Statistical Survival Analysis of Fish and Wildlife Tagging Studies

SURPH.1 Manual - Analysis of Release-Recapture Data For Survival Studies

Technical Manual

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Statistical Survival Analysis of Fish and Wildlife Tagging Studies

SURPH.1

Release Date: December 1994

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Forward

Program SURPH is the culmination of several years of research funded by Bonneville Power Administration to develop a comprehensive computer program to analyze survival studies of fish and wildlife populations. Development of this software was motivated by the advent of the PIT-tag (Passive Integrated Transponder) technology that permits the detection of salmonid smolt as they pass through hydroelectric facilities on the Snake and Columbia Rivers in the Pacific Northwest. Repeated detections of individually tagged smolt and analysis of their "capture-histories" permits estimates of downriver survival probabilities. Eventual installation of detection facilities at adult fish ladders will also permit estimation of ocean survival and upstream survival of returning salmon using the statistical methods incorporated in SURPH.1. However, the utility of SURPH.1 far exceeds solely the analysis of salmonid tagging studies. Release-recapture and radiotelemetry studies from a wide range of terrestrial and aquatic species have been analyzed using SURPH.1 to estimate discrete time survival probabilities and investigate survival relationships.

The interactive computing environment of SURPH.1 was specifically developed to allow researchers to investigate the relationship between survival and capture processes and environmental, experimental and individual-based covariates. Program SURPH.1 represents a significant advancement in the ability of ecologists to investigate the interplay between morphologic, genetic, environmental and anthropogenic factors on the survival of wild species. It is hoped that this better understanding of risk factors affecting survival will lead to greater appreciation of the intricacies of nature and to improvements in the management of our wild resources.

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Chapter 1

Introduction

There is increasing concern in the scientific community and in the public at large about natural and anthropogenic effects on the health of wild populations. Changes brought about by human activity can alter the ways animals interact with their environment. Consequently, it is important to understand the direct and indirect effects of the environmental milieu in which an individual animal finds itself.

A prime example is found on the Columbia and Snake Rivers in the northwestern United States. The desire to study the fate of salmon and steelhead populations native to these rivers was the motivation for the development of the SURPH methodology. Over the last century, major changes in river use have occurred on the Columbia and Snake Rivers. Sharp declines in salmon and steelhead runs have occurred concurrently with construction of hydroelectric projects, urbanization, and withdrawal of waters for irrigation. Hatchery production and mitigation projects—such as the construction of smolt bypass systems and adult fish ladders at the dams, smolt transportation programs and flow management—have been used in attempts to reverse the declines in salmon numbers and preserve salmon runs. However, very little is known about how environmental conditions, human actions, and mitigations may be affecting the survival of juveniles migrating to the ocean or adult salmonids returning to spawning streams.

Two technological developments have come together to help quantify survival relationships in the Columbia River Basin. The first new technology is the development of the PIT-tag (Passive Integrated Transponder) and the installation of PIT-tag detectors and slide-gate facilities at hydroprojects on the Columbia-Snake River systems. With this technology, juvenile salmon can be PIT-tagged, released and potentially detected at multiple dams as they migrate to the ocean. With proposed adult detector systems at various hydroprojects, these same fish might also be detected as they move upriver to spawn as adults. The result is the collection of capture history data that can be analyzed to estimate survival probabilities.

The second development is the advent of affordable high-speed computers that can numerically analyze increasingly sophisticated statistical models of tag-release studies. This manual describes statistical theory and computer software capable of not only extracting survival estimates but also characterizing relationships of survival rates with environmental covariates and the traits of individually marked fish and wildlife. The applications of the statistical models go far beyond the PIT-tag studies of salmon and steelhead on the Columbia and Snake Rivers. Applications of the methodology include the broader study of selection in wild populations based on the fates of individuals with differences in morphology, behavior, and genetics. Furthermore, using the statistical methods described in this manual, field experiments can be conducted to test relationships between the survival of wild populations and manipulative treatments applied over time or across the landscape. The methods presented in this manual have been used to analyze tagging studies of not only salmon but also molluscs, insects, mammals, and avian species. The goal of this manual is to convey the wide applicability and flexibility of analyses of tag-release studies to study survival relationships.

1.1 Background

Writing in 1652, Izaak Walton reported that Sir Francis Bacon studied salmon “by tying a riband...in the tail of some young Salmons...and then taking part of them again, with the known mark, at the same place, at their return from the sea which is usually about six months later” (from Cormack 1970). This appears to be the first reference to the use of animal marking to study a population. It would be almost three hundred years before David Lack pioneered the estimation of survival rates from the recoveries of bands from marked birds that had died (Lack 1951). Since that time, much has been written on the use of bands, tags, or radiotags to estimate population parameters, such as survival rates and abundance, and to delimit movements (see Seber 1982 for review).

This manual concentrates on methods that have been developed for estimation of survival probabilities and extensions of these models to investigate the effects of environmental factors and individual traits on survival. Animal marking studies can also be used to estimate other population parameters, such as abundance, density, and rates of movement between different habitats, but these methods are not covered here.

Statistical models for survival estimation have been developed for three types of tagging and resampling strategies. We will refer to all three strategies generically as *tag-release* sampling. In the first tag-release strategy, which we refer to as *release-recovery*, animals are captured, tagged with a number- or color-coded band, and released. The marked animals are subsequently resighted only once, usually upon death. Tagging may take place on one or several occasions throughout the duration of the study. The tag may identify the animals uniquely (e.g., the tag has a unique number) or may only indicate membership within a group of tagged animals (e.g., different groups are given tags of different colors). In Europe, ornithological studies usually investigate overall survival rates, and tags are collected from all possible mortality sources (Seber 1962, 1970, and 1972; Fordham and Cormack 1970). In the United States, the majority of release-recovery models have been concerned with tag returns from waterfowl upon harvest by hunters (Brownie et al. 1985). Besides survival probabilities, release-recovery models must also include parameters for recovery or reporting rates. Program SURPH is *not* set up to analyze data from release-recovery studies.

In the second tag-release strategy, which we refer to as *release-recapture*, animals are tagged with a uniquely coded band or ring and released, just as for the release-recovery methods. But in release-recapture studies, the resampling occasions consist of the recapture of tagged animals while still alive. The group of animals caught on each resampling occasion may include both previously marked and unmarked animals. The recaptures of marked animals are recorded and the unmarked animals are usually marked, and then all of the animals are released back into the environment. Some models for release-recapture data, such as the “Jolly-Seber model” (Jolly 1965, Seber 1965) use the ratio of marked-to-unmarked animals in the resamples to estimate birth rates and total abundance, as well as survival rates and capture probabilities. Other models, such as those presented by Cormack (1964), Burnham et al. (1987), and Lebreton et al. (1992), use only the data from previously marked animals, and estimate only survival and capture probabilities. Release-recapture data can be analyzed using Program SURPH to estimate survival and capture rates based on an extension of the Cormack (1964) model.

The third strategy, termed *known-fate*, uses radiotags or other sampling techniques to track the fate of each marked individual. In terrestrial radiotelemetry investigations, animals are

captured and fitted with small radio transmitters and released back onto the study site. Each transmitter has a unique signal. Resampling consists of triangulating on the radio signals until the animal is located and it is determined whether the animal is still alive. During the course of resampling, previously untagged animals may be captured and radiotagged to increase the sample numbers. Under ideal circumstances, each animal is relocated on each resampling occasion, obviating the need to include capture parameters in known-fate models (White 1983, White 1990). The establishment of upstream adult PIT-tag detectors with 100% scanning success at fish ladders holds the promise of providing known-fate data for returning adult salmon and steelhead on the Columbia-Snake River system. Other examples of known-fate studies include the study of sessile intertidal species. Program SURPH can be used to analyze known-fate data based on an extension of the White (1983) model.

For many years, the focus of tag-release models has been on the estimation of survival. The output of models we call *survival-estimation* models is a series of estimates of survival probabilities for the intervals between sampling events. Much of the early development of survival-estimation models for release-recover data was performed by Seber (1962, 1970, and 1972) and Cormack (1964). Fordham and Cormack (1970) used the models to estimate survival rates of Dominican gulls and included a statistical appendix by Cormack. Clobert et al. (1985) illustrated extensions of the Cormack model using data from studies of starlings, moths, and other animals. The monograph by Brownie et al. (1985) contains numerous models for analyzing tag returns from waterfowl hunters; this class of models has come to be known as Brownie models. A survival-estimation model for analyzing known-fate and radiotelemetry data was suggested by White (1983), who presented an example based on a tagging study of a population of elk. The models of Cormack (1964) and White (1983) form the basis for survival analyses in Program SURPH.

Survival-estimation models are seriously limited when it comes to assessing effects on survival or modeling survival relationships. The sequence of survival estimates from a tagging study are correlated, and there is no way to explicitly characterize relationships between survival probabilities and concomitant variables. Clobert et al. (1985) and Sandland and Kirkwood (1981) developed models with constraints on the survival and/or capture probabilities wherein

survival or capture probabilities for two or more periods are equated and the common probability is estimated. However, researchers are not likely to be satisfied knowing only that per-period survival probabilities fluctuate or that the probabilities in different periods are equal. Rather, they will wish to relate the fluctuations and equalities to the influence of some environmental variables or traits of the individual animals. For example, Clobert et al. (1985) reported a study of a starling population (*Sturnus vulgaris*) in Belgium where the Cormack (1964) survival estimation model was used to analyze the release-recapture data. The estimates were then plotted against the average October-March temperature, and a clear linear relationship was suggested. Unfortunately, correlations among survival estimates induced by the estimation procedure itself invalidate the correlation coefficient or a regression line of the relationship. This shortcoming has led to the current interest in statistical models that explicitly represent the relationships between survival probabilities and environmental and experimental conditions or individual traits (*covariates*). We refer to such models as *survival-effects* models. Survival-effects models may also include relationships between capture probabilities and covariates.

From the early 1900's biologists have studied selection by attempting to establish a relationship between an explanatory trait and survival. In a study on praying mantises, DiCesnola (1904) found that color was important to survival when the insect inhabited an environment in which it was not camouflaged. The relationship was presented as percentages of green and brown preying mantises that survived in green and brown environments. The results were extreme. By the end of the study, all the green preying mantises in a brown environment died and all the brown preying mantises in a green environment died. Thus, color of the insect was thought to be an agent of selection. However, no functional relationship was established.

Beginning in the 1980's, biologists began using more sophisticated statistical analyses to find evidence for selection. In a study on zooplankton, Byron (1982) used Pearson's χ^2 goodness-of-fit test (Hogg and Tanis 1983, pp. 414-420) to analyze a contingency table of observed percent survival in several different environments. Thornhill (1983) applied linear regression to survival data on the scorpionfly where the response variable was an estimate of number of days survived and the explanatory variable was body size. Schulze and Folt (1990) compared Kaplan-Meier survival curves to treatment groups of a crustacean (*Epischura lacustris*). However, well

into the 1980's, biologists relied mostly on descriptive relationships to provide evidence of selection (Endler 1986). The descriptive techniques ranged from plots of observed percent survival over time for different groups of animals, to tables comparing percent survival in a group, to some characteristic of that group such as average size (Bantok and Bayley 1973).

Most of the published studies on selection have relied on either comparing traits averaged over a group of animals to survival in the group, or have relied on data where individuals could be tracked and their fates determined. Averaging traits over a group can average out the effect of selection or make the effects more difficult to detect (Clobert and Lebreton 1985). By tracking the fates of individuals, one can establish a relationship between survival and an individual trait such as body size, thereby studying selection at the individual level. Thus, there was a need for statistical methods that can be used to test hypotheses about selection at the individual level. For this reason, Program SURPH was developed to investigate both environmental and individual-based covariates.

Papers including survival-effects and capture-effects models for tag-release data are still infrequent in the literature, though the pace of new publication is increasing. The earliest was a paper by North and Morgan (1979) in which a relationship between the survival rates of first-year grey herons (*Ardea cinerea*) and the mean winter temperature was built into a model for release-recapture data. Pollock et al. (1984) extended a Jolly-Seber type model to relate capture probabilities to sampling effort in a Canadian lobster fishery. Pollock et al. (1984) also presented a general theory for relating capture probabilities to a wide variety of environmental and individual variables. In their monograph, Burnham et al. (1987) adapted a Cormack-type model to relate survival rates in desert tortoises to carapace length (pp. 361-371). The monograph also presented a general approach to assessing dose-response relationships (pp. 372-378). Clobert and his colleagues (Clobert et al. 1985, 1987, 1988; Lebreton et al. 1992) are currently extending the theory of survival effects models. A very general extension of the Cormack model has been developed that permits modeling of both survival or capture probabilities as functions of external variables. The model has been implemented successfully in a computer program called SURGE. Examples of the utility of the SURGE model are given in Clobert et al. (1988) and Lebreton et al. (1992). Notable differences between Program SURPH and Program SURGE

(Clobert et al. 1988) are the ability to analyze known-fate data; the types of link functions for modeling survival and capture relationships; incorporation of both group- and individual-based covariates; and the presence of formal methods of testing hypotheses and performing model diagnostics. Figures 1.1 and 1.2 summarize the range of survival-estimation and survival-effects models that have been devised for the three sampling strategies.

Program SURPH is capable of analyzing data on group- and individual-based covariates. Group-based covariates affect the overall survival of all individuals within a particular tag group, or population. Examples of group-based covariates include site- or period-specific environmental variables such as temperature or vegetation. Multiple-population studies are required to study site-specific variables. Individual-based covariates, such as body size, are measured on each individual and can be analyzed using a single population of tagged animals. Program SURPH can be used to model survival and capture as functions of both individual- and group-based covariates.

1.2 Capabilities of Program SURPH

Program SURPH is an interactive, mouse-driven statistical program developed for the X-Windows computing environment under the UNIX operating system for SUN® workstations. SUN workstations were selected as the initial computing platform for SURPH because of their memory capacity and operating speed, important for iteratively solving the complex statistical models. Furthermore, SUN workstations have become a standard computing environment for numerous state and federal agencies dealing with salmon studies on the Columbia-Snake River systems. A revised program SURPH-PC is under development for operation on IBM®-compatible personal computers using the Microsoft Windows® operating system. Inquiries regarding the availability of SURPH-PC may be directed to the authors.

Program SURPH has a wide range of capabilities to model and assess survival and capture relationships based on known-fate (Table 1.1) and release-recapture data (Table 1.2). The modeling and testing capabilities include a choice of link functions that relate the capture and

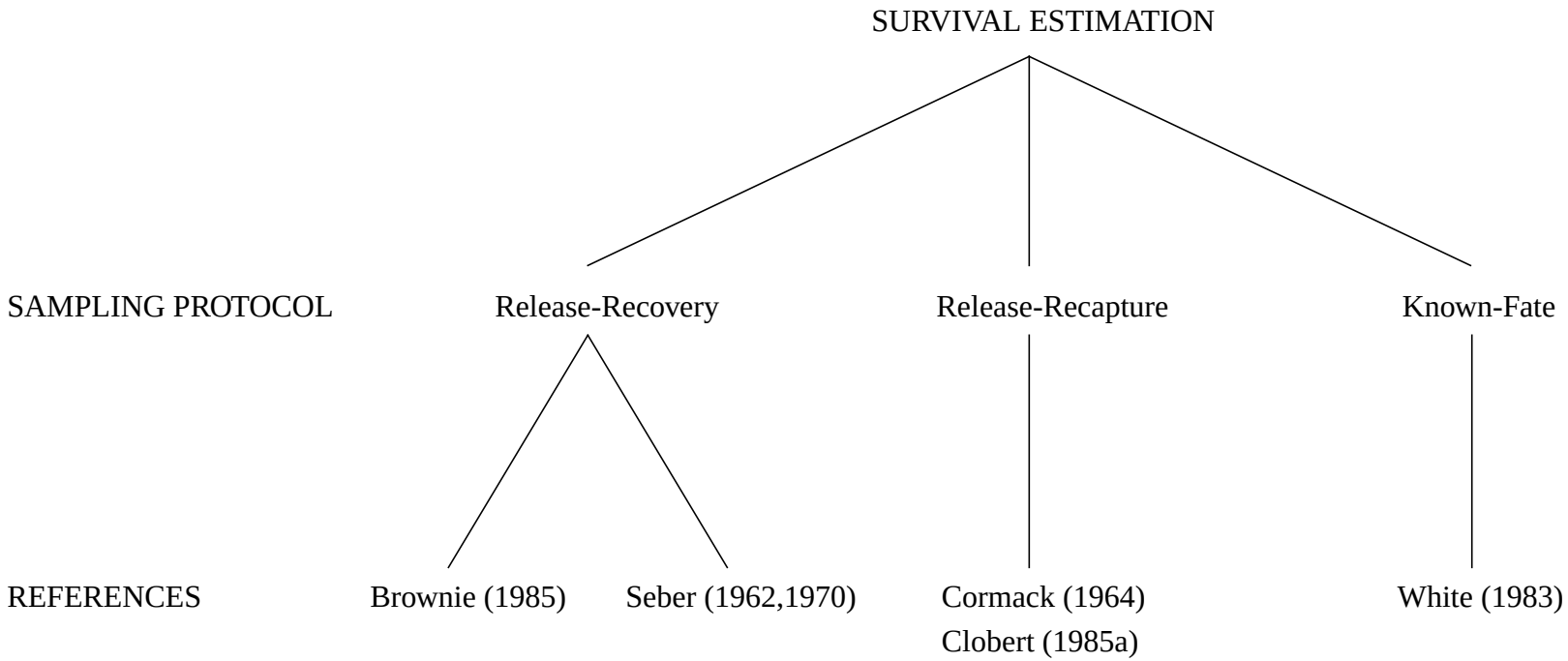


Figure 1.1 Diagram of available survival-estimation models for tag-release studies.

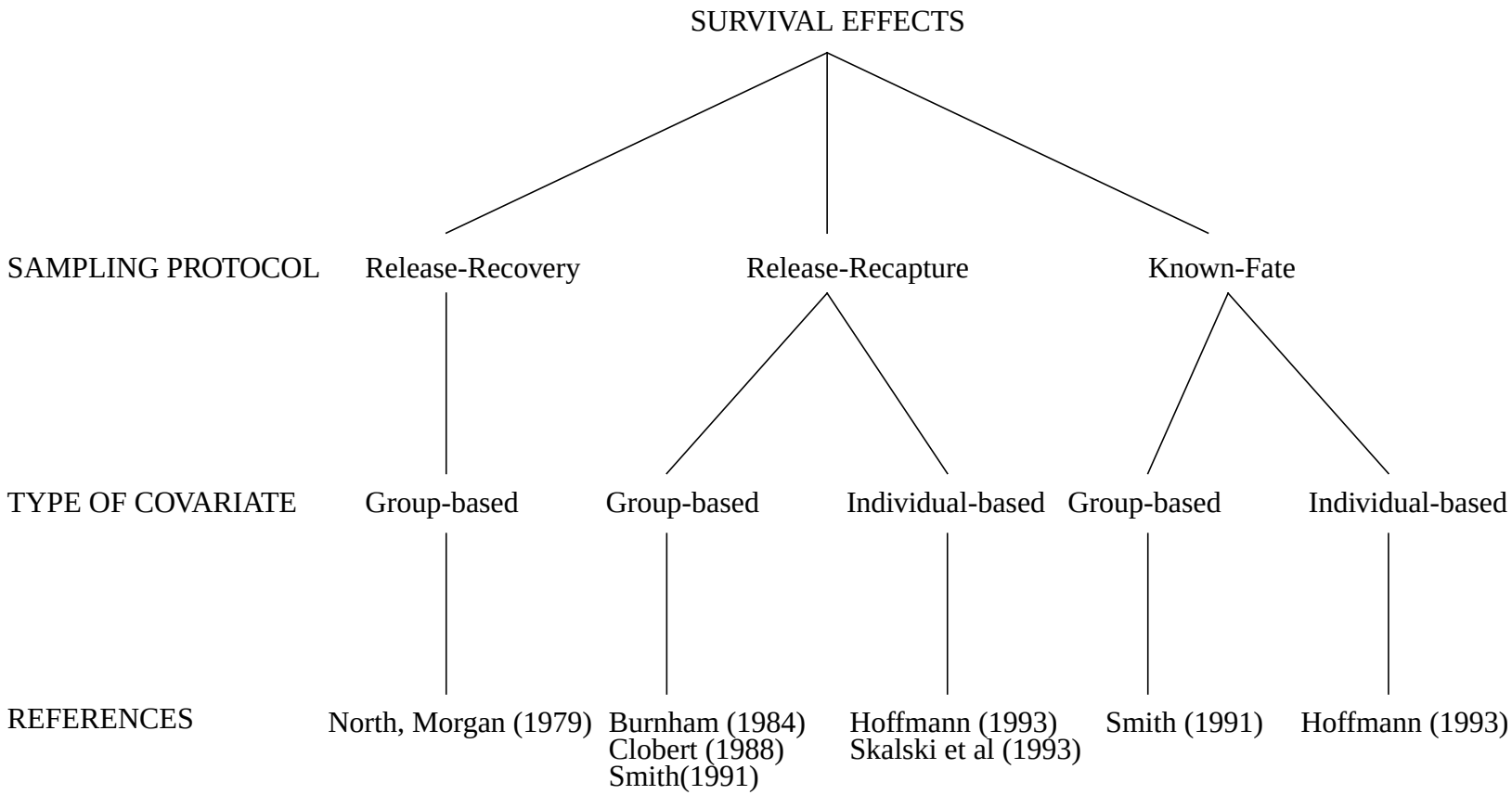


Figure 1.2 Diagram of available survival-effects models for tag-release studies.

Table 1.1 Summary of features of Program SURPH for known-fate data.

FUNCTION	COMPUTATION
Descriptive Statistics	a. Kaplan-Meier (1958) nonparametric estimates of survival functions.
	b. Empirical c.d.f.'s of individual-based covariates
	c. Kolmogorov-Smirnov test of equality of covariate c.d.f.'s.
	d. Period-specific survival estimates and variances (White 1983).
Survival Analysis	a. Modeling individual- and group-based covariates.
	b. Parameter estimates and variances.
	c. Plots of relative risk.
	d. Plots of survival function versus individual- and group-based covariate values.
Diagnostics	a. Plots of parametric versus nonparametric survival estimates.
	b. Plots of residuals.
	c. Goodness-of-fit tests.

Table 1.2 Summary of features of Program SURPH for release-recapture data.

FUNCTION	COMPUTATION
Descriptive Statistics	a. M-arrays of capture data (Burnham et al. 1987).
	b. Cormack (1964) estimates of capture and survival probabilities and variances.
	c. Empirical c.d.f.'s of individual-based covariates.
	d. Kolmogorov-Smirnov tests of equality of covariate c.d.f.'s.
Modeling Capture Probabilities	a. Manly-Parr (1968) estimates of capture probabilities.
	b. Log-linear analysis of Manly-Parr (1968) estimates.
	c. Modeling individual- and group-based covariates.
	d. Likelihood ratio tests (LRT) of capture process.
	e. Plots of capture process versus individual- and group-based covariate values.
	f. Parameter estimates and variances.
Modeling Survival Process	a. Modeling individual- and group-based covariates.
	b. Tests of survival relationships using LRT and ANODEV.
	c. Parameter estimates and variances.
	d. Plots of survival process versus individual- and group-based covariate values.
	e. Plots of relative risk.
Modeling Final Period	a. Modeling individual- and group-based covariates.
	b. LRT of parameter relationships.
Diagnostics	a. Plots of parametric versus nonparametric estimates of capture and survival probabilities.
	b. Plots of residuals.
	c. Goodness-of-fit tests.

survival probabilities to linear predictors (i.e., regression models). Capture and survival probabilities can be modeled using either a logistic-link function or a proportional hazards (log-log) link. In all cases, capture and survival probabilities can be characterized by period-, group-, and individual-specific effects.

Program SURPH, including both known-fate and release-recapture analyses, was devised to encompass the possible types of data sets that would ultimately be generated by Columbia-Snake River PIT-tag studies. Current juvenile PIT-tag detectors and slide-gate facilities generate release-recapture data that can be analyzed by Program SURPH. The eventual installation of adult PIT-tag facilities with 100% detection capabilities at upstream ladders will generate known-fate data that can also be analyzed by SURPH. Finally, with the prospect of both adult and juvenile PIT-tag facilities at Bonneville Dam (Figure 1.2), the juvenile tagging studies will generate data that is a composite of release-recapture and known-fate. The last interval from passage through Bonneville Dam as juveniles to redetection as returning adults provides known-fate data. For this reason, an unique capability of Program SURPH is the ability to model the last period as known-fate data to quantify and characterize ocean survival. Typically, release-recapture data will not permit estimates of survival in this last period. Rather, only the product of survival and capture probabilities can be estimated. Modeling in this case is usually limited to equality constraints among replicate release studies. The flexibility of Program SURPH will consequently allow analysis of a wide variety of terrestrial and aquatic tag-release studies.

Program SURPH is comprehensive in providing descriptive statistics, parameter estimates, model development, hypothesis testing, and model diagnostics (Tables 1.1 and 1.2). A useful feature of the interactive nature of Program SURPH is the ability to move easily between descriptive, estimation, testing, and diagnostic phases of tag data analysis to help identify the most descriptive yet parsimonious survival and capture models. This capability is reminiscent of some of the better statistical software for multiple regression. The parallels between SURPH software and regression software was intentional to rapidly acquaint investigators with this new methodology.

The software described in this manual is intended for biometricians and biologists involved in the analysis of fish and wildlife survival studies. Investigators will be best prepared to use the methods described in this manual if they have had a minimum of 2-3 college courses in applied statistics. These courses should include the general principles of statistical inference, regression analysis, and preferably experimental design and analysis of variance (ANOVA). In addition, readers should be familiar with tag-release theory. Valuable references on tag analysis may be found in Seber (1982), Clobert et al. (1985), Burnham et al. (1987), Lebreton et al. (1992), and Skalski and Robson (1992).

The remainder of this manual is organized as follows: Chapter 2 is an overview of a variety of statistical concepts and methods that provide the raw materials and tools upon which Program SURPH is built. Chapter 3 contains detailed development of methods for known-fate data. Analysis of release-recapture data is detailed in Chapter 4. Chapter 5 is a brief tutorial on system requirements, installation of the program, and the construction of input data files. Chapter 6 has examples of analyses of actual known-date and release-recapture data. Chapter 7 is a comprehensive catalog of all the windows and displays a SURPH user might encounter during data analysis. Chapters 8 and 9 are glossaries of terms and algebraic symbols used in this manual, respectively.

Chapter 2

Statistical Concepts and Methods

The theory underlying the assessment of effects on survival using SURPH is drawn from many difference sources; for example, tag-release theory, human epidemiology, maximum likelihood theory, and analysis of deviance. Elements of all these fields of study must be understood by any potential user of the SURPH software. This chapter is an introduction to the concepts on which the SURPH methodology is built.

Section 2.1 describes methods for modeling survival and capture processes for both continuous- and discrete-time data. Section 2.2 provides a general background on tag-release studies, including sampling protocols and concerns regarding the analysis of fish and wildlife survival studies. Section 2.3 covers the statistical method of maximum likelihood estimation. Section 2.4 discusses hypothesis testing using likelihood ratio tests and analysis of deviance. Section 2.5 discusses numerical procedures necessary to analyze complex survival models. Most biometricians should already be familiar with the material presented in Sections 2.3, 2.4, and 2.5 and may wish to familiarize themselves with details pertinent to wildlife tagging studies by reviewing the first two sections. Biologists, on the other hand, may wish to forego Sections 2.1 and 2.3 through 2.5 completely, focusing instead on the design and conduct of tagging studies discussed in Section 2.2. Investigators responsible for the analysis of tagging data will need to understand the information contained in Sections 2.1, 2.3, and 2.4.

2.1 Modeling Survival and Capture Relationships

The primary uses of Program SURPH are to evaluate and characterize relationships between measured covariates and survival probabilities. Modeling capture probabilities in release-recapture studies is usually a secondary objective. Section 2.1.1 explains the theory of continuous-time survival processes that underlies the discrete-time modeling of survival probabilities in SURPH. Section 2.1.2 discusses the range of mathematical functional forms that can be used to relate measured covariates to survival and capture probabilities in tag-release

models.

2.1.1 Continuous-time survival estimation

Let T be a nonnegative random variable representing the time elapsed from release to death of an individual from a homogeneous population. The *survivor function* for T, $S(t)$, is defined as the probability that T is equal to or greater than t. In other words, $S(t)$ is the probability an animal survives to at least time t:

$$S(t) = P(T \geq t), \quad 0 < t < \infty \ . \tag{2.1}$$

If T is absolutely continuous, then $S(t) = 1 - F(t)$, where $F(t)$ is the cumulative density function for time to death. Note that $S(0) = 1$ and $S(\infty) = 0$.

The *probability density function* (p.d.f.) of T is

$$f(t) = \lim_{\Delta t \to 0^+} \frac{P(t \leq T < t + \Delta t)}{\Delta t} = -\frac{dS(t)}{dt} \ . \tag{2.2}$$

By the definition of a p.d.f. for a nonnegative continuous random variable, $f(t) \geq 0$ for $0 \leq t < \infty$, and $\int_0^\infty f(u)du = 1$. Also, $S(t) = \int_t^\infty f(u)du$. The function $f(t)$ describes the distribution of lifetimes in the population.

The instantaneous rate of failure at time $T = t$, conditional on survival to time t, is given by the *hazard function* and is defined as

$$\lambda(t) = \lim_{\Delta t \to 0} \frac{P(t \leq T < t + \Delta t | (T \geq t))}{\Delta t} = \frac{f(t)}{S(t)} = \frac{-\frac{dS(t)}{dt}}{S(t)} \ . \tag{2.3}$$

From (2.3), $\lambda(t) = -\frac{d}{dt}\log S(t)$, because $\frac{d}{du}\log(x) = \frac{1}{x}\frac{dx}{du}$, so that by integrating we obtain

$$S(t) = exp\left(-\int_t^\infty \lambda(u)du\right) , \tag{2.4}$$

and the p.d.f. of T can be written as

$$f(t) = \lambda(t)exp\left(-\int_t^\infty \lambda(u)du\right) . \tag{2.5}$$

Rarely in the course of a survival study will a death time be observed for every single experimental subject. Some individuals may still be alive when the study is terminated; others may be “lost to follow-up” (i.e., they die before the end of the study, but the researchers are not aware of the time of death). When the death time of an experimental subject is not observed during the study, the death time is said to be *censored*.

It is far more common to estimate the survivor function (Eq. (2.1)) than the hazard (Eq. (2.3)) or probability density function (Eq. (2.5)). However, the three functions are equivalent in that each uniquely specifies the probability distribution of *T*. Kalbfleisch and Prentice (1980, Chapter 3) give methods of parameter estimation when a parametric distribution is assumed for the death times. More commonly, however, a nonparametric method due to Kaplan and Meier (1958) is used to estimate the survivor function. The estimate produced by the nonparametric method is known as the *Kaplan-Meier* or *product-limit* estimate.

The Kaplan-Meier estimate is used to estimate the survivor function when the population is assumed to be homogeneous with regard to survival rates. The estimate is based on the *empirical survivor function* (*ESF*). If there are no censored observations in a sample of size *n*, the ESF is defined as

$$\hat{S}(t) = \frac{\text{Number of observations} \geq t}{n} \qquad \text{for } t \geq 0 \ .$$

If all death times are distinct, the ESF is a step function that begins at $\hat{S}(0) = 1$ and decreases by $1/n$ just after each observed death time. In general, if there are d death times equal to t, the ESF decreases by d/n just after t.

The Kaplan-Meier estimate can be modified to give an unbiased estimate of the survivor function when there are censored observations. Let $t_1 < t_2 < \ldots < t_k$ be the distinct observed death times in a study with sample size n ($n \geq k$). "Ties" in death times are allowed; that is, more than one subject may die at each death time t_i, and we let d_i represent the number of deaths at time t_i ($i = 1, 2, ..., k$). In addition to the death times, there are also censoring times C_i for individuals whose death times are not observed. Let c_i be the number of subjects censored at time C_i. The Kaplan-Meier estimate of the survivor function in the presence of censoring is defined as

$$\hat{S}(t) = \prod_{i \in \{t_i, C_i\} < t} \frac{n_i - d_i}{n_i} \ , \tag{2.6}$$

where n_i is the number of individuals at risk at time t_i, i.e., the number of individuals alive and uncensored just prior to t_i ($n_i = n_{i-1} - d_{i-1} - c_{i-1}$). The Kaplan-Meier estimate reduces to the ESF if there is no censoring, because in that case, $n_1 = n$ and $n_i = n_{i-1} - d_{i-1}$. Variance estimates for $\hat{S}(t)$ are given in Kalbfleisch and Prentice (1980) and Lawless (1982). Lawless (1982) also includes a section on estimation of the cumulative hazard function in his chapter on nonparametric estimation of the survivor function. For known-fate data, Program SURPH provides Kaplan-Meier estimates modified for periodic, or discrete-time, sampling and associated variance estimates (see Section 3.6.1).

Tag-release methods rarely provide the precise measurements of death times required for the

Kaplan-Meier method. However, some researchers have been able to pinpoint the days of death for moderately sized samples of tagged animals using radio transmitters and intense follow-up. Pollock et al. (1989a) report on one such study of a black duck population where fifty female ducks were fitted with radios. After tagging, the location and status (alive, dead, or missing) of each bird were recorded daily from the date of release (8 November 1983 to 14 December 1983) until 15 February 1984. The expense of locating a reasonable number of radiotagged animals on a daily basis is probably prohibitive for most researchers; it is far more common for radiotagged birds to be located on a less frequent basis; weekly, for example.

In a second paper published describing the adaptation of the Kaplan-Meier method to studies of wild populations, Pollock et al. (1989b) use an example where 52 bobwhite quail were radiotagged and then located weekly for five months. The Kaplan-Meier method may still be applied if the sampling is not done daily and exact death times are not known. To calculate the estimate, however, it is necessary to assign a death time to each animal that dies. The animals that die in the interval (t_i, t_{i+1}) could be assigned any death time between t_i and t_{i+1}, and the choice of assignment appears to be arbitrary. One solution is to assume that any deaths that occur during a sampling interval occur uniformly throughout the interval. Table 1 in Pollock et al. (1989b) implies the use of the death time t_{i+1} for all individuals dying in the interval (t_i, t_{i+1}) while their Figure 1 implies assignment of death times uniformly throughout the interval. Similar assumptions must also be made for the censoring times of individuals censored within the interval (t_i, t_{i+1}). When death times are discrete (i.e., not exact), different assumptions about the time of death or time of censoring may lead to different conclusions.

The Kaplan-Meier method, as originally devised, applies to a single group of subjects, all entering the study at the same time, which is called “time zero”. In epidemiological studies, patients often do not enter the study at the same calendar time but all enter immediately after they have experienced a certain diagnosis or surgical procedure. Thus, time zero may refer to a different calendar time for each subject. It is assumed that the same survivor function applies to

each subject following the event, regardless of the actual calendar time. In tag-release studies, there is no such “landmark” event in the life of a subject that “sets the clock.” Rather, it is assumed that marked and unmarked animals experience the same hazards throughout the study period, so that if new animals are introduced to the study after the initial group is released, their time zero is assumed to be the same calendar time as the animals already released. This assumption is implicit in the adaptation of Kaplan-Meier methods to staggered-entry study designs proposed by Pollock et al. (1989a). The solution is to add the animals marked at time t_i to the “number at risk” at time t_{i+1} .

Release-recapture data cannot be analyzed properly using the Kaplan-Meier method. Unlike radio transmitters, passive tags do not provide death times of individual animals because dead animals are not subject to detection or recapture. Failure to recapture an animal may indicate either mortality or simply failure to recapture an animal that is alive. Release-recapture protocols rarely include searching for and recovering dead animals. The capture history data from release-recapture studies must be analyzed using likelihood models that include parameters for both capture and survival probabilities.

It is assumed under the Kaplan-Meier method that the population is homogeneous; that is, the same probability distribution for death times applies to all individuals in the biological population. However, this assumption is likely to be violated in any typical population. Because of inherent variation, some individuals are more likely to survive through any sampling interval than others, and the individual death times are influenced by intrinsic traits and exogenous factors. This is the incentive for using explanatory variables to model death times. Kalbfleisch and Prentice (1980) show how explanatory variables may be introduced to various parametric models, such as exponential, Gamma, or Weibull models. It is more common, however, not to assume a parametric model for survival times.

2.1.2 Discrete-time survival estimation

In studies of wild populations, it is often more interesting and appropriate to focus not on the

entire survivor function, but on the probability of surviving from one sampling event to the next. The exact death times are no longer important; just the intervals within which deaths occurred. There are two reasons for this difference in focus from human epidemiology. First, death times often cannot be determined exactly in wild populations. Second, in manipulative studies such as pesticide trials, the treatment effect may influence survival for only a small period of time following the application of the treatment. It is not necessary to study the entire survivor function to assess acute pesticide effects that quickly dissipate. Studying the entire function may even decrease power to detect effects occurring immediately after application.

There is a vast literature on tag-release models that includes interval-specific survival probabilities (survival-estimation models). The essential element common to all such models is the vector (S_1, S_2,..., S_K), where S_k (k = 1,..., K) is the conditional probability that an animal survives until sampling event k, given that it was alive just after event k-1. Periodic sampling naturally leads to consideration of conditional survival probabilities rather than instantaneous mortality rates, but there is still a continuous process at work. As before, let T be a random variable defined as the death time for an individual from a population with homogeneous survival rates. Let the hazard function be denoted $\lambda(t)$ and the survivor function $S(t)$. The conditional survival probability S_k can be written in terms of the continuous functions:

$$S_k = P(T > t_k | T \geq t_{k-1}) = \frac{S(t_k)}{S(t_{k-1})} = exp\left(-\int_{t_{k-1}}^{t_k} \lambda(u)du\right) . \qquad (2.7)$$

Now consider the simplest possible scenario for a single-population, single-release, release-recapture study, wherein the hazard function is constant for the duration of the study($\lambda(t) = \lambda$ for all t) and the sampling events are evenly spaced (i.e., the sampling intervals are of equal length). Let the times or locations of the sampling events be denoted t_1, t_2, t_3,..., t_K and let Δt be the width of the sampling intervals ($t_{k+1} - t_k = \Delta t$ for all k). In this case, the survival probabilities are equal:

$$S_k \equiv S = exp\left(-\int_{t_{k-1}}^{t_k} \lambda du\right) = exp(-\lambda \Delta t) \quad , \tag{2.8}$$

where S is the survival probability common to all periods.

In any realistic situation, the hazard function is not likely to be constant throughout the study. Differences in the hazard function from interval to interval will be reflected in differences in the respective cumulative hazard functions

$$\left(\int_{t_{k-1}}^{t_k} \lambda(u) du\right)$$

for each interval, in turn resulting in differences in the survival probabilities. If the sampling intervals are of equal length, then differences in the survival probabilities can be attributed solely to interval-to-interval differences in the hazard function. However, survival probabilities will also vary across sampling intervals if the intervals are of unequal lengths, even if the hazard function is constant. For example, suppose a constant hazard function gives the probability of surviving one week as 0.7. Then the probability of surviving a two-week-long period is $0.7^2 = 0.49$. Thus, if the sampling events are not evenly spaced, differences in the survival probabilities due to a varying hazard function are completely confounded with differences due to uneven lengths of sampling intervals. It is impossible to separate the two causes.

2.1.3 Covariate effects on survival and capture processes

2.1.3.1 Types of covariates

The nature of the study design is also strongly dependent on the type of covariates investigated. SURPH is capable of analyzing two important classes of covariates. The first class is *group-based*. River flow, temperature, and habitat quality are examples of group-based covariates.

All the tagged individuals within a particular population experience effects of the same level of the group covariates. Group covariates have been incorporated into known-fate and release-recapture models by Clobert et al. (1987), Smith (1991), Lebreton et al. (1992), and Smith and Skalski (to appear). Group-based covariates may be further classified into *time-invariant* (fixed) and *time-variant* measurements.

If the covariates that characterize populations are fixed, replicate populations with differing covariate values are required to study the relationship between covariates and survival rates, just as different levels of the independent variable must be observed to perform a linear regression analysis. Time-variant, group-based covariates can be accommodated in a periodic-sampling model, if it is assumed that the value of the time-variant covariate is constant within a particular sampling period and changes only at the times of the sampling occasions. That is, there is a vector of covariates $\underset{\sim}{x}_k$ to which an individual is subjected from sampling occasion k-1 until occasion k.

Individual-based measurements are the second important class of covariates. Examples of individual-based covariates include measurements of the morphology of the animals, their genotypic or phenotypic characteristics, behavioral or territorial differences, gender, and handling history. Individual covariates like body size have been incorporated into known-fate models (Kalbfleisch and Prentice 1980, White and Garrott 1990, Pollock et al. 1989) but have not previously been incorporated into release-recapture models.

Individual-based covariates can be either time-invariant (fixed) or time-variant. Time-invariant covariates have values that do not change (e.g., sex) or that change insignificantly during the course of the study. Fixed individual covariates are easier to model because the time of measurement does not matter; the relationship between the fixed covariate value and survival will be the same for all animals, regardless of when they entered the study.

In contrast, the relationship between time-variant covariates and survival depends on the time that the variable was measured. In a study with staggered entry of animals into the tagged population, covariate values are not comparable between animals measured at different times (i.e.,

upon entry into the study). For example, consider a pesticide study with weekly sampling occasions. A first set of tagged animals is assayed for blood contaminants just after the pesticide application that begins the study. The probability of surviving until the next sampling occasion can be modeled as a function of the contaminant level, because all animals were measured at the same time. Now suppose that at the second sampling occasion, a new set of animals is captured, measured for contaminants, tagged, and released. Unless all surviving animals in the first set are remeasured, the two sets cannot be used in the same regression model for survival in the next interval, because the covariate values are not comparable. The expected survival for an animal with a particular contaminant level measured on the second sampling occasion is not the same as that for an animal with the same level measured on the first occasion. When the covariates between groups of animals are not comparable, a separate analysis must be performed for each release group.

The relationship between survival and a time-variant individual-based covariate can be studied using a “single entry” design, wherein all tagged animals enter the study at the same time. Often, a variable will be known to vary over time, but will prove to be very difficult to monitor; for example, the degree of smoltification of a juvenile salmonid as it migrates downriver. In many such cases, the solution is to measure the variable at the time of release and to treat it subsequently as time-invariant, being careful in the interpretation of effects in subsequent periods. When a time-variant covariate is treated as fixed, the observed relationship between the covariates and survival can be expected to degrade over time, as the initial measurement becomes less indicative of the current value of the covariate.

Some covariates can be treated as either group- or individual-based covariates. Examples include gender or age class, where the multiple individuals with the same covariate values can be defined as unique populations. In a single-site, tag-release study, estimation of regression coefficients will be identical regardless of how these covariates are treated in the data analysis. However, tests of significance will differ appreciably. If treated as group covariates, replicated sites, each with the population divided into subpopulations, would be required to show reproducible differences between classes of individuals. Treated as individual-based covariates,

however, tests of significance are based on the inter-animal variation within a single population. This latter epidemiological approach to study design and analysis can be substantially more powerful in identifying significant survival effects. The epidemiological approach uses likelihood ratio tests (LRT) while group covariate effects must be tested using analysis of deviance (ANODEV) (see Section 2.4).

2.1.3.2 Quantities for comparing survival rates

This section describes several quantities that are used to characterize and contrast survival functions and probabilities. Implications to these quantities can help guide the selection of the appropriate link function.

The *odds ratio* and the effect on *relative risk* (Hosmer and Lemeshow 1989) are both used to contrast survival probabilities of two individuals with covariate vectors $\underset{\sim}{x}_1$ and $\underset{\sim}{x}_2$, respectively. If A is the event of interest and $P(A)$ is the probability of event A, then the odds ratio for the two individuals $(OR(\underset{\sim}{x}_1,\underset{\sim}{x}_2))$ is

$$OR(\underset{\sim}{x}_1\underset{\sim}{x}_2) = \frac{P(A|\underset{\sim}{X} = \underset{\sim}{x}_1)/(1 - P(A|\underset{\sim}{X} = \underset{\sim}{x}_1))}{P(A|\underset{\sim}{X} = \underset{\sim}{x}_2)/(1 - P(A|\underset{\sim}{X} = \underset{\sim}{x}_2))} \quad . \tag{2.9}$$

The numerator of (Eq. (2.9)) is the odds of success for an individual with covariate vector $\underset{\sim}{x}_1$ and the denominator is the odds of success for an individual with covariate vector $\underset{\sim}{x}_2$. The $OR(\underset{\sim}{x}_1, \underset{\sim}{x}_2)$ is a measure of how much more likely is a positive outcome under $\underset{\sim}{x}_1$ than under $\underset{\sim}{x}_2$.

Risk is the probability of a negative response (i. e., death) given present conditions. If death within an interval is denoted by the event $\bar{A}$, the *relative risk* $(RR(\underset{\sim}{x}_1, \underset{\sim}{x}_2))$ between two individuals with covariate vectors $\underset{\sim}{x}_1$ and $\underset{\sim}{x}_2$ is:

$$RR(\underset{\sim}{x}_1, \underset{\sim}{x}_2) = \frac{P(\bar{A}|\underset{\sim}{X} = \underset{\sim}{x}_1)}{P(\bar{A}|\underset{\sim}{X} = \underset{\sim}{x}_2)} \quad . \tag{2.10}$$

Relative risk $(RR(\underset{\sim}{x}_1, \underset{\sim}{x}_2))$ is a measure of how much more likely it is for an animal with covariate vector $\underset{\sim}{x}_1$ to have died in the interval than for an animal with covariate vector $\underset{\sim}{x}_2$.

Another quantity that characterizes survival potential is an animal's *life expectancy*. If T is the time to death, then the expected lifetime (i.e., $E(T|\underset{\sim}{x})$) of an animal with covariate vector $\underset{\sim}{x}$ can be expressed as

$$E(T|\underset{\sim}{x}) = \int_0^\infty t f(t|\underset{\sim}{x}) dt \,. \tag{2.11}$$

The *instantaneous relative risk* (IRR) between two individuals with covariate vectors $\underset{\sim}{x}_1$ and $\underset{\sim}{x}_2$, respectively, is the ratio of their hazard functions. For example, under the hazard link, the IRR is:

$$IRR(\underset{\sim}{x}_1, \underset{\sim}{x}_2) = \frac{\lambda_0(t) e^{\underset{\sim}{x}'_1 \underset{\sim}{\beta}}}{\lambda_0(t) e^{\underset{\sim}{x}'_2 \underset{\sim}{\beta}}} = e^{(\underset{\sim}{x}'_1 - \underset{\sim}{x}'_2)\underset{\sim}{\beta}} \,. \tag{2.12}$$

This quantity is a measure of the differences in risk between two animals on an instantaneous basis.

2.1.3.3 Link functions

Suppose an animal is subject to a set of fixed (time-invariant) covariate values $\underset{\sim}{x}$ (either intrinsic traits or exogenous factors) anticipated to influence its survival. When modeling the survival process on the continuous-time scale, it is typical to model the hazard function as a function of the covariates: $\lambda(t; \underset{\sim}{x}, \underset{\sim}{\beta})$, where $\underset{\sim}{\beta}$ is a vector of *effect parameters*. However, on the discrete-time scale, it is more common to model the survival probabilities in each sampling interval as functions of the covariates: $S_k(\underset{\sim}{x}, \underset{\sim}{\beta})$. In Program SURPH, the covariate relationships are assumed to be functions of the *linear predictor* $\underset{\sim}{x}'\underset{\sim}{\beta}$. The function that connects the linear predictor to the hazard function or survival probability is known as the *link function*. The most important link functions found in epidemiological literature are listed in Table 2.1.

Table 2.1 Definitions and properties of potential link functions for modeling capture and survival probabilities as functions of covariates. The parameter θ is a generic capture or survival probabilities.

Name	Link Function $\alpha + \underset{\sim}{x}'\underset{\sim}{\beta}$	Inverse Function[d, g] θ	Hazard Rate[a, e]	Life Expectancy[b, f] (Continuous Time)	Odds Ratio[c]	Response Relationship
Identity	θ	$\alpha + \underset{\sim}{x}'\underset{\sim}{\beta}$	N/A	N/A	$\frac{(\alpha + \underset{\sim}{x}'_1\underset{\sim}{\beta})(1-\alpha-\underset{\sim}{x}'_2\underset{\sim}{\beta})}{(\alpha + \underset{\sim}{x}'_2\underset{\sim}{\beta})(1-\alpha-\underset{\sim}{x}'_1\underset{\sim}{\beta})}$	• additive effect on survival probability
Log	$\log(\theta)$	$\theta e^{\underset{\sim}{x}'\underset{\sim}{\beta}}$	$\lambda_0(t)(\alpha + \underset{\sim}{x}'\beta)^{(e)}$	$\frac{E[t\|0]}{\alpha + \underset{\sim}{x}'\underset{\sim}{\beta}}$	$\frac{\theta^{e^{\underset{\sim}{x}'_1\underset{\sim}{\beta}}}\left(1-\theta^{e^{\underset{\sim}{x}'_2\underset{\sim}{\beta}}}\right)}{\theta^{e^{\underset{\sim}{x}'_2\underset{\sim}{\beta}}}\left(1-\theta^{e^{\underset{\sim}{x}'_1\underset{\sim}{\beta}}}\right)}$	• multiplicative effect on hazard rate • multiplicative effect on survival probability
Complementary Log	$\log(1-\theta)$	$1-(1-\theta)e^{\underset{\sim}{x}'\underset{\sim}{\beta}}$	N/A	N/A	$\frac{\left(1-(1-\theta)^{e^{\underset{\sim}{x}'_1\underset{\sim}{\beta}}}\right)(1-\theta)^{e^{\underset{\sim}{x}'_2\underset{\sim}{\beta}}}}{\left(1-(1-\theta)^{e^{\underset{\sim}{x}'_2\underset{\sim}{\beta}}}\right)(1-\theta)^{e^{\underset{\sim}{x}'_1\underset{\sim}{\beta}}}}$	• multiplicative effect on mortality probability
Logit or Log Odds	$\log\left(\frac{\theta}{1-\theta}\right)$	$\frac{exp(\alpha + \underset{\sim}{x}'\underset{\sim}{\beta})}{1+exp(\alpha + \underset{\sim}{x}'\underset{\sim}{\beta})}$	N/A	N/A	$e^{(\underset{\sim}{x}'_1 - \underset{\sim}{x}'_2)\underset{\sim}{\beta}}$	• additive effect on log odds ratio
Hazard or Log-Log	$\log(-\log(1-\theta))$	$\theta^{e^{\underset{\sim}{x}'\underset{\sim}{\beta}}}$	$\lambda_0(t)e^{\underset{\sim}{x}'\underset{\sim}{\beta}}$	$\frac{E[t\|0]}{e^{\underset{\sim}{x}'\underset{\sim}{\beta}}}$	$\frac{\theta^{e^{\underset{\sim}{x}'_1\underset{\sim}{\beta}}}\left(1-\theta^{e^{\underset{\sim}{x}'_2\underset{\sim}{\beta}}}\right)}{\theta^{e^{\underset{\sim}{x}'_2\underset{\sim}{\beta}}}\left(1-\theta^{e^{\underset{\sim}{x}'_1\underset{\sim}{\beta}}}\right)}$	• multiplicative effect on hazard rate • exponential effect on survival probability • multiplicative effect on life expectancy

Table 2.1 (cont.) Definitions and properties of potential link functions for modeling capture and survival probabilities as functions of covariates. The parameter θ is a generic capture or survival probabilities.

Name	Link Function $\alpha + \underset{\sim}{x}'\underset{\sim}{\beta}$	Inverse Function[d, g] θ	Hazard Rate[a, e]	Life Expectancy[b, f] (Continuous Time)	Odds Ratio[c]	Response Relationship
Complementary Log-Log	$\log(-\log(1-\theta))$	$1-(1-\theta)e^{\underset{\sim}{x}'\underset{\sim}{\beta}}$	N/A	N/A	$\dfrac{\left(1-(1-\theta)^{e^{\underset{\sim}{x}'_1\underset{\sim}{\beta}}}\right)(1-\theta)^{e^{\underset{\sim}{x}'_2\underset{\sim}{\beta}}}}{\left(1-(1-\theta)^{e^{\underset{\sim}{x}'_2\underset{\sim}{\beta}}}\right)(1-\theta)^{e^{\underset{\sim}{x}'_1\underset{\sim}{\beta}}}}$	• exponential effect on mortality probability

(a) Hazard rate is the instantaneous rate of mortality.

(b) Assuming constant hazard rate and time-invariant covariates $\underset{\sim}{x}'$.

(c) Measures relative odds of survival between individuals with covariates $\underset{\sim}{x}'_1$ and $\underset{\sim}{x}'_2$, respectively.

(d) Where $\theta = e^{\alpha}$ survival or capture probability with covariates equal to 0.

(e) Where $\lambda_0(t)$ is the hazard rate with covariates equal to 0.

(f) Where $E[t|0]$ is the expected life span with covariates equal to 0.

(g) Where $\theta = e^{(-e^{\alpha})}$ survival or capture probability with covariates equal to 0.

An important class of link functions are the *proportional hazards* (PH) functions (Feigl and Zelen 1965; Kalbfleisch and Prentice 1980, pp. 32-33). Program SURPH derives its name as an acronym for "SURvival with Proportional Hazards." However, other link functions may also be used in Program SURPH.

To describe the proportional hazard model, let $\lambda(t;\underset{\sim}{x})$ represent the hazard function at time t for an individual with covariates $\underset{\sim}{x}$. Initially, the covariates are assumed to be measured at the beginning of the study and to remain constant throughout the study. Under the PH model implemented in SURPH, we have

$$\lambda(t;\underset{\sim}{x}) = \lambda_0(t)e^{\underset{\sim}{x}'\underset{\sim}{\beta}} , \tag{2.13}$$

where $\lambda_0(t)$ is an arbitrary, unspecified baseline hazard function. That is, $\lambda_0(t)$ is the hazard function for an individual with covariate vector equal to $\underset{\sim}{0}(\underset{\sim}{x} = \underset{\sim}{0})$, or "baseline hazard." The covariates have a multiplicative effect on the hazard function, so that individuals with different covariates have proportional hazard functions. Provided the covariates do not change in value through time, the ratio of the hazard functions will also be constant through time. If $\underset{\sim}{x}_1$ and $\underset{\sim}{x}_2$ are vectors of covariates for two different individuals, the ratio of hazard functions can be written as:

$$\frac{\lambda(t;\underset{\sim}{x}_1)}{\lambda(t;\underset{\sim}{x}_2)} = \frac{\lambda_0(t)e^{\underset{\sim}{x}'_1\underset{\sim}{\beta}}}{\lambda_0(t)e^{\underset{\sim}{x}'_2\underset{\sim}{\beta}}} = e^{(\underset{\sim}{x}'_1 - \underset{\sim}{x}'_2)\underset{\sim}{\beta}} . \tag{2.14}$$

Now, consider the survival probabilities under discrete-time sampling for an animal subject to a vector of covariates. The conditional survival probability for a particular period i is the baseline probability raised to the power $e^{\underset{\sim}{x}'\underset{\sim}{\beta}}$, where

$$S_k(\underset{\sim}{x}) = exp\left(-\int_{t_{k-1}}^{t_k} \lambda_0(u)e^{\underset{\sim}{x}'\underset{\sim}{\beta}}du\right) = S_k^{e^{\underset{\sim}{x}'\underset{\sim}{\beta}}} . \tag{2.15}$$

Under the proportional hazards model (2.9), the link function implies that the survival probability is related to the linear predictor by a “log-log” transformation where

$$\ln(\ln S_k) = \underset{\sim}{x}'\underset{\sim}{\beta} \ . \tag{2.16}$$

Thus, this link function is sometimes called the “log-log link,” though we will use the term “hazard link.”

A second common link function is the logistic parameterization (Cox and Snell 1989):

$$S_k(\underset{\sim}{x}) = \frac{exp(\underset{\sim}{x}'\underset{\sim}{\beta})}{1 + exp(\underset{\sim}{x}'\underset{\sim}{\beta})} \ , \tag{2.17}$$

a common alternative for modeling survival probabilities. The logit-link function

$$ln\left(\frac{S}{1-S}\right) = \underset{\sim}{x}'\underset{\sim}{\beta} \tag{2.18}$$

relates the linear predictor to a nonlinear function of survival. Like the hazard link, the logit link is popular because of its mathematical property that bounds survival estimates within the admissable range of 0-1. Lebreton et al. (1992) extensively used the logit-link function in their monograph on tag analysis.

Lebreton et al. (1992) also describe the linear-link function for modeling survival where

$$S(\underset{\sim}{x}) = \underset{\sim}{x}'\underset{\sim}{\beta} \ . \tag{2.19}$$

However, a mechanistic argument for a linear-link function is generally absent. Instead, the choice of (2.19) is reminiscent of standard linear regression models often used in the absence of a well-defined response model.

A final important survival link function often used in epidemiology is the log link where

$$ln(S(\underset{\sim}{x})) = \underset{\sim}{x}'\underset{\sim}{\beta} \ , \tag{2.20}$$

derived from the survival function

$$S(\underset{\sim}{x}') = S_0 e^{\underset{\sim}{x}'\underset{\sim}{\beta}} . \tag{2.21}$$

The log link also gives a proportional hazards model; however, the effects on survival probabilities are multiplicative rather than exponential in nature.

For the four link functions for survival discussed so far (i.e., 2.16, 2.18, 2.19, and 2.20), complementary links can be established by modeling mortality (i.e., 1-*S*) rather than survival (*S*). Hence, a suite of possible response models are available to investigators. Program SURPH currently provides the two most important link functions for survival and capture probabilities; the hazard (log-log) and logit.

The selection of a particular link function is based on several considerations, including the nature of the process that gives rise to the survival probability, the response relationship implied, and the ease of calculating summary statistics (i.e., 2.9, 2.10, 2.11, 2.12). Both the log and hazard links have been used to describe continuous-time survival processes (Kalbfleisch and Prentice 1980), while the logit link is often used when the data are binomial counts of successes and failures (i.e., binomial outcomes of discrete events) (Hosmer and Lemeshow 1989). IRR and E(*T*) can be calculated from parameters under hazard link but not under the logit link. The hazard function is a description of instantaneous risk through time, whereas the logistic parameterization can only give a description of risk for an entire interval. Quantities useful for describing continuous processes, such as the instantaneous hazard rate and life expectancy, cannot be calculated from the logit link but are easily derived using the log- and hazard-link functions. The odds ratio is more easily calculated from the parameters under the logit link.

The alternative link functions (Table 2.1) can have dramatic differences in the shape of the response curve (Figure 2.1). The curves in Figure 2.1 are constrained to pass through the points of 100% mortality and 100% survival at the low and high end of the covariate gradient. These constraints maximize differences among the various link functions. When the range of survival probabilities is restricted, the differences among the link functions are much smaller. For example, Figure 2.2 shows a case where the survival functions are forced through the points of 70% and 100% survival. Here the logit, hazard, and complementary log functions are nearly

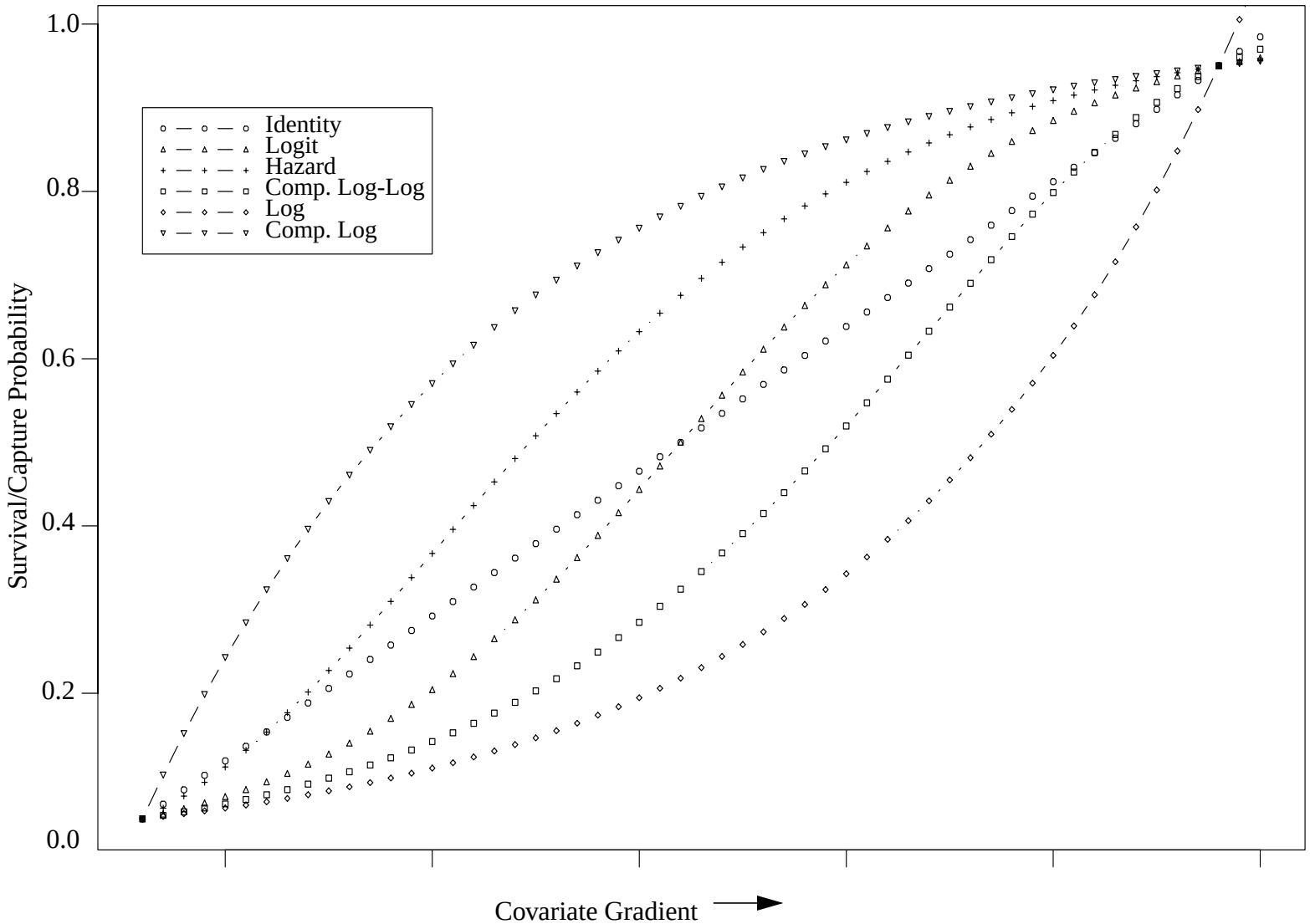


Figure 2.1 Graphical illustration of link functions for modeling relationships between covariates and capture or survival probabilities. All functions go through 0.0 at low end of covariate gradient and 1.0 at high end.

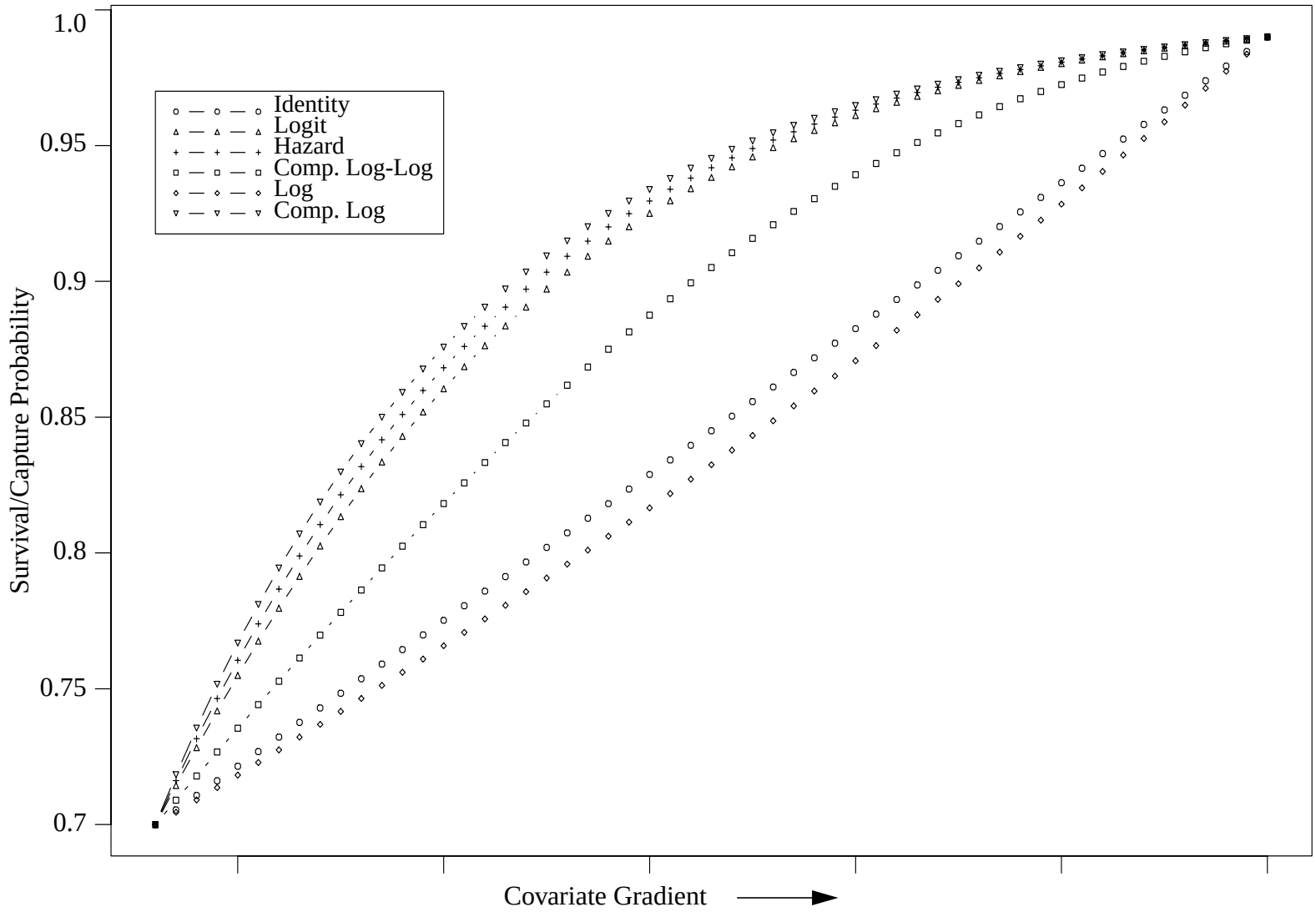


Figure 2.2 Graphical illustration of link functions for modeling relationships between covariates and capture or survival probabilities. Range of probabilities constricted to 0.7 to 1.0.

indiscernible within the restricted range of 0.7 and 1.0. In Figure 2.3, probabilities range from 0.0 to 0.3, and the logit, complementary log-log and log links all produce similar curves in the range. Outside the restricted ranges, the various link functions can vary widely. Consequently, if the estimated survival probabilities for a particular data set fall in a restricted range, extrapolation outside the range is not recommended.

In actual tag-release studies, the range of survival probabilities is usually relatively narrow. The similarity of link functions in restricted ranges implies that the choice of link functions in many analyses may not be critical with regard to fitted (predicted) survival probabilities and the resulting maximized likelihood value. Hence, inferences regarding tests of effects on survival (using likelihood ratio tests or analysis of deviance) will almost always be the same regardless of the link function employed. The major difference among link functions, then, is the interpretation of the parameters, and the implied effects on the hazard rate, life expectancy, and relative risk.

Instantaneous relative risk (Eq. (2.21)) and life expectancy (Eq. (2.20)) can be calculated from the parameters of the hazard link but not under the logit link. The hazard function is a description of instantaneous risk through time, whereas the logistic parameterization gives a description of risk for the entire interval. If environmental conditions are constant (i.e., $\lambda_0(t) = \lambda_0$), the life expectancy of an animal with covariate vector $\underset{\sim}{x}$ under the hazard link is:

$$E(T|\underset{\sim}{x}) = \frac{1}{\lambda_0 e^{\underset{\sim}{x}'\underset{\sim}{\beta}}} = \frac{E(T|0)}{e^{\underset{\sim}{x}'\underset{\sim}{\beta}}} \sim . \tag{2.22}$$

Thus, covariates have a multiplicative effect on life expectancy under the hazard link.

The probabilities of capture can also be modeled as functions of individual- and group-covariates. Although any of the link functions in Table 2.1 can be used, we recommend use of the logit link because capture probabilities in release-recapture models represent success probabilities for discrete-time events (the probability of being captured on a particular sampling occasion). Program SURPH can model capture probabilities in release-recapture studies using either the logit or hazard link.

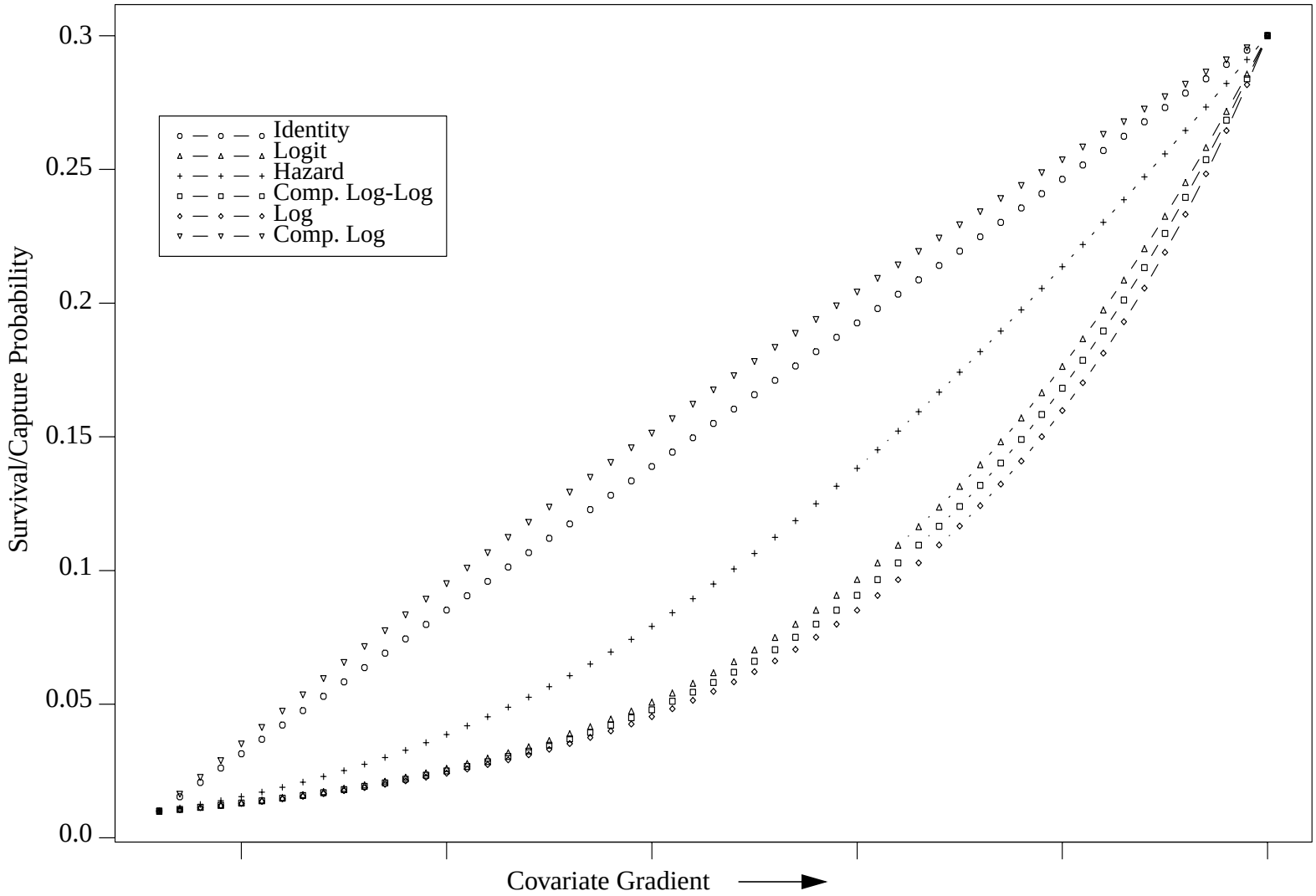


Figure 2.3 Graphical illustration of link functions for modeling relationships between covariates and capture and survival probabilities. Range of probabilities constricted to 0.0 to 0.3.

2.2 Design of Tag-Release Survival Studies

The ability to detect and quantify effects of covariates on survival rates is a powerful tool for fish and wildlife managers, regulatory agencies, population biologists, and others. Effects on survival may have both spatial and temporal aspects. Researchers might be interested in how survival rates differ among populations with different levels of a covariate within a particular time period, or they might wish to learn how survival probabilities at a particular site change through time as the level of a covariate changes. Multiple-site tag-release studies have both spatial and temporal aspects to their study design and are well-suited to the problem of assessment of effects.

Known-fate and release-recapture studies can be implemented to study survival over time intervals or over distances traveled. Thus, the experimental design can be thought of in one of two frames of reference: time or distance. For species that are faithful to a definable study area, survival of animals over time intervals and selection through time are the primary quantities of interest. Survival and selection over distance traveled are the primary quantities of interest in studies on migratory species where individuals share the same migratory route. Salmon smolt outmigration in the Columbia-Snake River system is an example where the frame of reference is distance. Other examples include studies on migratory birds, such as the Ross goose, where the migratory route is well-defined (Welty 1982). Known-fate and release-recapture studies can be applied equally well to studies on selection whether the frame of reference is time or distance (Schwarz 1988).

The type of covariates and the study designs used to investigate them will depend on the goals of the survival study. For example, agrochemical companies and regulatory agencies will wish to reach unambiguous conclusions regarding the effects of a pesticide on survival rates. To this end, they will conduct carefully controlled, multiple-site experiments according to the tenets of experimental design. The covariate of central interest will probably be the level of pesticide application on each site; a covariate that is defined at the population level. On the other hand, the questions of concern to population biologists, general ecologists, and others may not lend themselves to study by controlled experiments. Indeed, it may be impossible to control the

covariates. These researchers may seek general insights into factors influencing population dynamics, and may obtain information from observational studies. Observational or descriptive studies can be used to establish correlative, but not causal, relationships between environmental covariates and survival rates. Covariates for observational studies might include period- or site-specific factors and/or traits measured on individual animals to investigate selective pressures.

In the sense intended here, an *experimental study* is one that involves manipulation of the environment in a controlled and prescribed way. Federer (1973) provides a useful definition of an experiment as the collection of measurements or observations according to a prearranged plan for the purposes of obtaining evidence to test a theory or hypothesis. The goal is to isolate the effect of the manipulation on survival rates. In other words, experimental studies attempt to control for all environmental factors except for the factor being manipulated to allow us to demonstrate that changes are caused by the manipulation. An *observational study*, on the other hand, is one in which the covariate levels are not under the control of the investigator. The investigator conducts the tag-release study and records how covariates vary over space and time. Observational studies can be used to show that survival probabilities are correlated with covariates but cannot demonstrate causality because of the absence of experimental control. When an observational study shows correlation between covariates and survival, it can suggest hypotheses to be tested in subsequent experimental studies.

2.2.1 Principles of experimental design

Cox (1958) gives three conditions that prompt an experimental approach to answering a research question: (1) an objective of comparing treatment effects, (2) a substantial variation in response from plot to plot in the absence of a treatment effect, and (3) treatment differences that are relatively stable despite possible fluctuations in mean response levels. Fisher (1947) admonishes that the study must provide a valid estimate of the error variance with which to test hypotheses. This error variance is a measure of the extraneous variation that tends to mask the treatment effects. Fisher (1947) states that the correct measure of the error variance for testing treatment means is “one that contains all sources of variation inherent in the variation among

treatment means except that portion due specifically to the treatments themselves." To assure the validity of the comparison of treatments, an experimental design must adhere to the fundamental principles of replication, randomization, and experimental control.

If the effects of a treatment are to be demonstrated spatially (i.e., sites with different levels of the treatment have different survival rates), it is not sufficient to show that a single site with one level of the treatment differs from another site with a different level. The effects of the treatment in this case are completely confounded with the effects of any other differences between the two sites. The solution is replication, a basic technique in experimental design. *Replication* is the application of similar treatment conditions to two or more experimental units (sites). Replication accomplishes three major objectives: (1) It allows the experimenter to show that the treatment effect is repeatable; (2) it allows estimation of experimental error or error variability; and (3) it leads to a more precise estimate of treatment effects.

A slightly less stringent version of replication is seen in the design of a "controlled regression" study. In controlled regression, the levels of a covariate are under the control of the investigator and applied at random to experimental units. If a particular form is assumed for the relationship between a covariate and survival response, then each level of the covariate need not be exactly replicated. The assumed form of the relationship provides the opportunity to estimate the experimental error using the deviations from the model as a measure of variability. A classic example of a controlled regression study is the *dose-response* design, where differing levels of a treatment are applied to the replicate experimental units at random.

Randomization is employed to distribute the idiosyncratic characteristics of the experimental units over the treatment levels so that they will not systematically bias the outcome of the experiment. Thus, randomization provides a basis of obtaining unbiased estimates of the treatment effects in the face of unassigned variability among replicated experimental units. Randomization also helps to ensure that the measured responses are statistically independent (Kirk 1982). In this context, "random" does not mean "haphazard"; rather, that treatments are assigned to the experimental units in a probabilistic manner. The experimental design is a plan by

which treatments are randomized to sites. All familiar designs for linear models involve randomization, including randomized block, Latin square, split plot and the completely randomized design. All of these designs can be analyzed using Program SURPH.

The use of *experimental controls* implies that experimental units under treatment conditions are compared with units ("controls") treated identically except for the treatment under scrutiny. Often, treatment conditions will be compared to "null" or "normal" conditions. The null condition is often the complete absence of the treatment. In agricultural tests of a pesticide, for example, the control sites would not receive an application of the pesticide, though they may have an inert substance similar to the pesticide sprayed to control for the direct physical effects of the effort of applying the pesticide. Alternatively, the control condition may be an established level of an environmental factor for comparison with elevated or depressed levels of the factor.

Using the three principles outlined above, the choice of experimental design (i.e., the restrictions used in randomizing treatments to site) will depend on the environmental factors one wishes to control through blocking and the constraints imposed by the location and number of available sites. Typically, the simplest design that adequately controls for extraneous sources of variability should be selected. For simple comparisons of two treatments, completely randomized or paired designs will be adequate more often than not.

2.2.2 Release and sampling protocols

The basic elements of an animal survival study are the same for known-fate and release-recapture studies. The protocol consists of two components: (1) the designation of sampling events upon which survival information is obtained; and (2) a release design that specifies how newly tagged animals enter the study. The discussion below includes cases when the frame of reference is time or distance.

The first component is the designation of the sampling events. Sampling events are those occasions in time or those locations in space where survival status is determined in known-fate studies or where recapture efforts are made in release-recapture studies. The sampling events

divide the study into intervals. The term “interval” is generic and refers to the time or distance between sampling events. When time is the frame of reference, the intervals are called periods. When distance is the frame of reference, the intervals are segments. For the special case of salmon outmigration studies, the segments are river reaches. Figure 2.4 illustrates the numbering scheme for sampling events and intervals.

The sampling events are “snapshots,” giving a survivor profile of the marked animals at a point in time or space. The sampling events should be close enough in time or space that external environmental conditions within each interval vary as little as possible. If the conditions within an interval are not constant, individuals with one set of traits may be favored in one part of the interval and those with a different set of traits favored in a different part. In this case, the effects may cancel out, so that over the entire interval, no selection can be detected even though it occurred (Endler 1986, Chapter 4). Constancy of environmental conditions over an interval increases the chances of detecting and correctly interpreting selection if it exists. In addition, if the external conditions are to be used as group-based covariates in a multi-site study, volatile conditions within intervals makes it difficult to characterize the conditions in a meaningful way.

Figure 2.4, with sampling events depicted as single points along the line, illustrates the assumption that sampling events occur essentially instantaneously. That is, it is assumed that sampling events occur over a very short period of time or distance relative to the length of the intervals between events. Instantaneous sampling assures that the intervals over which survival is estimated are well-defined. If the events are not instantaneous (i.e., sampling occurs over a large span of time or space relative to the length of the intervals between sampling events), the beginning and end points of the intervals become “fuzzy.” A consequence of non-instantaneous sampling is illustrated in Figure 2.5. The figure illustrates the fate of two animals released at the same time in a known-fate study. Animal B actually survives for a longer time than A, yet A would be recorded as having survived the first interval and B would be recorded as not having survived. The probability of survival from release until the first sampling event is not a well-defined quantity when significant mortality can occur during a sampling event.

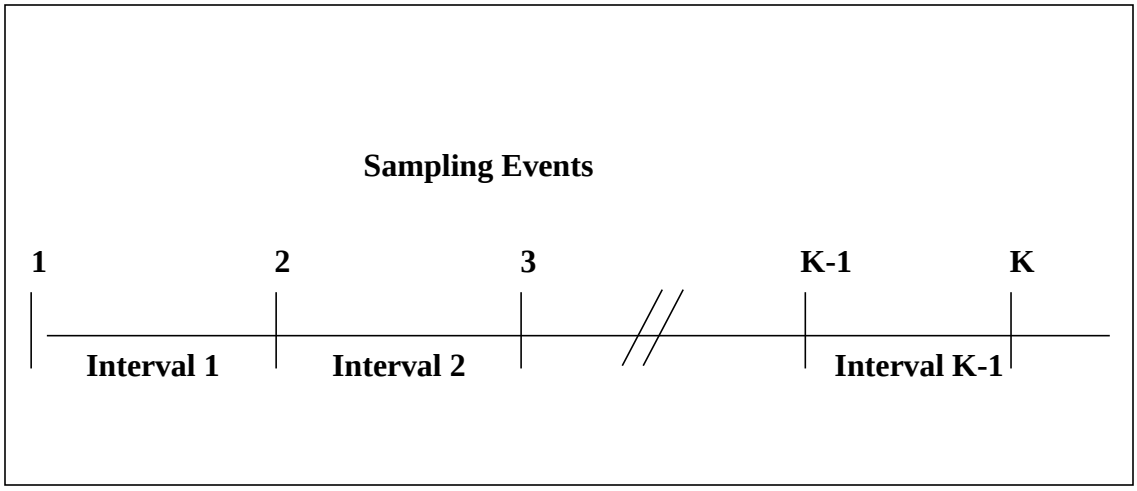


Figure 2.4 Schematic of the numbering system for the sampling events and intervals. The K sampling events divide the study into K-1 intervals over which survival is studied.

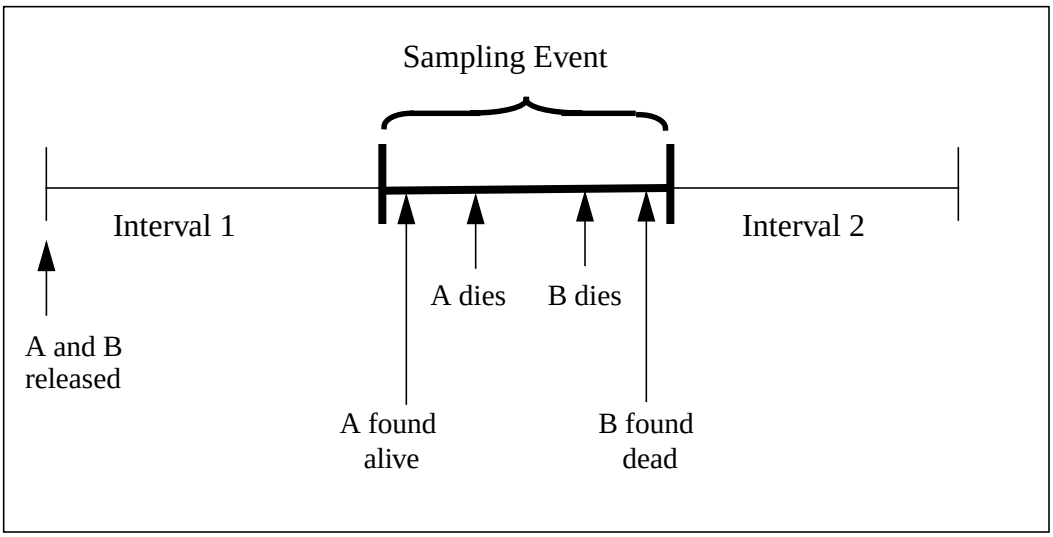


Figure 2.5 Illustration of a problem that can occur when mortalities can occur during a prolonged sampling event.

When the frame of reference is time, the problem is to find all the animals in the shortest time possible. The duration of a sampling event will depend on the techniques used for marking and recapturing the animals and on the number of personnel available. When the frame of reference is distance, fixed observation posts positioned at points along the migratory route assures that the instantaneous sampling assumption will be satisfied. It is important that the observation posts be operational until every survivor has passed the point.

The second component of the study protocol is the release design, which determines how tagged animals enter into the study. The release design consists of the number of populations included in the study and by the number of release groups per population. In this manual, for purposes of tag-release studies, the term “population” has a very specific meaning, not necessarily coinciding with the usual ecological definition. A population is a distinct group of animals to which the same levels of all group covariates apply, or which share common traits, such as sex or age class. For example, in a multi-site study, each site may be assumed to have a single, distinct population, with group covariates characterizing the sites. If survival is expected to differ between sexes, the analysis could include two populations on each site, defining males and females as separate populations (note that sex could also be defined as an individual-based indicator variable). In a study with the distance frame of reference, such as a juvenile salmon study on the Columbia River, populations might be defined by the time of release. For example, if releases are made at the same location on three separate occasions, the fish in each release are considered to be distinct populations.

A “release group” is defined as the collection of animals within a population marked and released at a particular sampling event. This definition differs from that used by Burnham et al. (1987) where a release group is defined to be the collection of animals captured and released at a particular sampling event, including previously marked individuals. Under the definition of Burnham et al. (1987), an animal is a member of as many release groups as the number of sampling events on which it was captured and released. Defining release groups according to the event when the animals were first captured and marked is convenient for our purposes, because animals are grouped by the event at which their individual covariates were measured. When the

frame of reference is time, the release groups are defined by the time when the animals entered into the study. When the frame of reference is distance, the releases are defined by the location where the animals entered the study. Accordingly, each animal is a member of only one release group, regardless of subsequent capture history. Within a release group, the covariates measured on each animal are comparable because they are measured at the same time or at the same place.

There are four basic study designs defined by the number of populations involved and the number of release groups within each population: (1) single-population, single-release design; (2) single-population, multiple-release design; (3) multiple-population, single-release design; and (4) multiple-population, multiple-release design.

2.2.2.1 Single-population single-release

In the single-population, single-release design (Figure 2.6), a single random sample of R animals is obtained from a designated biological population. This is also known as a *single-entry* release design. All individuals are measured and released into the study area simultaneously at Event 1. With this design, a survival-estimation model can be used to obtain estimates for interval-specific survival probabilities $S_1, S_2, \ldots, S_{K-1}$. With a survival-effects model, one can study relationships between the survival probability in each interval and group-based covariates specific to each interval. In addition, the relationship between survival in each interval and individual traits can be examined. The survival parameters shown in Figure 2.6 are defined as follows:

S = baseline, or intercept parameter for survival probabilities;

ρ_k = regression parameter describing the difference from the baseline survival probability for interval k (k= 2,..., K-1);

β_{kl} = regression parameter for the relationship between the lth (l = 1,..., L) individual-based covariate and survival probability in the kth interval (k= 1,..., K-1). These parameters are also referred to as selection parameters; and

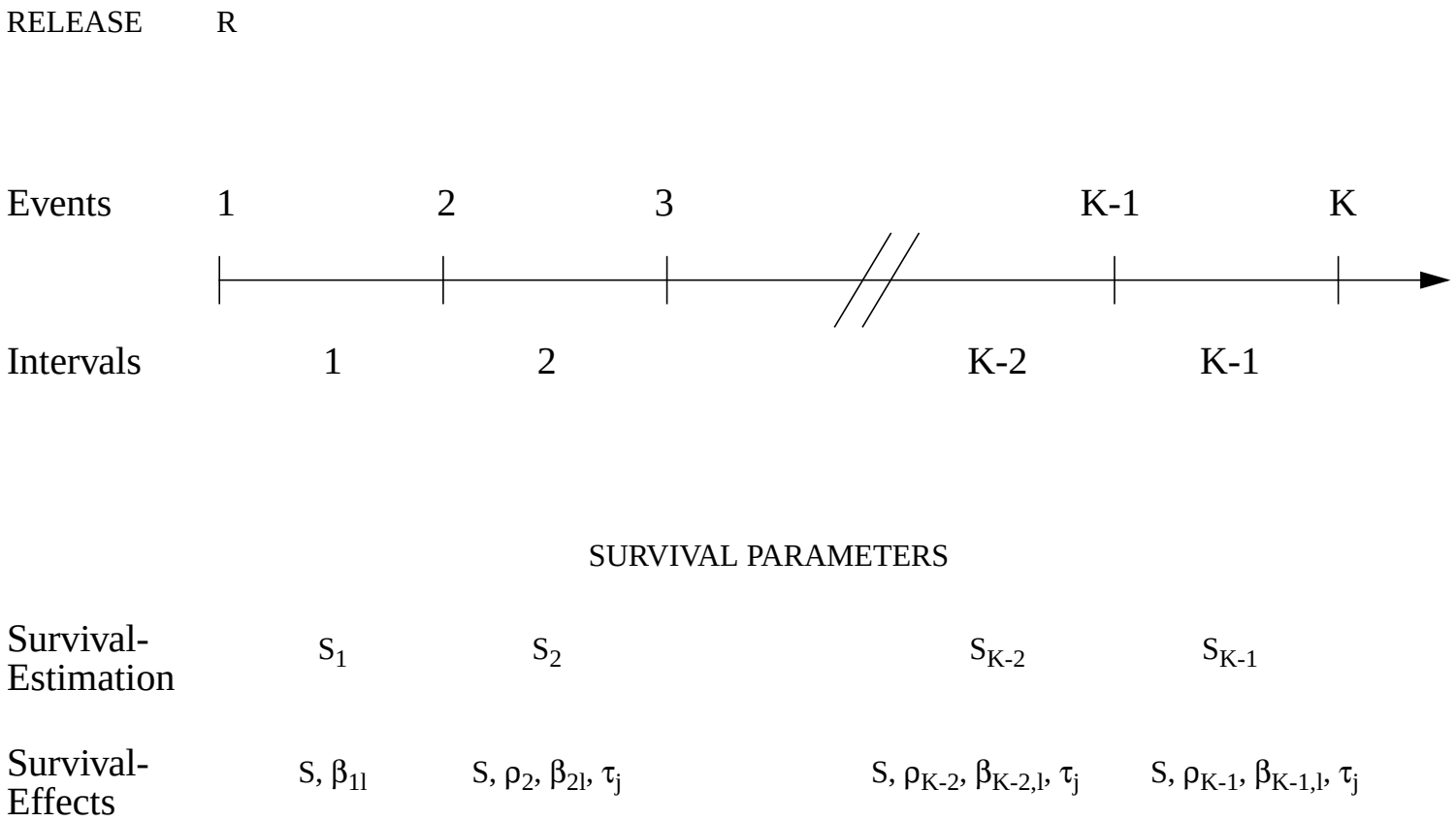


Figure 2.6 Schematic of single-population, single-release design, showing parameters that can be estimated using survival-estimation and survival-effects models. Design consists of a single release of *b* uniquely tagged animals at event 1.

τ_j = regression parameter for the relationship between survival probabilities and the *j*th interval-specific environmental (group-based) covariate (*j*=1,..., *J*).

Using release-recapture data, it is also necessary to model the capture probabilities. In a capture-estimation model, the event-specific capture probabilities are denoted P_2, P_3, …, P_K. The survival probability in the final interval and the capture probability on the final sampling event cannot be modeled separately. Release-recapture data have this restriction because it is impossible to know whether an animal not seen on the final sampling event died during the last interval or if it survived and eluded detection. It is possible to model the product of the probability of survival through the final interval and probability of detection at the final event ($S_{K-1}P_K$) (also known as the "product term"). In addition to the survival-process parameters above, the following parameters can be estimated using release-recapture data:

P = baseline, or intercept parameter for capture probabilities;

η_k = regression parameter describing the difference from the baseline capture probability for sampling event *k* (*k*= 3,..., *K*);

δ_{kl} = regression parameter for the relationship between the *l*th (*l* = 1,..., *L*) individual-based covariate and capture probability on the *k*th event (*k*= 2,..., *K*);

γ_j = regression parameter for the relationship between capture probabilities and the *j*th event-specific (group-based) covariate (*j*=1,..., *J*).

λ = baseline, or intercept parameter for product term; and

χ_l = regression parameter for the relationship between the *l*th (*l* = 1,..., *L*) individual-based covariate and the product term.

With only a single population, the product term cannot be modeled as a function of group-based covariates.

With the single-population, single-release design, one can test whether the survival process over time is related to external factors that vary with time (i.e., $H_0{:}\rho_k = 0$ or $H_0{:}\tau_j = 0$). In addition, hypotheses about the selection pressures among animals within sampling intervals (i.e., individual-based covariate effects) can be tested (i.e., $H_0{:}\beta_{kl} = 0$). Analogously, changes in capture probabilities over time (i.e., $H_0{:}\eta_k = 0$ or $H_0{:}\gamma_j = 0$) and as a function of individual-based covariates (i.e., $H_0{:}\delta_{kl} = 0$) can be tested.

2.2.2.2 Single-population multiple-release

In the single-population, multiple-release design (Figure 2.7) with K sampling events, there can be as many as K-1 release groups of size R_k (k = 1,..., K - 1), one on each sampling event except the last. The individuals in each release group are drawn from the same population. When releases of newly-marked animals occur at multiple sampling events, the release design is called *staggered-entry.* Without staggered entry, the number of marked animals surviving until the later stages of the study can be too small to estimate parameters with reasonable precision. The parameters that can be estimated are the same as for the single-population, single-release design. Time-variant individual-based covariates cannot be studied using the multiple-release design, because the covariates are measured at different times for the various release groups. Time-invariant individual covariates can be modeled, as the time of measurement is irrelevant. As in the single-release design, relationships can be investigated between the survival probability in each interval and group-based covariates specific to each interval.

2.2.2.3 Multiple-population single release

In the multiple-population, single-release design (Figure 2.8), a single release group, R_i (i = 1,..., I), is made at the beginning of the study in each of I populations. Animals from all populations are released on event 1. All releases and subsequent sampling events occur simultaneously (i.e., the same time or same location) in all populations. This design is essentially

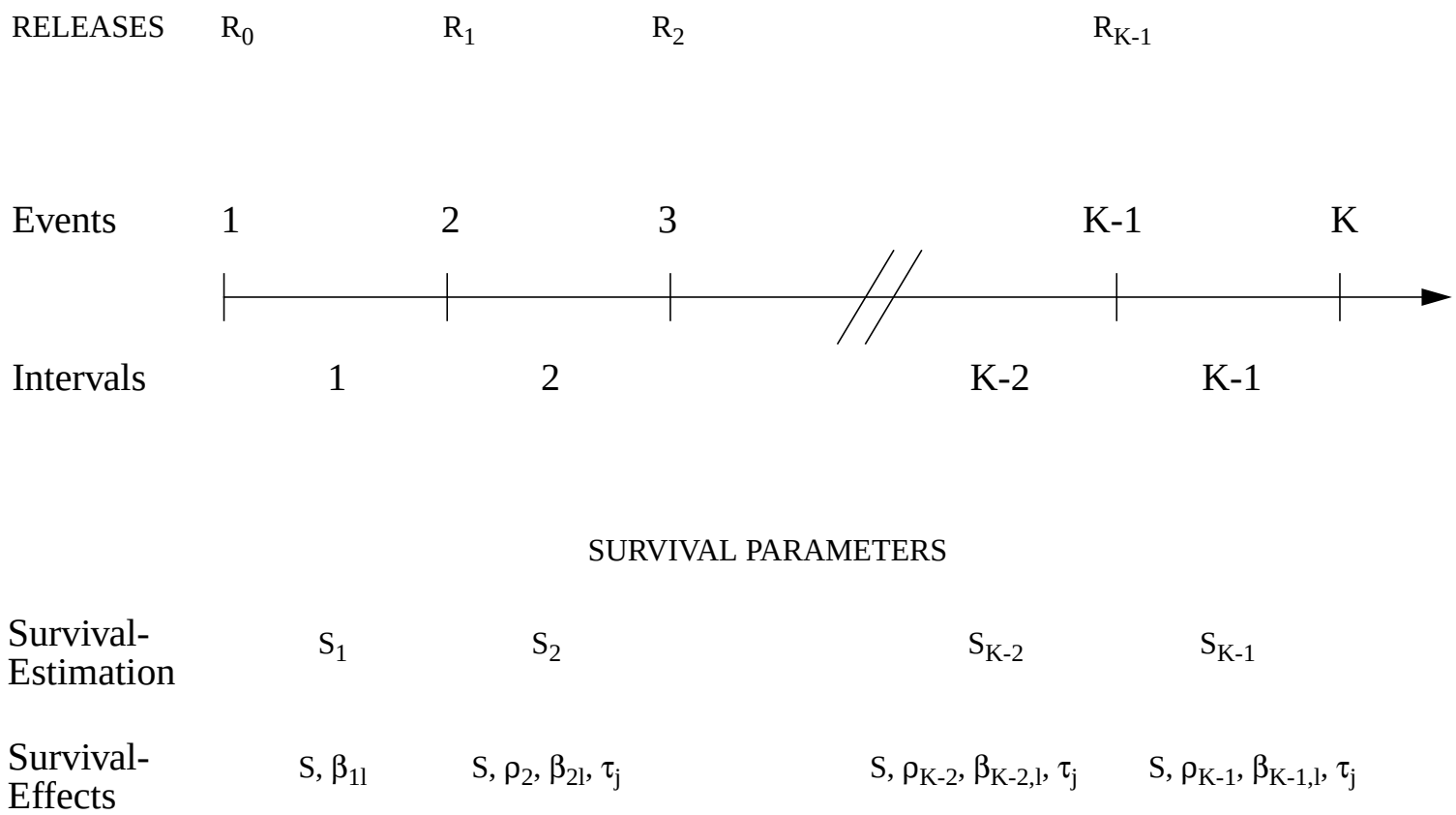


Figure 2.7 Schematic of single-population, multiple-release design, showing parameters that can be estimated using survival-estimation and survival-effects models. Design consists of as many as *K*-1 release groups {b_k (*k* = *1*,..., *K-1*)} of tagged animals. All animals are drawn from the same population.

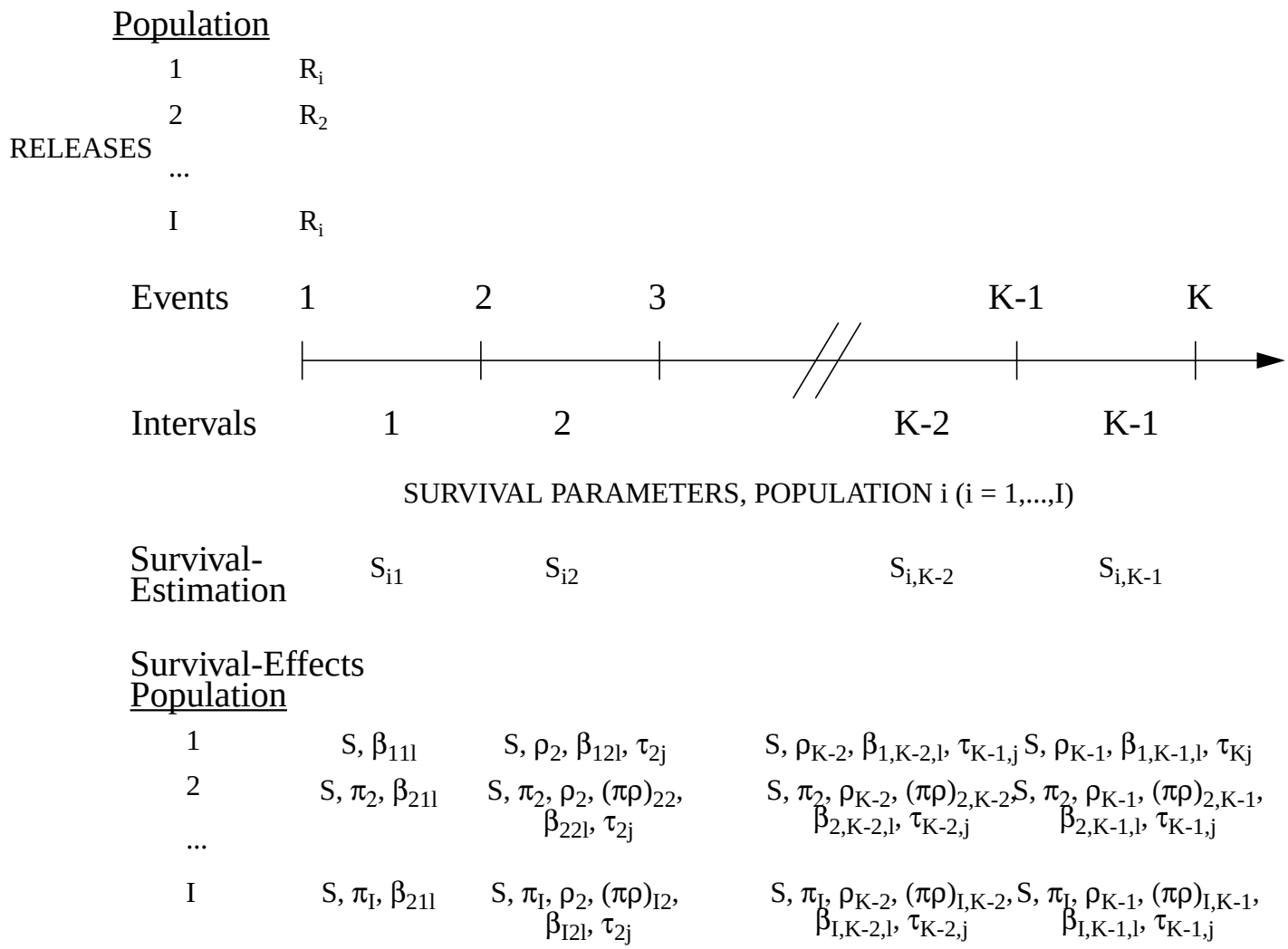


Figure 2.8 Schematic of multiple-population, single release design, showing parameters that can be estimated using survival-estimation and survival-effects models. Design consists of a single release, b_i (i = 1,..., I), of tagged animals in each of I populations. The sampling events occur at the same time or location for each population.

the single-population, single-release design carried out on two or more populations simultaneously. If the populations are defined by geographic location and environmental conditions vary among the locations, the effect on overall population survival rates of the environmental conditions (group-based covariates) can be modeled. Moreover, interactions between individual-based traits and environmental conditions can be investigated, shedding light on selection processes. When segments of a migration path are the focus of the study, the replicate populations are defined by the time of release. The study design can then be used to relate changes in survival probabilities to segment-specific conditions that change through time.

Using survival-estimation models, population- and interval-specific survival probabilities (S_{ik}, i = 1,...,I; k=1,...,K-1) can be estimated using a multiple-population design. Under a survival-effects model, the survival parameters that can be estimated with known-fate data are as follows (Figure 2.8):

S = baseline, or intercept parameter for survival probabilities;

π_i = regression parameter describing the difference from the baseline survival probability for population i (i = 2,..., I);

ρ_k = regression parameter describing the difference from the baseline survival probability for interval k (k = 2,..., K-1);

$(\pi\rho)_{ik}$ = regression parameter describing the interaction between population and interval effects on baseline survival probability (i = 2,..., I) and (k = 2,..., K-1);

β_{ikl} = regression parameter describing the relationship between the lth (i = 1,..., L) individual-based covariate and survival probability in the kth interval (k= 1,..., K-1) for the ith population (i = 1,..., I); and

τ_{kj} = regression parameter describing the relationship between survival probabilities in the kth interval (k= 1,..., K-1) and the jth (j = 1,..., J) environmental covariate

measured for all populations in the *k*th interval.

The following parameters can be estimated using release-recapture data, in addition to the survival-related parameters defined above:

P = baseline, or intercept parameter for capture probabilities;

ν_i = regression parameter describing the difference from the baseline capture probability for population i (i = 2,..., I);

η_k = regression parameter describing the difference from the baseline capture probability for event k (k = 3,..., K);

$(\nu\eta)_{ik}$ = regression parameter describing the interaction between population and event effects on baseline capture probability (i = 2,..., I) and (k = 3,..., K);

δ_{ikl} = regression parameter describing the relationship between the *l*th (i = 1,..., L) individual-based covariate and capture probability on the *k*th event (k= 2,..., K) for the *i*th population (i = 1,..., I);

γ_{kj} = regression parameter describing the relationship between capture probabilities on the *k*th event (k= 2,..., K) and the *j*th (j = 1,..., J) environmental covariate measured for all populations on the *k*th event;

λ = baseline, or intercept parameter for product term (product of final-interval survival and final-event capture probabilities);

φ_i = regression parameter describing the difference from the baseline product term for population i (i = 2,..., I);

χ_{il} = regression parameter for the relationship between the *l*th (i = 1,..., L) individual-

based covariate and product term for the ith population (i = 1,..., I); and

ω_j = regression parameter describing the relationship between product terms and the jth (j = 1,..., J) population-specific environmental covariate measured on the Kth (final) event.

Multiple-population designs allow significance testing for effects on survival probabilities of group-based covariates that vary among populations, in addition to those that vary across intervals. For individual-based covariates, one can test whether the regression parameters are equal across populations or intervals, i.e., whether or not selection occurs with the same intensity or in the same direction under the different environmental conditions experienced by each population in the study. Similarly, capture probabilities can be modeled as a function of population-specific or event-specific effects and their interactions.

2.2.2.4 Multiple-population multiple-release

The multiple-population multiple-release design (Figure 2.9) combines the aforementioned advantages of both multiple-population and multiple-release designs. That is, capture and survival probabilities can be modeled as functions of population-specific as well as interval-specific covariates, and sufficient numbers of animals are at risk in each interval for precise estimation of survival and capture probabilities.

2.3 Parameter Estimation

Whenever random sampling is used to gather data, the observed data and the values of any statistics used to summarize the data are realizations of random variables (Hoel et al. 1971). Statistics derived from random variables, have associated probability distributions. Probability distributions depend on a set of one or more unknown parameters. The parameters of interest here include survival and capture probabilities and regression coefficients that relate survival and capture to covariates. In survival studies, the random variables are the capture histories of the tagged animals. In some models, for instance, the data are summarized by obtaining a count of

	Population				
	1	R_{i1}	R_{i2}	R_{i3}	$R_{i,K-1}$
RELEASES	2	R_{21}	R_{22}	R_{23}	$R_{2,K-1}$
	...				
	I	R_{i1}	R_{I2}	R_{i3}	$R_{i,K-1}$

Events	1	2	3	K-1	K
Intervals	1	2		K-2	K-1

SURVIVAL PARAMETERS, POPULATION i (i = 1,...,I)

Survival-Estimation	S_{i1}	S_{i2}	$S_{i,K-2}$	$S_{i,K-1}$

Survival-Effects				
Population				
1	S, β_{11l}	$S, \rho_2, \beta_{12l}, \tau_{2j}$	$S, \rho_{K-2}, \beta_{1,K-2,l}, \tau_{K-1,j}$	$S, \rho_{K-1}, \beta_{1,K-1,l}, \tau_{Kj}$
2	S, π_2, β_{21l}	$S, \pi_2, \rho_2, (\pi\rho)_{22}, \beta_{22l}, \tau_{2j}$	$S, \pi_2, \rho_{K-2}, (\pi\rho)_{2,K-2}, \beta_{2,K-2,l}, \tau_{K-2,j}$	$S, \pi_2, \rho_{K-1}, (\pi\rho)_{2,K-1}, \beta_{2,K-1,l}, \tau_{K-1,j}$
...				
I	S, π_I, β_{21l}	$S, \pi_I, \rho_2, (\pi\rho)_{I2}, \beta_{I2l}, \tau_{2j}$	$S, \pi_I, \rho_{K-2}, (\pi\rho)_{I,K-2}, \beta_{I,K-2,l}, \tau_{K-2,j}$	$S, \pi_I, \rho_{K-1}, (\pi\rho)_{I,K-1}, \beta_{I,K-1,l}, \tau_{K-1,j}$

Figure 2.9 Schematic of multiple-population, multiple-release design, showing parameters that can be estimated using survival-estimation and survival-effects models. Design consists of as many as *K*-1 release groups $\{b_{ik}$ (i = 1,..., I; k = 1,..., K-1)$\}$ of uniquely-tagged animals in each of *I* populations.

animals for each of the possible histories. Under certain assumptions, these “cell counts” can be modeled as a sample from a multinomial distribution.

The problem of estimating unknown parameters of a probability distribution from sample data has long been a central concern in the field of statistics, and many methods have been proposed to solve the problem. One of the most well-known and widely-used is the method of *maximum likelihood (ML) estimation*, which was presented by Fisher (1922, 1925). The ML method provides a powerful means of deriving point estimates and, equally importantly, estimators of the sampling variances and covariances of the point estimators. Hypothesis testing and model building can also be performed using likelihood theory. The ML method is appealing for its conceptual justification and for its many large sample statistical properties. Maximum likelihood estimators are asymptotically unbiased, normally distributed, and maximally efficient (Wilks 1962, Rao 1973, Lehmann 1982).

2.3.1 Maximum likelihood theory

Suppose we have a set of discrete random variables $X_1, X_2, ..., X_n$ with joint probability function $f(\underset{\sim}{x};\underset{\sim}{\theta})$ where $\underset{\sim}{\theta}$ is a vector of parameters. In tag-release models, the random variables are usually a set of summary statistics derived from the counts of capture histories (multinomial cell counts). The joint probability function is based on the multinomial probability function with cell probabilities modeled as functions of survival and capture probabilities and regression coefficients for covariate effects. When treated as a function of the data, $f(\underset{\sim}{x};\underset{\sim}{\theta})$ gives the probability of the observed data, given the parameter values $\underset{\sim}{\theta}$.

When treated as a function of unknown parameters, on the other hand, the function $f(\underset{\sim}{x};\underset{\sim}{\theta})$ gives the “likelihood” of a set of parameters $\underset{\sim}{\theta}$ given the observed sample data $\underset{\sim}{x}$. The function is then called the *likelihood function* for $\underset{\sim}{\theta}$. To emphasize that the likelihood function is considered to be a function of the parameters, it is customary to use the notation $L(\underset{\sim}{\theta};\underset{\sim}{x})$, or simply $L(\underset{\sim}{\theta})$, for the likelihood function. The objective of the ML method is to find the set of parameter values

that maximizes the likelihood function for a given sample outcome. That is, the estimates are the parameter values under which the sample data are "most likely." The parameter values that maximize the likelihood function are known as *maximum likelihood estimates* (MLEs) and are denoted by $\hat{\underset{\sim}{\theta}}$.

Because likelihood functions are often formed as the product of many terms, it is generally easier to deal with the natural logarithm of the likelihood function, or "log-likelihood," which is composed of additive terms. The functions $L(\underset{\sim}{\theta})$ and $lnL(\underset{\sim}{\theta})$ have their maximum at the same value of $\underset{\sim}{\theta}$. Thus, the MLEs $\hat{\underset{\sim}{\theta}}$ are the solution to the following system of equations, known as the "likelihood equations":

$$\frac{\partial}{\partial \theta_1} lnL(\underset{\sim}{\theta}) = 0$$

$$\frac{\partial}{\partial \theta_2} lnL(\underset{\sim}{\theta}) = 0$$

$$\vdots$$

$$\frac{\partial}{\partial \theta_\nu} lnL(\underset{\sim}{\theta}) = 0$$

where ν is the number of parameters to be estimated.

When the likelihood equations can be solved analytically, the parameter estimators $\hat{\underset{\sim}{\theta}}$ are said to be in "closed form." That is, $\hat{\underset{\sim}{\theta}}$ can be written as a set of algebraic functions of the data. When closed forms are not possible (i.e., the likelihood equations cannot be solved analytically) there is a variety of numerical methods designed to find parameter values that maximize the likelihood function. Numerical methods can give estimates when no closed form estimators exist. Numerical optimization methods are discussed in Section 2.5.

As functions of the sample data, the MLEs are themselves random variables that will vary from sample to sample. Thus, a sampling variance is associated with each estimate. In addition, the estimators $\hat{\underset{\sim}{\theta}}$ are generally correlated, because they are estimated from the same data. Each pair of estimators has an associated sampling covariance. The variances and covariances make up the *covariance matrix*, which is usually denoted $\underset{\sim}{\Sigma}$:

$$\underset{\sim}{\Sigma} = \begin{bmatrix} Var(\hat{\theta}_1) & Cov(\hat{\theta}_1, \hat{\theta}_2) & Cov(\hat{\theta}_1, \hat{\theta}_3)\ldots & Cov(\hat{\theta}_1, \hat{\theta}_\nu) \\ Cov(\hat{\theta}_2, \hat{\theta}_1) & Var(\hat{\theta}_2) & Cov(\hat{\theta}_2, \hat{\theta}_3) & Cov(\hat{\theta}_2, \hat{\theta}_\nu) \\ Cov(\hat{\theta}_3, \hat{\theta}_1) & Cov(\hat{\theta}_3, \hat{\theta}_2) & Var(\hat{\theta}_3) & Cov(\hat{\theta}_3, \hat{\theta}_\nu) \\ \vdots & & \ddots & \\ Cov(\hat{\theta}_\nu, \hat{\theta}_1) & Cov(\hat{\theta}_\nu, \hat{\theta}_2) & Cov(\hat{\theta}_\nu, \hat{\theta}_3) & Var(\hat{\theta}_\nu) \end{bmatrix}_{\nu \times \nu}$$

The matrix is symmetric, since $Cov(\hat{\theta}_i, \hat{\theta}_j) = Cov(\hat{\theta}_j, \hat{\theta}_i)$. The variances and covariances are usually functions of the sample size and the unknown parameters themselves. Substituting the estimated parameter values of $\hat{\underset{\sim}{\theta}}$ into the expressions for the variances and covariances gives the estimated covariance matrix $\hat{\underset{\sim}{\Sigma}}$. The estimate of $Var(\hat{\theta}_i)$ is denoted $V\hat{a}r(\hat{\theta}_i)$ and the estimate of $Cov(\hat{\theta}_i, \hat{\theta}_j)$ is denoted $C\hat{o}v(\hat{\theta}_i, \hat{\theta}_j)$.

A property of the ML method is that the asymptotic covariance matrix of the estimators is easily (conceptually, at least) derived from the likelihood function itself. The covariance matrix is the inverse of the expected value of the negative of the matrix of mixed second partial derivatives of the log-likelihood. The matrix of expected values of second partial derivatives is known as the *Information matrix*, and is denoted $I(\underset{\sim}{\theta})$ (a function of $\underset{\sim}{\theta}$). The *ij*th element of $I(\underset{\sim}{\theta})$ is:

$$-E\left[\frac{\partial^2}{\partial\theta_i \partial\theta_j} lnL(\underset{\sim}{\theta})\right] .$$

The matrix $I(\underset{\sim}{\theta})$ is evaluated at the true parameter value $(\underset{\sim}{\theta})$. If the true values are unknown, the matrix can be evaluated at $\hat{\underset{\sim}{\theta}}$; the MLEs, giving the estimated covariance matrix:

$$\hat{\Sigma} = [I(\hat{\underset{\sim}{\theta}})]^{-1} .$$

The matrix $I(\hat{\underset{\sim}{\theta}})$ is known as the *observed Information matrix*.

The covariance matrix characterizes the likelihood function in the neighborhood of the maximum point. If the function is very peaked in a particular dimension, then a small movement away from the peak results in a greatly reduced likelihood. In the peaked case, the corresponding parameter can be estimated very precisely, i.e., the variance of the estimator is small. Alternatively, if the function is relatively flat in some dimension, then small movements away from the maximum value make little difference to the likelihood value. In the flat case, the variance is larger; i.e., the parameter is not estimated as precisely with the same sample size.

After variance estimates are obtained, one can rely on the asymptotic normality of MLEs to compute confidence intervals. An asymptotic $(1-\alpha)\times 100$ % confidence interval for θ is given by:

$$\hat{\theta} \pm Z_{1-\alpha/2}\sqrt{V\hat{a}r(\hat{\theta})}..$$

Asymptotic normality also suggests a statistic that can be used to test hypotheses of the form $H_0\colon\ \theta = \theta_0$, where θ_0 is a particular hypothesized value for the parameter θ. If $\hat{\theta}$ is normally distributed, then the test statistic:

$$Z = \frac{\hat{\theta} - \theta_0}{\sqrt{V\hat{a}r(\hat{\theta})}}$$

has a standard normal distribution when H_0 is true. To test hypotheses, Z is compared with appropriate quantiles of a standard normal variable ($Z \sim N(0, 1)$).

Despite its conceptual simplicity, the covariance matrix can be extremely difficult to derive, requiring complicated algebra. Most numerical optimization methods (see Section 2.5) use the inverse of the matrix of second partial derivatives, or an approximation to the matrix or its inverse, to find the maximum of the likelihood function. When numerical methods are used, $\hat{\Sigma} = I(\hat{\underset{\sim}{\theta}})^{-1}$ can be obtained from the final iteration of the numerical procedure.

2.3.2 Example of maximum likelihood estimation

Consider an experiment to estimate the probability that a coin will land "heads" up when flipped into the air. The probability of tossing a "head" is the unknown parameter p, and the probability of a "tails" is (1-p). The experiment consists of n trials, or flips of the coin, and the number of heads is recorded, denoted by x.

The number of heads in such an experiment is a random variable with a binomial distribution parameters n (known) and p. The binomial likelihood function for p (given n) is:

$$L(p|n, x) = \binom{n}{x} p^x (1-p)^{n-x} \quad .$$

The log-likelihood can then be written as

$$lnL(p|n, x) = ln\binom{n}{x} + xlnp + (n-x)ln(1-p) \quad .$$

The likelihood equation is found by taking the first derivative with respect to p, yielding

$$\frac{dlnL(p|(n, x))}{dp} = \frac{x}{p} - \frac{(n-x)}{(1-p)} = 0 \quad .$$

Solving for p in the above equation yields the familiar and reasonable MLE

$$\hat{p} = \frac{x}{n} \quad , \tag{2.23}$$

i.e., the estimate of the true probability of heads is equal to the proportion of heads observed in the sample. The variance of the estimated binomial parameter $\hat{p}$ is

$$Var(\hat{p}) = \frac{p(1-p)}{n} \quad . \tag{2.24}$$

The variance is estimated by substituting the parameter estimate (Eq. (2.22)) into the variance formula (Eq. (2.23)). The variance estimator for $\hat{p}$ can be written as

$$V\hat{a}r(\hat{p}) = \frac{\hat{p}(1-\hat{p})}{n} = \frac{x(n-x)}{n^3} \quad .$$

2.3.3 Precision

One of the goals of a survival study may be to estimate a model parameter with a high degree of precision. The other potential goal is to test the significance of a regression coefficient relating survival to measured covariates. Hypothesis tests are discussed in Section 2.4.

A common characterization of precision is the *coefficient of variation* (CV) for a parameter estimate, defined as:

$$CV(\hat{\theta}_i) = \frac{\sqrt{Var(\hat{\theta}_i)}}{\hat{\theta}_i} \times 100\% \ . \tag{2.25}$$

The CV provides a rapid means of assessing the relative certainty of a parameter estimate. For example, if the CV is 10%, then one is approximately 95% certain the estimate does not error by more than $\pm 20\%$. This translation of the CV to a measure of error is based on the expression for precision defined by

$$P\left(\left|\frac{\hat{\theta}-\theta}{\theta}\right| < \varepsilon\right) \geq 1-\alpha \ . \tag{2.26}$$

Expression (2.26) specifies that the relative error in estimation (i.e., $(\hat{\theta}-\theta)/\theta$) is less than ε, at least $(1-\alpha)$ 100% of the time. For example, a precision of $\pm 20\%$ of the true value of θ, 95% of the time specifies $\varepsilon = 0.20$ and $\alpha = 0.05$. Skalski and Robson (1992, p. 79) show that the probability expression (2.26) can be approximated as

$$P\left(\left|\frac{\hat{\theta}-\theta}{\theta}\right| < \varepsilon\right) \approx 1 - 2\Phi\left(\frac{100\varepsilon}{CV(\hat{\theta})}\right) = 1 - \alpha \quad , \tag{2.27}$$

where CV is expressed as a percentage and Φ devotes the cumulative standard normal distribution. In turn, expression (2.27) solves to the relationship that

$$\varepsilon = Z_{1-\alpha/2} CV(\hat{\theta}) \; .$$

For, $\alpha = 0.05$, $Z_{1-\alpha/2} = 1.96 \approx 2.0$, leading to the conclusion that one is approximately 95% certain the error in estimation is less than $\pm 2CV(\hat{\theta})$. Similarly, one can be approximately 80% certain the error in estimation is less than $\pm 1.3CV(\hat{\theta})$.

2.4 Hypothesis Testing

In any analysis of tag-release data, a criterion is needed to choose between competing models for describing the data. The process of model building is a series of selections between models. When we test for effects, we are choosing between two models; one that includes the effect of interest and one that does not. Program SURPH uses two basic types of statistical tests of hypothesis. When the inherent variability of the random variables is fully explained by the likelihood model, likelihood ratio tests (LRT) are performed. However, when extra-likelihood variability exists (variability not explicitly explained by the form of the likelihood), analysis of deviance (ANODEV) procedures are used to test hypotheses. Subsequent sections and chapters will describe when these two procedures are appropriate for a particular testing situation.

2.4.1 Likelihood ratio tests (LRT)

The ML method provides a useful, powerful, and general means of selecting between two models when one model is a special case of the other. The test is based on the ratio of the maximized likelihoods of the two models and is known as a *likelihood ratio test* (LRT). Two models are “nested,” or “hierarchical,” when one is a special case of the other. For example, Model A is nested in Model B if A can be derived from B by equating two or more parameters of B or by dropping one or more parameters from B. The special case model always has fewer parameters.

When choosing between two nested models, the *principle of parsimony* dictates that the model with more parameters should be selected if, and only if, the additional parameters provide a significantly better explanation of the observed data. A model with a larger number of parameters should be chosen only if the observed data is significantly more likely under that model. In LRT, the criterion by which nested models are judged is the relative values of the maximized likelihoods under each of the models. That is, the model with more parameters is said to provide a better explanation of the data than the other only if its maximized likelihood is significantly greater.

To formalize the discussion, ML estimation is a problem of searching the multi-dimensional space of possible values of the parameter vector $\underset{\sim}{\theta}$ (the "parameter space") for the point $\hat{\underset{\sim}{\theta}}$ that maximizes the function $L(\underset{\sim}{\theta})$. If we denote the parameter space Θ, then we can define the MLE $\hat{\theta}$ as parameter values such that:

$$L(\hat{\underset{\sim}{\theta}}) = \underset{\underset{\sim}{\theta} \in \Theta}{sup} L(\underset{\sim}{\theta}) .$$

The operator *sup* means "supremum," i.e., find the value of $\underset{\sim}{\theta}$ that maximizes the function $L(\underset{\sim}{\theta})$.

Now, considering the problem of choosing between two nested models, let us refer to the model with more parameters as the "full model," and to the special case model as the "reduced model." If we let the parameter space for the full model be denoted as Θ_F, then the parameter space for the reduced model, denoted Θ_R, is a subspace of Θ_F. For example, Θ_R may be the subspace where two parameters are equal to each other or where one or more parameters are equal to some hypothesized value(s). Thus, we can write the maximized likelihoods as:

$$L(\hat{\underset{\sim}{\theta}}_F) = \underset{\underset{\sim}{\theta} \in \Theta_F}{sup} L(\underset{\sim}{\theta})$$

and

$$L(\hat{\underset{\sim}{\theta}}_R) = \underset{\underset{\sim}{\theta} \in \Theta_R}{sup} L(\underset{\sim}{\theta}) \quad ,$$

where $\hat{\underset{\sim}{\theta}}_F$ and $\hat{\underset{\sim}{\theta}}_R$ are the MLEs under the full and reduced models, respectively. Because Θ_R is a subspace of Θ_F , it must be that $L(\hat{\underset{\sim}{\theta}}_R) \le L(\hat{\underset{\sim}{\theta}}_F)$. Since strict inequality usually holds, even when the additional parameters are not truly related to the data (the difference is explained wholly by sampling variability in this case), it is necessary to have a criterion to decide what is a significant increase in the likelihood and what can be explained by random sampling variability alone. LRTs provide such a criterion.

Likelihood ratio tests are used to test hypotheses of the form

H_0: Full model is not better than reduced model

versus

H_A: Full model is better than reduced model.

These hypotheses can be rewritten in terms of model parameters. For instance, the hypotheses to test whether survival probabilities in sampling intervals 1 and 2 are equal can be written as

$$H_0: S_1 = S_2$$

versus

$$H_A: S_1 \ne S_2 .$$

The full model in this case has one more parameter than the reduced model. The ratio of the maximized likelihoods is:

$$\lambda = \frac{L(\hat{\underset{\sim}{\theta}}_R)}{L(\hat{\underset{\sim}{\theta}}_F)} .$$

The LRT statistic is based on the difference in log-likelihoods:

$$-2\Lambda = -2(lnL\hat{\theta}_R - lnL(\hat{\theta}_F)) \quad . \tag{2.28}$$

If the null hypothesis is true, then the statistic $-2ln\lambda$ is asymptotically distributed as a central chi-squared random variable with $V_F - V_R$ degrees of freedom, where V_F is the dimension of Θ_F (number of parameters in the full model) and V_R is the dimension of Θ_R (number of parameters in the reduced model). The null hypothesis is rejected if $-2ln\lambda$ is greater than the quantile of the appropriate χ^2 distribution corresponding to the stated significance level (α) .

2.4.2 Non-hierarchical models

LRTs provide a framework for selecting among hierarchical models. In the course of model selection for any particular data set, however, it is likely that non-nested models will be considered. A simple example of four models for a multiple-population, multiple-interval, tag-release study is presented in Table 2.2. The subscripts in the model names refer to the possible dependence of the survival probabilities on space (*s*) and time (*t)*. For example, Model S_{st} has survival probabilities unique in space and time, while those in Model S_t depend only on time. The four models define two different hierarchies, namely $(S_{st} \rightarrow S_t \rightarrow S)$ and $(S_{st} \rightarrow S_s \rightarrow S)$. Models along either hierarchy could be compared using LRTs. However, S_t is not nested in S_s, and S_s is not nested in S_t. Thus, an LRT cannot be used to select between them. A different criterion is needed.

A criterion that has received some attention in tag-release literature (e.g., White 1990) is *Akaike's Information Criterion* (AIC) (Akaike 1973, Sakamoto et al. 1986). AIC forgoes formal testing by basing selection on the quantity:

$$\text{AIC} = -2\ln L(\hat{\underset{\sim}{\theta}}) + 2(\text{number of parameters estimated}). \tag{2.29}$$

The smaller the value of AIC, the better the fit of the model to the observed data. Thus, the model selection problem becomes, in effect, one of one-dimensional optimization rather than a multi-dimensional statistical hypothesis testing problem. Lebreton et al. (1992) have advocated the use

Table 2.2 Four alternative models for a multiple-population multiple-interval survival study.

Model	Description
S_{st}	Unique survival probability for each for each interval for each population
S_s	Probabilities population-specific, but constant across intervals
S_t	Probabilities interval-specific, but constant across populations
S	Common survival probability for all populations in all intervals

of only a few formal tests between the model selected under the AIC criterion and a few neighboring ones, thus “limiting the increase in the overall risk of false rejection of at least one null hypothesis otherwise caused by multiple tests.” Good results using AIC have been claimed for release-recapture analysis (Lebreton et al. 1992).

The AIC can be used not only for non-nested models, but also when the models of interest are strictly hierarchical. For example, suppose Model M_1 is obtained from M_0 by dropping a single parameter. Referring to Eq. (2.1), we see that AIC will select M_0 if $-2ln\lambda = -2(lnL_{M_0} - lnL_{M_1})$ is greater than 2. From the formal testing framework (LRT), we know that $-2ln\lambda$ has a χ^2 distribution with one degree of freedom when the null hypothesis (H_0:M_0 not better than M_1) is true. To reject this null hypothesis, when $-2ln\lambda$ is greater than 2.0, implies a significance level of 0.16. Questions of multiple testing aside, this procedure has given a risk of Type I error (α) in a single test of 16%. Thus, AIC can be used to identify a set of candidate models from a large number of non-hierarchical models, the criterion should be augmented by formal testing to choose the final model.

2.4.3 Analysis of deviance (ANODEV)

The final important concept in likelihood theory is that of the deviance of a model. The theory of analysis of deviance has largely been developed in the context of generalized linear models, where the data are a set of observed data values from individual study subjects. This context is assumed in the general introductory discussion below. However, analysis of deviance is used in SURPH to assess effects of group covariates, and the “observations” are group- and interval-specific survival probabilities, not measurements on individual subjects. Sections 3.5 and 4.5 give the details of analysis of deviance for known-fate and release-recapture data, respectively.

McCullagh and Nelder (1983) point out that “fitting a model to data may be regarded as a way of replacing a set of observed data values $\underset{\sim}{y}$ by a set of fitted values $\hat{\underset{\sim}{\mu}}$ derived from a model involving (usually) a smaller number of parameters.” The fitted values will not generally be

exactly equal to the observed data values, and a measure of how discrepant they are provides a good measure of how well the model fits the data. Of the many measures of discrepancy, the one of primary concern for SURPH modeling is formed from the logarithm of the ratio of likelihoods, and is known as the *deviance*.

When observations are made on individual subjects, models fit to a set of N observations can have up to N parameters. The simplest model, usually known as the *null model*, has only one parameter; it fits a common $\hat{\mu}$ to all observations. The null model is also sometimes referred to as the *grand mean model*. At the other extreme, the *full* or *saturated model* has N parameters, one parameter per observation, and generates $\hat{\mu}$'s that match the data exactly. For most data sets, the grand mean model is too simple, while the saturated model is uninformative because it does not summarize the data but merely repeats them in full. Most practical models will be intermediate between the null and full models, containing p parameters ($1 < p < N$). The basis for analysis of deviance is that the null model is nested in any intermediate model, and any intermediate model is nested in the full model.

The log-likelihood for the full model is the maximum attainable by any model for the data, and that for the null model is the minimum for any model. The two extremes provide a way to assess the discrepancy of an intermediate model. The deviance of a model is defined as twice the difference between the maximum log-likelihood attainable (full model) and that attained by the model under investigation. Symbolically,

$$D_M = 2\{lnL(\hat{\underset{\sim}{\theta}}_F) - lnL(\hat{\underset{\sim}{\theta}}_M)\} \tag{2.30}$$

where D_M is the deviance for Model M (the model under investigation), $\hat{\underset{\sim}{\theta}}_i$ are the MLEs under model i and $lnL(\hat{\underset{\sim}{\theta}}_i)$ is the maximum log-likelihood value under model i ($i = F$ or M).

The deviance of the null model (D_0) is known as the *total discrepancy* (McCullagh and Nelder 1983). The fit of an intermediate model can be assessed by examining how much of the total discrepancy it "explains" (how much smaller is its deviance than the total discrepancy), taking into account the number of parameters required to achieve the reduction in deviance. For

normal-theory linear models, the deviance for a particular model has an exact χ^2 distribution when the model is true. The deviance has an asymptotic χ^2 distribution for distributions other than normal, though McCullagh and Nelder (1983) warn that the χ^2 approximation for the deviance may be appropriate only for very large sample sizes. In the context of survival-effects models for tag-release data, Smith (1991) shows that an *F*-statistic derived from analysis of deviance (see Sections 3.5 and 4.5) was nominally distributed in a wide variety of scenarios with moderate release sizes.

Deviance has the attractive property of additivity for nested sets of models. For example, consider the nested set of models $(M_0, M_1, \ldots, M_F)$, where M_0 is the null model, M_F is the full model, and N_m is the total number of models under investigation. Model M_0 is nested in (a special case of) M_1, which is nested in M_2, and so on. Let ν_i be the number of parameters in M_i. The difference between the deviances of M_{i-1} and M_i is equal to the likelihood ratio statistic for testing M_{i-1} against M_i:

$$D_{i-1} - D_i = -2\{lnL(\hat{\underset{\sim}{\theta}}_{i-1}) - lnL(\hat{\underset{\sim}{\theta}}_i)\} \quad .$$

Accordingly, the difference in deviances is denoted $-2\Lambda_i$. The total discrepancy:

$$D_0 = -2\{lnL(\hat{\underset{\sim}{\theta}}_F) - lnL(\hat{\underset{\sim}{\theta}}_0)\} \quad ,$$

can also be written as the sum of the N_m likelihood ratio statistics:

$$D_0 = \sum_{i=1}^{N_m} -2\Lambda_i \, .$$

This decomposition of the total discrepancy suggests the construction of a table similar to the familiar normal theory method of analysis of variance (ANOVA) (Table 2.3). ANODEV decomposes discrepancies in the same way that ANOVA decomposes sums of squares, leading to an ANODEV table that is analogous to the ANOVA table. Extending the analogy to regression analyses, note that ANOVA tables are often used to display regression results. An auxiliary statistic is the "coefficient of determination," or R^2. An analog of R^2 based on deviance is given by

Table 2.3 Basic analysis of deviance table partitioning total deviance into model and residual deviance

Source	d.f.	Change in Deviance	DEV/d.f.	F
Total	$\nu_F - 1$	$D_o = 2\{lnL(\hat{\theta}_F) - L(\hat{\theta}_0)\}$		
Fitted Model	$\nu_M - 1$	$D^*_M = 2\{lnL(\hat{\theta}_M) - lnL(\hat{\theta}_0)\}$	$MD_M = D_M/(\nu_M - 1)$	$F_{\nu_M - 1, \nu_F - \nu_M} = \frac{MD_M}{MD_E}$
Residual	$\nu_F - \nu_M$	$D_E = 2\{lnL(\hat{\theta}_F) - lnL(\hat{\theta}_M)\}$	$MD_E = D_E/(\nu_F - \nu_M)$	

* D_M= can be further decomposed into a sum of single degree of freedom deviances

the percentage of the total discrepancy that is explained by the model under investigation. Symbolically, this is written as

$$R_M^2 = \frac{D_0 - D_M}{D_0}. \tag{2.31}$$

Alternative models may be informally compared, based on the proportion of total discrepancy explained by each model.

2.5 Numerical Optimization

To use the maximum likelihood estimation, methods are needed to find the maximum point of the likelihood (or log-likelihood) function. The method illustrated in Section 2.3 involves finding the roots of the system of equations obtained by differentiating the log-likelihood with respect to each parameter. This might be called the “analytical” optimization method. It leads to general algebraic expressions for the MLEs when the roots can be found analytically. Section 2.3 shows how the covariance matrix for the MLEs found by this method can be derived from the matrix of second partial derivatives of the log-likelihood (Information matrix).

There are many examples, however, of likelihood functions that lead to likelihood equations that cannot be solved analytically, or where it is prohibitively difficult to derive the Information matrix analytically. The solution in these situations is to use numerical methods to maximize the function. Numerical methods may be desirable even when analytical solutions are known to exist, but when the analytical solutions are too difficult to derive.

The best known numerical method is the Newton-Raphson (N-R) method. Other methods are variations on or approximations to the N-R method, and are sometimes referred to as quasi-Newton (q-N) methods. These methods are iterative: starting with an initial guess of the location of the maximum (the root of the likelihood equations), the methods use information obtained from evaluations of the log-likelihood function and possibly its derivatives to update the guess. The guess is improved iteratively until the series of parameter estimates converges. The N-R method and q-N methods are described below. The advantages and drawbacks of the various numerical

methods are discussed. Program SURPH relies exclusively on q-N methods because of the complexity of the likelihood models.

2.5.1 Newton-Raphson method

While the quasi-Newton methods are designed expressly for the problem of optimization, the Newton-Raphson method was devised for the more general problem of finding roots of a system of nonlinear equations. Thus, the N-R method is applied to the likelihood equations rather than the log-likelihood itself.

Suppose we wish to find the single parameter value θ_0 that maximizes the likelihood function $L(\theta)$. This is equivalent to finding the root of the likelihood equation $\frac{d}{d\theta}\log L(\theta)$. Let $g(\theta) = \frac{d}{d\theta}\log L(\theta)$. If we start with a trial solution $\theta_{(1)}$ in the neighborhood of θ_0, the Taylor approximation gives:

$$0 = g(\theta_0) \approx g(\theta_{(1)}) + (\theta_0 - \theta_{(1)})g'(\theta_{(1)})$$

where $g'(\theta)$ is the first derivative of $g(\theta)$ (i.e., the second derivative of $\log L(\theta)$) with respect to θ, evaluated at $\theta_{(1)}$. Rearranging this equation gives a new approximation to θ_0:

$$\theta_0 \approx \theta_{(1)} - \frac{g(\theta_{(1)})}{g'(\theta_{(1)})} \quad .$$

Thus, on each step of the iteration, a new trial solution is obtained:

$$\theta_{(i+1)} = \theta_{(i)} - \frac{g(\theta_{(i)})}{g'(\theta_{(i)})} \quad .$$

Iteration continues until $|\theta_{(i+1)} - \theta_{(i)}| < \varepsilon$ for some predetermined ε.

Suppose now that the parameter, $\underset{\sim}{\theta}$, is a vector of length p and we wish to find the maximum point $\underset{\sim}{\theta}_0$ that maximizes $L(\underset{\sim}{\theta})$. The likelihood equations are $\underset{\sim}{g}(\underset{\sim}{\theta})$, where

$g_i(\underset{\sim}{\theta}) = \frac{\partial}{\partial \theta_i} \log L(\underset{\sim}{\theta})$. The function $\underset{\sim}{g}(\underset{\sim}{\theta})$ is sometimes called the "score vector." Starting with an initial trial solution vector, the multivariate version of the N-R method is

$$\underset{\sim}{\theta}_{(i+1)} = \underset{\sim}{\theta}_{(i)} - H_{(i)}^{-1} \underset{\sim}{g}(\underset{\sim}{\theta}_{(i)}) \quad ,$$

where $H^{-1}{}_{(i)}$ and $\underset{\sim}{g}(\underset{\sim}{\theta}_{(i)})$ are the Information matrix and score vector, respectively, evaluated at $\underset{\sim}{\theta}_{(i)}$. The *jk*th element *of* $H_{(i)}$ is

$$\frac{\partial^2}{\partial \theta_j \partial \theta_k} \log L(\underset{\sim}{\theta}) \Big|_{\underset{\sim}{\theta} = \underset{\sim}{\theta}_{(i)}} .$$

Iteration continues until some convergence criterion is satisfied. A typical criterion is $\left\| \underset{\sim}{\theta}_{(i)} - \underset{\sim}{\theta}_{(i-1)} \right\| < \varepsilon$ where $\| \bullet \|$ is the Euclidean norm $(\|x\| = \sum x_i^2)$.

Implementation of the N-R method in a computer program requires that all the first partial and mixed second derivatives of the log-likelihood be coded. This can be extremely difficult, particularly if the program must be general enough to deal with many different study designs or parameterizations of survival in a multiple-population tag-release model. The derivatives must be calculated on each step of the iterative procedure. On some computers, this computation will be slow, especially if the number of parameters is great. In addition, the derivative matrix $H_{(i)}$ must be inverted on each step. Matrix inversion is a notoriously slow operation, and is susceptible to numerical instabilities if not programmed carefully. A benefit of the method, though, is that at the end of the final iteration, the observed Information matrix is available, which is inverted to estimate the covariance matrix.

2.5.2 Quasi-Newton methods

Quasi-Newton methods are used to avoid the difficulty of deriving and coding the first and second partial derivatives. The Broyden-Fletcher-Goldfarb-Shanno (BFGS) method requires only first derivatives (Press et al. 1986). It uses successive evaluations of the log-likelihood and the first derivatives to construct an approximation to the inverse Information matrix. That is, a sequence of

matrices $A_{(i)}$ is constructed with the property

$$\lim_{i \to \infty} A_{(i)} = [I(\hat{\underset{\sim}{\theta}})]^{-1} \quad .$$

Because convergence (it is to be hoped) occurs within a finite number of iterations, the value of A from the final iteration $(A_{(N)})$ is an estimate of the covariance matrix. The trial solution vector is updated as

$$\underset{\sim}{\theta}_{(i+1)} = \underset{\sim}{\theta}_{(i)} - A_{(i)} \underset{\sim}{g}(\underset{\sim}{\theta}_{(i)}) \quad .$$

Details of how $A_{(i)}$ is constructed and updated may be found in Press et al. (1986, pp. 307-310).

A second quasi-Newton method, due to Fletcher (1970) and known as “FLETCH,” uses no explicit evaluations of first or second derivatives. Instead, only the log-likelihood function is used, and difference equations are used to construct a series of approximations to the score vector and the Information matrix $I(\hat{\underset{\sim}{\theta}})$.

Code is available from outside sources for the quasi-Newton methods (Press et al. 1986, for BFGS; Vaessen 1984 for FLETCH). Of course, the user must provide code to evaluate the log-likelihood for both methods, and the first derivatives for BFGS. The FLETCH code appears to be more self-contained and readily adaptable. To build up reasonable approximations to the Information matrix, both BFGS and FLETCH require many more function evaluations than does N-R. The advantage is that coding of derivatives is avoided. Both programs provide, as by-products of the final iteration, the maximized function value for use in LRTs and a data structure that contains the estimated covariance matrix or the data that may be used to construct it.

Clearly, the main desideratum in selecting a numerical optimization method for a particular problem is the trade-off between coding derivatives and the number of function and derivative evaluations required. Although each iteration of the N-R algorithm will take more CPU time, the q-N methods will usually require so many more iterations and function evaluations per iteration that the total CPU time is greater for q-N. However, since CPUs are becoming exceedingly fast, this need not be a great concern. Because of the difficulty of coding second derivatives for the

SURPH models, particularly models for release-recapture data, the N-R method is not practical. Among the q-N methods, FLETCH is used in Program SURPH because the available code is much easier to use. One consequence of using FLETCH is that occasionally, SURPH will not find the MLEs because the method fails to converge. Invariably, failure to converge indicates that the data are too sparse to estimate all the parameters of the model being fit.

Chapter 3

Analysis of Known-Fate Data

3.1 Introduction

The distinguishing characteristic of a known-fate study is that the survival status of each tagged animal is known at each sampling event. Mortalities are known and assignable to the correct sampling intervals because there is no complicating interference from an incomplete capture process. However, known-fate data are generally more difficult to obtain than release-recapture data because of the large effort required to obtain reliable and complete records for every tagged animal. In wildlife investigations, radiotelemetry techniques are one of the few ways to generate reliable known-fate data. Known-fate data have also been collected by monitoring the "fate" of eggs by periodically inspecting nests for egg loss. Another example is the monitoring the "survival" of active nests by placing barriers across the opening of nesting boxes that the adult bird must remove each time it returns. Sessile organisms, such as intertidal mollusks, can also be monitored periodically to generate known-fate data without the use of radiotags (Hoffmann 1993). On the Columbia/Snake River system, known-fate data will be generated as PIT-tagged adult salmon and steelhead pass over adult ladders equipped with PIT-tag detector systems.

The use of radio transmitters to track animals in wildlife investigations is a relatively recent development. Advances in miniaturization of electronic equipment have resulted in transmitters that are small enough to be fitted to most mammals or birds and affordable enough that sufficiently large numbers of animals can be tagged. Among other applications, radio transmitters have been used to study diurnal usage of habitat by birds (Rothstein et al. 1984), patterns of flight activity in bats (Cooper and Charles-Dominique 1985), and in survival studies (Snyder 1985). In many situations, radiotelemetry is an attractive alternative to release-recapture procedures. Radiotelemetry can give estimates of survival rates with comparable precision using fewer tagged animals because the uncertainty of the capture process is eliminated. On the other

hand, radio transmitters are more expensive than passive tags, and the field effort of tracking radio signals may be greater than setting traps.

Previous statistical methods for analyzing known-fate data include multinomial likelihood models, survival models based on a proportional hazards assumption, and partial logistic regression models. Multinomial likelihood models (White 1983, White and Garrott 1990) can be used to estimate survival rates of animals within populations. The statistical model by White (1983) is of the survival-estimation type used to obtain a series of estimates of survival probabilities over time. This model allows specification of equality constraints on survival probabilities for different intervals, and the computer program SURVIV (White 1983) provides a flexible means of building and selecting models for known-fate data.

One limitation of the earlier multinomial models is that selection cannot be studied at the individual level. Program SURPH models known-fate data as multiple Bernoulli trials to estimate both interval-specific survival probabilities, and to model survival over time or across replicate populations as functions of group- and individual-based covariates.

3.2 Known-Fate Data

Using known-fate sampling, it is assumed that the fate of each tagged animal is known; and for those that die, the sampling interval where death occurred is known with certainty. That is, every tagged animal is either resighted alive on each sampling event after being tagged or found dead on the first sampling event after the time of death. However, fates of some animals can remain unknown if tags fail or are shed, or because animals are removed from the sample, either accidentally through handling mortality or purposefully to perform biopsies, for example. The fates of such animals are referred to as “censored.” Censored animals provide information on the survival process up until the point of censoring but not beyond that point. Models for known-fate data must be constructed to use whatever information is provided by such “known removals.” In summary, there are three possible scenarios for each tagged animal: (1) the animal survives to the end of the study and is detected at each sampling event after its release; (2) the animal dies sometime during the study and its carcass is found on the first sampling event after

its death; or (3) the animal is known to survive up to the point at which it is censored, due to tag failure, tag loss, or other known removal.

Because an animal in a known-fate study does not typically have to be recaptured to determine its fate, the sampling record for each marked animal is called a “survival history” rather than the more commonly used term “capture history.” Survival histories are made up of “1’s” to denote sampling events when the animal was alive when resighted; “0’s” to denote the event when the animal was found dead and all subsequent events; a “2” to denote the event on which the animal was removed alive or became a handling mortality, and a “3” to denote the first event on which the animal’s fate could not be determined due to tag loss or failure. The series of symbols over all resampling events give a record of the survival history of that animal (see Section 6.3 for more discussion of survival histories). With a staggered-entry design, it is also necessary to record the event when the animal was first tagged. Thus, for a study with K sampling events (see Figure 2.4), a series of K “1’s,” “0’s”, “2’s”, or “3’s” is needed to represent each survival history. The survival history of animals tagged on event 1 begins with “1,” while those tagged on subsequent sampling events have histories beginning “00...01.”

For example, in a known-fate study with $K = 4$ sampling events, the possible survival histories are listed in Table 3.1. Survival histories ending with “2” or “3” denote censored or truncated resampling records. With regard to the information provided for survival analysis and, hence, for the purposes of Program SURPH, there is no difference between an animal seen alive and then removed from the population on event k and an animal seen alive on event k and then “lost” due to tag failure on event k+1; the fate of both is censored after event k. Accordingly, the following treats both types of truncated history identically. Among animals tagged on event 1 (survival history beginning with “1”), there are four possible survival histories for those animals whose fate was known, and two possible histories for those lost. In general, if a release group is monitored on k sampling events, there are k+1 possible histories for those whose fate is known and k-1 for those lost, for a total of 2k. Thus, for a study with K sampling events and a staggered-entry release design, there is a total of

Table 3.1 Possible survival histories in a known-fate study with *K* = 4 sampling events.

History	Explanation
1111	Tagged on event 1 and survived until end of study
1110	Tagged on event 1 and died during sampling interval 3
1100	Tagged on event 1 and died during sampling interval 2
1000	Tagged on event 1 and died during sampling interval 1
1113	Tagged on event 1, detected alive on event 3, could not be located on event 4
112	Tagged on event 1, survived until event 3, removed from population on event 3
113	Tagged on event 1, detected alive on event 2, could not be located on event 3
12	Tagged on event 1, survived until event 2, removed from population on event 2
0111	Tagged on event 2 and survived until end of study
0110	Tagged on event 2 and died during sampling interval 3
0100	Tagged on event 2 and died during sampling interval 2
0113	Tagged on event 2, detected alive on event 3, could not be located on event 4
012	Tagged on event 2, survived until event 3, removed from population on event 3
0011	Tagged on event 3 and survived until end of study
0010	Tagged on event 3 and died during sampling interval 3

$$\sum_{k=1}^{K-1} 2k = K(K-1)$$

possible survival histories. Because there may be no newly marked animals on some sampling events and because of sampling variability, not all of the possible survival histories will be observed in all studies.

3.3 Survival-Estimation Models for Known-Fate Data

The statistical model used in SURPH to analyze known-fate data is a generalization of the multinomial likelihood model of White (1983). Before describing the SURPH models, the simpler model of White (1983) is presented to illustrate the basic concepts of survival estimation. Subsequent sections present the statistical models for assessing relationships between survival and group- and individual-based covariates.

3.3.1 Single population

3.3.1.1 Likelihood function

The survival histories are mutually exclusive and completely exhaustive; each tagged animal has one and only one of the possible survival histories. This condition, along with the assumptions of homogeneous survival probabilities and independent fates of tagged animals (see Section 3.3.1.3), allows known-fate data to be modeled as a sample from a multinomial distribution. The cells are the survival histories, and the cell probabilities depend on the probabilities of surviving through each sampling interval. The probability that an animal alive at the time of sampling event k survives until the event k+1 is denoted as S_k. If all animals have the same interval-specific survival probabilities, regardless of when they were first marked, the survival histories in Table 3.1 have the probabilities of occurrence reported in Table 3.2. Among uncensored animals, n_{jk} is the number of animals tagged on event j and last seen alive on event k, while n'_{jk} is the number of animals tagged on event j, seen alive on event k, and censored after event k.

Table 3.2 Probabilities of the possible survival histories in a known-fate study with K+1 = 4 sampling events (survival-estimation model).

History	Probability	Number
1111	$S_1S_2S_3$	n_{14}
1110	$S_1S_2(1 - S_3)$	n_{13}
1100	$S_1(1 - S_2)$	n_{12}
1000	$(1 - S_1)$	n_{11}
112 or 1113	S_1S_2	n'_{13}
12 or 113	S_1	n'_{12}
0111	S_2S_3	n_{24}
0110	$S_2(1 - S_3)$	n_{23}
0100	$(1 - S_2)$	n_{22}
012 or 0113	S_2	n'_{23}
0011	S_3	n_{34}
0010	$1 - S_3$	n_{33}

The data for the basic survival-estimation model of a known-fate study are the number of animals tagged on each event (b_k, for k = 1,..., K -1) and the vectors

$$\underset{\sim}{n} = (n_{1K}, \ldots, n_{11}, n_{2K}, \ldots, n_{22}, \ldots, n_{K-1,K}, n_{K-1,K-1})$$
$$\underset{\sim}{n}' = (n'_{1,K-1}, \ldots, n'_{12}, n'_{2,K-1}, \ldots, n'_{23}, \ldots, n'_{K-2,K-1}).$$

The multinomial probability density function for the survival history data is:

$$f(\underset{\sim}{n}, \underset{\sim}{n}' | \underset{\sim}{S}, \underset{\sim}{b}) = \frac{\left(\sum_{k=1}^{K-1} b_k\right)!}{\prod_{j=1}^{K-1}\left(\prod_{k=j}^{K} n_{jk}! \prod_{k=j+1}^{K-1} n'_{jk}!\right)}$$

$$\times (1-S_1)^{n_{11}} (S_1(1-S_2))^{n_{12}} \ldots (S_1 S_2 \ldots S_{K-2}(1-S_{K-1}))^{n_{1,K-1}} (S_1 S_2 \ldots S_{K-1})^{n_{1K}} S_1^{n'_{12}} \ldots (S_1 \ldots S_{K-2})^{n'_{1,K-1}}$$

$$\times (1-S_2)^{n_{22}} (S_2(1-S_3))^{n_{23}} \ldots (S_2 S_3 \ldots S_{K-1})^{n_{2K}} S_2^{n'_{23}} \ldots (S_2 \ldots S_{K-2})^{n'_{2,K-1}} \times \ldots \times (1-S_{K-1})^{n_{K-1,K-1}} S_{K-1}^{n_{K-1,K}}$$

$$\propto (1-S_1)^{n_{11}} S_1^{n_{12}+\ldots+n_{1K}+n'_{12}+\ldots+n'_{1,K-1}} (1-S_2)^{n_{12}+n_{22}} S_2^{n_{13}+\ldots+n_{1K}+n'_{13}+\ldots+n'_{1,K-1}+n_{23}+\ldots+n_{2K}+n'_{23}+\ldots+n'_{2,K-1}}$$

$$\times \ldots \times (1-S_{K-1})^{n_{1,K-1}+n_{2,K-1}+\ldots+n_{K-1,K-1}} S_{K-1}^{n_{1K}+n_{2K}+\ldots+n_{K-1,K}}. \tag{3.1}$$

When viewed as a function of the survival parameters with the observed data considered fixed, Eq. (3.1) is the likelihood function. This function assumes a simpler form if the following substitutions are made:

$$a_2 = n_{12} + n_{13} + \ldots + n_{1K} + n'_{12} + \ldots + n'_{1,K-1} = \sum_{k=2}^{K} n_{1k} + \sum_{k=2}^{K-1} n'_{1k}$$

$$a_3 = n_{13} + \ldots + n_{1K} + n'_{13} + \ldots + n'_{1,K-1} + n_{23} + \ldots + n_{2K} + n'_{23} + \ldots + n'_{2,K-1} = \sum_{j=1}^{2}\left(\sum_{k=3}^{K} n_{jk} + \sum_{k=3}^{K-1} n'_{jk}\right)$$

$$\vdots$$

$$a_{K-1} = n_{1,K-1} + n_{1K} + n'_{1,K-1} + \ldots + n_{K-2,K-1} + n_{K-2,K} + n'_{K-2,K-1} = \sum_{j=1}^{K-2}\left(\sum_{k=K-1}^{K} n_{jk} + n'_{j,K-1}\right)$$

$$a_K = n_{1K} + n_{2K} + \ldots + n_{K-1,K} = \sum_{j=1}^{K-1} n_{jK}$$

$$v_1 = n_{11} + a_2 = \sum_{k=1}^{K} n_{1k} + \sum_{k=2}^{K-1} n'_{0k}$$

$$v_2 = n_{12} + n_{22} + a_3 = \sum_{j=1}^{2}\left(\sum_{k=2}^{K} n_{jk} + \sum_{k=3}^{K-1} n'_{jk}\right)$$

$$\vdots$$

$$v_{K-2} = n_{1,K-2} + \ldots n_{K-2,K-2} + a_{K-1} = \sum_{j=1}^{K-2}\left(\sum_{k=K-2}^{K} n_{jk} + n'_{j,K-1}\right)$$

$$v_{K-1} = n_{1,K-1} + \ldots n_{K-1,K-1} + a_K = \sum_{j=1}^{K-1}\sum_{k=K-1}^{K} n_{jk}.$$

In general,

$$a_i = \sum_{j=1}^{i-1}\left(\sum_{k=i}^{K} n_{jk} + \sum_{k=i}^{K-1} n'_{jk}\right), \text{ for } i = 2,\ldots, K, \text{ and}$$

$$v_i = \sum_{j=1}^{i}\left(\sum_{k=i}^{K} n_{jk} + \sum_{k=i+1}^{K-1} n'_{jk}\right), \text{ for } i = 1,\ldots, K - 1.$$

The quantity a_k is the number of previously tagged animals detected alive on event k, while v_k is the number of tagged animals known to be alive and uncensored in the population immediately after event k (i.e., the number *at risk* in interval k). The simplified form of the likelihood function (3.1) is:

$$L(\underset{\sim}{S}|\underset{\sim}{v}, \underset{\sim}{a}) = \frac{\left(\sum_{k=1}^{K-1} b_k\right)!}{\prod_{k=1}^{K-1} a_{k+1}!(v_k - a_{k+1})!} \prod_{k=1}^{K-1} S_k^{a_{k+1}}(1 - S_k)^{(v_k - a_{k+1})} \quad . \tag{3.2}$$

3.3.1.2 Parameter estimation

Closed forms for the maximum likelihood estimators (MLEs) of the vector of survival probabilities are obtained by the usual method of taking partial derivatives of the logarithm of the likelihood with respect to the parameters and setting each derivative to zero. The solutions to this set of simultaneous equations (the likelihood equations) are the MLEs. The logarithm of the likelihood is as follows:

$$\log L = \sum_{k=1}^{K-1} \{a_{k+1}\log S_k + (v_k - a_{k+1})\log(1 - S_k)\} + C(\underset{\sim}{a}, \underset{\sim}{v})$$

where $C(\underset{\sim}{a}, \underset{\sim}{v})$ is a constant depending on the data but not on the parameters. The likelihood equations are:

$$\frac{\partial}{\partial S_k}\log L = \frac{a_{k+1}}{S_k} - \frac{v_k - a_{k+1}}{1 - S_k} = 0 \text{ for } k = 1, 2,..., K\text{-}1.$$

Solving the system of K likelihood equations gives the expressions for the MLEs:

$$\hat{S}_k = \frac{a_{k+1}}{v_k} \text{ for } k = 1, 2,..., K\text{-}1. \tag{3.3}$$

$\hat{S}_k$ is an unbiased estimator of S_k, unless v_k is zero, in which case the estimator is not defined.

The expression (3.3) for $\hat{S}_k$ is reminiscent of the estimate of the probability of success in a binomial trial (see Section 2.3.2). Indeed, if we condition on the number at risk at the beginning of interval k (i.e., v_k), the number surviving until the end of the interval is binomially distributed with parameters (v_k, S_k). For this reason, $\hat{S}_k$ is known in SURPH as the “binomial estimate” (see Section 3.5.1).

The variance of the maximum likelihood estimate $\hat{S}_K$, conditional on v_k is:

$$Var(\hat{S}_k|v_k) \approx \frac{S_k(1-S_k)}{v_k} \tag{3.4}$$

The variances are estimated by substituting estimates of the survival probabilities ($\hat{S}_k$) into variance formula (3.4). Program SURPH provides the MLEs of the survival probabilities (3.3), associated variance estimates (3.4), and standard errors ($\sqrt{V\hat{a}r(\hat{S})}$).

3.3.1.3 Assumptions

For the multinomial likelihood (3.2) to be valid, the following assumptions must be met:

A3.1) Individuals marked for the study are a representative sample from the biological population of interest.

A3.2) Survival probabilities are not affected by tagging or sampling. That is, tagged animals have the same probabilities as untagged animals.

A3.3) All sampling events are "instantaneous." That is, sampling takes a negligible amount of time or distance relative to the length of the intervals between sampling events.

A3.4) The fate of each tagged individual is independent of the fate of all others.

A3.5) All tagged individuals in the population alive at the beginning of a sampling interval have the same probability of surviving until the end of that interval.

A3.6) After being tagged and released, each animal is located on every sampling event until the animal dies or the study is completed, or until the animal is censored, in which case the event on which the animal is last seen alive is recorded without error.

A3.7) Each individual has the same probability of being censored on a particular sampling event, and the censoring process (i.e., probability of censoring) is independent of the survival process.

Assumptions (A3.1) and (A3.2) ensure that the information provided by the multinomial model can be applied to the biological population in general. Survivability might be adversely affected by the trauma of being physically handled and tagged. If death occurs during handling, the animal is simply discarded. If handling causes death after release as the result of handling stress or because the carrying of a tag introduces additional hardships, survival estimates will underestimate the true, natural probabilities of survival.

Assumption (A3.3) is violated if the resampling events themselves take a large amount of time relative to the interval between events. In this case, assumption (A3.5) is likely to be violated as well. This is because the amount of time between two consecutive sightings may be substantially different between tagged animals, implying that their per-interval survival probabilities differ. Figure 3.1 illustrates a situation where sampling events are long relative to sampling intervals. In this situation, animals A and B are both seen alive during event 2, so they are both said to be alive immediately after event 2. According to assumption (A4), A and B should have the same probability of surviving to event 3. However, due to the relatively long duration of the resampling events, nearly twice as much time elapses between sightings of A than between sightings of B. Therefore, we should not expect A's true probability of survival (S_A) to be equal to B's (S_B), even if they actually do have equal survivability over any fixed length of time.

Counts of the numbers of animals with each of the possible survival histories comprise the data from a known-fate survival study. Assumptions (A3.4) and (A3.5) allow the modeling of the data as a multinomial sample with cell counts equal to the number of animals with each history. Assumption (A3.4) assures independence of the trials, and assumption (A3.5) assures

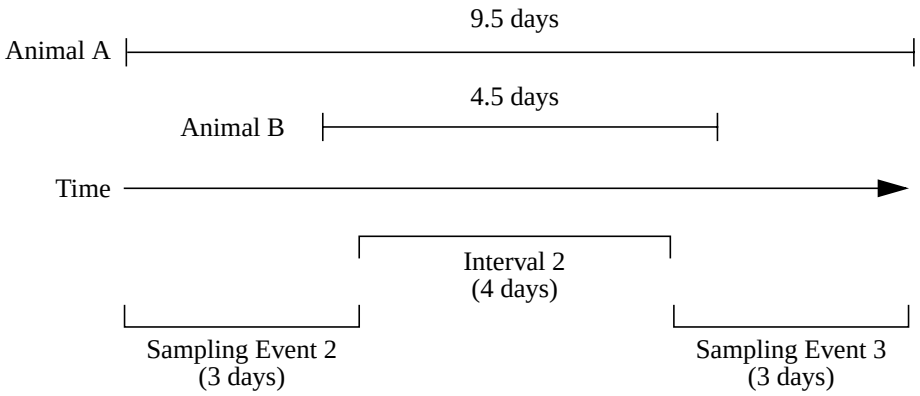


Figure 3.1 Illustration of effect of violation of instantaneous sampling assumption. To be seen alive on events 2 and 3, animal A had to survive 9.5, while animal B survived only 4.5 days, leading to unequal survival probabilities of survival.

that the same probabilities hold for each multinomial trial (one animal's fate), both of which are required assumptions for a multinomial sample.

Assumption (A3.4) would be violated if, for instance, the death of one marked animal increased the resources available to other marked animals, leading to their improved health and decreased mortality. Alternatively, the death of one tagged animal may focus predation on the remaining tagged animals, increasing their mortality rate. In either case, the effect is to bias the variance estimate but not the point estimates of survival.

In practice, assumption (A3.5) is likely to be violated in any particular population. The theory of natural selection tells us that we should expect variability in life expectancy. Pollock (1982) found estimates of abundance to be sensitive to inter-individual variability in survival probabilities. Variation in individual rates does not bias point estimates of survival, but results in overestimates of the sampling variance (i.e., $V\hat{a}r(\hat{S})$) derived from multinomial models (Feller 1968, p. 231). The result is valid but conservative estimates of variance and confidence intervals. Subsequent sections will describe statistical models that allow individual heterogeneity in survival probabilities.

The death time of a tagged animal may be censored (Assumptions A3.6 and A3.7) before the end of the study for any of the following reasons: the identifying tag does not remain attached to the animal; the tag (e.g., radio transmitter) fails before the end of the study; the tagged animal leaves the study site and is no longer susceptible to detection (e.g., moving outside the range of the radio tag's signal); the animal is trapped and purposely removed from the population (e.g., for bioassay, relocation, etc.).

Tag failure or absence from the study site may be either permanent or temporary. Intermittent tag failure or temporary emigration may result in an animal being detected alive on an event after which it was missing. For example, an animal's radio transmitter may be malfunctioning on one sampling event but working on a later event. Alternatively, a live tagged animal may have a radio transmitter that is working but is not detected because it has moved

beyond the range of the signal. If the animal returns within transmitter range on a later resampling event and remains alive, it will be detected. Such intermittent signal loss can be rectified. Clearly, if an animal is seen alive on resampling event *k*, we know that it was alive on events 1, 2, 3,..., *k*-1, whether or not we actually located the animal on those events. If the number of animals lost temporarily is small, the lost animals can be treated in the analysis identically to those that survived and were detected throughout. However, if the rate of temporary loss is high, such treatment can bias the survival estimates. In such cases, it may be safer to treat the animal as censored as of the first event it was "missing" and to ignore later detections. Alternatively, methods for release-recapture data presented in Chapter 4 can be applied, with capture probabilities representing the probability of a tagged individual being detected.

In some cases, censoring may not be independent of mortality. For example, if a predator takes a radio-tagged animal, it might destroy or dislodge the transmitter. If there is sufficient evidence that an animal was censored due to mortality, the censoring may be equated with death. That is, the analysis proceeds, treating the censored animal as if it had died during the interval of loss of signal. If lost animals are treated as deaths in a survival estimation model, then the quantity being estimated is *apparent survival* (i.e., the probability that an animal survives *and* remains detectable). Treating lost animals as deaths in a survival-effects model requires the further assumption that the rate of loss is independent of the factors that affect survival.

3.3.2 Multiple populations

For effect assessment to be powerful and convincing, replication and randomization of treatments are mandatory. If time is the frame of reference for survival probabilities (see Section 2.2), the strategy is to conduct independent known-fate studies on each of a set of study sites. The requirement of independence implies that the study sites must be spaced far enough apart that the animals do not mix (i.e., each site has a separate and distinct population, and the treatments are isolated). To avoid confounding treatment effects with time trends, the known-fate studies should be conducted simultaneously at each site. That is, the initial tagging of

animals and all subsequent resampling events take place at the same time on all study sites. Clearly, a large field crew is needed to conduct a multiple-population study.

When designing smolt survival studies on the Columbia-Snake River, and other instances where the frame of reference is distance, replication must take place over time. Whereas simultaneous sampling is required for spatially replicated studies (above), in temporally replicated studies, it is crucial that sampling takes place at the same locations for each replicate population. Inferences are to effects of changing environmental conditions on smolt survival in specific river reaches. In an experimental study, the ordering of treatments over time would be randomized to prevent confounding treatment effects with changing ambient river conditions.

The likelihood model (3.2) can be used for the analysis of the data from each of the independent survival study. Since the sampling, and hence the model, on each site is independent from all others, the likelihood function for the entire multiple-population study is the product of the likelihood functions for the individual populations. If there is a total of I populations, we can add a subscript i to each of the statistics and parameters in model (3.2) to indicate population. The resulting likelihood can then be written as:

$$L(\underset{\sim}{S}|\underset{\sim}{v}, \underset{\sim}{a}) = \prod_{i=1}^{I} \left\{ \frac{\left(\sum_{k=1}^{K-1} b_{ik}\right)!}{\prod_{k=1}^{K-1} a_{i,k+1}!(v_{ik} - a_{i,k+1})!} \prod_{k=1}^{K-1} S_{ik}^{a_{i,k+1}} (1 - S_{ik})^{(v_{ik} - a_{i,k+1})} \right\} \tag{3.5}$$

where

I = the total number of replicate populations;

K = the number of sampling events;

S_{ik} = the probability that a marked animal in population i, alive immediately after sampling event k, survives to event k+1 (i = 1,..., I; k = 1,..., K-1);

b_{ik} = the number of previously unmarked animals in population i that are marked and released on sampling event k (i = 1,..., I; k = 1,..., K - 1);

a_{ik} = the number of previously marked animals in population i detected alive on sampling event k (i = 1,..., I; k = 2,..., K; a_{i1} = 0);

v_{ik} = the number of marked animals known to be alive in population i immediately after sampling event k (i = 1,..., I; k = 1,..., K - 1).

The maximum likelihood estimators for the survival probabilities and the sampling variances of the estimators have the same form as Eqs. (3.3) and (3.4). For example, the survival probability estimates are:

$$\hat{S}_{ik} = \frac{a_{i,\,k+1}}{v_{ik}}, \text{ for } i = 1,..., I;\ k = 1,..., K.\text{-}1. \tag{3.6}$$

3.3.3 Alternative parameterization of survival-estimation model

For later development of survival-effects models (Section 3.4), it is useful to introduce an alternative parameterization for the survival-estimation models. The estimation model of the previous section included a separate survival probability for each interval for each population (S_{ik}). Under the alternative parameterization (see Section 2.2.2), each probability is defined as a function of a baseline, or intercept parameter (S), "main effects" for population (π_i) and interval (ρ_k), and an interaction between population and interval effects $(\pi\rho)_{ik}$:

$$S_{ik} = f(S, \pi_i, \rho_k, (\pi\rho)_{ik}) .$$

Constraints on the parameters are required to make all parameters identifiable. By convention, we use the following constraints: $\pi_1 = \rho_1 = (\pi\rho)_{1k} = (\pi\rho)_{i1} = 0$. Therefore, the survival probability in the first interval for the first population is S, and all other probabilities are

expressed relative to S. For example, if the hazard link is used, the survival probability for population *i* in interval *k* is:

$$S_{ik} = S^{\exp(\pi_i + \rho_k + (\pi\rho)_{ik})} .$$

If the full set of main effects and interaction parameters are included, there is a one-to-one correspondence with parameters of the survival-estimation model previously presented (3.3), and the two parameterizations are mathematically equivalent, regardless of the link function. The alternative parameterization provides a convenient method to model equalities among survival probabilities. For example, to define a model with probabilities equal for all populations within each interval but varying among intervals, all population main effects π_i and interaction effects $(\pi\rho)_{ik}$ are set equal to zero, leaving parameters for interval main effects only. Other models (see Table 2.2) can be defined similarly.

3.3.4 Individual-based survival-estimation model

Under the assumption that all animals have the same survival probability in each interval, the summary statistics $(\underset{\sim}{v}, \underset{\sim}{a})$ can be used to produce a simple form for the likelihood function (Eq. (3.5)). When the assumption of equal probabilities is relaxed (Section 3.4.2), the function must be written in terms of the survival histories of individual animals. The notation of the individual-covariate survival-effects model is complex (see Eq. (3.8) below). By rewriting the survival-estimation model on the basis of individual tagged animals, the transition to the individual-covariate model will be easier to understand.

Let t_{ikj} be the number of the event on which the *j*th tagged animal released on event *k* in population *i* was last seen alive. Let d_{ikj} be a variable that indicates whether or not a death time was observed for the *j*th tagged animal released on event *k* in population *i*. That is, d_{ikj} is equal to 0 if the animal was lost to follow-up and equal to 1 if a death time was observed. Also, by convention, d_{ikj} is 1 for animals that survive until the end of the study. Table 3.3 gives the

Table 3.3 Variables used to summarize survival histories for individual-based models. Study consists of K=4 sampling events

	History	Last Event Seen Alive (t_{ikj})	Death Time Observed (d_{ikj})
R_{i1}	1111	4	1
	1110	3	1
	1100	2	1
	1000	1	1
	1113	3	0
	112	3	0
	113	2	0
	12	2	0
R_{i2}	0111	4	1
	0110	3	1
	0100	2	1
	0113	3	0
	012	3	0
R_{i3}	0011	4	1
	0010	3	1

values of t_{ikj} and d_{ikj} for the possible histories in a known-fate study with $K = 4$ sampling events.

The individual-based formulation of the multiple-population, survival-estimation model (Eq. (3.5)) treats the survival history for each animal as a series of independent Bernoulli trials (i.e., survival through each interval is one Bernoulli trial). The likelihood function is the product of the likelihoods of the individual Bernoulli trials:

$$L(\underset{\sim}{S}) = \prod_{i=1}^{I} \prod_{k=1}^{K-1} \left\{ \prod_{j=1}^{b_{ik}} \left\{ (1 - S_{i,\, t_{ikj}})^{d_{ikj}} \prod_{m=k}^{t_{ikj}-1} S_{im} \right\} \right\} , \tag{3.7}$$

where, by convention, $S_{iK} = 0$, for all i.

3.4 Survival-Effects Models for Known-Fate Data

This section introduces models for known-fate data that include explicit relationships between survival probabilities and environmental and individual-based covariates. Such relationships are the heart of the SURPH methodology.

3.4.1 Models with group covariates

3.4.1.1 Single population

With a single population, SURPH can be used to investigate relationships between time-variant group covariates and interval-specific survival probabilities. If $\underset{\sim}{w}_k$ is the set of covariate measurements that apply to the population in interval k, then the likelihood function for the group-covariate model is derived as an extension of Eq. (3.2) where the survival probabilities are rewritten as $S_k = f(S, \underset{\sim}{w}_k, \underset{\sim}{\tau})$, where S is the intercept parameter, $\underset{\sim}{\tau}$ is the vector of effect parameters, and the function f is the link between the linear predictor $\underset{\sim}{w}'_k \underset{\sim}{\tau}$ and the survival probability. For example, if the logit link is used, the survival probability for interval k is:

$$S_k = \frac{exp(\alpha + \underset{\sim}{w}'_k \underset{\sim}{\tau})}{1 + exp(\alpha + \underset{\sim}{w}'_k \underset{\sim}{\tau})} ,$$

where $\alpha = \log\left(\frac{S}{1-S}\right)$. When group covariates are included in the single-population model, interval effects (ρ_k) must be omitted so that the model is not overparameterized. The group covariate model is typically of lower rank than the survival-estimation model (3.2), but the rank of the minimal sufficient statistic does not change. Consequently, closed-form expressions cannot be written for the parameters, and numerical methods are required to obtain maximum likelihood estimates and associated variances and covariances. Analysis of deviance is used to assess the statistical significance of group covariate effects in a single-population study. The method is described in Section 3.5.1.

3.4.1.2 Multiple populations

With multiple populations, SURPH is used to study relationships between population- or site-specific group covariates and population-specific survival probabilities on an interval-by-interval basis. The group covariates may be either time-variant or time-invariant. If $\underset{\sim}{w}_{ik}$ is the set of covariate measurements that apply to population *i* in interval *k*, then the likelihood function for the group-covariate model is an extension of Eq. (3.5), with survival probabilities S_{ik} replaced by the function $S_{ik} = f(S, \rho_k, \underset{\sim}{w}_{ik}, \underset{\sim}{\tau}_k)$, where S is the intercept parameter, ρ_k is the effect parameter for interval *k*, $\underset{\sim}{\tau}_k$ is the vector of covariate-effect parameters for period *k*, and *f* is the link function between the linear predictor $(\rho_k + \underset{\sim}{w}'_{ik}\tau_k)$ and the survival probability. When group covariates are used in multiple-population models, parameters for population effects (π_i) and population/interval interactions $(\pi\rho)_{ik}$ must be omitted to avoid overparameterization of the model. As in the single-population case, numerical methods are required to obtain maximum likelihood estimates for parameters of the multiple-population, group-covariate model. The analysis of deviance methods used to assess the statistical

significance of group covariate effects in a multiple-population study are described in Section 3.5.2.

3.4.2 Models with individual covariates

Section 3.3.4 introduced a formulation of the basic survival-estimation model based on individual tagged animals. The likelihood function is the product of likelihood functions for each individual tagged animal, which are, in turn, constructed as the product of a series of Bernoulli trial probabilities. In Section 3.3.4, we assumed that the Bernoulli probability for a particular interval was the same for each tagged animal in a given population (Eq. (3.7)). However, if survival probabilities depend upon characteristics of the individual animals (i.e., individual covariates), then animals with different levels of a covariate have different Bernoulli probabilities. Let S_{ikjm} be the probability of surviving interval *m* for the *j*th animal released on event *k* in population *i*. Continuing to assume that the fate of each individual is independent of that of all others, Eq. (3.7) can be rewritten with individual-specific survival probabilities as:

$$L(\underset{\sim}{S}) = \prod_{i=1}^{I} \prod_{k=1}^{K-1} \prod_{j=1}^{R_{ik}} \left\{ (1 - S_{ikj,\, t_{ikj}})^{d_{ikj}} \prod_{m=k}^{t_{ikj}-1} S_{ikjm} \right\} . \tag{3.8}$$

This model has a total of $\sum_{i=1}^{I} \sum_{k=1}^{K-1} \sum_{j=1}^{b_{ik}} (t_{ikj} - k + 1)$ survival parameters. Although maximum likelihood estimates can be obtained for all of these survival probabilities (i.e., $\hat{S}_{ikjm} = 1$ for $m = k, \ldots, t_{ikj} - 1$, and $\hat{S}_{ikj,\, t_{ikj}} = 0$), there are far too many parameters to be useful. To reduce the survival parameters to an informative number, the individual probabilities are modeled as a function of individual traits and, possibly, of group covariates as well. The survival-effects model is derived from Eq. (3.8) by replacing the survival probabilities S_{ikjm} with the function:

$$S_{ikjm} = f(S, \pi_i, \rho_m, (\pi\rho)_{im}, \underset{\sim}{x}_{ikj}, \underset{\sim}{\beta}_{im}, \underset{\sim}{w}_{im}, \underset{\sim}{\tau}_m) , \tag{3.9}$$

where S = baseline intercept parameter,

π_i = effect parameter for population *i*,

ρ_m = effect parameter for interval *m*,

$(\pi\rho)_{im}$ = parameter for interaction of effects of population *i* and interval *m*,

$\underset{\sim}{x}_{ikj}$ = vector of individual covariate measurements for the *j*th individual tagged on event *k* in population *i*,

$\underset{\sim}{\beta}_{im}$ = vector of regression parameters describing the relationship between the individual-based covariates and survival probability in the *m*th interval for the *i*th population,

$\underset{\sim}{w}_{im}$ = vector of group covariates that apply to population *i* in interval *m*, and

$\underset{\sim}{\tau}_m$ = vector of regression parameters describing the relationship between the population-specific group covariates and survival probability in interval *m*.

If group covariates are not included in the model, the full suite of population and interval effects and their interactions can be included. For example, if the hazard link is used, the survival probabilities are written as:

$$S_{ikjm} = S^{exp(\pi_i + \rho_m + (\pi\rho)_{im} + \underset{\sim}{x}'_{ikj}\beta_{im})} .$$

If group covariates are included, population effects (π_i) and population/interval interactions $(\pi\rho)_{ik}$ must be omitted to avoid overparameterization. For example, under the logit link:

$$S_{ikjm} = \frac{exp(\alpha + \rho_m + \underset{\sim}{w}'_{im}\tau_m + \underset{\sim}{x}'_{ikj}\beta_{im})}{1 + exp(\alpha + \rho_m + \underset{\sim}{w}'_{im}\tau_m + \underset{\sim}{x}'_{ikj}\beta_{im})} .$$

Numerical methods are required to obtain maximum likelihood estimates. Likelihood ratio statistics (Section 2.4.1) are used to test the statistical significance of the effects of individual covariates (Skalski et al. 1993).

3.4.3 Assumptions

The assumptions for survival-effects models are the same as for survival-estimation models (Section 3.3.1.3) with the adjustments described in this section.

If the focus of the study is the effect of environmental or individual-based variables on survival, and not on the baseline survival *per se*, then assumption (A3.2) may be replaced by a weaker version:

A3.2b) The probability of survival for every animal during each interval is affected in the same way by tagging and resampling.

Assumption (A3.2b) implies that there is no interaction between the effects of handling and the effects of the factors in question. It is assumed that the survivability of each animal is affected by handling in the same way, whatever other environmental influences it is subject to. If this assumption is made in a survival-estimation model, the actual survival estimates cannot be extrapolated to untagged animals, but the *differences* between survival in populations subject to different covariate levels are assumed to be unaffected. The differences in survival between populations are represented in survival-effects models by effect parameters. Thus, the effect parameters can be extrapolated to other non-handled populations, but the intercept parameter for survival (S) cannot.

By definition, assumption (A3.5) cannot apply when individual covariates are included in the model. Instead, for survival-effects models, (A3.5) is replaced by the following assumptions:

A3.8) The covariates for each population and each individual tagged animal are accurately measured.

A3.9) The relationship between covariates and survival probabilities is correctly modeled by the selected link function.

3.5 Testing Significance of Covariate Effects on Survival

Analysis of deviance is used to assess effects of group covariates by analyzing a series of hierarchical statistical likelihood models, from a maximally parameterized "full" model down to a minimal or "null" model. Section 2.4.3 includes a general description of the ANODEV method in the context of generalized linear models. Sections 3.5.1 and 3.5.2 specify how ANODEV is applied to known-fate data for single- and multiple-population studies, respectively. Finally, Section 3.5.3 briefly discusses how effects of individual covariates are tested using likelihood ratio statistics.

3.5.1 Analysis of deviance for group covariates in single-population study

The "full" model for a single-population, known-fate study is the survival-estimation model with a distinct survival probability in each interval (Eq. (3.2)). The full model contains a total of K-1 parameters, one survival probability for each of the K-1 intervals. The maximized likelihood for the full model is denoted $L(\hat{\underset{\sim}{\theta}}_F)$. The "null" model has just one parameter, a single survival probability common to all sampling intervals ($S_k \equiv S_0$). Under the null model, the common survival probability S_0 is a weighted average of the interval-specific estimates from the full model (Eq. (3.3)):

$$\hat{S}_0 = \frac{\sum_{k=1}^{K-1} a_{k+1}}{\sum_{k=1}^{K-1} v_k}. \tag{3.10}$$

The maximized likelihood for the null model is denoted $L(\hat{\underset{\sim}{\theta}}_0)$, and is obtained by evaluating Eq. (3.2) with all $S_k = \hat{S}_0$.

A single population cannot be used to evaluate the effects of a time-invariant group covariate. Multiple populations are required to test the significance of time-invariant factors, so

that varying levels of the covariate may be observed. However, single population studies can be used to study the relationship of interval-specific survival probabilities with time-variant (i.e., interval-specific) group covariates. Single-population studies are necessarily observational (no replication), though interval-specific conditions may be purposefully manipulated by researchers.

Suppose there is a total of J time-variant group covariates in a single-population, known-fate study. Table 3.4 lists the hierarchical models required to construct the ANODEV table. The table itself is shown in Table 3.5. Strictly speaking, the entries in the "Deviance" column for "Total" and "Mean" are not deviances. The construction of the ANODEV table requires their inclusion as defined in Table 3.5 to complete the parallel with the ANOVA table, which includes Total and Mean sums of squares. The "Corrected Total Deviance" is another name for the total discrepancy between the null and full models. The "Error Deviance" is the amount of the Corrected Total not "explained" by the covariates. There must be at least one degree of freedom for Error Deviance; thus, the maximum number of covariates that can be analyzed at one time is $K - 3$ $(1 \leq J \leq K - 3)$. The "Mean Deviance" for each source is the deviance divided by the associated number of degrees of freedom.

Unless covariates are uncorrelated, the deviance attributed to each covariate will depend on which other covariates are in the model. That is, the deviances for covariate effects are *nonorthogonal*. This nonorthogonality parallels linear regression analysis, where regression coefficients and reductions in sums of squares depend on other covariates in the model. When effects are nonorthogonal, a stepwise procedure can be used to choose the appropriate SURPH model. At the first step, the covariate that gives the largest (significant) difference in deviance from the null model is added to the model. Then, the next covariate that gives the largest difference from the model that contains the first covariate is added, and so on.

ANODEV is used to test the significance of the covariate effects, based on the amount of the Corrected Total explained by the covariates, as measured by the F-statistic:

$$F_{\nu,\, K-J-2} = \frac{\text{MD(Effect)}}{\text{MD(Err)}}, \tag{3.11}$$

Table 3.4 Hierarchical likelihood models required to construct ANODEV table for single-population known-fate study.

Model Name	Number of parameters[1]	Maximized likelihood	Linear predictor[2]
Full	K-1	$L(\hat{\underset{\sim}{\theta}}_F)$	–
Total Covariate	J + 1	$L(\hat{\underset{\sim}{\theta}}_M)$	$\underset{\sim}{w}'_k \underset{\sim}{\tau}$
Covariate 1	2	$L(\hat{\underset{\sim}{\theta}}_{M_1})$	$w_{k1}\tau_1$
Covariates 1 & 2	3	$L(\hat{\underset{\sim}{\theta}}_{M_{12}})$	$w_{k1}\tau_1 + w_{k2}\tau_2$
...	...	...	...
Covariates 1,2,...,J-1	J	$L(\hat{\underset{\sim}{\theta}}_{M_{12...J-1}})$	$w_{k1}\tau_1 + ... + w_{k,J-1}\tau_{J-1}$
Null	1	$L(\hat{\underset{\sim}{\theta}}_0)$	–

1. For models with covariates, the number of parameters is equal to the number of covariates in the model plus 1 for the intercept parameter.

2. w_{kj} is the value of the *j*th covariate in the *k*th interval; τ_j is the effect parameter for the *j*th covariate.

Table 3.5 Generic ANODEV table for single-population known-fate study.

Source	df	Deviance	Mean Deviance	F	R^2
Total	K-1	$-2lnL(\hat{\underset{\sim}{\theta}}_0)$			
Mean	1	$-2lnL(\hat{\underset{\sim}{\theta}}_F)$			
Corrected Total	K-2	$-2\{lnL(\hat{\underset{\sim}{\theta}}_0) - lnL(\hat{\underset{\sim}{\theta}}_F)\}$			
Covariate Total	J	$-2\{lnL(\hat{\underset{\sim}{\theta}}_0) - lnL(\hat{\underset{\sim}{\theta}}_M)\}$	$\frac{\text{Dev(Cov)}}{J}$	$F_{J,\,K-J-2} = \frac{\text{MD(Cov)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov)}}{\text{Dev(Cor)}}$
Covariate 1	1	$-2\{lnL(\hat{\underset{\sim}{\theta}}_0) - lnL(\hat{\underset{\sim}{\theta}}_{M_1})\}$	$\frac{\text{Dev(Cov}_1\text{)}}{1}$	$F_{1,\,K-J-2} = \frac{\text{MD(Cov}_1\text{)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov}_1\text{)}}{\text{Dev(Cor)}}$
Covariate 2 | Cov. 1	1	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{M_1}) - lnL(\hat{\underset{\sim}{\theta}}_{M_{12}})\}$	...	...	...
...	...	...	...	...	...
Covariate J | Cov. 1,2,..., J-1	1	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{M_{12...,J-1}}) - lnL(\hat{\underset{\sim}{\theta}}_M)\}$	$\frac{\text{Dev(Cov}_J\text{)}}{1}$	$F_{1,\,K-J-2} = \frac{\text{MD(Cov}_J\text{)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov}_J\text{)}}{\text{Dev(Cor)}}$
Error	K-J-2	$-2\{lnL(\hat{\underset{\sim}{\theta}}_M) - lnL(\hat{\underset{\sim}{\theta}}_F)\}$	$\frac{\text{Dev(Err)}}{(K-J-2)}$		

where ν is the number of covariate effects being tested, MD(Effect) is the mean deviance for the ν covariates, and MD(Error) is the mean deviance for error. When there is truly no effect of the covariates (i.e., the null hypothesis is true), the F-statistic has an asymptotic F-distribution with ν and $K - J - 2$ numerator and denominator degrees of freedom, respectively (Smith 1991).

An alternative to the F-statistic is the R^2 statistic, given by:

$$R^2 = \frac{\text{Dev(Effect)}}{\text{Dev(Cor)}}, \tag{3.12}$$

which measures the amount of the Corrected Total deviance explained by the covariate(s) of interest. Under the null hypothesis of no effects, R^2 is asymptotically distributed as a beta random variable with parameters $\frac{\nu}{2}$ and $\frac{K - \nu - 2}{2}$. When testing all covariates simultaneously, the F- and R^2-statistics are equivalent, because they are based on the same two independent variables (i.e., Dev(Cov) and Dev(Err), because Dev(Cor) = Dev(Cov) + Dev(Err)).

3.5.2 Analysis of deviance for group covariates in multiple-population study

The full model for a multiple-population, known-fate study is given by Eq. (3.5), the product of the independent single-population, survival-estimation models over the I populations. There are K-1 survival probabilities for each population, for a total of $I(K\text{-}1)$ parameters in the full model. The maximized likelihood for the full model is denoted $L(\hat{\underset{\sim}{\theta}}_F)$.

Using multiple populations, ANODEV is used to study relationships between population- or site-specific group covariates and population-specific survival probabilities on an interval-by-interval basis. SURPH maintains the interval-based orientation by defining the null model with interval-specific survival probabilities that are common to all I populations. Effectively, all populations are pooled; and a single survival-estimation model with parameters $(S_1, S_2, \ldots, S_{K-1})$ is applied to the pooled data, for a total of K-1 parameters in the null model.

This model is also called the “Interval Means” model, and the maximized likelihood is denoted $L(\hat{\underset{\sim}{\theta}}_{IM})$.

Suppose there is a total of *J* group covariates that vary across the multiple populations within each interval. The covariates may be time-variant or time-invariant, and may be quantitative measurements or indicator variables for blocks or treatment levels. The model that includes an effect parameter for each of the *J* covariates in each of the intervals is known as the “Total Covariate” model. The Total Covariate model has *K*-1 parameters for interval mean or baseline survival and *J*(*K*-1) for covariate effects.

To complete a hierarchy of models and compute the ANODEV table, models can be fitted to the data that include covariate effects in some intervals but not in others, or that include subsets of the covariate effects within particular intervals. Table 3.6 lists a typical hierarchy of models, and Table 3.7 gives the ANODEV table computed from the hierarchy. Strictly speaking, the entries in the “Deviance” column for “Total” and “Mean” are not deviances. The construction of the ANODEV table requires their inclusion, as defined in Table 3.7, to complete the parallel with the ANOVA table, which includes Total and Mean sums of squares. The “Corrected Total Deviance” is another name for the total discrepancy between the null and full models. The “Error Deviance” is the amount of the Corrected Total not “explained” by the covariates. There must be at least one degree of freedom for Error Deviance; thus, the maximum number of group covariates that can be analyzed at one time in a multiple-population study is $I-2$ $(1 \le J \le I-2)$. The “Mean Deviance” for each source is the deviance divided by the associated number of degrees of freedom.

The typical ANODEV for multiple populations first partitions the total deviance for covariates into contributions for each interval (Table 3.7). With known-fate data, the deviances for separate intervals are *orthogonal*. That is, the reduction in deviance obtained by adding all the covariate effects for a particular interval does not depend on the effects that are already in the model for other intervals. However, the reductions in deviance attributed to particular covariates

Table 3.6 Hierarchical likelihood models used to construct ANODEV table for multiple-population known-fate study.

Model Name	Number of parameters[1]	Maximized likelihood
Full	*I(K-1)*	$L(\hat{\underset{\sim}{\theta}}_F)$
Total Covariate	*K-1 + J(K-1)*	$L(\hat{\underset{\sim}{\theta}}_M)$
All Covariates, Interval 1	*K-1 + J*	$L(\hat{\underset{\sim}{\theta}}_{M_1})$
Covariate 1, Interval 1	*K-1 + 1*	$L(\hat{\underset{\sim}{\theta}}_{M_{1/1}})$
Covariates 1 & 2, Interval 1	*K-1 + 2*	$L(\hat{\underset{\sim}{\theta}}_{M_{1/12}})$
...	...	...
Covariates 1,2,..., *J-1* Interval 1	*K-1 + J-1*	$L(\hat{\underset{\sim}{\theta}}_{M_{1/12...J-1}})$
Covariates, Intervals 1 & 2	*K-1 + 2J*	$L(\hat{\underset{\sim}{\theta}}_{M_{12}})$
...	...	...
All Covariates, Intervals 1,2,..., *K-2*	*K-1 + J(K-2)*	$L(\hat{\underset{\sim}{\theta}}_{M_{12...K-2}})$
Null	*K-1*	$L(\hat{\underset{\sim}{\theta}}_{IM})$

1. For models with covariates, the number of parameters is equal to the number of covariate effect parameters in the model plus *K-1* for the interval-specific intercept parameters.

Table 3.7 Generic ANODEV table for multiple-population known-fate study.

Source	df	Deviance	Mean Deviance	F	R^2
Total	I(K-1)	$-2lnL(\hat{\underset{\sim}{\theta}}_{IM})$			
Mean	K-1	$-2lnL(\hat{\underset{\sim}{\theta}}_{F})$			
Corrected Total	(I-1)(K-1)	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{IM}) - lnL(\hat{\underset{\sim}{\theta}}_{F})\}$			
Covariate Total	J(K-1)	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{IM}) - lnL(\hat{\underset{\sim}{\theta}}_{M})\}$	$\frac{\text{Dev(Cov)}}{J(K-1)}$	$F_{J(K-1),\,df_{\text{ERR}}} = \frac{\text{MD(Cov)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov)}}{\text{Dev(Cor)}}$
Covariates; Interval 1	J	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{IM}) - lnL(\hat{\underset{\sim}{\theta}}_{M_1})\}$	$\frac{\text{Dev(Cov}_1\text{)}}{J}$	$F_{J,\,df_{\text{ERR}}} = \frac{\text{MD(Cov}_1\text{)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov}_1\text{)}}{\text{Dev(Cor)}}$
Covariate 1; Interval 1	1	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{IM}) - lnL(\hat{\underset{\sim}{\theta}}_{M_{1/1}})\}$	$\frac{\text{Dev(Cov}_1\text{)}}{J}$	$F_{1,\,df_{\text{ERR}}} = \frac{\text{MD(Cov}_{1/1}\text{)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov}_{1/1}\text{)}}{\text{Dev(Cor)}}$
Covariate 2 | Cov. 1; Interval 1	1	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{M_{1/1}}) - lnL(\hat{\underset{\sim}{\theta}}_{M_{1/12}})\}$	$\frac{\text{Dev(Cov}_{1/2}\text{)}}{1}$	$F_{1,\,df_{\text{ERR}}} = \frac{\text{MD(Cov}_{1/2}\text{)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov}_{1/2}\text{)}}{\text{Dev(Cor)}}$
...	...				
Covariate J | Cov. 1,2,..., J-1; Interval 1	1	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{M_{1/12...,J-1}}) - lnL(\hat{\underset{\sim}{\theta}}_{M_1})\}$	$\frac{\text{Dev(Cov}_{1/J}\text{)}}{1}$	$F_{1,\,df_{\text{ERR}}} = \frac{\text{MD(Cov}_{1/J}\text{)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov}_{1/J}\text{)}}{\text{Dev(Cor)}}$
Covariates; Interval 2	J	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{M_1}) - lnL(\hat{\underset{\sim}{\theta}}_{M_{12}})\}$	$\frac{\text{Dev(Cov}_2\text{)}}{J}$	$F_{J,\,df_{\text{ERR}}} = \frac{\text{MD(Cov}_2\text{)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov}_2\text{)}}{\text{Dev(Cor)}}$
...	...				
Covariates; Interval K-1	J	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{M_{12...,K-2}}) - lnL(\hat{\underset{\sim}{\theta}}_{M})\}$	$\frac{\text{Dev(Cov}_{\text{K-1}}\text{)}}{J}$	$F_{J,\,df_{\text{ERR}}} = \frac{\text{MD(Cov}_{\text{K-1}}\text{)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov}_{\text{K-1}}\text{)}}{\text{Dev(Cor)}}$
Error	(I-J-1)(K-1)	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{M}) - lnL(\hat{\underset{\sim}{\theta}}_{F})\}$	$\frac{\text{Dev(Err)}}{(I-J-1)(K-1)}$		

within the same interval are nonorthogonal. The stepwise procedure for adding covariates described in Section 3.5.1 can be used to build group covariate models for multiple populations.

We recommend a two-phase stepwise procedure for adding covariates to the ANODEV table to build group covariate models for multiple populations. In the first phase, the total covariate deviance is partitioned into contributions for each interval (i.e, all J covariates in each interval). Then the total covariate deviances for each interval are partitioned into contributions of each covariate in the second phase of the stepwise approach. For example, in the first step of the first phase, K-2 models are investigated, each including K-2 parameters for interval mean or baseline effects, and J parameters for covariate effects for interval k ($k = 1, ..., K-2$). The block of interval effects to enter the table first is determined by the model that has the greatest maximized likelihood among the K-2 candidates. Then, the next block of covariates that gives the largest difference from the model that contains the first block is added, and so on. The second phase proceeds analogously to the first, adding one interval-specific covariate effect on each step.

Hypothesis tests for covariate effects are based on the F-statistic:

$$F_{\nu,\,(I-J-1)(K-1)} = \frac{\text{MD(Effect)}}{\text{MD(Err)}}\ , \tag{3.13}$$

where ν is the number of covariate effects being tested, MD(Effect) is the mean deviance for the ν covariates, and MD(Error) is the mean deviance for error. When there is truly no effect of the covariates (i.e., the null hypothesis is true), the F-statistic has an asymptotic F-distribution with ν and $(I-J-1)(K-1)$ numerator and denominator degrees of freedom, respectively (Smith 1991).

3.5.3 Likelihood ratio tests for individual covariates

Likelihood ratio tests (LRTs) (Section 2.4.1) are not appropriate for group covariate effects because inter-replicate variability is not correctly accounted for (Smith 1991). However, Hoffmann (1993) showed that LRTs are appropriate for testing the significance of effects of

individual covariates when a saturated model (i.e., model Sst) is used for the design effects (i.e., population and interval) on survival.

For example, suppose we have a single-population, known-fate study with $K = 4$ sampling events. For each tagged animal, a condition index is calculated based on morphology (x_{kj} for the jth individual tagged on event k), and we wish to determine whether the index is significantly correlated with survival probabilities. A survival-effects model is used to estimate the effect parameter β_m for the condition index in interval m. Using the hazard link, the survival probability in interval m is written as:

$$S_{kjm} = S^{e^{\rho_m + x_{kj}\beta_m}}.$$

To test the hypotheses

$$H_0: \beta_m = 0 \quad \text{versus} \quad H_A: \beta_m \neq 0,$$

Eq. (3.8) is used to fit the model that includes the condition index effect and does not include the effect (i.e., $S_{kjm} = S^{e^{\rho_m}}$ for all kj; see Section 3.3.3). The likelihood ratio statistic is then computed Eq. (2.28) and compared to a χ^2-distribution with 1 degree of freedom.

3.6 SURPH Features for Analysis of Known-Fate Data

After data input to SURPH, the user can perform activities in three major areas. The user can (1) view descriptive tables and graphical displays based on the data, (2) fit a series of survival models to investigate relationships with group and individual covariates, and (3) view tabular and graphical information based on models fit to the data. All three activities are described in detail in Chapter 6 and especially Chapter 7. The theory for fitting models has been described in previous sections of this chapter. Chapter 7 is meant to be a tutorial, and omits detailed theoretical explanation of some of the tabular and graphical output of Program SURPH for known-fate data. This section explains the theory behind these features in more detail.

3.6.1 Binomial estimates of survival probabilities

SURPH automatically fits the survival-estimation model (Eq. (3.5)) and, upon request, provides a table of the survival estimates (Eq. (3.6)) (see "Data: Binomial Estimates" in Chapter 7). The estimates from the survival-estimation model are referred to in SURPH as "binomial estimates." For each estimate $\hat{S}_{ik}$, the table also gives the number at risk at the beginning of interval k (v_{ik}) and the number of those at risk that survived until the end of the interval $(a_{i,\,k+1})$. Kaplan-Meier survival estimates (Section 2.1.1) for population *i* can be derived from the binomial estimates as follows. Let t_k denote the time or location of sampling event *k*. Then the Kaplan-Meier estimate of the survivor function at t_k is:

$$\hat{S}(t_k) = \prod_{j=1}^{k} S_j \,. \tag{3.14}$$

3.6.2 Fitted models

3.6.2.1 Parameters estimated by SURPH

After fitting a model using SURPH, the maximum likelihood estimators for the model parameters can be displayed (see "Models: SURPH Parameter Estimates" in Chapter 7), along with a numerical approximation of the variance-covariance matrix based on difference equations. The parameters displayed are essentially those on the right-hand side of Eq. (3.9); i.e., the population and period effect parameters (see Section 3.3.3) and the slope parameters for group and individual covariates.

The internal workings of SURPH do not act directly upon the intercept parameter S. Instead, SURPH works with the logit of the intercept parameter:

$$S' = \log\left(\frac{S}{(1-S)}\right) \,. \tag{3.15}$$

The logistic scale is unrestricted [$(-\infty, \infty)$], as are all the effect parameters. Without this transformation, estimated values of the intercept parameter may fall outside the admissible range, causing problems with the iterative numerical procedure.Thus, the estimated intercept parameter that is displayed is not the one SURPH estimated, but the inverse transformation:

$$\hat{S} = \frac{exp(\hat{S}')}{1 + exp(\hat{S}')} . \tag{3.16}$$

Similarly, SURPH computes the approximate variance-covariance matrix based on the transformed variable S' but displays the matrix adjusted for the back-transformation:

$$\hat{Var}(\hat{S}) = \hat{Var}(\hat{S}')\{\hat{S}(1-\hat{S})\}^2 \quad \text{, and} \quad \hat{Cov}(\hat{S}, \hat{\theta}) = \hat{Cov}(\hat{S}', \hat{\theta})\{\hat{S}(1-\hat{S})\} \quad ,$$

where θ is any effect parameter.

3.6.2.2 SURPH parameters translated into probabilities

The SURPH user will rely mainly on the effect parameters (Section 3.6.2.1) to make inferences regarding influences on the survival process. However, it is also interesting to translate the effect parameters into the familiar scale of estimated survival probabilities for each interval. SURPH offers a tabular display of the parameter estimates translated into probabilities (see “Models: SURPH Probability Estimates” in Chapter 7).

For models that do not include individual covariates, the probability estimates are calculated as a straightforward function of the link function and the effect parameters:

$$\hat{S}_{ik} = f(\hat{S}, \hat{\pi}_i, \hat{\rho}_k, (\hat{\pi\rho})_{ik}, \underset{\sim}{w}_{ik}, \hat{\underset{\sim}{\tau}}_k) , \tag{3.17}$$

where $\hat{S}$ = the estimated intercept parameter,

$\hat{\pi}_i$ = the estimated effect parameter for population i,

$\hat{\rho}_k$ = the estimated effect parameter for interval k,

$(\widehat{\pi\rho})_{ik}$ = the estimated interaction between population i and interval k effects,

$\underset{\sim}{w}_{ik}$ = the vector of group covariates in interval k for population i,

$\hat{\underset{\sim}{\tau}}_k$ = the vector of covariate effect parameters for period k, and

f = the link function between the linear predictor and the survival probability.

Standard errors of the probability estimates are derived from the variance-covariance matrix of the SURPH parameters using the delta method (Seber 1982, pp. 7-9). The standard errors currently displayed are based only on the population and interval effects and on group covariate effects in the model.

When the model includes individual covariates, the probabilities are "integrated" over all individuals in population i and interval k according to the formula:

$$\hat{S}_{im} = \frac{\sum_{k=1}^{m-1} \sum_{j=1}^{R_{ik}} S_{ikjm}}{\sum_{k=1}^{m-1} R_{ik}} = \frac{\sum_{k=1}^{m-1} \sum_{j=1}^{R_{ik}} f(\hat{S}, \hat{\pi}_i, \hat{\rho}_m, (\pi\rho)_{im}, \underset{\sim}{x}_{ikj}, \hat{\underset{\sim}{\beta}}_{im}, \underset{\sim}{w}_{im}, \hat{\underset{\sim}{\tau}}_m)}{\sum_{k=1}^{m-1} R_{ik}}, \tag{3.18}$$

where $\underset{\sim}{x}_{ikj}$ = the vector of individual-based covariates for the jth animal released on the kth sampling event in population i,

$\underset{\sim}{\beta}_{im}$ = the vector of effect parameters for individual covariates in the mth sampling interval for population i,

and the other symbols are as in Eq. (3.17).

Code has not been installed in Program SURPH to calculate standard errors of the integrated probability estimates (Eq. (3.18)) when individual covariates are modeled.

3.6.2.3 Response curves for group covariates

For models including group covariates, SURPH provides a graphical display of the estimated response curves derived from the estimated parameters (see “Models: Survival Graphics: Group Covariate” in Chapter 7). The user selects an interval (k) and a covariate (l) to display. Values of the selected group covariate (w_{ikl}) are on the horizontal axis, ranging from the minimum observed value to the maximum, and the estimated survival probability is on the vertical axis. The plotted curve is:

$$y = f(\hat{S}, \hat{\pi}_i, \hat{\rho}_k, (\pi\rho)_{ik}, \bar{\underset{\sim}{x}}_i, \hat{\underset{\sim}{\beta}}_{ik}, \bar{\underset{\sim}{w}}_{k(l)}, \hat{\underset{\sim}{\tau}}_{k(l)}, x, \hat{\tau}_{kl}) \tag{3.19}$$

where $\bar{\underset{\sim}{x}}_i$ = a vector consisting of the average individual covariate values for individuals in population i;

$\bar{\underset{\sim}{w}}_{k(l)}$ = a vector consisting of the average across populations of each group covariate, other than that selected for display, in interval k;

$\hat{\underset{\sim}{\tau}}_{k(l)}$ = the vector of covariate effect parameters for interval k, excluding the effect of the selected parameter;

x = the value on the horizontal axis, i.e., values of the selected covariate (w_{ikl}); and

$\hat{\tau}_{kl}$ = the effect parameter for group covariate l in interval k.

3.6.2.4 Response curves for individual covariates

For models including individual covariates, SURPH provides a graphical display of the estimated response curves derived from the estimated parameters (see “Models: Survival Graphics: Individual Covariate (A)” in Chapter 7). The user selects an interval (k) and a covariate (l) to display. Values of the selected individual covariate (x_{il}) are on the horizontal axis, ranging from the minimum observed value to the maximum, and the estimated survival probability is on the vertical axis. The plotted curve is:

$$y = f(\hat{S}, \hat{\pi}_i, \hat{\rho}_k, (\pi\rho)_{ik}, \bar{\underset{\sim}{x}}_{i(l)}, \hat{\underset{\sim}{\beta}}_{ik(l)}, \bar{\underset{\sim}{w}}_k, \hat{\underset{\sim}{\tau}}_k, x, \hat{\beta}_{ikl}) \tag{3.20}$$

where $\bar{\underset{\sim}{x}}_{i(l)}$ = a vector consisting of the average individual covariate values, other than that selected for display, for individuals in population i;

$\hat{\underset{\sim}{\beta}}_{ik(l)}$ = the vector of covariate effect parameters for interval *k* and population *i*, excluding the effect of the selected parameter;

$\bar{\underset{\sim}{w}}_k$ = a vector consisting of the average across populations of each group covariate in interval *k*;

x = the value on the horizontal axis, i.e., values of the selected individual covariate (x_{il}); and

$\hat{\beta}_{ikl}$ = the effect parameter for individual covariate *l* in interval *k* and population *i*.

3.6.2.5 Nonparametric response curves

The response curve for individual covariates based on the SURPH parameters (Eq. (3.20)) can be superimposed on a "nonparametric" curve, or one that does not depend on the parameters of any particular model (see "Models: Survival Graphics: Individual Covariate (C)" in Chapter 7). The nonparametric curve can be thought of as the "moving average" survival as you move from the animals with the smallest values of the selected individual covariate to the animals with the largest values. The size of the "window" for the moving average ranges from a minimum of 8 individuals up to 20% of the entire number at risk in the selected interval.

The nonparametric curve is computed as follows:

1) The user selects an individual covariate (*l*), a sampling interval (*k*), and a population (*i*) for the display.

2) The animals in population *i* that were at risk in interval *k* are sorted from smallest to largest value of covariate *l*.

3) Beginning with smallest covariate value and window composed of the 8 individuals with the smallest covariate values, the binomial estimate (Eq. (3.3)) is computed. The estimated survival probability is plotted versus the mean covariate value for individuals in window.

4) In increments of one individual, the window size is increased to 20% of the number at risk by adding, at each step, the individual with the next largest value of the covariate. For each increment, the binomial estimate is computed and plotted versus the mean covariate value in the window.

5) Once the window is 20% of the number of animals at risk, the window is moved, one individual at a time, by dropping the individual with the smallest value from the window and adding the individual with the next largest value. At each step, the binomial survival estimate is computed and plotted versus the mean covariate value in the window.

6) Once the "right-end" of the window reaches the individual with largest covariate value, the window size is decreased in decrements of one individual at each step by dropping the individual with the smallest value of the covariate from the window, until the window size returns to the minimum of 8 animals. For each decrement, the binomial estimate is computed and plotted versus the mean covariate value in window.

The result is a non-smooth curve that does not depend on any particular model assumptions. For an adequate model of the individual covariate effect, the parametric response curve (Eq. (3.20)) should follow the nonparametric curve reasonably well.

3.6.2.6 Residual plots

One measure of the adequacy of a model fitted to data is how well the expected observations predicted by the model agree with what was actually observed. For SURPH models, we can compare the observed number of animals with each survival history with the number predicted by the model. The predicted numbers are obtained by computing expected survival probabilities for each individual animal (Eq. (3.9)) and then computing the expected probabilities for each survival history (e.g., Table 3.2). The probabilities are summed over all individuals to give the expected number of animals with each survival history in each population.

A residual is calculated for each possible history, based on the observed (O) and expected (E) number of animals with the survival history. For Poisson distributions, the following function, known as the Anscombe residual, is approximately normally distributed (Cox and Snell 1968):

$$r_A = \frac{\frac{3}{2}\left(O^{2/3} - \left(E - \frac{1}{6}\right)^{2/3}\right)}{E^{1/6}} \quad . \tag{3.21}$$

In a display available in SURPH (see “Models: Residual Plot” in Chapter 7), the Anscombe residual for each survival history is plotted against the decimal equivalent of the survival history taken as a binary number (e.g., 1110 base 2 = 14 base 10), with the plotting character equal to the number of the population. Because the r_A are approximately normal, any residuals greater than 2 in absolute value are potential outliers (i.e., $P(|Z| > 2.0) \approx 0.05$). If several large residuals occur, the user should investigate the corresponding survival histories to identify any patterns that might suggest a mechanism to explain why there are “too many” or “too few” of some survival histories.

SURPH also provides a plot of the residuals against quantiles of the normal distribution (see “Models: Quantile-Quantile Plot” in Chapter 7).

Chapter 4

Analysis of Release-Recapture Data

4.1 Introduction

In release-recapture studies, individual animals are identified with a unique mark, for example, a numbered band around the leg of a bird or a electronic PIT-tag injected into the body cavity of a migrating salmon. Individuals are captured, marked, and released back onto the study site, and periodically resampled for continued presence on the study site. The sampling record for each marked individual is the "capture history." Unlike known-fate studies, however, not every marked animal is sampled on each sampling event. Hence, release-recapture models differ from known-fate models in that the capture process must be modeled along with the survival process. Modeling the capture process increases the number of parameters that must be estimated, with a corresponding loss of statistical power and precision. Consequently, more animals must be marked in a release-recapture study to detect covariate effects than in a known-fate study. However, the cost per marked animal is generally much less.

The terms "release-recapture" and "capture history" imply that sampling consists of actual physical capture of marked animals. However, a "recapture" need only be the knowledge that the animal was alive on a sampling event. Thus, an animal need not be handled as long it can be identified when detected. We will use the more generic terms of "detected" or "not detected," that encompass both the physical practice of recapture and resighting data. For example, release-recapture data are collected from migrating juvenile salmon in the Snake and Columbia River system, using automatic PIT-tag detectors installed in juvenile bypass systems at the dams. The fish are never handled after the initial time of tagging.

The earliest useful general models of release-recapture data were presented by Jolly (1965), Seber (1965), and Cormack (1964). The so-called "Jolly-Seber model" includes a large suite of parameters, some of which are irrelevant to studies of survival. The ratio of marked-to-unmarked animals in the resamples is used to estimate birth rates (or recruitment) and total

abundance, while survival and capture probabilities are estimated using information only from previously marked animals. The Cormack (1964) model, by contrast, uses only the information from recaptures of previously marked animals, and includes parameters only for survival and capture probabilities. Clobert (1981) and Sandland and Kirkwood (1981) independently proposed modifications to the Cormack (1964) model, involving certain equality constraints among the survival and capture parameters.

The Jolly-Seber, Cormack, and Sandland-Kirkwood-Clobert (SKC) models are all capture- and survival-estimation models (Section 1.1), providing series of estimates of survival probabilities for each interval and capture probabilities for each event. Because the Jolly-Seber model also includes parameters for abundance and recruitment, the simpler Cormack and SKC models are more suitable when the focus of the study is strictly on survival parameters. More recently Clobert et al. (1985), Smith (1991), and Lebreton et al. (1992) have modeled the relationship of survival to characteristics that vary from group to group. Hoffmann (1992) developed release-recapture models incorporating individual-based covariates. Program SURPH incorporates the combined abilities to model the effects of both group and individual-based covariates on survival.

4.2 Release-Recapture Data

The data from a release-recapture study consist of measurements of characteristics for each interval and/or population (group covariates), measurements of traits of the individual marked animals (individual covariates), and the capture history for each marked animal. Capture histories are made up of “1’s” to denote sampling events when the animal was detected and “0’s” to denote the events when the animal was not detected. However, some individuals might be removed from the marked population at large before the end of the study, and, consequently, have truncated capture histories. Animals are removed if they are killed by the capture or sampling process itself (i.e., “handling mortalities”) or if they are purposely removed on a sampling event for biological sampling. On the Snake and Columbia Rivers, the PIT-tag detection systems are not capable of returning 100% of the detected fish back to the river, as required to obtain complete capture histories. Rather, some PIT-tagged fish are inadvertently shunted to barges and transported down the river. Marked animals removed from the population

with the researchers' knowledge are referred to as "known removals." The truncated capture history for a known removal ends with a "2" for the event on which it was removed. Removed animals provide information on the survival and capture processes up until the point of censoring, but not beyond that point. Models for release-recapture data must be constructed to use whatever information is provided by known removals.

The series of symbols ("0", "1", or "2") over all sampling events is the capture history of that animal (see Section 6.4 for more discussion of capture histories). With a staggered-entry design, it is also necessary to record the event when the animal was first tagged. Thus, for a study with *K* sampling events (see Figure 2.4), a series of *K* "1's," "0's", or "2's" is needed to represent each capture history. The capture history of animals tagged on event 1 begins with "1," while those tagged on subsequent sampling events have histories beginning "00...01."

For example, suppose we have a study with K = 4 sampling events, with newly marked animals released on events 1 through 3. The possible capture histories can be represented in the "recapture trees" shown in Figure 4.1, and summarized in Table 4.1. There are eight possible capture histories for animals tagged on event 1 (capture history beginning with "1") and not removed at any point in the study (sampled on three subsequent events). There are three possible histories ("112," "102," and "12") for animals removed from the population. In general, if a release group is released on sampling event *i*, there are 2^{K-i} possible capture histories for those not removed, and $\sum_{j=0}^{K-i-2} 2^j = (2^{K-i-1} - 1)$ for known removals. Summed over all possible release groups, there are $\sum_{i=1}^{K-1} 2^{K-i} = 2^K - 2$ possible capture histories for those not removed and $\sum_{i=1}^{K-1} (2^{K-i-1} - 1) = (2^{K-1} - K)$ for known removals. Because there may be no newly marked animals and/or no known removals on some sampling events and because of sampling variability, not all of the possible capture histories will be observed in all studies. Because the number of possible capture histories increases exponentially, the number of unobserved capture histories increases with the number of sampling events (*K*).

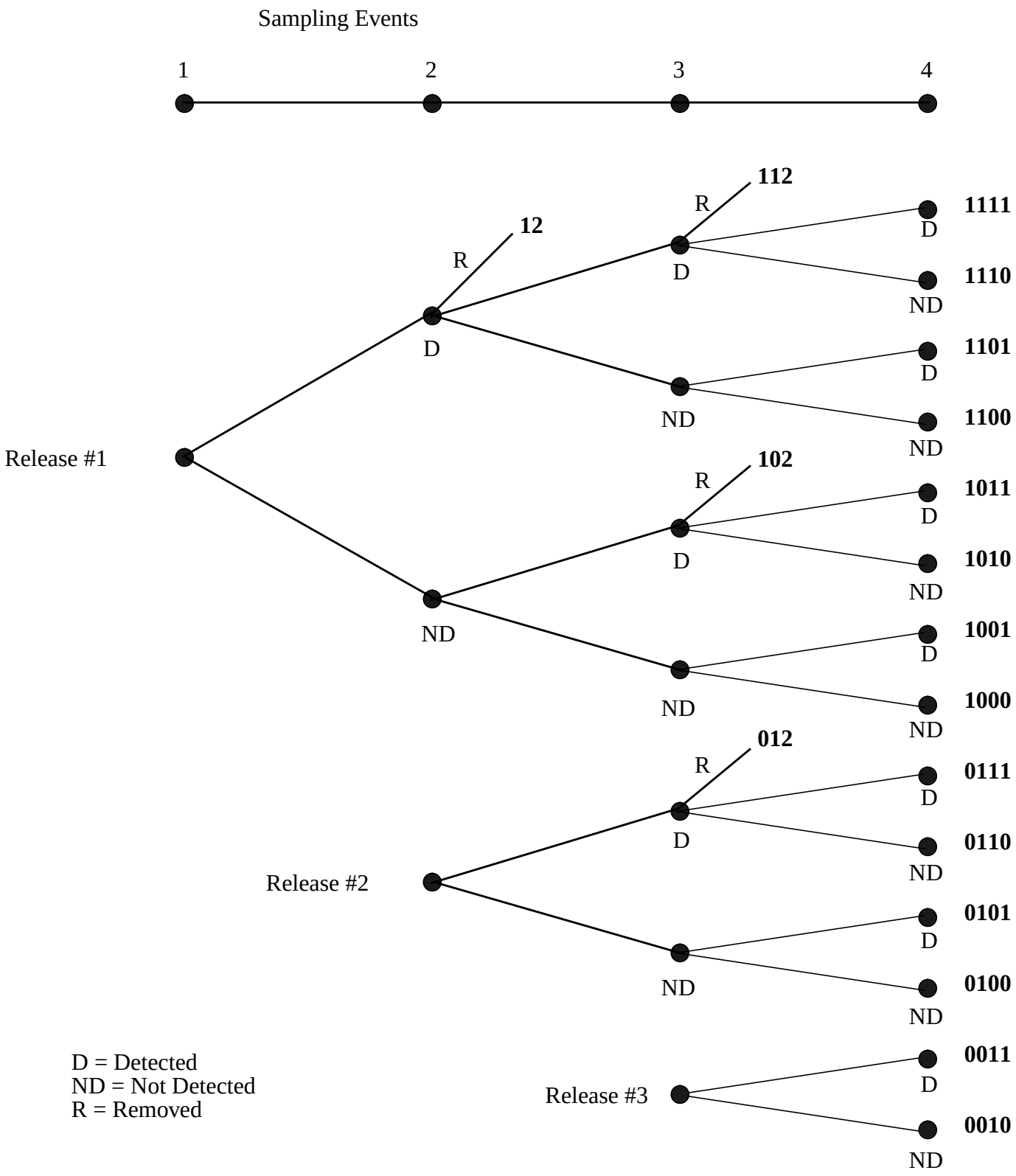


Figure 4.1 Recapture trees for a release-recapture study with *K* = 4 sampling events.

Table 4.1 Possible capture histories in a release-recapture study with *K* = 4 sampling events.

History	Explanation
1111	Tagged on event 1, detected on events 2, 3, and 4
1110	Tagged on event 1, detected on events 2 and 3, not detected on event 4
1101	Tagged on event 1, detected on events 2 and 4, not detected on event 3
1100	Tagged on event 1, detected on event 2, not detected on events 3 or 4
1011	Tagged on event 1, detected on events 3 and 4, not detected on event 2
1010	Tagged on event 1, detected on event 3, not detected on events 2 or 4
1001	Tagged on event 1, detected on event 4, not detected on events 2 or 3
1000	Tagged on event 1, not detected on events 2, 3, or 4
112	Tagged on event 1, detected on events 2 and 3, removed from population on event 3
12	Tagged on event 1, detected on event 2, removed from population on event 2
102	Tagged on event 1, not detected on event 2, detected on event 3, removed from population on event 3
0111	Tagged on event 2, detected on events 3 and 4
0110	Tagged on event 2, detected on event 3, not detected on event 4
0101	Tagged on event 2, not detected on event 3, detected on event 4
0100	Tagged on event 2, not detected on events 3 or 4
012	Tagged on event 2, detected on event 3, removed from population on event 3
0011	Tagged on event 3, detected on event 4
0010	Tagged on event 3, not detected on event 4

4.3 Capture - and Survival-Estimation Models for Release-Recapture Data

The statistical model used in SURPH for release-recapture data is a generalization of the likelihood model originally presented by Cormack (1964). First, a description of the Cormack (1964) model will be used to illustrate the basic concepts of survival estimation. Then, in later sections the SURPH models are described. Beginning with a survival-estimation model for a single population, subsequent sections present multiple-population models, and models incorporating group- and individual-based covariate effects on capture and survival probabilities.

4.3.1 Single population

4.3.1.1 Likelihood function

Assuming homogeneous survival and capture probabilities among animals, independent fates of tagged animals, and conditioning on the number of tagged animals in each release group (R_k), the counts of the capture histories in each release group constitute a multinomial sample. The multinomial cells are the capture histories; each animal falls into one and only one of the cells. The cell probabilities depend on the survival and capture probabilities. The probability that an animal alive at the time of sampling event k survives until the event k+1 is denoted S_k (k = 1,...,K-1), and the capture probability on event k is P_k (k = 2,...,K). If all animals have the same interval-specific survival and event-specific capture probabilities, regardless of when they were first marked, the survival histories in Table 4.1 have the probabilities of occurrence reported in Table 4.2. The subscripts for the number of animals with each history (n_j) are derived as the equivalent decimal value of the capture history interpreted as a binary number (e.g., 1101 base 2 = 13 base 10), so n_{13} is the number of animals with capture history 1101). Note that all capture histories between $j = 2$ and $j = 2^K - 1$ are observable for animals not removed from the population, while only a few capture histories, all with even-numbered j, are observable for known removals. Thus, when there are K -1 release groups (i.e., one release on each of the sampling events except the last), the overall likelihood is the product of K - 1 multinomial likelihoods:

$$L(\theta) \propto \prod_{i=1}^{K-1} \prod_{j=2^{K-i}}^{2^{K-i+1}-1} (\theta_j^{n_j} \times \theta'^{n'_j}_j) = \prod_{j=2}^{2^K-1} (\theta_j^{n_j} \times \theta'^{n'_j}_j)$$

Table 4.2 Capture histories, cell counts, and cell probabilities as functions of the survival and capture probabilities for K = 4 sampling events.

History	Probability	Count
1111	$\theta_{15} = S_1P_2S_2P_3S_3P_4$	n_{15}
1110	$\theta_{14} = S_1P_2S_2P_3(1-S_3(1-P_4))$	n_{14}
1101	$\theta_{13} = S_1P_2S_2(1-P_3)S_3P_4$	n_{13}
1100	$\theta_{12} = S_1P_2(1-S_2+S_2(1-P_3))(1-S_3)$ $+ S_2(1-P_3)S_3(1-P_4)$	n_{12}
1011	$\theta_{11} = S_1(1-P_2)S_2P_3S_3P_4$	n_{11}
1010	$\theta_{10} = S_1(1-P_2)S_2P_3(1-S_3+S_3(1-P_4))$	n_{10}
1001	$\theta_9 = S_1(1-P_2)S_2(1-P_3)S_3P_4$	n_9
1000	$\theta_8 = 1-S_1+S_1(1-P_2)(1-S_2)$ $+ S_1(1-P_2)S_2(1-P_3)(1-S_3)$ $+ S_1(1-P_2)S_2(1-P_3)S_3(1-P_4)$	n_8
112	$\theta'_{14} = S_1P_2S_2P_3$	n'_{14}
12	$\theta'_{12} = S_1P_2$	n'_{12}
102	$\theta'_{10} = S_1(1-P_2)S_2P_3$	n'_{10}
0111	$\theta_7 = S_2P_3S_3P_4$	n_7
0110	$\theta_6 = S_2P_3(1-S_3+S_3(1-P_4))$	n_6
0101	$\theta_5 = S_2(1-P_3)S_3P_4$	n_5
0100	$\theta_4 = 1-S_2+S_2(1-P_3)(1-S_3)$ $+ S_2(1-P_3)S_3(1-P_4)$	n_4
012	$\theta'_6 = S_2P_3$	n'_6
0011	$\theta_3 = S_3P_4$	n_3
0010	$\theta = 1-S_3+S_3(1-P_4)$	n_2

where θ_j and θ'_j are the probabilities of having capture history *j* for animals not removed and known removals, respectively. By convention, $\theta'^{n'_j}_j = 1$ are capture histories that are not observable for known removals.

In the probability expression for capture histories with no capture in the final interval (all even-numbered subscripts for animals not removed), there is a complex term reflecting the probability of never being detected after a particular interval. Let χ_k denote the probability of never being detected after the *k*th sampling event (*k* = 1, 2,..., *K*-1) (in Table 4.2, χ_3 occurs in θ_{14}, θ_{10}, θ_6 and θ_2; χ_2 occurs in θ_{12} and θ_4; and χ_1 occurs in θ_8). In general,

$$\chi_k = \sum_{j=k-1}^{K-1} \left\{ (1 - S_{j+1}) \prod_{l=k}^{j} (S_l(1 - P_{l+1})) \right\} , \tag{4.1}$$

with $S_K = 0$ and $\prod_{l=k}^{j} S_l(1 - P_{l+1}) = 1$ when $j < k$.

Because S_k, P_k, (1 - P_k) and χ_k occur in several θ_j and thus can be grouped together, the likelihood for a study with *K* = 4 sampling events can be rewritten as:

$$L(\underset{\sim}{S}, \underset{\sim}{P}) \propto \prod_{j=2}^{15} \theta_j^{n_j} = S_1^{n_{15}+n_{14}+n_{13}+n_{12}+n_{11}+n_{10}+n_9+n'_{14}+n'_{12}+n'_{10}} P_2^{n_{15}+n_{14}+n_{13}+n_{12}+n'_{14}+n'_{12}}$$

$$\times (1 - P_2)^{n_{11}+n_{10}+n_9+n'_{10}} \times \chi_1^{n_8} \times S_2^{n_{15}+n_{14}+n_{13}+n_{11}+n_{10}+n_9+n_7+n_6+n_5+n'_{14}+n'_{10}+n'_6}$$

$$\times P_3^{n_{15}+n_{14}+n_{11}+n_{10}+n_7+n_6+n'_{14}+n'_{10}+n'_6} \times (1 - P_3)^{n_{13}+n_9+n_5} \times \chi_2^{n_{12}+n_4}$$

$$\times S_3^{n_{15}+n_{13}+n_{11}+n_9+n_7+n_5+n_3} \times P_4^{n_{15}+n_{13}+n_{11}+n_9+n_7+n_5+n_3} \times \chi_3^{n_{14}+n_{10}+n_6+n_2}$$

This regrouping prompts the definition of several new variables to simplify and generalize the expression. Accordingly, let

a_k = the number of previously marked animals detected on event k ($a_1 = 0$),

c_k = the number of individuals detected for the last time on event k (not removed),

v_k = number of individuals marked on or prior to event k and known to be alive at event k+1;

$$v_k = \sum_{j=1}^{k} (b_j - c_j).$$

The likelihood for the K-event study can then be written as:

$$L(\underset{\sim}{S}, \underset{\sim}{P}) \propto \prod_{k=1}^{K-1} S_k^{v_k} P_{k+1}^{a_{k+1}} (1 - P_{k+1})^{v_k - a_{k+1}} \chi_k^{c_k} \tag{4.2}$$

where χ_k is defined as in Eq. (4.1).

Using release-recapture data, parameters S_{K-1} and P_K (parameters for the final interval) cannot be separately estimated. Unlike the previous intervals, it is impossible to separately estimate the proportion of those animals not detected on event K that died and the proportion that survived but were not detected. Only the product $S_{K-1}P_K = \lambda$ can be estimated. The likelihood can be written in terms of λ as:

$$L(\underset{\sim}{S}, \underset{\sim}{P}, \lambda) \propto \prod_{k=1}^{K-2} \left\{ S_k^{v_k} P_{k+1}^{a_{k+1}} (1 - P_{k+1})^{v_k - a_{k+1}} \right\} \lambda^{a_K} \prod_{i=1}^{K-1} \chi_i^{c_i} \tag{4.3}$$

The χ_i are written in terms of λ as follows:

$$\chi_k = \sum_{j=k-1}^{K-3} \left\{ (1 - S_{j+1}) \prod_{l=k}^{j} (S_l(1 - P_{l+1})) \right\} + (1 - \lambda) \prod_{j=k}^{K-2} (S_j(1 - P_{j+1})) \quad . \tag{4.4}$$

4.3.1.2 Parameter estimation

Analytical expressions for the maximum likelihood estimators (MLEs) of the S_k, P_k, and λ can be derived using the standard method of differentiating the log-likelihood with respect to each of the parameters and solving the resulting likelihood equations. The reader is referred to Cormack (1964) for the rather laborious details. The definition of two additional statistics is useful for expressing the estimates. Let

$r_k = a_k + b_k$ = the total number of animals detected on event k

and

$t_k = r_k - c_k$ = the total number detected on event k and on a later event.

The MLEs are as follows [from Cormack (1964)]:

$$\hat{S}_1 = \frac{t_1 r_2 - a_2 c_2}{b_1 t_2} \tag{4.5}$$

$$\hat{P}_2 = \frac{a_2}{b_1 \hat{S}_1} \tag{4.6}$$

and

$$\hat{S}_k = \frac{t_k v_k r_{k+1} - t_k a_{k+1} c_{k+1}}{r_k v_k t_{k+1}} \text{ for } k = 2, 3, \ldots, K - 2 \tag{4.7}$$

$$\hat{P}_k = \frac{a_k t_{k-1}}{r_{k-1} v_{k-1} \hat{S}_{k-1}} \text{ for } k = 3, 4, \ldots, K - 1 \tag{4.8}$$

$$\hat{\chi}_k = \frac{c_k}{r_k} \text{ for } k = 1, 2, ..., K - 1.$$

From $\chi_{K-1} = 1 - \hat{\lambda} = \frac{c_{K-1}}{r_{K-1}}$, we obtain

$$\hat{\lambda} = \frac{r_{K-1} - c_{K-1}}{r_{K-1}}. \tag{4.9}$$

Cormack (1964) gives variances and covariances for the survival probabilities. Program SURPH provides these Cormack (1964) estimates and variances as part of the initial summary statistics provided for each release-recapture data set. A unique aspect of Program SURPH is that release-recapture analyses are available when known removals of tagged animals occur at different recapture events. The Cormack (1964) parameter estimates (4.5 -4.9) and associated variances have been modified for known removals. As another part of the descriptive statistics for release-recapture studies, Program SURPH also provides *m*-arrays (Burnham et al. 1987, pp. 32-36; see Section 4.6.1.3) of the release-recapture data, modified for known removals of tagged animals at recapture events.

4.3.1.3 Special cases of basic model

Clobert et al. (1985) discuss some special cases of the Cormack (1964) survival estimation model for tag-recapture data that were proposed independently by Sandland and Kirkwood (1981) and Clobert (1981). Sandland-Kirkwood-Clobert models are essentially Cormack models with equality constraints among survival and/or capture probabilities. Clobert (1981) proposed models with various equality constraints, and Sandland and Kirkwood (1981) propose a model with a trap-dependence in the probability of capture. The most important models proposed are, in the nomenclature of Sandland and Kirkwood:

- Model (P, S) - Constant capture ($P_i = P$ for all i) and survival probabilities ($S_i = S$ for all i) for all intervals,

- Model (P_t, S) - Constant survival probability ($S_i = S$ for all i); capture probabilities depend on time,

- Model (P, S_t) - Constant capture probability ($P_i = P$ for all i); survival probabilities depend on time,

- Model (P_t, S_t) - Capture and survival probabilities depend on time.

Note that Model (P_t, S_t) is the Cormack model.

In all of the constrained models, numerical methods are required to maximize the likelihoods and obtain the MLEs of the constrained parameters. Clobert (1985) proposes likelihood ratio tests to choose an adequate and parsimonious model for any particular data set and includes several example analyses.

4.3.1.4 Assumptions

For the multinomial likelihood (4.3) to be valid, the following assumptions must be met:

A4.1) Individuals marked for the study are a representative sample from the population of interest.

A4.2) Survival and capture probabilities are not affected by tagging or sampling. That is, tagged animals have the same probabilities as untagged animals.

A4.3) All sampling events are "instantaneous." That is, sampling takes a negligible amount of time or distance relative to the length of the intervals between sampling events.

A4.4) The fate of each tagged individual is independent of the fate of all others.

A4.5) All tagged individuals alive at the beginning of a sampling interval have the same probability of surviving until the end of that interval.

A4.6) All tagged individuals alive at the time or location of a sampling event have the same probability of being detected on that event.

A4.7) Each individual detected on a particular sampling event has the same probability of

being removed on that event, and the probability of removal is independent of the survival process.

These assumptions are nearly identical to those for the known-fate, survival-estimation model. Refer to Section 3.3.1.3 for discussion of the assumptions. The release-recapture model requires additional assumptions regarding the detection process (A4.2 and A4.6).

4.3.2 Multiple populations

Replication of study sites and experimental conditions is required for effect assessment to be powerful and convincing. When multiple sites and populations are used, the sites must be spaced far enough apart that the animals do not mix, i.e., the populations are independent. For ease of inference, the release-recapture sampling at each site should occur simultaneously. That is, the sampling events should be coincident at all sites. For Columbia-Snake River smolt survival studies, replication occurs over time at the same series of river reaches. The use of the same river reaches over time is analogous to the simultaneous sampling necessary for spatially replicated investigations. Hence, when replication is over the landscape, the temporal dimension of the study must be held fixed for ease of inference. Alternatively, when replication is over time, the spatial dimension of the smolt outmigration studies must be held fixed for ease of interpretation.

Because the sampling is independent for all populations, a separate independent Cormack model (4.3) (or Sandland-Kirkwood-Clobert model) can be applied to the data from each of the populations. The overall likelihood function for the entire multiple-population study is then the product of the functions for the individual populations. If there is a total of I populations, and the Cormack (P_t, S_t) model is used on each, the overall likelihood is:

$$L \propto \prod_{i=1}^{I} \left(\prod_{k=1}^{K-2} \left(S_{ik}^{v_{ik}} P_{i,k+1}^{a_{i,k+1}} (1 - P_{i,k+1})^{v_{ik} - a_{i,k+1}} \right) \lambda_i^{a_{iK}} \prod_{k=1}^{K-1} \chi_{ik}^{c_{ik}} \right) \tag{4.10}$$

where

I = total number of replicate populations;

K = number of sampling events;

S_{ik} = probability that a marked animal in population i, known to be alive after the kth sampling event, survives until the (k + 1)th event (i = 1, 2,..., I; k = 1, 2,..., K – 2);

P_{ik} = probability that a previously marked animal in population i that is alive at the time of the kth sampling event is detected on that event (i = 1, 2,..., I; k = 2, 3,..., K - 1);

λ_i = probability that a previously marked animal in population i, known to be alive after the (K - 1)th sampling event, survives until the Kth event and is detected on the Kth event (i = 1, 2,..., I);

χ_{ik} = probability that a marked animal in population i is detected for the last time on event k (i = 1, 2,..., I; k = 1, 2,..., K - 1);

a_{ik} = number of previously marked animals detected on event k in population i (i = 1, 2,..., I; k = 2, 3,..., K);

v_{ik} = number of individuals marked on or prior to event k in population i, known to be alive at the time of event k + 1 (i = 1, 2,..., I; k = 1, 2,..., K - 1);

c_{ik} = number of individuals in population i, detected for the last time on event k (i = 1, 2,..., I; k = 1, 2,..., K – 1).

The maximum likelihood estimators for the survival and capture probabilities and the variances of the estimators have the same form as for the single population (4.5 - 4.9) where:

$$\hat{S}_{i1} = \frac{t_{i1} r_{i2} - a_{i2} c_{i2}}{b_{i1} t_{i2}} \text{ for i = 1, 2,..., I;} \tag{4.11}$$

$$\hat{P}_{i2} = \frac{a_{i2}}{b_{i1}\hat{S}_{i1}} \quad \text{for } i = 1, 2, \ldots, I; \tag{4.12}$$

$$\hat{S}_{ik} = \frac{t_{ik}v_{ik}r_{i,\,k+1} - t_{ik}a_{i,\,k+1}c_{i,\,k+1}}{r_{im}v_{ik}t_{i,\,k+1}} \quad \text{for } i = 1, 2, \ldots, I;\ k = 2, 3, \ldots, K - 2; \tag{4.13}$$

$$\hat{P}_{ik} = \frac{a_{ik}t_{i,\,k-1}}{r_{i,\,k-1}v_{i,\,k-1}\hat{S}_{i,\,k-1}} \quad \text{for } i = 1, 2, \ldots, I;\ k = 3, 4, \ldots, K - 1; \tag{4.14}$$

$$\hat{\chi}_{ik} = \frac{c_{ik}}{r_{ik}} \quad \text{for } i = 1, 2, \ldots, I;\ k = 1, 2, \ldots, K - 1.; \tag{4.15}$$

and where

$r_{ik} = a_{ik} + b_{ik}$ = the total number of animals in population i detected on event k,

$t_{ik} = r_{ik} - c_{ik}$ = the total number of animals in population i detected on event k and on a later event.

The Sandland-Kirkwood-Clobert models can be extended to multiple-population likelihood models by allowing equality constants, not only between intervals in a particular population, but also between populations in a particular interval or event. For example, for the capture probabilities, possible models are:

- Model P: A single constant capture probability for all events in all populations ($P_{ik} = P$ for all i and k).

- Model P_s: Capture probabilities depend on population but not on the sampling event ($P_{ik} = P_i$ for all k). This is equivalent to a single-population Model P (see Section 4.3.1.3) for each population.

- Model P_t: Capture probabilities depend on sampling event but not population ($P_{ik} = P_k$ for all i). This is equivalent to fitting a single-population Model P_t (see Section 4.3.1.3) with the data pooled across populations.

- Model P_{st}: A separate capture probability for each event for each population (P_{ik} unconstrained). This is equivalent to a single-population Model P_t for each population.

Analogous models for the survival probabilities (S, S_s, S_t, and S_{st}) are also possible, producing a total of 16 possible modeling combinations. For example, the model with an independent Cormack model for each population (4.10) is denoted P_{st}, S_{st}. These models are all available using SURPH methodology as special cases of the flexible modeling capabilities. In most cases, numerical methods are required to maximize the likelihoods of these extended Sandland-Kirkwood-Clobert models. However, analytical expressions are available for the MLEs of the P_{st}, S_{st} Model (4.11 - 4.15). In addition, because Model P_t, S_t ignores the differences in populations, pooling the data across all populations, the estimates can be obtained by applying (4.5 - 4.9) to the pooled statistics as if from a single population.

4.3.3 Alternative parameterization of estimation model

For later development of survival-effects models (Section 4.4), it is useful to introduce an alternative parameterization for the survival-estimation models. The estimation model of the previous section included a separate survival and capture probabilities for each interval for each population (S_{ik}, P_{ik}). Under the alternative parameterization (see Section 2.2.2), each probability is defined as a function of a baseline, or intercept parameter S, "main effects" for population (π_i) and interval (ρ_k), and an interaction between population and interval effects $(\pi\rho)_{ik}$:

$$S_{ik} = f(S, \pi_i, \rho_k, (\pi\rho)_{ik}) .$$

Constraints on the parameters are required to make all parameters identifiable. By convention, we use the following constraints: $\pi_1 = \rho_1 = (\pi\rho)_{1k} = (\pi\rho)_{i1} = 0$. Therefore, the survival probability in the first interval for the first population is S, and all other probabilities are expressed relative to S. For example, if the hazard link is used, the survival probability for population *i* in interval *k* is modeled as follows:

$$S_{ik} = S^{\exp(\pi_i + \rho_k + (\pi\rho)_{ik})} .$$

If the full set of main effects and interaction parameters are included, there is a one-to-one correspondence with parameters of the survival-estimation model previously presented (Eq. (4.10)); and the two parameterizations are mathematically equivalent, regardless of the link function. The alternative parameterization provides a convenient method to model equalities among survival probabilities. For example, to define a model with probabilities equal for all populations within each interval, but varying among intervals, all population main effects π_i and interaction effects $(\pi\rho)_{ik}$ are set equal to zero, leaving parameters for interval main effects only. Other SKC models can be defined similarly.

4.3.4 Individual-based survival-estimation model

Under the assumption that all animals have the same survival and capture probabilities in each interval, the summary counts $(\underset{\sim}{y}, \underset{\sim}{a}, \underset{\sim}{c})$ can be used to produce a simple form for the likelihood function (Eq. (4.10)). The simple formulation of the likelihood results from the fact that every animal with a particular capture history gives identical information regarding survival and capture probabilities. However, when the assumption of equal probabilities is relaxed (Section 4.4.2 below), the function must be written in terms of the capture histories of individual animals. The notation of the individual-covariate, survival-effects model is complex (see Eqs. (4.18) and (4.19) below). By rewriting the survival-estimation model on the basis of individual tagged animals, the transition to the individual-covariate model will be easier to understand.

Let t_{ikj} be the number of the event on which the *j*th tagged animal released on event *k* in population *i* was last seen alive. Let d_{ikj} be a variable that indicates whether or not the *j*th tagged animal released on event *k* in population *i* was removed (known removal) from the marked population on event t_{ikj}. By definition, d_{ikj} is equal to 0 if the animal was removed and equal to 1 if it was not known to be removed at any point in the study. Table 4.3 gives the values of t_{ikj} and d_{ikj} for the possible histories in a known-fate study with $K = 4$ sampling events. FInally, let I_{ikjm} be an indicator variable equal to 1, if the *j*th tagged animal released on event *k* in population *i* was detected on event *m*, and equal to 0, if it was not detected on event *m*.

The individual-based formulation of the multiple-population, survival-estimation model (Eq. (4.10)) is derived by treating the capture history for each individual as an independent multiple Bernoulli trial (i.e., a multinomial sample with sample size equal to 1). The likelihood function for each individual animal (trial) is:

$$L_{ikj}(\underset{\sim}{S}_i, \underset{\sim}{P}_i, \lambda_i) = Pr(\underset{\sim}{I}_{ikj}, d_{ikj}) = \prod_{m=k}^{t_{ikj}-1} S_{im} P_{i,m+1}^{I_{ikjm}} (1 - P_{i,m+1}^{1-I_{ikjm}}) \times \chi_{i,t_{ikj}}^{d_{ikj}} \ , \tag{4.16}$$

where χ_{iK} is defined to be equal to 1 and, as before, $S_{i,K-1}P_{iK}$ is replaced by λ_i wherever the product appears in (4.16). If the fate of each animal is independent of the fates of all others, the likelihood model is a product of the independent multiple Bernoulli likelihood functions:

$$L(\underset{\sim}{S}, \underset{\sim}{P}, \underset{\sim}{\lambda}) = \prod_{i=1}^{I} L_{ikj}(\underset{\sim}{S}_i, \underset{\sim}{P}_i, \lambda_i) \ . \tag{4.17}$$

4.4 Capture- and Survival-Effects Models for Release-Recapture Data

This section introduces models for release-recapture data that include explicit relationships between survival and capture probabilities, and environmental and individual-based covariates. Such relationships are the heart of the SURPH methodology.

Table 4.3 Variables used to summarize capture histories for individual-based models. Study consists of *K*=4 sampling events.

	History	Last Event Seen Alive (t_{ikj})	Remained in Popn. (d_{ikj})
R_{i1}	1111	4	1
	1110	3	1
	1101	4	1
	1100	2	1
	1011	4	1
	1010	3	1
	1001	4	1
	1000	1	1
	112	3	0
	12	2	0
	102	3	0
R_{i2}	0111	4	1
	0110	3	1
	0101	4	1
	0100	2	1
	012	3	0
R_{i3}	0011	4	1
	0010	3	1

4.4.1 Group covariate effects

4.4.1.1 Single population

With a single population, SURPH can be used to investigate relationships between time-variant group covariates and interval-specific survival probabilities. If $\underset{\sim}{w}_k$ is the set of covariate measurements that apply to the population in interval *k*, then the likelihood function for the group-covariate model is derived as an extension of equation (4.2) where the survival probabilities are rewritten as $S_k = f(S, \underset{\sim}{w}_k, \underset{\sim}{\tau})$, where S is the intercept parameter, $\underset{\sim}{\tau}$ is the vector of effect parameters, and the function *f* is the link between the linear predictor $\underset{\sim}{w}'_k\underset{\sim}{\tau}$ and the survival probability. For example, if the logit link is used, the survival probability for interval *k* is:

$$S_k = \frac{exp(\alpha + \underset{\sim}{w}'_k\underset{\sim}{\tau})}{1 + exp(\alpha + \underset{\sim}{w}'_k\underset{\sim}{\tau})} ,$$

where $\alpha = \log\left(\frac{S}{1-S}\right)$. When group covariates are included in the single-population model, interval effects (ρ_k) must be omitted so that the model is not overparameterized. The group covariate model is typically of lower rank than the survival-estimation model (4.2), but the rank of the minimal sufficient statistic does not change. Consequently, closed-form expressions cannot be written for the parameters, and numerical methods are required to obtain maximum likelihood estimates, and associated variances and covariances. Analysis of deviance is used to assess the statistical significance of group covariate effects on survival in a single-population study. This method is described in Section 4.5.1.

4.4.1.2 Multiple populations

With multiple populations, SURPH is used to study relationships between population- or site-specific group covariates and population-specific survival probabilities, on an interval-by-interval basis. The group covariates may be either time-variant or time-invariant. If $\underset{\sim}{w}_{ik}$ is the set of covariate measurements that apply to population *i* in interval *k*, then the likelihood function for the group-covariate model is an extension of Eq. (4.10), with survival probabilities S_{ik}

replaced by the function $S_{ik} = f(S, \rho_k, \underset{\sim}{w}_{ik}, \underset{\sim}{\tau}_k)$, where S is the intercept parameter, ρ_k is the effect parameter for interval k, $\underset{\sim}{\tau}_k$ is the vector of covariate-effect parameters for period k, and f is the link function between the linear predictor $(\rho_k + \underset{\sim}{w}'_{ik}\tau_k)$ and the survival probability. When group covariates are used in multiple-population models, parameters for population effects (π_i) and population/interval interactions $(\pi\rho)_{ik}$ must be omitted to avoid overparameterization of the model. As in the single-population case, numerical methods are required to obtain maximum likelihood estimates for parameters of the multiple-population, group-covariate model. The analysis of deviance methods used to assess the statistical significance of group covariate effects on survival in a multiple-population study are described in Section 4.5.2.

4.4.2 Individual covariate effects

Section 4.3.4 introduced a formulation of the basic survival- and capture-estimation model based on individual tagged animals. The likelihood function is the product of likelihood functions for each individual tagged animal, which are, in turn, constructed as multiple Bernoulli trial probabilities. In Section 4.3.4, we assumed that the Bernoulli probabilities were the same for all tagged animals in a given population (Eq. (4.16)). However, if survival or capture probabilities depend upon characteristics of the individual animals (i.e., individual covariates), then animals with different levels of a covariate have different Bernoulli probabilities. Let S_{ikjm} be the probability of surviving interval m, and P_{ikjm} be the probability of being detected on event m for the jth animal released on event k in population i. Continuing to assume that the fate of each individual is independent of that of all others, Eq. (4.16) can be rewritten with individual-specific probabilities as:

$$L_{ikj}(\underset{\sim}{S}_i, \underset{\sim}{P}_i, \lambda_i) = Pr(\underset{\sim}{I}_{ikj}, d_{ikj}) = \prod_{m=k}^{t_{ikj}-1} S_{ikjm} P_{ikj,m+1}^{I_{ikjm}} (1 - P_{ikj,m+1})^{1 - I_{ikjm}} \times \chi_{ikj,t_{ikj}}^{d_{ikj}} , \quad (4.18)$$

where χ_{ikjK} is defined to be equal to 1 and $S_{ikj,K-1}P_{ikjK}$ is replaced by λ_{ikj} wherever the product appears in (4.18).

As expressed, this model (4.18) with individual-specific S_{ikjm} and P_{ikjm} is overparameterized, making estimation impossible without simplification. To reduce the survival and capture parameters to an useful number, the individual probabilities are modeled as a function of individual traits and, possibly, group covariates as well. A survival- and capture-effects model is derived from Eq. (4.18), for example, by replacing the survival probabilities S_{ikjm} with the function:

$$S_{ikjm} = f(S, \pi_i, \rho_m, (\pi\rho)_{im}, \underset{\sim}{x}_{ikj}, \underset{\sim}{\beta}_{im}, \underset{\sim}{w}_{im}, \underset{\sim}{\tau}_m) , \tag{4.19}$$

where S = baseline intercept parameter;

π_i = effect parameter for population i;

ρ_m = effect parameter for interval m;

$(\pi\rho)_{im}$ = parameter for interaction of effects of population i and interval m;

$\underset{\sim}{x}_{ikj}$ = vector of individual covariate measurements for the jth individual tagged on event k in population i;

$\underset{\sim}{\beta}_{im}$ = vector of regression parameters describing the relationship between the individual-based covariates and survival probability in the mth interval for the ith population;

$\underset{\sim}{w}_{im}$ = vector of group covariates that apply to population i in interval m; and

$\underset{\sim}{\tau}_m$ = vector of regression parameters describing the relationship between the population-specific group covariates and survival probability in interval m.

If group covariates are not included in the model, the full suite of population and interval effects and their interactions can be included. For example, if the hazard link is used, the survival probabilities are written as:

$$S_{ikjm} = S^{exp(\pi_i + \rho_m + (\pi\rho)_{im} + \underset{\sim}{x}'_{ikj}\beta_{im})} .$$

If group covariates are included, population effects (π_i) and population/interval interactions $(\pi\rho)_{ik}$ must be omitted to avoid overparameterization. For example, under the logit link:

$$S_{ikjm} = \frac{exp(\alpha + \rho_m + \underset{\sim}{w}'_{im}\tau_m + \underset{\sim}{x}'_{ikj}\beta_{im})}{1 + exp(\alpha + \rho_m + \underset{\sim}{w}'_{im}\tau_m + \underset{\sim}{x}'_{ikj}\beta_{im})} .$$

Capture-effects models are constructed in a completely analogous manner. Numerical methods are required to obtain maximum likelihood estimates. Likelihood ratio statistics (Section 2.4.1) are used to test the statistical significance of the effects of individual covariates on survival (Skalski et al. 1993).

4.4.3 SURPH modeling of capture probabilities

It is important to choose an appropriate parsimonious model of the capture process before modeling the survival process because the estimates of capture and survival parameters are not independent in release-recapture models. Using an inappropriate model for the capture probabilities can lead to incorrect conclusions regarding survival. For example, suppose a model with a separate capture probability for each population on each event is used when, in fact, a constant capture probability model would suffice. Although the capture model is overparameterized, the survival parameters remain unbiased. However, estimating more capture parameters than necessary can lead to imprecision in the survival estimates, decreasing the power to detect effects on survival. On the other hand, using a model that is too restrictive on the capture probabilities can lead to bias in the survival estimates, making survival effects difficult to distinguish. It is the philosophy of SURPH analysis to describe as much of the variability in the data due to capture probabilities as necessary and possible before turning to the modeling of the survival process.

It is possible to model the capture probabilities with the same detail as survival probabilities are modeled in SURPH. An investigator has a choice of link functions for the capture process independent of the selection of the function for survival probabilities. After a model for the capture process is selected, the choice can be “locked in” before proceeding to the modeling of the survival process. The capture process can be modeled as a function of indicator

variables for design factors such as interval and location effects, as well as covariates at the group- and individual-level.

Program SURPH provides investigators with two alternative approaches for assessing effects and modeling the capture process. One approach is based on a subset of the capture data, providing a means to assess effects on the capture process independent of the survival process. This approach is based on the techniques used by Manly and Parr (1968) to estimate capture probabilities in their open-population abundance model. The second approach uses the complete capture data and likelihood ratio tests to select a model for the capture process. In the second approach, the capture process is investigated using a saturated model to describe the survival process. In other words, while modeling the capture process, the survival probabilities are assumed to be unique for each sampling interval in each population. The two approaches to modeling the capture process are described in detail below.

4.4.3.1 Modeling capture process using Manly-Parr estimates

A method of modeling the capture probabilities that is independent of the survival model is suggested by the Manly-Parr abundance estimation model (Manly and Parr, 1968). When estimating abundance, survival, and birth rates with release-recapture data, it is necessary also to estimate capture probabilities. The Manly-Parr (1968) model estimates P_k, the capture probability for the *k*th sampling event in a single population survey using the following data:

g_k = the number of animals marked before sampling event *k* that were detected both on event *k* and on at least one later event,

h_k = the number of animals marked before sampling event *k* that were not detected on event *k*, but were detected on at least one later event.

The total of these two variable, $g_k + h_k$, gives the number of marked animals that are known to have been alive at the time of sampling event *k*, and g_k gives the number of these that were actually detected on that event. Thus, an estimate of the capture probability is

$$\hat{P}_k = \frac{g_k}{g_k + h_k} \tag{4.20}$$

With multiple populations, a second subscript is added. That is, $\hat{P}_{ik} = \dfrac{g_{ik}}{g_{ik} + h_{ik}}$ for the *k*th sampling event and *i*th population (i = 1, 2,..., I; k = 2, 3,..., K - 1). Program SURPH allows the user to display Manly-Parr estimates of the capture probabilities, adjusted for known removals (see Section 4.6.1.1 for details of the adjustment algorithm).

Consider a general study with I populations and K sampling events. An I x (K - 2) x 2 contingency table can be built from the g_{ik} and h_{ik} as shown in Figure 4.2. The method of fitting log-linear models to contingency tables (Bishop et al. 1975) can be used to choose among basic models for the capture probabilities. In general, the log-likelihood for any log-linear model of the I x (K - 2) x 2 table can be written as:

$$lnL \propto \sum_{i=1}^{I} \sum_{k=2}^{K-1} (g_{ik} ln(\hat{P}_{ik}) + h_{ik} ln(1 - \hat{P}_{ik})) \tag{4.21}$$

For example, expressions for $\hat{P}_{ik}$ under four candidate models are as follows:

$$P_{st}: \ \hat{P}_{ik} = \frac{g_{ik}}{g_{ik} + h_{ik}}$$

$$P_s: \ \hat{P}_{ik} = \frac{g_{i\bullet}}{g_{i\bullet} + h_{i\bullet}}$$

$$P_t: \ \hat{P}_{ik} = \frac{g_{\bullet k}}{g_{\bullet k} + h_{\bullet k}}$$

$$P: \ \hat{P}_{ik} = \frac{g_{\bullet\bullet}}{g_{\bullet\bullet} + h_{\bullet\bullet}}$$

Population 1

Event	g	h	Total
2	g_{12}	h_{12}	$g_{12}+h_{12}$
3	g_{13}	h_{13}	$g_{13}+h_{13}$
⋮	⋮	⋮	⋮
K-1	$g_{1,K-1}$	$h_{1,K-1}$	$g_{1,K-1}+h_{1,K-1}$
Total	$g_{1\bullet}$	$h_{1\bullet}$	$g_{1\bullet}+h_{1\bullet}$

Population 2

g	h	Total
g_{22}	h_{22}	$g_{22}+h_{22}$
g_{23}	h_{23}	$g_{23}+h_{23}$
⋮	⋮	⋮
$g_{2,K-1}$	$h_{2,K-1}$	$g_{2,K-1}+h_{2,K-1}$
$g_{2\bullet}$	$h_{2\bullet}$	$g_{2\bullet}+h_{2\bullet}$

Population 3

Event	g	h	Total
2	g_{32}	h_{32}	$g_{32}+h_{32}$
3	g_{33}	h_{33}	$g_{33}+h_{33}$
⋮	⋮	⋮	⋮
K-1	$g_{3,K-1}$	$h_{3,K-1}$	$g_{3,K-1}+h_{3,K-1}$
Total	$g_{3\bullet}$	$h_{3\bullet}$	$g_{3\bullet}+h_{3\bullet}$

• • •

Population I

g	h	Total
g_{I2}	h_{I2}	$g_{I2}+h_{I2}$
g_{I3}	h_{I3}	$g_{I3}+h_{I3}$
⋮	⋮	⋮
$g_{I,K-1}$	$h_{I,K-1}$	$g_{I,K-1}+h_{I,K-1}$
$g_{I\bullet}$	$h_{I\bullet}$	$g_{I\bullet}+h_{I\bullet}$

Total

g	h	Total
$g_{\bullet 2}$	$h_{\bullet 2}$	$g_{\bullet 2}+h_{\bullet 2}$
$g_{\bullet 3}$	$h_{\bullet 3}$	$g_{\bullet 3}+h_{\bullet 3}$
⋮	⋮	⋮
$g_{\bullet,K-1}$	$h_{\bullet,K-1}$	$g_{\bullet,K-1}+h_{\bullet,K-1}$
$g_{\bullet\bullet}$	$h_{\bullet\bullet}$	$g_{\bullet\bullet}+h_{\bullet\bullet}$

Figure 4.2 Contingency table for modeling capture probabilities using Manly-Parr (1968) estimates.

where the "•" notation denotes summation over the indicated subscript. For more complicated dependencies among the cell probabilities it is not possible to write analytical expressions for $\hat{P}_{ik}$ and iterative methods are used.

The Manly-Parr (1968) approach to modeling the capture process can be further generalized to include individual-covariate effects. Each of the $(g_{ik} + h_{ik})$ animals known to be alive at the time or location of sampling event k can be viewed as an independent Bernoulli trial with result 0 if the animal was not detected and 1 if the animal was detected. The success (detection) probability for each of these Bernoulli trials can be written as a function of design factors and group- and individual-covariate effects:

$$P_{ikj} = f(P, \nu_i, \eta_k, (\nu\eta)_{ik}, \underset{\sim}{x}_{ij}, \underset{\sim}{\delta}_{ik}, \underset{\sim}{w}_{ik}, \underset{\sim}{\gamma}_k) , \tag{4.22}$$

where P_{ikj} = detection probability for jth animal known to be alive on sampling event k in population i;

P = baseline intercept parameter;

ν_i = effect parameter for population i;

η_k = effect parameter for event k;

$(\nu\eta)_{ik}$ = parameter for interaction of effects of population i and event k;

$\underset{\sim}{x}_{ij}$ = vector of individual covariate measurements for the jth individual known to be alive on event k in population i;

$\underset{\sim}{\delta}_{ik}$ = vector of regression parameters describing the relationship between the individual-based covariates and capture probability on the kth event for the ith population;

$\underset{\sim}{w}_{ik}$ = vector of group covariates that apply to population i on event k;

$\underset{\sim}{\gamma}_k$ = vector of regression parameters describing the relationship between the population-specific group covariates and capture probability in event k; and

$f(\bullet)$ = the link function for capture probabilities.

Assuming that each Bernoulli trial is independent, the overall likelihood function can be written as follows:

$$L \propto \prod_{i=1}^{I} \prod_{k=2}^{K-1} \prod_{j=1}^{g_{ik}+h_{ik}} P_{ikj}^{I_{ikj}} (1 - P_{ikj})^{1 - I_{ikj}} \quad , \tag{4.23}$$

where I_{ikj} is an variable that indicates whether the *j*th animal known to be alive on event *k* in population *i* was detected on event *k*.

The possible capture probability models investigated by SURPH are not necessarily nested. In the case where the models are not nested, LRT's cannot be used and another statistical criterion must be used. Instead, Akaike's Information Criterion (AIC) (Sakamoto et al. 1986) defined as:

$$AIC = -2 lnL + 2p \tag{4.24}$$

where *p* is the number of parameters in the log-linear model, is a reasonable criterion for choosing the appropriate model. The model with minimum AIC is selected as the appropriate model. Program SURPH automatically checks to see if two capture models are nested, in which case LRT is performed. Alternatively, AIC is provided for each capture model investigated, and can be used to identify the most appropriate model for the capture process. After a parsimonious capture model has been selected, the capture model is held constant (i.e., locked) while the survival process is then investigated.

4.4.3.2 Modeling capture process jointly with saturated survival model

The alternative to selecting a capture model using the Manly-Parr (1968) subset of the data, is to model the capture probabilities jointly with survival probabilities, using a fully saturated model for survival with interval-by-population specific survival probabilities (i.e., the S_{st} model). Computer simulation studies have shown that an unbiased selection of a capture model is possible using the joint survival-capture model (4.18) when the survival process is first

fully saturated with unique $\hat{S}_{ik}$'s. Program SURPH permits testing of candidate capture probability models under a saturated survival process using LRT if models are nested and AIC regardless of model hierarchies.

The likelihood function for modeling capture probabilities jointly with a saturated survival model is derived from equations (4.16), (4.17), and (4.18) based on the following expression:

$$L_{ikj}(\underset{\sim}{S}_i, \underset{\sim}{P}_i, \lambda_i) = Pr(\underset{\sim}{I}_{ikj}, d_{ikj}) = \prod_{m=k}^{t_{ikj}-1} S_{ik} P_{ikj,m+1}^{I_{ikjm}} (1 - P_{ikj,m+1})^{1 - I_{ikjm}} \bullet \chi_{ikj,t_{ikj}}^{d_{ikj}} \tag{4.25}$$

where P_{ikjm} = detection probability on sampling event *m* for *j*th animal tagged on sampling event *k* in population *i*.

To model effects on capture probabilities, P_{ikjm} is replaced with the expression:

$$P_{ikjm} = f(P, \nu_i, \eta_k, (\nu\eta)_{ik}, \underset{\sim}{x}_{ij}, \underset{\sim}{\delta}_{ik}, \underset{\sim}{w}_{ik}, \underset{\sim}{\gamma}_k), \tag{4.26}$$

P = baseline intercept parameter;

ν_i = effect parameter for population *i*;

η_k = effect parameter for event *k*;

$(\nu\eta)_{ik}$ = parameter for interaction of effects of population *i* and event *k*;

$\underset{\sim}{x}_{ikj}$ = vector of individual covariate measurements for the *j*th individual tagged on event *k* in population *i*;

$\underset{\sim}{\delta}_{im}$ = vector of regression parameters describing the relationship between the individual-based covariates and capture probability on the *m*th event for the *i*th population;

$\underset{\sim}{w}_{im}$ = vector of group covariates that apply to population *i* on event *m*;

$\underset{\sim}{\gamma}_m$ = vector of regression parameters describing the relationship between the population-specific group covariates and capture probability in event *m*; and

$f(\bullet)$ = the link function for capture probabilities.

When release-recapture studies are based on a single-release protocols (i.e., no staggered entry) and there are no known removals, the Manly-Parr estimates of capture probabilities are also the MLEs for Model Pst,Sst. In this situation the two approaches to model selection for capture probabilities are asymptotically equivalent. For smaller release sizes under the single-release protocol, model selection based on the Manly-Parr data is slightly more powerful than joint with a saturated survival model. For the staggered-release protocol the approach based on joint survival/capture modeling is more powerful. The only exception to this rule of thumb is when both the capture and survival processes are functions of quantitative group- and individual-based covariates. In this case, the Manly-Parr approach of Section 4.4.3.1 is preferred.

We generally recommend the capture model be based on the Logistic link-function. However, Program SURPH permits the use of the Hazard link if desired.

4.4.4 Modeling effects on final-interval product term

In the last sampling interval in release-recapture studies, it is typically impossible to differentiate the fates of death and escapement for individuals not detected. As such, the parameter

$$\lambda = S_{k-1} p_k$$

describes the joint probability of surviving the time interval and being detected in the last sampling interval. The complement, $1 - \lambda$, is therefore the probability of not surviving or surviving and not being re-detected:

$$1 - \lambda = 1 - S_{k-1} p_k = (1 - S_k) + S_{k-1}(1 - p_k)$$

Typically this complex term would be simply modeled as a function of the design factor of population membership. Program SURPH easily accommodates the section between a constant λ and a population specific λ_i.

The Columbia-Snake River smolt survival studies prompt a much more flexible modeling of the last interval joint survival-capture parameter (λ). The future installation of both smolt

and adult PIT-tag facilities at Bonneville Dam holds the possibility of estimating ocean survival rates of salmon if the adult facilities provide 100% detection rate. With the proposed 100% detection rate at adult ladders, the last term λ represents an overall ocean survival rate (i.e., natural survival x harvest escapement).

Program SURPH therefore provides the capability of modeling λ as a function of design factors (i.e., population), group covariates (e.g., mean ocean temperature, harvest effort) and individual-based covariates (e.g., smolt condition factor at time of release). Modeling of the λ's is recommended after both P-modeling and S-modeling is completed. Selection of λ -models can be based on either LRT and AIC.

4.4.5 Assumptions

The assumptions for models of release-recapture data that include covariate effects on survival, detection or final-period product terms (i.e., effects models) are the same as for estimation models (Section 4.3.1.4) with the adjustments described in this section.

If the focus of the study is the effect of environmental or individual-based variables on survival, and not on the baseline survival per se, then assumption (A4.2) may be replaced by a weaker version:

A4.2b) The probabilities of survival and detection are affected by tagging and resampling identically for every animal.

Assumption (A4.2b) implies that there is no interaction between the effects of handling and the effects of the factors in question. It is assumed that the survivability of each animal is affected by handling in the same way, whatever other environmental influences it is subject to. If this assumption is made in a survival-estimation model, the actual survival estimates cannot be extrapolated to untagged animals, but the *differences* between survival in populations subject to different covariate levels are assumed to be unaffected. The differences in survival between

populations are represented in survival-effects models by effect parameters. Thus, the effect parameters can be extrapolated to other, non-handled populations, but the intercept parameter for survival (S) cannot.

By definition, assumptions (A4.5) and (A4.6) cannot apply when individual covariates are included in the model. Instead, for survival-and capture-effects models, (A4.5) is replaced by the following assumptions:

A4.8) The covariates for each population and each individual tagged animal are accurately measured.

A4.9) The relationship between covariates and survival probabilities is correctly modeled by the selected link function.

A4.10) The relationship between covariates and capture probabilities is correctly modeled by the selected link function.

A4.11) The relationship between covariates and the final-interval product term is correctly modeled by the selected link function.

4.5 Testing Significance of Covariate Effects on Survival

Analysis of deviance (Section 2.4.3) is used to assess effects of group covariates on survival probabilities. Using release-recapture, an appropriate model of the capture probabilities must be selected (see Section 4.4.3) before the analysis of deviance is performed for the effects on survival. Then, to construct the ANODEV table, a series of hierarchical models is computed for the survival probabilities, from a maximally parameterized “full” model down to a minimal, or “null” model. Each model in the hierarchy shares the same structure for the capture probabilities so that only the survival modeling differs among models. Sections 4.5.1 and 4.5.2 specify how ANODEV is applied to release-recapture data for single- and multiple-population

studies, respectively. Finally, Section 4.5.3 briefly discusses how effects of individual covariates are tested using likelihood ratio statistics.

4.5.1 Analysis of deviance for group covariates in single-population study

The parameters of the "full" model for a single-population release-recapture study are distinct survival probabilities for each sampling interval (i.e., the S_t Model for survival probabilities) plus whatever parameters were selected to describe the capture process in the first step (Section 4.4.3). Thus the full model contains a total of K-2 parameters for survival, one for each sampling interval except the last. The maximized likelihood for the full model is denoted $L(\hat{\underset{\sim}{\theta}}_F)$. The "null" model has just one parameter for survival, a single survival probability common to all sampling intervals ($S_k \equiv S_0$). The maximized likelihood for the null model is denoted $L(\hat{\underset{\sim}{\theta}}_0)$.

A single population cannot be used to evaluate the effects of a time-invariant group covariate. Multiple populations are required for time-invariant factors, so that varying levels of the covariate may be observed. However, single population studies can be used to study the relationship of interval-specific survival probabilities with time-variant (i.e., interval-specific) group covariates. Single-population studies are observational by definition (no replication), though interval-specific conditions may be purposefully manipulated by researchers.

Suppose there is a total of J time-variant group covariates in a single-population release-recapture study. Table 4.4 lists the hierarchical models required to construct the ANODEV table. The table itself is shown in Table 4.5. Strictly speaking, the entries in the "Deviance" column for "Total" and "Mean" are not deviances. The construction of the ANODEV table requires their inclusion as defined in Table 4.5 to complete the parallel with the ANOVA table, which includes Total and Mean sums of squares. The "Corrected Total Deviance" is another name for the total discrepancy between the null and full models. The "Error Deviance" is the amount of the Corrected Total not "explained" by the covariates. There must be at least one degree of freedom

for Error Deviance, thus the maximum number of covariates that can be analyzed at one time is $K-4$ $(1 \le J \le K-4)$. The "Mean Deviance" for each source is the deviance divided by the associated number of degrees of freedom.

Unless covariates are uncorrelated, the deviance attributed to each covariate will depend on which other covariates are in the model. That is, the deviances for covariate effects are *nonorthogonal*. This nonorthogonality parallels linear regression analysis, where regression coefficients and reductions in sums of squares in depend on other covariates in the model. When effects are nonorthogonal, a stepwise procedure can be used to choose the appropriate SURPH model. At the first step, the covariate that gives the largest (significant) difference in deviance from the null model is added to the model. Then, the next covariate that gives the largest difference from the model that contains the first covariate is added, and so on.

ANODEV is used to test the significance of the covariate effects, based on the amount of the Corrected Total explained by the covariates, as measured by the F-statistic:

$$F_{\nu,\, K-J-3} = \frac{\text{MD(Effect)}}{\text{MD(Err)}} \tag{4.27}$$

where ν is the number of covariate effects being tested, MD(Effect) is the mean deviance for the ν covariates, and MD(Error) is the mean deviance for error. When there is truly no effect of the covariates (null hypothesis is true), the F-statistic has an asymptotic F-distribution with ν and $K-J-3$ numerator and denominator degrees of freedom, respectively (Smith, 1991).

An alternative to the F-statistic is the R^2 statistic, given by:

$$R^2 = \frac{\text{Dev(Effect)}}{\text{Dev(Cor)}}, \tag{4.28}$$

which measures the amount of the Corrected Total deviance explained by the covariate(s) of interest. Under the null hypothesis of no effects, R^2 is asymptotically distributed as a Beta random variable with parameters $\frac{\nu}{2}$ and $\frac{K-\nu-3}{2}$. When testing all covariates simultaneously,

Table 4.4 Hierarchical likelihood models required to construct ANODEV table for single-population release-recapture study.

Model Name	Number of parameters for survival[1]	Maximized likelihood	Linear predictor[2]
Full	K-2	$L(\hat{\underset{\sim}{\theta}}_F)$	–
Total Covariate	J + 1	$L(\hat{\underset{\sim}{\theta}}_M)$	$\underset{\sim}{w}'_k \underset{\sim}{\tau}$
Covariate 1	2	$L(\hat{\underset{\sim}{\theta}}_{M_1})$	$w_{k1}\tau_1$
Covariates 1 & 2	3	$L(\hat{\underset{\sim}{\theta}}_{M_{12}})$	$w_{k1}\tau_1 + w_{k2}\tau_2$
...	...	...	...
Covariates 1,2,...,J-1	J	$L(\hat{\underset{\sim}{\theta}}_{M_{12...J-1}})$	$w_{k1}\tau_1 + ... + w_{k,J-1}\tau_{J-1}$
Null	1	$L(\hat{\underset{\sim}{\theta}}_0)$	–

1. For models with covariates, the number of parameters is equal to the number of covariates in the model plus 1 for the intercept parameter.

2. w_{kj} is the value of the *j*th covariate in the *k*th interval; τ_j is the effect parameter for the *j*th covariate.

Table 4.5 Generic ANODEV table for single-population release-recapture study.

Source	df	Deviance	Mean Deviance	F	R^2
Total	K-2	$-2lnL(\hat{\underset{\sim}{\theta}}_0)$			
Mean	1	$-2lnL(\hat{\underset{\sim}{\theta}}_F)$			
Corrected Total	K-3	$-2\{lnL(\hat{\underset{\sim}{\theta}}_0) - lnL(\hat{\underset{\sim}{\theta}}_F)\}$			
Covariate Total	J	$-2\{lnL(\hat{\underset{\sim}{\theta}}_0) - lnL(\hat{\underset{\sim}{\theta}}_M)\}$	$\frac{\text{Dev(Cov)}}{J}$	$F_{J,\,K-J-3} = \frac{\text{MD(Cov)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov)}}{\text{Dev(Cor)}}$
Covariate 1	1	$-2\{lnL(\hat{\underset{\sim}{\theta}}_0) - lnL(\hat{\underset{\sim}{\theta}}_{M_1})\}$	$\frac{\text{Dev(Cov}_1\text{)}}{1}$	$F_{1,\,K-J-3} = \frac{\text{MD(Cov}_1\text{)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov}_1\text{)}}{\text{Dev(Cor)}}$
Covariate 2 | Cov. 1	1	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{M_1}) - lnL(\hat{\underset{\sim}{\theta}}_{M_{12}})\}$	...	...	...
...	...	...	...	...	...
Covariate J | Cov. 1,2,..., J-1	1	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{M_{12...,J-1}}) - lnL(\hat{\underset{\sim}{\theta}}_M)\}$	$\frac{\text{Dev(Cov}_J\text{)}}{1}$	$F_{1,\,K-J-3} = \frac{\text{MD(Cov}_J\text{)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov}_J\text{)}}{\text{Dev(Cor)}}$
Error	K-J-3	$-2\{lnL(\hat{\underset{\sim}{\theta}}_M) - lnL(\hat{\underset{\sim}{\theta}}_F)\}$	$\frac{\text{Dev(Err)}}{(K-J-3)}$		

the F- and R^2-statistics are equivalent because they are based on the same two independent variables (i.e., Dev(Cov) and Dev(Err), because Dev(Cor) = Dev(Cov) + Dev(Err)).

4.5.2 Analysis of deviance for group covariates in multiple-population study

The parameters of the "full" model for a multiple-population release-recapture study are distinct survival probabilities for each sampling interval for each population (i.e., the S_{st} Model for survival probabilities) plus whatever parameters were selected to describe the capture process in the first step (Section 4.4.3). Thus the full model contains a total of K-2 parameters for survival for each population (one probability for each sampling intervals except the last) for a total of $I(K-2)$ parameters. The maximized likelihood for the full model is denoted $L(\hat{\underset{\sim}{\theta}}_F)$.

Using multiple populations, ANODEV is used to study relationships between population- or site-specific group covariates and population-specific survival probabilities, on an interval-by-interval basis. SURPH maintains the interval-based orientation by defining the null model with interval-specific survival probabilities that are common to all I populations. Effectively, all populations are pooled, and a single survival-estimation model with survival probabilities $S_1, S_2, \ldots, S_{K-2}$ is applied to the pooled data (i.e., $S_{ik} \equiv S_k$), for a total of K-2 survival parameters in the null model. This model is also called the "Interval Means" model, and the maximized likelihood is denoted $L(\hat{\underset{\sim}{\theta}}_{IM})$.

Suppose there is a total of J group covariates that vary across the multiple populations within each interval. The covariates may be time-variant or time-invariant, and may be quantitative measurements or indicator variables for blocks or treatment levels. The model that includes an effect parameter for each of the J covariates in each of the intervals is known as the "Total Covariate" model. The Total Covariate model has K-2 parameters for interval mean or baseline survival probabilities and J(K-2) for covariate effects.

To complete a hierarchy of models and compute the ANODEV table, models can be fitted to the data that include covariate effects in some intervals but not in others, or that include subsets of the covariate effects within particular intervals. Table 4.6 lists a typical hierarchy of

models and Table 4.7 gives the ANODEV table computed from the hierarchy. Strictly speaking, the entries in the “Deviance” column for “Total” and “Mean” are not deviances. The construction of the ANODEV table requires their inclusion as defined in Table 4.7 to complete the parallel with the ANOVA table, which includes Total and Mean sums of squares. The “Corrected Total Deviance” is another name for the total discrepancy between the null and full models. The “Error Deviance” is the amount of the Corrected Total not “explained” by the covariates. There must be at least one degree of freedom for Error Deviance, thus the maximum number of group covariates that can be analyzed at one time in a multiple-population study is $I - 2$ $(1 \leq J \leq I - 2)$. The “Mean Deviance” for each source is the deviance divided by the associated number of degrees of freedom.

The typical ANODEV for multiple populations first partitions the total deviance for covariates into contributions for each interval (Table 4.7). With release-recapture data, the contributions of covariates in separate intervals are *nonorthogonal*. That is, the reduction in deviance obtained by adding all the covariate effects for a particular interval depends on the effects that are already in the model for other intervals. The reductions in deviance attributed to specific covariates within the same interval are also nonorthogonal.

We recommend a two-phase stepwise procedure for adding covariates to the ANODEV table to build group covariate models for multiple populations. In the first phase, the total covariate deviance is partitioned into contributions for each interval (i.e., all J covariates in each interval). For example, in the first step of this phase, K-2 models are investigated, each including K-2 parameters for interval mean, or baseline effects, and J parameters for covariate effects for interval k $(k = 1, ..., K - 2)$. The block of interval effects to enter the table first is determined by the model that has the greatest maximized likelihood among the K-2 candidates. Then, the next block of covariates that gives the largest difference from the model that contains the first block is added, and so on. The total covariate deviances for each interval are partitioned into contributions of each covariate in the second phase of the stepwise approach. This phase proceeds analogously to phase 1, and to the approach described in Section 4.5.1.

Hypothesis tests for covariate effects are based on the F-statistic:

Table 4.6 Hierarchical likelihood models used to construct ANODEV table for multiple-population release-recapture study.

Model Name[1]	Number of parameters for survival[2]	Maximized likelihood
Full	I(K-2)	$L(\hat{\underset{\sim}{\theta}}_F)$
Total Covariate	K-2 + J(K-2)	$L(\hat{\underset{\sim}{\theta}}_M)$
All Covariates, Interval 1	K-2 + J	$L(\hat{\underset{\sim}{\theta}}_{M_1})$
Covariate 1, Interval 1	K-2 + 1	$L(\hat{\underset{\sim}{\theta}}_{M_{1/1}})$
Covariates 1 & 2, Interval 1	K-2 + 2	$L(\hat{\underset{\sim}{\theta}}_{M_{1/12}})$
...	...	...
Covariates 1,2,..., J-1 Interval 1	K-2 + J-1	$L(\hat{\underset{\sim}{\theta}}_{M_{1/12...J-1}})$
Covariates, Intervals 1 & 2	K-2 + 2J	$L(\hat{\underset{\sim}{\theta}}_{M_{12}})$
...	...	...
All Covariates, Intervals 1,2,..., K-3	K-2 + J(K-3)	$L(\hat{\underset{\sim}{\theta}}_{M_{12...K-3}})$
Null	K-2	$L(\hat{\underset{\sim}{\theta}}_{IM})$

1. All models share the same structure for the capture probabilities; only the survival modeling differs among models.

2. For models with covariates, the number of parameters for survival is equal to the number of covariate effect parameters in the model plus K-2 for the interval-specific intercept parameters.

Table 4.7 Generic ANODEV table for multiple-population release-recapture study.

Source	df	Deviance	Mean Deviance	F	R^2
Total	I(K-2)	$-2lnL(\hat{\underset{\sim}{\theta}}_{IM})$			
Mean	K-2	$-2lnL(\hat{\underset{\sim}{\theta}}_{F})$			
Corrected Total	(I-1)(K-2)	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{IM}) - lnL(\hat{\underset{\sim}{\theta}}_{F})\}$			
Covariate Total	J(K-2)	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{IM}) - lnL(\hat{\underset{\sim}{\theta}}_{M})\}$	$\frac{\text{Dev(Cov)}}{J(K-2)}$	$F_{J(K-1),\,df_{\text{ERR}}} = \frac{\text{MD(Cov)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov)}}{\text{Dev(Cor)}}$
Covariates; Interval 1	J	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{IM}) - lnL(\hat{\underset{\sim}{\theta}}_{M_1})\}$	$\frac{\text{Dev(Cov}_1\text{)}}{J}$	$F_{J,\,df_{\text{ERR}}} = \frac{\text{MD(Cov}_1\text{)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov}_1\text{)}}{\text{Dev(Cor)}}$
Covariate 1; Interval 1	1	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{IM}) - lnL(\hat{\underset{\sim}{\theta}}_{M_{1/1}})\}$	$\frac{\text{Dev(Cov}_1\text{)}}{J}$	$F_{1,\,df_{\text{ERR}}} = \frac{\text{MD(Cov}_{1/1}\text{)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov}_{1/1}\text{)}}{\text{Dev(Cor)}}$
Covariate 2 | Cov. 1; Interval 1	1	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{M_{1/1}}) - lnL(\hat{\underset{\sim}{\theta}}_{M_{1/12}})\}$	$\frac{\text{Dev(Cov}_{1/2}\text{)}}{1}$	$F_{1,\,df_{\text{ERR}}} = \frac{\text{MD(Cov}_{1/2}\text{)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov}_{1/2}\text{)}}{\text{Dev(Cor)}}$
...	...				
Covariate J | Cov. 1,2,..., J-1; Interval 1	1	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{M_{1/12...,J-1}}) - lnL(\hat{\underset{\sim}{\theta}}_{M_1})\}$	$\frac{\text{Dev(Cov}_{1/J}\text{)}}{1}$	$F_{1,\,df_{\text{ERR}}} = \frac{\text{MD(Cov}_{1/J}\text{)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov}_{1/J}\text{)}}{\text{Dev(Cor)}}$
Covariates; Interval 2	J	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{M_1}) - lnL(\hat{\underset{\sim}{\theta}}_{M_{12}})\}$	$\frac{\text{Dev(Cov}_2\text{)}}{J}$	$F_{J,\,df_{\text{ERR}}} = \frac{\text{MD(Cov}_2\text{)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov}_2\text{)}}{\text{Dev(Cor)}}$
...	...				
Covariates; Interval K-2	J	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{M_{12...,K-3}}) - lnL(\hat{\underset{\sim}{\theta}}_{M})\}$	$\frac{\text{Dev(Cov}_{\text{K-2}}\text{)}}{J}$	$F_{J,\,df_{\text{ERR}}} = \frac{\text{MD(Cov}_{\text{K-1}}\text{)}}{\text{MD(Err)}}$	$\frac{\text{Dev(Cov}_{\text{K-1}}\text{)}}{\text{Dev(Cor)}}$
Error	(I-J-1)(K-2)	$-2\{lnL(\hat{\underset{\sim}{\theta}}_{M}) - lnL(\hat{\underset{\sim}{\theta}}_{F})\}$	$\frac{\text{Dev(Err)}}{(I-J-1)(K-2)}$		

$$F_{\nu,\,(I-J-1)(K-2)} = \frac{\text{MD(Effect)}}{\text{MD(Err)}} \tag{4.29}$$

where ν is the number of covariate effects being tested, MD(Effect) is the mean deviance for the ν covariates, and MD(Error) is the mean deviance for error. When there is truly no effect of the covariates (null hypothesis is true), the F-statistic has an asymptotic F-distribution with ν and $(I-J-1)(K-2)$ numerator and denominator degrees of freedom, respectively (Smith, 1991).

4.5.3 Likelihood ratio tests for individual covariates

Likelihood ratio tests (LRTs) (Section 2.4.1) are not appropriate for group covariate effects because inter-replicate variability is not correctly accounted for (Smith, 1991). However, Hoffmann (1993) showed that LRTs are appropriate for testing the significance of effects of individual covariates when a saturated model (i.e., Model Sst) is used for the design effects (population and interval) on survival. As in ANODEV for group covariates, a structure for the model of capture probabilities is chosen in a first analysis phase (Section 4.4.3), and used for all models of individual effects on survival.

For example, suppose we have a multiple-population release-recapture study with $K = 4$ sampling events. For each tagged animal, a condition index is calculated based on morphology (x_{ikj} for the *j*th individual tagged in population *i* on event *k*), and we wish to determine whether the index is significantly correlated with survival probabilities. A survival-effects model is used to estimate the effect parameter β_{im} for the condition index for population *i* in interval *m*. Using the Hazard link, the survival probability is written as:

$$S_{ikjm} = S^{e^{\pi_i + \rho_m + (\pi\rho)_{im} + x_{ikj}\beta_{im}}}.$$

To test the hypotheses

$$H_0\colon \beta_{im} = 0 \qquad \text{versus} \qquad H_A\colon \beta_{im} \neq 0$$

(Eq. (4.18)) is used to fit the model that includes the condition index effect, and a model that does not include the effect (i.e., $S_{ikjm} = S^{e^{\pi_i + \rho_m + (\pi\rho)_{im}}}$ for all ikj; see Section 4.3.3). The

likelihood ratio statistic is then computed (Eq. (2.28)) and compared to a χ^2-distribution with 1 degree of freedom.

4.6 SURPH Features for Analysis of Release-Recapture Data

After data input to SURPH, the user can perform activities in three major areas. The user can (1) View descriptive tables and graphical displays based on the data; (2) Fit a series of survival models to investigate relationships with group and individual covariates; and (3) View tabular and graphical information based on models fit to the data. All three activities are described in detail in Chapter 6 and especially Chapter 7. The theory for fitting models has been described in previous sections of this chapter. Chapter 7 is meant to be a quick reference guide to SURPH features, and omits detailed theoretical explanation of some of the tabular and graphical output of Program SURPH for release-recapture data. This section explains the theory behind these features in more detail.

4.6.1 Data description

4.6.1.1 Manly-Parr estimates of capture probabilities

The technique used by Manly and Parr (1968) to estimate capture probabilities is introduced in Section 4.4.3.1. Program SURPH provides the option of viewing the capture probability estimates under the Manly-Parr model (see “Data: Manly-Parr Estimates” in Chapter 7). Three tables are provided by SURPH when Manly-Parr estimates are requested. The first is a table of capture probability estimates (see Eq. (4.20) in Section 4.4.3.1), not adjusted for known removals. The second table gives the removal proportions on each sampling event in each population, and the third gives the capture probabilities adjusted for known removals.

When there are known removals (see Section 4.2) in a release-recapture study, the Manly-Parr (1968) estimates of capture probabilities (Eq. (4.20)) are biased, underestimating the true values. To understand why the bias exists, consider the definitions of the variables g_{ik} and h_{ik}:

g_{ik} = the number of animals marked before sampling event *k* that were detected both on event *k* and on at least one later event,

h_{ik} = the number of animals marked before sampling event *k* that were not detected on event *k*, but were detected on at least one later event.

Only animals detected on event *k* can be removed on that event. Thus, known removals decrease the number of animal that could contribute to g_{ik} but not to h_{ik}. To correct for the bias, h_{ik} must be adjusted downward:

$$h'_{ik} = (1 - r_{ik})h_{ik} \tag{4.30}$$

and

$$\hat{P}_{ik} = \frac{g_{ik}}{g_{ik} + h'_{ik}} \tag{4.31}$$

where r_{ik} is the proportion of animals detected on event *k* that were removed. This estimate of the capture probability is unbiased.

4.6.1.2 Reduced M-arrays

To summarize release-recapture data, Burnham et al (1987) introduced the so-called “Full M-array” and “Reduced M-array.” Reduced M-arrays have been incorporated into Program SURPH. The reduced M-array is illustrated here using simulated data. Suppose a release-recapture study with *K*=4 sampling occasions is conducted on a single population. One hundred animals are marked on the first sampling event, 50 on the second event, and 40 on the third. The observed capture history data are listed in Table 4.8. Table 4.9(a) shows which capture histories contribute to each cell of the reduced M-array, while Table 4.9(b) shows the numbers for the simulated data set. The “Total Released” for a particular event includes both animals tagged and released for the first time, and previously-marked animals detected on that event and re-released (i.e., not removed). The cells labeled “Event Next Detected” contain two numbers. To the left of the colon is the total number detected; to the right is the number of these that were known to be removed on that event. In Table 4.9 (a) the first column in each cell, to the left of the colon, gives the capture histories that contribute to the number detected, and the second column, to the right of the colon, gives the capture histories that represent known removals.

4.6.2 Fitted models

4.6.2.1 Parameters estimated by SURPH

After fitting a model using SURPH, the maximum likelihood estimators for the model parameters can be displayed (see “Models: SURPH Parameter Estimates” in Chapter 7), along with a numerical approximation of the variance-covariance matrix based on difference equations. The parameters displayed are essentially those on the right-hand side of (Eq. (4.19)); i.e., the population and period effect parameters (see Section 4.3.3) and the slope parameters for group and individual covariates.

The internal workings of SURPH do not act directly upon the intercept parameter S. Instead, SURPH works with the logit of the intercept parameter:

$$S' = \log\left(\frac{S}{(1-S)}\right) . \tag{4.32}$$

The logistic scale is unrestricted [$(-\infty, \infty)$], as are all the effect parameters. Without this transformation, estimated values of the intercept parameter may fall outside the admissible range, causing problems with the iterative numerical proceudre.Thus, the estimated intercept parameter that is displayed is not the one SURPH estimated, but the inverse logistic transformation:

$$\hat{S} = \frac{exp(\hat{S}')}{1 + exp(\hat{S}')} . \tag{4.33}$$

Similarly, SURPH computes the approximate variance-covariance matrix based on the transformed variable S' but displays the matrix adjusted for the back-transformation:

$\hat{Var}(\hat{S}) = \hat{Var}(\hat{S}')\{\hat{S}(1-\hat{S})\}^2$, and $\hat{Cov}(\hat{S}, \hat{\theta}) = \hat{Cov}(\hat{S}', \hat{\theta})\{\hat{S}(1-\hat{S})\}$, where θ is any effect parameter.

Table 4.8 Simulated release-recapture data for illustration of reduced M-array.

History	Count
1111	8
1110	1
1101	5
1100	11
1011	3
1010	7
1001	9
1000	42
112	3
12	7
102	4
0111	2
0110	8
0101	10
0100	25
012	5
0011	10
0010	30

Table 4.9 Illustration of reduced M-array for release-recapture study with K = 4 sampling events.

(a) Capture histories contributing to each cell of the reduced M-array.

		Event Next Detected			
Event	Total Released	2	3	4	Never Detected
1	R_1	1111:12 1110 1101 1100 12 112	1011:102 1010 102	1001	1000
2	R_2 1111 1110 1101 1100 112		1111:112 1110 012 112 0111 0110 012	1101 0101	1100 0100
3	R_3 1111 1110 1011 1010 0111 0110			1111 1011 0111 0011	1110 1010 0110 0010

(b) Reduced M-array for simulated study.

		Event Next Detected			
Event	Total Released	2	3	4	Never Detected
1	100	35:7	14:4	9:0	42
2	78		27:8	15:0	36
3	69			23:0	46

4.6.2.2 SURPH parameters translated into probabilities

The SURPH user will rely mainly on the effect parameters (Section 4.6.2.1) to make inferences regarding influences on the survival process. However, it is also interesting to translate the effect parameters into the familiar scale of estimated survival probabilities for each interval. SURPH offers a tabular display of the parameter estimates translated into probabilities (see “Models: SURPH Probability Estimates” in Chapter 7).

For models that do not include individual covariates the probability estimates are calculated as a straightforward function of the link function and the effect parameters:

$$\hat{S}_{ik} = f(\hat{S}, \hat{\pi}_i, \hat{\rho}_k, (\widehat{\pi\rho})_{ik}, \underset{\sim}{w}_{ik}, \hat{\underset{\sim}{\tau}}_k) , \tag{4.34}$$

where $\hat{S}$ = the estimated intercept parameter,

$\hat{\pi}_i$ = the estimated effect parameter for population i,

$\hat{\rho}_k$ = the estimated effect parameter for interval k,

$(\widehat{\pi\rho})_{ik}$ = the estimated interaction between population i and interval k effects,

$\underset{\sim}{w}_{ik}$ = the vector of group covariates in interval k for population i,

$\hat{\underset{\sim}{\tau}}_k$ = the vector of covariate effect parameters for period k, and

f = the link function between the linear predictor and the survival probability.

Standard errors of the probability estimates are derived from the variance-covariance matrix of the SURPH parameters using the delta-method (Seber, 1982, pp 7-9). The standard errors currently displayed are based only on the population and interval effects and on group covariate effects in the model.

When the model includes individual covariates, the probabilities are “integrated” over all individuals in population i and interval k according to the formula:

$$\hat{S}_{im} = \frac{\sum_{k=1}^{m-1} \sum_{j=1}^{R_{ik}} S_{ikjm}}{\sum_{k=1}^{m-1} R_{ik}} = \frac{\sum_{k=1}^{m-1} \sum_{j=1}^{R_{ik}} f(\hat{S}, \hat{\pi}_i, \hat{\rho}_m, (\pi\rho)_{im}, \underset{\sim}{x}_{ikj}, \hat{\underset{\sim}{\beta}}_{im}, \underset{\sim}{w}_{im}, \hat{\underset{\sim}{\tau}}_m)}{\sum_{k=1}^{m-1} R_{ik}}, \tag{4.35}$$

where $\underset{\sim}{x}_{ikj}$ = the vector of individual-based covariates for the *j*th animal released on the *k*th sampling event in population *i*,

$\underset{\sim}{\beta}_{im}$ = the vector of effect parameters for individual covariates in the *m*th sampling interval for population *i*,

and the other symbols are as in (Eq. (4.28)).

Code has not been installed in Program SURPH to calculate standard errors of the integrated probability estimates (Eq. (4.29)) when individual covariates are modeled.

4.6.2.3 Response curves for group covariates

For models including group covariates, SURPH provides a graphical display of the estimated response curves derived from the estimated parameters (see “Models: Survival Graphics: Group Covariate” in Chapter 7). The user selects an interval (*k*) and a covariate (*l*) to display. Values of the selected group covariate (w_{ikl}) are on the horizontal axis, ranging from the minimum observed value to the maximum, and the estimated survival probability is on the vertical axis. The plotted curve is:

$$y = f(\hat{S}, \hat{\pi}_i, \hat{\rho}_k, (\pi\rho)_{ik}, \bar{\underset{\sim}{x}}_i, \hat{\underset{\sim}{\beta}}_{ik}, \bar{\underset{\sim}{w}}_{k(l)}, \hat{\underset{\sim}{\tau}}_{k(l)}, x, \hat{\tau}_{kl}) \tag{4.36}$$

where $\bar{\underset{\sim}{x}}_i$ = a vector consisting of the average individual covariate values for individuals in population i,

$\bar{\underset{\sim}{w}}_{k(l)}$ = a vector consisting of the average across populations of each group covariate, other than that selected for display, in interval *k*,

$\hat{\underset{\sim}{\tau}}_{k(l)}$ = the vector of covariate effect parameters for interval *k*, excluding the effect of the selected parameter,

x = the value on the horizontal axis; i.e., values of the selected covariate (w_{ikl}), and

$\hat{\tau}_{kl}$ = the effect parameter for group covariate l in interval k.

4.6.2.4 Response curves for individual covariates

For models including individual covariates, SURPH provides a graphical display of the estimated response curves derived from the estimated parameters (see "Models: Survival Graphics: Individual Covariate (A)" in Chapter 7). The user selects an interval (k) and a covariate (l) to display. Values of the selected individual covariate (x_{il}) are on the horizontal axis, ranging from the minimum observed value to the maximum, and the estimated survival probability is on the vertical axis. The plotted curve is:

$$y = f(\hat{S}, \hat{\pi}_i, \hat{\rho}_k, (\pi\rho)_{ik}, \bar{\underset{\sim}{x}}_{i(l)}, \hat{\underset{\sim}{\beta}}_{ik(l)}, \bar{\underset{\sim}{w}}_k, \hat{\underset{\sim}{\tau}}_k, x, \hat{\beta}_{ikl}) \tag{4.37}$$

where $\bar{\underset{\sim}{x}}_{i(l)}$ = a vector consisting of the average individual covariate values, other than that selected for display, for individuals in population i,

$\hat{\underset{\sim}{\beta}}_{ik(l)}$ = the vector of covariate effect parameters for interval k and population i, excluding the effect of the selected parameter,

$\bar{\underset{\sim}{w}}_k$ = a vector consisting of the average across populations of each group covariate in interval k,

x = the value on the horizontal axis; i.e., values of the selected individual covariate (x_{il}), and

$\hat{\beta}_{ikl}$ = the effect parameter for individual covariate l in interval k and population i.

4.6.2.5 Nonparametric response curves

The response curve for individual covariates based on the SURPH parameters (Eq. (4.31)) can be superimposed on a "nonparametric" curve, or one that does not depend on the parameters of any particular model (see "Models: Survival Graphics: Individual Covariate (C)" in Chapter 7). The nonparametric curve can be thought of as the "moving average" survival as you move

from the animals with the smallest values of the selected individual covariate to the animals with the largest values. The size of the "window" for the moving average ranges from a minimum of 8 individuals up to 20% of the entire number at risk in the selected interval.

The nonparametric curve is computed as follows:

1) The user selects an individual covariate (*l*), a sampling interval (*k*), and a population (*i*) for the display.

2) The animals in population *i* that were at risk in interval *k* are sorted from smallest to largest value of covariate *l*.

3) Beginning with smallest covariate value and window composed of the 8 individuals with the smallest covariate values, the reduced M-array (Section 4.6.1.3) is computed for individuals in window. From the M-array, the number "released" on occasion *k* (M_{kk}) and the number next seen again on occasion k+1 ($M_{k,\,k+1}$) are obtained. The ratio $\frac{M_{k,\,k+1}}{M_{kk}}$ is an estimate of the product of S^*_k and P^*_{k+1} ($S^*_k P^*_{k+1}$) for the individuals in the window. The survival estimate is isolated by dividing the ratio by the Manly-Parr estimate of capture probability on event *k* (Section 4.4.3) for population *i*:

$$S^*_k = \frac{(M_{k,\,k+1} / M_{kk})}{\hat{P}_{i,\,k+1}} \tag{4.38}$$

The survival estimate is plotted versus the mean covariate value for individuals in window.

4) In increments of one individual, the window size is increased to 20% of number at risk by adding, at each step, the individual with the next largest value of the covariate. For each increment, the survival estimate is computed as in Step 3 and plotted versus the mean covariate value in window.

5) Once the window is 20% of the number at risk, the window is moved, one individual at a time, by dropping the individual with smallest value from the window and adding the individual with the next largest value. At each step, the survival estimate is computed and plotted against the mean covariate value in window.

6) Once the "right-end" of the window reaches the individual with largest covariate value, the window size decreased in decrements of one individual at each step by dropping the individual with the smallest value of covariate from the window, until the window size returns to the minimum of 8 animals. For each decrement, the survival estimate is computed and plotted against the mean covariate value in window.

The result is a non-smooth curve that does not depend on any particular model assumptions. For an adequate model of the individual covariate effect, the parametric response curve (Eq. (4.31)) should follow the nonparametric curve reasonably well.

4.6.2.6 Residual plots

One measure of the adequacy of a model fitted to data is how well the expected observations predicted by the model agree with what was actually observed. For SURPH models, we can compare the observed number of animals with each capture history with the number predicted by the model. The predicted numbers are obtained by computing expected survival and capture probabilities for each individual animal (Eq. (4.19)) and then computing the expected probabilities for each capture history (e.g., Table 4.2). The probabilities are summed over all individuals to give the expected number of animals with each capture history in each population.

A residual is calculated for each possible history based on the observed (O) and expected (E) number of animals with the survival history. For Poisson distributions the following function, known as the Anscombe residual, is approximately normally distributed (Cox and Snell, 1968):

$$r_A = \frac{\frac{3}{2}\left(O^{2/3} - \left(E - \frac{1}{6}\right)^{2/3}\right)}{E^{1/6}} \quad . \tag{4.39}$$

In a display available in SURPH (see “Models: Residual Plot” in Chapter 7), the Anscombe residual for each survival history is plotted against the decimal equivalent of the survival history taken as a binary number (e.g., 1110 base 2 = 14 base 10), with the plotting character equal to the number of the population. Because the r_A are approximately normal, any residuals greater than 2.0 in absolute value are potential outliers (i.e., $P(|Z| > 2.0) \approx 0.05$). If several large residuals occur, the user should investigate the corresponding capture histories to identify any patterns that might suggest a mechanism to explain why there are “too many” or “too few” of some capture histories.

SURPH also provides a plot of the residuals against quantiles of the normal distribution (see “Models: Quantile-Quantile Plot” in Chapter 7).

Chapter 5

Installing Program SURPH and Creating Data Files

5.1 System Requirements

To run SURPH, the following equipment and support are necessary:

1. A SUN workstation with at least 1 MB of free memory. The amount of free memory above 1 MB will determine the speed of the program execution.
2. The UNIX operating system.
3. Some version of an X-windowing system. SURPH has been run using XView and several other X-window managers (e.g., uwm, twm). It should run under any window manager that uses X.
4. A color monitor. Although color is not necessary, it is helpful in viewing certain graphics.

5.2 Installing SURPH

Step One: Accessing the executable and other files.

Use anonymous ftp or Mosaic to log in to the host site and download the necessary files. The address of the host site is **ftp://opus.cqs.washington.edu/public/surph**. To get the files via ftp, at the UNIX prompt type

> **ftp opus.cqs.washington.edu**

At the login prompt, type “anonymous”, then use your login id as the password.

To get the files via Mosaic, type **ftp://opus.cqs.washington.edu/public/surph** in the new URL pop-up window.

The files are:

1. README (ascii mode) Contains these instructions, including any revisions since this manual was printed.

2. SURPH.tar.Z (binary mode) Compressed “tape archive.” Use uncompress and tar utilities to extract the following files:

surph	(binary mode) Contains the entry program.
omni	(binary mode) Contains the release-recapture program.
telem	(binary mode) Contains the known-fate program.
*.info	(ascii mode) These are help files; they include help_main.info, anodev.info, menu.info, xv.info, desc_stat.info, and splots.info.

3. SURPH.data.tar.Z (binary mode) Compressed “tape archive” containing data files.

4. SURPH.manual.tar.Z (binary mode) Compressed “tape archive” containing this manual.

Step Two: Setting the PATH environment variable.

Set the PATH environment variable to include the directory that contains downloaded SURPH files.

Step Three: Setting the SURPH environment variable.

Create and set a new environment variable called SURPH. This variable should contain the name of the directory that SURPH is installed in (that is, the same directory that was added to the path variable in the previous step).

Step Four: Setting the HELPPATH variable.

Add to (or create) the environment variable HELPPATH to include the directory where the *.info files will reside. This directory can be different from the directory that SURPH is installed in, but it doesn’t have to be.

After these four steps are performed, SURPH should be operational.

Send questions or bug reports to surph@cqs.washington.edu.

5.3 SURPH Data Files

5.3.1 Introduction

This section describes the format required for SURPH data files. Whether a study uses release-recapture or known-fate sampling to collect data, the following information must be provided in every SURPH data file:

1. A brief verbal description, or title, for the data set.
2. The number of discrete populations in the data set.
3. The number of sampling intervals (i.e., intervals between sampling events). If there are *K* sampling events, then there are *K*-1 sampling intervals.
4. A definition of each group covariate. For each covariate, the data file should include a name, an indication of whether the covariate varies from interval to interval, and the measurements of the variable for each population.
5. The number of animals newly tagged and released in each population at each sampling event except the last (new animals are not tagged on the last sampling events).
6. The number of characters used for individual identification (ID) codes. If codes are not listed in the data file, the user should indicate an "ID length" of 0 characters.
7. The name of each individual covariate.
8. For every tagged individual in the study: the identification code, if desired; the capture or survival history; and the measurements for each individual covariate in the same order as the names provided above (#7).

Below are details on how the required information must be arranged in the data file. Rules for capture or survival histories are also provided, particularly for animals that are known to have been removed from the population on a particular sampling event.

Figure 5.1 illustrates the first section (the "Header") of a SURPH data file for a hypothetical release-recapture study. This simulated data set was used to generate most of the "snapshots" of the program found in Chapter 7. Each piece of information provided to SURPH is identified

```
Data
Simulated data based on 1993 PIT-tagged chinook salmon paired turbine releases
# 3 paired releases for total of 6 populations
number_of_populations 6
# 5 sampling events give 4 sampling intervals
number_of_intervals 4

group_covariate name treatment time 0
    0.000000
    1.000000
    0.000000
    1.000000
    0.000000
    1.000000
group_covariate name mid_release time 0
    0.000000
    0.000000
    1.000000
    1.000000
    0.000000
    0.000000
group_covariate name late_release time 0
    0.000000
    0.000000
    0.000000
    0.000000
    1.000000
    1.000000
group_covariate name ATPase time 1
8.3         25.5    29.1    28.8
9.0         20.42   25.9    33.02
9.3         22.56   34.14   39.28
7.5         20.2    29.0    23.6
8.5         21.4    34.0    25.3
9.0         21.3    23.9    23.6

individual_covariate length
individual_covariate weight
individual_covariate condix
number_tagged
1000  250  0  0
1000  250  0  0
1000  250  0  0
1000  250  0  0
1000  250  0  0
1000  250  0  0
length_of_ids 10
data
7F7E644A5A      1 0 0 0 0       141 31.4 1.12
7F7F0F554E      1 0 0 0 0       144 33.6 1.12
# 7F7F0F5C7D transported by barge from Lower Granite Dam
7F7F0F5C7D      1 2             156 39.9 1.04
7F7F103974      1 0 1 0 0       146 34.9 1.11
7F7F112C28      1 0 2           139 29.5 1.09
7F7F112F77      1 1 0 0 0       124 21.3 1.12
7F7F15131F      0 1 0 1 0       132 24.6 1.08
```

Figure 5.1 Header and beginning of data block for hypothetical release-recapture data file.

Table 5.1 Data file keywords.

Keyword	Purpose
Data	First word on first line of every file. Identifies file as a data file.
number_of_populations npop	Number that follows the keyword is the number of populations.
number_of_intervals nint number_of_periods nper	Number that follows the keyword is the number of sampling intervals.
group_covariate gcov	First word on line that describes a group covariate.
name	On gcov line; character string that follows the keyword **name** is the name for the group-based covariate.
time	On gcov line; number that follows the keyword **time** is 0 if covariate is time-independent and 1 if time-dependent.
individual_covariate icov	Character string that follows the keyword is the name of an individual-based covariate.
number_tagged ntag	Block of numbers that follows the keyword is the number of newly-marked animals released in each population at each sampling event.
full_hist	Must appear on a separate line before the keyword **data** if capture histories for removed animals are extended with 0's after the removal event. The keyword **full_hist** is absent if capture histories of removed animals are truncated after the removal.
length_of_ids idlen	Number that follows the keyword is the length (number of characters) of the code used to identify individual animals.
data	Identifies beginning of Data Block. Data that follow are ID codes, capture or survival histories, and covariate measurements for individual animals.
enddata	Identifies end of Data Block

with a "keyword" (Table 5.1). In many cases, several synonymous keywords can be used to

identify the same information. Novice users may prefer to use the longer, fully-descriptive keywords, while more experienced users may prefer the shorter, more cryptic ones. Synonymous keywords are grouped together in Table 5.1. In the text that follows, keywords appear in bold type. Examples of such keywords in the first few lines of Figure 5.1 are **Data**, **number_of_populations**, and **group_covariate**. Each data file consists of two sections: the "Header", which begins with the keyword **Data** and extends to the keyword **data**, where the "Data Block" begins.

5.3.2 Header format

The first line of every data file is the single keyword **Data**, which identifies the file as a data file and distinguishes it from model files produced when fitted models are saved (the first line of a model file is the keyword **Models**). The second line is the verbal description, or title of the data set. The title appears at the top of most display screens in SURPH, allowing easy identification of the data being analyzed. The title is also saved in model files, so the program can ensure that any model files the user attempts to load are compatible with the data being analyzed.

The next two lines define the dimension of the data set. The example data file (Figure 5.1) has six populations ("**number_of_populations** 6") and four sampling intervals ("**number_of_intervals** 4").

Comments can be placed in the data file at any point after the data title. Lines beginning with the character "#" are comments, and ignored when SURPH reads data files.

In the example data set, the six populations represent three paired treatment/control releases. The next section of the data file defines group covariates that assign each population to the appropriate treatment level and pair, allowing modeling of the effects of treatment and blocking factors. The treatment and release-pair covariates are time-invariant indicator variables. For example, the line "**group_covariate name** treatment **time** 0" defines a time-invariant group covariate named "treatment." The next six lines give the covariate value for each of the six populations. Because the covariate is time-invariant, there is one value on each line. Populations

2, 4, and 6 are the treatment populations. The release-pairs are defined similarly, with group covariates named “mid_release” and “late_release.” Individuals from each population were sampled at each sampling event, and the sample average ATPase activity used as a group covariate to characterize the entire population. The fourth group covariate line (“**group_covariate name** ATPase **time** 1”) defines the ATPase variable. Because the covariate changes between sampling intervals (**time** 1), the next six lines give the covariate values for each interval for each population.

For each individual covariate, the data file contains one line (**individual_covariate** *covariate_name*) to define the covariate name. In the example data set, measurements of length, weight, and condition index (e.g., “condix”) are defined. The covariate values for each individual are provided below in the Data Block.

The numbers of animals marked and released at each sampling event in each population are in a block following the keyword **number_tagged**. In the example, 1000 animals were released on the first event in each population, and 250 were released on the second event. No newly marked animals were released on the third or fourth events.

The optional keyword **full_hist** is used if capture or survival histories (see Sections 5.3 and 5.4) for censored animals are extended with 0’s after the removal event. If the capture or survival histories are truncated after the removal event, the keyword **full_hist** is omitted.

The keyword **length_of_ids** must appear at some point in every SURPH data file. Following the keyword is the length (number of characters) of the ID code used for each individual. In the example, ID codes are 10 characters long (**length_of_ids** 10). If no ID codes are listed in the data file, the “length” is 0 (**length_of_ids** 0).

The keyword **data** indicates the end of the Header and the beginning of the Data Block.

5.3.3 Data Block format

The keyword **data** signals the beginning of the Data Block. The Data Block contains one line for each animal marked during the study. In the example (Figure 5.1), the total number of animals from all six populations is 7500; hence, there are 7500 lines in the Data Block. The record for each individual includes the ID code, if used (see **length_of_ids** above); the capture or survival history, with digits separated by spaces; and the values of each individual covariate measured on the individual, listed in the order in which the covariate names were defined in the Header. For example, the individual with PIT-tag code 7F7F103974 (Figure 5.1) was 146 millimeters long, weighed 34.9 grams, and had a condition index of 1.1. See Sections 5.3 and 5.4 for explanations of the capture and survival histories.

Individual records within the Data Block are ordered by population. That is, all records for Population 1 appear before records for Populations 2, 3, and so on. Thus, the example file would include first the records for the 1250 animals tagged in Population 1, then the 1250 for Population 2, and so on. Within the sections for each population, the records for the individual animals can be listed in any order; records need not be listed in the order that the individuals were marked.

The last line of every data file is the keyword **enddata**, signaling the end of the Data Block and the end of the entire file. SURPH provides notification of an error if **enddata** is encountered "too soon" or "too late" (i.e., the number of records in the Data Block is not equal to the total number of marked animals declared in the **ntag** block of the Header).

5.4 Rules for Survival Histories (Known-Fate Studies)

A survival history is the record of the sampling events at which an individual was detected alive. Survival histories for individuals that were not known to be removed consist of a series of K digits, where K is the number of sampling events. If an individual is detected alive, a "1" is recorded in the survival history for the particular interval. If an animal is detected but is found dead, a "0" is recorded. Individuals not released at the first event, but captured and marked at the second event have survival histories beginning with the digits "0 1." For example, an individual

marked at the second event, then redetected at the third and fourth events, but not at the fifth event, would have a survival history of “0 1 1 1 0.” Survival histories for animals newly marked at the third event begin with “0 0 1,” and so on.

In known-fate studies, each marked individual is queried at every event, and it is determined whether the animal has survived or died since the previous event. Thus, survival histories in known-fate studies cannot have “0’s” between two “1’s”; the first “0” following the release occasion indicates mortality. Thus, an individual in a known-fate study could have a survival history of “0 0 1 1 0”, which indicates release on the third occasion, detection on the fourth, and then death. However, an animal in a known-fate study could not have a survival history of “0 1 0 0 1” for example, because the zero on the fourth event indicates that the animal died; it could not then be redetected on later sampling events.

There are two distinct types of known removals in known-fate studies. For example, in a study using radio-tags, animals are removed from the sample if: (1) they are captured alive and removed from the study site (e.g., handling mortality or for biopsy); or (2) their radio transmitter fails and their survival status cannot be determined. Survival histories for removals of the first type are recorded the same as removals for release-recapture, with a code of “2” for the removal event. For example, in a study including five sampling events, if an animal survives to the third event and is removed on that event, the truncated survival history is “1 1 2” (“1 1 2 0 0” if extended: **full_hist** keyword included). For removals of the second type (i.e., radio transmitter failure), a code of “3” is recorded on the first occasion on which the individual could not be located. In the five-sampling event study above, an animal that was known to survive until the third event, but could not be located on the fourth event or thereafter, would have a survival history of “1 1 1 3” (“1 1 1 3 0,” if extended). With regard to information provided for survival estimation, survival histories “1 1 2” and “1 1 1 3” are equivalent; both animals provide information for the first two sampling intervals but none for any subsequent interval.

5.5 Rules for Capture Histories (Release-Recapture Studies)

A capture history is the record of the sampling events on which the individual was either detected alive or not detected. Capture histories for individuals that were not censored consist of

a series of *K* digits, where *K* is the number of sampling events. If an individual is detected, a “1” is recorded in the capture history for that particular event. If not detected, a “0” is recorded. In the example file (Figure 5.1), the individual coded 7F7F103974 was marked and released at the first event, redetected at the third event, but not detected on events 2, 4, or 5. Thus, the capture history is “1 0 1 0 0.” Individuals not released at the first event, but captured and marked at the second event have capture histories beginning with the digits “0 1”. For example, individual 7F7F15131F (Figure 5.1) was marked on the second event and then redetected on the fourth event, for a capture history of “0 1 0 1 0”. Capture histories for animals newly marked on the third event begin with the digits “0 0 1”, and so on.

In release-recapture studies, a failure to detect a marked individual may be due to mortality or to imperfect sampling of surviving individuals. Thus, capture histories typically consist of a series of interspersed “1’s” and “0’s” (see example data set, Figure 5.1).

There are a number of ways that marked animals may become known removals from a release-recapture study. For example, if physical trapping is used, animals may be killed by trapping or handling; or live animals may be purposely removed for biopsy. In the automatic data collection system for PIT-tags on the Snake River, the system fails to divert a portion of the tagged fish back into the river. These fish are transported by barge, rather than returned to the river. For known removals, the code “2” is used to denote the event when the animal is removed. The code “2” indicates that the individual survived the interval but was removed from the study before contributing survival information for subsequent intervals. For example, individual 7F7F112C28 (Figure 5.1) was removed after being detected alive at the third event, for a truncated capture history of “1 0 2”.

Often, SURPH users will record capture data in a spreadsheet, with one column for each sampling event and one row for each marked animal. The Data Block for the data file can then be generated by saving the spreadsheet in a text format. For data files produced in this way, it can be convenient to present capture histories for removed individuals with “extended 0’s” after the removal event, so there is a numeric code for each event. For example, individual 7F7F112C28 (Figure 5.1) would have an extended capture history of “1 0 2 0 0”. If capture

histories in the Data Block are extended, the keyword **full_hist** must appear in the Header. If **full_hist** does not appear in the Header, SURPH assumes that capture histories are truncated after removal events.

Chapter 6

Annotated Examples of SURPH Analysis

Previous chapters have discussed the general framework for the design and analysis of survival studies. The inferential basis to assess individual-based and group-level covariates in an animal tagging study were presented in earlier chapters. This chapter demonstrates these statistical principles using a series of examples of known-fate and release-recapture studies. The examples presented illustrate the assessment of the effects of both individual-based and group-level covariates on survival and/or capture probabilities. The examples present analyses of both manipulative experiments and observational studies, however, they do not exhaust the analysis potential of SURPH.

The data files for the examples are included on the same disk or tape that contains the program. Specific filenames are given within each example. Users are strongly encouraged to work through these example analyses to become acquainted with the computational operations of SURPH before proceeding to the analysis of their own studies.

There are two separate discussions for each example within this chapter: (1) analysis of the various data sets, and (2) instructions on how to use SURPH to perform the analysis. Two different fonts are used to distinguish text related to the two separate goals. The regular font is used to explain the analysis, and the *italic font* is used to instruct the user on the mechanics of SURPH. For further instructions on using SURPH commands (command sequences), accessing SURPH windows, and viewing SURPH graphics, see the User Guide in Chapter 7.

6.1 Known-Fate Examples

Four known-fate studies are presented in this section. The basic characteristics of the four examples are as follows:

Example #1: Single-population observational study of temperature effects on black duck (*Anas rubripes*) survival over time,

Example #2: Multiple-population observational study of the relationship of habitat characteristics with bobwhite quail (*Colinus virginianus*) survival,

Example #3: Single-population observational study of the effects of organism size and tidal height on blue mussel (*Mytilus edulis*) survival,

Example #4: Multiple-population experimental study of effects of pesticide application on nest box abandonment rates by starlings (*Sturnus vulgaris*).

6.1.1 Black duck survival study

This example shows how survival probabilities over time can be modeled as a function of time-variant covariates measured at the population level in a single-population study. The observational nature of the study is reminiscent of a classical regression analysis. However, this example differs from regression analysis in that the dependent variable is a survival rate, and the response model is the nonlinear proportional hazards relationship.

Conroy et al. (1989) used radiotelemetry to monitor winter survival and cause-specific mortality of female American black ducks (*Anas rubripes*) captured at three sites in New Jersey and Virginia. In the analysis by Conroy et al. (1989), the effects of mean daily temperatures on survival were inconclusive. Decreased temperature appeared to be weakly related to increased mortality. The SURPH analysis sheds more light on the temperature-survival relationship.

The tagging scheme consists of a single-entry design with all ducks present in period 1. For the SURPH analysis, the period from 14 December to 8 February was divided into eight one-week sampling periods. A total of 50 radiotagged ducks were known to be alive on December 15, 1983. Two had radio failures within the first week, and were dropped from the analysis (Table 6.1). It was thought that cold temperatures during winter months would decrease survival. Table 6.2 lists several potential covariates used to characterize weekly temperatures. Those that were explored were the average maximum temperature (“avgmax”) and the average minimum temperature (“avgmin”) for each week during the 8-week study; the minimum temperature (“min”) for each week during the 8-week study; and finally, the number of days within each week that the minimum temperature was less than 0 degrees Celsius(“min<0”). Although the ducks consisted of both yearlings and adults, all were assumed to be homogeneous (for purposes of illustration); only the environmental covariates were considered.

To begin the SURPH session, at the prompt, type “surph blackduck8.dat”:

```
> surph blackduck8.dat
```

Left-click on the ***Known-Fate Button****. This begins the program for known-fate data analysis and loads the datafile “blackduck8.dat”.*

Table 6.1 **Survival histories for the 48 radiotagged black ducks. The number to the left of the colon is the number of ducks that survived to that sampling occasion. The number to the right of the colon is the number of radiotags that failed during the following period. Thus, at the third sampling occasion, 45 ducks were detected. However, between the third and fourth sampling occasions, 4 radiotags failed. Thus, of the 45 ducks that were known to be alive on the third sampling occasion, only 41 could be tracked beyond the third sampling occasion.**

	Survived to Occasion							
	1	2	3	4	5	6	7	8
Number Known Alive	48	47:0	45:4	39:0	34:2	28:0	25:0	24:0

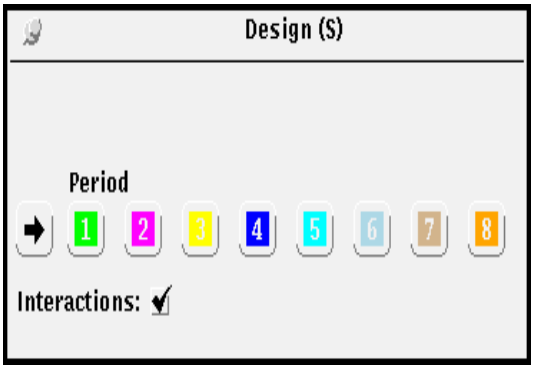
Table 6.2 Period-specific temperature data used in the analysis of the black duck survival study.

Period	Dates	avgmax[1]	avgmin[2]	min[3]	min < 0[4]
1	14 Dec - 20 Dec	42.14	32.14	19	4
2	21 Dec - 27 Dec	31.43	16.29	4	6
3	28 Dec - 3 Jan	37.86	19.29	13	7
4	11 Jan - 17 Jan	43.00	23.00	14	7
5	18 Jan - 24 Jan	31.00	15.00	9	7
6	18 Jan - 24 Jan	25.29	8.43	-7	6
7	19 Jan - 31 Jan	46.86	27.29	22	5
8	1 Feb - 7 Feb	40.29	23.71	9	5

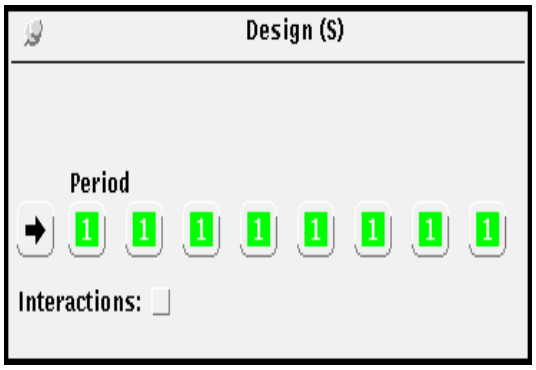
1. Average daily maximum temperature for period.
2. Average daily minimum temperature for period.
3. Minimum temperature during period.
4. Number of days where minimum temperature was less than 0° C.

With a single-population study, there are two standard models that can be computed using the S Design Button Pad. The simplest model has a single parameter, and estimates a single common survival probability for all periods. This model is called the “S” Model, or the Grand Mean Model. The other model has a unique survival for each period. This model is called the “St”, or Full Model. For a single population, the “St” Model is the fully parameterized model. A likelihood ratio test can be used to compare the “S” and “St” models, and to determine whether the more fully parameterized model provides a statistically (p-value < 0.10) improved fit.

*Go to the **Modeling Pull-Down Button**, and bring up the button pads for **S Design** and **S Group** (**Modeling -> S Design** and **Modeling -> S Group**). Using the Quick Button on the left side of the **S Design** Button Pad, change the buttons from “1, 2, 3, 4, 5, 6, 7, 8” to all “1’s”.*



St Model

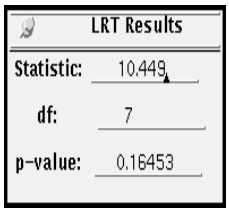


S Model

*In the **Name** field in the SURPH Base Window, enter the name “S” or “Grand Mean”. Left-click on **Begin Estimate** to estimate the parameter value for model “S”. Once the model “S” has been fit, change the button settings, again using the Quick Button, back to “1, 2, 3, 4, 5, 6, 7, 8”. In the **Name** field in the SURPH Base Window, enter the name “St” or “Full Model”. Left-click on **Begin Estimate** to estimate the parameters for model “St”.*

*To compare the fit of these two models using the likelihood ratio test, select the “S” model in the **Master Models List**, then select the “St” model in the **Testable Models List**. A pop-up window will appear that displays the value of the test statistic (10.449; see Chapter 2 for calculating formula), the change in number of parameters (7; also known as the degrees of*

freedom), and the probability of observing this or a greater value of the test statistic under a chi-square distribution with 7 degrees of freedom (p-value = 0.165).



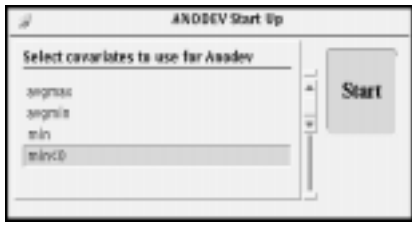
*Access the binomial estimates (**Data Button -> Binomial Estimates**). The binomial survival estimate for period "i" is computed by dividing the number known alive at the end of the period (i.e., on occasion "i+1") by the total number of animals at risk at the beginning of the period (i.e., on occasion "i"). Thus, for the fourth period, there were 39 black ducks known to be alive at the beginning of the fourth period; the 39 in the denominator (Table 6.3). At the end of the fourth period, only 34 of those 39 black ducks were known to be alive; the 34 in the numerator. Thus, the fractional survival estimate is 34/39, and the decimal equivalent is 0.872. The binomial estimates should be considered when deciding upon a model, as they provide a nonparametric estimate of the survival probabilities. When using known-fate data in SURPH, the binomial estimates of survival will be identical to the SURPH survival estimates for the fully parameterized model. The fully parameterized SURPH model and the binomial model are two parameterizations of the same model. For this data set, because there are multiple periods but only one population, the fully parameterized model is the "St" model.*

The fully parameterized model does not significantly improve the fit. However, the binomial estimates (Table 6.3) do show some variation in survival probabilities for the different periods. It is possible that important differences in survival may be obscured by the 7 degrees of freedom in the overall likelihood ratio test (LRT). Because the binomial estimates suggest that the period-specific survival probabilities differ, it might be possible to explain the variation in survival probabilities as a function of one of the various temperature variables. Because the temperature variables are highly correlated with each other, four separate Analysis of Deviance (ANODEV) Tables were calculated, each based on only one of the group-covariate variables.

Table 6.3 Binomial survival estimates for the black duck data set. The decimal number on line 1 is the binomial survival estimate. The fraction on line 2 is the numbers of animals used to compute the decimal estimate.

	Period							
	1	2	3	4	5	6	7	8
Binomial Estimate	0.979 (47/48)	0.957 (45/47)	0.951 (39/41)	0.872 (34/39)	0.875 (28/32)	0.893 (25/28)	0.960 (24/25)	1.000 (24/24)

To analyze the effects of the "min<0" group covariate on survival, left-click on the ***Anodev Button*** *within the* ***S Group Pop-Up****. This causes the* ***Anodev Start Up Window*** *to appear. Select the group covariate "min<0", and left-click on the* ***Start Button****.*



An ***Analysis of Deviance Table*** *will appear shortly, with three default models fit. The three models are the Grand Mean Model, the Full Model, and the Total Covariate Model. Since the only covariate included in this analysis is "min<0", the Total Covariate Model is the model that has fit "min<0" (Figure 6.1).*

For each group covariate, a model was fit that included a parameter for the group covariate, and the fit of this model was compared to the Grand Mean and Full Models. Only the group covariate that counted the number of days that the minimum temperature was below freezing ("min<0") showed a statistically significant relationship to black duck survival (two-sided *p*-value = 0.039) (Figure 6.1). Therefore, it appears that the best model for the data is one that includes a baseline survival parameter and a parameter that relates the value of the group covariate "min<0" to the survival probability for each period.

All models that are created using the ANODEV procedure are not automatically transferred into the ***Master Models List****. Therefore, before a model that was fit under the ANODEV procedure can be accessed from within the SURPH Base Window, it must be manually transferred to the* ***Master Models List****. To transfer a model to the* ***Master Models List****, select the model from the ANODEV* ***Available Models List****, then left-click on the* ***Transfer Model to Master List Button****. Once the best fit model is in the* ***Master Models List****, select it. All future discussion will concern the best fit model.*

Once a model has been selected, the values of the estimated parameters, and the associated variance-covariance matrix (Figure 6.2) can be accessed under the **Models Button**.The fitted survival model for this data set can be written as: $S_i = S^{exp(\beta x_i)}$ or, with fitted parameter values

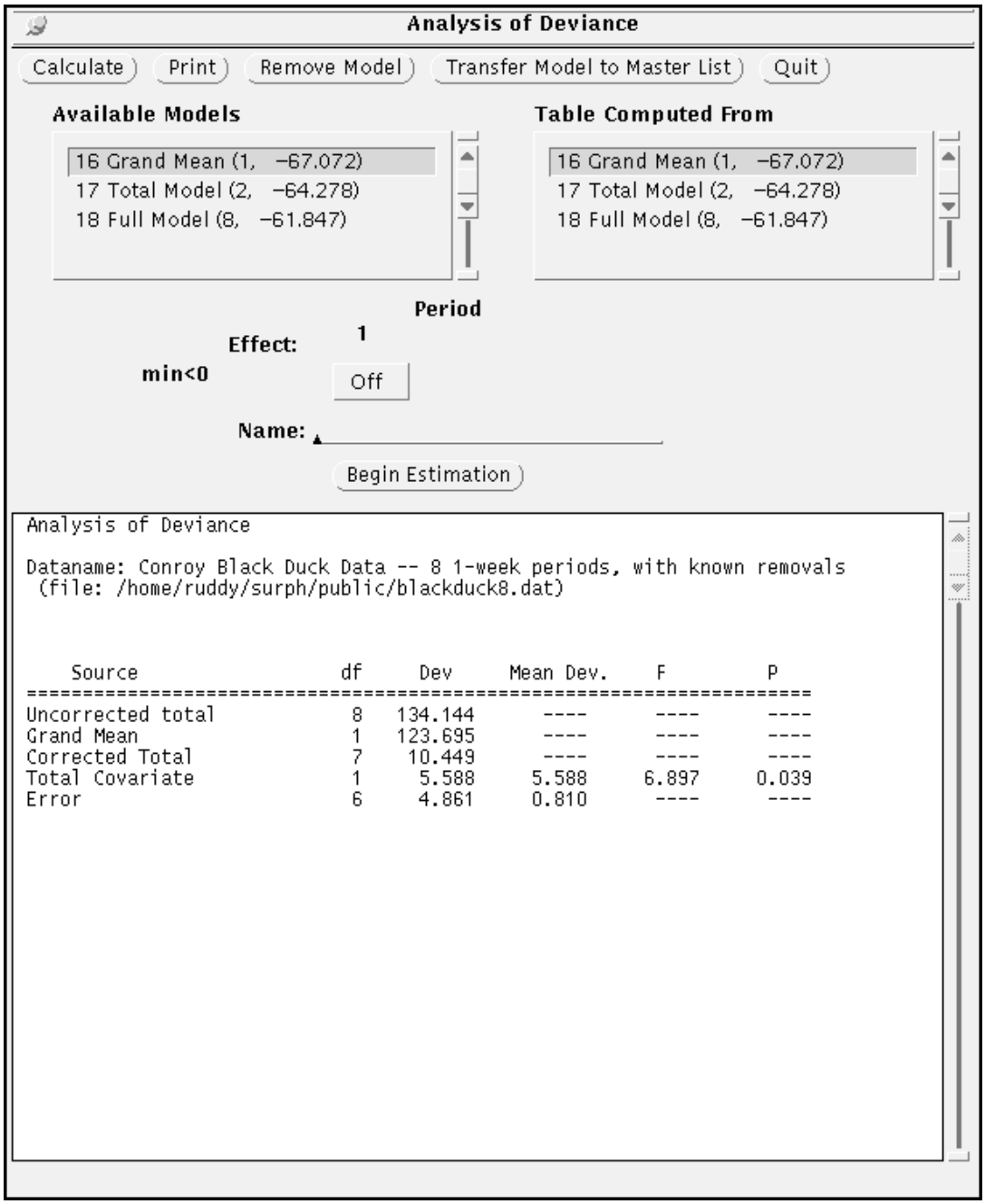


Figure 6.1 **Analysis of deviance window for the group covariate "min<0" using the black duck data set. The total covariate model in the ANODEV Table assesses the fit of the model that includes the group covariate "min<0". This analysis shows that inclusion of "min<0" significantly improves (*p*=0.039, two-tailed, *p*=0.020, one-tailed) the model fit.**

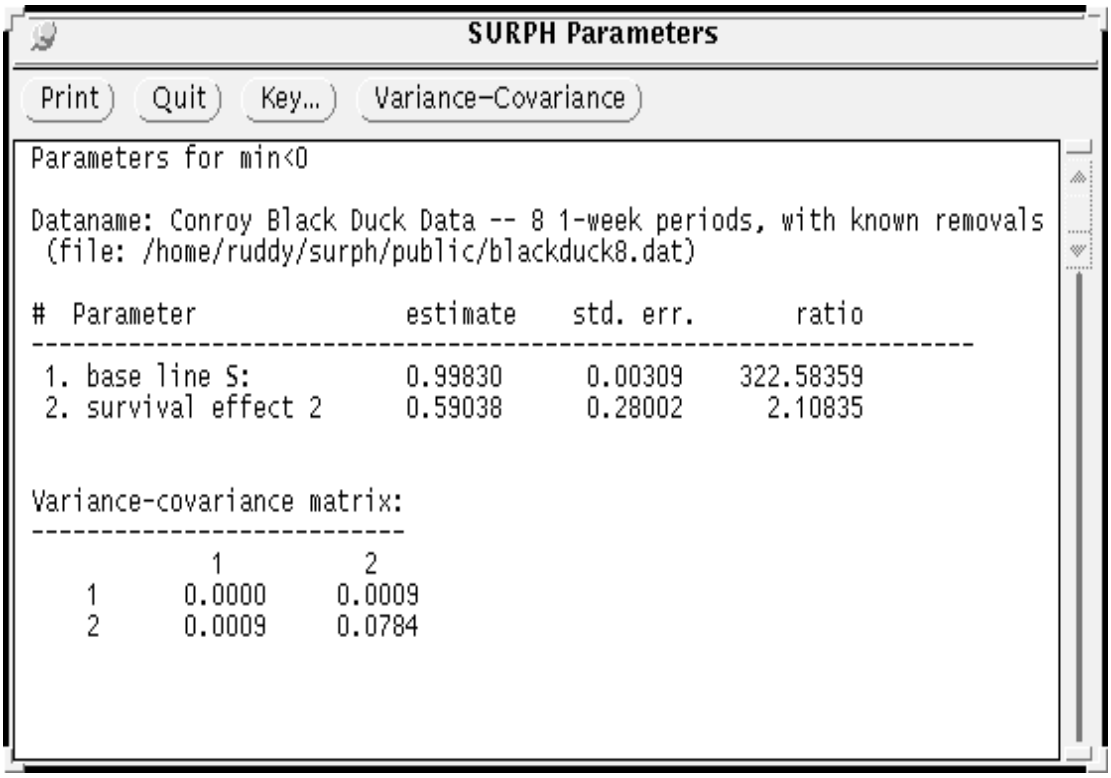


Figure 6.2 SURPH parameter estimates and the variance-covariance matrix for the model that includes the group covariate "min<0" using black duck data set.

as: $S_i = 0.9983S^{exp(0.59038\beta x_i)}$, where the x_i are the values of the time-variant group covariate "min<0".

*To access the **SURPH Parameters** for the best fit model, and to calculate the Variance-Covariance Matrix, follow the command sequence **Models Button -> SURPH Parameters**. This will access a pop-up window that displays the values of the **SURPH Parameters** for the model selected within the **Master Models List**. This pop-up will not have the variance-covariance matrix displayed at this point. To calculate the standard errors of the parameters, and to display the variance-covariance matrix, left-click on the **Variance-Covariance Button** within the **SURPH Parameters** pop-up window (Figure 6.2).*

To assess the fit of the model that includes the group covariate "min<0", several diagnostic plots can be examined. One plot compares the binomial survival estimates for each of the periods to the fitted curve under the SURPH model (Figure 6.3).

*To access the plot of the fitted model against the group covariate "min<0", select the best fit model from the **Master Models List**; then follow the command sequence **Models -> Survival Curves -> Group**. A group-covariate plot for survival will appear. To choose the desired covariate, go to the **Covariate Pull-Down Menu** in the bottom, left-hand portion of the window. Right-click on the down-arrow, then left-click on "min<0". The horizontal axis of this plot displays the range of the group covariate. The vertical axis of this plot displays the estimated survival probabilities for each period. The plot displays the binomial survival estimates ("bull's-eye" points) and the fitted SURPH curve for the selected model (Figure 6.3).*

The Group-Covariate Survival Curve shows that the SURPH curve appears to fit the binomial estimates well. The plot shows that the SURPH survival curve decreases with increasing numbers of days below freezing; or that survival decreases the longer a cold spell lasts.

The plot of the Binomial Estimates for period survival versus the SURPH model estimates (Figure 6.4) is another diagnostic used to assess how well the survival estimates from the fitted SURPH model correspond to the binomial estimates. If the SURPH survival estimates and the binomial estimates correspond, the displayed points should lie near the 45° line.

*Access the plot of **Binomial Estimates vs. SURPH Survival Estimates** (Figure 6.4), **(Models Button -> Binomial Estimates**). The values for the SURPH survival estimates are computed using the model that is currently selected within the **Master Models List**. The*

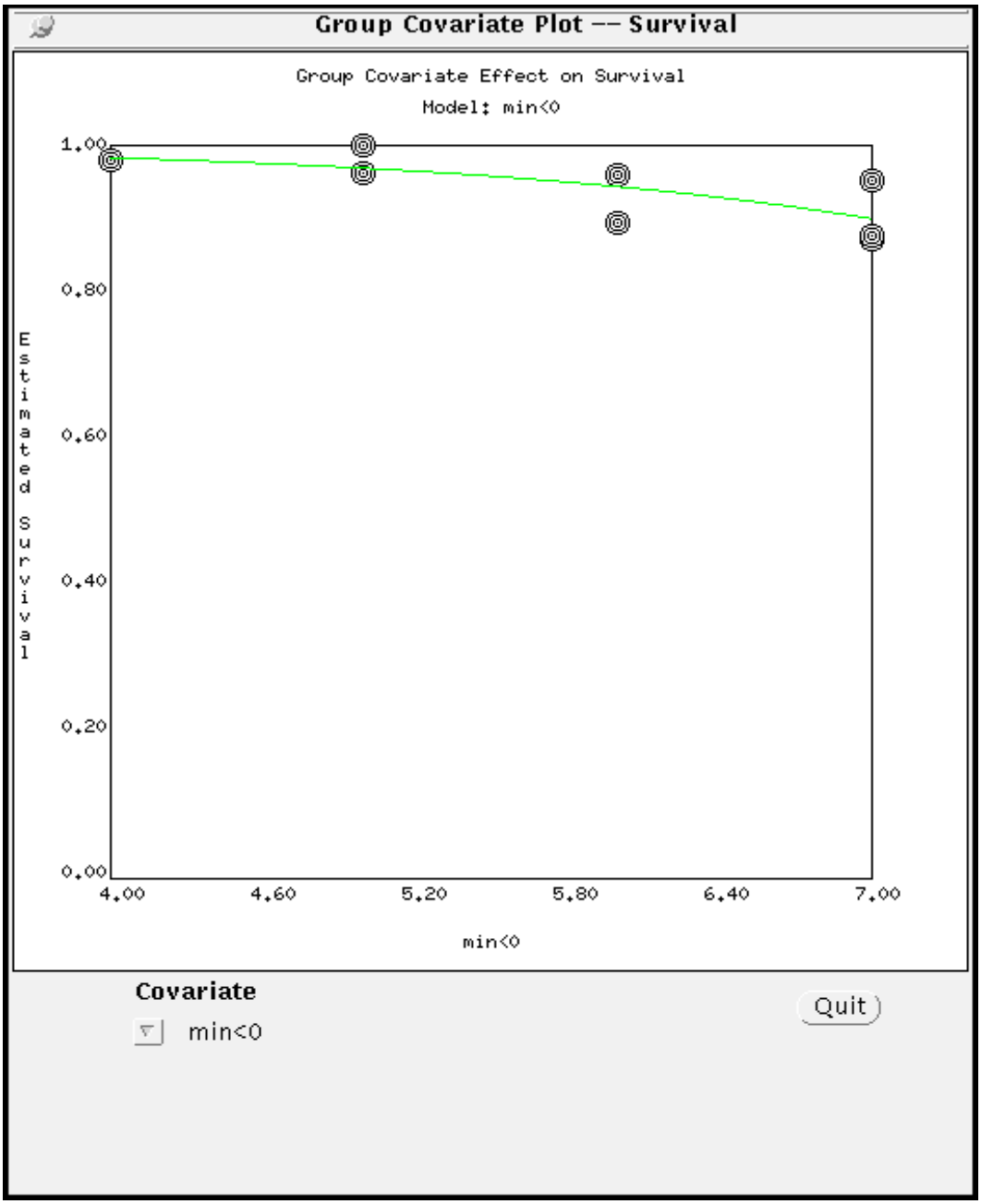


Figure 6.3 **The SURPH group covariate curve pop-up window plots the SURPH model estimates (fitted line) as a function of the group covariate "min<0". The large round ("bull's-eye") points displayed on the graph are the binomial estimates of survival for each period for the black duck data set.**

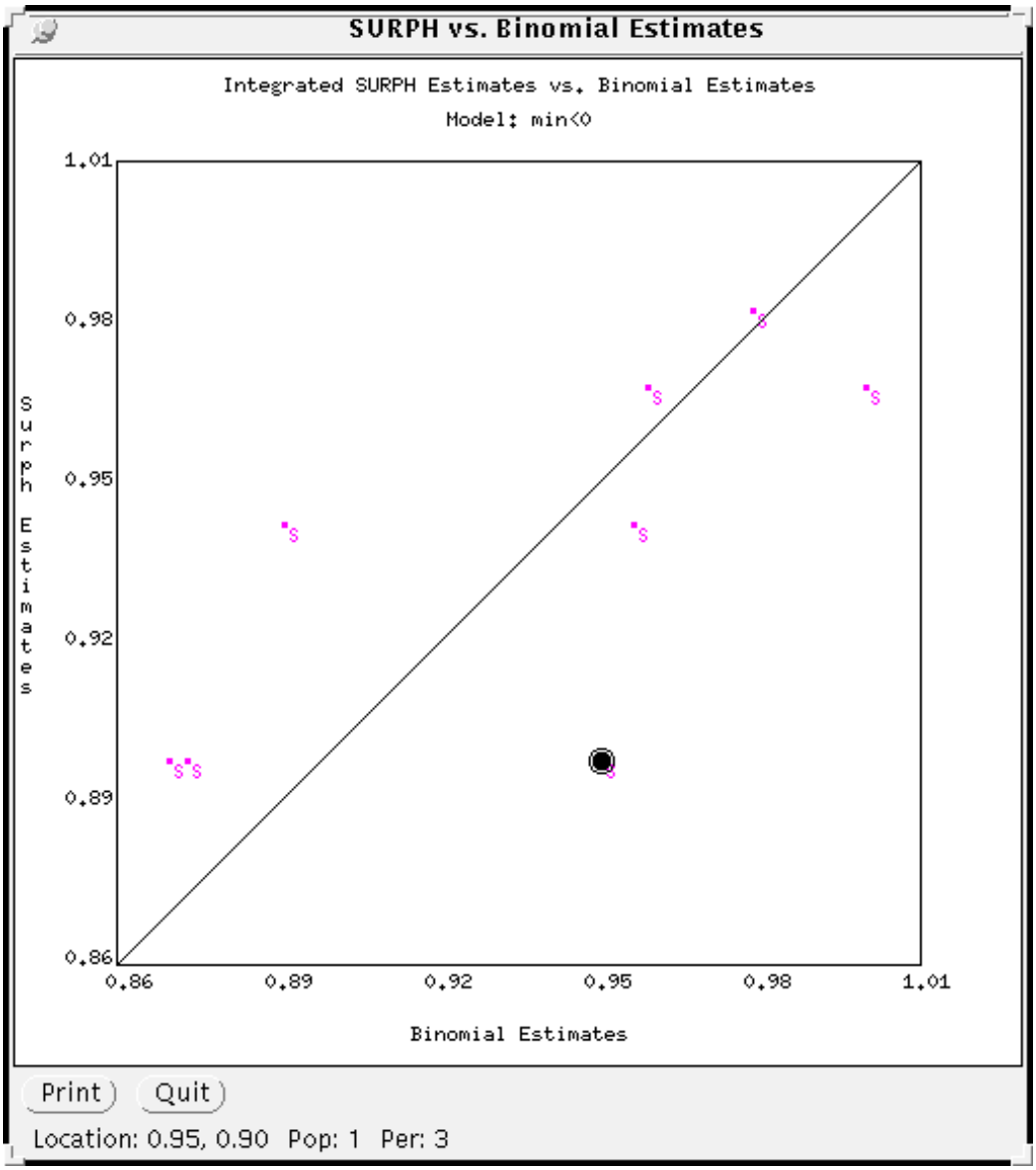


Figure 6.4 **The SURPH Survival Estimates for the model that includes the group covariate "min<0" versus the Binomial Estimates. A 45° line indicates where the two estimates are equal. In the example, the survival estimate for period 3 has been selected. The window footer displays the binomial estimate (0.95) and the SURPH estimate (0.90) for the selected point.**

vertical axis of this display are SURPH survival probability estimates. The horizontal axis of this display are binomial survival probability estimates. A 45° line is included to show the user where the two probability estimates are equal. Thus, if the SURPH estimates perfectly correspond to the binomial estimates, all points will lie along this line. A point may be selected from within the display. To select a point, position the mouse cursor above the point and left-click. The binomial and SURPH estimates for this point will be displayed in the window footer, as well as the population and period this point represents. In Figure 6.4, the selected point represents the binomial and SURPH estimates of survival for period 3. The binomial estimate is 0.95, whereas the SURPH estimate with the fitted covariate predicts a survival probability of 0.90.

This graphic shows some disparity between the two sets of estimates. However, the differences between the estimates are not great (the maximum difference between a binomial survival estimate and a SURPH survival estimate for any period is 0.05); and the current SURPH model is fit with 6 fewer parameters than the fully parameterized model (Figure 6.4). The fitted SURPH survival estimates for the selected model are also available in text form (Figure 6.5). The display gives the model estimate of survival for each period and the standard error of the estimate (in parentheses) (e.g., $\hat{S}_3 = 0.899$ with a standard error of 0.027).

*Access the SURPH estimates of survival (Figure 6.5) (**Models Button -> SURPH Probabilities**). The calculated estimates of survival displayed are for the model that is currently selected within the **Master Models List**. If the variance-covariance matrix for the selected model has not been computed, only the survival estimates for each period will appear. To display the standard errors of the estimates, left-click on the **Variance Button**.*

Based upon diagnostics and model fit, the model that includes the group covariate “min<0” provides an insight into the relationship between black duck survival and temperature. It appears that survival decreases the longer a cold spell lasts.

This data set also includes values for several individual covariates. The individual covariates are age, weight, wing length, and condition index. Analysis of the effects of individual covariates showed no significant contribution by any of the individual covariates to the model fit. Thus, discussions concerning the analysis of individual covariates are not included with this example.

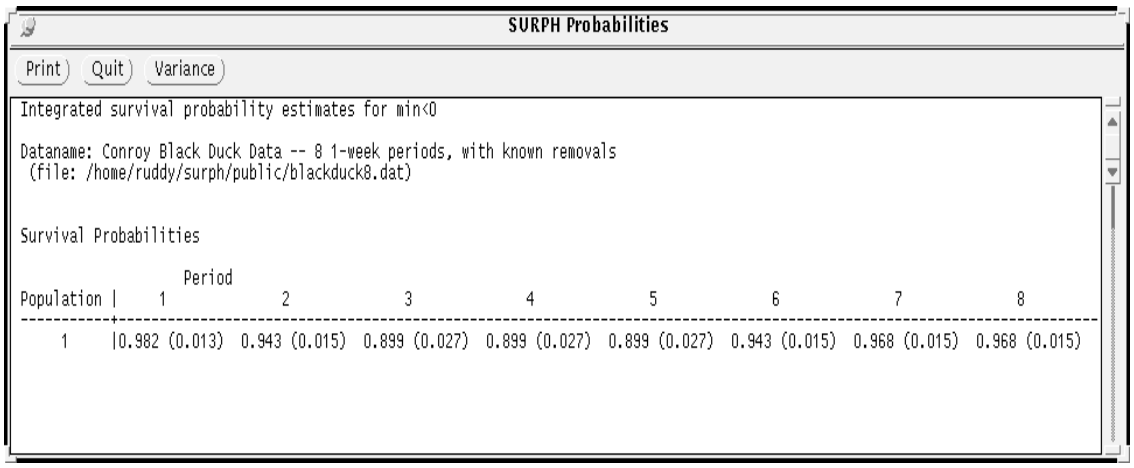


Figure 6.5 **Survival estimates for the model that includes an intercept parameter and a single regression parameter for the group covariate "min<0". The initial display gives only the survival probability estimates. To display the standard errors of the probabilities, it is necessary to left-click the Variance button in the control panel of this text pane.**

6.1.2 Northern bobwhite quail survival study

Researchers from The Institute of Wildlife and Environmental Toxicology (TIWET), Clemson University, Clemson, South Carolina, studied Northern bobwhite quail (*Colinus virginianus*) on nine sites in Iowa farmland in the spring of 1989. The study was part of a large-scale test of pesticide application methods. The study was designed with three treatments (pesticide application methods), randomized to the study sites in three blocks. For purposes of this illustration, the treatments and blocks were ignored; instead, three characteristics of the sites potentially related to survival were analyzed. This example analysis will focus on the relationship between the three site characteristics and survival probabilities on the seven sites that had sufficient data. (Table 6.4).

The researchers released adult Northern bobwhite quail onto the study sites using a staggered-entry design. Monitoring of the quail occurred over a 12-week period. For the purposes of this example, the data were collapsed into 6 two-week intervals. The number of release groups varied from site to site. Table 6.5 lists values by site for the habitat covariates "proportion edge," "proportion cropland," and "proportion pond" used in the survival analysis. Under typical circumstances, a simple regression of habitat traits versus survival at the seven sites would be conducted. However, the circumstances are exacerbated by the potential to conduct such a regression analysis on each of the 5 period-specific survival estimates. Such classical approaches to the survival analysis ignore the fact that the repeated survival estimates of a site are correlated and the propagation of experimental-wise Type I error rate with repeated analysis.

To begin the SURPH session, at the prompt, type "surph bobwhite.dat".

> surph bobwhite.dat

Left-click on the ***Known-Fate Button.*** *This begins the program for known-fate data analysis and loads the datafile "bobwhite.dat".*

With multiple populations and more than three sampling occasions, there are four basic survival models that can be constructed. These basic models assess the spatial and temporal variability of survival, but do not allow the user to infer any relationship between the survival

Table 6.4 Data from 1989 radiotelemetry study of Northern bobwhite quail in Iowa farmland. Numbers within the table represent numbers known alive from each release group on each occasion.

Populations	Occasion					
	1	2	3	4	5	6
#1	4	3	2	2	1	0
(3 release groups)			1	0	0	0
				3	3	3
#2	2	2	2	2	1	1
(3 release groups)		3	3	2	2	0
					1	1
#3	4	3	1	0	0	0
(3 release groups)		1	1	1	1	1
			1	1	1	0
#4	1	1	0	0	0	0
(5 release groups)		2	2	2	1	0
			1	1	1	1
				1	1	1
					2	2
#5	5	4	4	2	2	1
(4 release groups)			2	2	0	0
				1	1	1
					2	1
#6	2	2	2	2	2	2
(4 release groups)		2	2	1	0	0
				1	1	1
					2	1
#7	4	4	3	2	2	2
(3 release groups)		1	0	0	0	0
			2	2	1	0

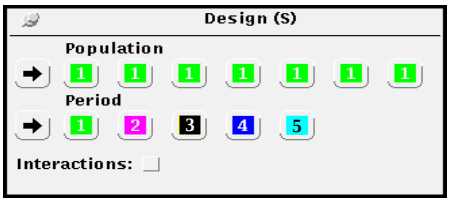
Table 6.5 Period-specific binomial estimates of survival and site characteristics for the 1989 radiotelemetry study of Northern bobwhite quail in Iowa farmland.

				Binomial Estimates				
Population	Proportion Edge	Proportion Crop	Proportion Pond	$\hat{S}_1$	$\hat{S}_2$	$\hat{S}_3$	$\hat{S}_4$	$\hat{S}_5$
1	0.040	0.69	0.019	0.75 (3/4)	0.67 (2/3)	0.67 (2/3)	0.80 (4/5)	0.75 (3/4)
2	0.040	0.56	0.004	1.00 (2/2)	1.00 (5/5)	0.80 (4/5)	0.75 (3/4)	0.50 (2/4)
3	0.075	0.90	0.008	0.75 (3/4)	0.50 (2/4)	0.67 (2/3)	1.00 (2/2)	0.50 (1/2)
4	0.020	0.63	0.008	1.00 (1/1)	0.67 (2/3)	1.00 (3/3)	0.75 (3/4)	0.80 (4/5)
5	0.030	0.63	0.000	0.80 (4/5)	1.00 (4/4)	0.67 (4/6)	0.60 (3/5)	0.80 (4/5)
6	0.060	0.89	0.000	1.00 (2/2)	1.00 (4/4)	0.75 (3/4)	0.75 (3/4)	0.80 (4/5)
7	0.110	0.92	0.000	1.00 (4/4)	0.60 (3/5)	0.80 (4/5)	0.75 (3/4)	0.67 (2/3)

probabilities and independent variables. The four basic design effects models are: (1) the model that has a single survival parameter, the “S” or Grand Mean Model; (2) the model that has a common parameter for all populations but a unique survival parameter for each period, the “St” or Period Means Model; (3) the model that has a common parameter for all periods but a unique survival parameter for each population, the “Ss” Model; and (4) the model that has a unique survival parameter for each period, each population, and for all interactions between the periods and populations, the “Sst” or Full Model.

*Go to the **Modeling Pull-Down Button**, and bring up the button pads for **S Design** and **S Group** (**Modeling -> S Design** and **Modeling -> S Group**). Using the Quick Buttons on the left side of the **S Design Button Pad**, left-click to change the buttons to all “1’s”.*

S Model



St Model

Ss Model

Sst Model

*In the **Name** field in the SURPH Base Window, enter the name “S” or Grand Mean Model. Left-click on **Begin Estimate** to estimate the parameter value for model “S”. Once the model “S” has been fit, change the button settings, again using the Quick Button, to “1, 2, 3, 4, 5” in the bottom row (Period), but keep the top row (Population) all “1’s”. In the **Name** field in the SURPH Base Window, enter the name “St” or “Period Means Model”. Left-click on **Begin Estimate** to estimate the parameter values for model “St”. Then, fit the “Ss” model, with unique parameters for each population (top row of **S Design** is “1, 2, 3, 4, 5, 6, 7”) and a common parameter for all periods (bottom row of **S Design** is all “1’s”). Finally, fit the “Sst” or “Full Model,” with a unique parameter for each population and period. Check the interactions box to fully parameterize this model.*

*To access the **Binomial Estimates** (Table 6.5), use the command sequence **Data -> Binomial Estimates**. A pop-up window will appear that gives the binomial estimates for each period and population. In period 3, population 5, there were 6 bobwhite known to be alive at the start of period 3. Of these, 4 were known to be alive at the end of period 3. Thus the binomial estimate for period 3, population 5 is (4/6) or 0.667. Recall from Section 6.6.1 that the binomial estimates of survival are identical to the SURPH survival estimates for the fully parameterized model. For this data set, because there are multiple populations and multiple periods, the fully parameterized model is the "Sst" model.*

Of the four basic survival models, the "S" model is the most parsimonious model that adequately fits to the bobwhite data based on the LRT. Comparing the survival estimates from the SURPH model ("S") to those from the binomial estimates (Table 6.5), this result is somewhat surprising since the binomial estimates for survival range from 0.500 to 1.000. However, since the sample sizes for many of the estimates are very small, there is little power to detect statistically significant differences in survival probability estimates.

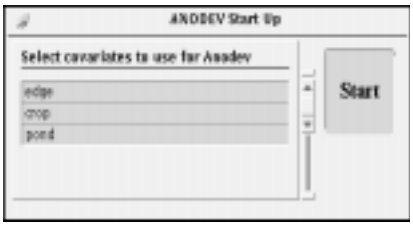
Analysis of deviance was used to investigate survival-habitat relationships. The site specific habitat characteristics were proportion of habitat edge to total area, proportion of site covered by ponds, and proportion of site planted in crops ("edge", "pond", and "crop", respectively). Unlike the black duck example (Section 6.1.1), where each covariate was analyzed with a separate analysis of deviance, all group covariates in this case were analyzed concurrently. The ANODEV fits three standard models: (1) the "Full Model" (35 parameters; this is also the "Sst" Model), (2) the "Period Means Model" (5 parameters; this is also the "St" Model), and (3) the "total covariate model," which has unique parameters to account for period effects (Period Means Model) and adds a unique parameter for each covariate in each of the five periods (20 parameters: 5 {for Period Means Model} + 15 {for a unique parameter for each of five periods for each of three group covariates}). These calculations yield an ANODEV Table that partitions the total deviance into a corrected total deviance, a total covariate deviance, and an error deviance. Within each period, the total covariate deviance was partitioned into the single degree of freedom contributions of "crop", "edge", and "pond" (Table 6.6).

*To analyze the effects of adding group covariates to the model, left-click on the **Anodev Button** within the **S Group Button Pad** (**Modeling -> S Group -> Anodev**). This causes the **Anodev***

Table 6.6 Analysis of deviance table for 1989 radiotelemetry study of Northern bobwhite quail in Iowa farmland.

Source	df	Deviance	Mean Dev.	F	P(F)
Total	35	143.670			
Pd Means	5	125.074			
Corrected Total	30	18.596			
Model Total	15	8.118	0.539	0.770	.690
Period 1	3	1.164	0.381	0.545	.659
pond	1	0.715	0.715	1.021	.328
edge|pond	1	0.161	0.161	0.229	.639
crop|edge, pond	1	0.288	0.288	0.413	.530
Period 2	3	5.266	1.755	2.513	.098
edge	1	1.840	1.840	2.628	.126
pond| edge	1	3.192	3.192	4.557	.050
crop|pond, edge	1	0.234	0.234	0.335	.571
Period 3	3	0.050	0.017	0.024	.995
crop	1	0.026	0.026	0.038	.848
edge| crop	1	0.017	0.017	0.024	.879
pond| edge, crop	1	0.006	0.006	0.009	.927
Period 4	3	0.747	0.249	0.357	.785
pond	1	0.323	0.323	0.462	.507
crop|pond	1	0.405	0.405	0.582	.457
edge|crop, pond	1	0.017	0.017	0.025	.878
Period 5	3	0.891	0.297	0.425	.737
edge	1	0.203	0.203	0.290	.598
crop| edge	1	0.644	0.644	0.923	.352
pond| crop, edge	1	0.044	0.044	0.063	.806
Error	15	10.4778	0.699		

Start Up window *to appear. Select all of the group covariates, and left-click on the* ***Start button****.*



An ***Analysis of Deviance Table*** *will appear shortly, with the three default models fit. The three default models are the Period Means Model, the Full Model, and the Total Covariate Model. The total covariate deviance is based on 15 degrees of freedom. These 15 degrees of freedom can be partitioned into the separate contributions of the three group covariates in each period, each effect with a single degree of freedom.*

The total covariate deviance can be decomposed into the five orthogonal period contributions. The three degrees of freedom for each period can be further decomposed into the contributions of the covariates within each period (Chapter 3). The contributions of the covariates within each period are not orthogonal (i.e., the value obtained for the contribution depends on the order in which the covariates are added to the model). For each period, a stepwise procedure was used. At each step, the covariate that resulted in the greatest reduction in deviance was added to the model.

Use the ***ANODEV Table*** *to investigate the influence of each group covariate. The ANODEV window can be divided into two portions: (1) The top portion, a control panel, which allows the user to create, name, and manipulate models; and (2) the bottom portion, a text pane, which displays the* ***ANODEV Table****.*

To add an effect to the model, use the buttons within the top portion on the ***ANODEV Table****. Left-clicking on a button changes its designation from "Off" to "On" or vice versa. When a button is "on" ("depressed"), a parameter will be included to estimate the effect of the covariate in the corresponding period. For example, in the top portion of Figure 6.6, all buttons are depressed for the first two periods. This means that 6 effect parameters will be estimated (in addition to the Period Means Model) that will account for the effects of edge, crop, and pond in the first two periods.*

To compute an ***ANODEV Table****, complete the following steps:*

1) Run the three default models using the ANODEV option (described above).

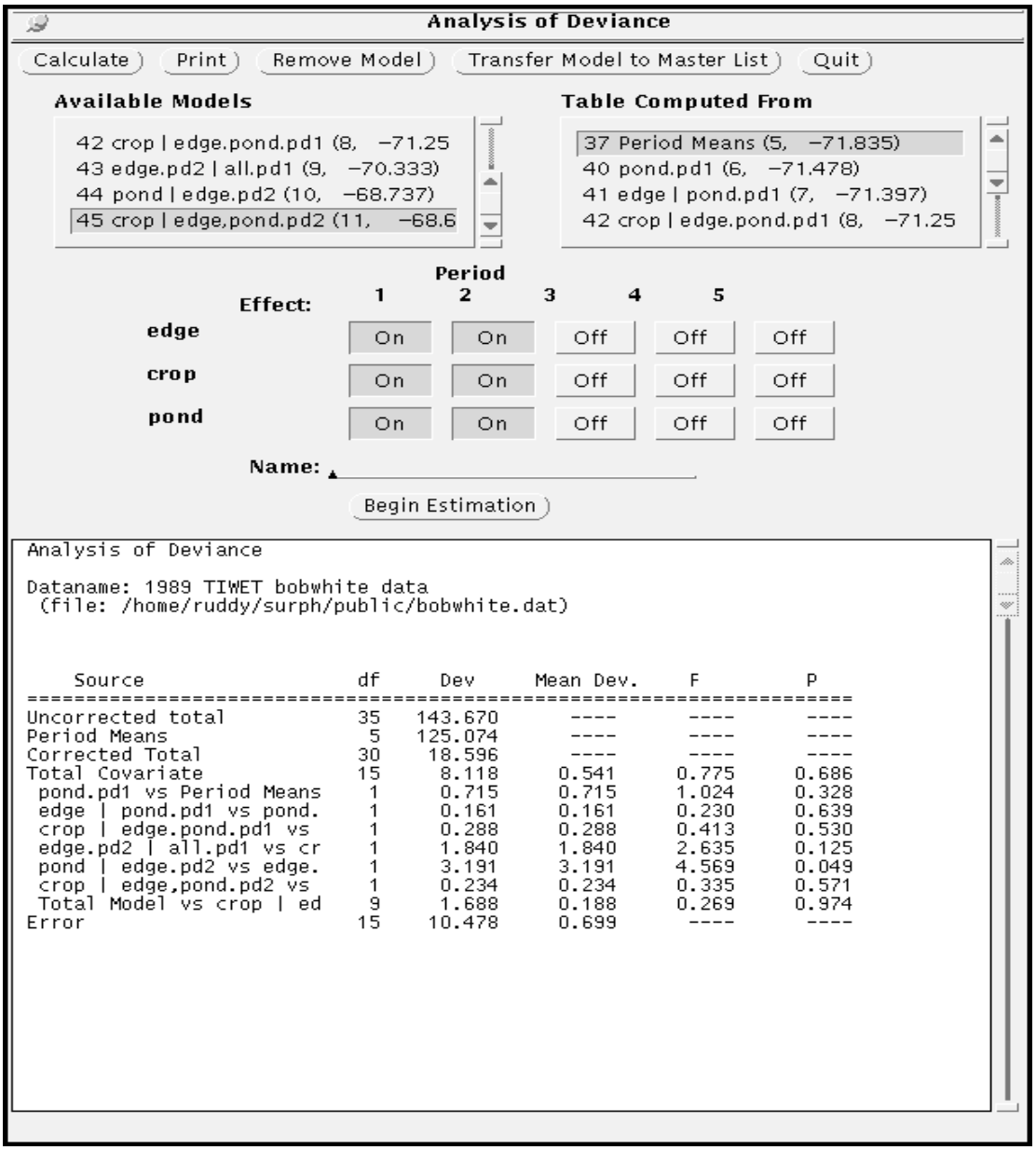
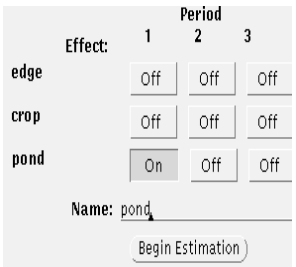
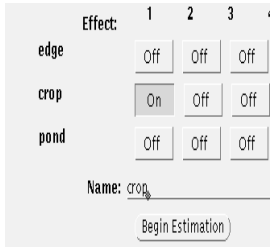
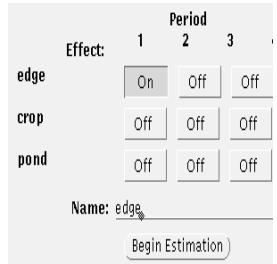


Figure 6.6 **The Analysis of Deviance Table for the Northern bobwhite quail data with the three group covariates included. This ANODEV Table has partitioned the total covariate deviance into the contributions from the first and second periods. The only variable that is statistically significant is pond | edge in period 2 (*p*=0.049, two-tailed).**

2) *Separately run all single-parameter, group-covariate models for a particular period. For this data set, this would involve running a separate model that included a pond effect only, a crop effect only, and an edge effect only (see below).*







3) *Select (left-click) one of the group-covariate models calculated in Step 2 from the* ***Available Models List****. Left-clicking on the model name in the* ***Available Models List*** *will transfer a copy of the model from the* ***Available Models List*** *to the* ***Table Computed From List****.*

4) *Left-click on the* ***Calculate Button****. This will create the* ***ANODEV Table****. Note the amount of deviance explained by each model.*

5) *Select the group-covariate model from the* ***Table Computed From List*** *and left-click on* ***Remove Model Button****. This will delete the copy of the group-covariate model from the* ***Table Computed From List****. Go to Step 3 and repeat until all single-parameter, group-covariate models have been analyzed.*

6) *Add the single-parameter, group-covariate model that explained the greatest amount of deviance to the* ***Table Computed From List****. Go to Step 2, and run all two-parameter models that include the best single-parameter model. Continue this stepwise process until all group covariates have been added for the period. In Figure 6.6, notice that in Period 1, pond was added first, followed by edge, then crop. In Period 2, edge was added first, then pond, then crop.*

Analysis of Deviance Tables *can only be computed using hierarchical or nested models. When a model that is not nested within the* ***Table Computed From List*** *is selected from the* ***Available Models List****, a warning pop-up will appear that states, "This model is not sorted within the list." When such a message appears, it may be necessary to remove models from the* ***Table Computed From List****, using the* ***Remove Model Button****.*

The analysis indicates there is slight evidence for a pond effect in the second period (Table 6.6). However, in the model that contains a single parameter for pond in the second period, the effect is not statistically significant ($\alpha = 0.10$). The effect of the pond variable is only significant

if an edge effect for the second period is included first, then the pond effect is added. Thus, even though there is slight evidence of a pond effect in the second period, the result is so tenuous as to suggest that the Period Means Model is the best model.

Once a model has been chosen, several diagnostics can be examined to assess model fit. Residual plots can be used to show if estimates from the SURPH model are close to the observed survival histories (Figure 6.7). If the model fits the data well, then most of the residual points should lie within the range [-2,+2].

*To access the plot of **Residuals versus Survival History**, use the command sequence **Models -> Residuals Plots -> vs. Survival History**. The values for the SURPH survival estimates are computed using the model that is currently selected within the **Master Models List**. The vertical axis of this display is the value of the standardized residual. In normal theory, 96% of the residual points should lie in the range [-2,+2]. The horizontal axis of this display is the decimal equivalent to the survival history. Because survival histories without censoring are composed entirely of strings of "1's" and "0's", each survival history can be thought of as a binary number. The horizontal axis of this graph is the decimal equivalent to the binary number the survival history represents. For example, the history 111111 has a decimal equivalent of 63 (Chapter 7). Points can be selected from the display. Position the mouse cursor above the point and left-click. The population, survival history, observed value, expected value, and residual value for this point will be displayed in the footer of the window. The observed value is the number of animals within the population that had the corresponding survival history. The expected value is the product of the survival probabilities associated with the survival history, estimated using the SURPH model, times the number of animals released. For example, in Figure 6.7, the selected point is from Population 6, and has a survival history of 111111. This survival history translates into surviving throughout the entire study. The probability of surviving all periods is the product of the individual probabilities for surviving each period. Thus, the probability of observing 111111 for this data set is (0.28). Two animals had this survival history. The model predicts only 0.55 animals would have this survival history, resulting in a standardized residual for this survival history of 1.01.*

Examination of the residuals versus survival history plot indicates that the Period Means Model fits reasonably well. All points have standardized residuals that fall within the range [-2,+2].

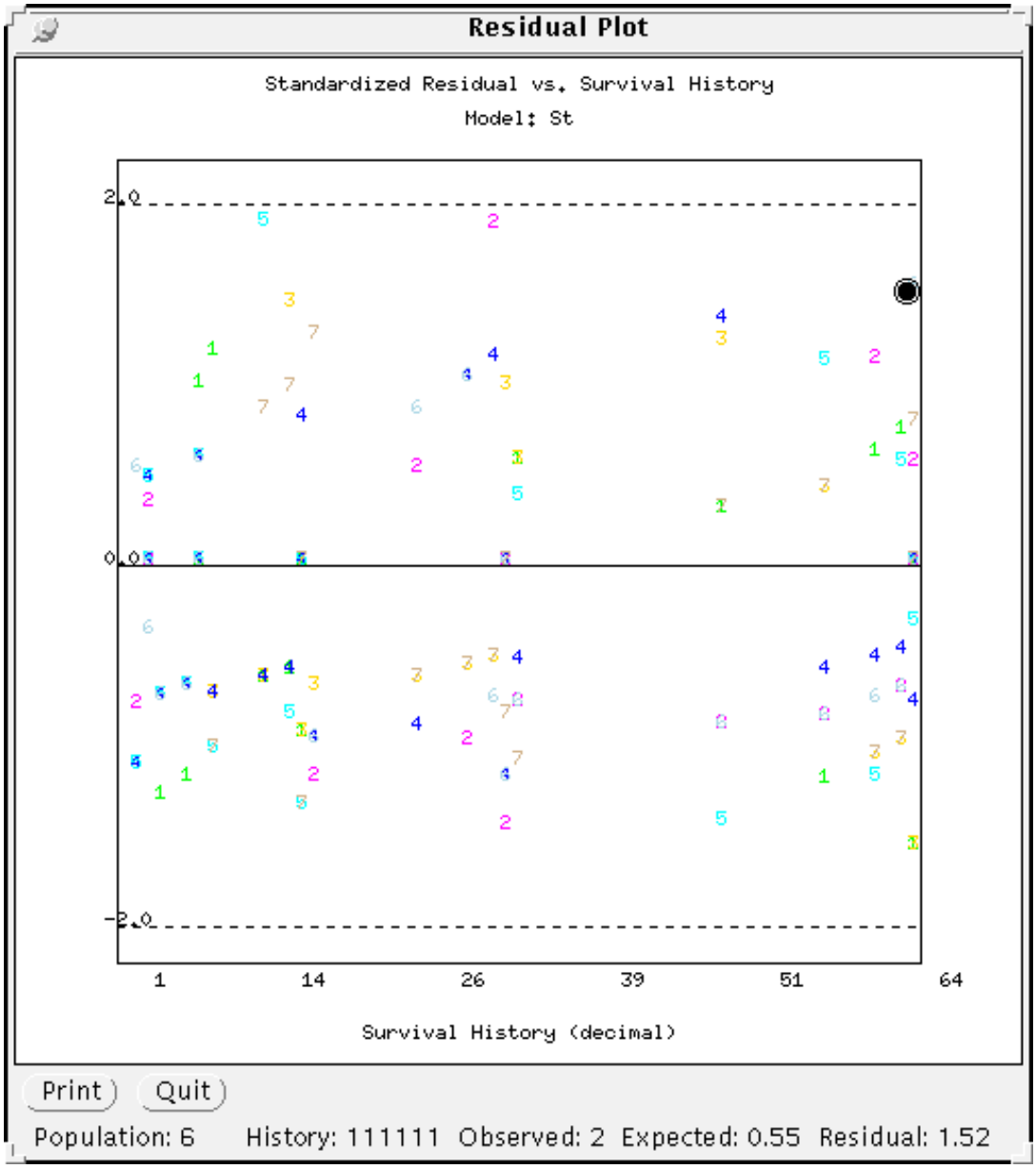


Figure 6.7 **This plot displays the value of the standardized residuals [using an Anscombe transformation (McCullagh and Nelder 1983)] versus the decimal equivalent of the survival history for the Period Means Model using the bobwhite data. The small black circle in the upper right-hand corner indicates a survival history that was selected by the user. Text in the window footer indicates that the selected point is from population 6, has a survival history of 111111, and that 2 animals with this survival history were observed, while only 0.55 animals were expected, resulting in a standardized residual of 1.52.**

A second diagnostic is the SURPH versus Binomial Estimates plot (Figure 6.8). This plot displays the disparity between the binomial estimates of survival (the fully parameterized model—“Sst”), and the SURPH estimates of survival (a reduced model). Instructions on how to access this plot are available in Section 6.1.1—the black duck example. The SURPH versus Binomial Estimates plot indicates that there is some disparity between the model and the binomial estimates. Notice that the points form a series of horizontal lines. This is because the Period Means Model has a single survival probability for each period for all populations. Examination of this plot indicates that the greatest differences between the model and the binomial estimates occurs during the second period. This suggests that something is not being accounted for during the second period. The “pond | edge” effect was marginally significant in the second period, and may partially explain this disparity. However, even when the pond and edge effects are fit in the second period, the residual and binomial plots do not improve drastically. Recall that this data set was selected from one that had treatment and block factors, but that these were ignored for purposes of this example. Of course, for the true data set, the treatment and block effects would not be ignored; and it may be that these effects could explain the disparity observed in the example data set.

Overall, the Period Means Model appears to fit the data adequately, with the possible exception of the second period. It may be that site-specific habitat characteristics do significantly effect the survival of bobwhite quail. However, from the current study, such a conclusion is tenuous. Part of the problem lies with the small release sizes, which do not allow for much power to determine specific effects unless those effects are substantial. Larger release sizes or more sites would be needed to confirm or refute these conclusions.

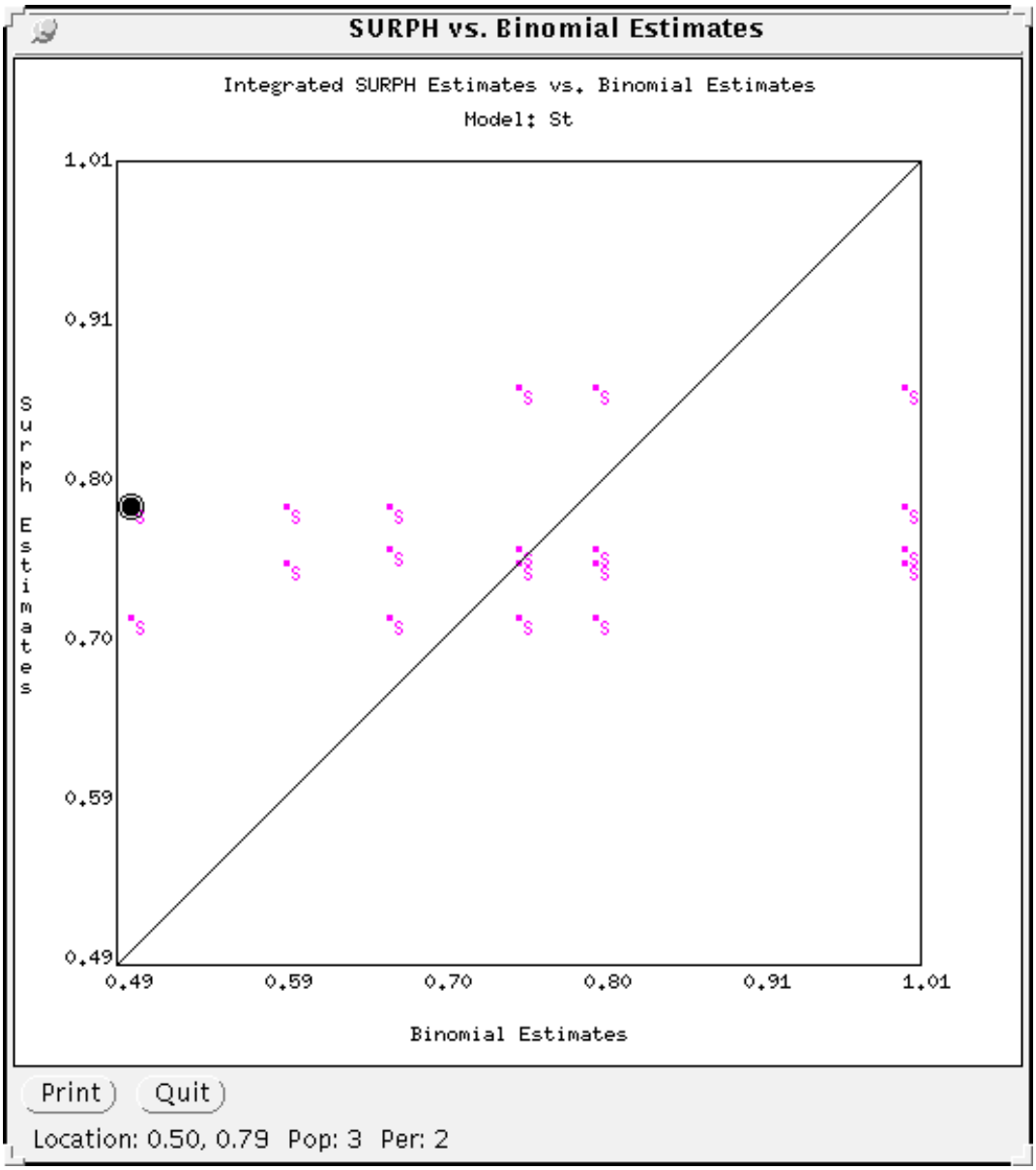


Figure 6.8 **The plot of the SURPH survival estimates versus the binomial estimates for the Period Means Model using the bobwhite data. The selected point indicates that population 3 in period 2 has a binomial estimated survival probability of 0.50, and a period means estimated survival probability of 0.79.**

6.1.3 Blue mussel survival study

A known-fate study of the blue mussel (*Mytilus edulis*) was conducted on a 15 x 10 m area on the west bank of Jackson Beach Biological Preserve, Friday Harbor, WA (Hoffmann 1992). The major predators were whelks (*Thais canaliculata*) that feed on mussels during high tide. During this study, low tides that exposed the study area occurred during the day, forcing the whelks to retreat to avoid desiccation. The purpose of this study was to determine the relationship between the size and tidal height of individual blue mussels and their survival.

The study design was a single-population multiple-release design. Two samples of mussels were marked by etching a number into the shell of each and coloring the number with a bright enamel. The first sample of 99 mussels was marked on 9 July 1991 and the second sample of 50 mussels on 24 July 1991. Resighting attempts occurred on 24 July, 8 August, and 25 August 1991 to coincide with tides that exposed the study area. The periods between surveys were approximately 2 weeks each and the sampling occasions lasted approximately 4-6 hours. Mussels that were not resighted were assumed to have died during the previous survey period.

Three covariates, functions of size of the mussel and location, were measured at the time of marking each mussel. “Width” of the mussel was measured across the lateral dimension, “depth” of the mussel was measured across the dorsal-ventral plane, and “height” by its elevation above or below an arbitrarily chosen beach mark. A fourth covariate, “size”, was computed as the maximum cross-sectional area (*Size = width x depth*). Average group size and tidal height have previously been recognized in the literature as factors influencing the survival of mussels (Suchanek 1979; Paine 1971, 1980, 1984; Palmer 1980). It is likely that two potential mortality sources, predation and physiological stress (Suchanek 1979) discriminated among individuals on the basis of size and tidal height. Marked mussels in this study represented a wide range of sizes and tidal heights. The range of sizes and heights are illustrated using SURPH output of histograms of covariates (Figures 6.9 and 6.10). The data can be found in mussel.dat. There are no group covariates.

*Go to the **Data Pull-Down Menu** on the SURPH Base Window, and bring up the pop-up window for **Individual Covariates** (**Data -> Individual Covariates**). This will access a*

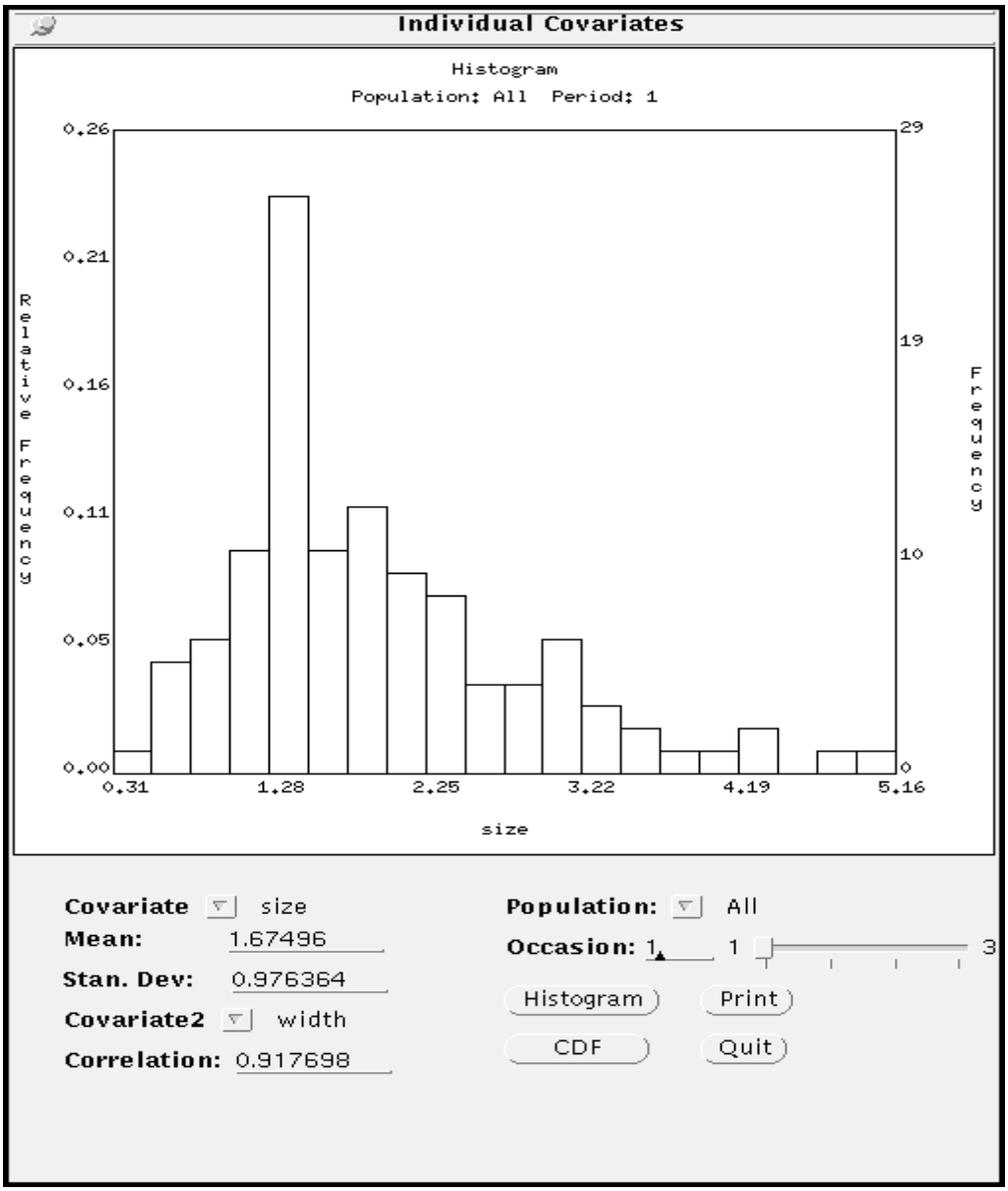


Figure 6.9 **A plot of the range of sizes of marked blue mussels on the first[t] sampling occasion (Occasion 1). The left vertical axis is the relative frequency, the right vertical axis is the absolute frequency, and the horizontal axis is the range of sizes in the study.**

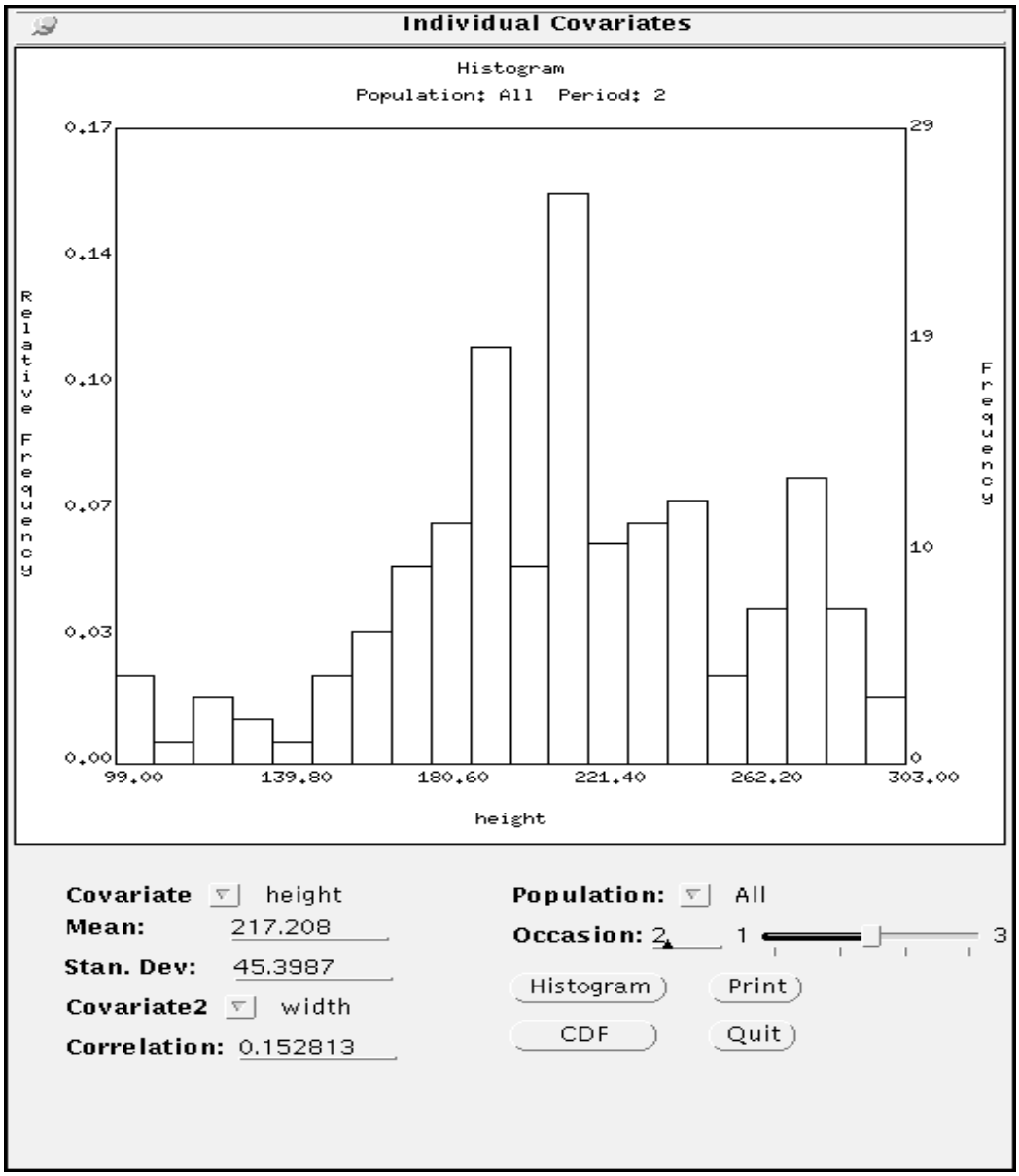
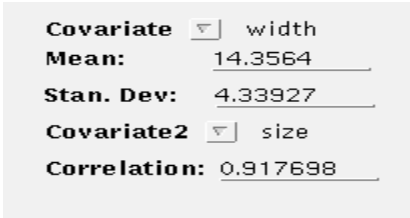


Figure 6.10 A plot of the range of tidal heights above the arbitrary set point for marked mussels known to be alive immediately after the second occasion (Occasion 2).

pop-up window that displays a histogram of the individual-covariate values, the mean and standard deviation of the displayed covariate, and the correlation between the selected covariate and any other individual covariate the user selects. This window also allows you to follow the values of the individual covariates through time (use the slide bar to change occasion) for one or all populations (Use the ***Population Pull-Down Menu*** *to display the covariate values for another population. This is not important for this example since there is only one population.). To compute the correlation between "width" and "size", select "width" from the* ***Covariate Pull-Down Menu****, and select "size" from the* ***Covariate2 Pull-Down Menu*** *(see below). To reproduce either Figure 6.9 or 6.10, select size or height respectively from the* ***Covariate Pull-Down Menu****.*



One way to investigate which of the individual covariates may affect the survival process is to use the CDF plot, and the associated Kolmogorov-Smirnov (K-S) test statistic (Zar 1984), available from the **Individual Covariates** pop-up window. The K-S test statistic is used to determine whether those individuals known to be alive share a common distribution with those individuals not known to be alive. Since all individuals begin the study alive, the CDFs can be used to determine whether individuals are dying in a random fashion, thus both CDFs would be similar for each occasion, or if there is some pattern to the deaths, in which case the CDFs would diverge.

On the lower right-hand corner of the ***Individual Covariate*** *pop-up window, left-click on the* ***CDF Button****. This will change the histogram display to a cumulative distribution function display (Figure 6.11). The green (dashed) line displays the CDF of the individual covariate for individuals that were known to be alive on the occasion selected. The purple (solid) line displays the CDF of the individual covariate for individuals that were not known to be alive on the occasion selected. Select "size" from the* ***Covariate Pull-Down Menu****, and move the slide*

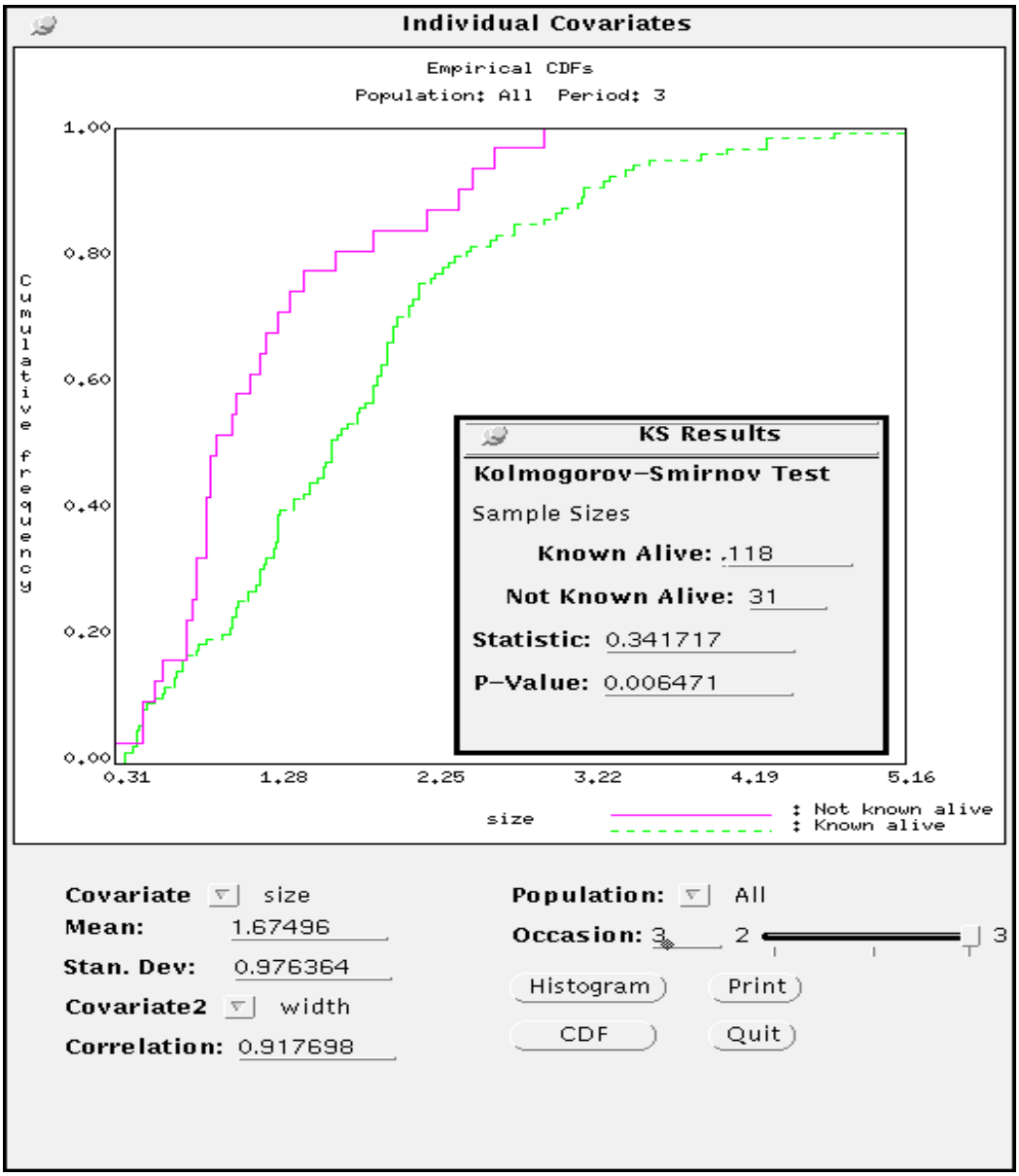
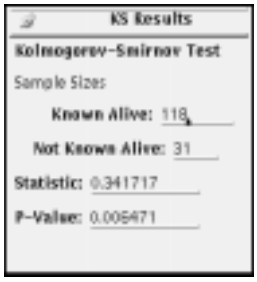


Figure 6.11 **The CDF plot indicates that mussels of smaller size are significantly less likely to be alive by the third occasion (Occasion 3). The difference between the two CDF curves attains a maximum value of 0.342. Under the Kolmogorov-Smirnov Test, the p-value (0.006) indicates the probability of observing such a difference if the two distributions were equivalent. Thus, it is unlikely that the difference observed is a chance occurrence due to sampling.**

*bar between occasions 2 and 3. A **K-S Results** pop-up window that displays the results of a Kolmogorov-Smirnov Test of equality between the two CDFs will automatically appear.*



For both occasions, using the individual covariate "size", there is a significant difference ($p < 0.01$) between the two CDFs. Smaller mussels are less likely to be known alive. The **K-S Results** pop-up window also displays the sample size for each of the CDFs and the value of the test statistic. Individual covariates that have significant K-S tests are candidates for evaluation of individual effects in subsequent SURPH survival modeling.

A comparison of two design effects models available for survival indicates that the "St" model has a significantly better fit than the "S" model ($p = 0.024$). Regardless of the results of this test, when fitting an individual-covariate model it is advisable to use a fully parameterized design effects model (Hoffmann 1993). Little power is lost if the fully parameterized design effects model is overly general. There is a desire to attribute only individual effects to the individual covariates, while avoiding spurious effects due to incorrect parameterization of the design effects model. Thus, beginning with the fully parameterized design effects model—the "St" model for this data set—fit a variety of models that include the individual covariates. Several of the individual covariates (e.g., width and size, width and depth) are highly correlated, as is expected since they are either functionally or biologically related. Thus, it should be expected that similar fits may be achieved with several of the individual covariates.

Examination of the binomial estimates (Table 6.7) shows high survival throughout the study, but different survival probabilities for the different periods. Because the release sizes were quite large, even small differences in survival were statistically detectable. This is why the fully parameterized "St" model was selected, even though the range of survival probabilities is relatively small [0.825, 0.939]. Recall in the bobwhite example that the range of survival probabilities was [0.500, 1.000], but due to small release sizes, there were no statistically

Table 6.7 Binomial estimates of period-specific survival of blue mussels at Jackson Beach Biological Preserve, Friday Harbor, WA. The upper decimal number is the binomial survival estimate. The lower fraction gives the numbers of animals used to compute the binomial estimate.

	Period		
	1	2	3
Binomial Estimate	0.939 (93/99)	0.825 (118/143)	0.873 (103/118)

significant differences in the survival probabilities across periods. Thus, these two data sets, bobwhite and mussel, demonstrate the relationship between release size and statistical power to detect differences in survival probabilities.

The **Sampling Summary** (Figure 6.12) allows the user to follow the fate of each release group. The sampling summary details the number of mussels released, by period, and gives the survival of each release separately. This table also details when censoring occurred and how many animals were involved. For this data set, there was no censoring.

> *To access the **Sampling Summary**, follow the command sequence (**Data -> Sampling Summary**). This command sequence causes a pop-up window to appear that follows the fate of each release group through time (Figure 6.12). This allows the user to see if different release groups behaved differently, how many animals were used to estimate each survival probability, and how many animals were censored. At each occasion beyond the release, there are two classes of animals, those that were censored and those that were not censored. The two classes are separated by a colon, non-censored to the left, censored to the right. Thus, in the second occasion, 50 mussels were marked; 35 survived until the next occasion, and none were censored. There was no censoring in this data set, thus all numbers to the right of the colons are zero.*

From studying the sampling summary, there does appear to be somewhat differing survivals for the 2 release groups during the 2nd period (0.89 for release group 1, and 0.70 for release group 2). The two release groups are combined for the overall survival estimate in this period (S_2 = 0.825), but since the second release group had much lower survival, and more small animals, the lower survival estimate in the second period may be solely a function of decreased survival of the smaller mussels that were just added to the study. This implies that smaller mussels may have poorer survival than larger mussels.

Recall that K-S Test results (Figure 6.11) suggested that several of the individual covariates may significantly affect survival of the mussels. The covariate “size” seemed to be most likely, since it had the largest difference in the CDFs. The effects of all individual covariates were investigated.

> *To fit models that include individual covariates, access the **S-Modeling Individual Button Pads** for all of the individual covariates (**Modeling -> S Individual -> size/height/width/***

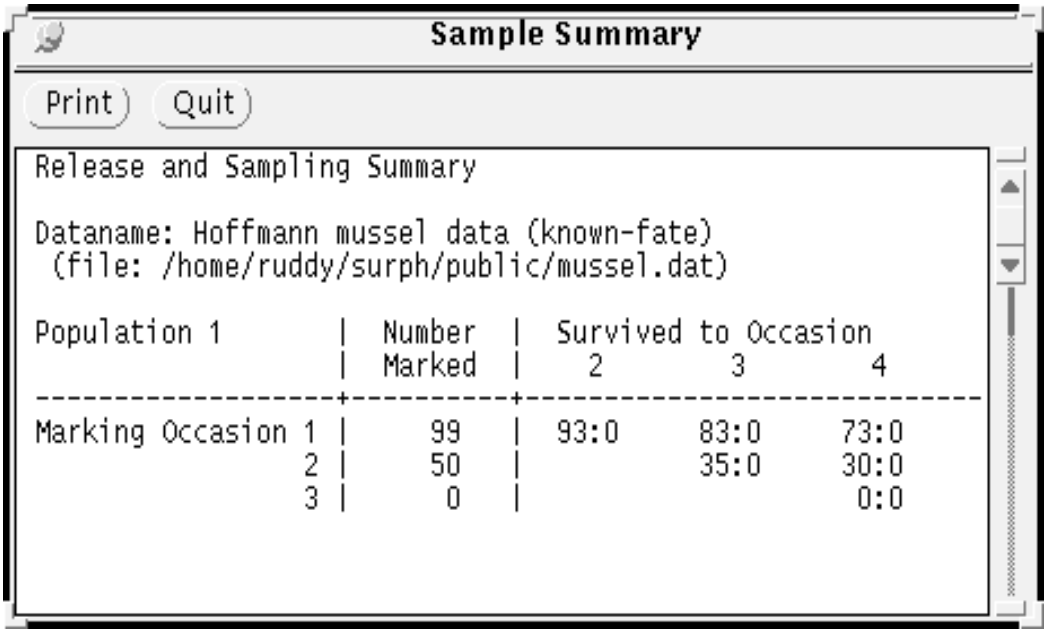
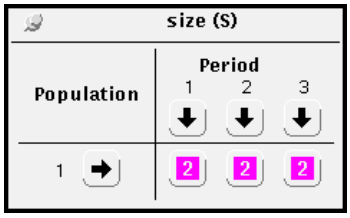
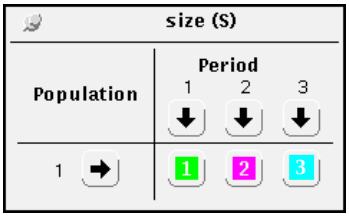


Figure 6.12 The sampling summary for the blue mussel data set. This graphic details the fate of mussels throughout the study.

depth). *Check to make certain that the "St" model is the design effects model. To fit a common individual-covariate effect on survival for all periods, within the* ***Individual Button Pad****, set all buttons for the chosen covariate to a common non-zero number. To fit a period specific individual survival effect, within the* ***Individual Button Pad****, set all buttons for the chosen covariate to a different non-zero number. A button set to zero within the* ***Individual Button Pad*** *indicates that no parameter will be estimated for the individual survival effect for that population and period.*



Common Effect



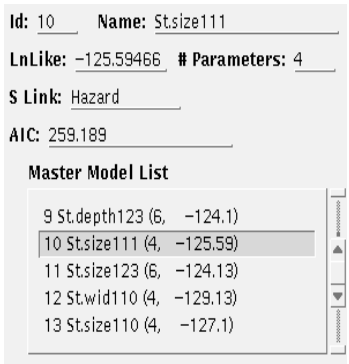
Period-Specific Effect

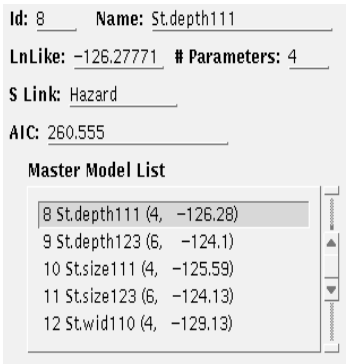
Notice that the ***Individual Button Pad*** *on the left, for the individual covariate "size", is set to all "2's". This parameterization will fit a common survival effect for "size". The identical model would be specified if the buttons were set to all "1's" or all "3's". It doesn't matter which non-zero number is chosen, just that all buttons share the same number. For clarity sake, throughout this example, all models are named by concatenating the design effects model name, the individual covariate, and the parameterization of the individual-covariate effect model. Therefore, a model with an "St" design effects model, and a common effect for the individual covariate "size" will be named "St.size111", whereas a model with an "St" design effects model, and period-specific effects for the individual covariate "size" will be named "St.size123".*

Models that included common and period-specific effects for each of the individual covariates were fit. After fitting these eight models, nested models were compared using the LRT, while non-nested models were compared using Akaike's Information Criterion (AIC).

On the SURPH Base Window, in the upper left-hand corner, there is an area that displays certain characteristics of the model that is selected in the ***Master Models List****. In the upper right-hand corner, there is an area that displays certain characteristics of the model that is selected in the* ***Testable Models List****. For nested models, select the model with more parameters ("full model") within the* ***Master Models List****, and the model with fewer parameters ("reduced model) in the* ***Testable Models List****. A pop-up will appear that gives the results of a LRT between the two models. If there is a significant difference between the two models, the full model provides a significantly better fit. Alternatively, for models that are not nested, use the Akaike's Information Criterion (AIC on the SURPH Base Window) to make*

similar comparisons. The AIC uses the log-likelihood, but "penalizes" each model based on the number of parameters estimated. The principle of AIC-based model selection is that the "best" model is the one with the minimum AIC. In the example below, the AIC for St.size111 is 259.189, and the AIC for St.depth111 is 260.555. Thus, based on the AIC, St.size111 is the better model.





The results from the models that included individual-covariate effects suggested that several of the individual covariates significantly affected survival, and that the effects were constant throughout the study, not period-specific. Of the models fit with a common individual-covariate effect, the covariate "size" had the minimum AIC.

Next, the model with a common "size" effect across all periods and the "St" design for design effects was used as the base model, and each of the remaining individual covariates was added. None of the subsequent models significantly improved the fit. Thus, the best model for the mussel data set includes a common "size" effect across all periods and period-specific baseline survival.

Once a model has been selected, check whether the parametric SURPH curve for the chosen model fits the nonparametric survival probability estimates (Figure 6.13).

To display the SURPH survival curve and the individual-based nonparametric estimates of survival, highlight the model St.size111 in the ***Master Models List****. Select the survival curves graphic from the SURPH Base Window (****Models -> Survival Curves -> Individual****). From the* ***Covariate Pull-Down Menu*** *on the lower left portion of the* ***Individual Survival Curves Pop-Up window****, left-click on "size" to display the estimated SURPH curve. To overlay the nonparametric curve, left-click on the* ***Non-Parametric Button*** *(Figure 6.13).*

Alternatively, to see the relative risk associated with an individual covariate, use the command sequence ***Models -> Survival Curves -> Individual****, then select the* ***Relative Risk Button****.*

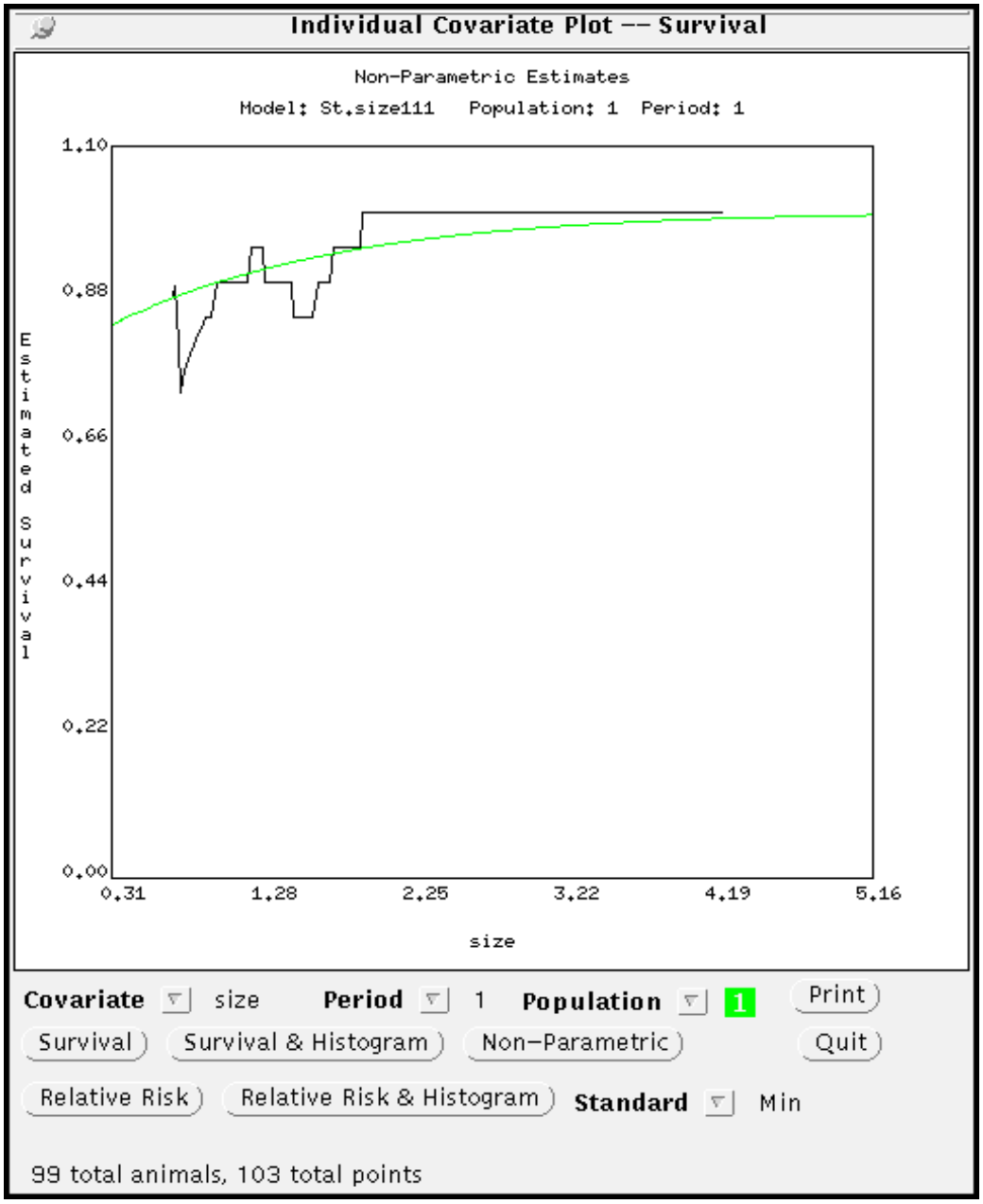


Figure 6.13 The SURPH Individual-Covariate Curve pop-up window for the model "St.size111". The buttons on the control panel have been set for the first period (Period 1) for the first population (Population 1). The smooth curve is the SURPH model fit for survival as a function of the variable "size," whereas the jagged line represents the nonparametric ("running average") estimates of survival.

If desired, a histogram of the individual covariate may be overlaid by selecting the ***Relative Risk & Histogram Button****.*

The SURPH survival curve for the model that includes the individual covariate "size" closely approximates the nonparametric curve (Figure 6.13). This evidence confirms that the SURPH model fits the data reasonably well.

Now that a model has been chosen, access the **SURPH Parameters** *(Figure 6.14) (For instructions on how to access* **SURPH Parameters** *and* **Probabilities***, see Section 6.1.1). In the* **SURPH Parameters** *window, parameters are listed in order of entry into the model, and are not descriptive (e.g., survival effect 4 refers to the effect of the individual covariate "size"). To understand the effects associated with each of the parameters, the user can left-click on the* **Key Button***. A text window will appear that provides the user with a description of each parameter, and how parameters are combined to give various survival estimates. For further explanation of the* **Key***, see Chapter 7.*

The standard errors of parameters 2 and 3 (Figure 6.14) indicate that the parameters for the period offsets are not statistically different from zero under the current model (p-value = 0.094 for H_0: θ_2=0 and 0.210 for H_0: θ_3 = 0). If the model "St.size111" is compared to the model "S.size111", the LRT (p-value = 0.113) shows that the two parameters that are used to estimate the period effects (parameters 2 and 3) do not significantly improve the fit (α < 0.10). This explains why these two parameters are not statistically different from zero. When fitting models that include individual covariates, the recommended protocol calls for the use of fully parameterized design effects model. However, once the individual-covariate effects have been fit, a reduced model can be chosen. Therefore, the user can stay with the model "St.size111", or use the reduced model "S.size111". The conclusions from either model are generally the same.

Finally, examine the integrated SURPH Probabilities (Chapter 3) for the model "St.size111" (Figure 6.15). They correspond well to the binomial estimates. This model appears to fit well. This study indicates that for blue mussels in the Jackson Beach Biological Preserve, Friday Harbor, Washington, larger mussels seem to have better survival than smaller mussels.

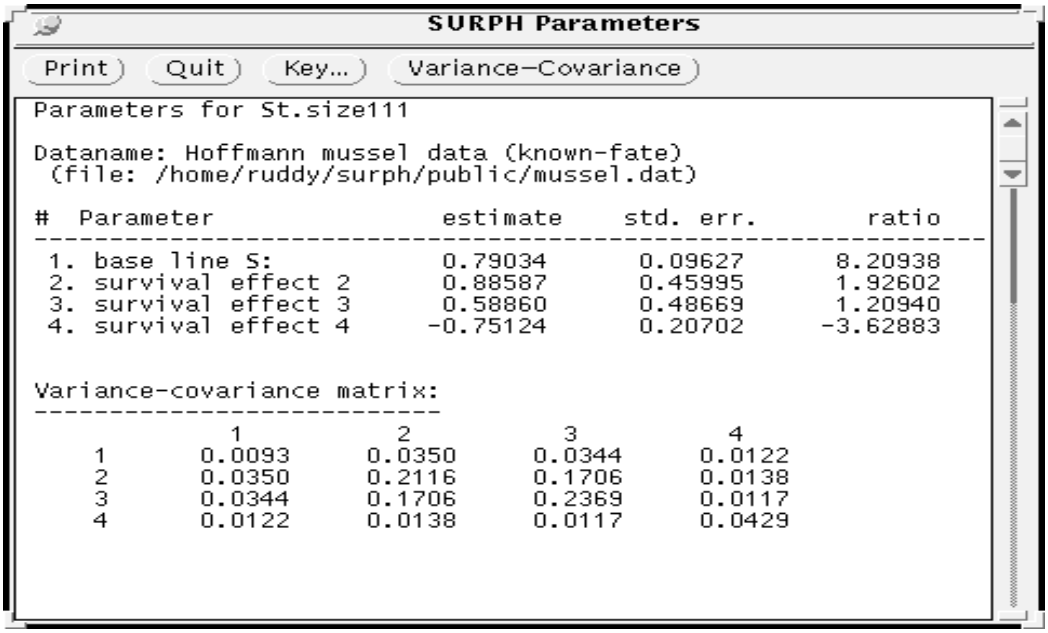


Figure 6.14 The SURPH Parameters window displays the value of the estimate for each parameter and, once the variance-covariance matrix is computed, the standard error of each estimate and the ratio of the estimate to its standard error.

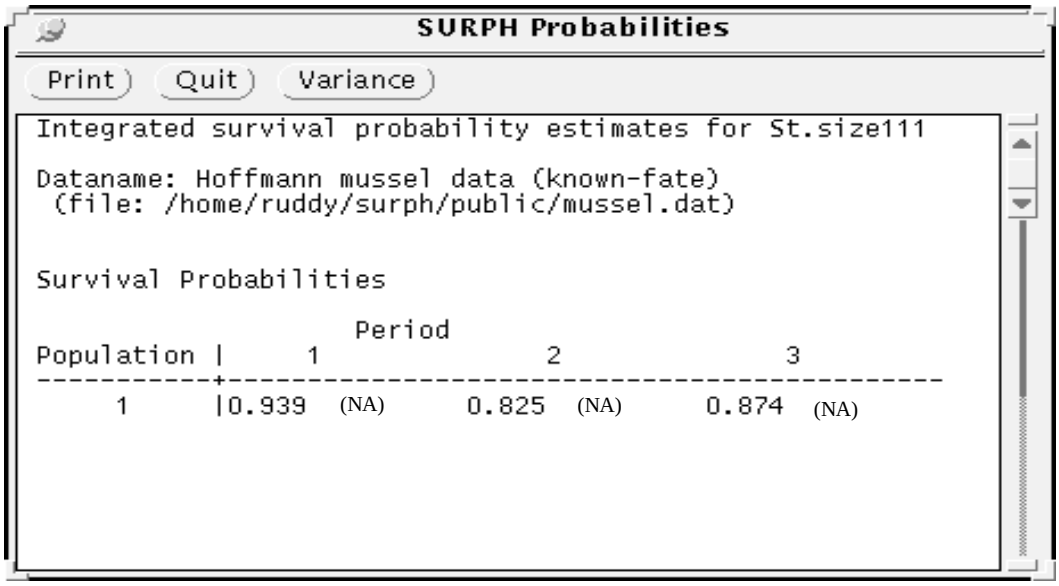


Figure 6.15 The integrated SURPH survival probabilities for the model St.size111 for the blue mussel data. Under each period designation, the number to the left is the integrated SURPH survival probability; the number in parentheses to the right is the standard error of the estimate. For models with individual covariates, the standard error designation is "NA"—not available.

6.1.4 Starling Nest Box Abandonment Study

The final example of known-fate analysis illustrates a novel approach to generating known-fate data. On the same nine sites used in the bobwhite quail example (Section 6.1.2), the TIWET researchers conducted a study of nest box abandonment by starlings (*Sturnus vulgaris*). The purpose was to assess the effects of two different pesticide application methods on nest box abandonment rates. The nine sites were grouped into three blocks of three sites, based on site characteristics. Within each block, one site was randomly chosen to be a control; and the two pesticide application methods were assigned at random to the remaining two sites. The pesticide was applied before the beginning of the starling nesting season. The data for this example can be found in the datafile nestbox.dat.

A number of nest boxes were placed on each site. After the nesting season began, active nests were identified from periodic visits to the boxes. The date on which an active nest was discovered was deemed "time zero" for that nest, and it was then monitored for four weeks. New nests were discovered throughout the entire duration of the study. Hence, not every nest had the same calendar date for its time zero. In this way, the study is more like survival studies on humans following surgical procedures than like traditional tag-release studies where all marked animals have the same time zero based on calendar date. Survival probabilities from this study are not for absolute time periods (e.g., April 7 through April 21), but relative to the start of nesting activity. The "periods," then, relate to phases of the nesting period, from egg laying to fledging.

From the date of first egg laying (i.e., initiation), nests were monitored by means of toothpicks lodged in the entrance of the nest box in the morning of each weekday (nests were not visited on weekends). The toothpick was placed in a way that required the adult bird to remove it to get through the entrance. Dislodgment of the toothpick was assumed to be a positive indicator of adult presence. A toothpick still in place at the entrance after one day (or three days in the case of weekends) was taken as evidence that the nest was no longer active; the adults had either died or abandoned the nest.

The hallmark of a radiotelemetry study is that every marked animal can be sampled on every sampling occasion, with a definite determination of survival or death. Regarding the continued

“survival” of a nest, the use of toothpicks across the entrance of nest boxes provided the same information. The data from the study are not used to analyze the survival probabilities of individual birds, but the probabilities of nest “survival” throughout the nesting period.

For the purposes of this analysis, the daily sampling data were collapsed down to four weekly sampling occasions. These data are shown in Table 6.8. Sample sizes were relatively large; but of the 200 nests initiated, only 11 nest abandonments occurred.

Based on the binomial estimates of survival (i.e., model “Sst”), there are no great differences among the populations. Per-period survival probabilities ranged from 0.833 to 1.000 (Table 6.9), with no definite pattern indicated. When the “S” model (Sections 6.1.1 and 6.1.2) is compared to the “St” and the “Sst” models, this conclusion is confirmed. The “St” and the “Sst” models do not provide a statistically significant improved fit based on the LRT ($p = 0.15$ and $p = 0.41$, respectively).

Analysis of deviance was used, as in the black duck and bobwhite examples, to explore the effects of the group covariates: blocks, and the three treatment levels (one control and two pesticide application methods). As with the bobwhite example, all group covariates were analyzed concurrently. Since the block and treatment deviances within a given period are not orthogonal—that is, the value for the deviance depends on the order the parameters entered—it was necessary to determine the order of entry of the independent variables into the model for each period separately. For this analysis, the block effects were entered before the treatment effects. After the block effects were entered, a stepwise procedure was used to select the order of entry of the treatment effects. Of the two possible treatment effects, the treatment effect that caused the greatest reduction in deviance when added to the block effects was entered first.

None of the group covariates had a significant ($p < 0.10$) effect on the nest abandonment rate in any period (Table 6.10). Because a small number of nest boxes were abandoned, there is little evidence of block or treatment effects; abandonment rates were all quite low. Neither pesticide application methods nor blocks caused any detectable effects on nest box survival.

Table 6.8 Data from 1989 study of nest box abandonment among starlings in Iowa farmland. The data are the number of active nests on each sampling occasion.

			Sampling Occasion			
Site	Block	Treatment	1	2	3	4
1	A	C	20	20	19	18
2	A	T_1	19	18	18	17
3	A	T_2	21	21	19	18
4	B	C	22	22	22	22
5	B	T_1	16	16	15	15
6	B	T_2	6	6	6	5
7	C	C	24	24	23	23
8	C	T_1	39	39	39	39
9	C	T_2	33	33	33	32

Table 6.9 Binomial estimates of period-specific survival of starling nest boxes. The decimal number is the binomial survival estimate. The fraction gives the numbers of nests used to compute the decimal estimate.

Population	Period 1	Period 2	Period 3
1	1.000 (20/20)	0.950 (19/20)	0.947 (18/19)
2	0.947 (18/19)	1.000 (18/18)	0.944 (17/18)
3	1.000 (21/21)	0.905 (19/21)	0.947 (18/19)
4	1.000 (22/22)	1.000 (22/22)	1.000 (22/22)
5	1.000 (16/16)	0.938 (15/16)	1.000 (15/15)
6	1.000 (6/6)	1.000 (6/6)	0.833 (5/6)
7	1.000 (24/24)	0.958 (23/24)	1.000 (23/23)
8	1.000 (39/39)	1.000 (39/39)	1.000 (39/39)
9	1.000 (33/33)	1.000 (33/33)	0.970 (32/33)

Table 6.10 The ANODEV Table for the starling nest box data. None of the group covariates significantly affected nest box abandonment in any period.

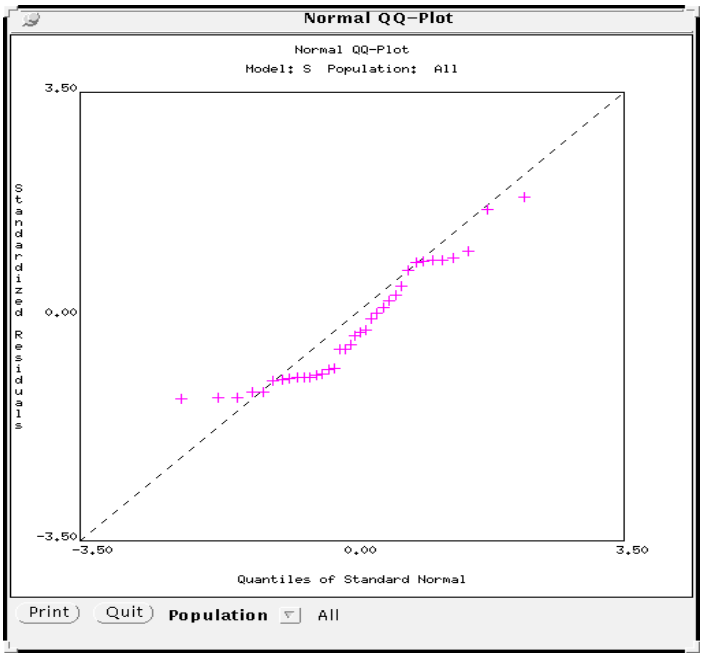
Source	df	Deviance	Mean Dev.	F	P(F)
Total	27	105.758			
Period Means	3	82.544			
Corrected Total	24	23.214			
Model Total	12	12.093	1.008	1.087	0.443
Model, Period 1	4	4.756	1.189	1.283	0.330
Blocks	2	2.420	1.210	1.305	0.307
Trt. 1	1	2.337	2.337	2.521	0.138
Trt. 2|Trt. 1	1	0.010	0.010	0.011	0.919
Model, Period 2	4	2.84	0.710	0.766	0.568
Blocks	2	2.314	1.157	1.249	0.322
Trt. 1	1	0.501	0.501	0.541	0.476
Trt. 2|Trt. 1	1	0.021	0.021	0.023	0.882
Model, Period 3	4	4.498	1.125	1.213	0.355
Blocks	2	2.463	1.231	1.329	0.301
Trt. 2	1	2.035	2.035	2.196	0.164
Trt. 1|Trt. 2	1	0.002	0.002	0.002	0.963
Error	12	11.121	0.927		

Since there are no significant group-covariate effects, diagnostics associated with the “S” and the “St” models were examined. These two models were chosen because the “St” model is the base model for ANODEV, but when the “St” model was compared to the “S” model using the LRT, the inclusion of period effects did not significantly improve the fit of the model. Two types of residual plots are available in SURPH. The first is a normal quantile-quantile plot (“q-q plot”). The q-q- plot compares the values of the sorted standardized residuals with the expected percentiles of the standard normal distribution. Deviations from the expected 45 degree line indicate skewness and kurtosis (Zar 1984). The second type of residual plot shows the values of the standardized residuals versus the decimal equivalent of the corresponding survival histories (Section 4.6.2.6).

> *To access the **Q-Q Residuals Plot**, use the command sequence **Models -> Residuals Plots -> q-q plot**. The values for the SURPH survival estimates are computed using the model that is currently selected within the **Master Models List**. The vertical axis of this plot is the value of the standardized residual. The horizontal axis of this plot is the value of the standard normal percentile. If the standardized model residuals are truly distributed N(0,1), the points should lie along the 45 degree line.*

Examination of the q-q residual plots (Figure 6.16) indicates that the transformed residuals do not conform strictly to the normal assumptions for either model. However, the standardized residuals are quite close to the expected residuals from a N(0,1) distribution. In addition, the residual versus survival history plot (Figure 6.17) does not indicate any large deviations from the expected values for either the “S” or the “St” model (further discussion about the residual plots and instructions on how to access the residual plots can be found in Section 6.1.2).

Finally, neither the blocks nor the pesticide application methods appear to explain the slight variations observed in the survival probabilities. All sites had high nest box survival. It appears from this study that the application of pesticide to a nesting site did not cause starlings to abandon their nests.



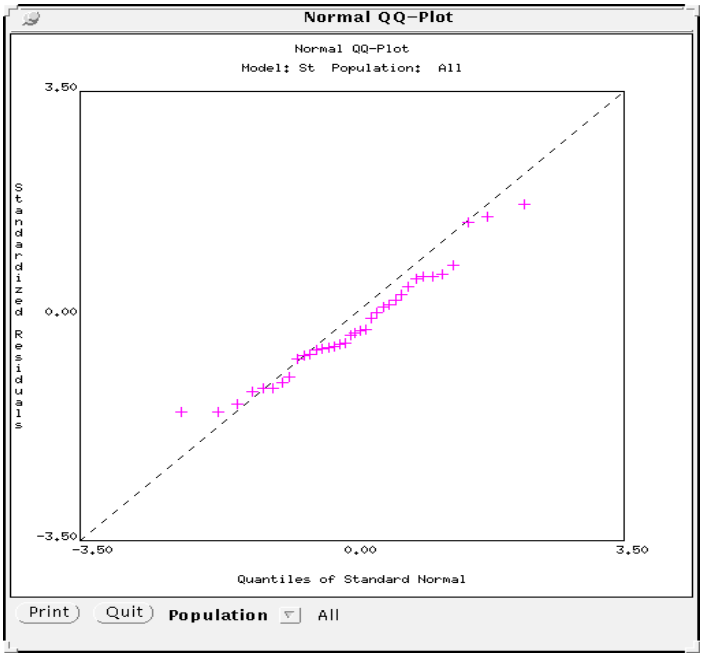
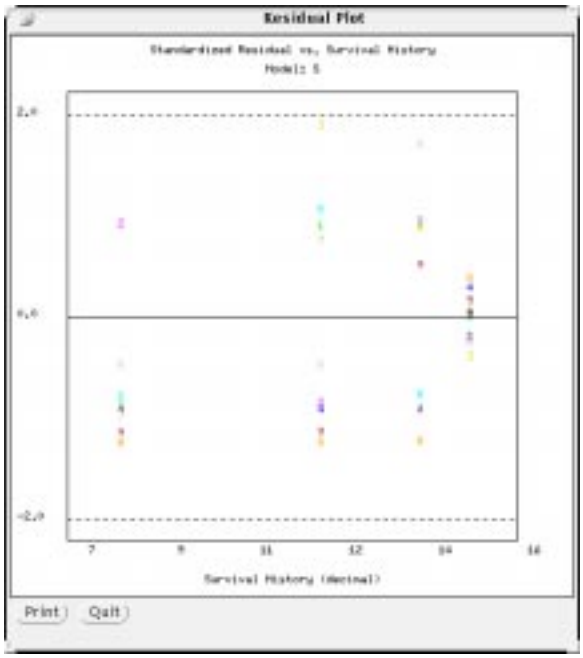


Figure 6.16 The Normal Q-Q plots of the residuals for both the "S" (upper) and "St" (lower) models for the starling nest box data set. The vertical axis designates the value of the standardized residuals. The horizontal axis designates the percentiles of a standard normal distribution.



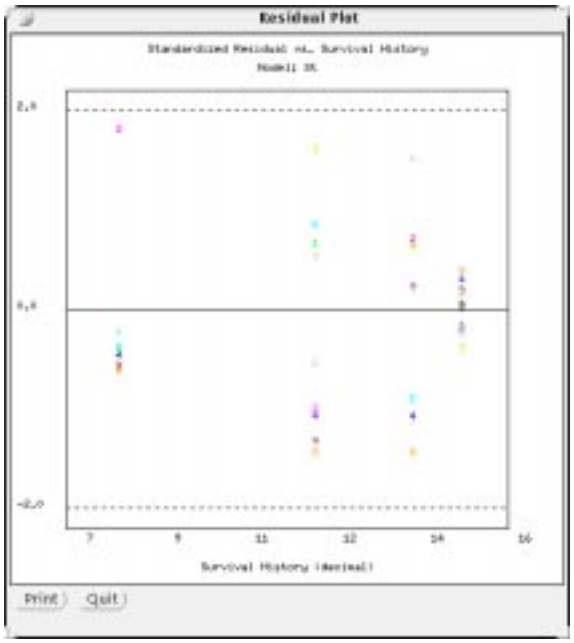


Figure 6.17 The residual versus survival history plots for models "S" (upper) and "St" (lower) for the starling nest box data set. Both models appear to fit the data well, as none of the points lie outside the [-2, 2] range. The vertical axis of this plot is the value of the standardized residual. The horizontal axis of this plot is the decimal equivalent of the survival history.

6.2 Release-Recapture Examples

In this section, four examples of release-recapture studies are analyzed. The examples were selected to illustrate a range of possible study designs and analyses that may be encountered. The first three release-recapture examples are derived from research conducted in 1993 on the migration of juvenile chinook salmon (smolts), (*Oncorhyncus tshawytscha*) in the Snake River in the northwestern United States. The fourth example illustrates how SURPH can be used to analyze paired-release data of the type treated in the monograph by Burnham et al. (1987). The approach is demonstrated with the hypothetical data set used as the major example in the monograph.

Scientists with the National Marine Fisheries Service (NMFS) began experimenting with implanted electronic tags for juvenile salmon research in 1983. Since then, the Passive Integrated Transponder tag, or "PIT-tag," has become a mainstay of research on salmon migration in the Columbia and Snake River drainages. A PIT-tag consists of a microchip and antenna encased in a tiny glass capsule. Individually coded tags are injected into the body cavity of juvenile fish using a hypodermic syringe, and the PIT-tagged fish are returned to the river. PIT-tag detectors are installed in juvenile bypass facilities at several dams in the Columbia/Snake Rivers system. After the initial tagging, no further handling is required, because the detectors at the dams automatically record the passage of PIT-tagged fish. The capture history for each PIT-tagged fish is the record of the dams where the fish were detected and where they were not detected. Thus, we can estimate and model survival probabilities for PIT-tagged fish on stretches of river between successive dams (i.e., sampling segments), and probabilities of detection at each dam (i.e., sampling locations).

Each of the first three examples involves the release of chinook salmon smolts in the Snake River drainage in Idaho and eastern Washington in the spring of 1993 (Figure 6.18). Fish were monitored from the point of release to McNary Dam, just below the confluence of the Snake and Columbia Rivers. Fish passed the following dams, from uppermost to farthest downstream: Lower Granite, Little Goose, Lower Monumental, Ice Harbor and McNary. All but Ice Harbor Dam were equipped with PIT-tag detectors.

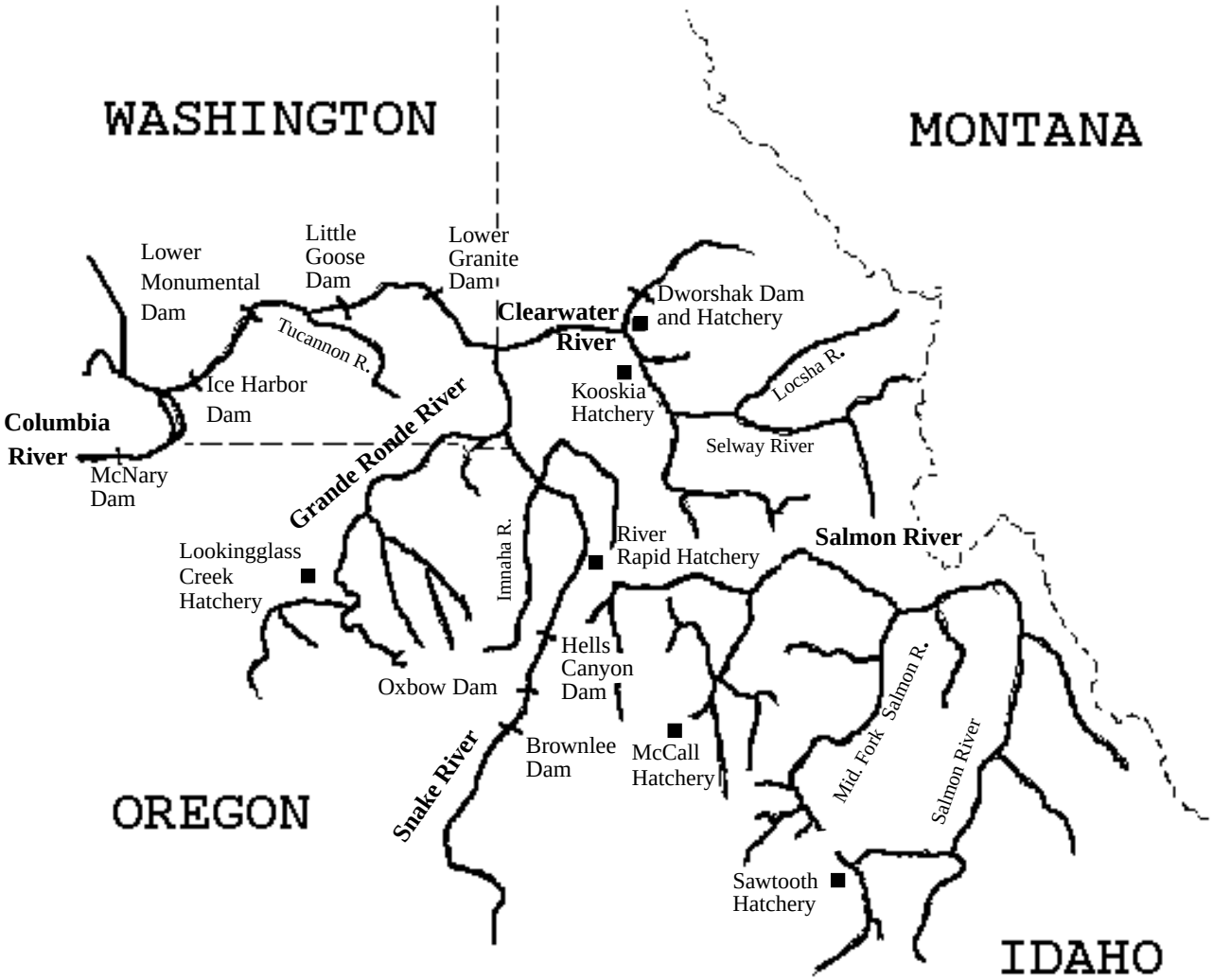


Figure 6.18 Map of the Snake River drainage showing locations of dams with PIT-tag facilities in 1993.

The juvenile bypass facilities have been designed to divert fish away from the turbines and, at some dams, to collect fish for the smolt transportation program. In the transportation program, smolts are removed from the river and moved downstream in barges to avoid further dam passage and possible adverse river conditions. Thus, to return detected fish to the river so that detection on multiple sampling events is possible, mechanisms called “slide gates” have been installed in the pipes that normally deliver the fish to transportation barges. In 1993, slide gates were operational at Lower Granite and Little Goose Dams. Because there was no slide gate at Lower Monumental Dam, detections at Lower Monumental and McNary Dams were pooled into a single sampling event; detection at either dam constituted a “capture” on the final sampling event. Thus, there are three sampling intervals (river reaches): release-to-Lower Granite; Lower Granite-to-Little Goose, and Little Goose-to-Lower Monumental/McNary. Survival probabilities can be modeled for the first two reaches. Because the slide gates are not 100% efficient in diverting fish from transportation, some fish were not returned to the river. PIT-tag detectors are in place to identify those fish that are not returned to the river, so that they can be treated as “known removals” in the release-recapture data.

The basic characteristics of the four examples are as follows:

Example #1: Multiple-population experimental study to assess effect of timing of release from a hatchery on the in-river survival of chinook salmon smolts.

Example #2: Single-population observational study of the relationship between the body lengths of individual chinook salmon smolts and in-river survival.

Example #3: Multiple-population observational study of the relationship between migration distance and in-river survival of chinook salmon smolts reared at and released from various hatcheries.

Example #4: Hypothetical paired control-treatment release design to estimate mortality of salmon smolts passing through a hydroelectric turbine (simulated data from Burnham et al. 1987).

The SURPH Base Window for Release-Recapture looks very similar to the SURPH Base Window for Known-Fate. However, capture probabilities and the product of survival and capture in

the final period (hereinafter called the “product term” or “product”) can now be modeled in addition to survival effects. The effects on the product term will be not be specifically modeled in the PIT-tag examples. Instead, the fully parameterized model for the design effects on the product will be used. Example #4 includes a hypothesis test for equality of product terms between the control and treatment releases.

6.2.1 Study of timing of release from hatchery

A study of the effect of timing of release on in-river smolt survival was conducted in 1993 by personnel of the Dworshak National Fish Hatchery (U.S. Fish and Wildlife Service). Releases were made on each of three dates: 8 April, 22 April, and 6 May, 1993. On each date, approximately 250 PIT-tagged spring chinook salmon smolts were released from each of six raceways at the hatchery. For the purposes of this illustration (to simplify the example by reducing the total number of populations), replicate raceways were pooled randomly so that each date had three releases; each of the releases had approximately 500 fish. Thus, there is a total of 9 populations; 3 replicates of each of three "treatment levels" (release dates). The goal of this analysis is to determine if there are significant differences in in-river survival among fish released on different dates.

The file "dworshak.dat" contains the data for this example. There are two group covariates, called "middle" and "late," which indicate whether the population was released at the middle (22 April) or late date (6 May), respectively. There is one individual covariate, "length," which will not be investigated in this example (see Section 6.2.2 for an example analysis of an individual covariate).

> *To begin the SURPH session, at the UNIX prompt, type "surph dworshak.dat". Left-click on the* ***Release-Recapture Button*** *to begin the example analysis.*

The final period product terms will be not be specifically modeled for the PIT-tag examples. Instead, the fully parameterized model for the design effects on the product term will be used. For this example, the button settings for the fully parameterized product design effect model should read "1, 2, 3, 4, 5, 6, 7, 8, 9".

With SURPH, capture probabilities can be modeled using either of two distinct approaches. Using the **Modeling: P-Only Button**, only the "Manly-Parr subset" of the data is used to estimate capture probabilities (see Section 4.4.3); no survival model is assumed during this process. If capture is modeled under the P-Only scenario, the best capture model is selected and "Locked" before any survival modeling commences. Once the capture model is locked, the model for capture probabilities cannot be reparameterized.

Using the **Modeling: Joint S-P Button**, all of the data is utilized; and capture and survival are modeled concurrently. Typically, capture probabilities are modeled first, while the survival model is held constant. During the initial step of modeling capture probabilities, the fully parameterized design effects model is used for survival probabilities (i.e., unique time- and period-specific survival probabilities; "Sst"). Also, the fully parameterized design effects model is used for the product terms (for details on the product term, see Section 4.4.4). Once the best capture model has been selected, survival probabilities are modeled. However, because no modeling buttons are "locked" during Joint S-P Modeling, both capture and survival models can be reparameterized throughout the modeling process. Modeling using the Joint S-P approach can be an iterative procedure. One advantage of Joint Modeling is that, without quitting and restarting SURPH, the user can alternate capture models to see how the assumptions of each capture model affect the results of the survival models.

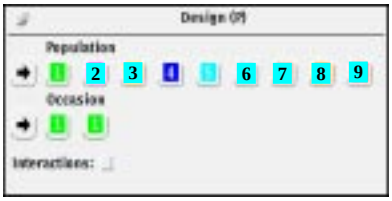
If there are no individual covariates, the same capture model is typically chosen whether the P-Only or the Joint S-P Modeling approach is used. For this example data set, both P-Only Modeling and Joint S-P Modeling will be illustrated. Whenever individual covariates that could affect capture are included, the user is advised to use P-Only Modeling to parameterize the capture model. This is because P-Only Modeling allows the user to model capture independently of any survival model. The absence of any assumed survival model decreases the chance that individual effects that should be attributed to the survival process will be spuriously attributed to the capture process or vice versa. See Section 6.2.2 for an example in which P-Only Modeling should be used to develop the capture model.

> *To begin, access the capture design and group effect button pads for* ***P-Only Modeling*** *(****Modeling: P-Only -> P Design/P Group****).*

As with survival modeling (Sections 6.1.1-4), several of the capture models that have been described in the literature have been given standard names. A fully parameterized capture model—with separate effects for all populations, all sampling events, and their interactions—is called the "Pst" model. The "Pst" model is so named because capture probabilities ("P") vary through space ("s") and time ("t"). The "Pt" model has event-specific capture probabilities that are common to all populations (probabilities vary through time). Similarly, the "Ps" model has

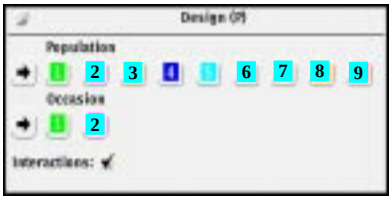
population-specific capture probabilities that are constant across sampling events (probabilities vary through space). And finally, a capture model that has a single common parameter for all populations and all sampling events is called the “P” model (capture probabilities are constant). In this example, the “sampling events” refer to the different dams (locations in space), and the populations refer to different releases (changes in time). SURPH refers to sampling events as “occasions” regardless of whether they are locations in space or occasions in time.

“P” Model



“Ps” Model

“Pt” Model

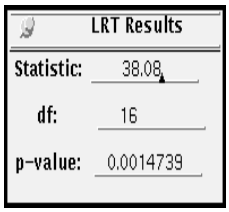


“Pst” Model

*On the **Capture** (“P”) **Design Button Pad**, the quick buttons operate identically to the quick buttons on the **Survival Design Button Pad** (See Section 6.1.1 and Chapter 7). The default model that initially appears is the “Pst” model. To change from the “Pst” model to the “Ps” model, position the mouse cursor above the quick button in the occasion row, and left-click. This action changes the button settings in the occasion row from “1, 2” to “1, 1”. Left-click on the interactions check-box to remove interactions. The **P Design Button Pad** should now resemble the “Ps” model above. To get the “Pt” model, left-click on the occasion quick button to go back to the “1, 2” button setting. Then left-click on the population quick button to change the button settings in the population row from “1, 2, 3, 4, 5, 6, 7, 8, 9” to all “1’s”. The **P Design Button Pad** should now resemble the “Pt” model above. Finally, use the quick buttons to specify the “P” model. Estimate and name all four models (Set buttons to specify the model, type the name in the **Name** field, then left-click on **Begin Estimate**).*

*To compare the fit of any two models using the likelihood ratio test, select one model in the **Master Models List**, then select a competing model in the **Testable Models List**. For*

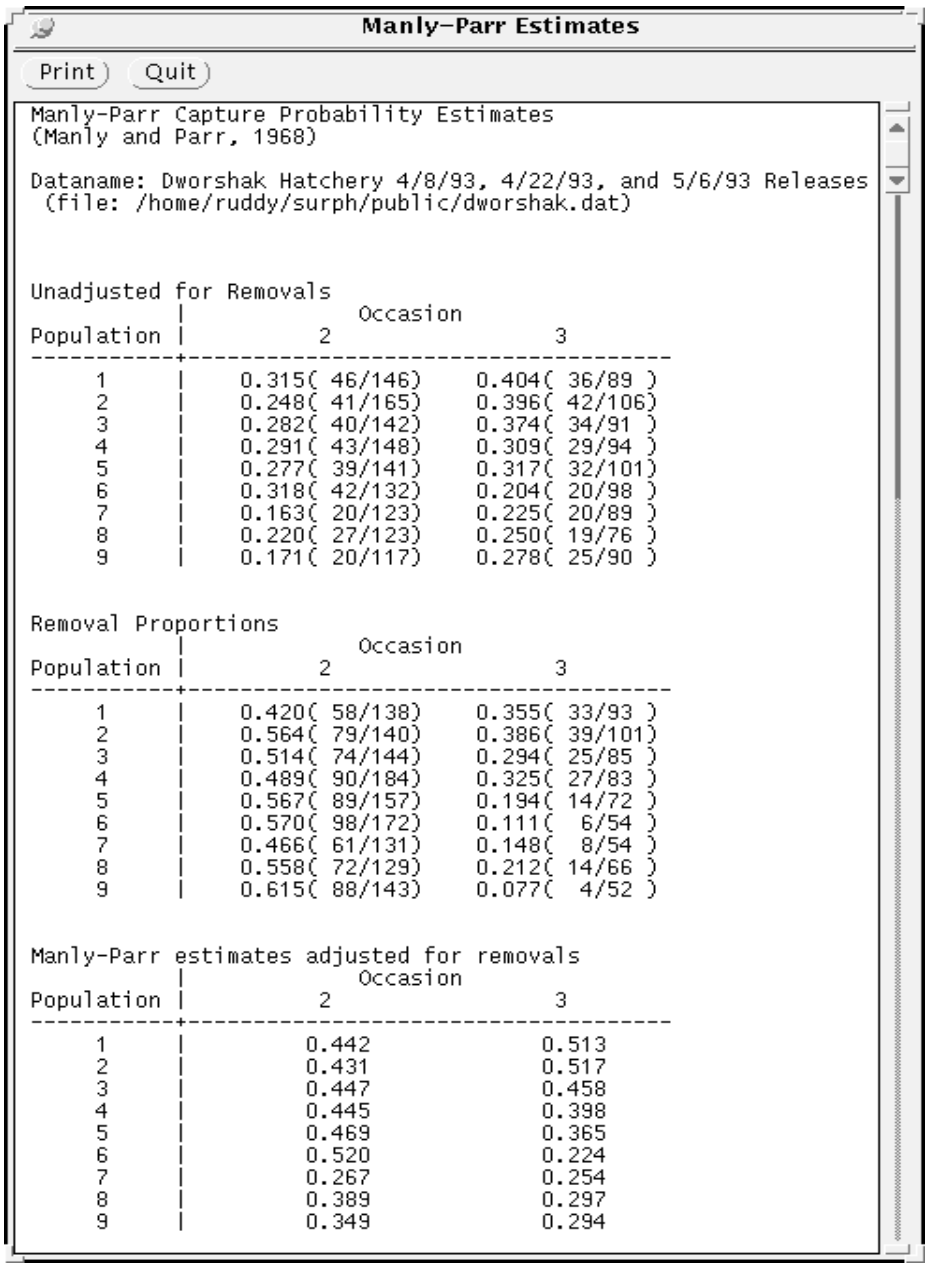
*example, select the "Pt" model in the **Master Models List**, then select the "Pst" model in the **Testable Models List**. A pop-up window will appear that displays the value of the test statistic (38.08; See Section 2.4.1 for calculating formula), the change in number of parameters (16; also known as the degrees of freedom), and the probability of observing this or a greater value of the test statistic under a chi-square distribution with 16 degrees of freedom (p-value = 0.0015).*



Comparison of the first four models using LRT indicates that the "Pst" model provides a significantly better fit than any of the other models ($p < 0.10$). However, up to this point, the structure of the study design has been ignored. Recall that the study consists of three replicate releases of salmon smolts at three different times. Thus, the timing of the releases, as well as the dams where the fish were detected, could influence the capture probabilities. Although the Pst model accounts for capture probabilities that vary in space and time, a model with fewer parameters could provide a similar fit. The time of release is a group covariate; thus, the modeling of capture effects related to time of release will use the **P Group Button Pad**. The **Cormack/ Jolly-Seber (CJS) Estimates** (Section 4.3.2) and the **Data Listing** can be used as guides for model parameterization.

*Access the **P Group Button Pad**. There are several ways of parameterizing the model to include effects due to release timing. Models can be constructed that include both design and group effects. A model that has a "Pst" design, however, is already fully parameterized, and no group effects may be added. Thus, it is necessary to begin with an unsaturated design effects model. In this instance, the data suggest either a "P" design effects model, which would imply similar capture probabilities at both dams or a "Pt" design effects model, which would imply differing capture probabilities, but constant capture probabilities across all releases. With either model for design effects ("P" or "Pt") any or all of the group effects may be used to fit the model. Use LRT or AIC to determine the model that provides the best fit without unnecessary parameters.*

*To access the **Manly-Parr Estimates** (Figure 6.19), use the command sequence **Data -> Manly-Parr**. The **Manly-Parr Estimates** (Section 4.4.3.1) provide nonparametric estimates of capture probabilities. The Manly-Parr estimates of capture probabilities will be identical to*



Manly-Parr Estimates

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Manly-Parr Capture Probability Estimates
(Manly and Parr, 1968)

Dataname: Dworshak Hatchery 4/8/93, 4/22/93, and 5/6/93 Releases
(file: /home/ruddy/surph/public/dworshak.dat)

Unadjusted for Removals

Population	Occasion 2	Occasion 3
1	0.315(46/146)	0.404(36/89)
2	0.248(41/165)	0.396(42/106)
3	0.282(40/142)	0.374(34/91)
4	0.291(43/148)	0.309(29/94)
5	0.277(39/141)	0.317(32/101)
6	0.318(42/132)	0.204(20/98)
7	0.163(20/123)	0.225(20/89)
8	0.220(27/123)	0.250(19/76)
9	0.171(20/117)	0.278(25/90)

Removal Proportions

Population	Occasion 2	Occasion 3
1	0.420(58/138)	0.355(33/93)
2	0.564(79/140)	0.386(39/101)
3	0.514(74/144)	0.294(25/85)
4	0.489(90/184)	0.325(27/83)
5	0.567(89/157)	0.194(14/72)
6	0.570(98/172)	0.111(6/54)
7	0.466(61/131)	0.148(8/54)
8	0.558(72/129)	0.212(14/66)
9	0.615(88/143)	0.077(4/52)

Manly-Parr estimates adjusted for removals

Population	Occasion 2	Occasion 3
1	0.442	0.513
2	0.431	0.517
3	0.447	0.458
4	0.445	0.398
5	0.469	0.365
6	0.520	0.224
7	0.267	0.254
8	0.389	0.297
9	0.349	0.294

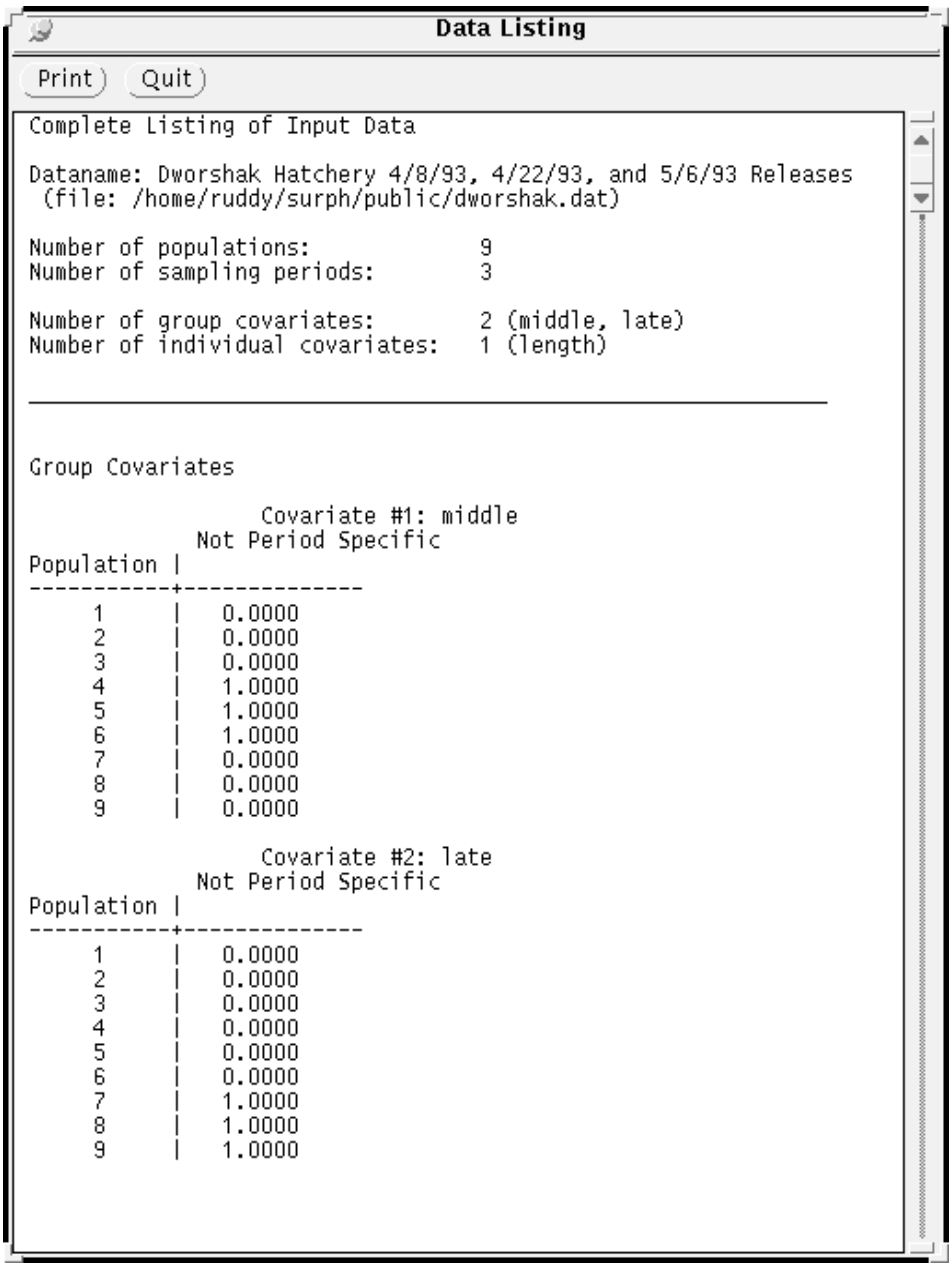
Figure 6.19 Manly-Parr estimates of capture probabilities for smolts released from Dworshak Hatchery. The capture probabilities for the two "occasions" refer to detections at Lower Granite and Little Goose Dams. The fractions in parentheses are used to calculate the estimates.

the SURPH estimates for the fully parameterized design effects ("Pst") model. The fully parameterized SURPH model for this example has a total of 18 parameters. For each population, both the numbers used to compute the capture probability (the fractional numbers in parentheses), and the decimal equivalent are given. The Manly-Parr pop-up window consists of three separate tables. The upper table gives the capture probability estimates (see Eq. (4.20) in Section 4.4.3.1), not adjusted for known removals. The middle table gives the removal proportions on each sampling event in each population, and the lower table gives the capture probabilities adjusted for known removals (Section 4.6.1.1).

Access the ***Data Listing*** *(****Data -> Data Listing****). This text window (Figure 6.20) allows the user to verify that the data file is organized as intended. For the Dworshak Hatchery releases, the* ***Data Listing*** *indicates that there are 9 populations and 3 sampling periods. The 9 populations are segregated into 3 groups by the use of the group covariates "middle" and "late". The Group Covariate portion of this window indicates that the 9 populations are arranged such that the first 3 populations are from the early release (neither "middle" nor "late"), the second 3 populations are from the "middle" release, and the final 3 populations are from the "late" release. For further discussion on the* ***Data Listing****, see Chapter 7.*

The **Manly-Parr Estimates** (**Data -> Manly-Parr**) suggest that there may be significantly different capture probabilities at each dam, and that the capture probabilities appear to change for the three releases, but that the capture probabilities are similar for the three replicates (Figure 6.19) at each time of release. This implies that the best model for capture may be a model that has the "Pt" design effects model and includes separate parameters for both middle and late releases under the **P Group Button Pad** (see capture model parameterization below). Alternative models for group effects were estimated. The most basic group effects model is the null model, which includes no group effects. The null model has all "0's" on the **P Group Button Pad**. The most complex model of group effects for this data set has distinct parameters for each sampling occasion for both middle and late releases (button rows for middle and late release are both set to "1, 2"; see capture model parameterization below). Between these two extremes are a variety of models that can be estimated; some that include a single parameter for both occasions (button rows are set to "1, 1" for a group effect), and others that do not include a parameter for a given occasion or covariate (button rows are set to "1, 0" or "0, 1" for a group effect). The fits of alternative models were compared using LRT or AIC.

On the SURPH Base Window, in the upper left-hand corner, there is an area that displays certain characteristics of the model that is selected in the ***Master Models List****. The same*



Data Listing

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```
Complete Listing of Input Data

Dataname: Dworshak Hatchery 4/8/93, 4/22/93, and 5/6/93 Releases
 (file: /home/ruddy/surph/public/dworshak.dat)

Number of populations:             9
Number of sampling periods:        3

Number of group covariates:        2 (middle, late)
Number of individual covariates:   1 (length)

_____________________________________________________________


Group Covariates

                  Covariate #1: middle
              Not Period Specific
Population |
-----------+--------------
     1     |   0.0000
     2     |   0.0000
     3     |   0.0000
     4     |   1.0000
     5     |   1.0000
     6     |   1.0000
     7     |   0.0000
     8     |   0.0000
     9     |   0.0000

                  Covariate #2: late
              Not Period Specific
Population |
-----------+--------------
     1     |   0.0000
     2     |   0.0000
     3     |   0.0000
     4     |   0.0000
     5     |   0.0000
     6     |   0.0000
     7     |   1.0000
     8     |   1.0000
     9     |   1.0000
```

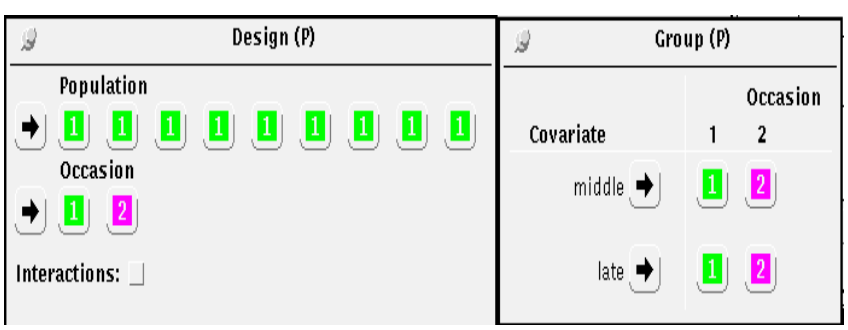
Figure 6.20 Data listing for the Dworshak Hatchery data set. This pop-up window provides an overview of the data file and its organization.

characteristics of the model that is selected in the ***Testable Models List*** *are displayed in the upper right-hand corner. To compute a LRT for nested models, select the model with more parameters ("full model") in the* ***Master Models List****, and select the model with fewer parameters ("reduced model") in the* ***Testable Models List****. A pop-up window will appear that gives the results of the LRT between the two models. If there is a significant difference between the two models, the full model provides a significantly better fit. Alternatively, for models that are not nested, use the AIC to make comparisons. The AIC uses the log-likelihood, but "penalizes" each model based on the number of parameters estimated (Section 2.4.2). The principle of AIC-based model selection is that the "best" model is the one with the minimum AIC.*

Another set of models was estimated that included the "P" model of design effects, and identical group effects to the suite of models under the "Pt" design effects. Again, nested models were compared using the LRT; non-nested models were compared using the AIC. None of the models of group-covariate effects with the "P" model of design effects had a smaller AIC than the capture model with "Pt" design effects, and separate parameters for both middle and late group effects (see capture model parameterization below).

When P-Only Modeling is used, after a capture model has been chosen, the model must be "locked" before survival modeling may proceed.

To lock the capture model, select the desired model within the ***Master Models List****, then left-click on the* ***Lock Button*** *on the SURPH Base Window.*



Final Capture Model Parameterization

After the capture model is "Locked", the **Modeling: P-Only Button** *is disabled, and the* **Modeling: Joint S-P Button** *is used to model survival probabilities. This, then, is a good*

place to illustrate how to model both capture and survival using the **Modeling: Joint S-P Button**. *Quit SURPH, then restart using the same commands as before. This time, however, all modeling will use pop-ups accessed under the* **Modeling: Joint S-P Button**.

To quit SURPH, select the ***Quit Button*** *on the SURPH Base Window. A pop-up window will appear to ask if the models that have been estimated should be saved. If you wish to save the models, select "yes", if not, select "no." If "yes" is selected, a* ***Store Model File*** *pop-up will appear. In the* ***File Name Field****, enter the name of the file in which to store the models. If the file name that is specified already exists, that data will be overwritten by the new information.*

To restart the SURPH session, at the UNIX prompt type "surph dworshak.dat." Left-click on the ***Release-Recapture Button*** *to begin the example analysis.*

Before any joint modeling is done, access the capture, survival, and product design effects and group effects button pads. The initial button settings on each button pad are the default settings for capture, survival, and the product term. Under S-P Modeling, both the survival and capture are modeled simultaneously, though typically, only one process is manipulated at any given time. No specific modeling of the product term will occur in this example. Instead, the fully parameterized design effects model for the product term will be used (the button settings for the design effects of the product term should read "1, 2, 3, 4, 5, 6, 7, 8, 9").

Access the ***Capture****,* ***Survival*** *and* ***Product Design Effects*** *and* ***Group Effects Button Pads*** *(****Modeling: Joint S-P -> P Design/P Group/S Design/S Group/Product Design/ Product Group****). This series of commands should access six separate button pads. Notice that the default settings for the P, S and Product modeling buttons are the fully parameterized design effects models.*

Estimate the same sequence of models for capture probabilities as before, keeping the default "Sst" survival model and the default Product Design Effects model. Estimate all four models of design effects on capture described previously ("P", "Ps", "Pt", "Pst"), then estimate the suite of group effects capture models described in the ***P-Only Modeling*** *section above. Identify the model that has the smallest AIC.*

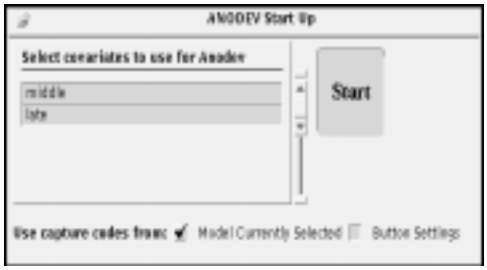
Once again, the "Pst" provides the best fit of the four basic models of design effects on capture probabilities. Also, when the models that include group-covariate effects to account for the different release times are fit, the best fit to the capture data is provided once again by the model that has the "Pt" model of design effects on capture, and separate parameters for both middle and late release capture effects (see capture model parameterization above). Typically, it will not

matter which modeling approach (P-Only or Joint S-P) is used to model capture probabilities, for the same capture model will be chosen, as occurred in this case. For a particular model of capture probabilities, results of survival modeling will be identical regardless of the approach used to select the capture model.

*To access the **CJS Estimates**, use the command sequence **Data -> CJS Estimates**. The **CJS Estimates** (Section 4.3.2) provide nonparametric estimates for capture, survival and the product term. The CJS estimates of capture, survival and the product term probabilities will be identical to the SURPH estimates for the fully parameterized model. The fully parameterized SURPH model for this example ("Pst" model of design effects on capture, an "Sst" model of design effects on survival, and "λs" model of design effects on the product term), has a total of 45 parameters. For each population, the estimated probabilities are given along with standard errors in parentheses.*

CJS estimates of survival probabilities (Figure 6.21) suggest that survival may depend on the river reach and on the timing of the release. The group effects on survival were modeled using ANODEV (Sections 4.5.2). Both group covariates were included in this analysis, and a stepwise procedure was used to determine the order of entry of the group effects into the model (see Sections 6.1.2, and 6.1.4 for detailed examples of this process).

*Access the **S Group Button Pad** (**Modeling: Joint S-P -> S Group**). Select the best fit capture model from the **Master Models List**. Left-click on the **Anodev Button** on the **S Group Button Pad**. This will cause another pop-up window to appear, the **ANODEV Start Up**. Select both group covariates (middle and late) in the "Select covariates to use for Anodev" list. In the bottom of the **ANODEV Start Up** pop-up window, select the check-box labelled, "Model currently selected", and select the **Start Button**.*



*Three default models will be estimated (Section 4.5.2), and the basic **ANODEV Table** will appear shortly. Use a stepwise procedure to determine order of entry of the group covariates into the model, as in Sections 6.1.2 and 6.1.4.*

Cormack/Jolly-Seber Estimates

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Cormack/Jolly-Seber Estimates
(Cormack, 1964; Jolly, 1965; Seber, 1965)

Dataname: Dworshak Hatchery 4/8/93, 4/22/93, and 5/6/93 Releases
 (file: /home/ruddy/surph/public/dworshak.dat)


Survival Probabilities

            |              Period
Population  |      1                2
------------+-----------------------------------
     1      |   0.640 (0.048)  0.714 (0.080)
     2      |   0.662 (0.045)  0.796 (0.080)
     3      |   0.658 (0.050)  0.747 (0.092)
     4      |   0.849 (0.063)  0.644 (0.090)
     5      |   0.686 (0.050)  0.802 (0.105)
     6      |   0.682 (0.046)  1.037 (0.174)
     7      |   1.003 (0.149)  0.494 (0.115)
     8      |   0.677 (0.069)  0.855 (0.164)
     9      |   0.881 (0.111)  0.549 (0.114)


Capture Probabilities

            |              Occasion
Population  |       2               3
------------+-----------------------------------
     1      |   0.442 (0.040)  0.513 (0.050)
     2      |   0.431 (0.037)  0.517 (0.046)
     3      |   0.447 (0.041)  0.458 (0.051)
     4      |   0.445 (0.041)  0.398 (0.050)
     5      |   0.469 (0.041)  0.365 (0.048)
     6      |   0.520 (0.041)  0.224 (0.043)
     7      |   0.267 (0.045)  0.254 (0.047)
     8      |   0.389 (0.046)  0.297 (0.054)
     9      |   0.349 (0.050)  0.294 (0.048)


Product of Final Period Survival/Capture
Population |
------------+------------------
     1      |   0.600 (0.063)
     2      |   0.677 (0.059)
     3      |   0.567 (0.064)
     4      |   0.518 (0.067)
     5      |   0.552 (0.065)
     6      |   0.417 (0.071)
     7      |   0.435 (0.073)
     8      |   0.365 (0.067)
     9      |   0.521 (0.072)
```

Figure 6.21 Cormack/Jolly-Seber estimates for survival, capture, and the product term for smolts released from the Dworshak Hatchery. The capture probabilities for the two "occasions" refer to detections at Lower Granite and Little Goose Dams. The survival probability for "Period 1" is for the stretch of river from release at the hatchery to Lower Granite Dam. "Period 2" is Lower Granite Dam to Little Goose Dam.

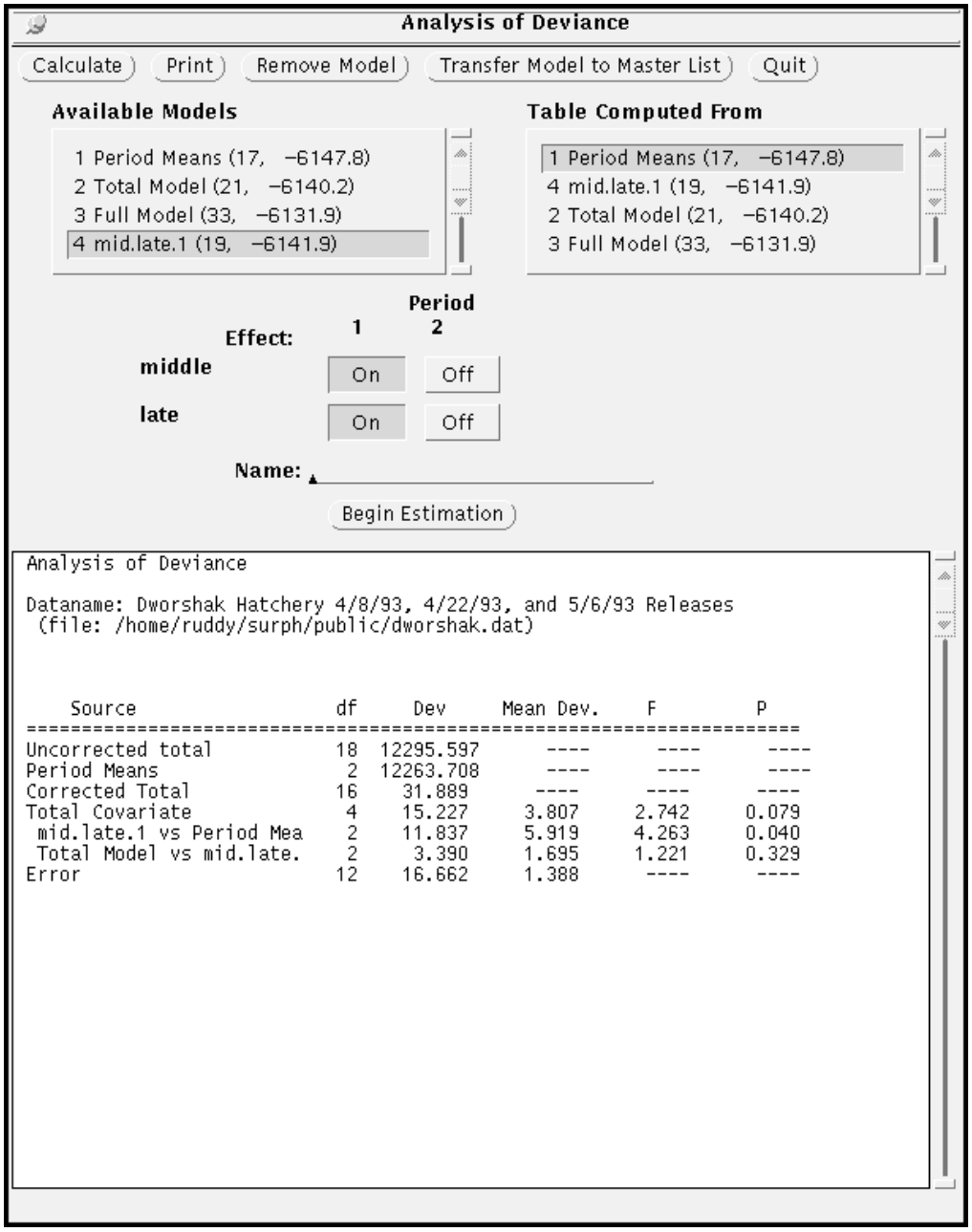
*Use the **ANODEV Table** to investigate the influence of each group covariate. The ANODEV window can be divided into two portions: (1) The top portion, a control panel, which allows the user to create, name, and manipulate models; and (2) the bottom portion, a text pane, which displays the **ANODEV Table**.*

*The **ANODEV** under **Joint S-P Modeling** works identically to the **ANODEV** with known-fate data (Sections 6.1.1, 6.1.2, and 6.1.4). To define new models to partition the total group-covariate effect, use the buttons within the top portion on the **ANODEV Table**. Left-clicking on a button changes its setting from "Off" to "On" or vice versa. When a button is "on" ("depressed"), a parameter will be included in the model to estimate the effect of the covariate in the corresponding period. For example, in the top portion of Figure 6.22, both buttons are depressed for the first period. This means that two effect parameters will be estimated (in addition to the Period Means Model) that will account for the effects of the middle and late releases in the first period. Recall that for this data set, the "periods" are actually river reaches.*

The ANODEV indicated that the model should include effects of the middle and late releases in the first reach only. Within the first reach, the order in which the group covariates were entered into the model was not important. Regardless of the covariate chosen, the first group covariate entered was not significant, but the second group covariate entered was significant. Therefore, both were entered simultaneously to account for this behavior (Figure 6.22). In the second reach ("Period 2"), neither group covariate significantly improved the model ($p > 0.10$). Therefore, the model that was ultimately chosen had the "Pt" model for design effects on capture, separate effects of for middle and late releases on capture at both dams, the "St" model for design effects on survival, and separate effects of middle and late release on survival in the first reach (Figure 6.23).

*Models that are created using the ANODEV procedure are not automatically available in the **Master Models List** on the SURPH Base Window. Therefore, before a model that was fit under the ANODEV procedure can be accessed from the SURPH Base Window, it must be manually transferred to the **Master Models List**. To transfer a model to the **Master Models List**, select the model from the ANODEV **Available Models List**, then left-click on the **Transfer Model to Master List Button**. Once the best fit model is in the **Master Models List**, select it. All future discussion will concern the best fit model (Figure 6.23).*

To determine if the model fits the data well, several diagnostics are available. Many are identical to those used in known-fate data analysis (Sections 6.1.1-4). Two diagnostics examined



Source	df	Dev	Mean Dev.	F	P
Uncorrected total	18	12295.597	----	----	----
Period Means	2	12263.708	----	----	----
Corrected Total	16	31.889	----	----	----
Total Covariate	4	15.227	3.807	2.742	0.079
mid.late.1 vs Period Mea	2	11.837	5.919	4.263	0.040
Total Model vs mid.late.	2	3.390	1.695	1.221	0.329
Error	12	16.662	1.388	----	----

Figure 6.22 Analysis of deviance table for three releases from Dworshak Hatchery. This table indicates that release timing had a significant ($p < 0.10$) effect on survival within the first reach (mid.late.1 versus period means), but not the second reach (total model versus mid.late.1).

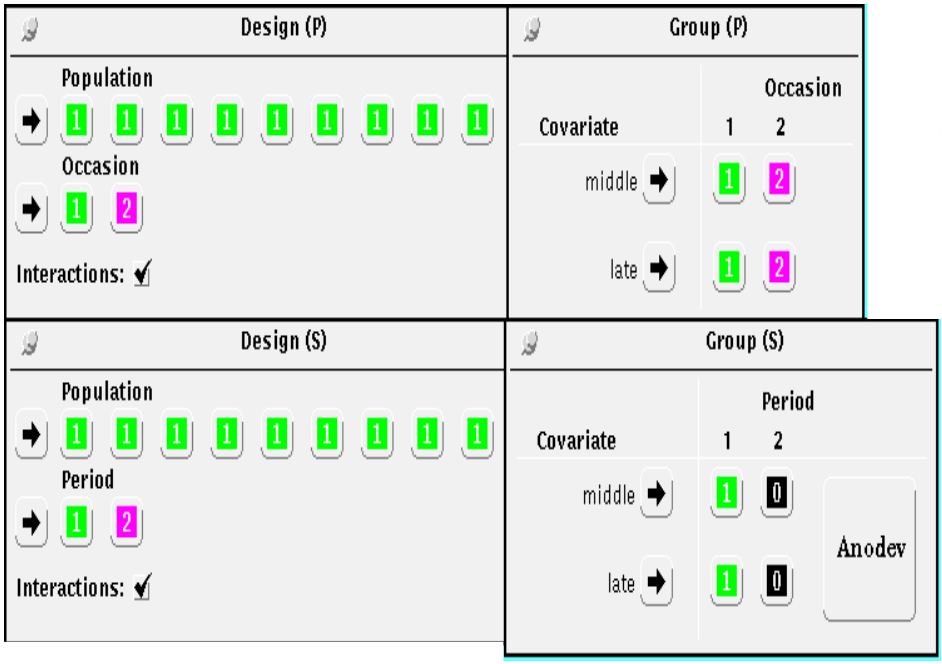


Figure 6.23 The parameterization of the capture and survival effects for the final model for the Dworshak Hatchery data set.

for this data set were the **Residuals versus Capture History Plot** (Section 6.1.2), and the **Quantile-Quantile Plot** (Section 6.1.4). Both plots indicated that the chosen model fits well.

In the **Residuals vs. Capture History Plot** (Figure 6.24), poor fit to the data is indicated when greater than 5% of the values of the standardized residuals lie outside the range [-2,2]. For this model of the Dworshak Hatchery data set, all but one of the standardized residuals fall within the range [-2,2]. This indicates that the model provides a good fit to the data.

In the **Quantile-Quantile Plot** (q-q plot; Figure 6.25), poor fit is indicated by deviations from the 45° line, and by values of the standardized residuals that are far beyond the range [-2,2] (Zar 1984). For this model, there is some indication that the standardized residuals do not strictly conform to the normality assumption, as evidenced by the deviation from the 45° line. However, the deviation is minor, and again, this plot indicates that the model fits the data adequately.

> *Access the SURPH estimates of capture and survival probabilities (Figure 6.26) (**Models Button -> SURPH Probabilities**). The estimates of capture and survival probabilities are for the model that is currently selected in the **Master Models List**. Initially, only the probability estimates for each period will appear. To display the standard errors of the estimates (the parenthetical number to the right of each estimate), left-click on the **Variance Button**.*

The SURPH probabilities associated with the final model (Figure 6.26) indicate that within the first reach, survival increased with later release time. However, in the second reach, survival was independent of release time. The overall survival from release to Little Goose Dam ($S_1 \cdot S_2$) was best for those fish that were in the late release group ($0.577 = 0.770 \cdot 0.741$), because the late release group had highest survival in the first reach (0.770), and all release groups had the same survival in the second reach (0.741). However, when the standard errors were calculated using the delta method to propagate the variance, and the confidence ranges were calculated assuming normal theory, there was no statistical difference ($\alpha = 0.05$) between the overall survival for the early (0.489; SE = 0.03), middle (0.557; SE = 0.04) and the late (0.577; SE = 0.04) releases.

These conclusions are in slight disagreement with the CJS estimates. The CJS estimates show a substantial range, [0.494, 1.037], of survival probabilities within the second reach, but

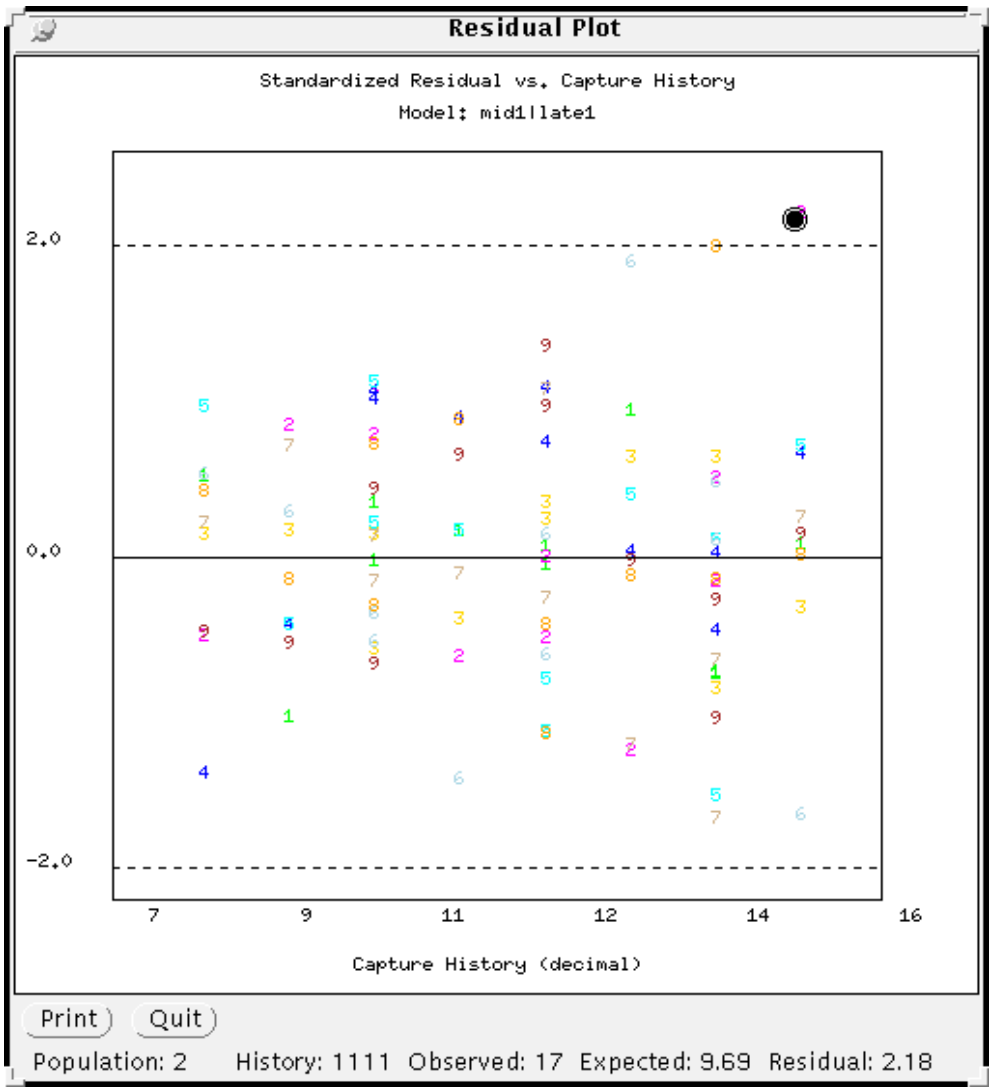


Figure 6.24 The residual versus capture history plot for the final model of the Dworshak Hatchery data set. The fitted model appears to fit the data well, as only one of the standardized residuals lies outside the range [-2,2].

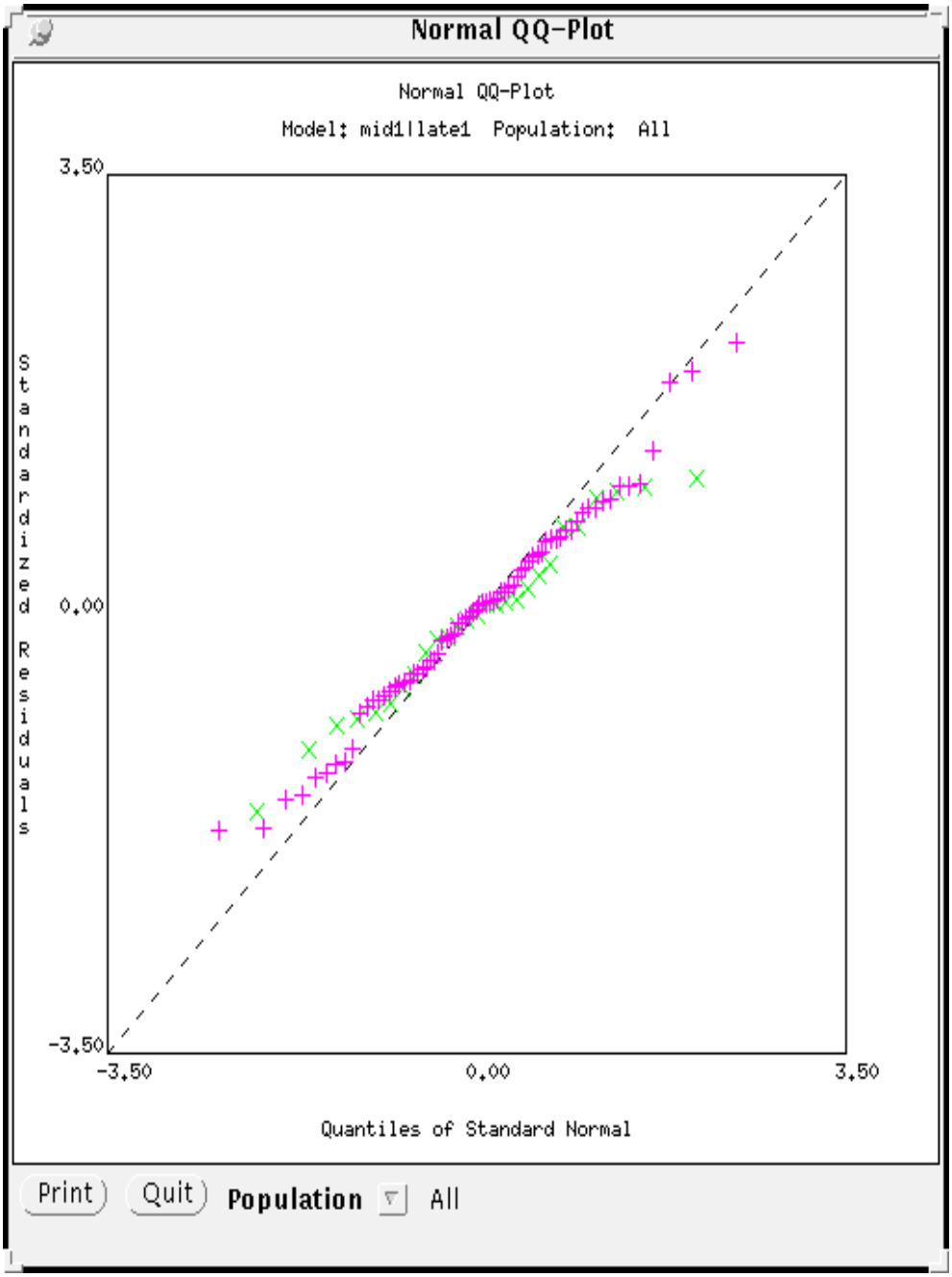
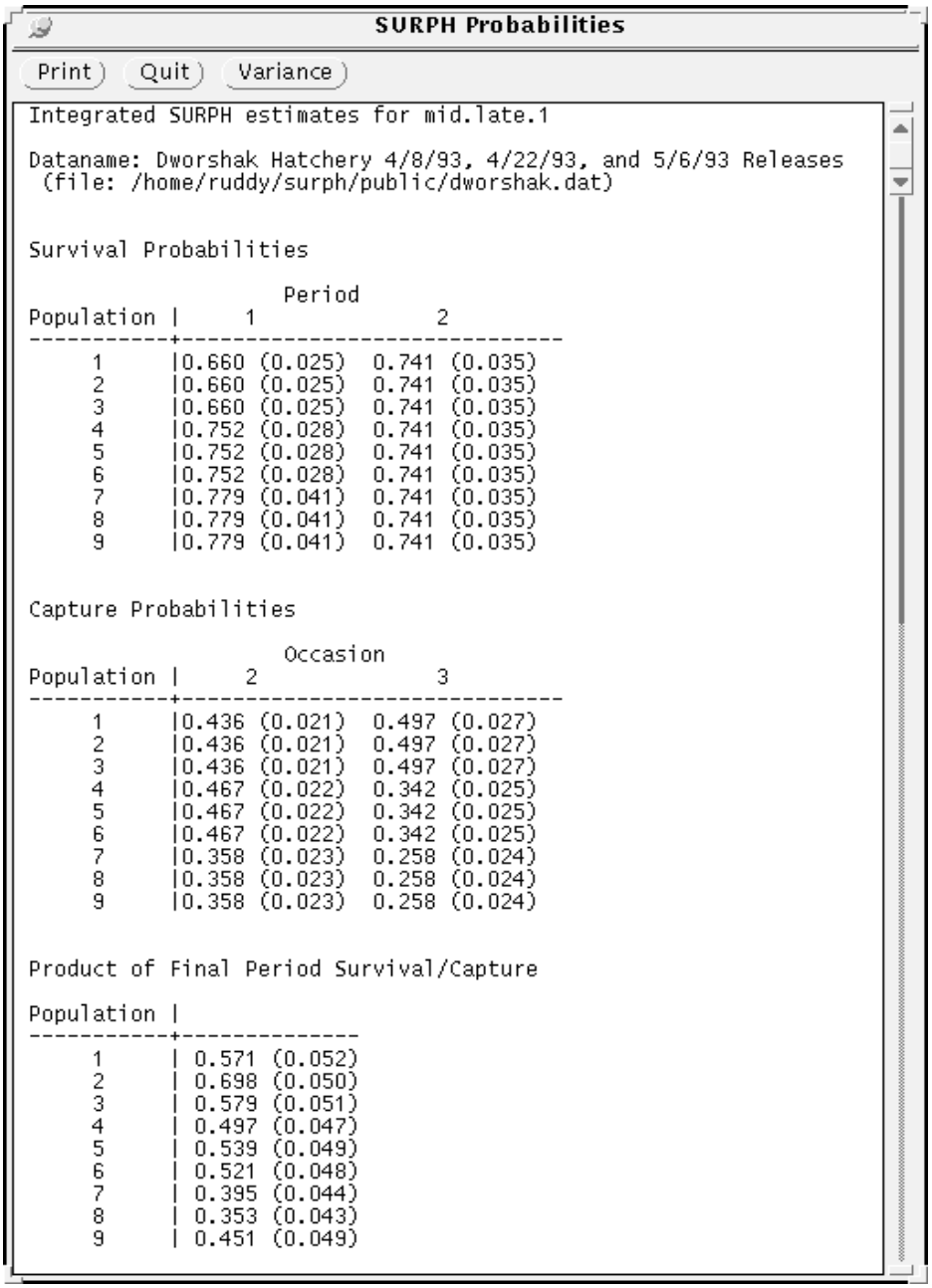


Figure 6.25 The normal Q-Q plot of the standardized residuals for the final model of the Dworshak Hatchery data set. The vertical axis designates the values of the standardized residuals. The horizontal axis designates quantiles of a standard normal distribution.



SURPH Probabilities

Print Quit Variance

```
Integrated SURPH estimates for mid.late.1

Dataname: Dworshak Hatchery 4/8/93, 4/22/93, and 5/6/93 Releases
 (file: /home/ruddy/surph/public/dworshak.dat)


Survival Probabilities

                      Period
Population |     1                2
-----------+-------------------------------
     1     |0.660 (0.025)  0.741 (0.035)
     2     |0.660 (0.025)  0.741 (0.035)
     3     |0.660 (0.025)  0.741 (0.035)
     4     |0.752 (0.028)  0.741 (0.035)
     5     |0.752 (0.028)  0.741 (0.035)
     6     |0.752 (0.028)  0.741 (0.035)
     7     |0.779 (0.041)  0.741 (0.035)
     8     |0.779 (0.041)  0.741 (0.035)
     9     |0.779 (0.041)  0.741 (0.035)


Capture Probabilities

                      Occasion
Population |     2                3
-----------+-------------------------------
     1     |0.436 (0.021)  0.497 (0.027)
     2     |0.436 (0.021)  0.497 (0.027)
     3     |0.436 (0.021)  0.497 (0.027)
     4     |0.467 (0.022)  0.342 (0.025)
     5     |0.467 (0.022)  0.342 (0.025)
     6     |0.467 (0.022)  0.342 (0.025)
     7     |0.358 (0.023)  0.258 (0.024)
     8     |0.358 (0.023)  0.258 (0.024)
     9     |0.358 (0.023)  0.258 (0.024)


Product of Final Period Survival/Capture

Population |
-----------+--------------
     1     | 0.571 (0.052)
     2     | 0.698 (0.050)
     3     | 0.579 (0.051)
     4     | 0.497 (0.047)
     5     | 0.539 (0.049)
     6     | 0.521 (0.048)
     7     | 0.395 (0.044)
     8     | 0.353 (0.043)
     9     | 0.451 (0.049)
```

Figure 6.26 The integrated SURPH estimates of survival, capture, and final period product probabilities for the final model of the Dworshak Hatchery data set. To the right of each estimate, the standard error of the estimate is shown in parentheses.

ANODEV indicated the differences were not significant. The CJS estimates also indicate that the middle release had the highest overall survival of the three release groups, because the early release had poorer survival in the first reach and the late release group had poorer survival in the second reach.

6.2.2 Relationship of fish length to survival

In the spring of 1993, NMFS and UW scientists made seven releases of PIT-tagged chinook salmon for the "Snake River Survival Study" (Iwamoto et al. 1984). The releases occurred near the Nisqually John boat landing, about 30 km upstream from Lower Granite Dam. Run-of-river fish were collected by purse-seine, and previously untagged hatchery-reared yearling chinook salmon were selected to be PIT-tagged and re-released. The length of each PIT-tagged fish was recorded. One release of the seven, comprising 1405 fish, was chosen for this example. The purpose of this example is to explore the relationship between the length of the individual fish and their survival probabilities through stretches of the river. The file "reservoir.dat" contains the data for this example.

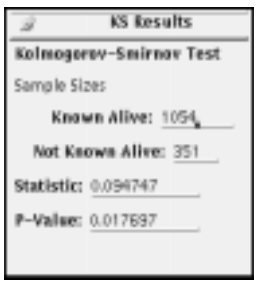
With release-recapture data, capture probabilities can be modeled using either of two distinct approaches (Section 6.2.1). However, if individual covariates that could affect capture rates are present, the user is advised to use "P-Only Modeling" to model the capture probabilities. This is because P-Only Modeling allows the user to model capture independently of any survival model. The absence of any assumed survival model decreases the chance that individual effects that should be attributed to the survival process will be spuriously attributed to the capture process or vice versa. Because the length of the salmon could affect both the capture and survival processes, capture probabilities will be modeled using P-Only Modeling.

> *To begin the SURPH session, at the UNIX prompt type "surph reservoir.dat". Left-click on the* ***Release-Recapture Button*** *to begin the analysis.*
>
> *Access the capture design and individual effects button pads for* ***P-Only Modeling*** *(****Modeling: P-Only -> P Design/P Individual****). Notice that there are no group covariates for this data set.*

Of primary interest in this example is the effect of length on survival and capture. If length affects either survival or capture, the distribution of lengths of fish that are observed should differ from the distribution of lengths of fish that are not observed. One way to investigate whether the length affects either the capture or survival process is to use the cumulative distribution function (CDF) plot, and the associated two-sample Kolmogorov-Smirnov (K-S) test statistic (Zar 1984), available from the **Individual Covariates** pop-up. The K-S test statistic is used to determine

whether those individuals known to be alive on a particular occasion share a common distribution with those not known to be alive. Since all individuals begin the study alive, the CDFs can be used to determine whether individuals are dying in a random fashion, thus both CDFs would be similar, or if there is some pattern to the deaths, in which case the CDFs would diverge.

*Access the **Individual Covariates** pop-up window (**Data -> Individual Covariates**), and left-click on the **CDF Button** at the lower right-hand corner of the window. This will change the default histogram display to a cumulative distribution function display (Figure 6.27). The green (dashed) line displays the empirical CDF of the selected individual covariate for individuals that were known to be alive on the selected occasion. The purple (solid) line displays the empirical CDF of the individual covariate for individuals that were not known to be alive. Select "length" from the **Covariate Pull-Down**, and move the slide bar to occasion 2. The **KS Results** pop-up will appear, displaying the results of the Kolmogorov-Smirnov test of equality between the two CDFs.*



The CDF indicates a significant difference between the distributions (p = 0.0177; K-S Table), suggesting that there is an effect of length on capture and/or survival (Figure 6.27).

The **CJS Estimates** (Figure 6.28) suggest that the two dams have different capture probabilities. Because there is one population and three recapture opportunities, there are only two available models of design effects on capture probabilities. The model of design effects can have either a single overall capture probability that is the same at both dams (the "P" model) or separate capture probabilities at each dam (the "Pt" model). Based on the LRT (p = 0.04), the model with separate capture probabilities (i.e., the "Pt" or fully parameterized model of design effects) at each dam was selected.

The individual covariate "length" could have an effect on either capture or survival probabilities, or both. We recommend investigating the effect on capture first, so that capture effects are not spuriously identified as effects on survival. Recall that while investigating

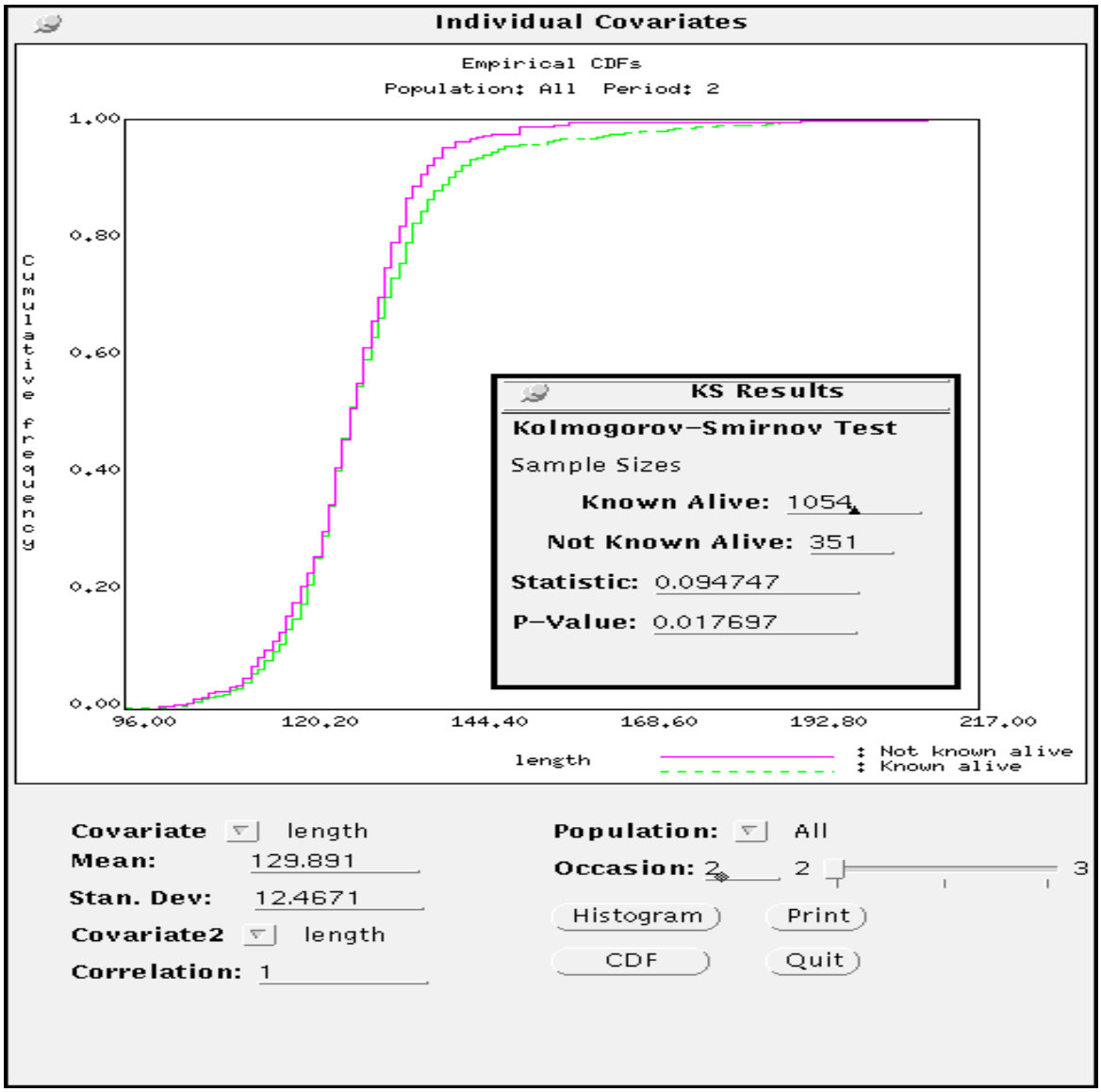
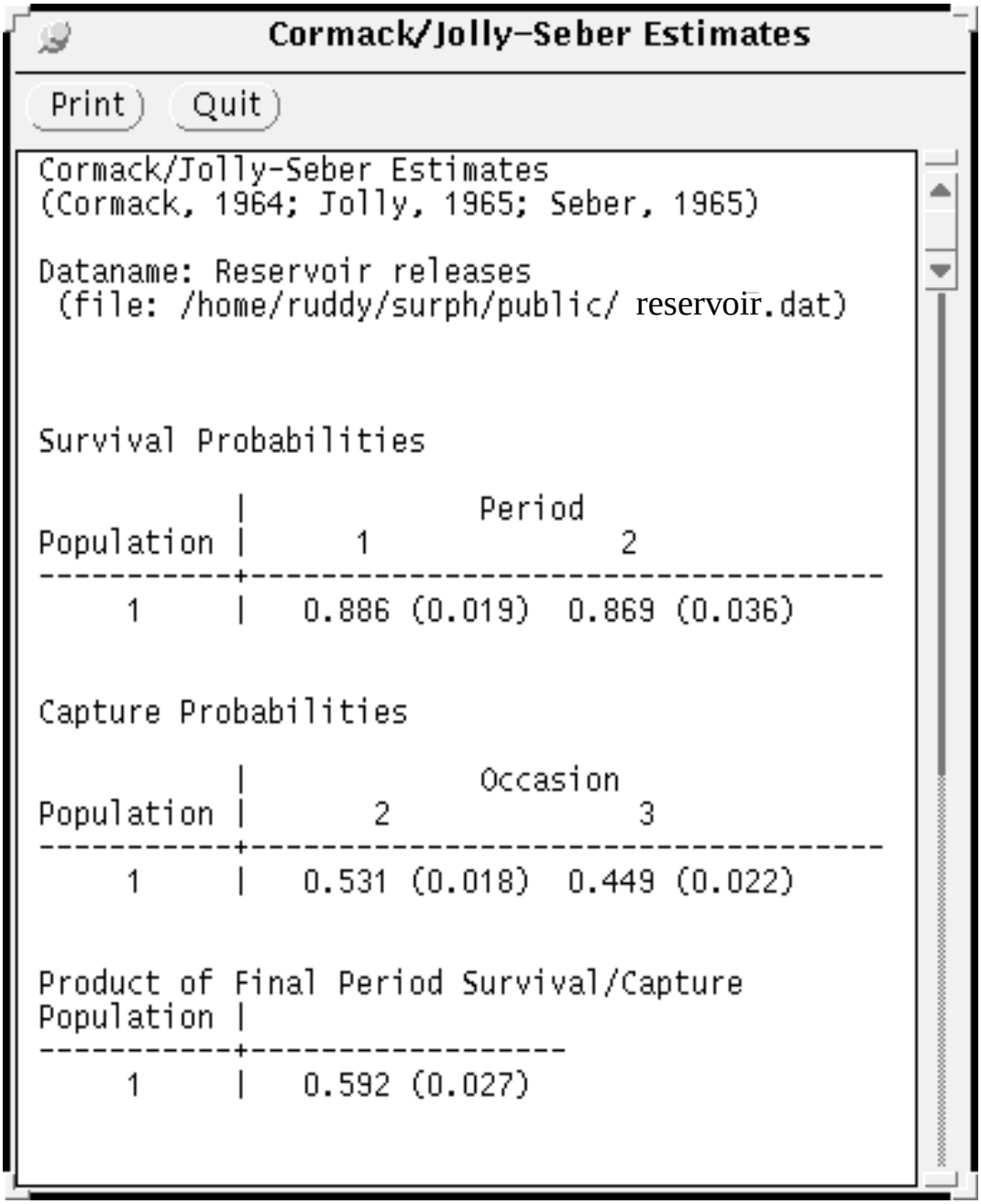


Figure 6.27 **The Empirical Cumulative Distribution Function (CDF) plot for the individual covariate "length" for the reservoir data set. CDFs are plotted for those fish known alive at Lower Granite Dam and those not known alive. The difference between the two distributions attains a maximum value of 0.095. The p-value (0.017) for the K-S test is the probability of observing such a difference if the two distributions were truly equivalent.**



Cormack/Jolly-Seber Estimates

Print Quit

```
Cormack/Jolly-Seber Estimates
(Cormack, 1964; Jolly, 1965; Seber, 1965)

Dataname: Reservoir releases
 (file: /home/ruddy/surph/public/ reservoir.dat)



Survival Probabilities

           |              Period
Population |      1               2
-----------+-------------------------------------
     1     |   0.886 (0.019)  0.869 (0.036)


Capture Probabilities

           |              Occasion
Population |       2               3
-----------+-------------------------------------
     1     |   0.531 (0.018)  0.449 (0.022)


Product of Final Period Survival/Capture
Population |
-----------+------------------
     1     |   0.592 (0.027)
```

Figure 6.28 Cormack/Jolly-Seber estimates of the capture, survival, and final period product probabilities for the reservoir data set. The numbers in parentheses to the right of the estimates are the estimated standard errors.

individual-covariate effects (Section 6.1.3), the fully parameterized model of design effects on capture (and on survival and the product term if joint modeling is used) is recommended. Thus, regardless of the conclusion reached in the design effects portion of modeling, the individual effects would be modeled in conjunction with the “Pt” model of design effects.

> *Choose the “Pt” model from the **Master Models List**. Using the **P Individual Covariate Button Pad**, estimate two additional models. First, model a common effect of the individual covariate “length” on capture (set the buttons on the **P Individual Covariate Button Pad** to “1, 1”). For the second model, model distinct effects for the individual covariate “length” on capture (set the buttons on the **P Individual Covariate Button Pad** to “1, 2”). Use the LRT to decide which of the three individual covariate models (i.e., no effect “0, 0”, a common effect “1, 1”, or distinct effects “1, 2”) is the most appropriate model.*

The LRT indicates that no length effect should be included in the capture model. Thus, the capture model for this data set is the “Pt” model, with no individual effects.

> *Select the “Pt” model from the **Master Models List** and select the **Lock Button**. Access the survival design and individual effects button pads (**Modeling: Joint SP -> S Design/S Individual**).*

As with capture modeling, there are only two design effects models available, “S” and “St”. The model of design effects on survival can be used to determine whether both reaches had similar or differential average survival. However, because the individual effects are of primary interest in this example, estimate only the fully parameterized model design effects on survival (i.e., the “St” model).

> *As with capture, estimate the two individual effects (button settings “1,1” and “1,2”) models for survival.*

Comparing the models using LRT (Sections 6.1.1 and 6.2.1) indicates that the model that has distinct “length” effects on survival in each reach is not significantly (p = 0.20) better than the model that has a common “length” effect on survival. Thus, the model that has the “Pt” capture model, and the “St” survival model with a common “length” effect provides the best fit to the data without any unnecessary parameters. This model was named “Pt.St.S_len11”. All further discussion will concern the “Pt.St.S_len11” model.

*To **Rename** a model, use the command sequence **Models -> Change Name**. A **Change Model Name Pop-Up** will appear. Type the new name into the **New Name** field, then select **Change**. Then, select the "Pt.St.S_len11" model from the **Master Models List**.*

Several model diagnostics are available to the user. In this example, since "length" could affect both capture and survival, the fitted SURPH model should be compared to the nonparametric estimates of both the capture and survival probabilities.

*Access the **Individual Covariate Effects Capture Curves** (**Models -> Capture Curves -> Individual**). Since the final SURPH model does not include an effect of "length" on capture, the SURPH curve is a horizontal line. Left-click on the **Non-Parametric Button** to observe the nonparametric estimates of capture probabilities (Section 4.6.2). To view curves for other occasions, right-click on the occasion pull-down menu indicator, then select the occasion of interest.*

The nonparametric estimates of capture suggest no effect of length at either dam, consistent with the lack of a "length" effect on the capture probabilities in the "Pst.St.S_len11" model (Figure 6.29). Thus, the capture model appears to be properly parameterized.

The "Pst.St.S_len11" model should be compared to the nonparametric estimates of the survival probabilities (Figure 6.30).

*Access the **Individual Covariate Effects Survival Curves** (**Models -> Survival Curves -> Individual**). Since SURPH has included an effect of "length" on survival, the SURPH survival curve is not a horizontal line. Left-click on the **Non-Parametric Button** to observe the nonparametric estimates of survival probabilities (Section 4.6.2.5).*

*To see a histogram for the lengths of fish released, select the **Survival & Histogram Button**. Although the range of fish lengths goes from 96-217 cm, the majority of the fish were between 100-150 cm (Figure 6.31). The functions of other buttons on the **Individual Covariate Effects Survival Curves Pop-Up** are described in Chapter 7.*

The SURPH model provides a fair fit to the nonparametric estimates, particularly over the most common range of 100-150 cm. The SURPH model indicates that larger fish have slightly better survival than smaller fish. However, this increase in survival is slight. For both reaches, the smallest fish (96 cm) had an estimated survival of approximately 82%, while the largest fish (217 cm) had an estimated survival of approximately 95% (Figure 6.31). The majority of the fish

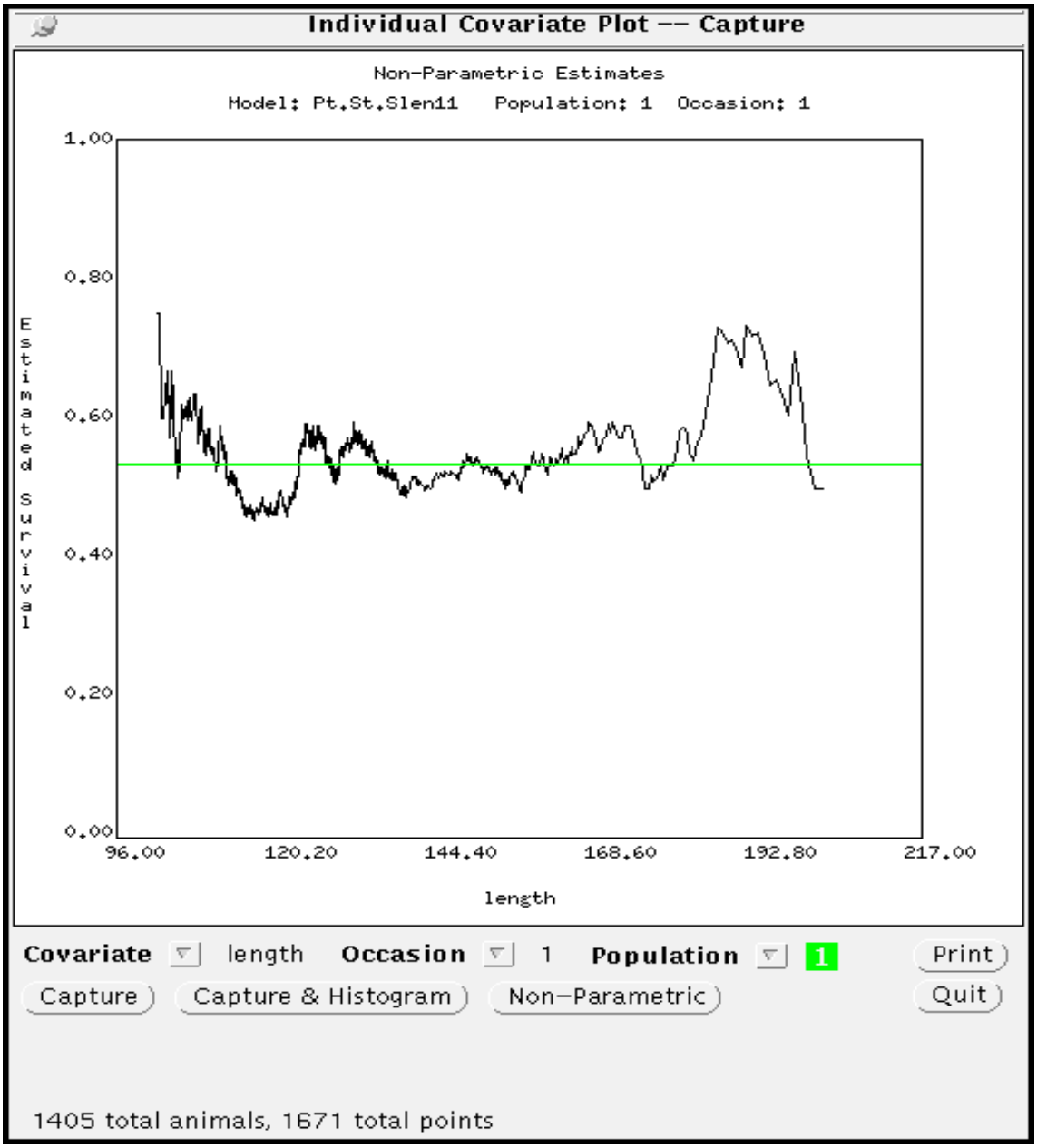
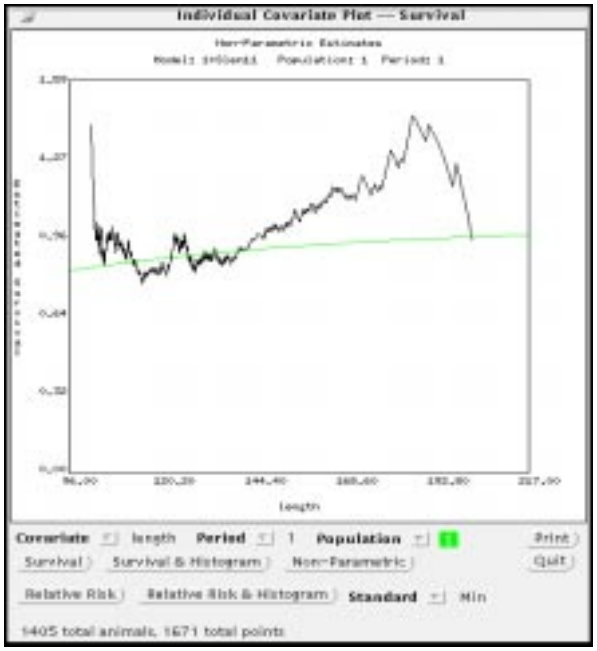


Figure 6.29 A plot of both the nonparametric ("running average") capture probability estimates (the jagged line) and the fitted SURPH model (model "Pt") capture probability estimates (the horizontal line). The plot shown is for Lower Granite Dam ("occasion 1").



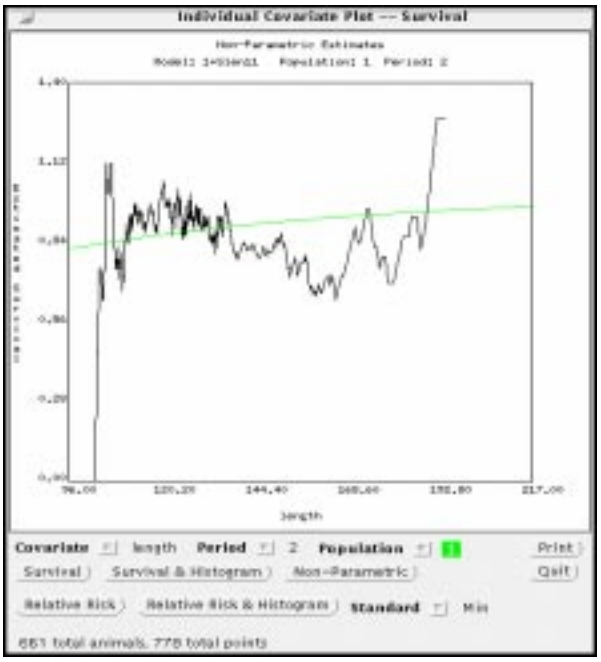


Figure 6.30 Plots of both the nonparametric ("running average") survival probability estimates (the jagged line) and the fitted SURPH model (model "Pt.St.Slen11") survival probability estimates (the horizontal line). The upper plot is for the first "period", the stretch of river from release to the tailrace of Lower Granite Dam. The lower plot is for the second "period", from Lower Granite Dam to Little Goose Dam.

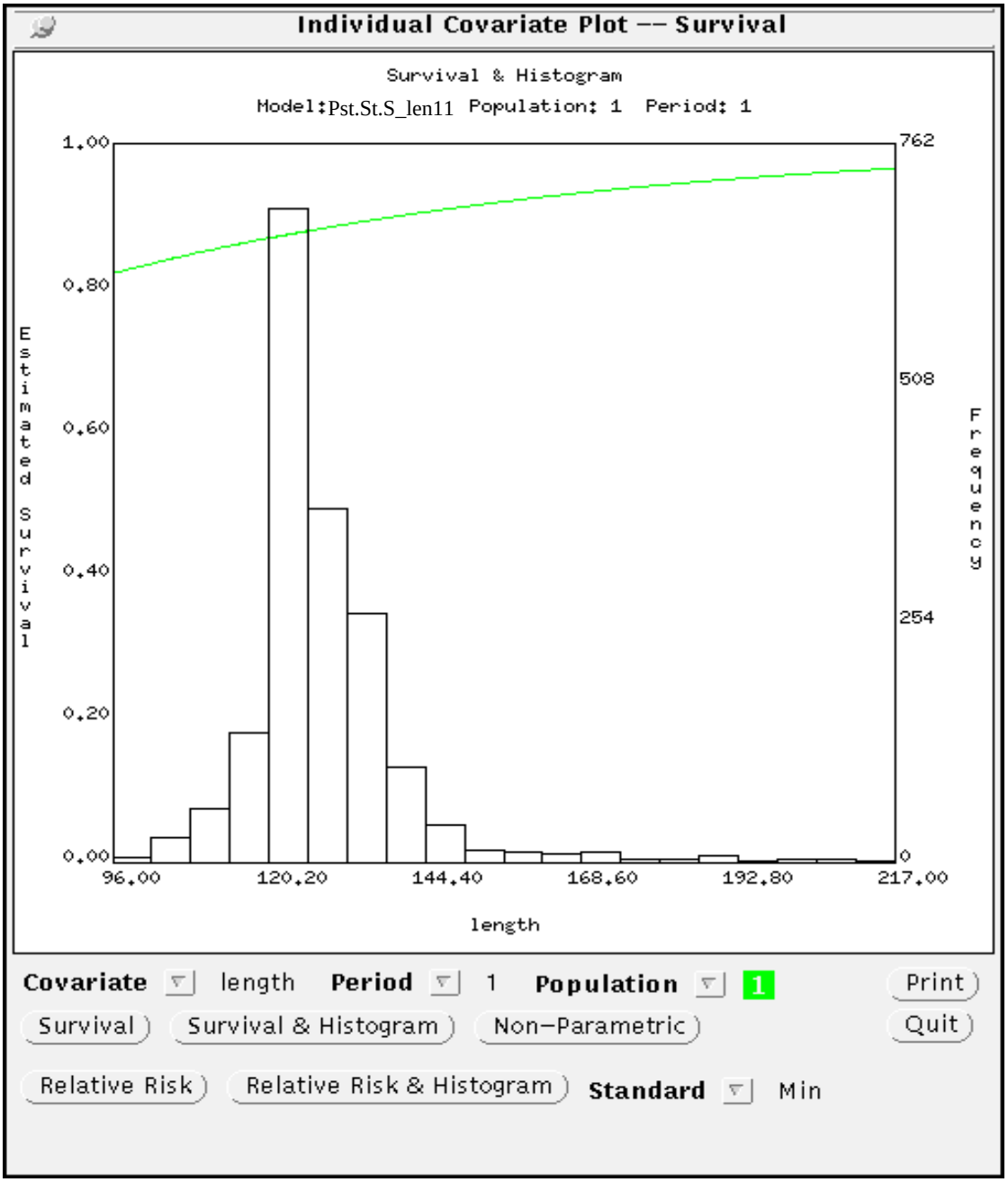


Figure 6.31 **Histogram of the lengths of fish that were known to be alive at the end of the first period. The smooth curve is the fitted SURPH survival curve for the model "Pt.St.Slen11" during the first period. The left vertical axis is estimated survival. The right vertical axis is the absolute frequency of observed lengths. The horizontal axis is the fish length in millimeters.**

released were between 100-150 cm, and the range of estimated survival over this reduced size range is only 84-90%.

A second diagnostic plot that can be viewed is the SURPH versus CJS Estimates plot. In this plot, integrated SURPH estimates (Section 4.6.2.2) are compared to the CJS estimates (Figure 6.32).

> *Access the plot of* ***SURPH Estimates vs. CJS Estimates****,* ***(Models Button -> SURPH vs. CJS Estimates****). The values for the SURPH capture and survival estimates are computed using the model that is currently selected in the* ***Master Models List****. Along the vertical axis of this display are SURPH probability estimates. Along the horizontal axis of this display are Cormack/Jolly-Seber probability estimates. If the SURPH estimates perfectly correspond to the CJS estimates, all points would lie along the overlaid 45˚ line. Capture probability estimates are denoted by a "P"; survival probability estimates are denoted by an "S". A point may be selected from within the display. To select a point, position the mouse cursor above the point and left-click. The CJS and SURPH estimates for this point will be displayed in the window footer, as well as the population and period this estimate represents. In Figure 6.32, the selected point represents the survival estimates for period 2. The CJS estimate of survival is 0.87, and the SURPH estimate is 0.88.*

Again, the SURPH model is in reasonable agreement with the CJS estimates. All points lie very near the 45° line.

Finally, the Q-Q Plot of residuals (Section 6.2.1) should be considered. This residual plot (Figure 6.33), although sparse because of the limited number of possible capture histories, indicates that the residuals are approximately normal. The graph has two different plotting characters. The (red) crosses denote uncensored capture histories; the (green) "X's" denote censored capture histories (known removals). For this data set, the three (green) "X's" indicate that there were three capture histories for animals removed at Lower Granite or Little Goose Dams.

In conclusion, this example data set was used to explore the effects of length on both capture and survival probabilities for juvenile chinook salmon migrating down the Snake River. The analysis indicates that there was no length effect on capture at either dam, but that there was a

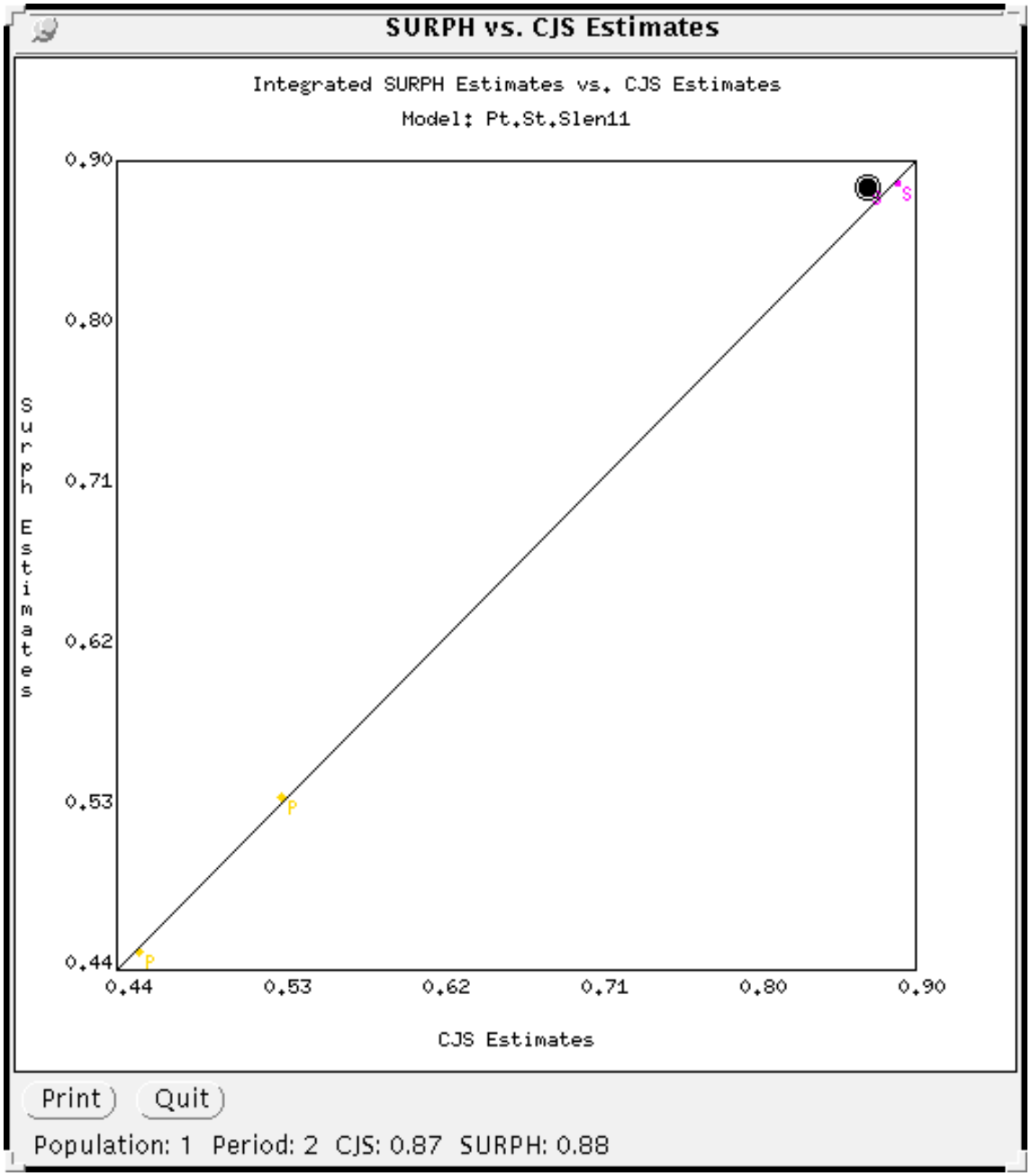


Figure 6.32 SURPH versus CJS estimates of survival and capture probabilities. Along the horizontal axis are CJS estimates of capture and survival probabilities. Along the vertical axis are the integrated SURPH estimates of capture and survival probabilities for model "Pt.St.Slen11" of the reservoir data set. Capture and survival probabilities are plotted with the characters "P" and "S," respectively. Information about the selected point appears in the window footer.

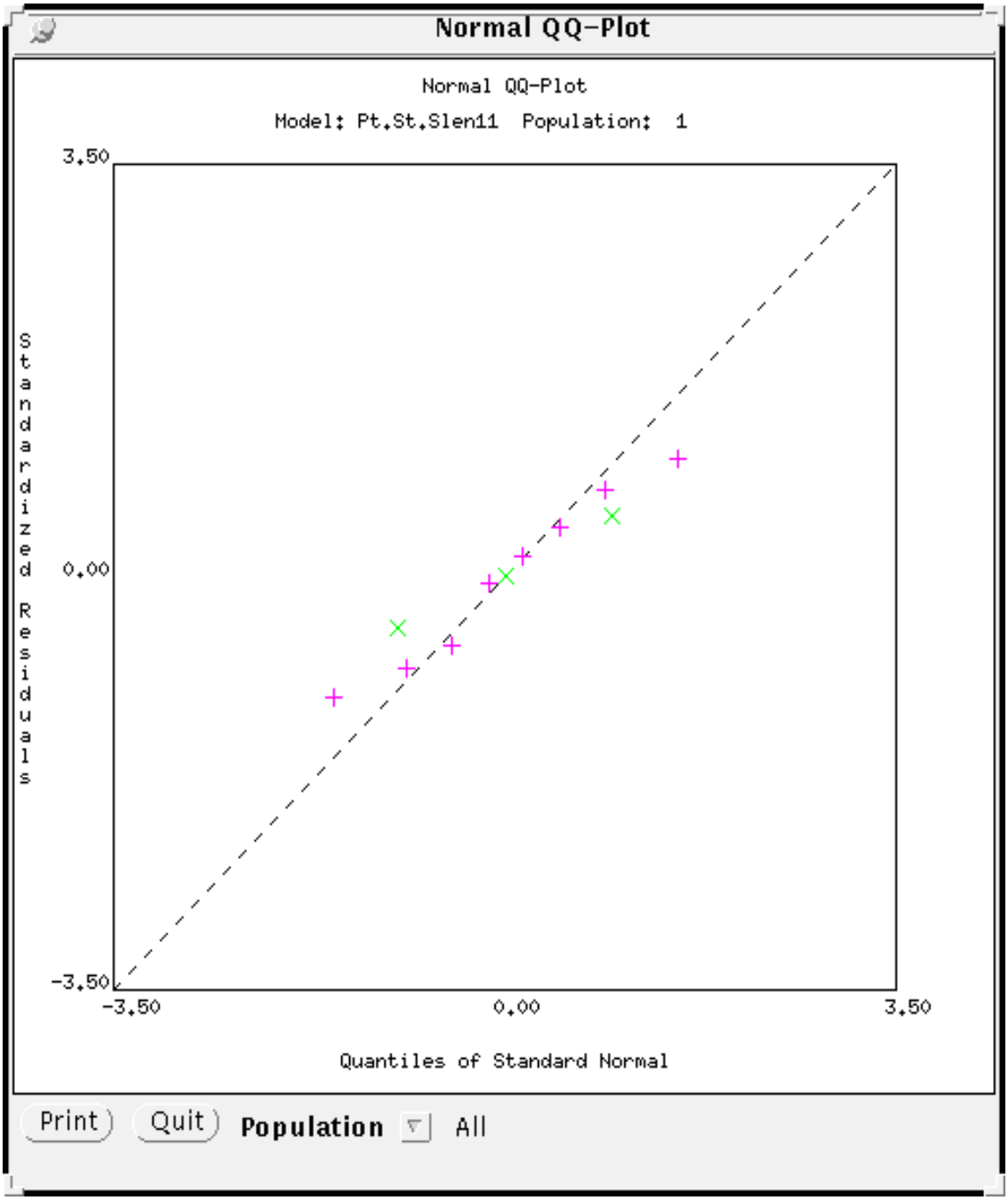


Figure 6.33 Normal Quantile-Quantile Plot for the standardized residuals of the fitted model "Pt.St.Slen11" of the reservoir data set. Along the vertical axis are values of the standardized residuals for the model. Along the horizontal axis are expected values under the standard normal distribution. Crosses ("+") denote uncensored capture histories; "X's" denote censored capture histories.

slight effect of length on survival within both reaches. There was a small, but significant, increase in survival with increasing length in both reaches.

6.2.3 Relationship of migration distance to survival

PIT-tagged yearling chinook salmon were released from the Upper Snake River Basin from six different hatcheries in 1993, as parts of experiments conducted at each hatchery independently. The hatcheries are scattered throughout the Snake River drainage (Figure 6.18), with a wide range of distances to Lower Granite Dam. The purpose of this analysis is to investigate the relationship between the distance the yearling chinook traveled and their survival rates to Lower Granite Dam.

Several of the hatchery investigations included treatment groups of fish that were manipulated in a way that might affect their survival. In this example, we attempted to identify the releases from each hatchery that most closely reflected “normal” release conditions, i.e., the “control” groups. In cases where several releases were made from a hatchery at the same time, we pooled across releases to effectively create one population of marked fish per release date at each hatchery. Table 6.11 summarizes the releases from hatcheries in 1993, and gives the distance (km) from the point of release to Lower Granite Dam. Although the individual covariate “length” is available, individual effects will not be modeled here. Examples that include modeling of individual effects can be found in Sections 6.1.3 and 6.2.2. The data for this example are in the file “distance.dat.”

There is no reason to believe that there should be any effect of the distance travelled on the capture probability upon arrival at Lower Granite Dam; therefore, models that included effects of the group covariate “distance” on capture were not considered. The “P”, “Ps”, “Pt” and “Pst” models of design effects on capture were consequently computed. Of these, the “Pst” (fully parameterized) model of design effects on capture provided significantly better fit than any of the reduced models. The “Pst” model of design effects on capture has a unique capture probability for each release at each dam. The “Pst” model of design effects on capture was used as the capture model during the ANODEV procedure for assessing “distance” effects on survival.

The ANODEV procedure indicated (Figure 6.34) that the group covariate “distance” significantly affected survival within the first reach (release to Lower Granite Dam; $p < 0.001$), but did not indicate (Figure 6.34) that the group covariate should be included within the second

Table 6.11 Information for 1993 releases of PIT-tagged yearling chinook salmon from hatcheries in the Snake River drainage.

Population	Hatchery	Release Site	Distance (km) to Lower Granite Dam	Release Date	Release Size
1	Dworshak	Dworshak	116	4/08	1,467
2	Dworshak	Dworshak	116	4/22	1,460
3	Dworshak	Dworshak	116	5/06	1,445
4	Kooskia	Kooskia	176	4/19	1,171
5	Lookingglass	Lookingglass	235	4/07	999
6	Lookingglass	Imnaha River	135	4/12	1,991
7	McCall	McCall	467	4/03	2,993
8	McCall	McCall	467	4/09-5/05	1,501
9	Rapid River	Rapid River	277	4/17	2,985
10	Sawtooth	Sawtooth	748	4/20	799

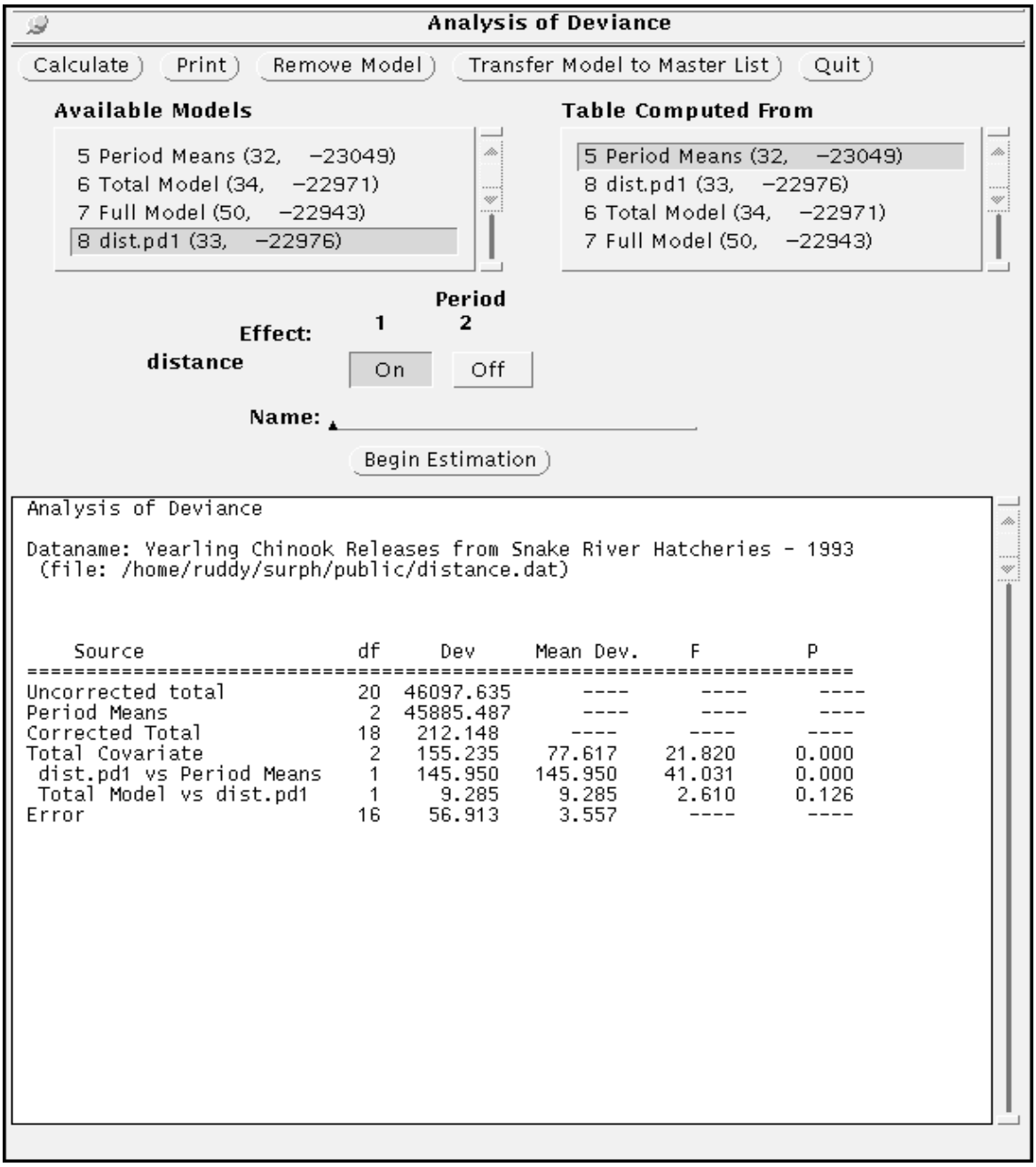
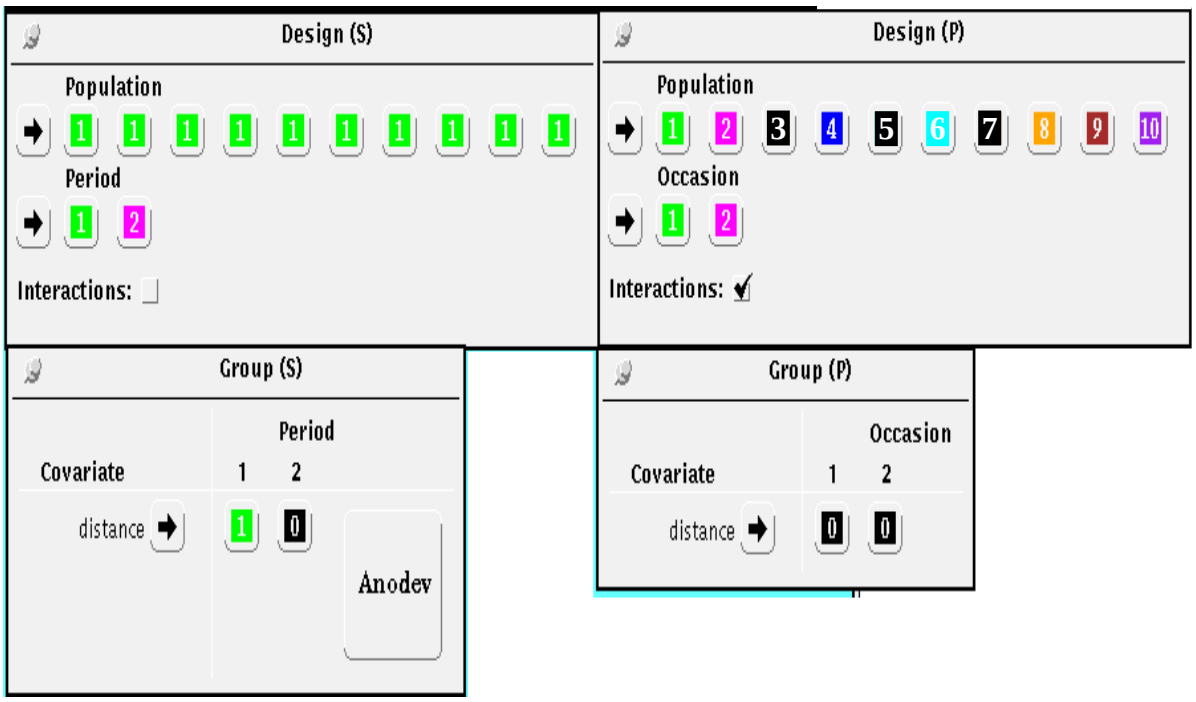


Figure 6.34 ANODEV Table for the effect of distance on survival. In the first reach, the effect of the group covariate "distance" had a significant effect on survival (p-value < 0.001), whereas in the second reach there was no significant effect (p-value = 0.126)

reach (Lower Granite to Little Goose; p = 0.126). The fit of “distance” to the survival model in the second reach is a conditional probability; it is conditional on “distance” having been fit to the survival model in the first reach (see Section 4.5.1). Thus, the model that was ultimately chosen from the ANODEV procedure to best represent the data had a “Pst” model of design effects on capture, an “St” model of design effects on survival (“Period Means Model”), and an effect of the group covariate “distance” on survival within the first reach (see below).



Button Settings for the model “Pst.St.dist10”.

Name the model that had a “Pst” model of design effects on capture, an “St” model of design effects on survival (“Period Means Model”), and an effect of the group covariate “distance” on survival within the first reach “Pst.St.dist10”. All further discussions will concern the “Pst.St.dist10” model.

To assess the fit of the model, the SURPH probability estimates can be compared to the Cormack-Jolly/Seber estimates. There are several different ways of comparing the SURPH probabilities to the CJS estimates. One way is to compare the estimates of capture and survival probabilities using the SURPH Probabilities and the CJS Estimates text windows. The same comparison can be viewed in a graphical format by accessing the SURPH versus CJS Estimates plot from the **Models** pull-down menu.

*Select the "Pst.St.dist10" model from the **Master Models List**. Access the **SURPH Probabilities** (**Models -> SURPH Probabilities**) and the **CJS Estimates** (**Data -> CJS**). Also access the **SURPH vs. CJS Estimates** (**Models -> SURPH vs. CJS Estimates**).*

Comparison of the probability estimates under the SURPH model to the CJS estimates shows some discrepancy between the estimates of survival (Figures 6.35 and 6.36). The agreement between the SURPH model and the CJS estimates is not as good in the second period as it is in the first period (Figure 6.37). This is due, in large part, to the estimates at the extremes of the distance data; Population 3 (116 km; $\hat{S}_{CJS} = 0.62$, $\hat{S}_{SURPH} = 0.80$) and Population 10 (748km; $\hat{S}_{CJS} = 1.15$, $\hat{S}_{SURPH} = 0.80$). Because SURPH probability estimates are constrained to the range [0,1], no SURPH model will be able to fit a CJS estimate above 1.00 well. Thus, although Program SURPH does not have a leverage statistic, given the (x, y) position of population 10, it is quite probable that this one point strongly affects the fit of the SURPH model. There are no replicates from this distance (i.e., 748 km) to indicate the expected spread. The relatively low estimate of survival for Population 3 is not consistent with estimates of survival from other fish also released 116 km away from Lower Granite Dam (Populations 1 and 2). The other CJS estimates of survival for this distance were much closer to the SURPH estimate of 0.80; thus, the survival estimate of 0.62 could be an outlier. Whatever the cause, this estimate cannot be modeled as an effect of distance.

Another plot that compares the SURPH model to the CJS estimates is the group-covariate plot. This plot shows the fitted SURPH survival curve for the model "Pst.St.dist10" as a smooth curve, and the CJS estimates for each population as "bull's-eyes."

*Access the Group Covariate Curve for Survival (**Models -> Survival Curves -> Group**).*

The group-covariate survival plot (Figure 6.38) shows that, during the first period, survival decreased drastically with distance. The fitted SURPH curve provides good agreement with the CJS estimates. In the second period (Figure 6.39)), there is no group effect, so the SURPH curve is a horizontal line. When the CJS probability estimates for the second period are plotted against distance, there is no pattern to the scatter, and the horizontal line seems to provide an adequate fit. Although the fit is not as good as for the first period, the lack of trend is the predominant feature.

SURPH Probabilities

Print Quit Variance

```
Integrated SURPH estimates for Pst.St.dist10

Dataname: Yearling Chinook Releases from Snake River Hatcheries - 1993
 (file: /home/ruddy/surph/public/distance.dat)


Survival Probabilities

                      Period
Population |     1                2
-----------+-----------------------------
     1     |0.725 (0.011)  0.798 (0.017)
     2     |0.725 (0.011)  0.798 (0.017)
     3     |0.725 (0.011)  0.798 (0.017)
     4     |0.696 (0.010)  0.798 (0.017)
     5     |0.665 (0.009)  0.798 (0.017)
     6     |0.716 (0.010)  0.798 (0.017)
     7     |0.525 (0.010)  0.798 (0.017)
     8     |0.525 (0.010)  0.798 (0.017)
     9     |0.642 (0.009)  0.798 (0.017)
    10     |0.325 (0.021)  0.798 (0.017)


Capture Probabilities

                      Occasion
Population |     2                3
-----------+-----------------------------
     1     |0.410 (0.018)  0.435 (0.024)
     2     |0.483 (0.018)  0.333 (0.021)
     3     |0.383 (0.017)  0.260 (0.019)
     4     |0.423 (0.020)  0.256 (0.022)
     5     |0.484 (0.021)  0.598 (0.026)
     6     |0.411 (0.015)  0.367 (0.019)
     7     |0.426 (0.020)  0.461 (0.026)
     8     |0.445 (0.015)  0.390 (0.019)
     9     |0.507 (0.013)  0.392 (0.016)
    10     |0.369 (0.038)  0.285 (0.041)


Product of Final Period Survival/Capture

Population |
-----------+--------------
     1     | 0.525 (0.029)
     2     | 0.505 (0.026)
     3     | 0.401 (0.023)
     4     | 0.402 (0.028)
     5     | 0.697 (0.028)
     6     | 0.485 (0.023)
     7     | 0.629 (0.030)
     8     | 0.528 (0.022)
     9     | 0.580 (0.019)
    10     | 0.499 (0.055)
```

Figure 6.35 Survival, capture, and final period product probability estimates from the model "Pst.St.dist10." In the parentheses to the right of each estimate is the standard error of that estimate.

Cormack/Jolly-Seber Estimates

Print Quit

```
Cormack/Jolly-Seber Estimates
(Cormack, 1964; Jolly, 1965; Seber, 1965)

Dataname: Yearling Chinook Releases from Snake River Hatcheries - 1993
 (file: /home/ruddy/surph/public/distance.dat)


Survival Probabilities

            |              Period
Population  |      1                2
------------+-------------------------------------
     1      |   0.657 (0.028)  0.746 (0.048)
     2      |   0.739 (0.031)  0.790 (0.065)
     3      |   0.835 (0.060)  0.616 (0.074)
     4      |   0.668 (0.043)  0.708 (0.087)
     5      |   0.672 (0.024)  0.870 (0.040)
     6      |   0.669 (0.025)  0.759 (0.047)
     7      |   0.563 (0.029)  0.731 (0.052)
     8      |   0.503 (0.018)  0.804 (0.044)
     9      |   0.680 (0.017)  0.866 (0.041)
    10      |   0.264 (0.029)  1.153 (0.191)


Capture Probabilities

            |              Occasion
Population  |       2               3
------------+-------------------------------------
     1      |   0.438 (0.023)  0.497 (0.028)
     2      |   0.476 (0.024)  0.330 (0.028)
     3      |   0.334 (0.028)  0.283 (0.029)
     4      |   0.436 (0.032)  0.299 (0.034)
     5      |   0.492 (0.023)  0.574 (0.028)
     6      |   0.432 (0.020)  0.405 (0.024)
     7      |   0.403 (0.024)  0.468 (0.029)
     8      |   0.457 (0.018)  0.399 (0.022)
     9      |   0.494 (0.015)  0.355 (0.019)
    10      |   0.440 (0.045)  0.248 (0.048)


Product of Final Period Survival/Capture
Population |
------------+------------------
     1      |   0.615 (0.036)
     2      |   0.500 (0.039)
     3      |   0.438 (0.041)
     4      |   0.474 (0.051)
     5      |   0.663 (0.033)
     6      |   0.541 (0.031)
     7      |   0.639 (0.035)
     8      |   0.541 (0.027)
     9      |   0.521 (0.025)
    10      |   0.432 (0.075)
```

Figure 6.36 Cormack/Jolly-Seber estimates of survival, capture, and final period product probabilities for the ten hatchery releases used to study the relationship between distance and survival. Populations are not ordered in strictly increasing distance from Lower Granite Dam.

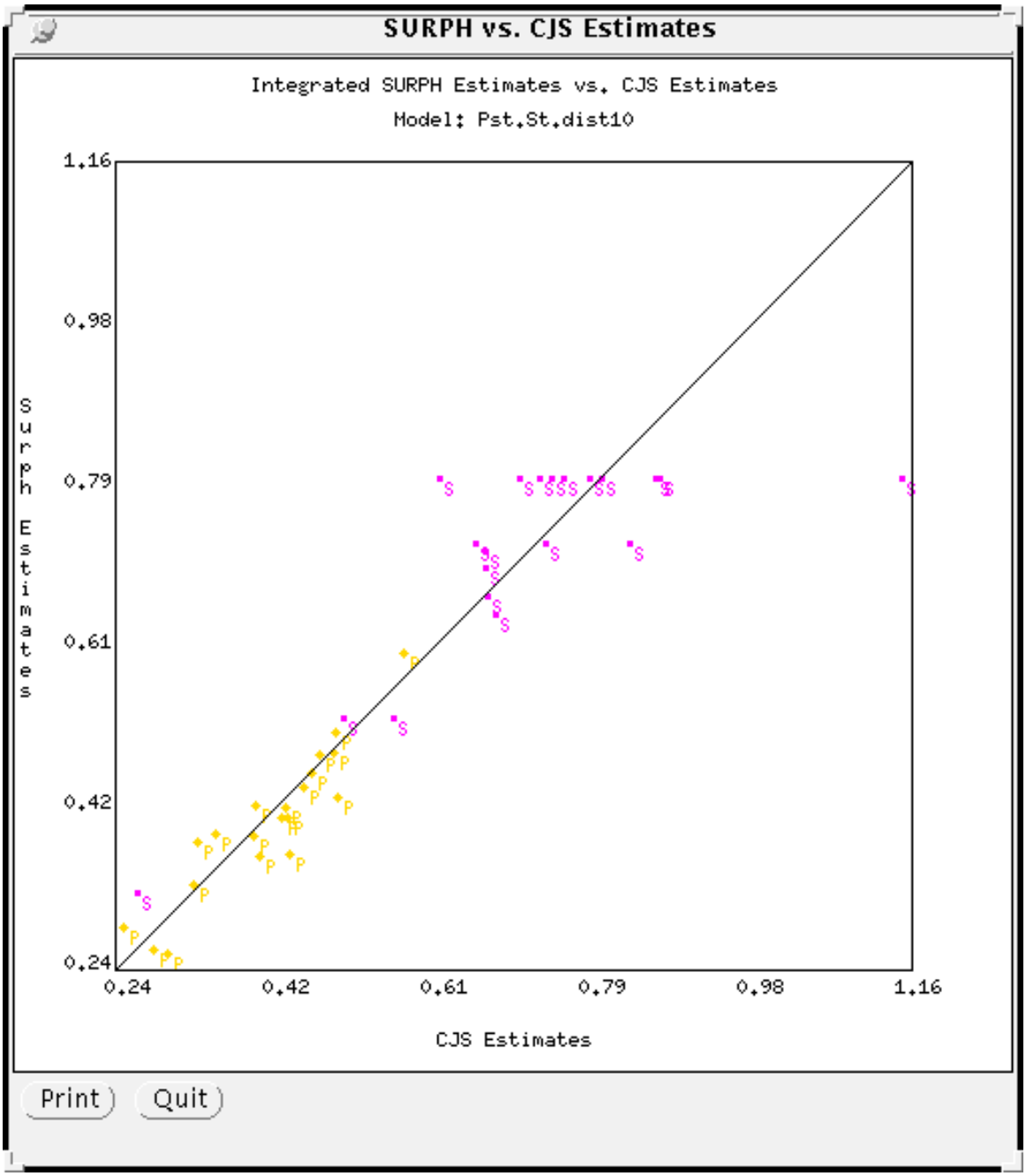


Figure 6.37 SURPH versus CJS estimates plot for the model "Pst.St.dist10" using the data set "distance.dat." Along the horizontal axis are the CJS estimates of capture and survival probabilities. Along the vertical axis are the SURPH estimates of capture and survival probabilities. Capture and survival probabilities are plotted with the characters "P" and "S," respectively.

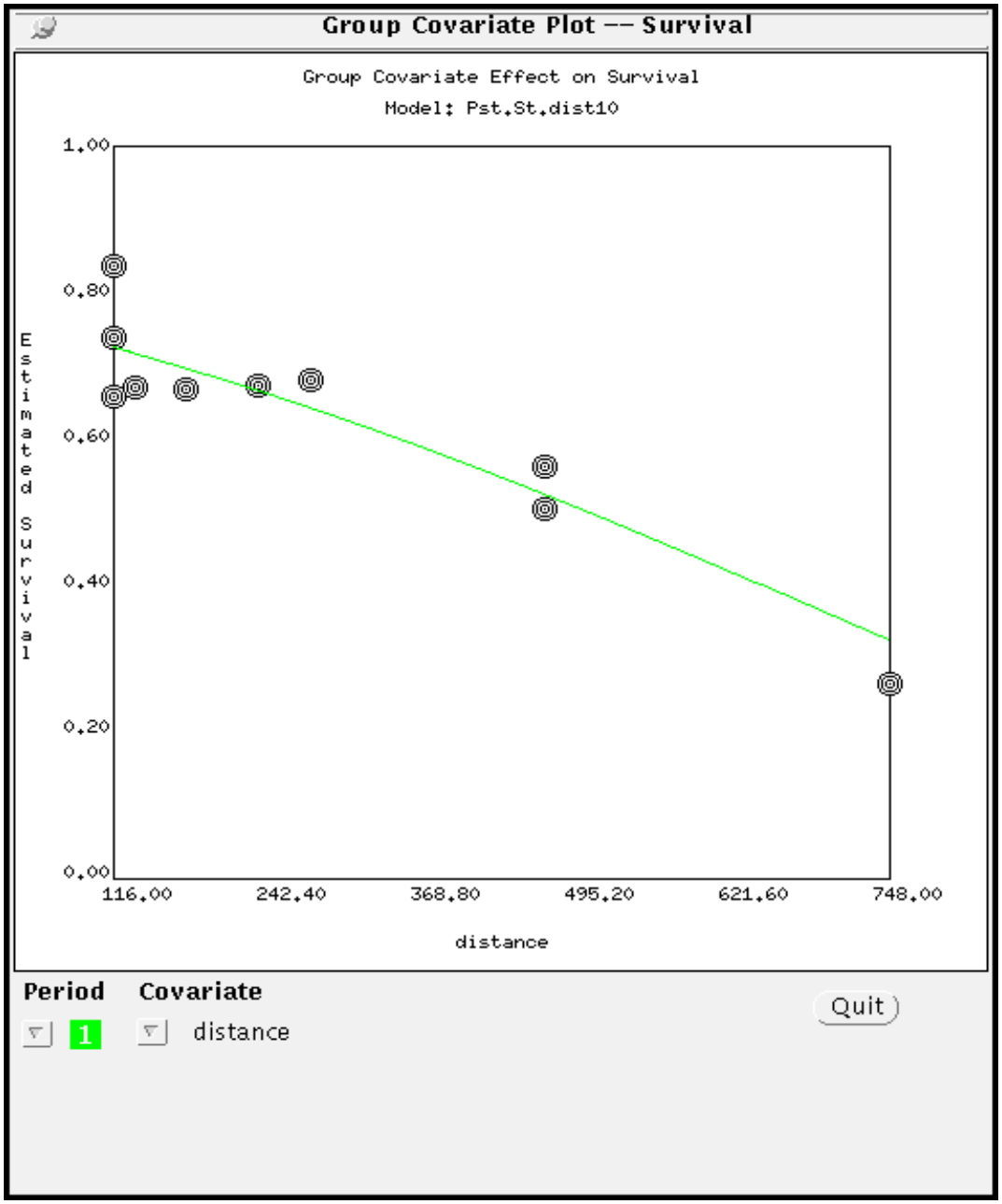


Figure 6.38 The effect of the group covariate "distance" on survival in the first reach. The smooth curve is the fitted SURPH curve for the model "Pst.St.dist10." The "bull's-eye" points are the CJS estimates of survival, plotted against distance.

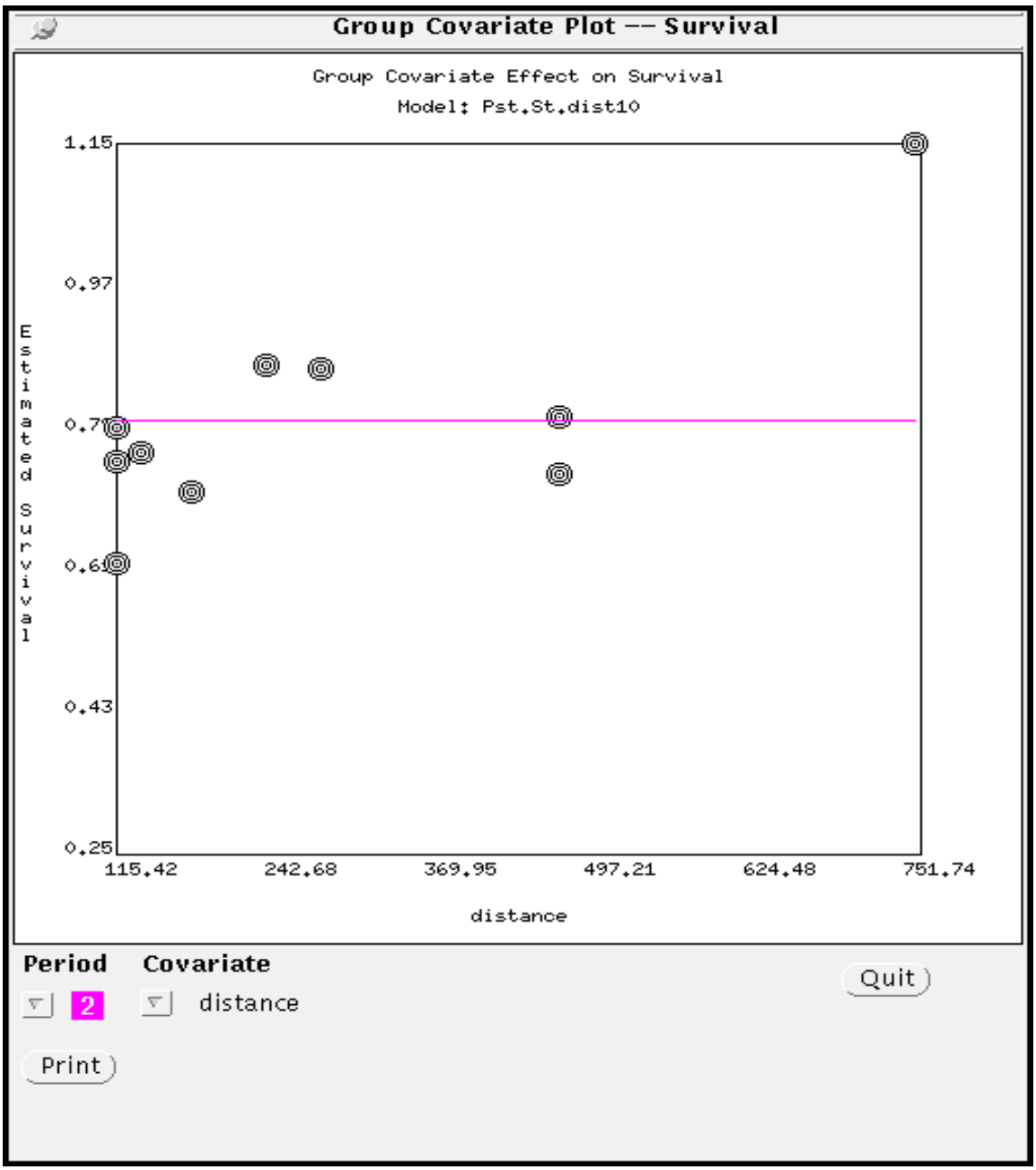


Figure 6.39 The effect of the group covariate "distance" on survival in the second reach. The horizontal line is the fitted SURPH curve for the model "Pst.St.dist10." The "bull's-eye" points are the CJS estimates of survival, plotted against distance. The SURPH curve is a horizontal line because there is no effect of "distance" in the second reach.

Finally, the residuals plot was accessed (***Models -> Residuals Plots -> vs. Capture Histories***). The residuals versus capture history plot (Figure 6.40) showed that the "Pst.St.dist10" model does not have any large outliers. Thus, the evidence indicates that the best model for this data set includes a survival effect due to distance from release point to the first dam. As distance to the first dam increased, survival decreased. In the second reach, no such trend was evident.

However, because there is a large discrepancy between the CJS and SURPH survival estimates for the second period, further analysis was undertaken. The data set was altered, and each of the populations was assigned a group-covariate designation using an indicator or "dummy" variable (Table 6.12). This new data is in the file "distance.2.dat".

> *Quit the current version of SURPH using the* ***Quit Button****. The models that were estimated should be saved for future reference. A series of pop-up windows will give instructions on how to save the models to a file.*
>
> *Indicator variables can take on the values "0" or "1". A "1" is used to indicate that the datum belongs to the group, whereas a "0" is used to indicate that the datum does not belong to the group. In "distance.2.dat", the indicator variable is used to delineate the various populations. For example, in Table 6.12, the "Kooskia" population (Population 4), has a "1" in the fourth position, and "0's" elsewhere.*

In the previous analysis, much of the error term in the ANODEV was associated with the fit of the model for the second reach. In the model "Pst.St.dist10", however, the overall estimate of the survival probabilities in the second period had been fit, and there was considerable scatter. Therefore, for the second analysis, the survival estimates within the second reach were uniquely estimated for each release. Once this was done, only the error associated with the first reach was used to estimate the effect of the group covariate "distance" in the first reach. Using the data construct in "distance.2.dat", the significance of adding the group covariate "distance" to the first period cannot be tested automatically in SURPH, but the ANODEV Table can be constructed using a combination of design and group-covariate effects on survival. As with the data set "distance.dat", the "Pst" model of design effects on capture was used to model the capture probabilities. Next, a specific sequence of survival models was estimated.

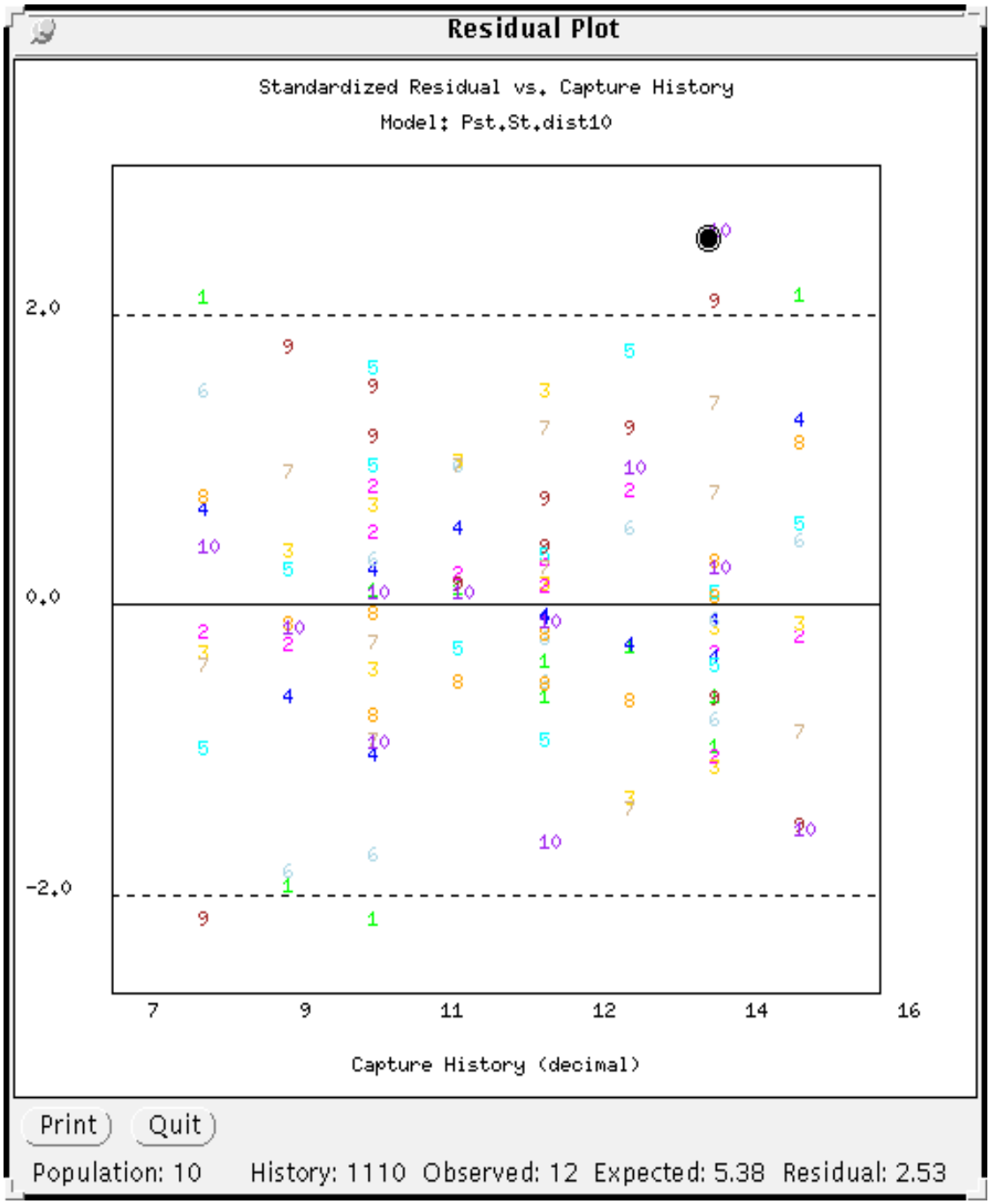


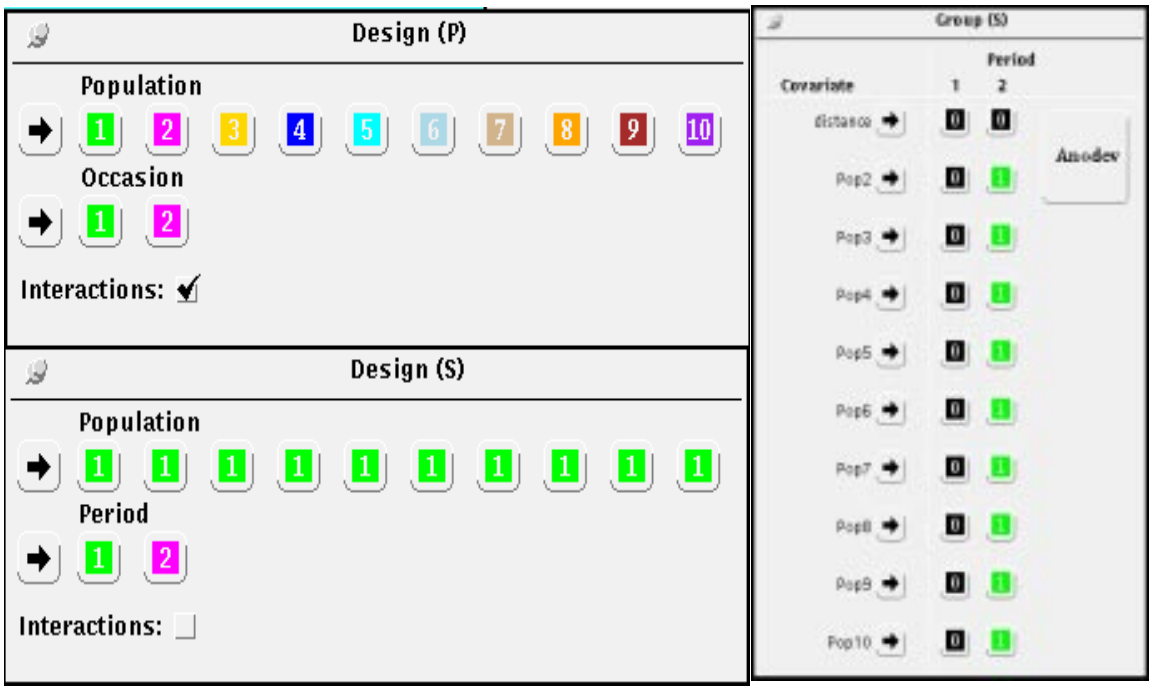
Figure 6.40 Standardized residuals versus capture history plot for the model "Pst.St.dist10" using the data set "distance.dat".

Table 6.12 Indicator variable coding for 10 populations in the data set "distance.2.dat". For SURPH, the indicator variable for the first population is not included in the data file.

Population	Hatchery	Population									
		1	2	3	4	5	6	7	8	9	10
1	Dworshak	1	0	0	0	0	0	0	0	0	0
2	Dworshak	0	1	0	0	0	0	0	0	0	0
3	Dworshak	0	0	1	0	0	0	0	0	0	0
4	Kooskia	0	0	0	1	0	0	0	0	0	0
5	Lookingglass	0	0	0	0	1	0	0	0	0	0
6	Lookingglass	0	0	0	0	0	1	0	0	0	0
7	McCall	0	0	0	0	0	0	1	0	0	0
8	McCall	0	0	0	0	0	0	0	1	0	0
9	Rapid River	0	0	0	0	0	0	0	0	1	0
10	Sawtooth	0	0	0	0	0	0	0	0	0	1

Begin SURPH, this time with the data file "distance.2.dat". Access the ***Capture*** *and* ***Survival Design*** *and* ***Group Button Pads*** *(****Modeling: Joint S-P -> P Design/P Group/S Design/ S Group****.)*

The models of design effects on survival that were estimated were the "Pst.Sst" and the "Pst.St" models. In addition, two group effects models were also estimated. Beginning with the "Pst.St" model, the effects of the group covariates "Pop2" through "Pop10" were added for the second period only. This model was named "Pst.St.Pop01". This model fits unique survival estimates in the second reach (see below). The parameters that were included to account for the



Button Settings for Model "Pst.St.Pop01"

unique estimates for each release in the second period significantly improved the model fit ($P(\chi^2_9) \geq 83.344 \cong 0$). Finally, the model that included both the effect of distance in the first period and the unique parameters for each release in the second period was estimated. This model was named "Pst.St.Pop01.dist10".

Begin with the "Pst.St" model. Using the ***S Group Button Pad****, change the buttons for "Pop2" through "Pop10" in the second period from "0's" to "1's". Name this model "Pst.St.Pop01". Use LRT to compare the model "Pst.Sst" to the model "Pst.St.Pop01". Confirm that the inclusion of the extra parameters in model "Pst.St.Pop01" significantly improved the model fit.*

To create the final model, begin with Pst.St.Pop01, and using the ***S Group Button Pad****, change the button for "distance" in the first period from a "0" to a "1". Name this model "Pst.St.Pop01.dist10".*

An ANODEV Table (Table 6.13) was created from the models "Pst.Sst", "Pst.St.Pop01", and "Pst.St.Pop01.dist10". There are 9 degrees of freedom between the Full Model (i.e., "Pst.Sst") and the model with unique estimates of survival for each release in second reach, but a common estimate of survival for all releases in the first reach (i.e., "Pst.St.Pop01"). These 9 degrees of freedom can be partitioned into an effect of the group covariate "distance" in the first reach (with 1 degree of freedom), and the remainder is considered the error (with 8 degrees of freedom). For the ANODEV Table, we were interested in the effect of "distance" on survival in the first reach. The corrected total deviance for the ANODEV Table is based on the difference between the log-likelihoods of the Full Model and the model with a common estimate of survival for all releases in the first reach (i.e., 2*(lnL("Pst.Sst") - lnL("Pst.St.Pop01")). The portion of the corrected total deviance that is explained by the group covariate "distance" in the first reach is assessed by comparing the fit of the model that includes "distance" to the model with the common estimate of survival in the first reach (i.e., 2*(lnL("Pst.St.Pop01.dist10") - lnL("Pst.St.Pop01")). The error term is the amount of deviance between the model that has fit the effect of "distance" in the first reach and the Full Model (i.e., 2*(lnL("Pst.Sst") - lnL("Pst.St.Pop01.dist10")).

Again, ANODEV indicates a significant effect of "distance" on survival in the first reach ($F_{1,8} = 35.164$, p-value < 0.001). As distance from the hatchery to Lower Granite Dam increases, survival decreases. This is the same conclusion that was drawn from the original data set. However, in the second example, we redefined the error term to account for the "lack of fit" within the first reach only. Using the data set "distance.2.dat, the final model for the first period can be defined as

$$\hat{S}_1(d) = 0.791^{\exp(0.002 \times d)} .$$

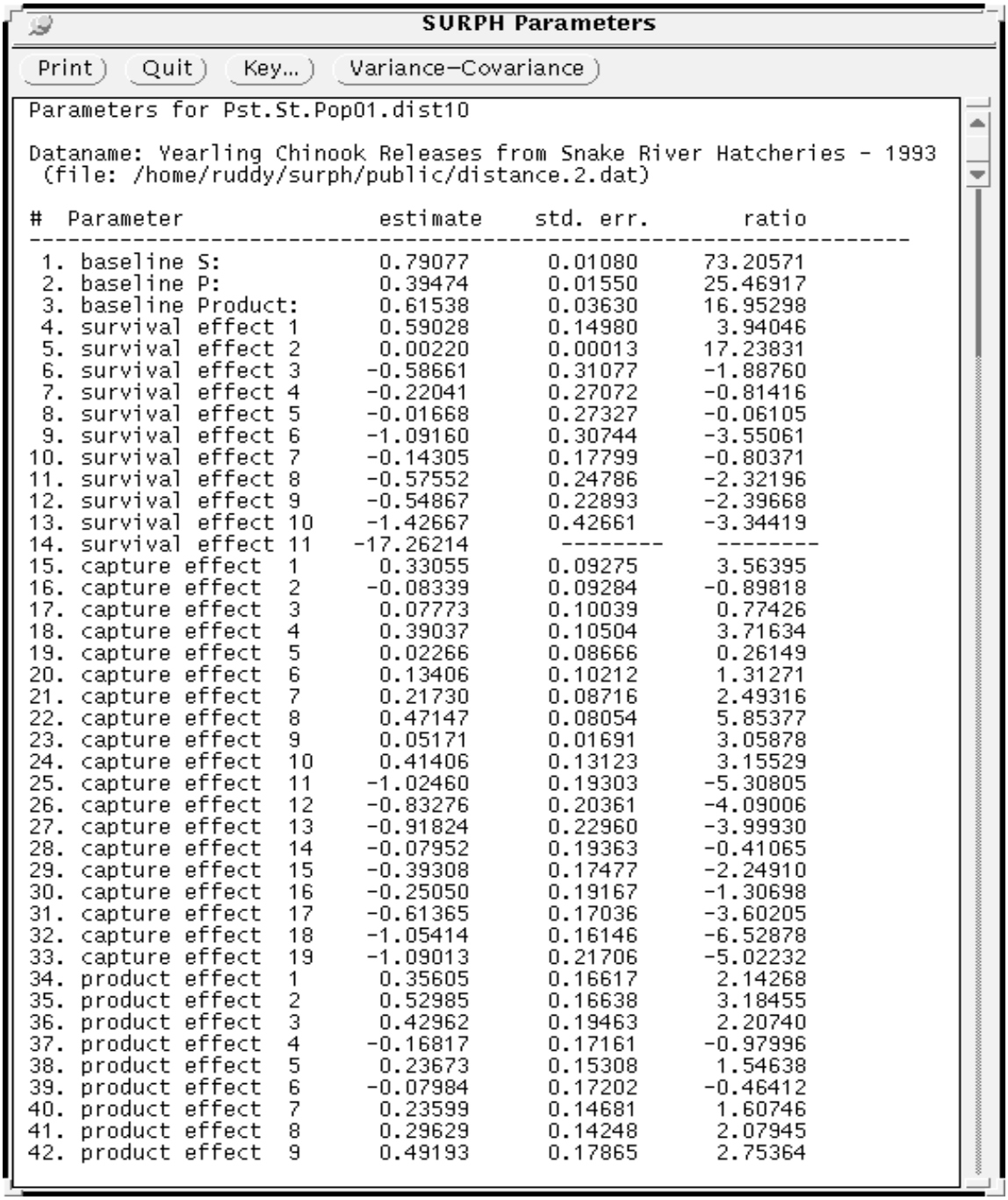
Table 6.13 ANODEV Table to assess the effect of the group covariate "distance" on survival in the first reach, while modeling all variability in survival probabilities in the second reach. This analysis used the data set "distance.2.dat".

Source	df	Deviance	Mean Deviance	F	Prob(F)
Corrected Total	9	128.747			
Distance	1	104.930	104.930	35.164	<0.001
Error	8	23.874	2.984		

*The fitted equation was derived using the **SURPH Parameters** window (Figure 6.41), accessed by the command sequence **Models -> SURPH Parameters**. Use the **Parameter Key** (Figure 6.42; select the **Key Button** on the upper control panel) to see that the fifth parameter is the slope parameter for the effect of "distance" in the first period.*

Both the SURPH versus CJS Estimates plot (Figure 6.43) and the SURPH probability estimates for the model "Pst.St.Pop01.dist10" (Figure 6.44) indicate that the model "Pst.St.Pop01.dist10" provides a much better fit for the second period than did "Pst.St.dist10" (Figures 6.36 and 6.37). This is expected, as in model "Pst.St.dist10", only a single common parameter was used to fit the 10 survival probabilities within the second period, but in model "Pst.St.Pop01.dist10", an additional 9 parameters were included to provide a unique parameter for each survival probability within the second period. The estimates of the survival probabilities within the first period have not change much.

This example showed how to add group-covariate effects to a model and how to test the significance of these effects. It also showed that when non-standard models are needed, the data set and the analysis can often be adapted. This allows the user to continue operating within the SURPH modeling framework.



SURPH Parameters

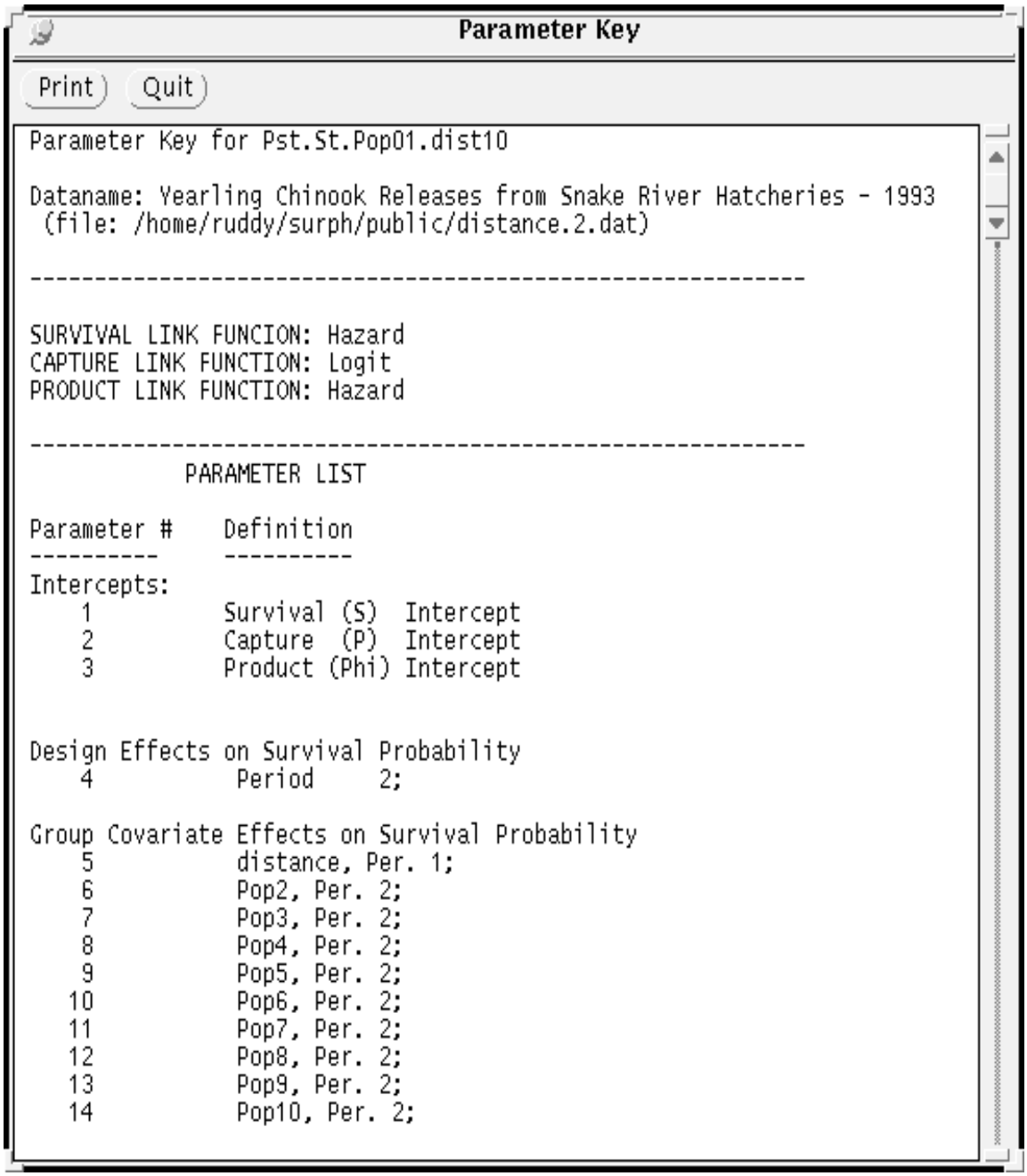
Print | Quit | Key... | Variance-Covariance

Parameters for Pst.St.Pop01.dist10

Dataname: Yearling Chinook Releases from Snake River Hatcheries - 1993
(file: /home/ruddy/surph/public/distance.2.dat)

#	Parameter	estimate	std. err.	ratio
1.	baseline S:	0.79077	0.01080	73.20571
2.	baseline P:	0.39474	0.01550	25.46917
3.	baseline Product:	0.61538	0.03630	16.95298
4.	survival effect 1	0.59028	0.14980	3.94046
5.	survival effect 2	0.00220	0.00013	17.23831
6.	survival effect 3	-0.58661	0.31077	-1.88760
7.	survival effect 4	-0.22041	0.27072	-0.81416
8.	survival effect 5	-0.01668	0.27327	-0.06105
9.	survival effect 6	-1.09160	0.30744	-3.55061
10.	survival effect 7	-0.14305	0.17799	-0.80371
11.	survival effect 8	-0.57552	0.24786	-2.32196
12.	survival effect 9	-0.54867	0.22893	-2.39668
13.	survival effect 10	-1.42667	0.42661	-3.34419
14.	survival effect 11	-17.26214	--------	--------
15.	capture effect 1	0.33055	0.09275	3.56395
16.	capture effect 2	-0.08339	0.09284	-0.89818
17.	capture effect 3	0.07773	0.10039	0.77426
18.	capture effect 4	0.39037	0.10504	3.71634
19.	capture effect 5	0.02266	0.08666	0.26149
20.	capture effect 6	0.13406	0.10212	1.31271
21.	capture effect 7	0.21730	0.08716	2.49316
22.	capture effect 8	0.47147	0.08054	5.85377
23.	capture effect 9	0.05171	0.01691	3.05878
24.	capture effect 10	0.41406	0.13123	3.15529
25.	capture effect 11	-1.02460	0.19303	-5.30805
26.	capture effect 12	-0.83276	0.20361	-4.09006
27.	capture effect 13	-0.91824	0.22960	-3.99930
28.	capture effect 14	-0.07952	0.19363	-0.41065
29.	capture effect 15	-0.39308	0.17477	-2.24910
30.	capture effect 16	-0.25050	0.19167	-1.30698
31.	capture effect 17	-0.61365	0.17036	-3.60205
32.	capture effect 18	-1.05414	0.16146	-6.52878
33.	capture effect 19	-1.09013	0.21706	-5.02232
34.	product effect 1	0.35605	0.16617	2.14268
35.	product effect 2	0.52985	0.16638	3.18455
36.	product effect 3	0.42962	0.19463	2.20740
37.	product effect 4	-0.16817	0.17161	-0.97996
38.	product effect 5	0.23673	0.15308	1.54638
39.	product effect 6	-0.07984	0.17202	-0.46412
40.	product effect 7	0.23599	0.14681	1.60746
41.	product effect 8	0.29629	0.14248	2.07945
42.	product effect 9	0.49193	0.17865	2.75364

Figure 6.41 The SURPH Parameters for the model "Pst.St.Pop01.dist10" using the data set "distance.2.dat". Once the variance-covariance matrix has been computed, the display also includes the standard error and the ratio of the estimate to its standard error.



Parameter Key

Print Quit

```
Parameter Key for Pst.St.Pop01.dist10

Dataname: Yearling Chinook Releases from Snake River Hatcheries - 1993
 (file: /home/ruddy/surph/public/distance.2.dat)

-------------------------------------------------------------

SURVIVAL LINK FUNCION: Hazard
CAPTURE LINK FUNCTION: Logit
PRODUCT LINK FUNCTION: Hazard

-------------------------------------------------------------
            PARAMETER LIST

Parameter #    Definition
----------     ----------
Intercepts:
    1          Survival (S)  Intercept
    2          Capture  (P)  Intercept
    3          Product (Phi) Intercept


Design Effects on Survival Probability
    4           Period     2;

Group Covariate Effects on Survival Probability
    5           distance, Per. 1;
    6           Pop2, Per. 2;
    7           Pop3, Per. 2;
    8           Pop4, Per. 2;
    9           Pop5, Per. 2;
   10           Pop6, Per. 2;
   11           Pop7, Per. 2;
   12           Pop8, Per. 2;
   13           Pop9, Per. 2;
   14           Pop10, Per. 2;
```

Figure 6.42 The Parameter Key for the model "Pst.St.Pop01.dist10" using the data set "distance.2.dat".

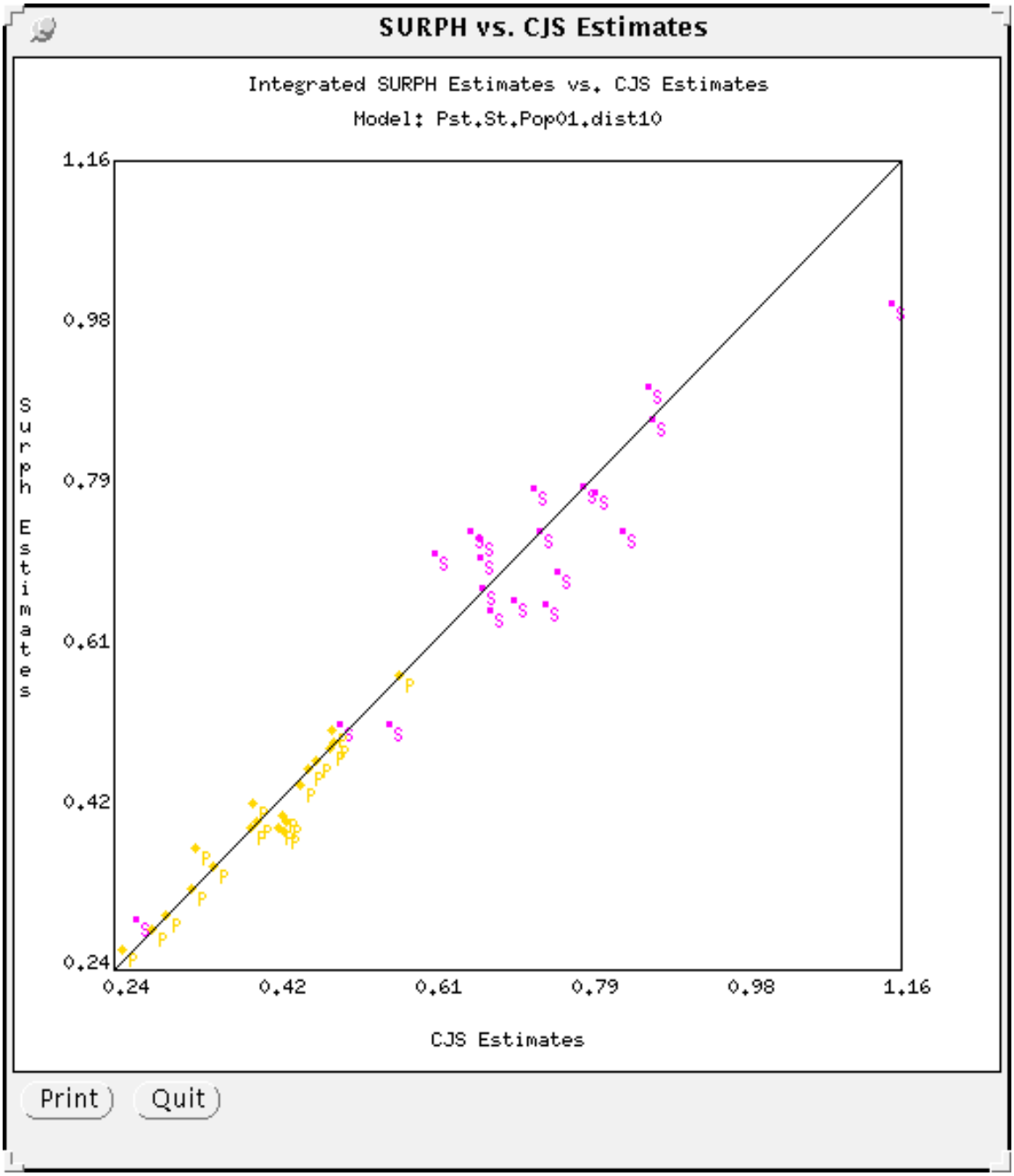


Figure 6.43 **SURPH versus CJS estimates plot for the model "Pst.St.Pop01.dist10" using the data set "distance.dat". Along the horizontal axis are the CJS estimates of capture and survival probabilities. Along the vertical axis are the SURPH estimates of capture and survival probabilities. Capture and survival probabilities are plotted with the characters "P" and "S," respectively.**

SURPH Probabilities

Print Quit Variance

```
Integrated SURPH estimates for Pst.St.Pop01.dist10

Dataname: Yearling Chinook Releases from Snake River Hatcheries - 1993
 (file: /home/ruddy/surph/public/distance.2.dat)


Survival Probabilities

                     Period
Population |     1                2
-----------+-----------------------------
     1     |0.738 (0.010)  0.655 (0.034)
     2     |0.738 (0.010)  0.790 (0.055)
     3     |0.738 (0.010)  0.712 (0.060)
     4     |0.707 (0.010)  0.659 (0.067)
     5     |0.674 (0.009)  0.867 (0.036)
     6     |0.729 (0.010)  0.693 (0.036)
     7     |0.518 (0.009)  0.788 (0.041)
     8     |0.518 (0.009)  0.783 (0.038)
     9     |0.649 (0.009)  0.903 (0.038)
    10     |0.295 (0.018)  1.000 (-----)


Capture Probabilities

                     Occasion
Population |     2                3
-----------+-----------------------------
     1     |0.395 (0.015)  0.497 (0.028)
     2     |0.476 (0.018)  0.330 (0.028)
     3     |0.375 (0.016)  0.283 (0.029)
     4     |0.413 (0.020)  0.299 (0.035)
     5     |0.491 (0.021)  0.574 (0.028)
     6     |0.400 (0.015)  0.405 (0.024)
     7     |0.427 (0.020)  0.468 (0.029)
     8     |0.448 (0.016)  0.399 (0.022)
     9     |0.511 (0.013)  0.355 (0.019)
    10     |0.407 (0.015)  0.259 (0.036)


Product of Final Period Survival/Capture

Population |
-----------+--------------
     1     | 0.615 (0.036)
     2     | 0.500 (0.039)
     3     | 0.438 (0.041)
     4     | 0.474 (0.053)
     5     | 0.663 (0.033)
     6     | 0.541 (0.031)
     7     | 0.639 (0.035)
     8     | 0.541 (0.027)
     9     | 0.521 (0.025)
    10     | 0.452 (0.047)
```

Figure 6.44 The integrated SURPH estimates of survival, capture and product term probabilities for the model "Pst.St.Pop01.dist10" using the data set "distance.2.dat". In the parentheses to the right of each estimate is the standard error of that estimate.

6.2.4 Burnham et al. turbine mortality study

The American Fisheries Society monograph by Burnham et al. (1987) (hereafter referred to as the “Burnham monograph”) was primarily concerned with the analysis of paired, “control/ treatment” releases. Such paired releases can be used to assess the effects on survival of fish through hydroelectric turbines or other routes of dam passage. In a “turbine trial,” the treatment group of fish is released directly into the turbine unit while the control group is released into the tailrace below the dam. It is assumed that fish from the two releases mix together thoroughly as they move downstream, so that survival and capture probabilities are common between the two groups, except for the difference caused by turbine passage of the treatment fish. The parameter of most interest is S_T (our notation), the probability of surviving turbine passage. The Burnham monograph provides a suite of sampling protocols and alternative models for release-recapture data generated in such a paired-release study. The purpose of this example is to show how SURPH can be used to perform the analysis recommended in the Burnham monograph under the “complete capture histories” protocol. Data from the “general numerical (simulated) example data set” from the Burnham monograph are used. The SURPH analysis does not include all the tests of assumptions that are provided in the Burnham monograph. The data for this example are in the file “burnham.dat.”

The sampling protocols described in Burnham et al. (1987) include “first capture histories,” where only the location of the first “recapture” of each fish is known; “partial capture histories,” where multiple tags are used to give information on the locations of the first two recaptures (“scheme A”); and the “complete capture histories” protocol, where distinct individual marks allow the compilation of complete records of detection at all downstream sampling sites. This is the type of data required by SURPH, and we will restrict our attention to the “complete capture histories” sampling protocol.

The Burnham monograph (Section 2.4.10, pp. 129-143) identify a suite of possible models for paired-release data. Table 6.14 repeats Table 2.2 of Burnham et al. (1987), with model names modified to agree with our notation. The table lists models from the most general to most restricted. Model $H_{K-1,S}$ amounts to what we call “Model (Pst, Sst),” wherein both survival and

Table 6.14 Suite of models for paired-release recapture data (Burnham et al. 1987). Notation: E means that the parameter is assumed to be equal for the treatment and control groups; D means that the parameter is allowed to differ between the two groups.

Dam k = 1→		2	→	3	→	4	→	K-1	K
Model	S_1	P_2	S_2	P_3	S_3	P_4	→	P_{K-1}	λ
H_0	E	E	E	E	E	E	→	E	E
H_{1S}	D	E	E	E	E	E	→	E	E
H_{2P}	D	D	E	E	E	E	→	E	E
H_{2S}	D	D	D	E	E	E	→	E	E
H_{3P}	D	D	D	D	E	E	→	E	E
H_{3S}	D	D	D	D	D	E	→	E	E
•	•	•	•	•	•	•		•	•
•	•	•	•	•	•	•		•	•
•	•	•	•	•	•	•		•	•
$H_{K-1,P}$	D	D	D	D	D	D	→	D	E
$H_{K-1,S}$	D	D	D	D	D	D	→	D	D

capture probabilities depend on “site” and “time” (i.e., all parameters differ between reaches and release groups). At the other extreme, under Model H_0 all parameters are common between the two groups; i.e., the model we call “(P_t,S_t).” Another notable model is H_{1s}, wherein all survival and capture probabilities are common between the two populations except for the first reach, where the passage effects on survival are evident. Note that the series of parameters listed in the heading of Table 6.14 can be thought of as ordered chronologically; the events leading to S_1 occur before those for P_2, which is before S_2, and so on.

The recommended analysis (hereafter called the “Burnham analysis”) consists of a series of tests to determine the appropriate model of the data, and then estimation of S_T from the selected model. The hypothesis tests begin with a test of the most general model $H_{K-1,S}$ against $H_{K-1,P}$, which has a common final period product parameter for the two groups. If the product terms are not found to be significantly different, then Model $H_{K-1,P}$ is tested against $H_{K-2,S}$, i.e., a test for equality of the parameters $P_{t,K-1}$ and $P_{c,K-1}$. Testing continues in this way, increasing the number of common parameters as warranted until a test finds a significant difference between two parameters. The “treatment” effect is deemed to persist through the time of the earliest parameter that was found to be common between the two groups. The Burnham monograph shows how each test in the series of tests between models can be computed using the appropriate 2×2 contingency table based on the observed data. The contingency table tests have not been incorporated into SURPH, but asymptotically equivalent likelihood ratio tests can be computed using SURPH.

There are two aspects of the Burnham analysis of paired releases that do not conform to our general recommendations regarding analysis of release-recapture data using SURPH. First, the analysis switches back and forth between modeling capture and survival probabilities, whereas our usual approach is to model the capture process first and then to proceed to modeling of the survival process. Second, the button settings used in SURPH to parameterize design effects do not allow a mixture of common parameters among populations in some periods and unique in others.

Instead, a small “trick” is required to fit the series of Burnham models; a “dummy” or “indicator” group covariate for the treatment effect is defined for the two populations. In the input file, assuming the treatment group capture history data is listed first, the group covariate is defined by the lines (see Section 5.2):

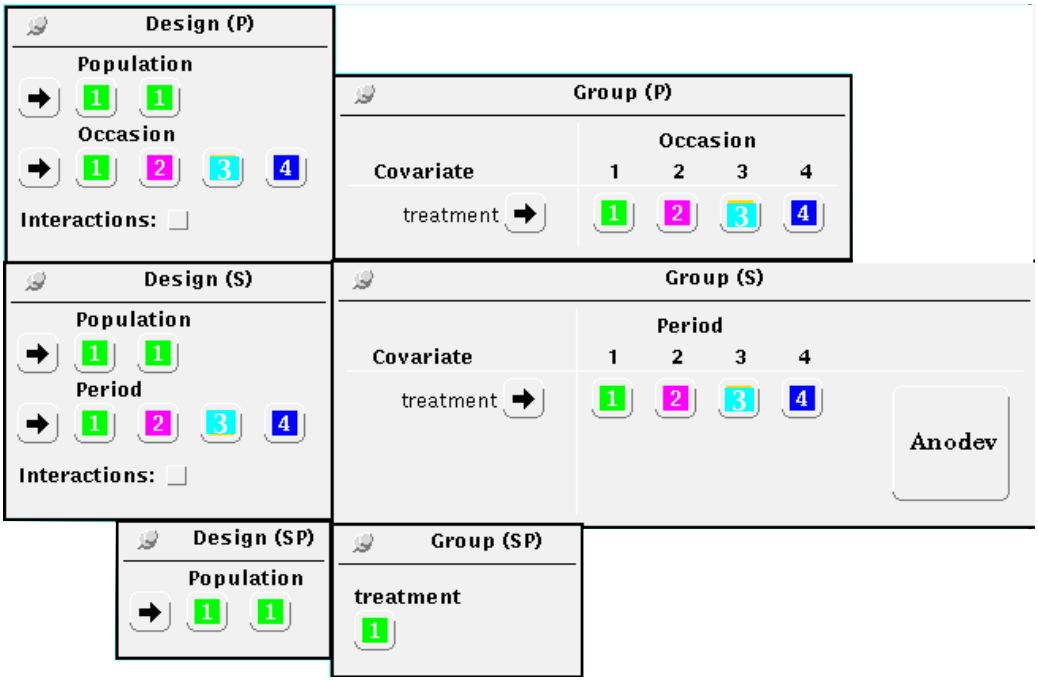
number_of_populations 2
group_covariate name treatment time 0
1
0.

> *At the UNIX prompt, type “surph burnham.dat,” then left-click on the “Release-Recapture button to begin SURPH. Access the design and group effects button pads for capture, survival, and the product term in the final period (**Modeling: Joint S-P -> P Design/P Group/S Design/S Group/Product Design/Product Group**).*
>
> *Specify Model “H5s” using both design and group effects: parameterize the design effects on capture as a “Pt” model, and the design effects on survival as an “St” model. Then, using the group effects button pads, add a separate parameter for each period for both capture and survival. For the product term, use a common parameter for both populations (design effects), and add a group effect. When you have finished setting all the buttons, the button pads should appear as shown below. Enter “H5s” in the Name field and left-click on the Begin Estimation button to fit the model. If the buttons are correctly set, Model “H5s” will have 18 parameters.*

Testing begins with the product term in final period. The product term is the probability that an individual both survived the final reach and was recaptured at the final dam. The first test in the series tests whether the product terms are equal for the control and treatment groups.

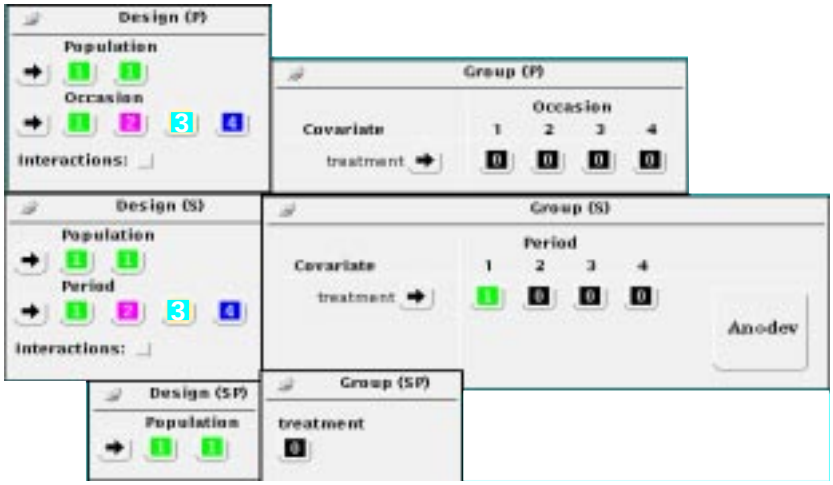
> *This test is accomplished by setting the Group (SP) treatment button to “0” (i.e., no effect of treatment in the product term), and using the LRT to determine whether the added parameter in the Full Model statistically improved the fit. Name the new model “H5p.” Test “H5p” against “H5s” by selecting “H5p” from the Master List and “H5s” from the Testable List. The additional parameter in “H5s” (i.e., treatment effect on product term) did not statistically improve the fit (p-value = 0.358).*

The test of the product term indicated the probability was common between the control and treatment groups. The Burnham analysis continues by alternately removing the treatment effect on capture at a particular dam, or on survival through a particular reach.



Button settings for Model "H5s".

The sequence of tests alternates testing common capture probabilities, then common survival probabilities. To test whether a common capture effect was shared by both the treatment and control group at the fourth dam, begin with model "H4p" selected in the Master List, and remove the treatment effect on capture on the fourth occasion (i.e., set the Group Covariate button for capture on the fourth occasion to "0"). Name this model "H4s" and compute the LRT to test against the "H4p" model. Next, test whether a common survival effect was shared by both the treatment and control group in the fourth "period". Begin with model "H4s", and remove the treatment effect on survival in the fourth period (i.e., set the Group Covariate button for survival on the fourth "period" to "0"). Name this model "H3p" and use the LRT to test against the "H4s" model. Continue this sequence of alternately removing a treatment effect on capture or survival until you get to model "H1s." The button settings for model "H1s" are shown below.



Button settings for Model "H1s".

Finally, remove the treatment effect on survival in the first period to arrive at the model with no treatment effects for either capture or survival. This model has a "Pt" capture model and an "St" survival model, and common product terms for the two populations. Name this model "H0." When "H0" is compared to "H1s", the LRT indicates a highly significant difference in survival (p-value < 0.001) in the first reach.

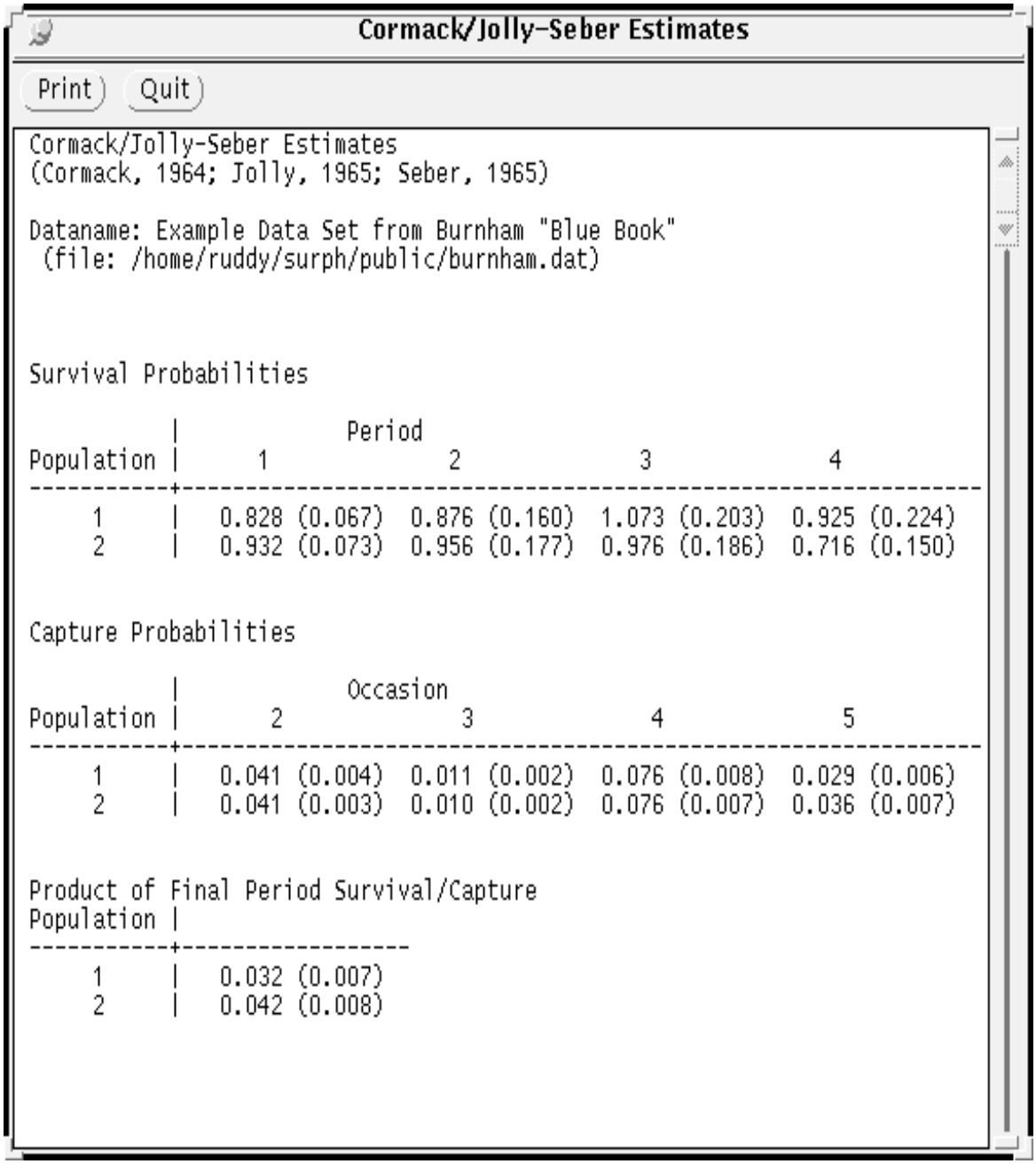
When the model that has common capture probabilities for both control and treatment groups at each dam and common survival probabilities for both control and treatment groups in each reach (i.e., Model H_0) was compared to the model that had common capture probabilities for both control and treatment groups at each dam and different survival probabilities for both control and treatment groups in the first reach (i.e., Model H_{1s}), the LRT indicated that the survival probabilities were significantly different in the first reach. There were no statistically significant ($p < 0.10$) treatment effects on any other parameters. Thus the Burnham analysis selects Model H_{1S}; i.e., "Pt" model of design effects on capture, an "St" model of design effects on survival, and a treatment effect on survival in the first period (i.e., reach). Table 6.15 compares the results of the likelihood ratio tests to those from the contingency table tests presented in Burnham et al. (1987).

As in all previous examples, once a model has been selected, certain diagnostics should be consulted to assess the goodness of fit of the model. For this example, first compare the Cormack/ Jolly-Seber estimates (Figure 6.45) to the SURPH estimates from Model H_{1s} (Figure 6.46). The

Table 6.15 Comparison of the p-values from the LRT in SURPH and the contingency table tests done by Burnham et al. (1987). The null hypothesis in each case tests whether the full model (on the left) fits significantly better than the reduced model (on the right). All tests have one degree of freedom.

	LRT		Contingency Table	
Models Tested	χ^2	p-value	χ^2	p-value
H5s vs. H4p	0.84	0.358	0.84	0.360
H4p vs. H4s	0.28	0.597	0.28	0.607
H4s vs. H3p	0.05	0.817	0.01	0.930
H3p vs. H3s	0.18	0.669	0.21	0.646
H3s vs. H2p	0.03	0.855	0.16	0.690
H2p vs. H2s	0.15	0.694	0.15	0.694
H2s vs. H1p	0.005	0.945	0.01	0.945
H1p vs. H1s	0.02	0.889	0.02	0.889
H1s vs. H0	29.63	<0.001*	29.63	<0.001*

* - The only LRT and contingency table test that was found to be statistically significant (p-value < 0.001).



Cormack/Jolly-Seber Estimates

Print Quit

```
Cormack/Jolly-Seber Estimates
(Cormack, 1964; Jolly, 1965; Seber, 1965)

Dataname: Example Data Set from Burnham "Blue Book"
 (file: /home/ruddy/surph/public/burnham.dat)



Survival Probabilities

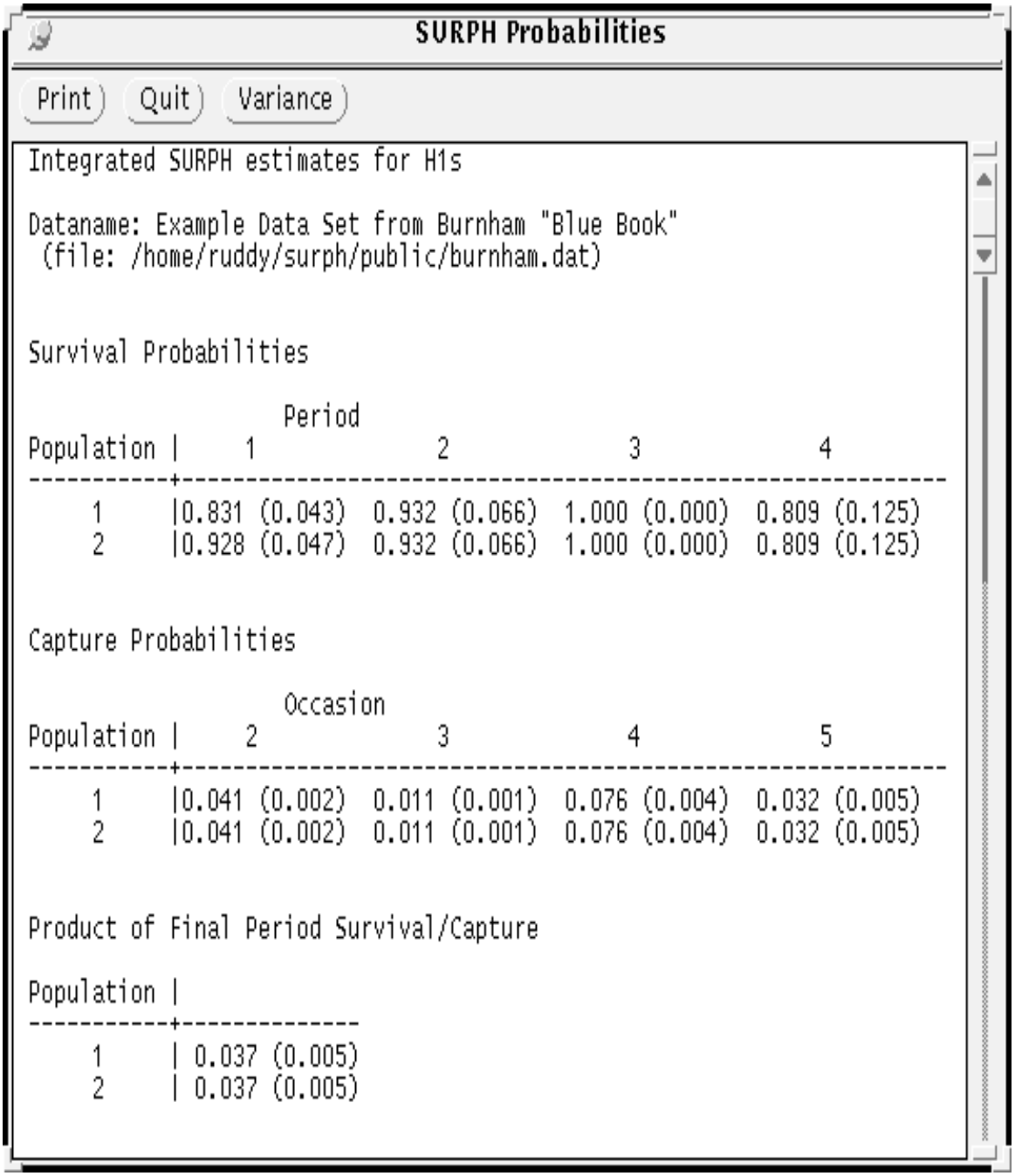
           |             Period
Population |      1              2              3              4
-----------+-------------------------------------------------------------
     1     |   0.828 (0.067)  0.876 (0.160)  1.073 (0.203)  0.925 (0.224)
     2     |   0.932 (0.073)  0.956 (0.177)  0.976 (0.186)  0.716 (0.150)


Capture Probabilities

           |             Occasion
Population |       2              3              4              5
-----------+-------------------------------------------------------------
     1     |   0.041 (0.004)  0.011 (0.002)  0.076 (0.008)  0.029 (0.006)
     2     |   0.041 (0.003)  0.010 (0.002)  0.076 (0.007)  0.036 (0.007)


Product of Final Period Survival/Capture
Population |
-----------+------------------
     1     |   0.032 (0.007)
     2     |   0.042 (0.008)
```

Figure 6.45 CJS estimates of capture, survival and final period product probabilities for the Burnham et al**. (1987) data set. Estimated standard errors are in parentheses.**




```
Integrated SURPH estimates for H1s

Dataname: Example Data Set from Burnham "Blue Book"
 (file: /home/ruddy/surph/public/burnham.dat)


Survival Probabilities

                    Period
Population |     1              2              3              4
-----------+-------------------------------------------------------------
     1     |0.831 (0.043)  0.932 (0.066)  1.000 (0.000)  0.809 (0.125)
     2     |0.928 (0.047)  0.932 (0.066)  1.000 (0.000)  0.809 (0.125)


Capture Probabilities

                    Occasion
Population |     2              3              4              5
-----------+-------------------------------------------------------------
     1     |0.041 (0.002)  0.011 (0.001)  0.076 (0.004)  0.032 (0.005)
     2     |0.041 (0.002)  0.011 (0.001)  0.076 (0.004)  0.032 (0.005)


Product of Final Period Survival/Capture

Population |
-----------+--------------
     1     | 0.037 (0.005)
     2     | 0.037 (0.005)
```

Figure 6.46 SURPH probability estimates for the model "H1s" using the Burnham et al. (1987) data set.

SURPH versus CJS Estimate plot (**Models -> SURPH vs. CJS Estimates**) indicates close agreement between the SURPH model estimates and the CJS estimates.

Because a group effect on survival was included in the first period, another graphic that was accessed was the group effects plot (**Models -> Survival Curves -> Group**). In the first period (Figure 6.47), the SURPH curve fits the CJS estimates of survival, and indicates that the treatment group has poorer survival the control group. Subsequent "periods" (i.e., reaches) do not include group effects on survival. Therefore, the SURPH curves in all but the initial "period" are horizontal lines; the control group and the treatment group have equal survival. Although the group-covariate plots indicate a continuous measure along the horizontal axis, this is an artifact. Treatment is an indicator variable, and takes on only the values 0 (control) or 1 (treatment).

Having verified that Model H_{1S} fits the data adequately, we turn to the turbine passage survival probability S, the parameter of primary interest in the analysis. Turbine passage can be estimated as the ratio of the survival probability in the first reach for the treatment group to that of the controls. In the parameterization of the SURPH model, using the hazard link, this is:

$$\hat{S_T} = \frac{\hat{S}_{T1}}{\hat{S}_{C1}} = \frac{\hat{S}^{e^{\hat{\tau}}}}{\hat{S}} = \hat{S}^{e^{\hat{\tau}}-1}. \tag{6.1}$$

The parameter estimates for Model H_{1S} are listed in Figure 6.48. For Eq. (6.1), $\hat{S}$ is parameter #1, "baseline S," and $\hat{\tau}$ is parameter #7, the fourth survival effect in the model. Thus, the turbine passage survival probability is $0.92765^{e^{0.89934}-1} = 0.896$. Application of the delta-method gives a standard error of 0.093:

$$Var(\hat{S}^{e^{\hat{\tau}}-1}) \approx \left(\frac{\partial g}{\partial S}\right)^2 Var(\hat{S}) + \left(\frac{\partial g}{\partial \tau}\right)^2 Var(\hat{\tau}) + 2\left(\frac{\partial g}{\partial S}\right)\left(\frac{\partial g}{\partial \tau}\right) Cov(\hat{S}, \hat{\tau}) \tag{6.2}$$

where

$$g = g(S, \tau) = S^{e^{\tau}-1}$$

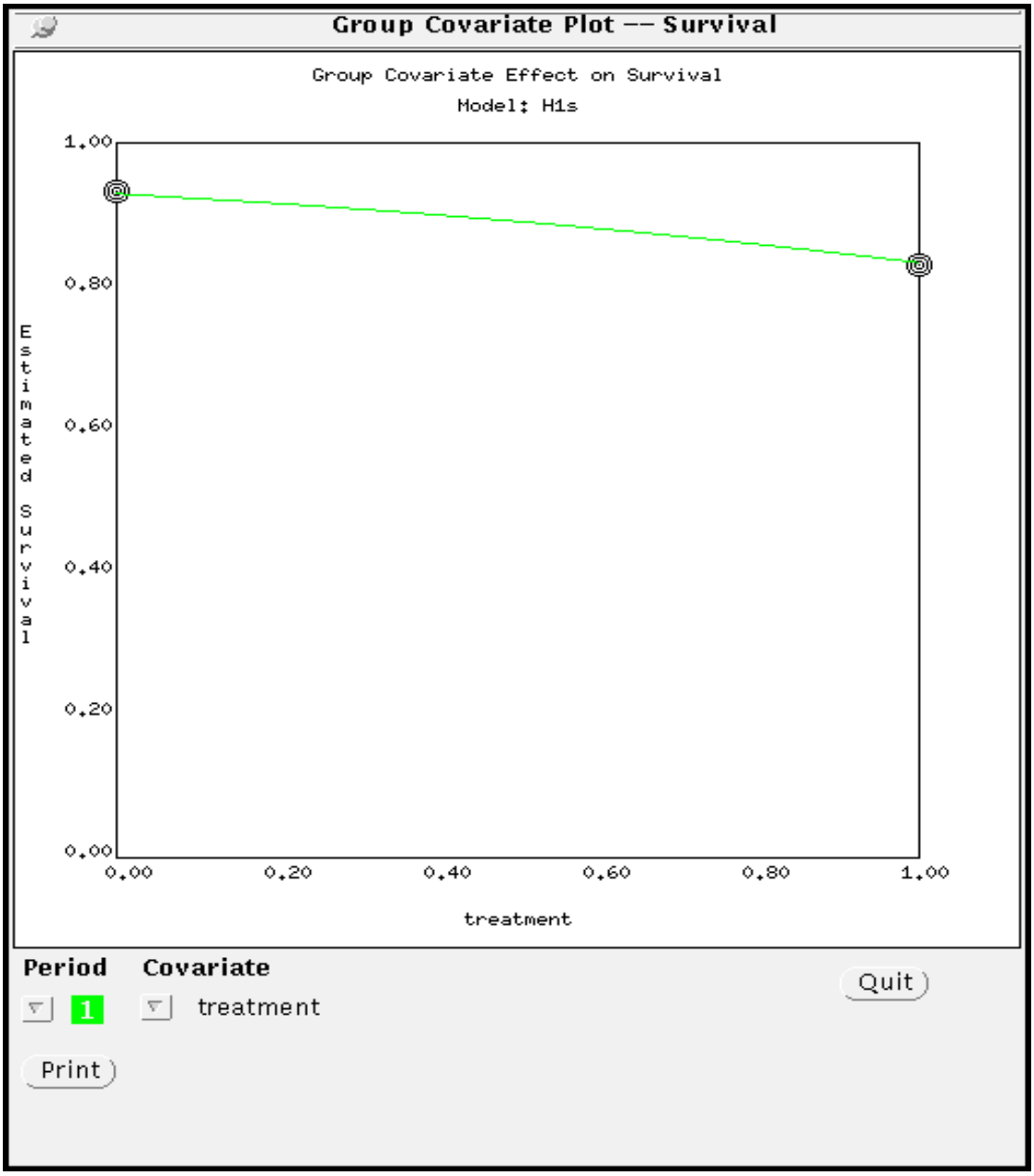


Figure 6.47 **Effect of the "dummy" or "indicator" covariate for treatment on survival in the first reach for the data set burnham.dat. Survival of the treatment group is significantly (p-value < 0.001) less than the survival of the control group. The smooth curve is the SURPH curve for the model "H1s". The "bull's-eye" points are the CJS estimates of survival in the first reach.**

SURPH Parameters

Print | Quit | Key... | Variance-Covariance

```
Parameters for H1s

Dataname: Example Data Set from Burnham "Blue Book"
 (file: /home/ruddy/surph/public/burnham.dat)

#  Parameter                 estimate    std. err.       ratio
-------------------------------------------------------------------
 1. baseline S:              0.92765      0.04732     19.60452
 2. baseline P:              0.04114      0.00224     18.39926
 3. baseline Product:        0.03731      0.00548      6.81239
 4. survival effect 1       -0.05988      1.50547     -0.03978
 5. survival effect 2      -11.06764    290.24975     -0.03813
 6. survival effect 3        1.03821      1.01927      1.01859
 7. survival effect 4        0.89934      0.43486      2.06811
 8. capture effect  1       -1.39231      0.08770    -15.87507
 9. capture effect  2        0.65695      0.08017      8.19461
10. capture effect  3       -0.24790      0.16173     -1.53286


Variance-covariance matrix:
---------------------------
```

	1	2	3	4	5	6	7	8
1	0.0022	-0.0001	0.0000	0.0604	0.0641	0.0338	0.0199	0.0021
2	-0.0001	0.0000	-0.0000	-0.0026	-0.0030	-0.0015	-0.0008	-0.0001
3	0.0000	-0.0000	0.0000	0.0000	0.0037	0.0036	0.0000	0.0000
4	0.0604	-0.0026	0.0000	2.2664	2.0676	0.7067	0.5247	0.1020
5	0.0641	-0.0030	0.0037	2.0676	84244.9150	0.8607	0.5469	0.0875
6	0.0338	-0.0015	0.0036	0.7067	0.8607	1.0389	0.3009	0.0169
7	0.0199	-0.0008	0.0000	0.5247	0.5469	0.3009	0.1891	0.0177
8	0.0021	-0.0001	0.0000	0.1020	0.0875	0.0169	0.0177	0.0077
9	0.0021	-0.0001	0.0000	0.1046	0.1971	0.0155	0.0175	0.0059
10	0.0025	-0.0001	0.0008	0.0678	0.1854	0.1376	0.0208	0.0029

	9	10
1	0.0021	0.0025
2	-0.0001	-0.0001
3	0.0000	0.0008
4	0.1046	0.0678
5	0.1971	0.1854
6	0.0155	0.1376
7	0.0175	0.0208
8	0.0059	0.0029
9	0.0064	0.0029
10	0.0029	0.0262

Figure 6.48 SURPH parameter estimates associated standard errors, and variance/covariance matrix for the model "H1s" of the data set burnham.dat.

$$\frac{\partial g}{\partial S} = (e^{\tau} - 1)S^{e^{\tau} - 2}$$

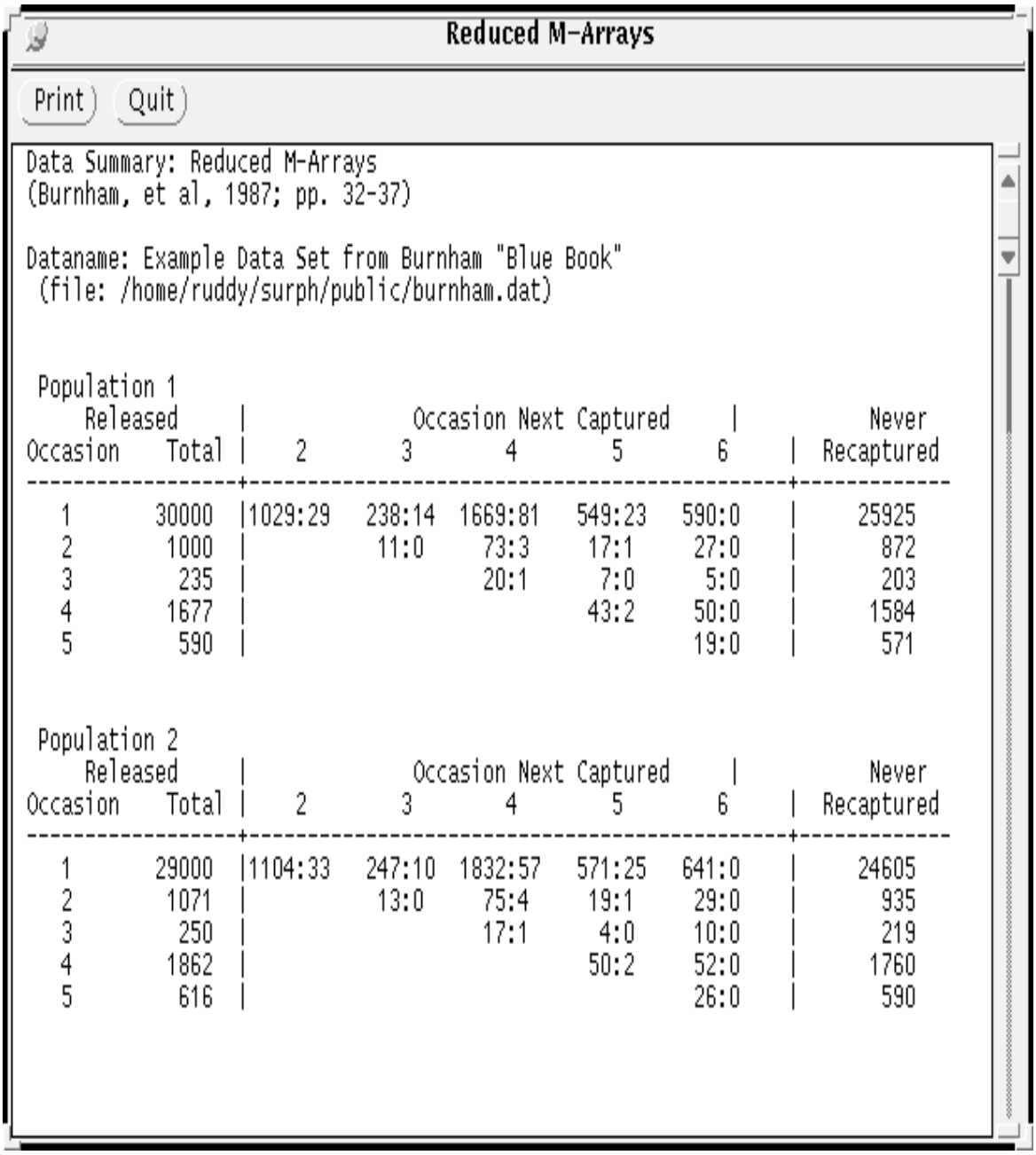
$$\frac{\partial g}{\partial \tau} = \ln S(e^{\tau} - 1)S^{e^{\tau} - 1}$$

Alternatively, under Model H_{1S}, the turbine passage survival probability S_T can be estimated using the "relative recovery method" (Ricker 1975; Burnham et al. 1987). The simple estimate under this method is the ratio of the proportion of fish from each group detected at least once downstream:

$$\hat{S}_T = \frac{r_T / R_T}{r_C / R_C}, \tag{6.3}$$

where R_T and R_C are the numbers of fish released r_C are the numbers recovered at least once in the treatment and control groups, respectively. When it is appropriate (i.e.,under Model H_{1S}), Eq. (6.3) gives a much more precise estimate than Eq. (6.1). The information required for the relative recovery method can be obtained from the reduced M-arrays (Figure 6.49).

To access the reduced M-Arrays, use the command sequence ***Data -> M-Arrays****. The reduced M-Arrays follow the fate of each release. Once detected, the animal can either be re-released or removed from the study. The number of animals with each of these two fates are separated by a colon in the M-Array Table. For example, for the first population, 30,000 fish were released on the first occasion. Of these, 1029 (the number to the left of the colon) were first seen alive on occasion 2, but 29 of the 1029 (the number to the right of the colon) were removed from the study. On the third occasion, 238 fish from the first release were recaptured for the first time, but 14 were removed from the study. In addition, of the 1000 fish that were released on the second occasion, 11 were detected on the third occasion. Because this is a single release study, newly marked fish were only released on the first occasion. Fish that are released on subsequent occasions must have been recaptured on that occasion. For example, on the third occasion, 235 fish were released. These 235 fish are the 238 fish released on occasion 1 that were first detected on occasion 3, plus the 11 fish released on occasion 2 that were first detected on occasion 3, minus the 14 fish that were removed (235 = 238 + 11 - 14). The column to the far right enumerates the number of fish released that were never detected.*



Reduced M-Arrays

Print Quit

Data Summary: Reduced M-Arrays
(Burnham, et al, 1987; pp. 32-37)

Dataname: Example Data Set from Burnham "Blue Book"
(file: /home/ruddy/surph/public/burnham.dat)

Population 1

Released		Occasion Next Captured					Never
Occasion	Total	2	3	4	5	6	Recaptured
1	30000	1029:29	238:14	1669:81	549:23	590:0	25925
2	1000		11:0	73:3	17:1	27:0	872
3	235			20:1	7:0	5:0	203
4	1677				43:2	50:0	1584
5	590					19:0	571

Population 2

Released		Occasion Next Captured					Never
Occasion	Total	2	3	4	5	6	Recaptured
1	29000	1104:33	247:10	1832:57	571:25	641:0	24605
2	1071		13:0	75:4	19:1	29:0	935
3	250			17:1	4:0	10:0	219
4	1862				50:2	52:0	1760
5	616					26:0	590

Figure 6.49 **Reduced M-arrays for data set burnham.dat. M-arrays can be used to calculate treatment effects based on the relative recovery method.**

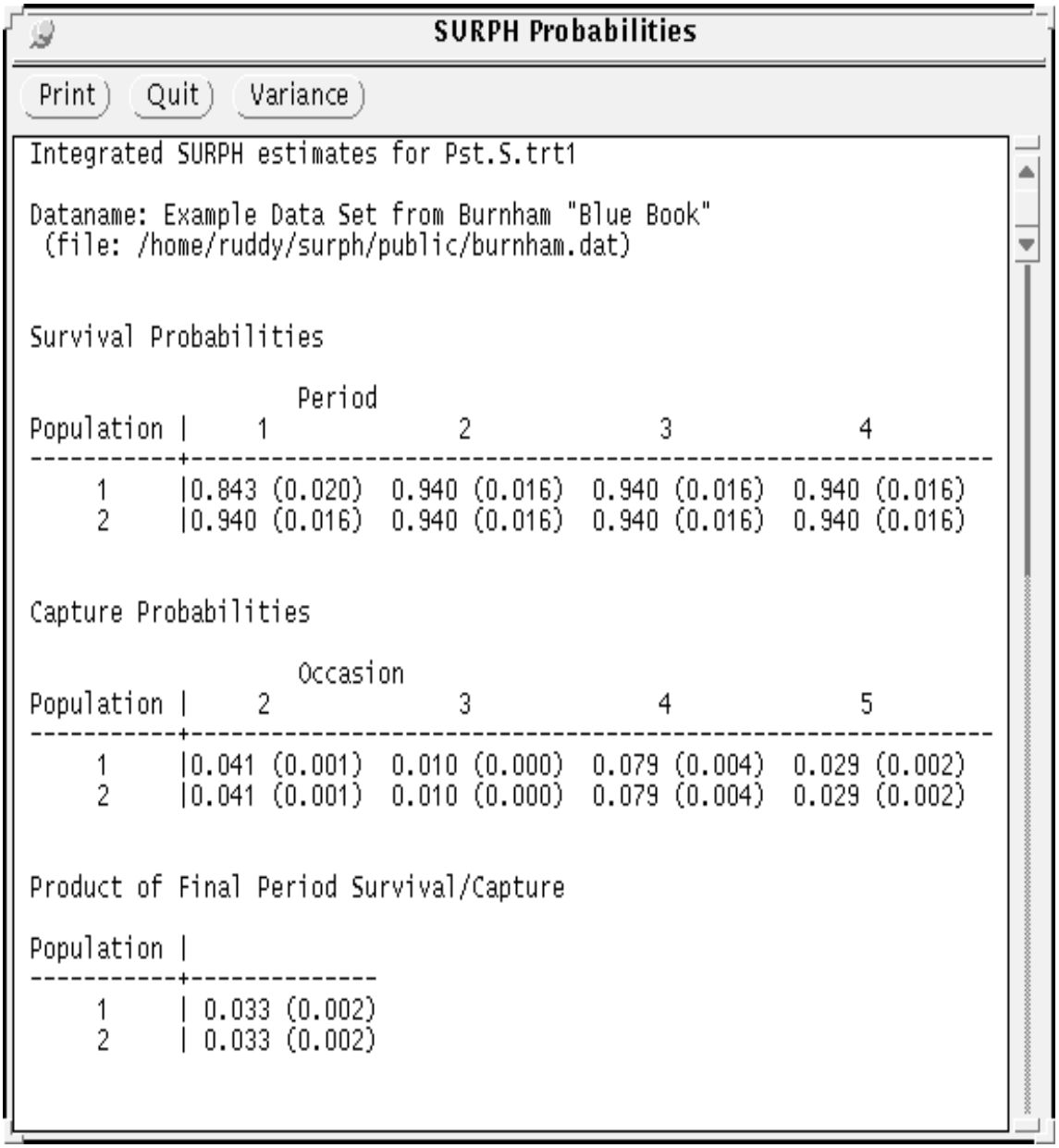
In this example, the estimate based on relative recoveries is $\hat{S}_T = \frac{4075/30000}{4395/29000} = 0.896$, with standard error (see Burnham et al. 1987):

$$\hat{S}_T^2\left(\frac{1}{r_T} - \frac{1}{R_T} + \frac{1}{r_C} - \frac{1}{R_C}\right) = 0.018 .$$

This concludes the Burnham analysis. However, SURPH allows further flexibility in modeling. Examining the CJS estimates (Figure 6.45), it is apparent that although the estimates of survival differ among the different reaches, there is considerable error associated with the estimates. The large standard errors of the survival estimates are due to the minuscule recapture probabilities. Similarly, in the SURPH model "H1s," the standard errors of the parameters that are associated with the "period" effects (Figure 6.48, parameters 4, 5 and 6) indicate that these parameters may be superfluous. The imprecise nature of the survival estimates suggests that it might not be necessary to model survival with four design effects (Model "St", which has unique survival estimates for each reach), as the current model does; a single design effect may be sufficient (Model "S", which has a common survival estimate for all reaches).

> *On the **Survival Design Button Pad**, change the button settings for period from "1, 2, 3, 4" to "1, 1, 1, 1". The new parameterization will fit a common effect for both populations for all reaches. The "1" in group covariate button pad for the first period will still allow for the effect of a treatment effect in the first reach. Name this new model "Pst.S.trt1" and use LRT to compare it to the model selected in the Burnham analysis (i.e., "H1s").*

The additional three parameters that were estimated for Model "H1s" do not significantly improve the fit (p-value = 0.759). Diagnostics for the reduced model (i.e., "Pst.S.trt1") were examined, but are not shown here. It was found that the reduced model provided an adequate fit to the data. Under this model (Figure 6.50), the SURPH estimate of survival for the control group was constant for all downstream reaches (i.e., $\hat{S} = 0.94$ for all periods). The treatment group experienced reduced survival in the first reach after the treatment (i.e., $\hat{S} = 0.84$ for the first period), but afterward had the same survival as the control group (i.e., $\hat{S} = 0.94$ for subsequent periods).



SURPH Probabilities

Print Quit Variance

```
Integrated SURPH estimates for Pst.S.trt1

Dataname: Example Data Set from Burnham "Blue Book"
 (file: /home/ruddy/surph/public/burnham.dat)


Survival Probabilities

                    Period
Population |     1              2              3              4
-----------+-------------------------------------------------------------
     1     |0.843 (0.020)  0.940 (0.016)  0.940 (0.016)  0.940 (0.016)
     2     |0.940 (0.016)  0.940 (0.016)  0.940 (0.016)  0.940 (0.016)


Capture Probabilities

                    Occasion
Population |     2              3              4              5
-----------+-------------------------------------------------------------
     1     |0.041 (0.001)  0.010 (0.000)  0.079 (0.004)  0.029 (0.002)
     2     |0.041 (0.001)  0.010 (0.000)  0.079 (0.004)  0.029 (0.002)


Product of Final Period Survival/Capture

Population |
-----------+--------------
     1     | 0.033 (0.002)
     2     | 0.033 (0.002)
```

Figure 6.50 SURPH survival, capture and final period product probabilities for the model "Pst.S.trt1" of the data set burnham.dat.

Under Model “Pst.S.trt1” the estimated turbine passage survival probability is $0.94049^{e^{1.02651}-1} = 0.896$, with standard error 0.040 (see Eq. (6.2)). Thus, we see that this more parsimonious model has given a much more precise estimate than under Model H_{1S}, though not as precise as the relative recovery estimate.

This analysis has shown that SURPH can be used to analyze data in the fashion that was proposed in the Burnham et al. (1987) monograph. In addition, SURPH allows further flexibility in modeling equalities among parameters, leading to more precise estimates of treatment effects.

Chapter 7

Using Interactive Program SURPH

Program SURPH provides an interactive windows environment for summarizing and analyzing known-fate and release-recapture data. This chapter provides instructions on how to use the interactive program, windows and cursor/mouse (Section 7.1). Furthermore, this chapter provides an illustrated index of the program options, directives and data displays. Section 7.2 provides guidance for the use of Program SURPH in the analysis of release-recapture. This section also describes the use of SURPH in the analysis of known-fate data where the operations are the same as for release-recapture data. Section 7.3 provides additional descriptions of the program options unique to the analysis of known-fate data.

7.1 Fundamentals in Windows operations

We have included an introductory section that outlines how to use a mouse, how to re-size windows, how to access pull-down and pull-right menus, and how to store text pane information. Also included within this section are descriptions of some conventions and definitions used throughout Chapter 7.

7.2 Analysis of release-recapture data

Program options available for the analysis of release-recapture data are summarized in Table 7.1. The order of the listing is based on a typical sequence of data analysis steps. Specifically, the ordering includes file input/output, descriptive statistics of the data set, modeling of capture and survival probabilities, and model diagnostics. Specific program options are cross-listed in the index of this manual.

7.3 Analysis of known-fate data

The majority of program options available for the analysis of known-fate data are identical to program options for release-recapture data. Only options unique to known-fate data are included in Section 7.3 and summarized in Table 7.2. For all other program options, consult Section 7.2 and Table 7.1. The order of the listing is based on a typical sequence of data analysis steps. Specifically, the ordering includes descriptive statistics of the data set, modeling survival probabilities and model diagnostics. Specific program options are cross-listed in the index of this manual.

Table 7.1: Listing of SURPH options for analysis of release-recapture data and associated page number where operational description can be found.

Program Options	Page
Basic Mouse Instructions	7.7
Some SURPH Window Definitions and Conventions	7.13
Pull-Down Mouse Instructions	7.19
Testing Nested Models: Master and Testable Lists	7.21
Storing Text Pane Information	7.23
SURPH Introductory Window	7.25
SURPH Base Window: Release-Recapture	7.27
File Pull-Down Menu	7.31
File: Load Data	7.33
File: Load Models	7.35
File: Store Models	7.37
Data Pull-Down Menu	7.39
Data: Cormack/Jolly-Seber Estimates	7.41
Data: Manly-Parr Estimates	7.43
Data: M-Arrays	7.45
Data: Individual Covariates: Histogram of Data	7.47
Data: Individual Covariates: Cumulative Distribution Function of the Data	7.51
Data: Data Transformations: Group Covariates	7.53
Data: Data Transformations: Individual Covariates	7.55
Data: Data Listing	7.57
Capture Modeling Pull-Down Menu	7.59
Capture Modeling: Design Factors Button Pad	7.61
Capture Modeling: Examples	7.63
Capture Modeling: Group Covariates	7.65
Capture Modeling: Individual Covariates	7.67
Quick Button Pad : Instructions 1	7.69
Quick Button Pad : Instructions 2	7.71
Capture Modeling: Link Function	7.73

Table 7.1 (cont'): Listing of SURPH options for analysis of release-recapture data and associated page number where operational description can be found.

Program Options	Page
Capture Modeling: Locking Model	7.75
Joint Modeling Pull-Down Menu	7.77
Joint Modeling: Capture Design Factors Button Pad	7.81
Joint Modeling: Capture Modeling Pop-Up Message	7.83
Joint Modeling: Capture: Group Covariates	7.85
Joint Modeling: Capture: Individual Covariates	7.87
Joint Modeling: Capture: Link Function	7.89
Joint Modeling: Survival Design Factors Button Pad	7.91
Joint Modeling: Survival Modeling - Examples	7.93
Joint Modeling: Survival: Group Covariates	7.95
Joint Modeling: Survival: Individual Covariates	7.97
Joint Modeling: Survival: Link Function	7.99
Joint Modeling: Product Design Factors Button Pad	7.101
Joint Modeling: Product: Group Covariates	7.103
Joint Modeling: Product: Individual Covariates	7.105
Joint Modeling: Product-Link Function	7.107
Analysis of Deviance: Group Covariate Button Pad	7.109
ANODEV Start-Up	7.111
Analysis of Deviance Table (A): Beginning	7.113
Analysis of Deviance Table (B): Partitioning Total Covariate Deviance	7.117
Analysis of Deviance Table (C): Duplicate Models	7.119
Analysis of Deviance Table (D): Quitting	7.121
Models Pull-Down Menu	7.123
Models: SURPH Parameter Estimates	7.127
Models: SURPH Parameters: Key Legend	7.129
Models: SURPH Parameters: Variance-Covariance	7.133
Models: SURPH Probability Estimates	7.135
Models: Model Graphics: SURPH Estimates vs. CJS Estimates	7.137
Models: Survival Graphics: Group Covariates	7.139
Models: Survival Graphics: Individual Covariates (A) - SURPH Curve	7.141

Table 7.1 (cont'): Listing of SURPH options for analysis of release-recapture data and associated page number where operational description can be found.

Program Options	Page
Models: Survival Graphics: Individual Covariates (B) - SURPH Curve and Histogram	7.145
Models: Survival Graphics: Individual Covariates (C) - SURPH Curve and Non-Parametric Analogue	7.147
Models: Survival Graphics: Individual Covariates (D) - Relative Risk Curve	7.149
Models: Survival Graphics: Individual Covariates (E) - Relative Risk Curve and Histogram	7.151
Models: Capture Graphics: Group Covariates	7.153
Models: Capture Graphics: Individual Covariates (A) - SURPH Curve	7.155
Models: Capture Graphics: Individual Covariates (B) - SURPH Curve and Histogram	7.157
Models: Capture Graphics: Individual Covariates (C) - SURPH Curve and Non-Parametric Analogue	7.159
Models: Product Graphics: Group Covariates	7.161
Models: Product Graphics: Individual Covariates (A) - SURPH Curve	7.163
Models: Product Graphics: Individual Covariates (B) - SURPH Curve and Histogram	7.165
Models: Product Graphics: Individual Covariates (C) - SURPH Curve and Non-Parametric Analogue	7.167
Models: Residual Plot	7.169
Models: Quantile-Quantile Plot	7.171
Models: Change Model Names	7.173
Models: Discard Model	7.175
Help Dialog Box	7.177
Quit Dialog Box	7.179

7.3 Analysis of known fate data

The majority of program options available for the analysis of known fate data are identical to program options for release-recapture data. Only options unique to known fate data are included in Section 7.3 and summarized in Table 7.2. For all other program options, consult Section 7.2 and Table 7.1. The order of the listing is based on a typical sequence of data analysis steps. Specifically, the ordering includes descriptive statistics of the data set, modeling survival probabilities and model diagnostics. Specific program options are cross-listed in the index of this manual.

Table 7.2: Listing of unique SURPH options for analysis of known fate data and associated page number where operational description can be found.

Program Options	Page
SURPH Base Window: Known-Fate	7.181
Data Pull-Down Menu	7.185
Data: Binomial Estimates	7.187
Data: Sampling Summary	7.189
Survival Modeling: Pull-Down Menu	7.191
Models Pull-Down Menu	7.193
Models: Model Graphics: Binomial Estimates	7.195

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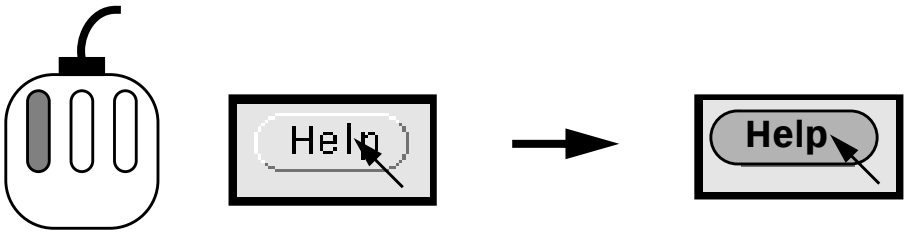
All functions within SURPH are accessed via the mouse. There are only a few times that you must type information while in SURPH. You, therefore, must be thoroughly familiar with mouse operations before any data analysis is performed using SURPH.

When using the mouse, a floating black arrow (the pointer) indicates your position on the screen or within the window.

The mouse is used to move the pointer around the screen, to select buttons in SURPH, to access menus, to dismiss pop-up windows, to resize text panes, and to place the cursor in text fields.

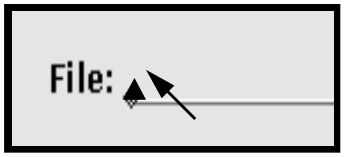
In the instructions that follow, we use several terms to describe the functions of the three-button mouse:

"Left-click": When the pointer covers an object such as a button or a text field, depress and release the left mouse button to select this object. In SURPH, when a button is selected, the button gets darker or the number within the button changes. In the first example, left-clicking on the **Help Button** causes the button to darken, and accesses the "Help" function.

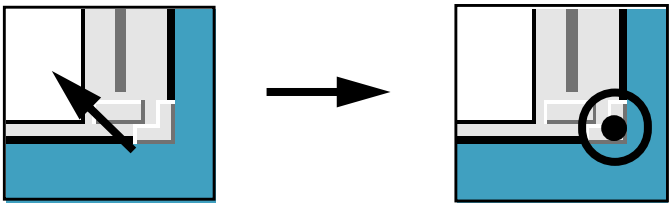


In the second example, left-clicking on a button pad increases the value of the button by one. This type of button is used for model parameterization.

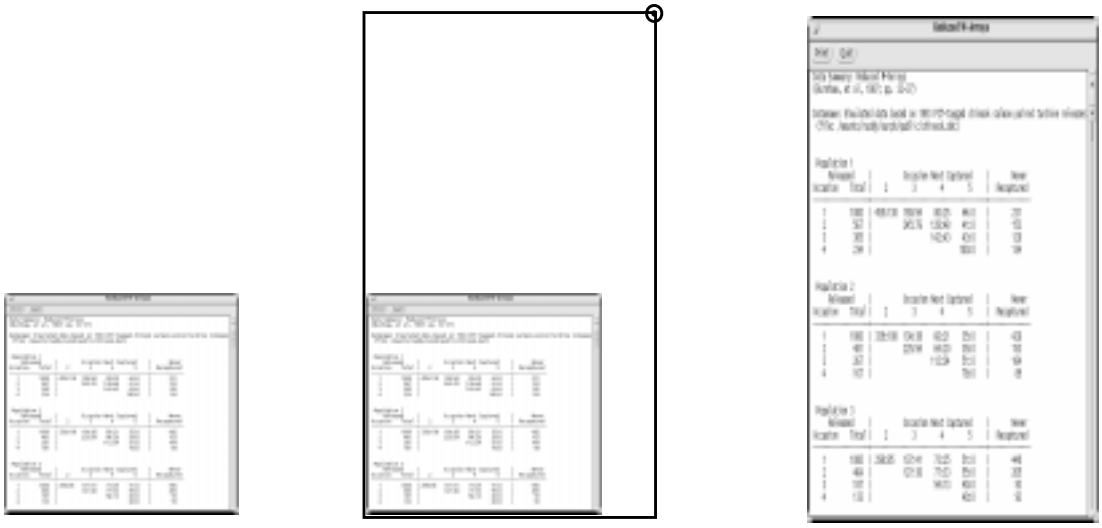
To type in a text field, use the mouse to point at the text field, then left-click. A triangular cursor appears within the text field at the pointer position. In the following example, you could now enter a file name in the text field.



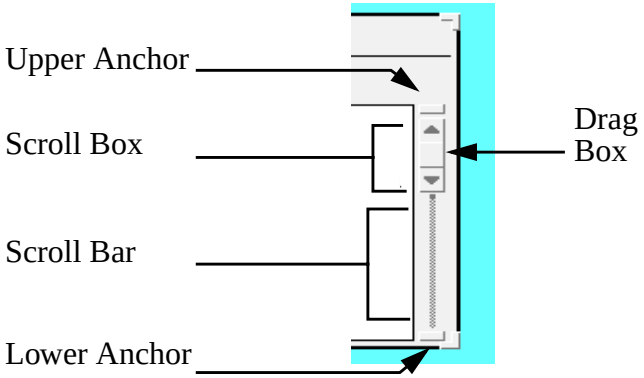
"Left-hold": Left-hold is used to change the size of windows that allow re-sizing, and to move the scroll bar on text windows. When the pointer covers the corner of a text window, it changes from an arrow to a small circle. To resize a text window, move the pointer to one corner, until the arrow becomes a circle, as shown here.



Depress the left mouse key and hold down. When you move the mouse while holding the left button, the corner of the window will move with you. This allows you to alter the dimensions of the window. Release the mouse button when the window is the desired size. In the example, we enlarge an M-Array text window.



All text windows have a scroll bar that extends vertically along the right-hand side of the border; a scroll box that consists of an up-arrow, a down-arrow, and a drag-box; and upper and lower anchors. These scrolling devices are used to move through the text pane from one screen display to the next. The scrolling devices allow you to move through the text pane in four different ways.



1. To scroll through a document one screen (page) at a time, left-click while the arrow is on the scroll bar. The scroll bar allows you to move either up or down within the document. To move down (up), make certain the arrow is below (above) the scroll box. To move through multiple pages, use left-hold instead of left-click.

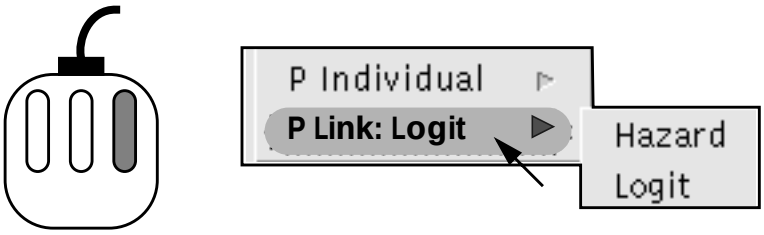
2. To scroll through a document one line at a time, left-click while the arrow is one the scroll box. The scroll indicator allows you to move either up or down within the document. To move down (up), make certain the arrow is on the scroll-box arrow pointing down (up). To move through multiple lines, use left-hold instead of left-click

3. To go to the beginning (end) of a document displayed in a text window, left-click when the arrow is on the upper (lower) anchor.

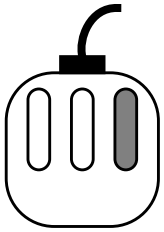
4. An alternative way to move multiple lines or pages is to use the drag box. Place the mouse arrow on the drag box and left-hold while moving the drag box up or down the scroll bar.

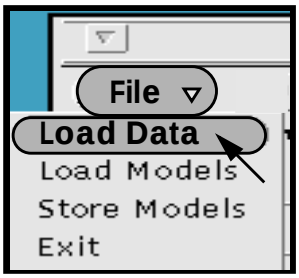
"Right-click": When the pointer covers a button or menu choice that has a small triangle that points downward, depress and release the right mouse button to access a pull-down menu. When a button is selected, the button gets darker. In the example, when you right-click on the **File Button,** a pull-down menu appears that allows you to select one of four options. You would then left-click on the option you wish to use.

When the pointer covers a button or menu choice that has a small triangle that points to the right, depress the right mouse button to access a pull-right menu. In this example, when you right-click on **P Link: Logit**, a pull-right menu appears that allows you to select either the **Hazard** or **Logit** link. The **P Individual** is shown to illustrate the difference in shading between selected and non-selected choices.



“Right-hold”: Right-hold is used to perform the same mouse operations as right-click. However, instead of depressing the right mouse button and releasing, depress the right mouse button and hold. While holding the right button down, move the mouse until the option you are interested in is selected (i.e. the option is darkened), then release the right mouse button. In the example, the right-hold was used to access the **File Button** pull-down menu. While holding the right mouse button, the pointer was moved to **Load Data** and released. This action implemented the **Load Data** function.





The middle button is not used for anything in SURPH.[1]

1. For further instructions on how to use the mouse, consult the section on using the mouse in your User’s Guide.

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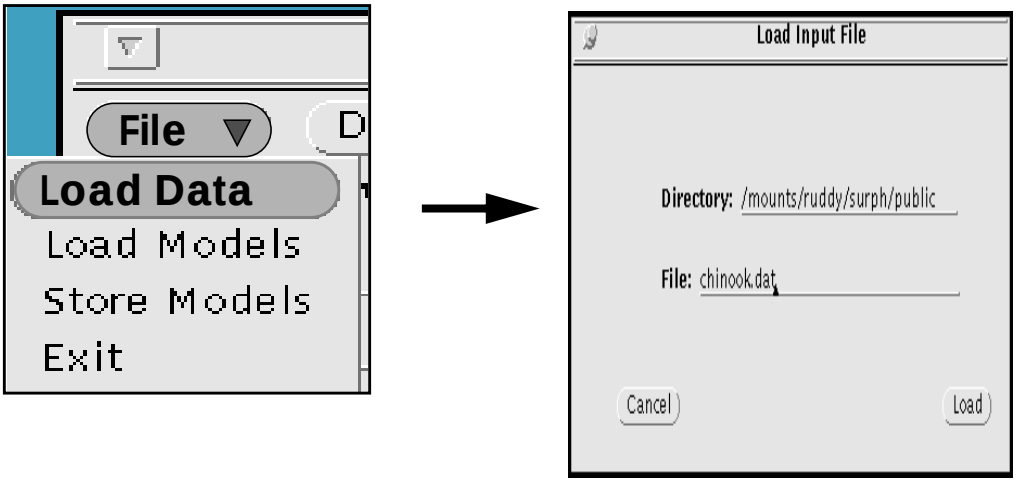
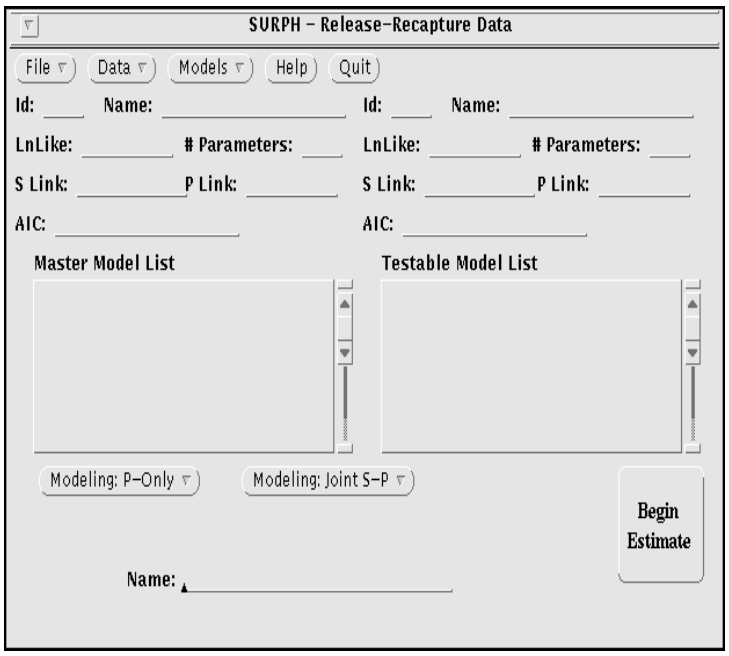
Conventions

All commands in SURPH are accessed using the mouse keypad. Throughout this chapter, command paths will be included along with captured screen graphics to facilitate learning SURPH. The “command paths” are the listings of the necessary selections you must make to obtain the graphical display shown on that page. For example, to obtain the Load Data Window, you must right-click on **File**, then left-click on **Load Data**. This command path is illustrated as **File -> Load Data**. The result of this command path is the appearance of the Load Data Window.

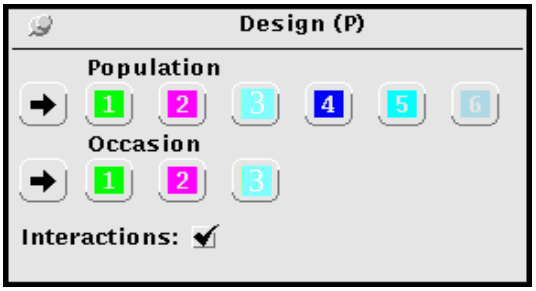


Definitions

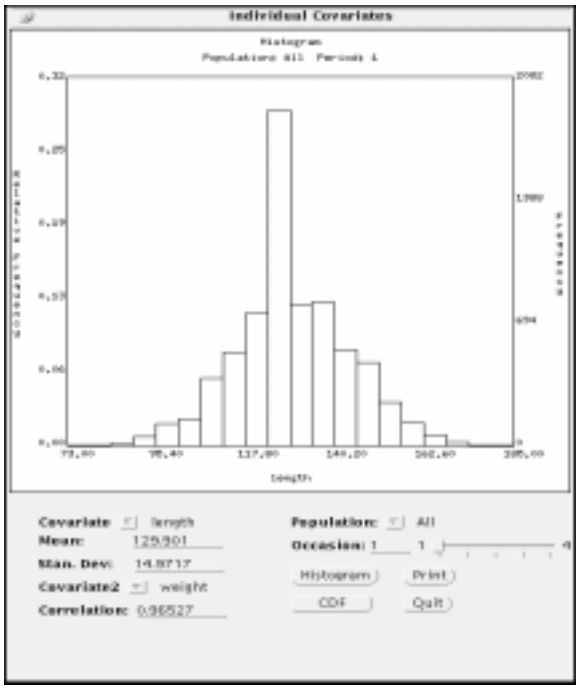
Button - A Button is a device that allows you to implement functions. Examples of Buttons on the SURPH Base Window are **File**, **Data**, **Models**, **Help**, **Quit**, **Modeling: P-Only**, **Modeling: Joint S-P**, and **Begin Estimate**.



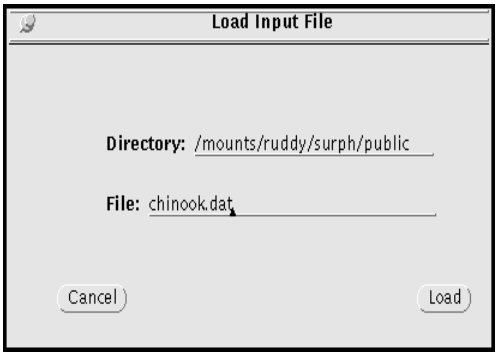
Button Pad - A Button Pad is a device that allows you to change the model parameterization. Button Pads are defined for all Capture (P), all Survival (S), and all Product (SP) design factors, group covariates and individual covariates. Left-click on a button within the button pad to change the model parameterization. For further Button Pad illustrations, see Quick Button Pad Instructions .



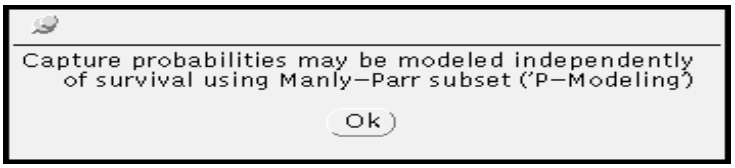
Graphics Window - A Graphics Window displays information graphically. An example of a Graphics Window is the Pop-Up that appears after you selects **Data -> Individual Covariates**.



Input/Output Window - An Input/Output Window in SURPH allows you to load data and to load or store models. An example of an Input/Output Window is the Load Data Window under **File -> Load Data**.

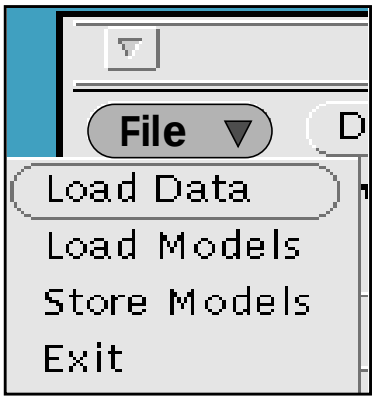


Message Window - A Message Window in SURPH is used to query or enlighten you. An example of a Message Window is the Pop-Up that appears after you initially choose to model capture probabilities under the **Modeling: Joint S-P Button**.

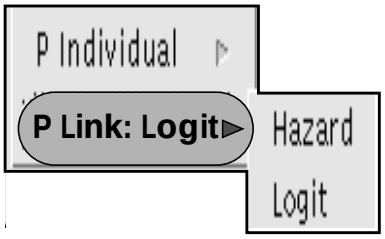


Pop-Up Window - A Pop-Up Window in SURPH is any window that appears following a command. Examples of Pop-Up Windows are Message Windows that query or enlighten you, Text Windows that present text information, Graphics Windows that present graphical information, and Input/Output Windows that allow you to store or load files. Pop-Ups are usually used for temporary tasks or displays. All Pop-Up Windows have a push-pin in the upper left-hand corner. To dismiss a Pop-Up window, left-click on the push-pin.

Pull-Down Menu - A Pull-Down Menu gives you additional options under a Button. Pull-Down Menus are accessed by right-clicking on a Button with a triangle that points downward. Examples of Buttons with Pull-Down Menus are **File**, **Data**, **Models**, **Modeling: P-Only**, and **Modeling: Joint S-P**.

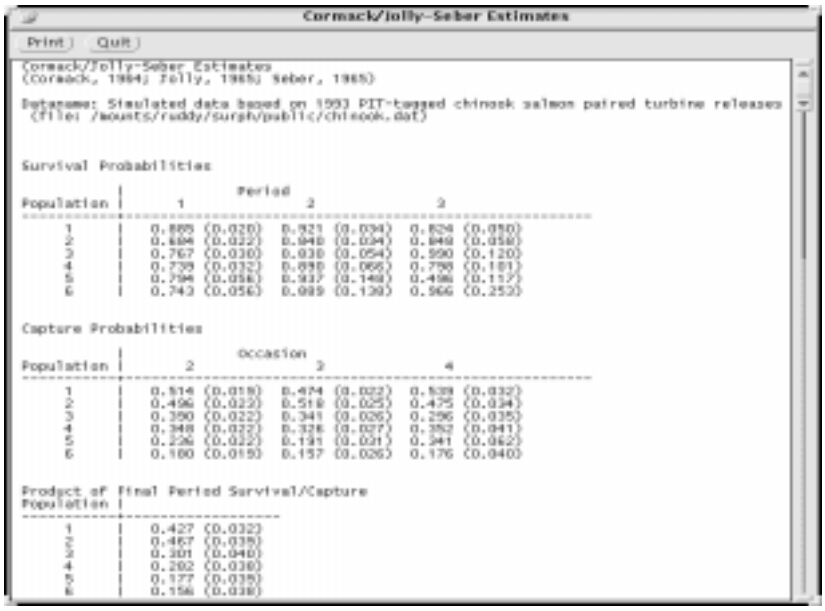


Pull-Right Menu- A Pull-Right Menu gives you additional options under a Pull-Down Menu choice. Pull-Right Menus are accessed by right-clicking on a Pull-Down Menu option with a triangle that points to the right. An example of a Pull-Down Menu with a Pull-Right Menu is **Modeling: P-Only -> P Link: Logit**.



Text Field - A Text Field is a region on a Pop-Up Window that allows you to enter text, usually a directory path or a file name. Text fields are used in SURPH to name models, to name new variables, to load data, and to load and store models. In the example, both the underlined area following **Directory:** and **File:** are text fields that can be edited by you. In this particular example, you has instructed the program to look for the data file named “chinook.dat” in the directory “/mounts/ruddy/surph/public”.

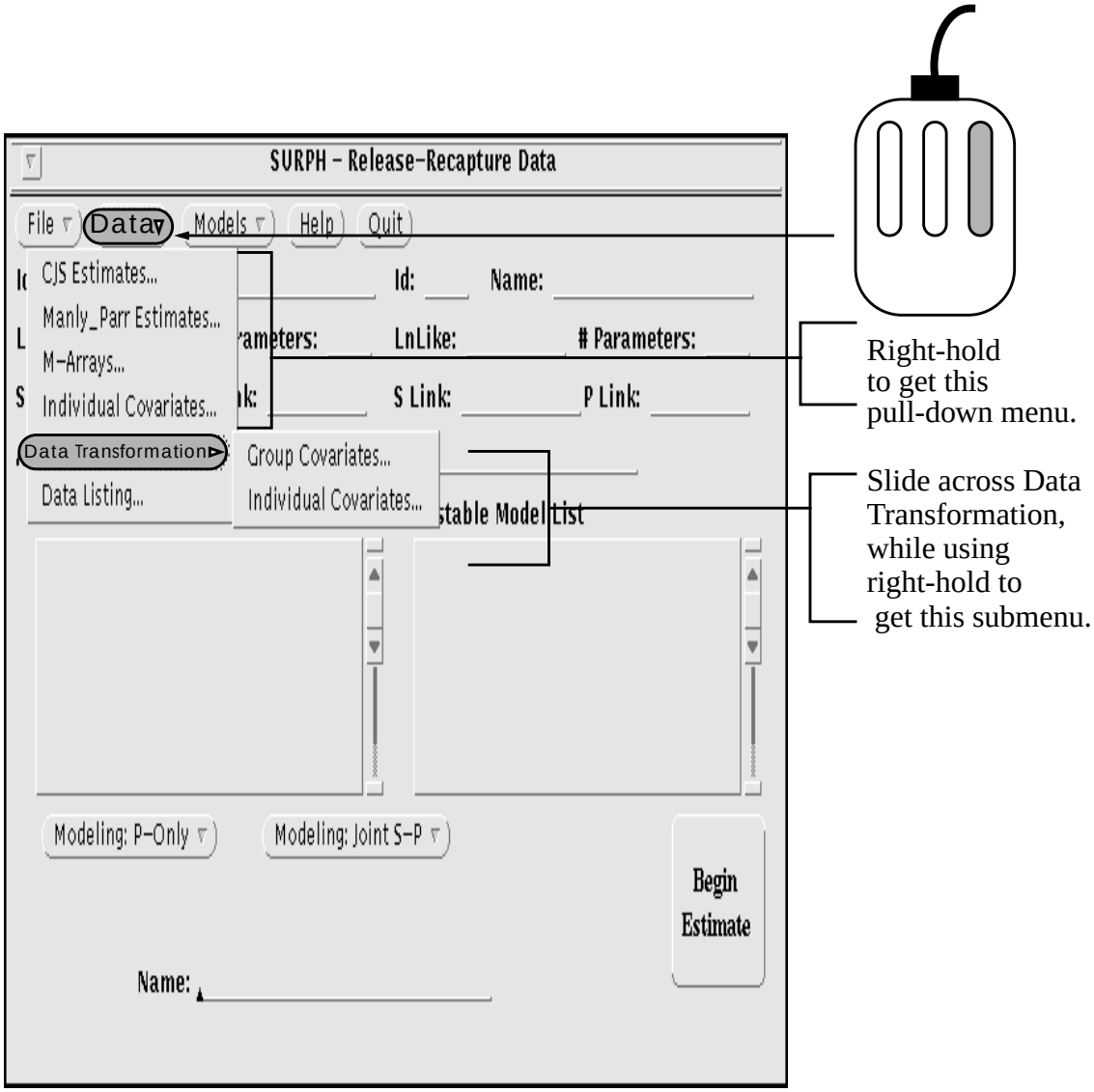
Text Window - A Text Window displays text information. In SURPH, text windows are used to display various summary statistics and model estimates for the current data set. An example of a text window is the window that displays Cormack/Jolly-Seber Estimates (**Data -> CJS Estimates**). This window displays estimated capture and survival probabilities based on the model parameterization of Cormack (1964), Jolly (1965) and Seber (1965).



Text windows generally consist of the Text Pane, where the information is displayed, and a small “control panel”, which in most cases contains a **Print** button and a **Quit** button.

When you quit SURPH, all information associated with a particular data set is no longer accessible. At times, you may wish to retain the information within the text window for further inspection after you have exited SURPH. To learn how to do so, see Storing Text Pane Information.

Pull-Down Menu Mouse Instructions



This is the pull-down and pull-right menu the user gets if he accesses the **Data Button** and the **Data Transformation** menu option.

Right-hold to get the pull-down.

Move the mouse down to select **Data Transformation**, then move sideways to the right, while holding the right mouse key down to get the pull-right menu. Release the right mouse key when the cursor covers the desired option (i.e., Group Covariates or Individual Covariates).

Alternatively, you may right-click on the **Data Button**, right-click on the **Data Transformation** option in pull-down, then left-click on the desired option in the pull-right menu.

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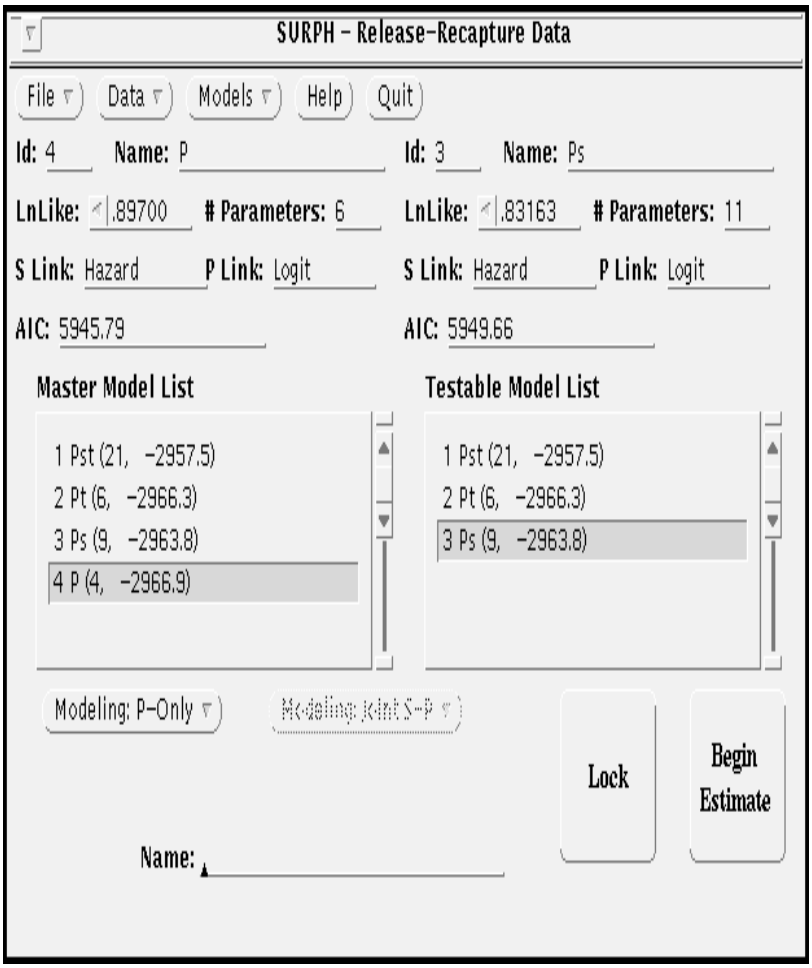
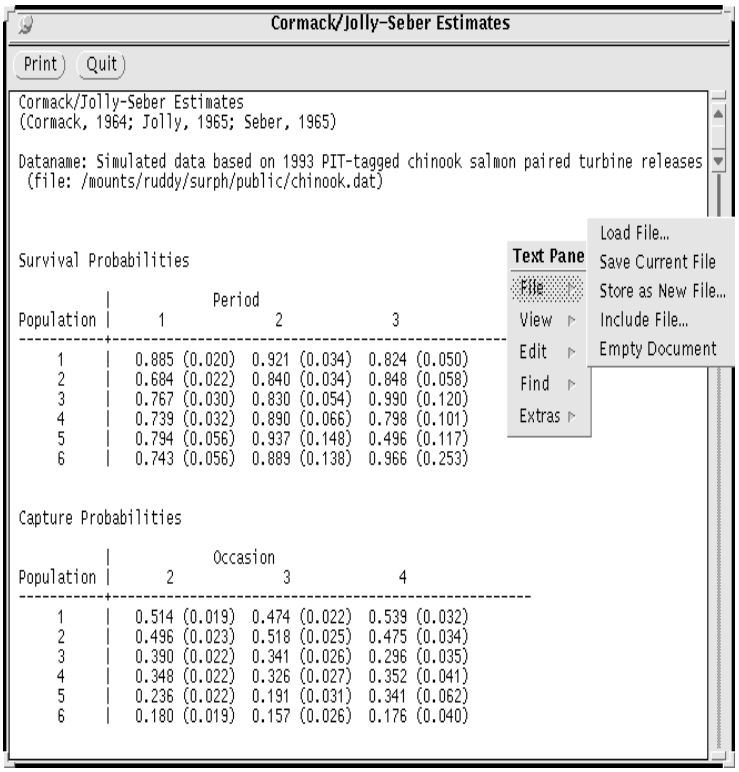


This graphic shows the typical appearance of the SURPH Base Window after you estimate a series of models for capture probabilities under **Modeling: P-Only**. After a series of capture models is estimated, you have the opportunity to choose which capture model will be retained for the survival modeling phase of the data analysis. All models that have been estimated during the current SURPH session, and those that have been loaded from previously-saved SURPH model files, appear within the **Master Model List**. For a model to appear in the **Testable Model List**, one of two conditions must be met. Either the selected model within the **Master Model List** is nested within the model in the **Testable Model List** or the model within the **Testable Model List** is nested within the selected model within the **Master Model List**. Two models are said to be “nested”, or “hierarchical”, when one model is a special case of the other. For example, Model A is

nested in Model B if Model A can be derived from Model B by either equating two or more parameters of B or by simply dropping one or more parameters of B.

To decide which model best fits the data, SURPH allows you to compare nested models using the Likelihood Ratio Test (LRT) (Wald 1943), and to compare non-nested models using Akaike's Information Criterion (AIC) (Akaike 1973). To test nested models using the LRT, select a model from the Master Model List. Nested models will appear within the **Testable Model List**. When you select a model in the **Testable Model List**, a pop-up window will appear. This pop-up window displays the change in Deviance between the two models (Test Statistic), the difference in the number of parameters estimated between the two models (df), and the probability of detecting a change in Deviance of such magnitude if the more complex model does not improve the fit (p-value).



To write text from a text pane to a file (e.g., the output from **Data -> Manly-Parr**), use the mouse to move the pointer onto the text pane, and right-click. This will cause the **Text Pane Menu** to appear. Right-click on "**File**" to bring up the pull-right menu. Then left-click on the "**Store as New File**" option. A **Text: Store** Pop-Up Window will appear. You can now store the file in a text file that can be editted using a text editor, and printed using standard UNIX utilities.

Occasionally, the display within the text window is too wide to be seen without enlarging the window. If this is the case, then the display is typically too wide to be printed using the **Print Button**. To print the entire contents of the display, you must save the output text to a new text file, import the new text file into a text editor, and print the file from the text editor. Even when the information fits comfortably within the text pane, and can be printed in its entirity using the **Print Button**, this technique can be used to save the text for future reference.

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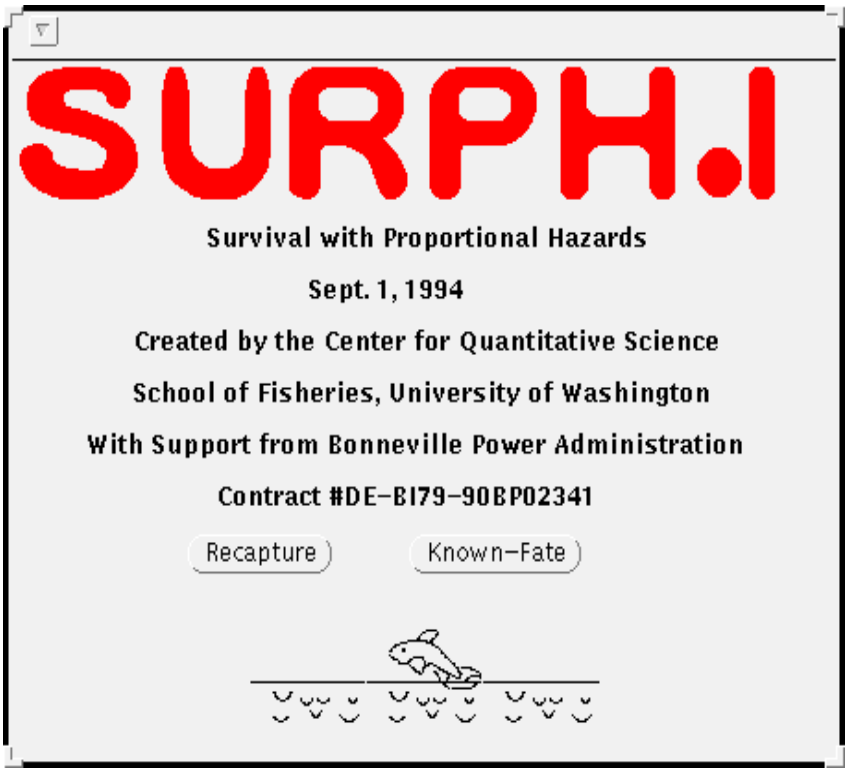

To begin a SURPH session, type either

> **surph** *datafile*

or

> **surph**

In the first case, the user specifies the datafile that will be used in the analysis on the command line. In the second case, the user does not specify the datafile at this time; the datafile to be used in the analysis will be specified once the SURPH Base Window appears (See **SURPH Base Window** and **File: Load Data** entries in Chapter 7).

To continue, the user must select whether the data are from a Release-Recapture study (**Recapture Button**) or a Known-Fate study (**Known Fate Button**). Once the appropriate button is selected, the SURPH Base Window will appear.

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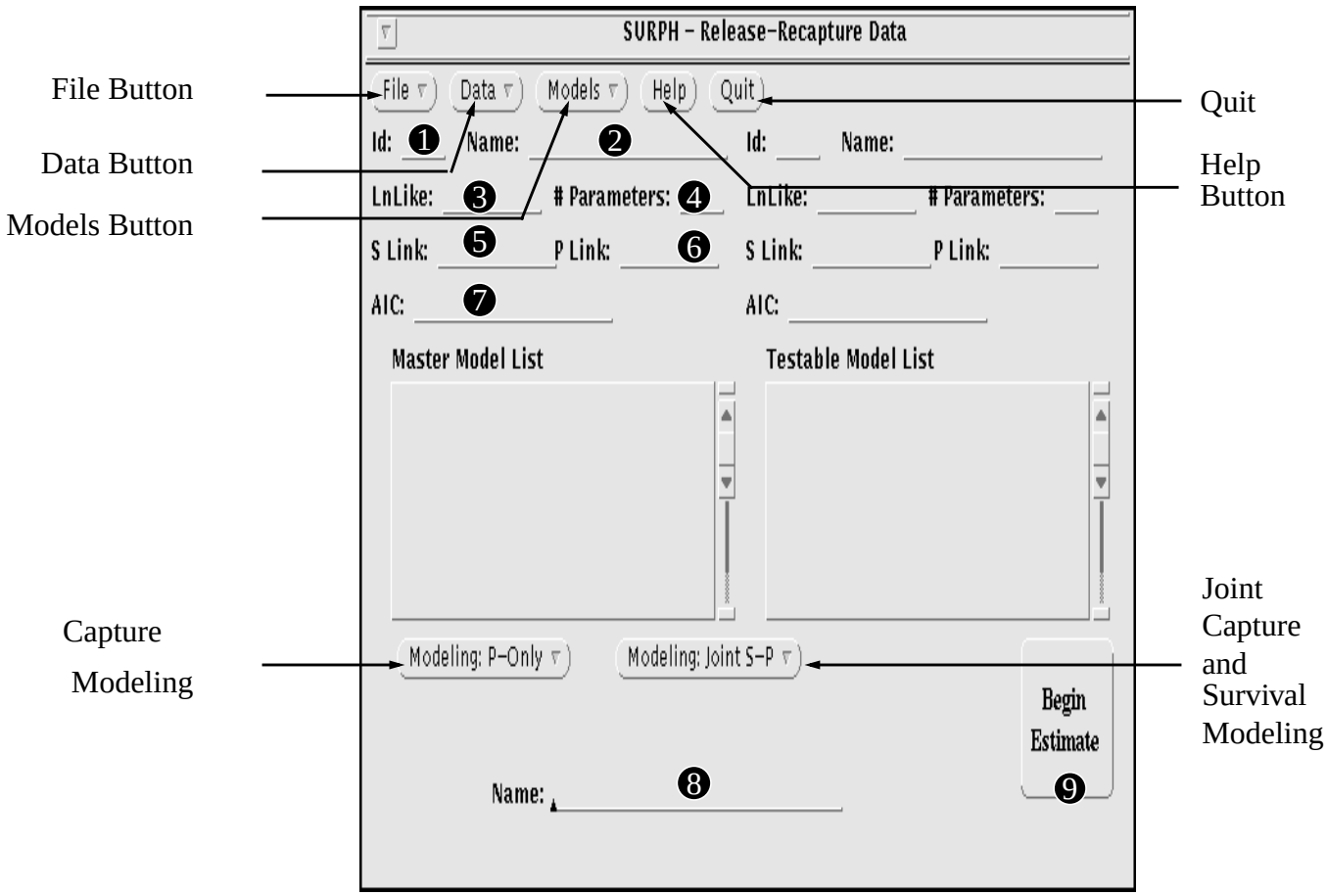


This is the SURPH Base Window for Release-Recapture data files, the first window that appears after you select the Release-Recapture modeling option from the SURPH Introductory Window. The SURPH Introductory Window appears when the program is started with a command line:

> **surph** *datafile*

All data summaries, modeling operations, graphics, and diagnostics are accessed from the SURPH Base Window.

Overview of Command Buttons

The pull-down menu accessed by the **File Button** is used to load data files, and to load or store model files. The **File** pull-down can also be used to end the SURPH session. Because the data file was specified on the command line, the Load Data command (**File -> Load Data**) is disabled.

The pull-down menu accessed by the **Data Button** has choices for graphical data display; computed Cormack (1964), Jolly (1965), Seber (1965) survival and capture probability estimates and Manly-Parr (Manly and Parr 1968) capture probability estimates; summary statistics in the form of M-Arrays (Burnham et al. 1987); data transformations; and echoing input data to the screen.

The pull-down menu accessed by the **Models Button** allows display of model estimates and graphical displays of model fit. This button also allows you to discard models and change model names.

The **Help Button** explains the use of the various buttons. To see further instructions, left-click on this button.

The **Quit Button** ends the SURPH session.

The **Modeling: P-Only Button** is used to parameterize the capture-only model. When this button is used, the capture process is modelled as an extension of the Manly-Parr (1968) Model and uses only a subset of the total release data. Menu choices under the **Modeling: P-Only Button** allow you to model the capture process at the population or individual level, and allow you to specify the link function. For further descriptions of the functions associated with this button, see

Capture Modeling .

The **Modeling: Joint S-P Button** is used to parameterize the joint survival/capture model. When this button is used, the capture process and survival process are modelled jointly. Menu choices under the **Modeling: Joint S-P Button** allow you to model the capture and survival processes at the population or individual level, and allow you to specify the link functions for both. The final period product of capture and survival can also be modelled at the population or individual level, and you can specify the link function. For further descriptions of the functions associated with this button, see

Joint Modeling: Pull-Down Menu .

The SURPH Base Window has two lists of estimated models, the **Master Model List** and the **Testable Model List**. The **Master Model List** contains all models that have been estimated during the current SURPH session, and those that have been loaded from previous SURPH sessions. The **Testable Model List** contains

models that can be compared to the model that has been selected from the **Master Model List**. For a model to appear within the **Testable Model List**, either the model within the **Testable Model List** is nested within the model selected from the **Master Model List**, or the model selected from the **Master Model List** is nested within the model in the **Testable Model List**

(See Testing Nested Models: Master and Testable Lists).

Numbered Features

The numbered spaces 1-7 refer to attributes of the model selected from the **Master Model List**. Analogous spaces in the upper right-hand portion of the SURPH Base Window refer to attributes of the model selected within the **Testable Model List**.

❶ Displays the Model ID Number of the selected model in the **Master Model List**.

❷ Displays the name of the selected model in the **Master Model List**.

❸ Displays the Log-Likelihood of the selected model in the **Master Model List**.

❹ Displays the number of parameters estimated in the selected model in the **Master Model List**.

❺ Displays the link function for the survival parameters of the selected model in the **Master Model List**.

❻ Displays the link function for the capture parameters of the selected model in the **Master Model List**.

❼ Displays Akaike's Information Criterion (Akaike 1973) - This is used to help determine the best fitting models when the models are not nested.

The space numbered 8, and the button numbered 9 are used to create new models:

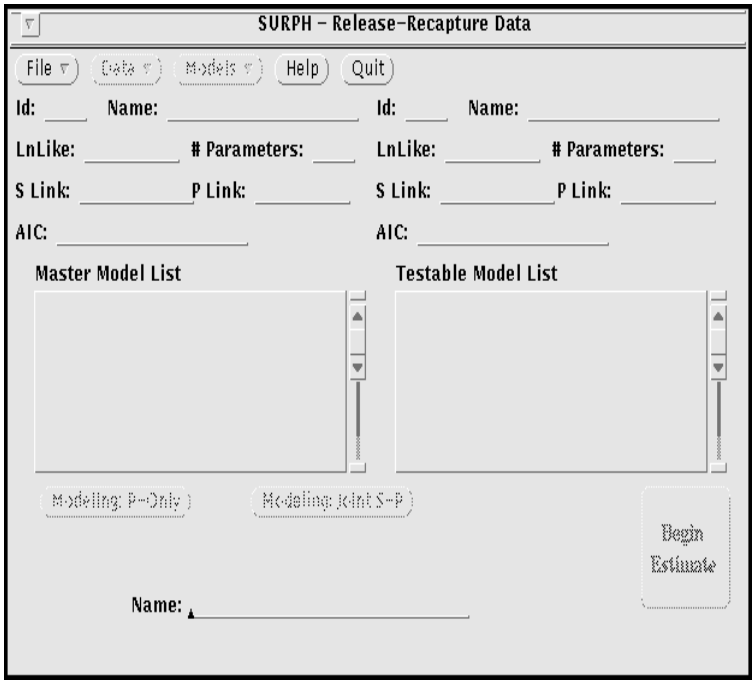
❽ This field allows you to name the model prior to running the estimation procedure. If you does not specify a name for the model, the name "Model 'n'" is assigned, where "n" is the Model ID Number. If you have a model you wish to rename, see the section for the **Models Button**.

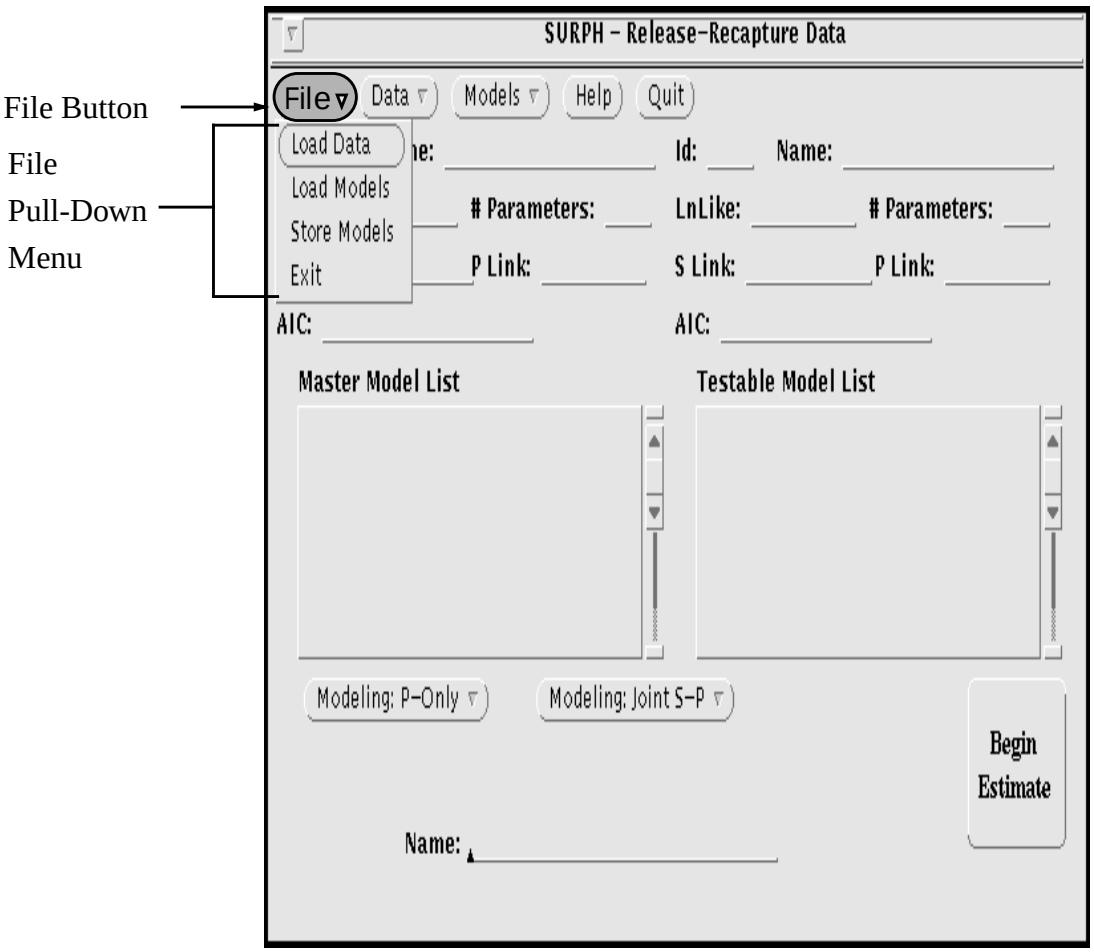
❾ Left-clicking on this button initiates the numerical optimization routine to estimate the parameters of the model specified in the modeling options under **Modeling: P-Only** or **Modeling: Joint S-P**.

If you start SURPH without specifying an input data file on the command line:

> **surph**

not all buttons are activated (see below). Before these de-activated buttons can be used, data must be loaded. To load data, right-click on the **File Button**. A pull-down menu will appear. Left-click on **Load Data**. The **Load Input File** window will appear. If your data file is in the directory from which you started SURPH, left-click in the **File** text field and type the name of the file that contains your data. If your data is in a different directory, left-click in the **Directory** text field and change the directory path in the **Directory** field, then left-click in the **File** field and enter the file name in the blank **File** field. Left-click on the **Load Button** in the **Load Input Data** window to load the data.





To access this pull-down menu, right-click on the **File Button**.

The commands available from this pull-down menu are:

Load Data - Load a data file to be analyzed (See **Load Data**).

Load Models - Load previously developed and stored models (See **Load Models**).

Store Models - Save models from the **Master Model List** for future retrieval (See **Store Models**).

Exit - Quit SURPH

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This pop-up window (**File -> Load Data**) is used to load data for SURPH. Alternatively, the data file can be specified on the UNIX command line by typing:

> **surph** *datafile*

Data files for SURPH consist of definitions of the dimensions of the data (e.g., number of populations), followed by recapture data for each tagged animal. Examples of data files can be found in Chapter 6.

To specify the directory where the data file is located, left-click on the **Directory** field, and type the directory path. To specify the data file, left-click on the **File** field, and type the data file name. Once the correct directory has been specified and the data file name has been entered in the **File** field, initiate loading by left-clicking on the **Load Button**.

In this example, the file “chinook.dat” in the directory “/mounts/ruddy/surph/public” would be loaded.

Left-click on the **Cancel Button** to dismiss this window without loading data.

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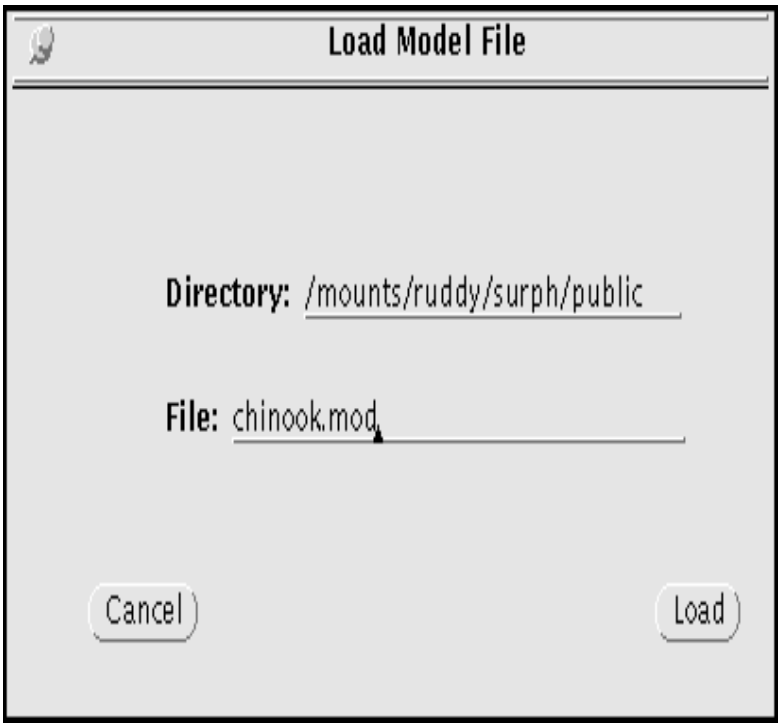

This pop-up window (**File -> Load Model**) allows you to load previously stored SURPH models into the **Master Model List**. Models must have been saved using SURPH during a previous modeling session. Model files are formatted ASCII files that contain all pertinent information regarding the stored SURPH models.

To specify the directory where the model file is located, left-click on the **Directory** field, and type the correct directory path. To specify the file that contains the previously stored models, left-click on the **File** field, and type the name of the model file. Once the correct directory has been specified and the name of the model file has been entered into the **File** field, left-click on the **Load Button** to load models.

In this example, the file “chinook.mod” in the directory “/mounts/ruddy/surph/public” would be loaded. “Chinook.mod” holds models that were saved during a previous SURPH session. After loading, these models would be accessible to you in SURPH, just as if they had been created in the current session.

Left-click on the **Cancel Button** to dismiss this window without loading models.

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This pop-up window (**File -> Store Model**) allows you to store SURPH models from the **Master Model List** to a disk file. Model files are formatted ASCII, containing all pertinent information regarding the SURPH models.

To specify the directory where the models are located, left-click on the **Directory** field, and type the directory path. To specify the file where the models are located, left-click on the **File** field, and type the name of the model file. Once the correct directory has been specified and the file name has been entered into the field, left-click on the **Store Button** to store the models.

In this example, the model file “chinook.mod” would be created in the directory “/mounts/ruddy/surph/public”. “Chinook.mod” would hold all models that had been estimated during the current SURPH session. After the models have been stored, these models can be loaded during future SURPH sessions.

Left-click on the **Cancel Button** to dismiss this window without storing models.

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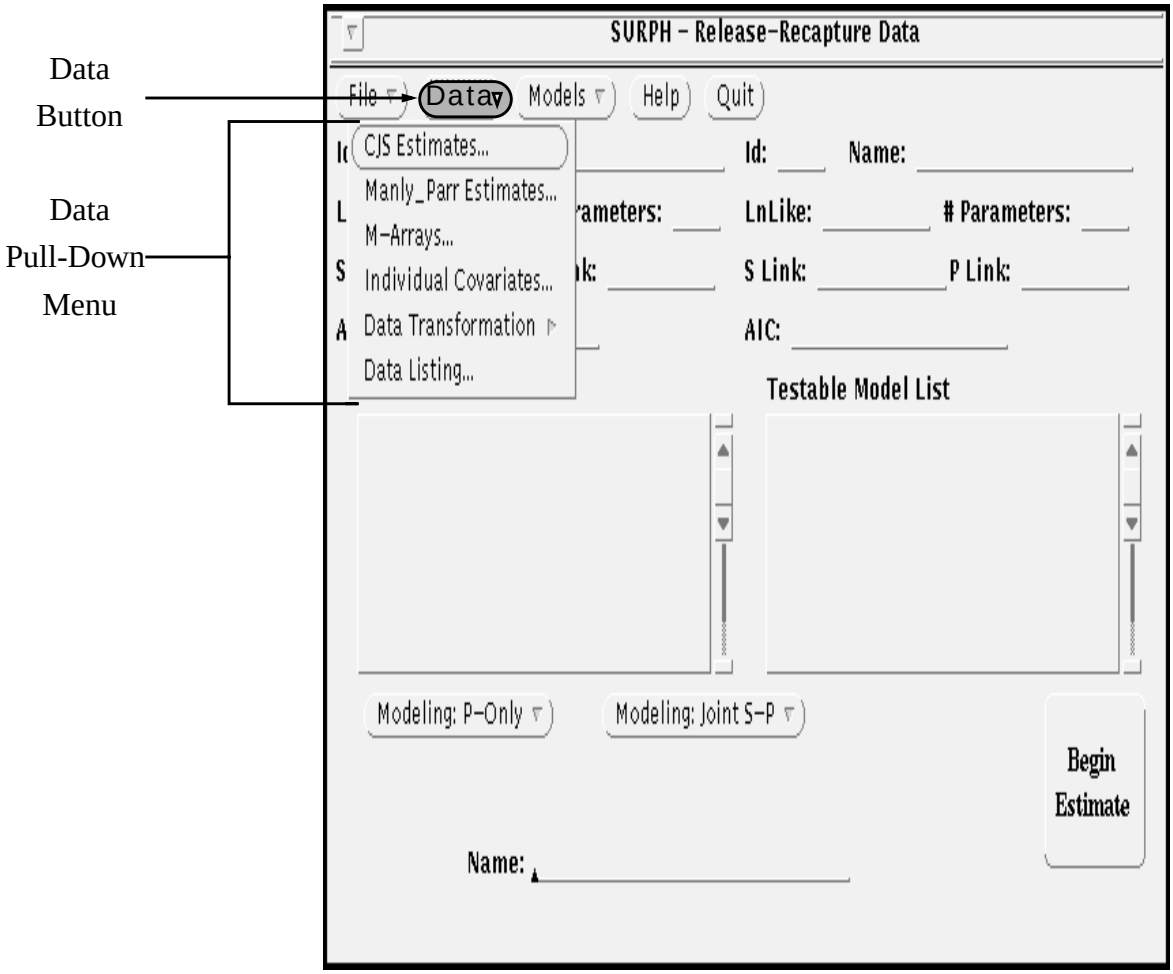


To access this pull-down menu, right-click on the **Data Button**.

The commands available from this menu produce data summaries and transformations:

CJS Estimates - Provides Cormack (1964), Jolly (1965), Seber (1965) estimates of survival and capture probabilities. For further information, see Data: Cormack/Jolly-Seber Estimates.

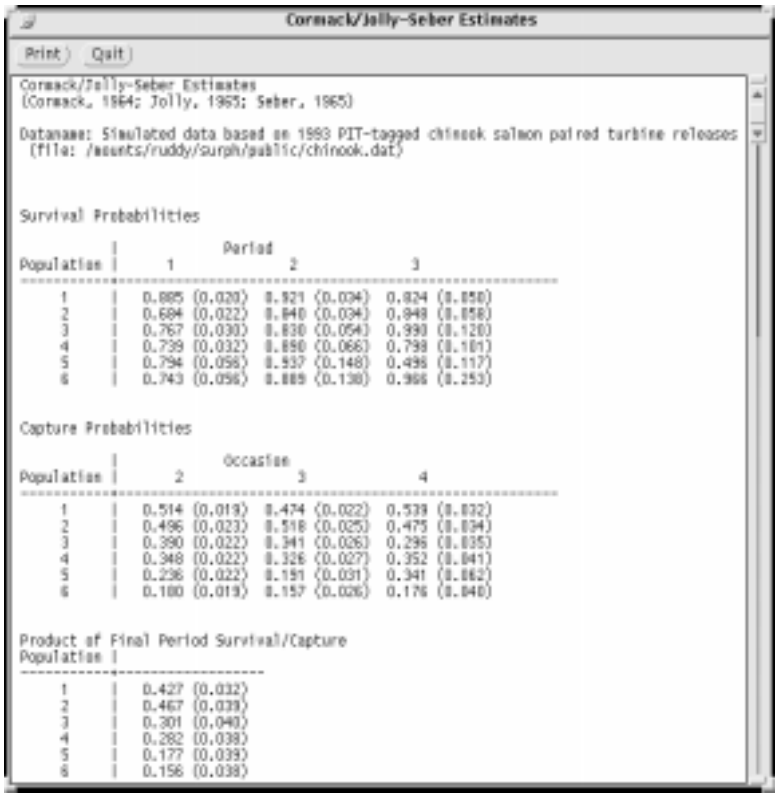
Manly-Parr - Provides estimates of capture probabilities using the Manly-Parr (1968) method, which is independent of the survival process. For further information, see Data : Manly Parr.

M-Arrays - Provides release-recapture summary statistics (Burnham et al. 1987). For further information,
see Data : M-Arrays .

Individual Covariates - Displays graphical representations (histograms and cumulative distribution functions) of the data, by covariate, by population, by period. For further information,
see Individual Covariates - Histogram or
Individual Covariates - CDF Plot .

Data Transformation - Allows transformations of covariate data. Examples of transformations are squares, square roots, cross products, reciprocals and natural logarithms. For further information,
see Data Transformations: Group Covariates or
Data Transformations: Individual Covariates

Data Listing - Gives a complete listing of the input data in a formatted display. For further information,
see Data Listing .



Cormack/Jolly-Seber Estimates

Print Quit

```
Cormack/Jolly-Seber Estimates
(Cormack, 1964; Jolly, 1965; Seber, 1965)

Dataname: Simulated data based on 1993 PIT-tagged chinook salmon paired turbine releases
 (file: /mounts/ruddy/surph/public/chinook.dat)


Survival Probabilities

           |            Period
Population |     1              2              3
-----------+-------------------------------------------------------
     1     |  0.885 (0.020)  0.921 (0.034)  0.824 (0.050)
     2     |  0.684 (0.022)  0.840 (0.034)  0.848 (0.058)
     3     |  0.767 (0.030)  0.830 (0.054)  0.990 (0.120)
     4     |  0.739 (0.032)  0.850 (0.066)  0.798 (0.101)
     5     |  0.794 (0.056)  0.537 (0.148)  0.496 (0.117)
     6     |  0.743 (0.056)  0.889 (0.130)  0.966 (0.253)


Capture Probabilities

           |            Occasion
Population |      2             3              4
-----------+-------------------------------------------------------
     1     |  0.514 (0.019)  0.474 (0.022)  0.539 (0.032)
     2     |  0.496 (0.023)  0.518 (0.025)  0.475 (0.034)
     3     |  0.390 (0.022)  0.341 (0.026)  0.296 (0.035)
     4     |  0.348 (0.022)  0.326 (0.027)  0.352 (0.041)
     5     |  0.236 (0.022)  0.191 (0.031)  0.341 (0.062)
     6     |  0.180 (0.019)  0.157 (0.026)  0.176 (0.040)


Product of Final Period Survival/Capture
Population |
-----------+-----------------
     1     |  0.427 (0.032)
     2     |  0.467 (0.039)
     3     |  0.301 (0.040)
     4     |  0.282 (0.038)
     5     |  0.177 (0.039)
     6     |  0.156 (0.038)
```

This text pane (**Data -> CJS Estimates**) shows the Cormack (1964), Jolly (1965), Seber (1965) survival and capture probability estimates. The parenthetical number beside each probability estimate is the estimated standard error for that parameter. For example, for Population 1 in Period 1, the estimated survival probability is 0.885, with an estimated standard error of 0.020, while the estimate of the product of final period survival and capture probabilities for Population 3 is 0.301, with an estimated standard error of 0.040.

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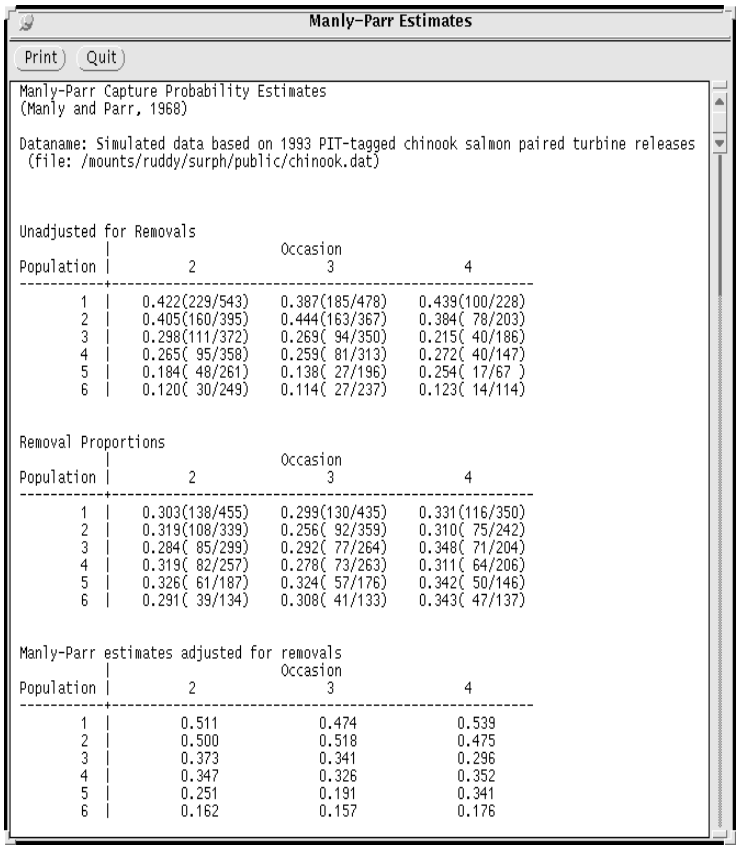

Manly-Parr Estimates

Print Quit

Manly-Parr Capture Probability Estimates
(Manly and Parr, 1968)

Dataname: Simulated data based on 1993 PIT-tagged chinook salmon paired turbine releases
(file: /mounts/ruddy/surph/public/chinook.dat)

Unadjusted for Removals

Population	Occasion 2	3	4
1	0.422(229/543)	0.387(185/478)	0.439(100/228)
2	0.405(160/395)	0.444(163/367)	0.384(78/203)
3	0.298(111/372)	0.269(94/350)	0.215(40/186)
4	0.265(95/358)	0.259(81/313)	0.272(40/147)
5	0.184(48/261)	0.138(27/196)	0.254(17/67)
6	0.120(30/249)	0.114(27/237)	0.123(14/114)

Removal Proportions

Population	Occasion 2	3	4
1	0.303(138/455)	0.299(130/435)	0.331(116/350)
2	0.319(108/339)	0.256(92/359)	0.310(75/242)
3	0.284(85/299)	0.292(77/264)	0.348(71/204)
4	0.319(82/257)	0.278(73/263)	0.311(64/206)
5	0.326(61/187)	0.324(57/176)	0.342(50/146)
6	0.291(39/134)	0.308(41/133)	0.343(47/137)

Manly-Parr estimates adjusted for removals

Population	Occasion 2	3	4
1	0.511	0.474	0.539
2	0.500	0.518	0.475
3	0.373	0.341	0.296
4	0.347	0.326	0.352
5	0.251	0.191	0.341
6	0.162	0.157	0.176

This text pane displays Manly-Parr (1968) capture probability estimates (**Data -> Manly-Parr**) for each sampling occasion and population. The first table displays the uncorrected point estimates of the capture probabilities and the number of captures used in their calculations. The formulas for the capture probabilities are given in Section 4.6. For example, in Population 1, 478 animals were caught both before and after the 3rd sampling occasion, and of those, 185 were also captured on the 3rd sampling occasion, for a capture probability estimate of 185/478 = 0.387. These estimates are biased when trap mortality or known removal of captured animals occurs.

The second table displays the proportion and fraction of the captured animals that were removed from each population on each sampling occasion. For example, in Population 1, 435 animals were caught on the 3rd sampling occasion, and of those, 130 were either killed or removed, for a removal proportion of 130/435 = 0.299.

The final table displays the estimated capture probabilties corrected for trap mortality and known removals. For an explanation of the adjustment procedure, see Section 4.6.

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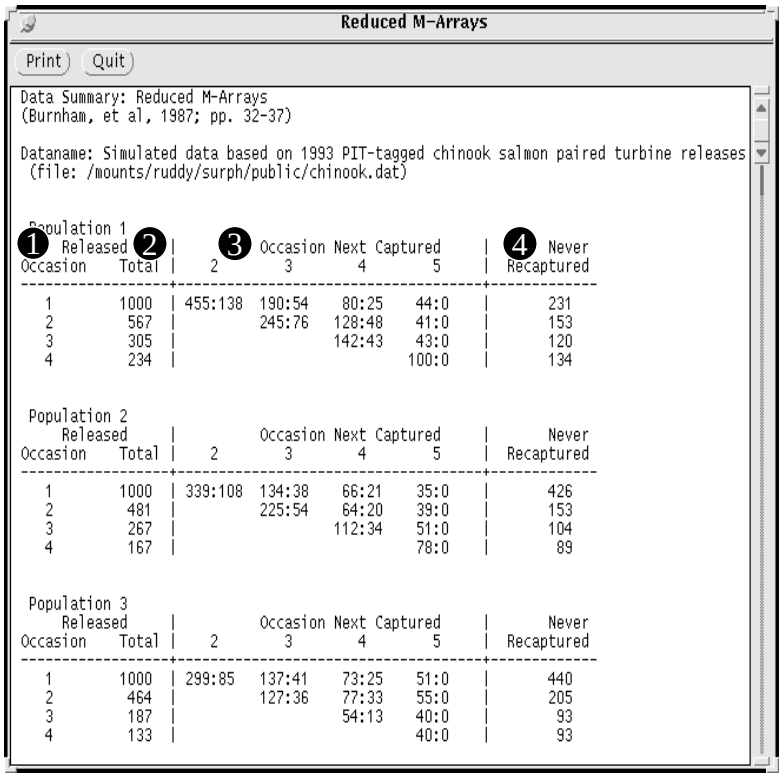

Reduced M-Arrays

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```
Data Summary: Reduced M-Arrays
(Burnham, et al, 1987; pp. 32-37)

Dataname: Simulated data based on 1993 PIT-tagged chinook salmon paired turbine releases
 (file: /mounts/ruddy/surph/public/chinook.dat)


 Population 1
❶  Released ❷ |     ❸ Occasion Next Captured     | ❹ Never
Occasion    Total |    2        3        4        5     |  Recaptured
------------------+-----------------------------------+-------------
   1        1000  | 455:138  190:54    80:25    44:0    |       231
   2         567  |          245:76   128:48    41:0    |       153
   3         305  |                   142:43    43:0    |       120
   4         234  |                             100:0    |       134


 Population 2
     Released     |          Occasion Next Captured     |       Never
Occasion    Total |    2        3        4        5     |  Recaptured
------------------+-----------------------------------+-------------
   1        1000  | 339:108  134:38    66:21    35:0    |       426
   2         481  |          225:54    64:20    39:0    |       153
   3         267  |                   112:34    51:0    |       104
   4         167  |                              78:0    |        89


 Population 3
     Released     |          Occasion Next Captured     |       Never
Occasion    Total |    2        3        4        5     |  Recaptured
------------------+-----------------------------------+-------------
   1        1000  | 299:85   137:41    73:25    51:0    |       440
   2         464  |          127:36    77:33    55:0    |       205
   3         187  |                    54:13    40:0    |        93
   4         133  |                              40:0    |        93
```

This text pane (**Data -> M-Arrays**) displays numbers of animals released and subsequently recaptured, in the format of the “reduced M-array” of Burnham et al. (1987). There is one table for each population. The elements of the table for each population are:

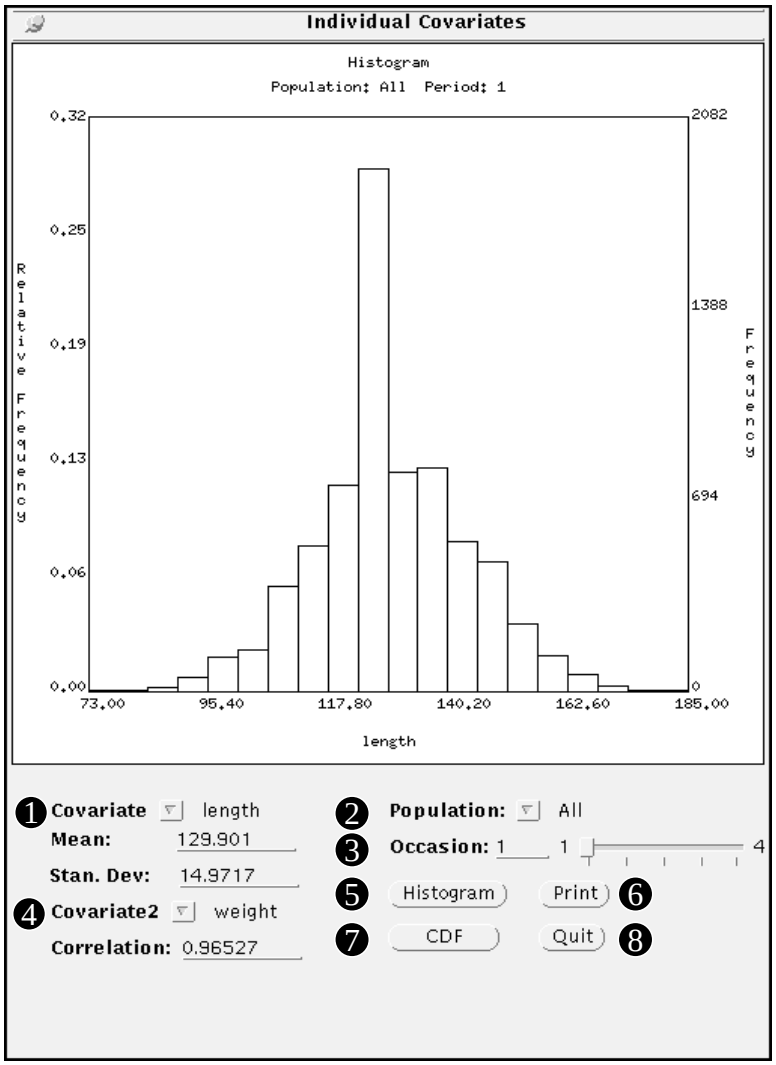
❶ Release Occasion — Occasion of release of marked animals.

❷ Total Released — Number of animals seen and released at this occasion. This total includes animals marked and released for the first time, as well as previously-marked animals recaptured on this sampling occasion, and re-released.

❸ Occasion Next Captured — For each release occasion, the number of animals first recaptured again on each subsequent occasion. The number to the left of the colon is the total number of animals captured. To the right of the colon is the number of animals not re-released, due either to trap mortality or other known removal.

❹ Never Recaptured — For each release occasion, the number of animals that were never again seen after the initial release.

In the example shown, 1000 animals in Population 1 were marked and released on occasion 1. Of these, 455 were recaptured on the 2nd sampling occasion. Of the 545 animals not seen on occasion 2, 190 were recaptured on occasion 3. Of the 455 recaptured on occasion 2, 138 were removed. The other 317 were combined with 250 newly marked animals on occasion 2 for a total of 567 released on occasion 2. A total of 435 animals from Population 1 were recaptured on occasion 3 (190 + 245), and of those 130 (54 + 76) were removed. The remaining 305 were released on occasion 3, with no newly marked animals.



This graphic (**Data -> Individual Covariates**) displays histograms of individual covariate data. Histograms display individual covariate data from all animals from the selected population known to be alive on the selected occasion. Different individual covariates may be selected using the covariate pull-down menu (❶). Similarly, the different populations may be selected using the population pull-down menu (❷). To access either, right-click on the small arrow adjacent to the appropriate keyword (**Covariate** or **Population**).

Numbered Features

❶ Covariate Pull-Down Menu. This menu allows you to select the individual covariate to be viewed. Right-click on the downward

pointing arrow to access the menu. Left-click on a menu choice to select a covariate.

❷ Population Pull-Down Menu. This menu allows you to select the population to be viewed. Right-click on the downward pointing arrow to access the menu. Left-click on a menu choice to select a population. The menu includes a choice to view data for all populations simultaneously.

❸ Occasion Designation. This slide-bar allows you to select the occasion to be viewed. Pull slide bar (left-hold on the small rectangle on the slide bar and move mouse sideways) across to increment or decrement the occasion designation.

❹ Covariate2 Pull-Down Menu - This menu allows you to select a second individual covariate to use in conjunction with the individual covariate selected above (❶) in computing the simple correlation (see below). Right-click on the downward pointing arrow to access the menu. Left-click on a menu choice to select a covariate.

❺ **Histogram Button**. Displays the data as a histogram (as shown here).

❻ **Print Button**. Sends a copy of the screen to the printer.

❼ **CDF Button**. Displays the cumulative distribution of covariate values for recaptured and non-recaptured animals. The cumulative distribution plot is explained under

Individual Covariates - CDF Plot .

❽ **Quit Button**. Quits this window.

Statistical Functions:

Mean - Displays the arithmetic mean for the selected covariate for the selected population. Data from all animals in the population,

regardless of marking occasion, are combined for this calculation. In this example data set, we have designated “length” as our primary covariate. The mean length for all animals released was 129.901.

Stand. Dev. - Displays the standard deviation for the covariate and the population currently selected. Data from all animals in the population, regardless of marking occasion, are combined for this calculation. In this example data set, we have designated “length” as our primary covariate. The standard deviation of the length for all animals released was 14.9717.

Correlation - Displays the simple correlation (Zar 1984) between the covariate selected from the **Covariate** pulldown menu and the covariate selected from the **Covariate2** pulldown menu. Data from all animals in the population, regardless of marking occasion, are combined for this calculation. In the example, we have designated “length” as our primary covariate and “weight” as Covariate2. The correlation between “length” and “weight” in this example data set is 0.96.

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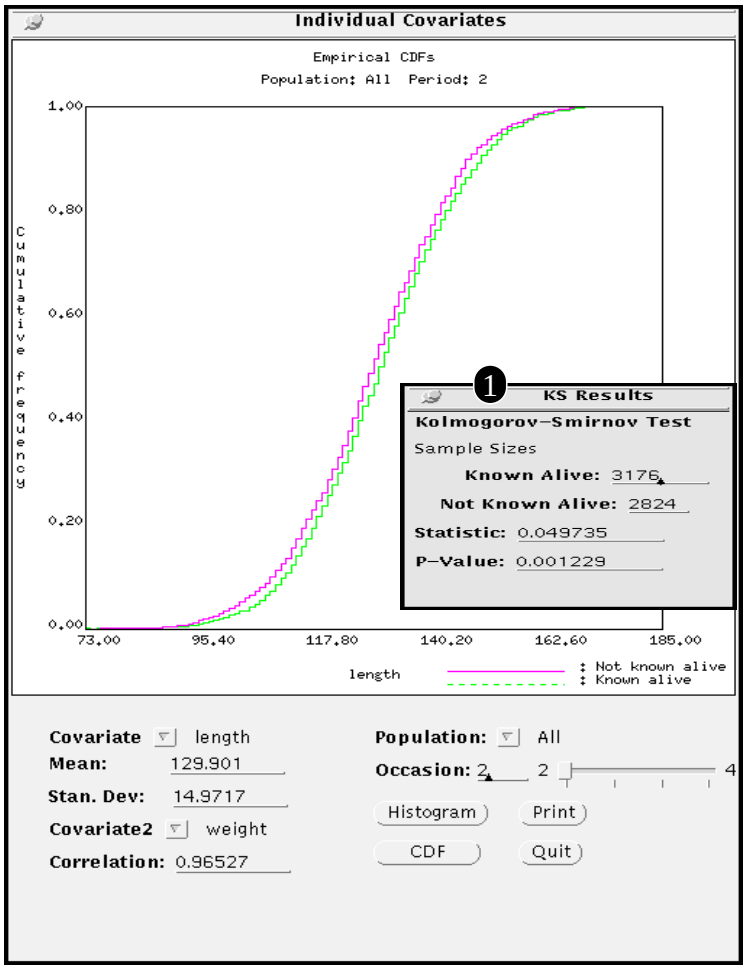
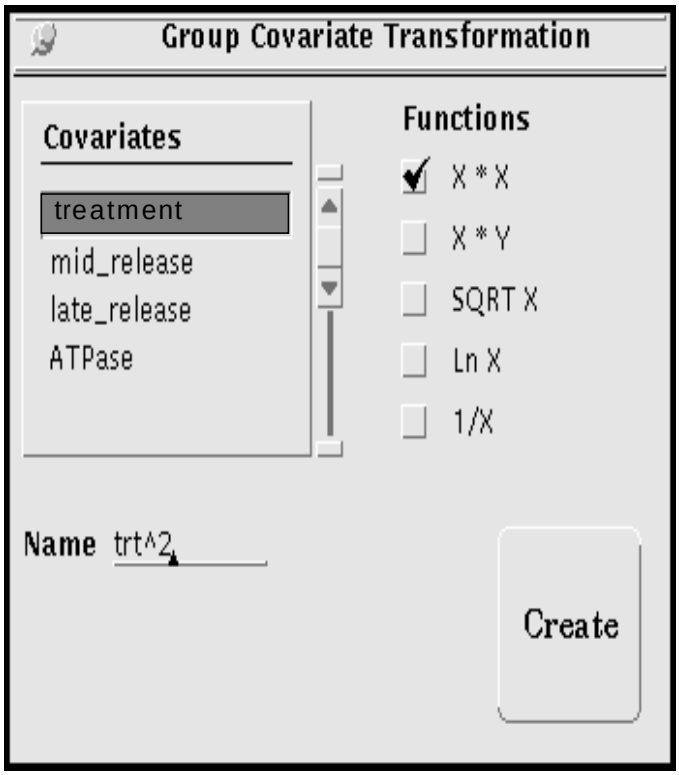


This graphic (**Data -> Individual Covariates**) displays cumulative distribution functions (cdfs) of individual covariate data. Two cumulative distributions are displayed: one for previously marked animals that were known to be alive on the selected occasion (recaptured on the selected occasion or later), and one for those not known to be alive (captured for the last time prior to the selected occasion). Large differences between the curves may indicate some selective effect of the individual factor on capture, survival, or both.

For further information concerning other functions in this window, see Individual Covariates: Histogram .

In addition to the graphic display of cdfs, the Kolmogorov-Smirnov test for homogeneity of discrete distributions is automatically computed. The K-S pop-up window (❶) displays the number of animals known alive, the number of animals not known alive, the maximum difference between the two empirical distributions (Statistic), and the

probability (P-Value) of observing such a difference if the two samples were from identical distributions.



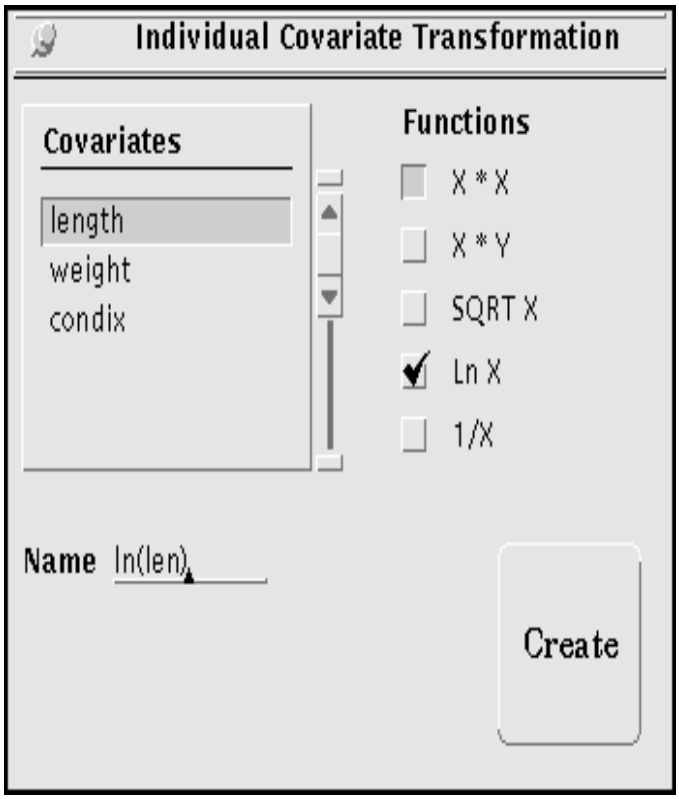
This window (**Data -> Data Transformations -> Group Covariates**) is used to generate new Group Covariates that are functions of the currently defined Group Covariates. To create new data that are a transformation of current data, select the covariate(s) from the Covariates List and the functional transformation from the Function List. To name the new Covariate, type the name you desire in the blank line following "Name" prior to pushing the **Create Button**. If you forget to include a name for the new variable, a pop-up window will appear and advise you to name the new variable. You cannot create a new variable without naming it. To create the new Covariate, place the arrow key above the **Create Button**, then left-click.

Available functional manipulations are:

X*X	Square the value of the selected Covariate.
SQRT (X)	Take the Square Root of the value of the selected Covariate
Ln (X)	Take the Natural Logarithm of the value of the selected Covariate.
1/ (X)	Take the Reciprocal of the value of the selected Covariate

X*Y Multiply the value of one selected Covariate by the value of another selected Covariate

In the example window, left-clicking on the **Create Button** will create a new variable "*trt^2*". The values of *trt^2* for each population will be equal to the square of the values for *treatment*.



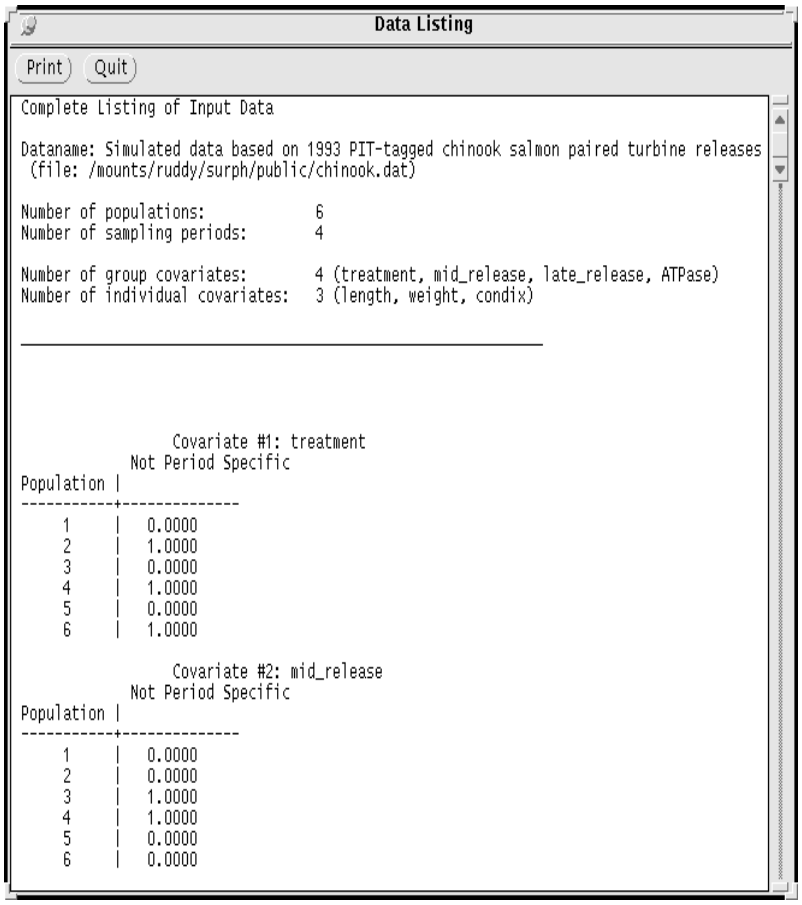
This window (**Data -> Data Transformations -> Individual Covariates**) is used to generate new Individual Covariates that are functions of the currently selected Individual Covariate data. To create new data that are a transformation of current data, select the covariate(s) from the Covariates List and the functional transformation from the Function List. To name the new Covariate, type the name you desire in the blank line following “Name” prior to pushing the **Create Button**. If you forget to include a name for the new variable, a pop-up window will appear and advise you to name the new variable. You cannot creat a new variable without naming it. To create the new Covariate, place the arrow key above the **Create Button**, then left-click.

Available functional manipulations are:

X*X	Square the value of the selected Covariate.
SQRT (X)	Take the Square Root of the value of the selected Covariate.
Ln (X)	Take the Natural Logarithm of the value of the selected Covariate.
1/ (X)	Take the Reciprocal of the value of the selected Covariate.

X*Y Multiply the value of one selected Covariate by the value of another selected Covariate.

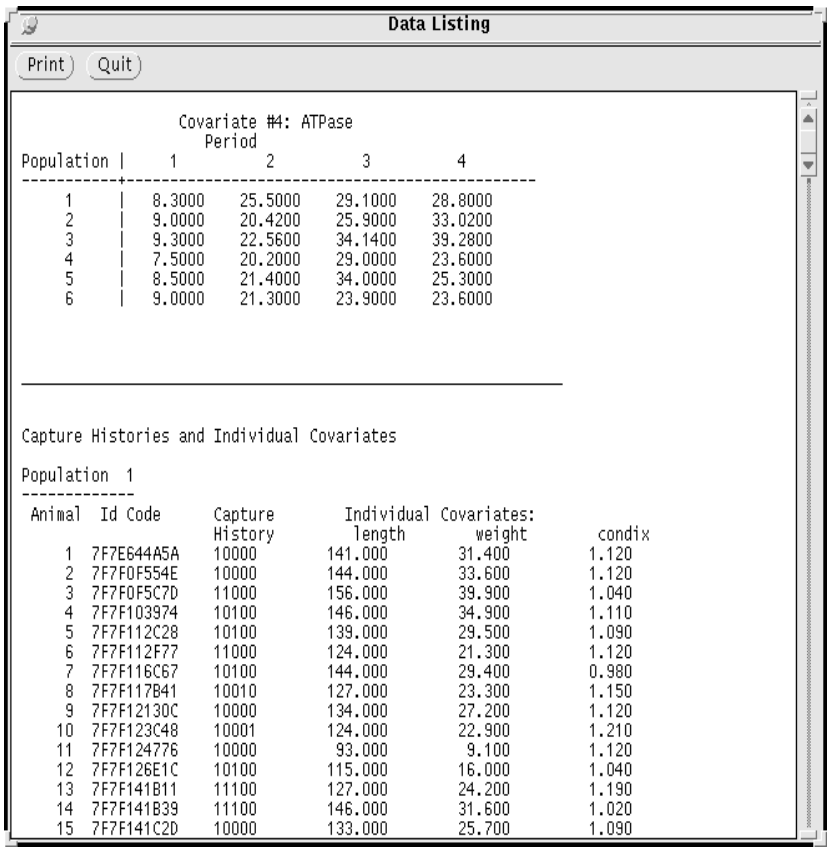
In the example window, left-click on the **Create Button** to create a new variable "*ln(len)*". The values in *ln(len)* will be equal to the Natural Logarithm of the values in *length*.



This text window (**Data -> Data Listing**) displays the input data.

An example of a data listing for chinook.dat is displayed. As the data listing was too long to display in a single graphic, portions of the listing are shown in two different graphics. In the upper graphic, the data listing gives the name of the data file (/mounts/ruddy/surph/public/chinook.dat), the number of populations in the data set (6), the number of sampling periods (4), the number and names of the group covariates, and the number and names of the individual covariates. Also displayed in the upper graphic are two examples of time independent group covariates. The first group covariate is treatment. Indicator variables denote which populations are (1's) and are not (0's) within the treatment group. Thus, populations 2, 4, and 6 are the treatment populations, whereas populations 1, 3, and 5 are non-treatment populations. Similarly, for the second group covariate (mid_release), populations 3 and 4 are mid-release groups, whereas populations 1, 2, 5, and 6 are not mid-release groups. Since both of these group covariates were time-independent, a single value is given for each population.

In the lower graphic, ATPase is a time-dependent group covariate. The values of ATPase must be defined for each period for each population. For population 1, the mean ATPase changes from a value of 8.3 in the 1st period, to 25.5 in 2nd period, to 29.1 in 3rd period, and to 28.8 in 4th period. Below the ATPase values, capture histories and the values of the individual covariates are displayed. The first 15 animals in population 1 are displayed. Each line within this portion of the data listing pertains to an individual animal. For example, the 6th animal in chinook.dat has the unique ID code 7F7F112F77 and has an associated capture history of 11000. This animal (7F7F112F77) was 124 mm in length, weighed 21.3 grams, and had a condition index of 1.120 at first capture.



Data Listing

Print Quit

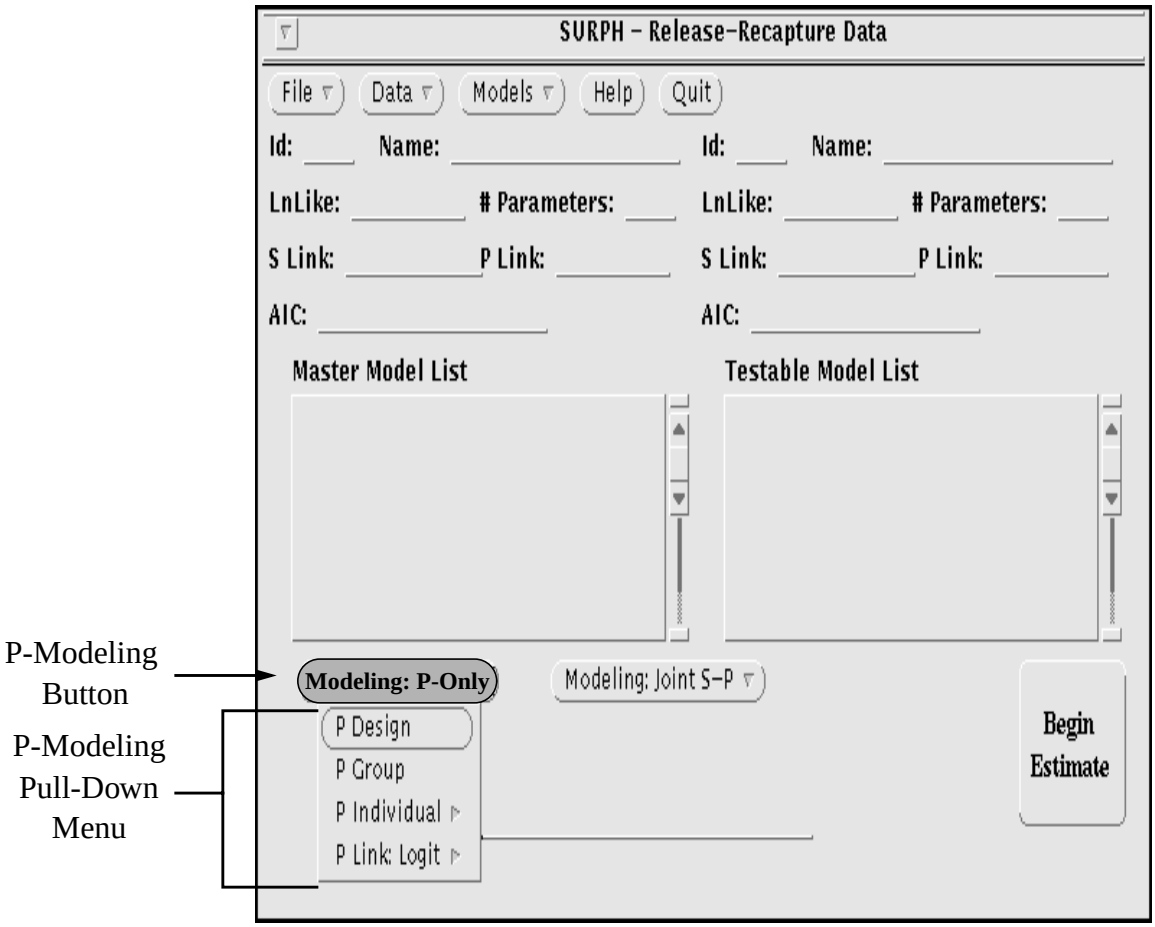
Covariate #4: ATPase

Population	Period 1	2	3	4
1	8.3000	25.5000	29.1000	28.8000
2	9.0000	20.4200	25.9000	33.0200
3	9.3000	22.5600	34.1400	39.2800
4	7.5000	20.2000	29.0000	23.6000
5	8.5000	21.4000	34.0000	25.3000
6	9.0000	21.3000	23.9000	23.6000

Capture Histories and Individual Covariates

Population 1

Animal	Id Code	Capture History	Individual Covariates: length	weight	condix
1	7F7E644A5A	10000	141.000	31.400	1.120
2	7F7F0F554E	10000	144.000	33.600	1.120
3	7F7F0F5C7D	11000	156.000	39.900	1.040
4	7F7F103974	10100	146.000	34.900	1.110
5	7F7F112C28	10100	139.000	29.500	1.090
6	7F7F112F77	11000	124.000	21.300	1.120
7	7F7F116C67	10100	144.000	29.400	0.980
8	7F7F117B41	10010	127.000	23.300	1.150
9	7F7F12130C	10000	134.000	27.200	1.120
10	7F7F123C48	10001	124.000	22.900	1.210
11	7F7F124776	10000	93.000	9.100	1.120
12	7F7F126E1C	10100	115.000	16.000	1.040
13	7F7F141B11	11100	127.000	24.200	1.190
14	7F7F141B39	11100	146.000	31.600	1.020
15	7F7F141C2D	10000	133.000	25.700	1.090



This is the pull-down menu that is displayed when you right-click on the **P-Modeling Button**. Using this menu, you create models of capture probabilities independent of the survival process (see Section 4.4.1).

The menu choices available from this pull-down menu specify elements of models of capture probabilities:

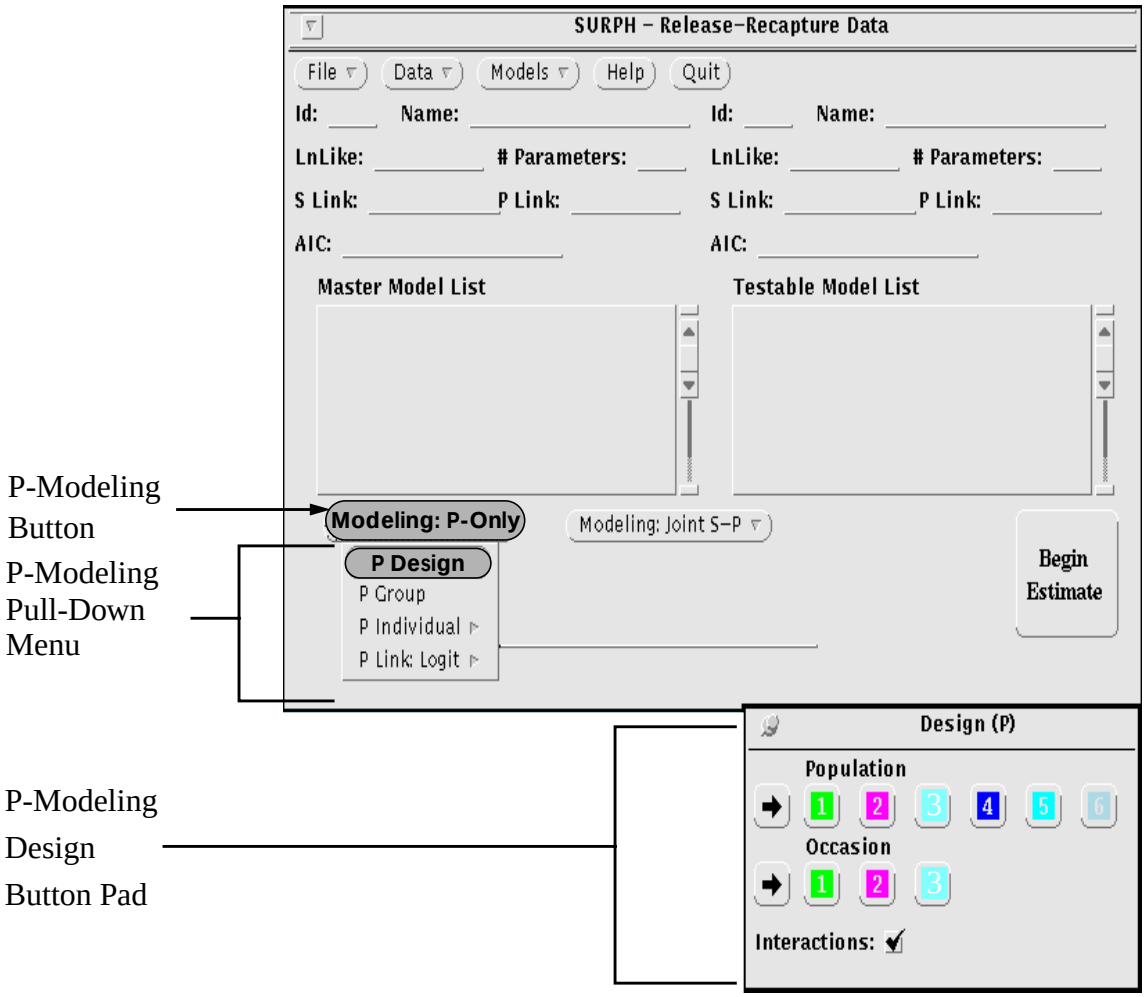
P Design - Specify effects of experimental design factors. A Button Pad will appear that allows you to specify period and population-specific capture parameters (see Capture Modeling: Design Factors).

P Group - Specify group covariate effects. A Button Pad will appear that allows you to specify parameters for period-specific group covariate effects on capture

probabilities
(see Capture Modeling: Group Covariates).

P Individual - Specify individual covariate effects. For each covariate selected, a Button Pad will appear. This Button Pad allows you to specify parameters for period and population-specific effects on capture probabilities (see Capture Modeling: Individual Covariates).

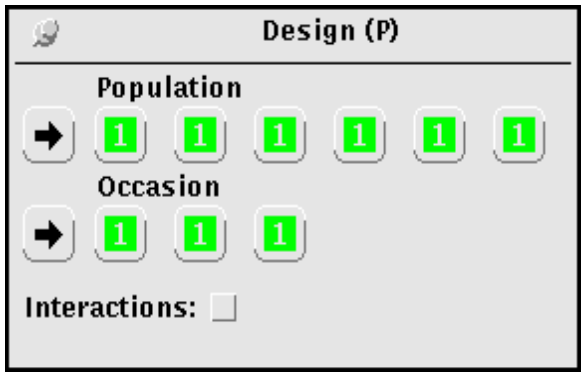
P Link - Specify the function that links covariate effects to capture probabilities. The default link is Logit. Alternatively, the Hazard link function can be specified
(see Capture Modeling: Link Function).



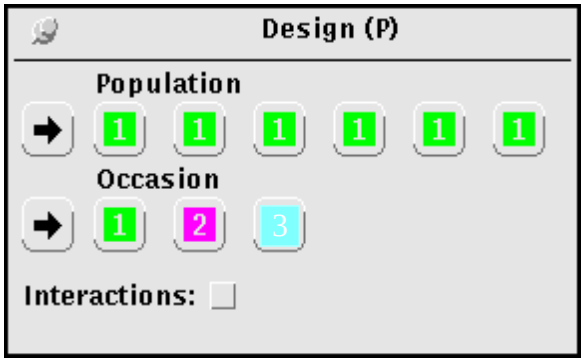
The P-Design Button Pad (**Modeling: P-Only -> P Design** or **Modeling: Joint S-P -> P Design**) allows you to model capture probabilities as a function of the design factors population and occasion. Unique button settings within the population or occasion row indicate unique effects for each population or occasion, whereas duplicated button settings within the population or occasion row indicate a shared parameter. For example, in the Design Button Pad shown above, all occasion and population effects are estimated with unique parameters, for there are unique settings on each button within a row, and there are interactions among the populations and occasion effects. Left-click on the individual buttons or use the Quick Buttons (see Quick Buttons - Instructions) to change button settings.

The example above shows **Model Pst**, with main effects for space (population) and time (occasion) and interactions among all population and occasion effects. Other standard capture models are illustrated under Capture Modeling - Examples .

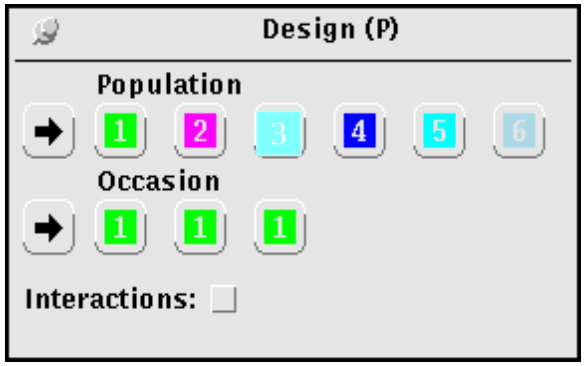
Example of Four Major Design Factor Models



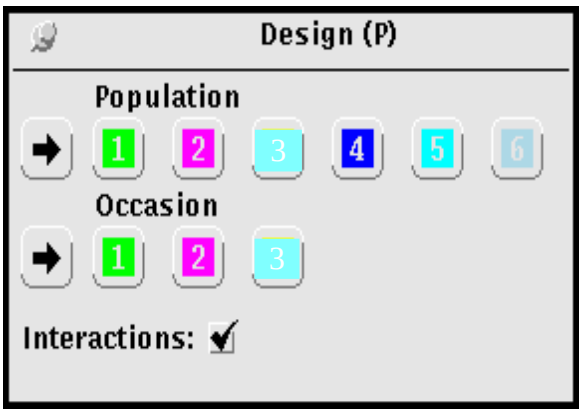
This display illustrates the simplest of the capture models. Only one parameter is estimated; a common capture probability for all populations and on all occasions. This is also known as **Model P**.



This display illustrates **Model Pt**. Under this model, there is a common capture parameter across populations on each sampling occasion, but capture probabilities vary across occasions.



This display illustrates **Model Ps**. Under this model, the capture probability for each population is constant over all occasions, but capture probabilities vary among populations.



The final display illustrates the most general of design factor models. Under **Model Pst**, capture probabilities are unique on each occasion for each population. Note that the interaction checkbox must be checked to fully parameterize this option. If interactions are not checked, the population and occasion effects are additive (a “main effects” model).

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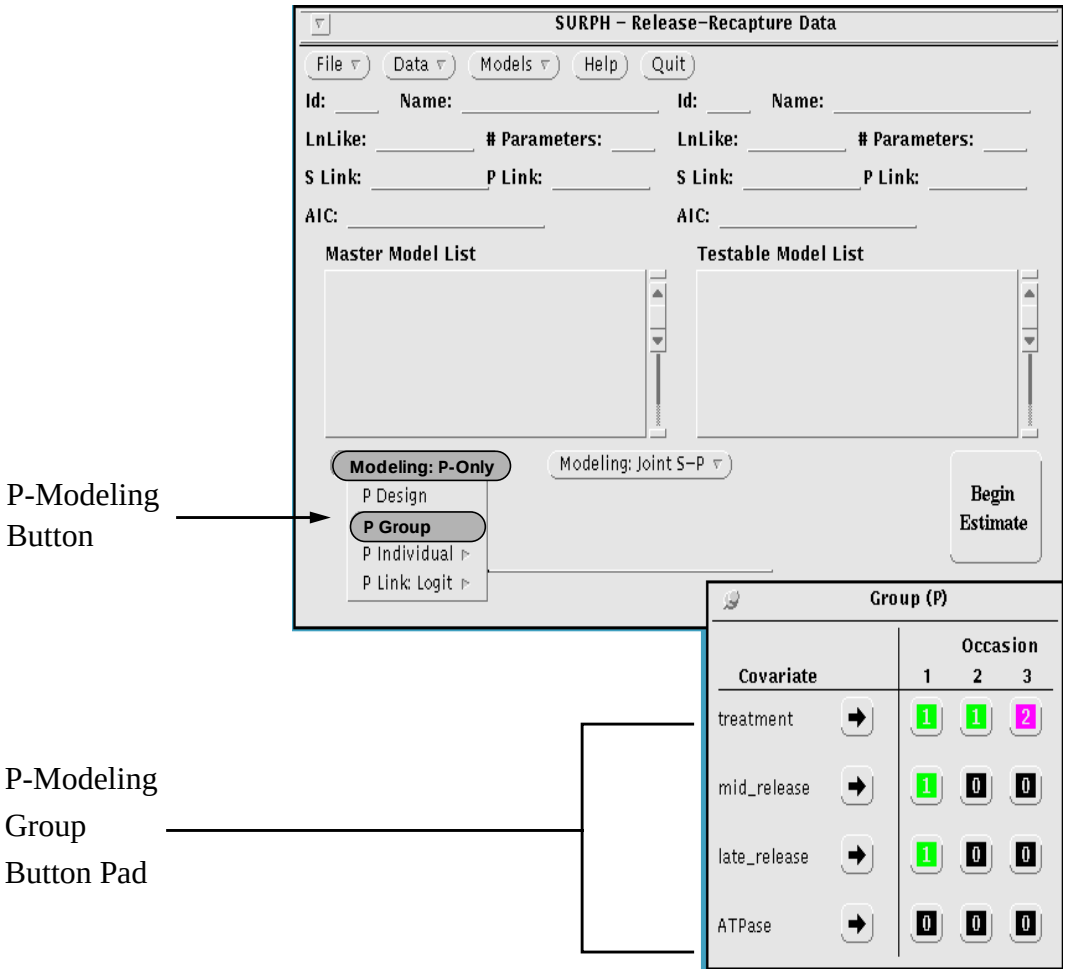
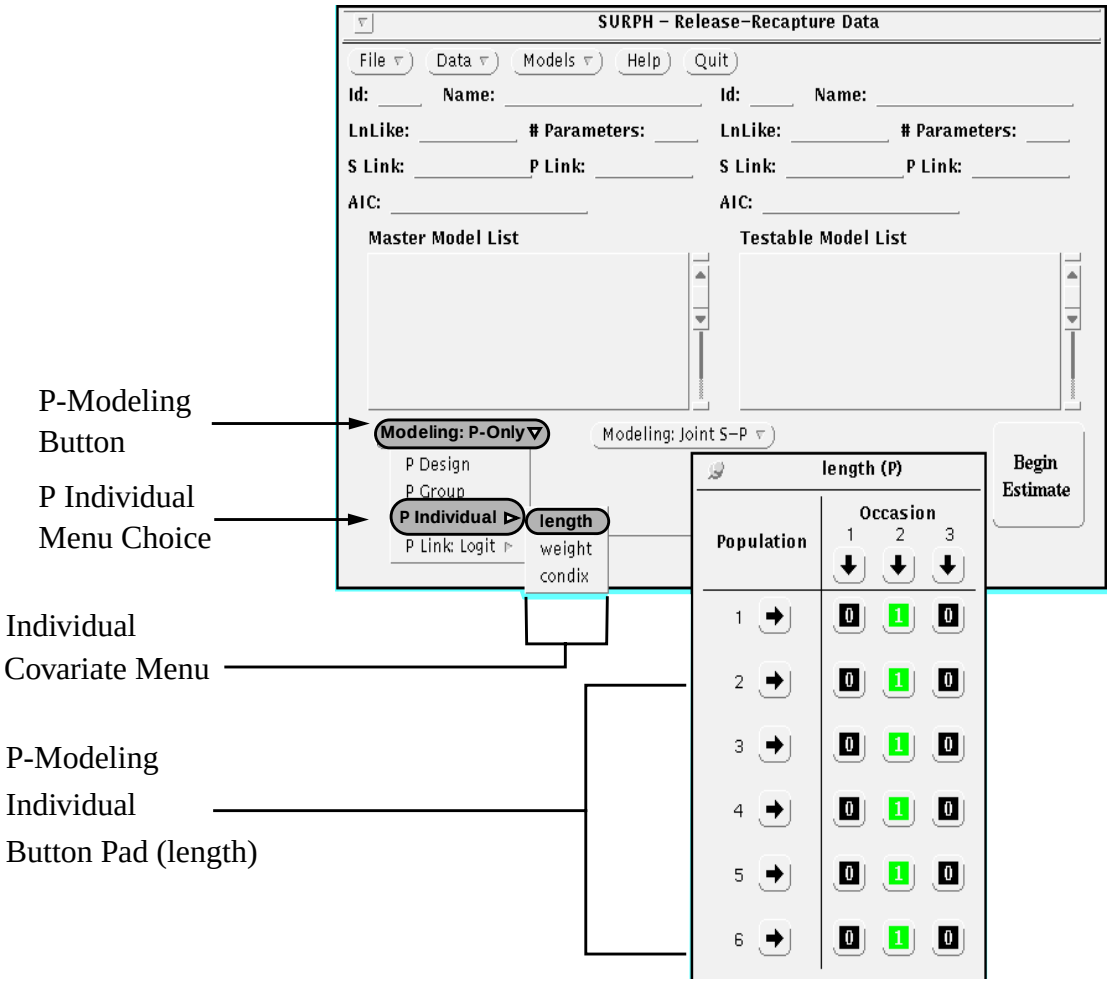


The Group Covariate Button Pad (**Modeling: P-Only -> P Group** or **Modeling: Joint S-P -> P Group**) allows you to model capture probabilities as a function of Group Covariates. You change the parameterization of the capture model by altering the button settings on the Button Pad. A zero indicates that no effect is estimated for that covariate on that occasion, whereas non-zero settings indicate that a parameter is estimated for the effect of that covariate. If the same button setting is used for more than one occasion for a particular covariate, a common parameter is estimated for the effect of the covariate on all occasions sharing the setting. If different button settings are used, separate parameters are estimated. Left-click on the individual buttons or use the Quick Buttons (see Quick Buttons - Instructions) to change button settings.

The model specified above has a common treatment effect on occasions 1 and 2, and a different treatment effect on occasion 3. In addition, there is a mid_release effect on occasion 1, but not on occasions 2 or 3, and a late-release effect on occasion 1, but not on occasions 2 or 3. Note that the treatment, mid_release and late_release settings are independent. The “1” settings for treatment on occasions 1 and 2, the “1” setting for mid-release on occasion 1, and the “1” setting for late_release on occasion 1 do not indicate that the same parameter is used for the three covariates.



The P-Modeling Individual Covariate Button Pad (**Modeling: P-Only -> P Individual** or **Modeling: Joint S-P -> P Individual**) allows you to model capture probabilities as a function of Individual Covariates. You access the **P-Modeling Individual Button Pad** by selecting the covariate of interest from the submenu under **P Individual**. You change the parameterization of the capture model by altering the button settings within the **P-Modeling Individual Button Pad**. A zero indicates that no effect is estimated for the covariate on that occasion for that population, whereas non-zero settings indicate that a parameter is estimated for the effect of the covariate. If the same button setting is used for a particular covariate, a common parameter is estimated for the effect of the covariate for all populations and on all occasions sharing the setting. If different button settings are used, separate parameters are estimated. Left-click on the individual buttons or use the Quick Buttons

(see Quick Buttons - Instructions) to change button settings.

The current example shows a capture model with a common length covariate effect for all populations on occasion 2 (all “1’s”), and no length effects on other occasions (all “0’s”).

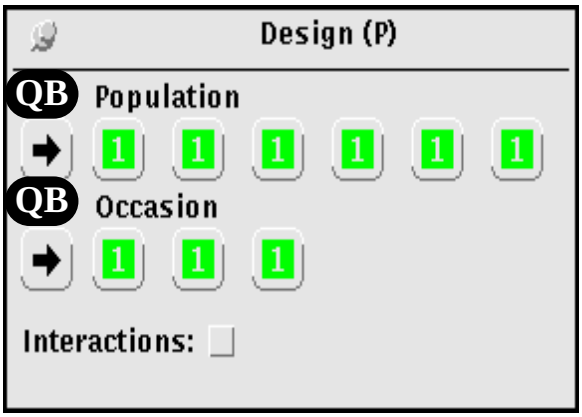
Illustration of Quick Button Use for Design Factors

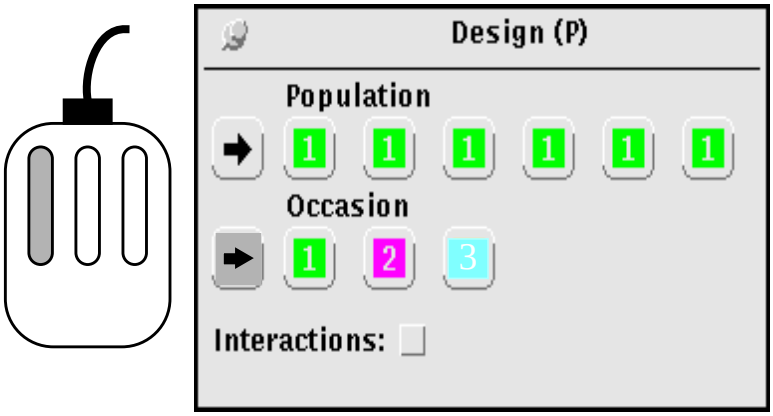
The quick buttons (arrow keys labelled QB in the diagram) allow you to change the parameters in the model (button settings) quickly. The use of quick buttons (QB) for Design Factor Button Pads is illustrated below. The use of quick buttons for all other Button Pads is illustrated on the following page.

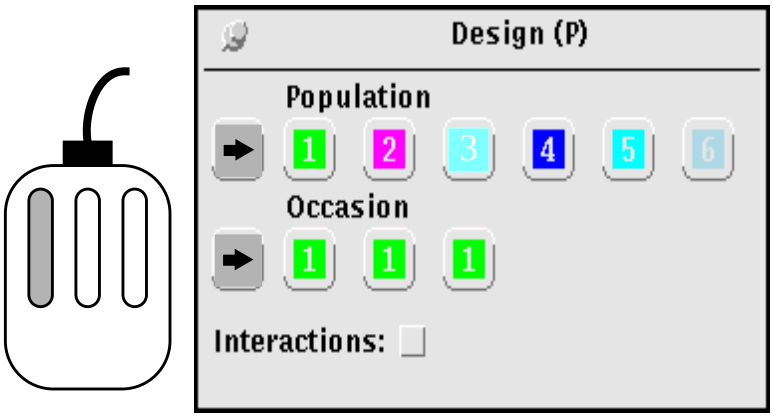
Left-clicking on the Quick Button alternates between a single parameter for all buttons in the row, and a distinct parameter for each button.

Hence, to go from the first illustrated setting to the second, left-click on the QB for Occasions. Note, the display changes from “111” to “123”.

Similarly, to go from the second to the third illustrated setting, left-click on the QB for Populations, and then left-click on the QB for Occasions. This changes the Population row from “1111” to “123456”, and changes the Occasion row from “123” to “111”.







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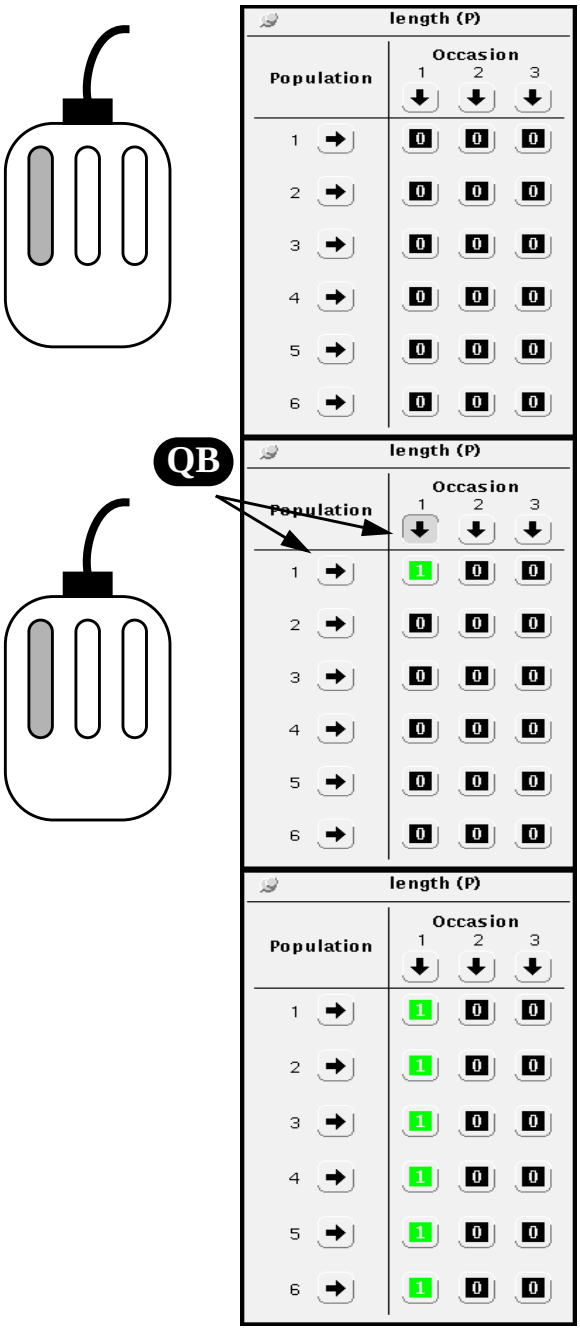
Illustrations of Quick Button Use for Group and Individual Covariate Modeling

The quick buttons (QB) for the group and individual covariate modeling respond slightly differently than the quick buttons for the Design Factors (see previous page). The quick button for individual covariates copies the parameter designation on the first button in the row or column to all buttons within that row or column.

In the example, the first model has no individual parameters fit in the capture model (all buttons set to “0”). Left-clicking on the button in the first row-first column changes that button from a “0” to a “1”. Left-clicking on the “Occasion” quick button in column 1 copies the “1” in the first row-first column throughout the entire first column. You can copy a setting across rows similarly.



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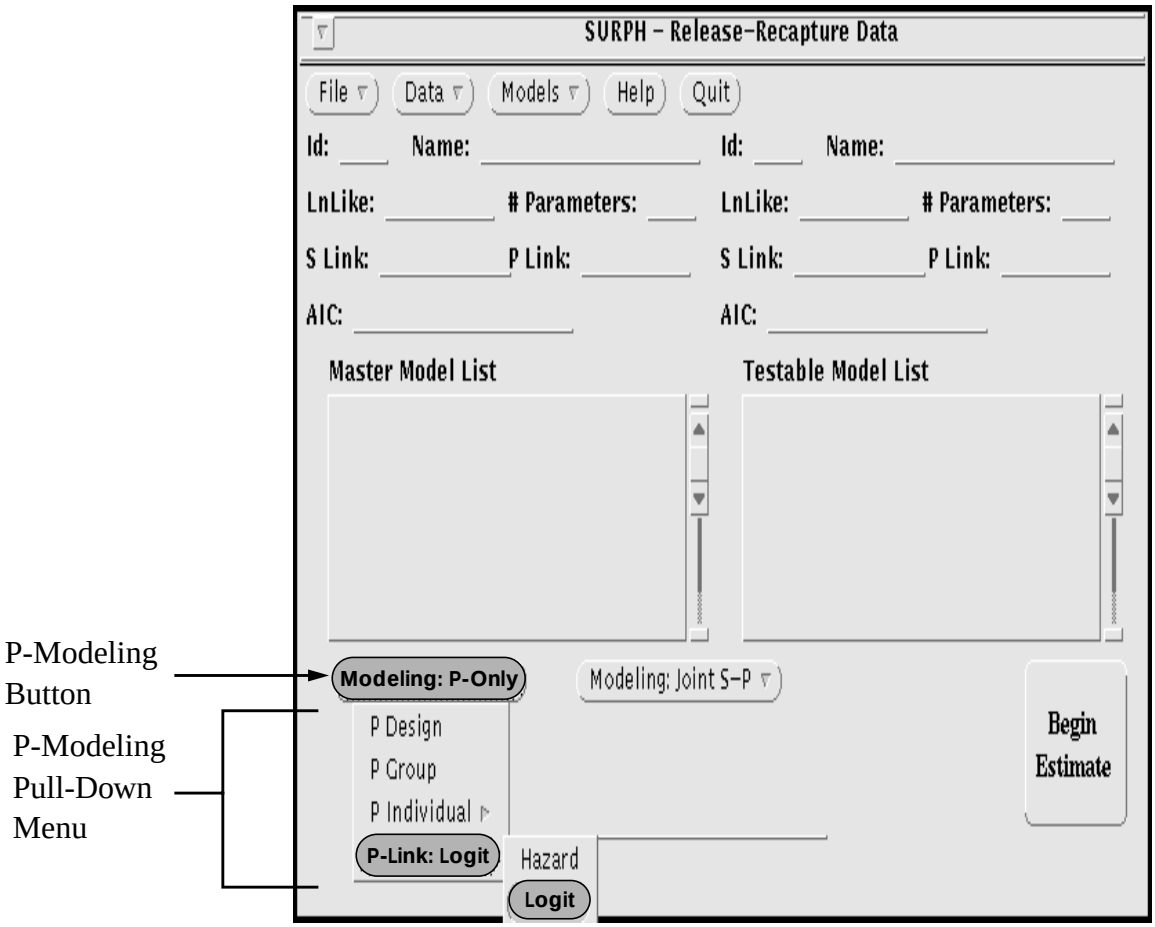

The P-Modeling Link Function (**Modeling: P-Only -> P-Link** or **Modeling: Joint S-P -> P-Link**) allows you to specify whether effects on the capture will be linked to capture probabilities using a Hazard Function link or a Logit Function link. The default link for capture modeling is Logit.

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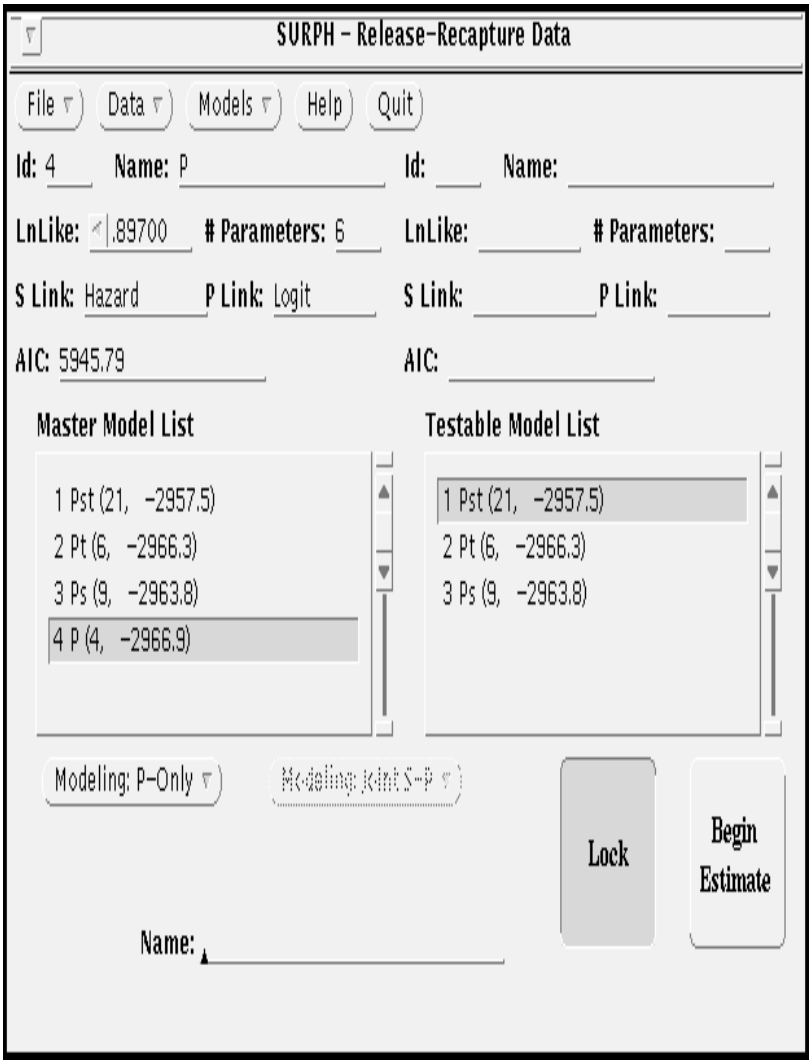

This graphic shows the typical appearance of the SURPH Base Window after you estimate a series of models for capture probabilities under **Modeling: P-Only**. After a series of capture models is estimated, you have the opportunity to choose which capture model will be retained for the survival modeling portion of the data analysis. The capture model that is chosen is then “locked”. Once the capture model has been locked (left-click on the **Lock Button**), you cannot change the model for capture probabilities during subsequent survival analysis.

In the above example, capture model “P” is selected in the Master Model List. Left-click on the **Lock Button** to specify the “P” model for capture probabilities. All subsequent models of survival specified under the Modeling: Joint S-P Button will have the “P” model specified for capture probabilities.

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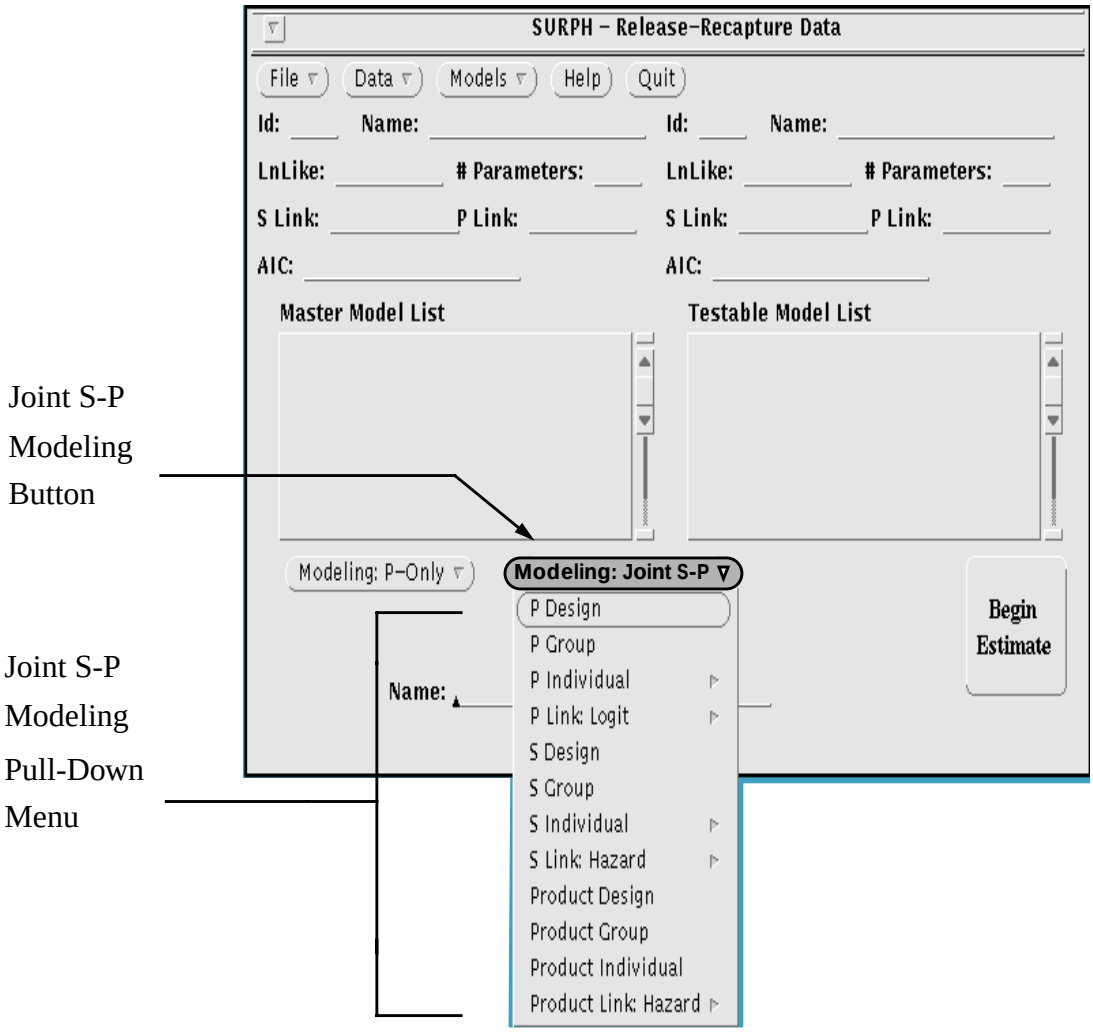

This is the pull-down menu displayed when you right-click on the **Modeling: Joint S-P Button**. Using this menu, you create models of capture and survival jointly (see Section 4.4.3).

The commands available from this pull-down menu specify models for capture and survival probabilities:

P Design - Specify effects of the experimental design factors on capture probabilities. A Button Pad will appear that allows you to specify occasion and population-specific effects (see Capture Modeling: Design Factors).

P Group - Specify group covariate effects on capture probabilities. A Button Pad will appear that allows you to specify parameters for occasion-specific group covariate effects
(see Capture Modeling: Group Covariates).

P Individual - Specify individual covariate effects on capture probabilities. For each covariate selected, a Button Pad will appear. This Button Pad allows you to specify parameters for occasion and population-specific effects
(see Capture Modeling: Individual Covariates).

P Link - Specify the function that links covariate effects to capture probabilities. The default link is Logit. Alternatively, the Hazard link function can be specified
(see Capture Modeling: Link Function).

S Design - Specify effects of the experimental design factors on survival probabilities. A Button Pad will appear that allows you to specify period and population-specific effects on survival probabilities
(see Survival Modeling: Design Factors).

S Group - Specify group covariate effects on survival probabilities. A Button Pad will appear that allows you to specify parameters for period-specific group covariate effects
(see Survival Modeling: Group Covariates).

S Individual - Specify individual covariate effects on survival probabilities. For each covariate selected, a Button Pad will appear. This Button Pad allows you to specify parameters for period and

population-specific effects
(see Survival Modeling: Individual Covariates).

S Link - Specify the function that links covariate effects to survival probabilities. The default link is Hazard. Alternatively, the Logit link function can be specified
(see Survival Modeling: Link Function).

Product Design - Specify effects of the experimental design factors on the final period capture-survival probabilities. A Button Pad will appear that allows you to specify population effects
(see Product Modeling: Design Factors).

Product Group - Specify group covariate effects on the final period capture-survival probabilities. A Button Pad will appear that allows you to specify parameters for group covariate effects
(see Product Modeling: Group Covariates).

Product Individual - Specify individual covariate effects on the final period capture-survival probabilities. A single Button Pad will appear that includes all individual covariates. This Button Pad allows you to specify population-specific effects
(see Survival Modeling: Individual Covariates).

Product Link - Specify the function that links covariate effects to the final period capture-survival probabilities. The default link is Hazard. Alternatively, the Logit link function can be specified
(see Product Modeling: Link Function).

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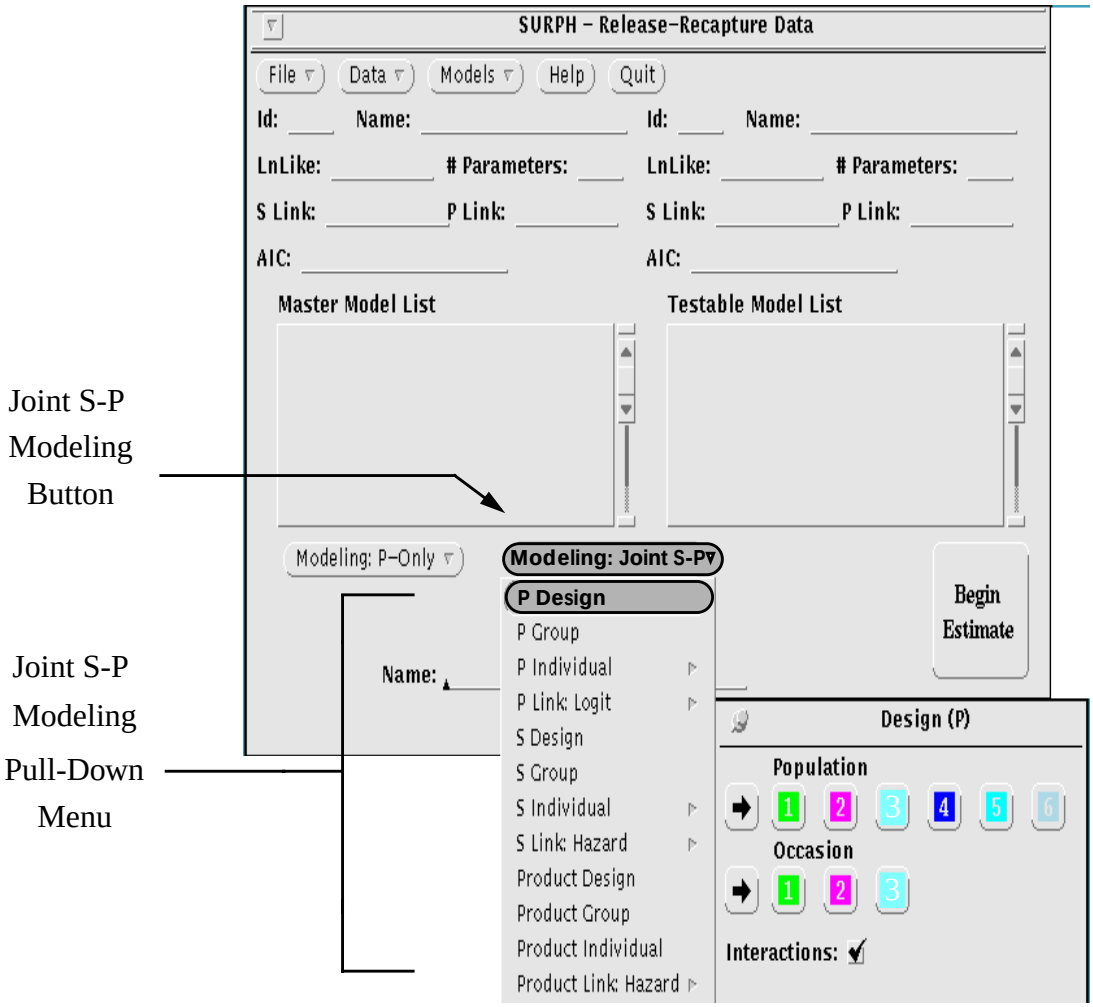


This Button Pad (**Modeling: Joint S-P -> P Design**) allows you to model capture probabilities as a function of the experimental design factors for Population and Occasion. This function is fully described under Capture Modeling: Design Factors.

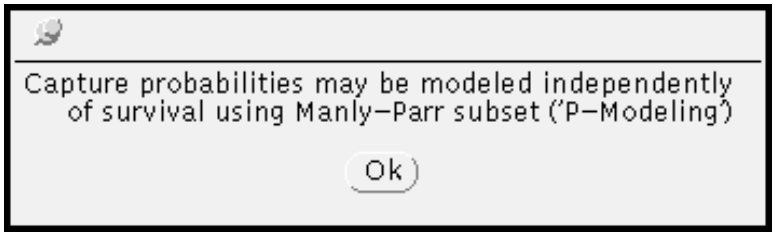
The current example shows **Model Pst**, with main effects for space (population) and time (occasion), and interactions among all population and occasion effects. Other standard capture models are illustrated under

Capture Modeling - Examples.

There is a subtle difference between modeling the capture process using the **Modeling: Joint S-P Button**, rather than the **Modeling: P-Only Button**. Under the **Modeling: P-Only Button**, an extension of the Manly-Parr (1968) model is used to model the capture process. Only a subset of the data is used
(see Data Summary: Manly-Parr).

Under P-Only modeling, the models for the capture probabilities are independent of the survival process, and no survival model is implied during the capture modeling (see Section 4.4.1). Under the **Modeling: Joint S-P Button**, however, capture and survival are modelled jointly. Thus the capture probabilities are not independent of the survival process.

Conclusions regarding the capture model might depend on the jointly-defined survival model. Simulation studies have shown that if **Model Sst** is used for survival probabilities (unique parameters for all period and population main effects and interactions) conclusions regarding the capture model will generally be identical whether **P-Only** or **Joint S-P** modeling is used.



This pop-up message informs you that there are two separate ways to approach modeling the capture histories (see Joint Modeling: Capture Design Factors).

The pop-up message appears when you select a capture modeling option from the **Modeling: Joint S-P** menu before selecting any survival modeling option. The message is a reminder that the capture probabilities can be modeled independently.

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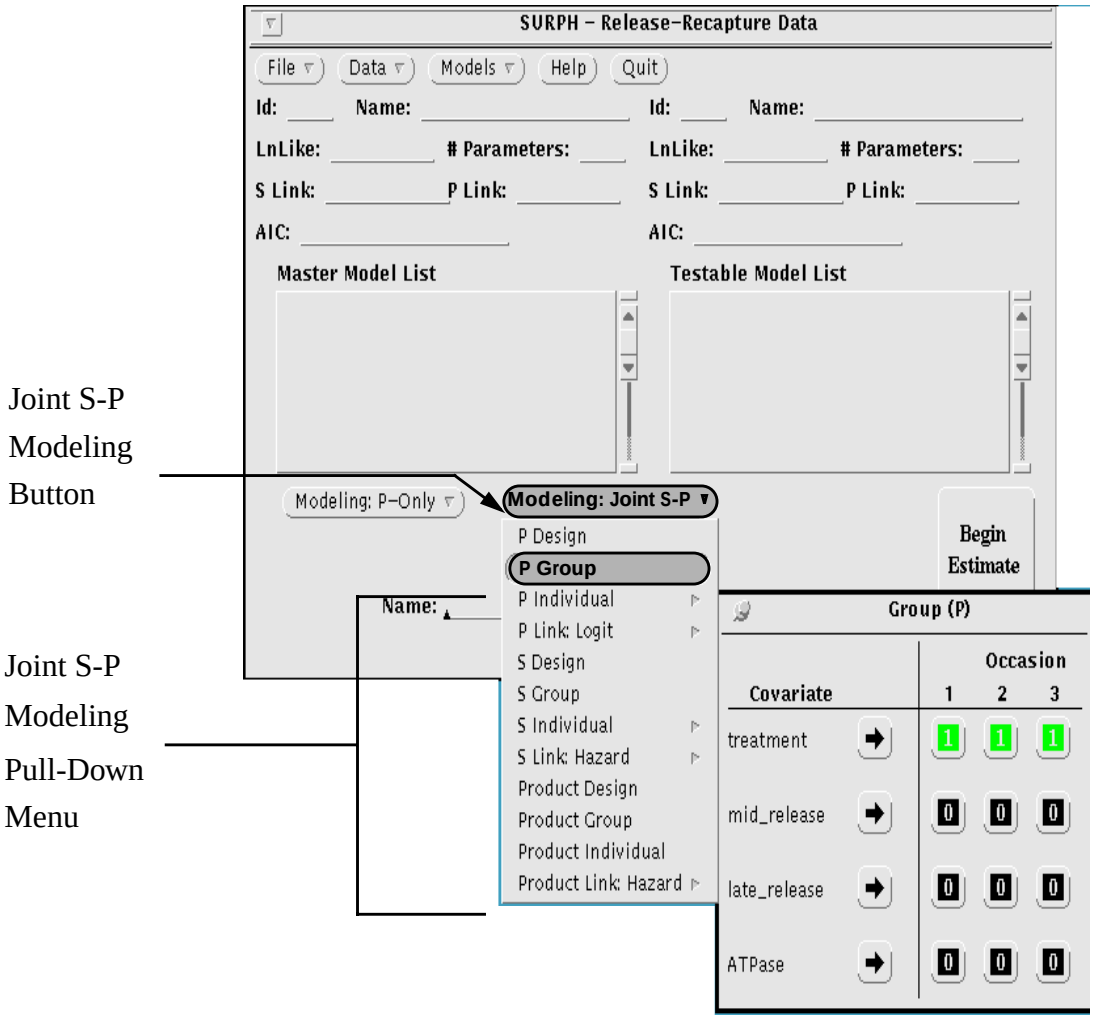

The P-Modeling Group Covariate Button Pad (**Modeling: Joint S-P -> P Group** or **Modeling: P-Only -> P Group**) allows you to model capture probabilities as a function of Group Covariates. This function is fully described under

Capture Modeling: Group Covariates .

The current example shows a capture model with a common treatment covariate effect throughout all occasions (all “1’s” in the upper row), and no other group covariate effects (all “0’s” elsewhere).

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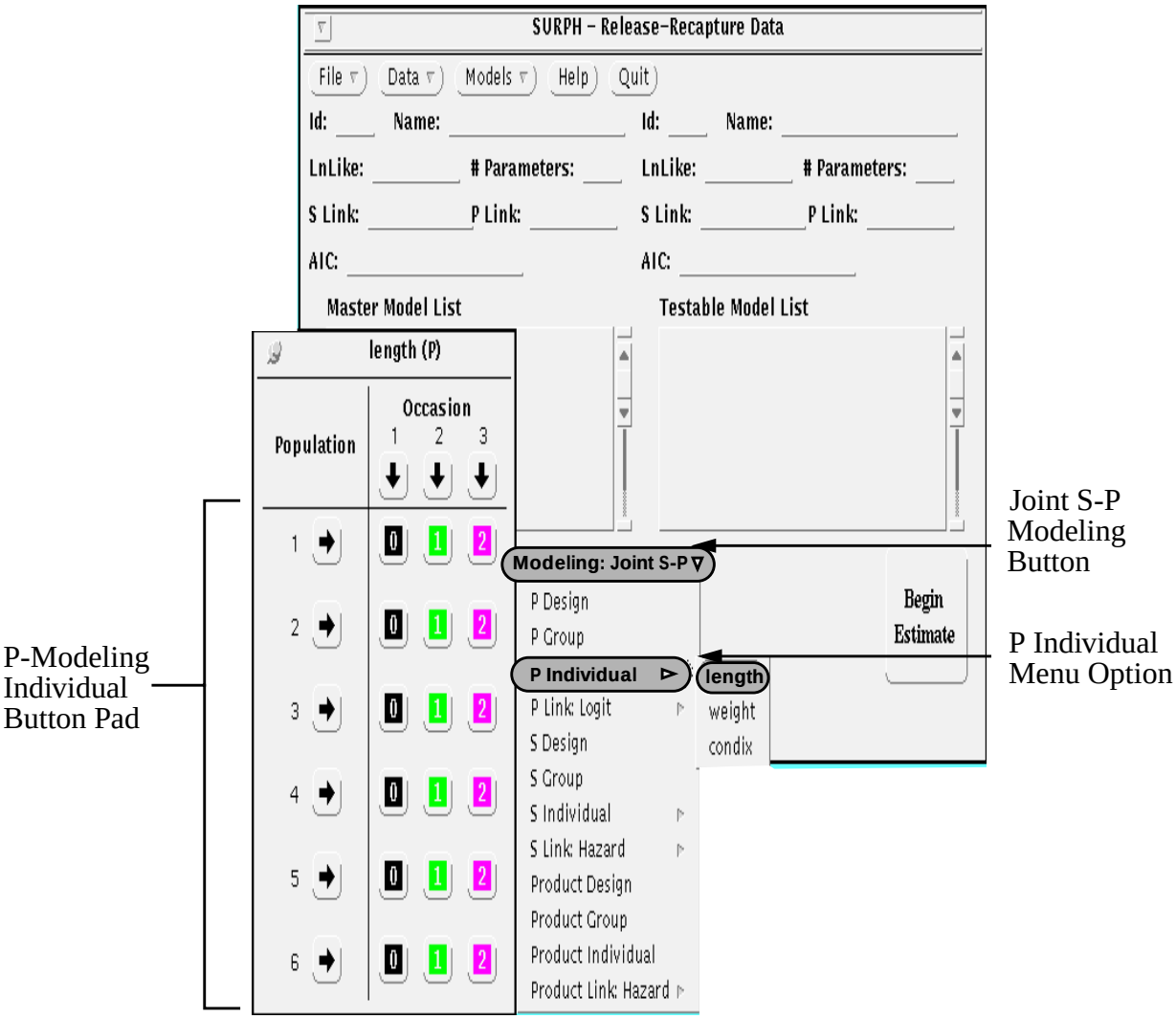

The P-Modeling Individual Covariate Button Pad (**Modeling: Joint S-P -> P Individual** or **Modeling: P-Only -> P Individual**) allows you to model capture probabilities as a function of Individual Covariates. This function is fully described under Capture Modeling: Individual Covariates .

The current example shows a capture model with no length effects on occasion 1 (all “0’s” in the first column), a common length effect for all populations on occasion 2 (all “1’s” in the second column), and a second common, but different, length effect on occasion 3 (all “2’s in the third column).

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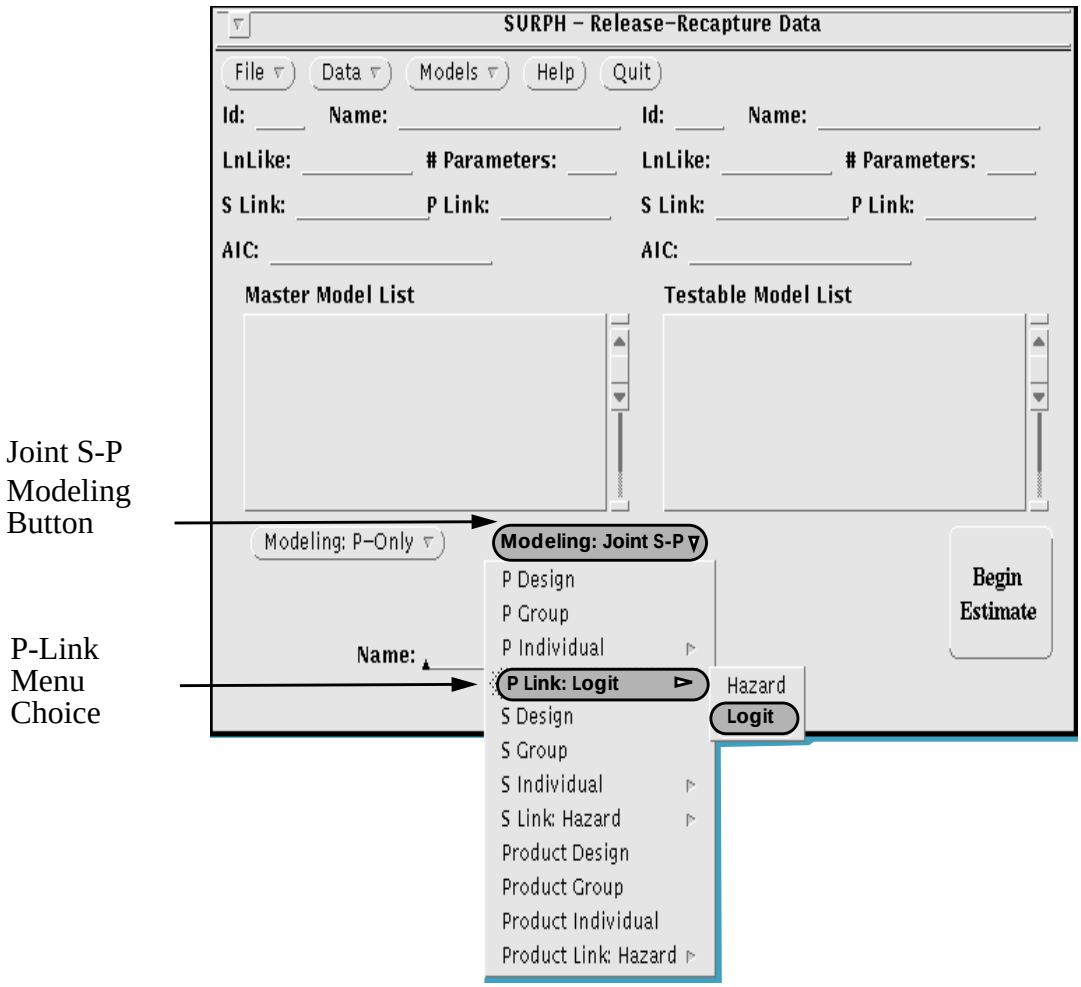

The P-Modeling Link Function (**Modeling: Joint S-P -> P-Link or Modeling: P-Only -> P-link**) allows you to specify whether effects on the capture will be linked to capture probabilities using a Hazard Function link or a Logit Function link. The default link for capture modeling is Logit.

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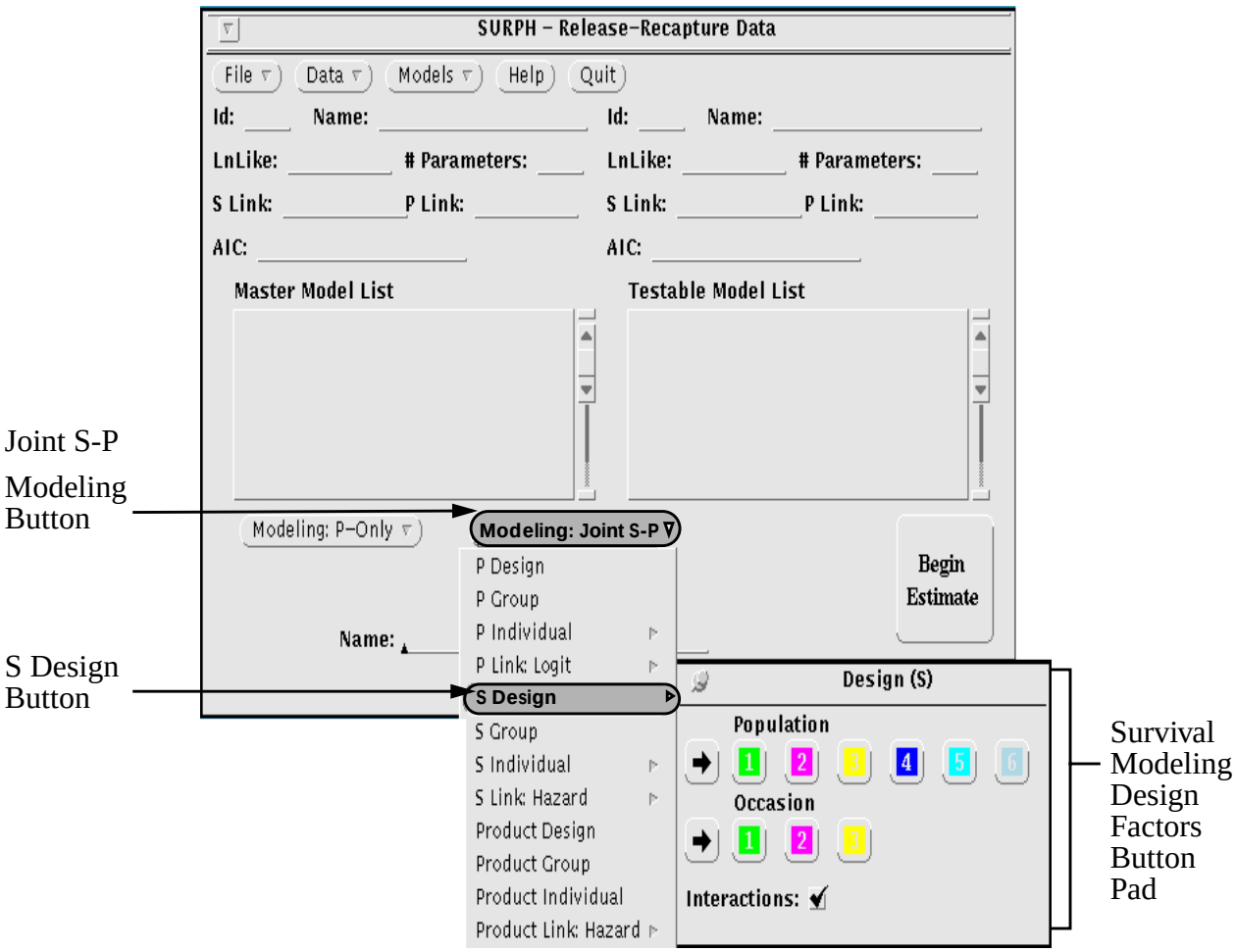

The S-Design Button Pad (**Modeling: Joint S-P -> S Design**) allows you to model survival probabilities as a function of the design factors population and period. Unique button settings within the population or period row indicate unique effects for each population or period, respectively, whereas duplicated button settings within the population or period row indicate shared parameters. In the example above, all population and period main effects and interactions are estimated with unique parameters, for there are unique button settings on each button within a row, and the interaction box has been checked. Left-click on the individual buttons or use the Quick Buttons (see Quick Buttons - Instructions) to change button settings.

The example above shows **Model Sst** for survival probabilities, with main effects for space (population) and time (period) and interactions among all population and period effects. Other standard survival models are illustrated under Survival Modeling - Examples .

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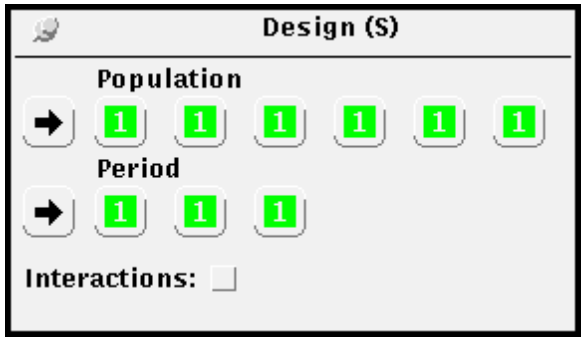
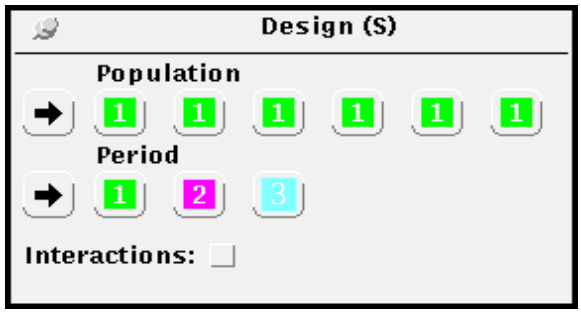
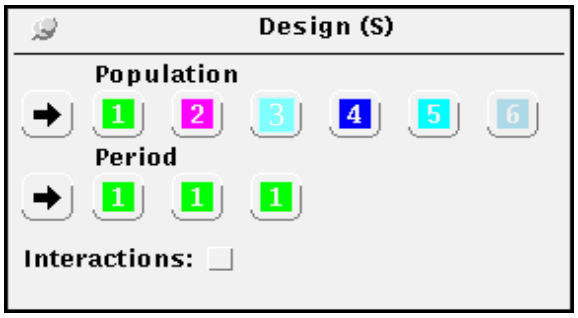
Example of Four Major Design Factor Models



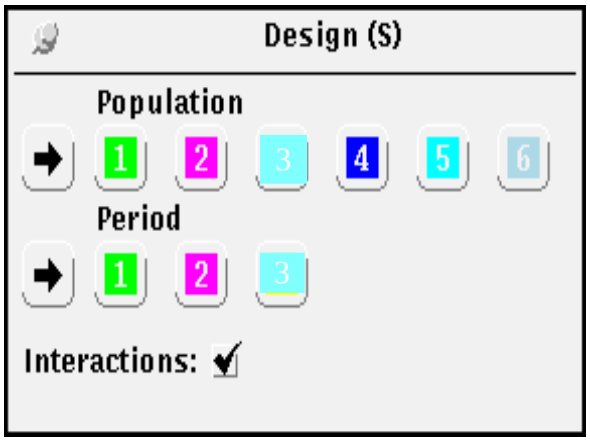
This display illustrates the simplest of the survival models. Only one parameter is estimated; a common survival probability for all populations and in all periods. This is also known as **Model S**.



This display illustrates **Model St**. Under this model, there is a common survival parameter across populations during each sampling period, but survival probabilities differ among periods.



This display illustrates **Model Ss**. Under this model, the survival probability for each population is constant across all periods, but survival probabilities vary among populations.



The final display illustrates the most general of design factor models. Under **Model Sst**, survival probabilities are unique during each period for each population. Note that the interaction checkbox must be checked to fully parameterize this option. If interactions are not checked, the population and period effects are additive (a “main effects” model).

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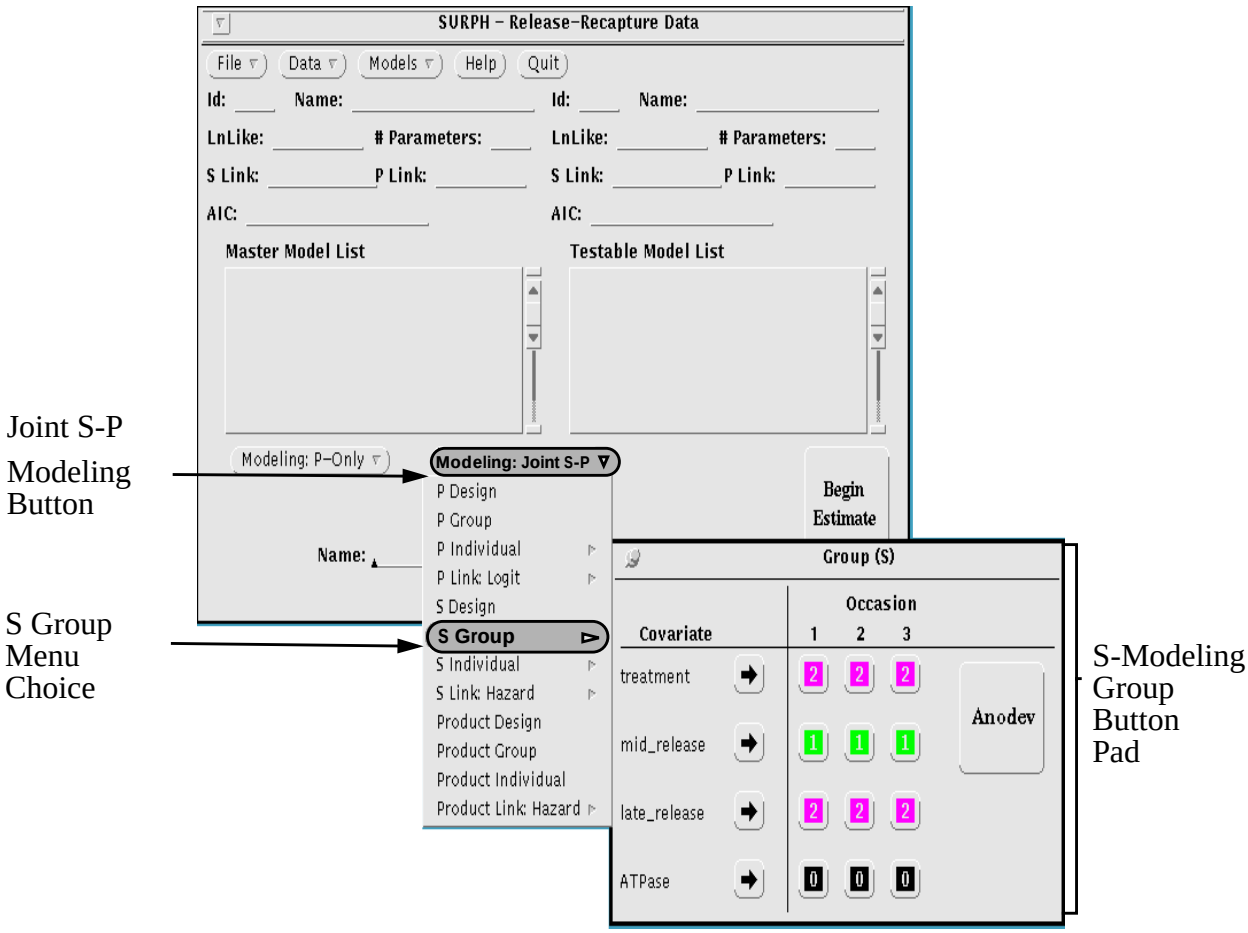
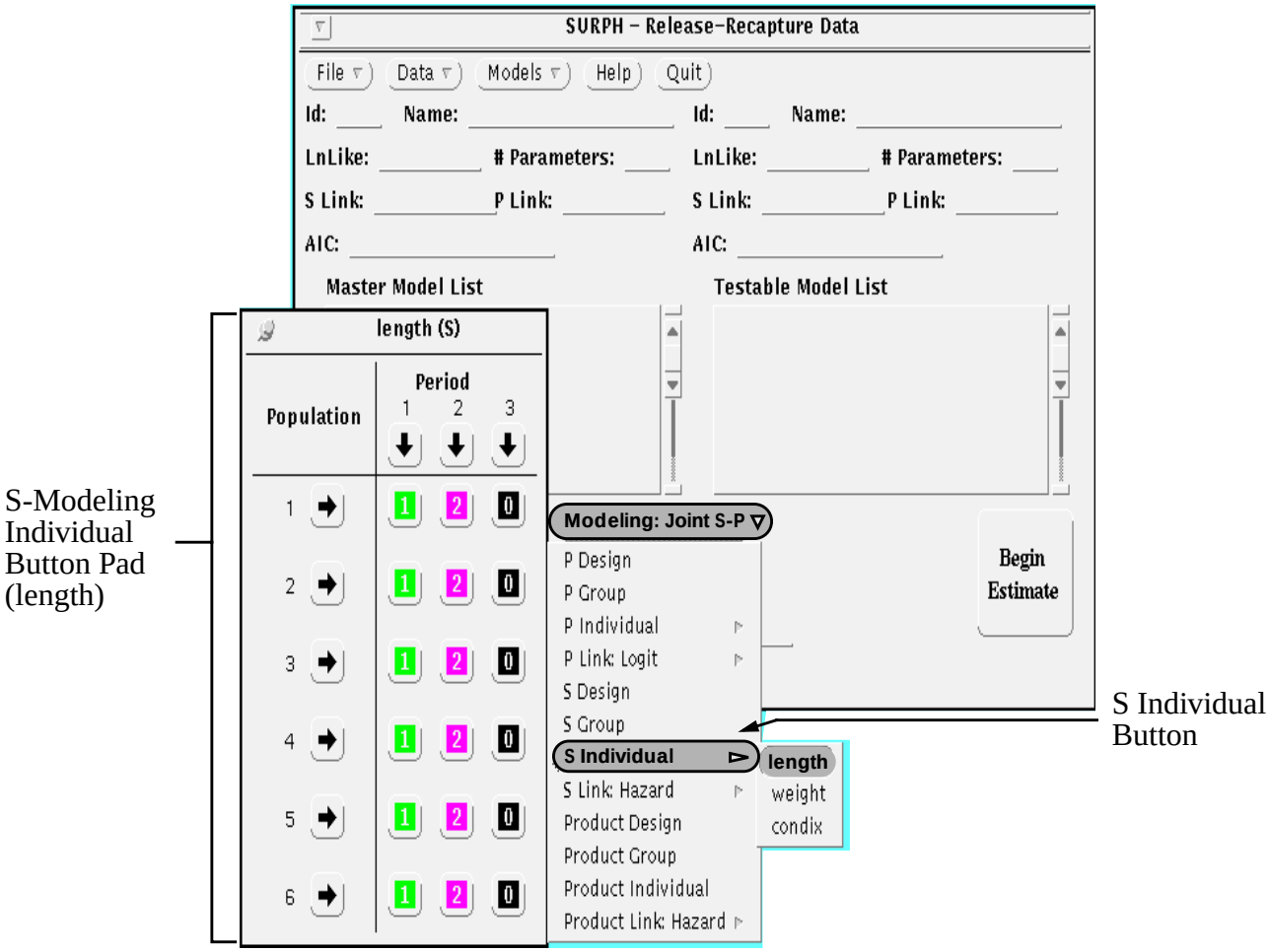


The Survival Modeling Group Covariate Button Pad (**Modeling: Joint S-P -> S Group**) allows you to model survival probabilities as a function of Group Covariates. You change the parameterization of the survival model by altering the button settings on the **S-Modeling Group Covariate Button Pad**. A zero indicates that no effect is estimated for that covariate in that period, whereas non-zero settings indicate that a parameter is estimated for the effect of that covariate. If the same button setting is used for more than one period for a particular covariate, a common parameter is estimated for the effect of the covariate during all periods sharing the setting. If different button settings are used, separate parameters are estimated. Left-click on the individual buttons or use the Quick Buttons (see Quick Buttons - Instructions) to change button settings.

The model specified above has a common treatment effect during all periods (all “2’s” across the treatment row), a common mid_release effect during all periods (all “1’s” across the mid_release row), and a common late_release effect during all periods (all “2’s” across the late_release row). Note that the treatment, mid_release and late_release

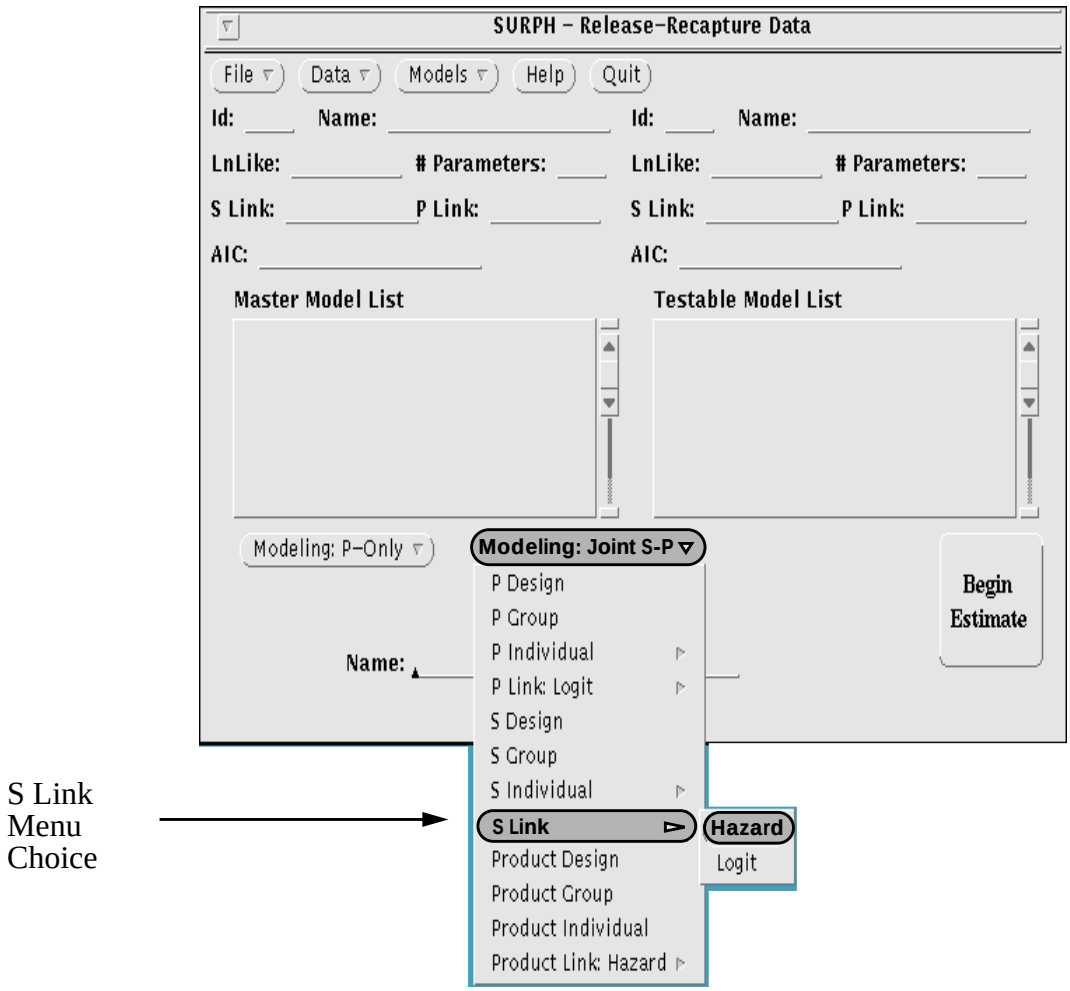
settings are independent. The “2” settings for treatment and the “2” setting for late_release do not indicate that the same parameter is used for both covariates.

Alternatively, you can investigate the effects of Group Covariates using Analysis of Deviance. To use Analysis of Deviance to assess Group Covariate effects, left-click on the **Anodev Button**. For further information on Analysis of Deviance, see ANODEV and all pages associated with Analysis of Deviance.



The Survival Modeling Individual Covariate Button Pad (**Modeling: Joint S-P -> S Individual**) allows you to model survival probabilities as a function of Individual Covariates. You access the **S-Modeling Individual Button Pad** by selecting the covariate of interest from the pull-right menu under **S Individual**. You change the parameterization of the survival model by altering the button settings within the **S-Modeling Individual Button Pad**. A zero indicates that no parameter is estimated for the covariate in that period for that population, whereas non-zero button settings indicate that a parameter is estimated for the covariate. If the same button setting is used for a particular covariate, a common parameter is estimated for all populations and periods sharing that designation. If different button settings are used, separate parameters are estimated. Left-click on the individual buttons or use the Quick Buttons to change button settings (see Quick Buttons - Instructions).

The example above shows a survival model with a common length effect for all populations in the 1st period (all “1’s” in the first column), a different common length effect for all populations in the 2nd period (all “2’s” in the second column), and no length effect elsewhere (all “0’s” in the third column).



The Survival Modeling Link Function (**Modeling: Joint S-P -> S Link**) allows you to specify whether effects on the survival process will be linked to survival probabilities using a Hazard Function link or a Logit Function link. The default link for survival modeling is Hazard.

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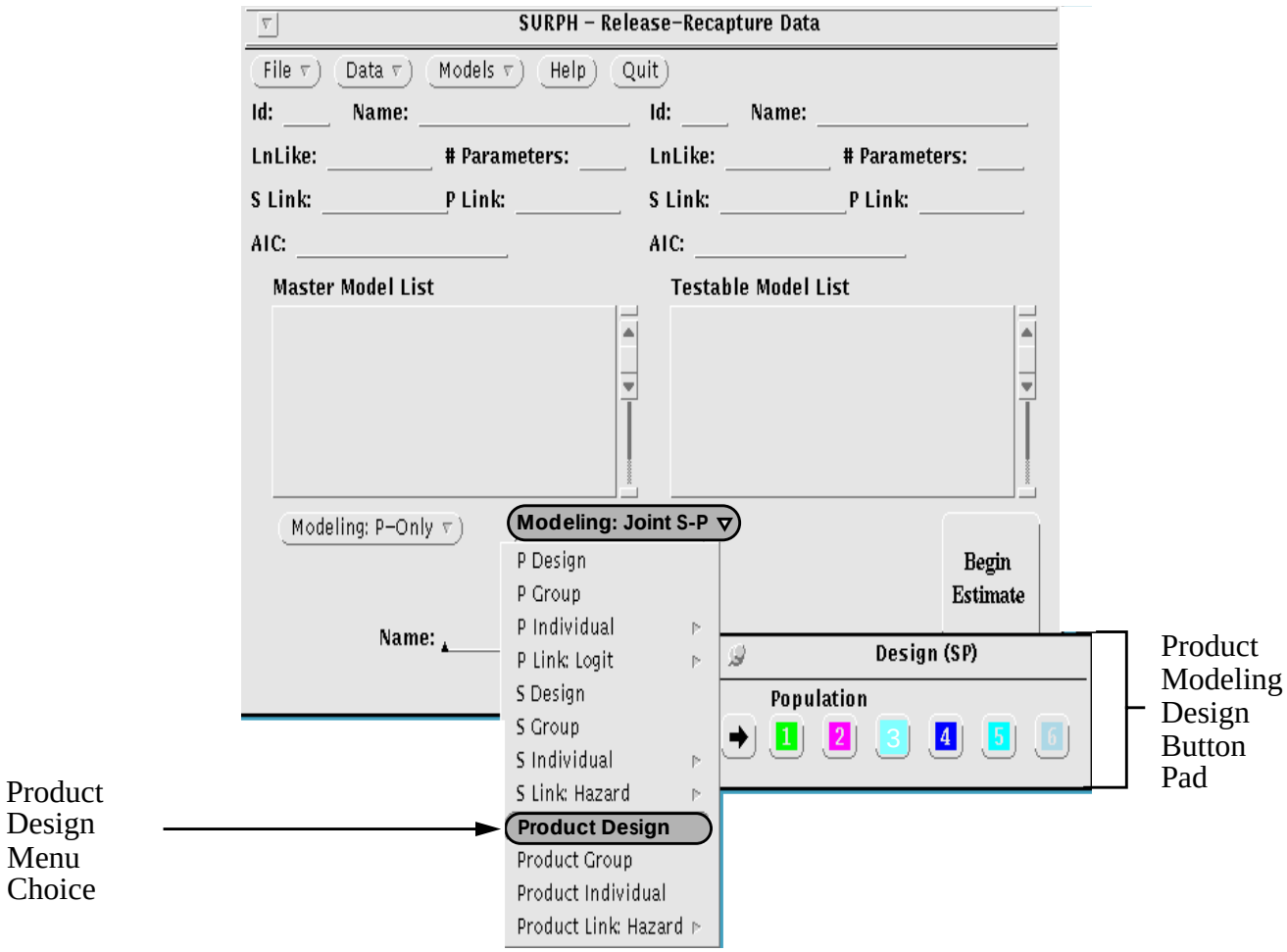

In the final recapture occasion, although it is not possible to separately estimate capture and survival effects, it is possible to estimate effects on the product (Survival x Capture). The Product Design Button Pad (**Modeling: Joint S-P -> Product Design**) allows you to model the final period product as a function of population-specific effects. You change the parameterization of the product model by changing the button settings within the **Product Modeling Design Button Pad**. Unique button settings within the population row indicate unique effects for each population. Duplicated button settings within the population row indicate shared parameters for multiple populations. For the example above, all population effects are estimated with unique parameters, as each button in the **Product Modeling Design Button Pad** is set uniquely.

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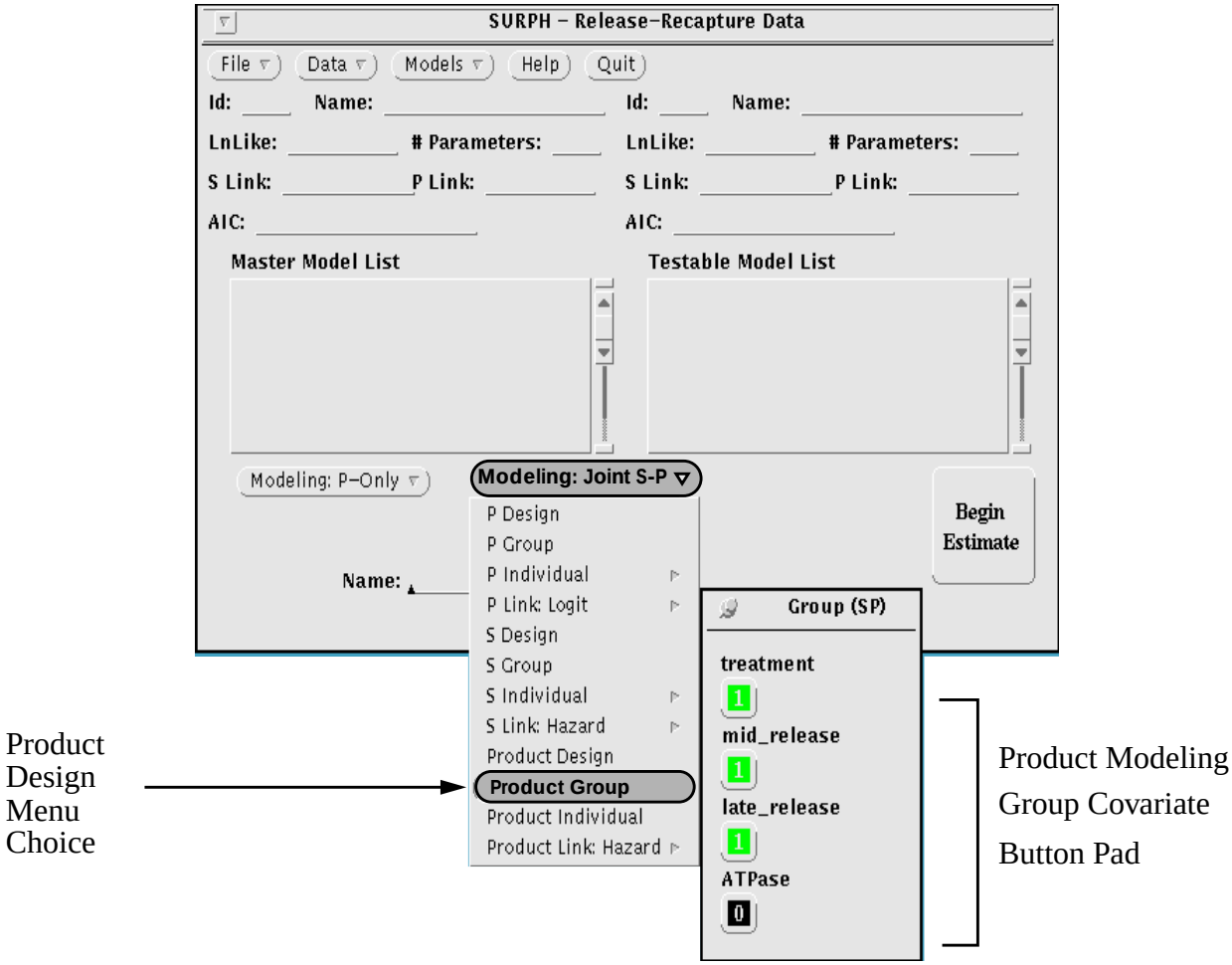

The Product Group Button Pad (**Modeling: Joint S-P -> Product Group**) allows you to model the final period product (Survival x Capture) probabilities as a function of Group Covariates. You change the parameterization of the product model by altering the buttton settings within the **Product Modeling Group Covariate Button Pad**. A zero indicates that no effect is estimated for that covariate, whereas a one indicates that a parameter is estimated for the effect of that covariate. Left-click on the individual buttons or use the Quick Buttons (see Quick Buttons - Instructions) to change button settings.

The model specified above shows a product model with effects of treatment, mid_release, and late_release covariates (a “1” for each covariate). No parameter is estimated for the effect of ATPase (a “0” beneath the ATPase covariate). Note that the treatment, mid_release and late_release settings are independent (i.e. the “1” settings do not indicate that the same parameter is used for all three covariates).

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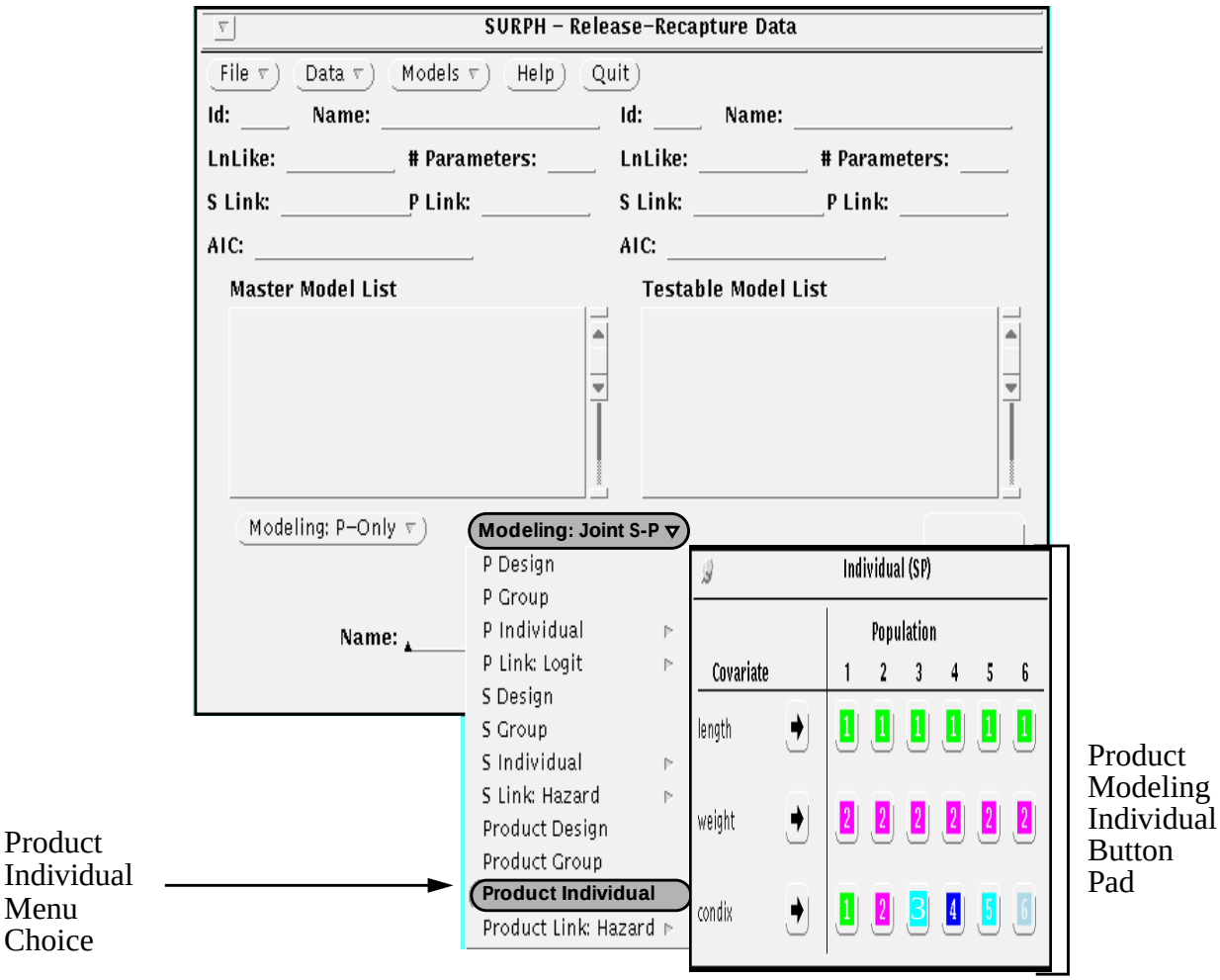
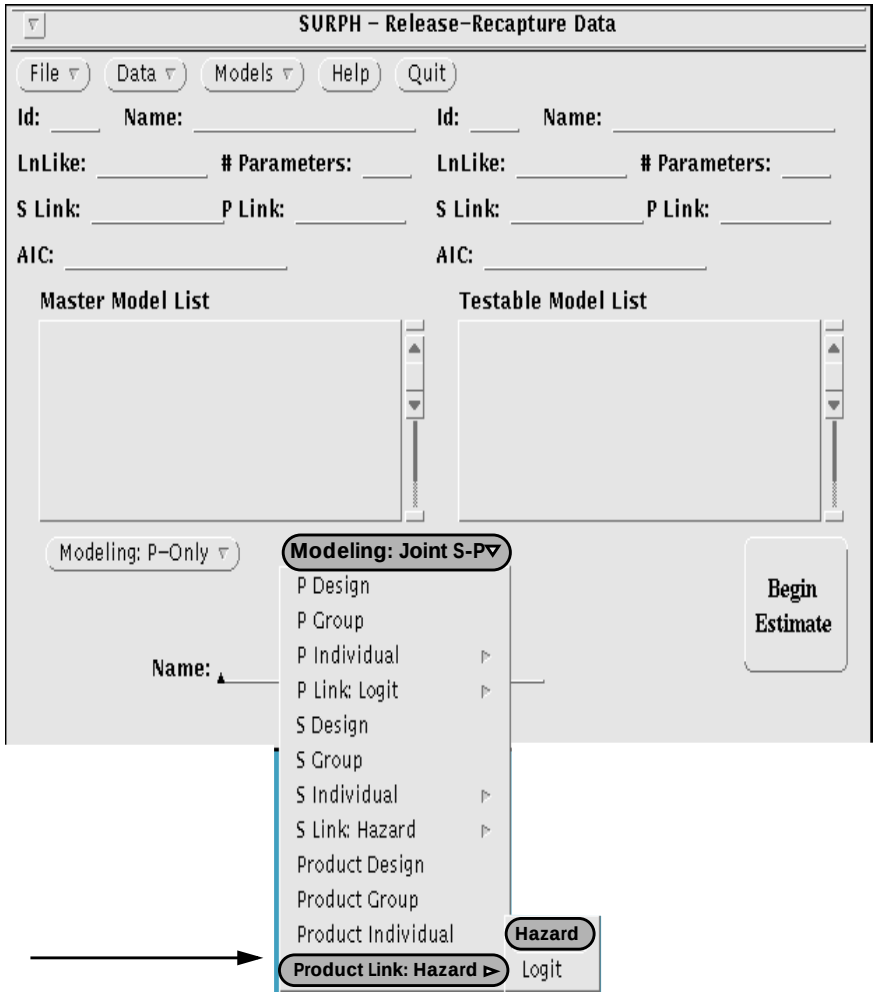


The Product Modeling Individual Covariate Button Pad (**Modeling: Joint S-P -> Product Individual**) allows you to model the final period product (Survival x Capture) probabilities as a function of Individual Covariates. You access the **Product Modeling Individual Button Pad** by left-clicking on the Product Individual Menu Choice. You change the parameterization of the product model by changing the button settings within the **Product Modeling Individual Button Pad**. A zero indicates that no effect is estimated for that covariate, whereas non-zero numbers indicate that a parameter is estimated for the effect of that covariate. If the same button setting is used for a particular covariate, a common parameter is estimated for the effect of the covariate for all populations sharing that setting. If different button settings are used, separate parameters are estimated. Left-click on the individual buttons or use the Quick Buttons to change button settings (see Quick Buttons - Instructions).

The model specified above shows a product model with a common length effect for all populations (all “1’s”), a common weight effect for all populations (all “2’s”), and unique condix (condition index) effects for each population (Button settings are “123456”).

Note that the length, weight and condix settings are independent. Thus, if a common length effect for all populations had been parameterized with all “1’s”, and a common weight effect for all populations had been parameterized with all “1’s”, the model would estimate a common effect for weight, and a separate common effect for length. The model would be no different from the model shown above, where the common length effect for all populations is indicated by all “1’s”, and the common weight effect for all populations is indicated by all “2’s”.



Product Link Menu Choice

The Product Modeling Link Function (**Modeling: Joint S-P -> Product Link**) allows you to specify whether effects on the final period product (Survival x Capture) will be linked to the product probabilities using a Hazard Function link or a Logit Function link. The default link for final product modeling is Hazard.

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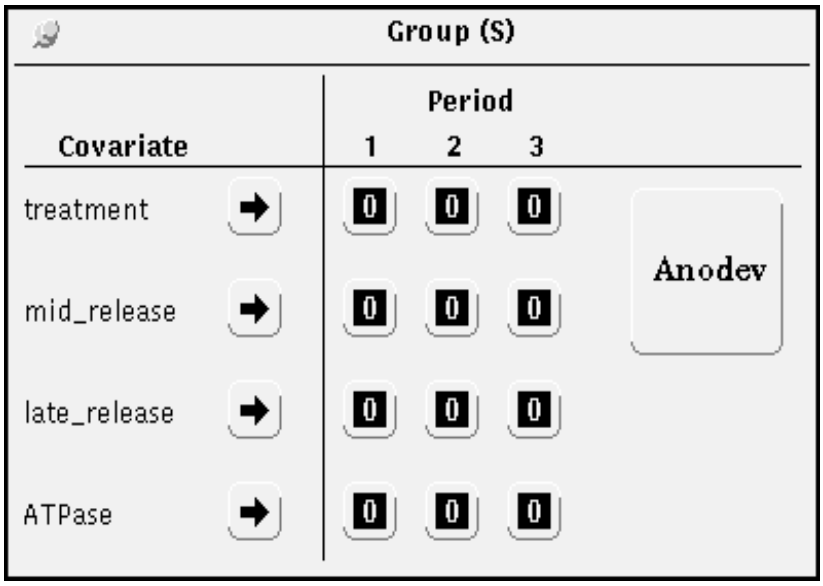

This Button Pad (**Modeling: Joint S-P -> S Group**) allows the user to model group covariate effects on survival. The user can test the significance of the group covariate effects using the likelihood ratio approach (see Section 2.4.1 and Survival Modeling: Group Covariates) or using the Analysis of Deviance approach (see Section 2.4.3). To analyze the data using Analysis of Deviance, left-click on the **Anodev Button**. SURPH will prompt the user to select the group covariates to analyze (see ANODEV Start Up), and will then run three default models required for ANODEV (the Full Model, the Period Means Model, and the Total Model). An Analysis of Deviance Table will appear when all calculations are completed (see all pages associated with Analysis of Deviance).

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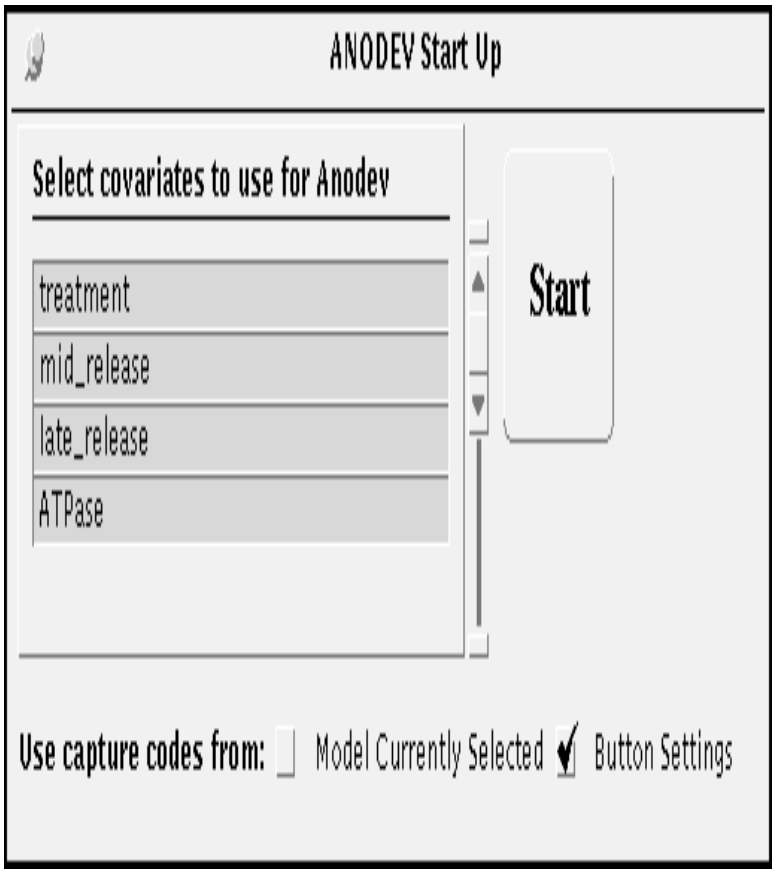
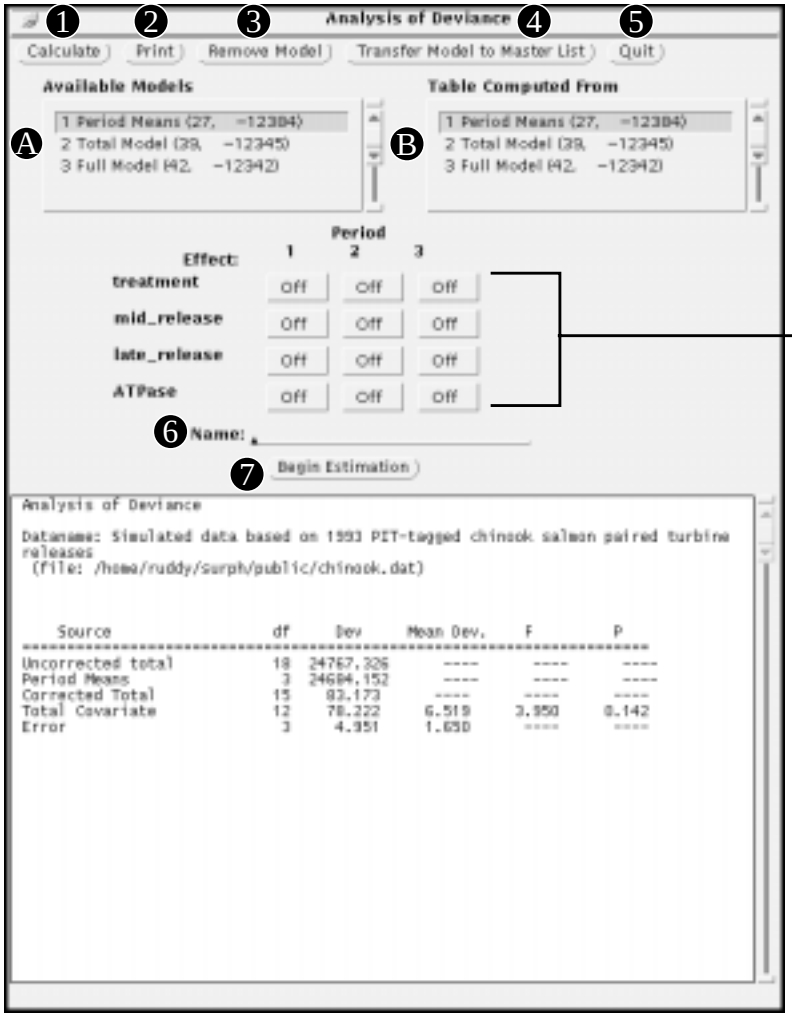


This pop-up window appears after you initiate the Analysis of Deviance option (**Modeling: Joint S-P -> S Group -> Anodev**). You must select the group covariates that will be used during the Analysis of Deviance. You select a group covariate by left-clicking on the group covariate name in the list beneath “Select covariates to use for ANODEV”. Group covariates that have been selected will appear darkened. You remove a group covariate from those that will be used during the Analysis of Deviance by left-clicking on a selected covariate name.

You must also select the capture model that is to be used during the analysis. If the “Model Currently Selected” checkbox is checked, the model for capture probabilities during ANODEV is the same as that in the model currently selected in the Master Model List in the Base Window. If the “Button Settings” checkbox is checked, the capture model is read from the current settings on the Button Pads for capture probabilities.

After selecting the group covariates to analyze, and the model for capture probabilities, left-click on the **Start Button** to initiate Analysis of Deviance. When the start button is pushed, the three "standard models" (Full, Period Means, and Total Covariate Models) are estimated (see Sections 3.5 and 4.5). After the standard models are complete, the Analysis of Deviance Table appears (see Analysis of Deviance Table (A) .



ANODEV Button Pad

This window (**Modeling: Joint S-P -> S Group -> ANODEV**) contains a control panel (top) for guiding Analysis of Deviance and a text pane (bottom) for displaying ANODEV results. The main features of the ANODEV Table are the following:

Ⓐ **Available Models List** - A list of models available for potential use in computing ANODEV Tables. All models in this list have the model for capture probabilities and involve the group covariate effects on survival selected at the ANODEV start-up.

Ⓑ **Table Computed From List** - A list of models that you selected from the **Available Models List** to be used to compute an ANODEV Table. This list always contains the Full, Period Means, and Total Covariate Models. The other models in the list form a hierarchical set that is used to partition the Total Covariate Deviance. A model is added to the **Table Computed From List** by selecting (left-clicking) on the model in the

Available Models List. If the model selected fits in the hierarchy currently defined by the models in the **Table Computed From List**, the model is added to the **Table Computed From List**. If a new hierarchy is desired, models must first be removed from the **Table Computed From List** (see **Remove Model Button**).

❶ **Calculate Button -** Left-click to compute the ANODEV Table from the models currently in the **Table Computed From List**.

❷ **Print Button -** Left-click to send a copy of the current ANODEV Table to the printer.

❸ **Remove Model Button -** Left-click to remove the currently selected model from the **Table Computed From List**. Models must be removed from the **Table Computed From List** if an alternative hierarchy (partition of the Total Deviance) is to be investigated.

❹ **Transfer Model Button -** Left-click to transfer the currently selected model from the **Available Models List** to the **Master Model List** on the **SURPH Base Window**. While they are legitimate SURPH models, the three standard models and any models estimated from the ANODEV Button Pad (see below) are by default not listed on the **Master Model List** on the SURPH Base Window. On the basis of ANODEV results, it is frequently desirable to transfer selected models from the ANODEV **Available Models List** to the **Master Model List**, for functions not available from the ANODEV Table (e.g., display of parameter estimates; residual plots; individual covariate modeling).

❺ **Quit Button -** Left-click to quit Analysis of Deviance. This is the only way to leave ANODEV; the pushpin in the left-hand corner of the ANODEV Table is disabled. You are asked to confirm the intent to quit ANODEV
(see Analysis of Deviance Table (C)).

❻ **Model Name Field -** Left-click on the horizontal line to place the cursor in the field, then type the name for a new model.

❼ **Begin Estimation Button -** Left-click to fit the model currently defined by the ANODEV Button Pad. If the model has already been estimated, a warning appears (see Analysis of Deviance Table (B)). After estimation is complete, the model is added to the Available Models List. If a name for the model is not specified in the **Model Name Field**, the model's name is "Model 'n'", where 'n' is the model number.

ANODEV Button Pad - While performing Analysis of Deviance, new models may be estimated to partition the Total Covariate Deviance into contributions of specific covariates in each period. ANODEV models are specified on the **ANODEV Button Pad** rather than the usual **Survival- Group Covariate Button Pad**. The **ANODEV Button Pad** functions similar to the **Group Covariate Button Pad**, except that it is not possible to define equalities among parameters across periods.

ANODEV Text Pane - Displays the results of Analysis of Deviance. The Dataname and file from which the data were read are listed at the top of the pane, followed by the Analysis of Deviance table, based on the models in the current **Table Computed From List** (see Section 4.5 for a full explanation of the ANODEV Table). When the ANODEV Table first appears, the displayed ANODEV Table is computed from the Full, Period Means, and Total Covariate Models (i.e., the Total Covariate Deviance is displayed, but it is not partitioned in any way).

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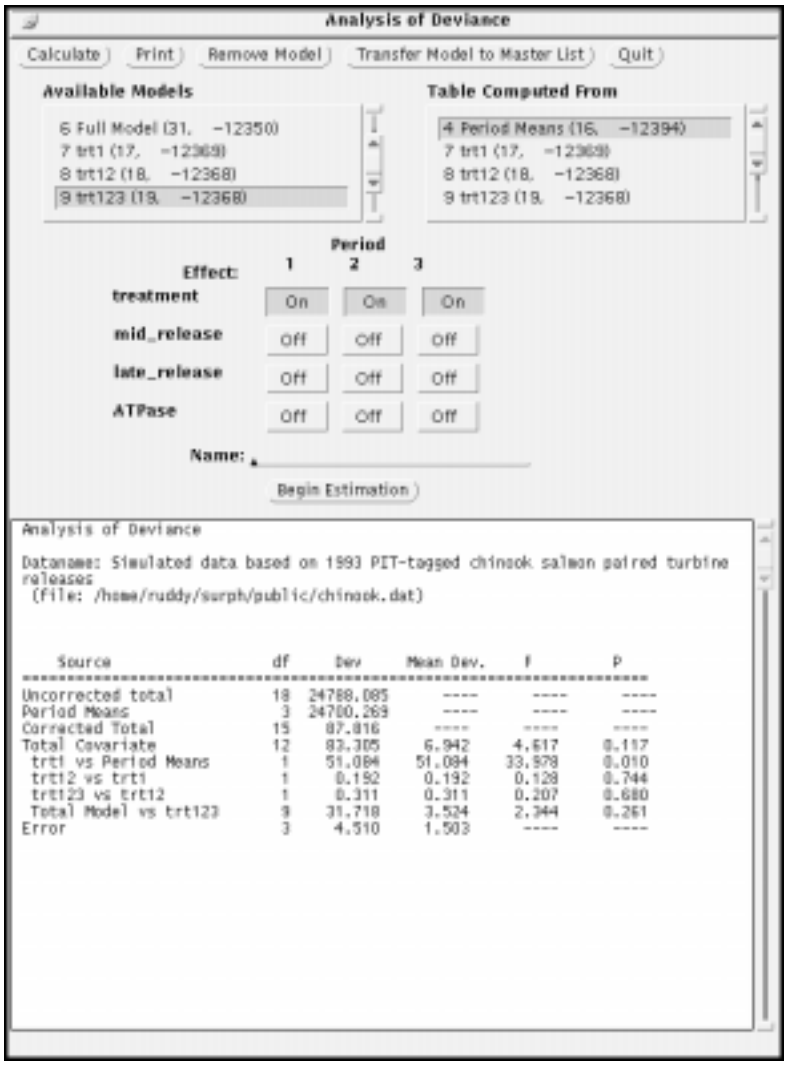
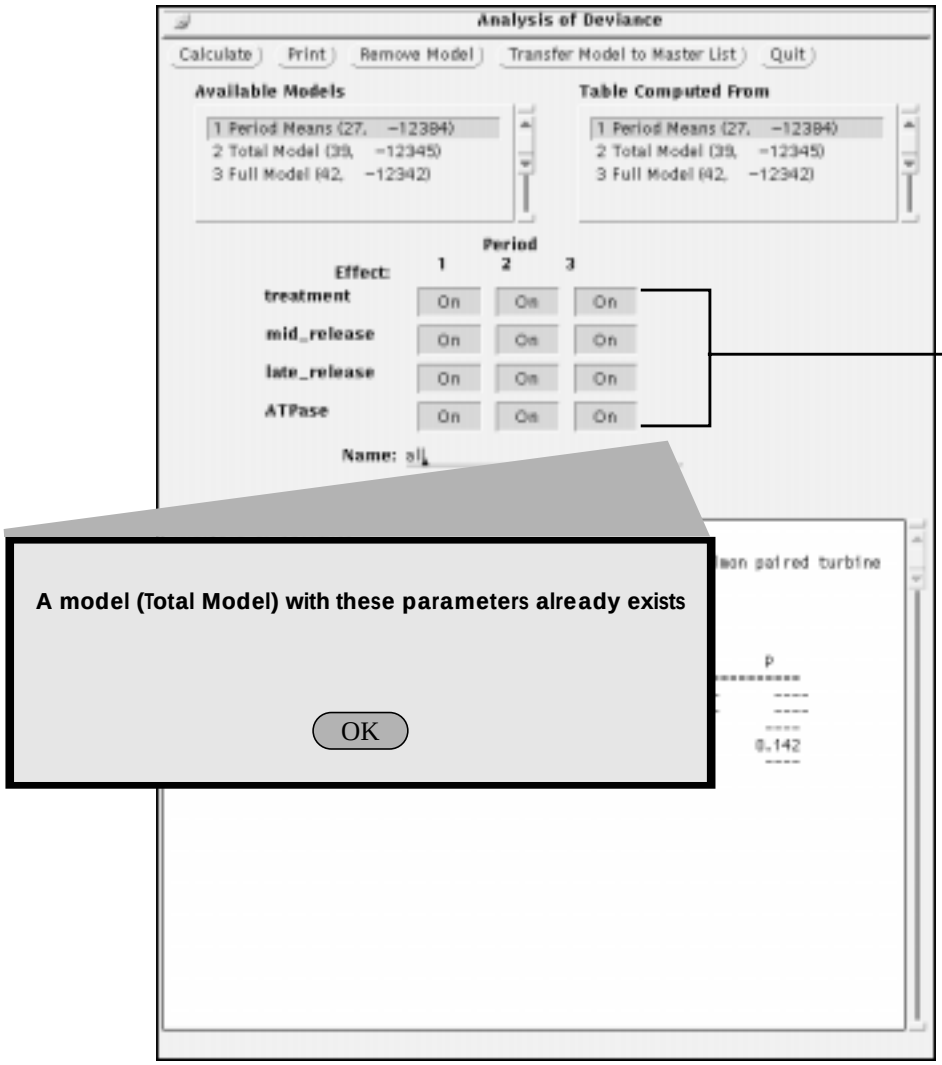


Analysis of Deviance can be used to test the significance of group covariate effects on survival. New models that partition the Total Covariate Deviance into contributions of specific covariates in each period can be created by adding (On) or deleting (Off) parameters using the ANODEV Button Pad. After a series of hierarchical models have been estimated, you can create an ANODEV Table. Left-click on model names in the **Available Models List** to move them to the **Table Computed From List**. Then, to create the ANODEV Table, left-click on the **Calculate Button**.

In the example above we have estimated three nested models (labelled above as trt1, trt12, trt123). Model “trt1” has a treatment effect estimated in period 1, model “trt12” has separate treatment effects estimated in periods 1 and 2, and model “trt123” has separate treatment effects estimated in periods 1, 2, and 3. You read the ANODEV Table as you would an ANOVA Table. Thus, the only significant group covariate effect from this

set of nested models is a treatment effect in period 1 (p=0.01). Recall that due to non-orthogonality, the treatment effect in subsequent periods may be affected by whether the treatment effect in the first period has been included in the model. Therefore, you may also wish to estimate the treatment effects in periods 2 and 3 independent of the effect in period 1.



ANODEV

Button Pad

When an ANODEV model that has already been estimated is specified, a message window informs you of this duplication.

In the example, using the Modeling Buttons, we have attempted to run the Total Covariate Model under an alternative name. The message window informs us that this model already exists.

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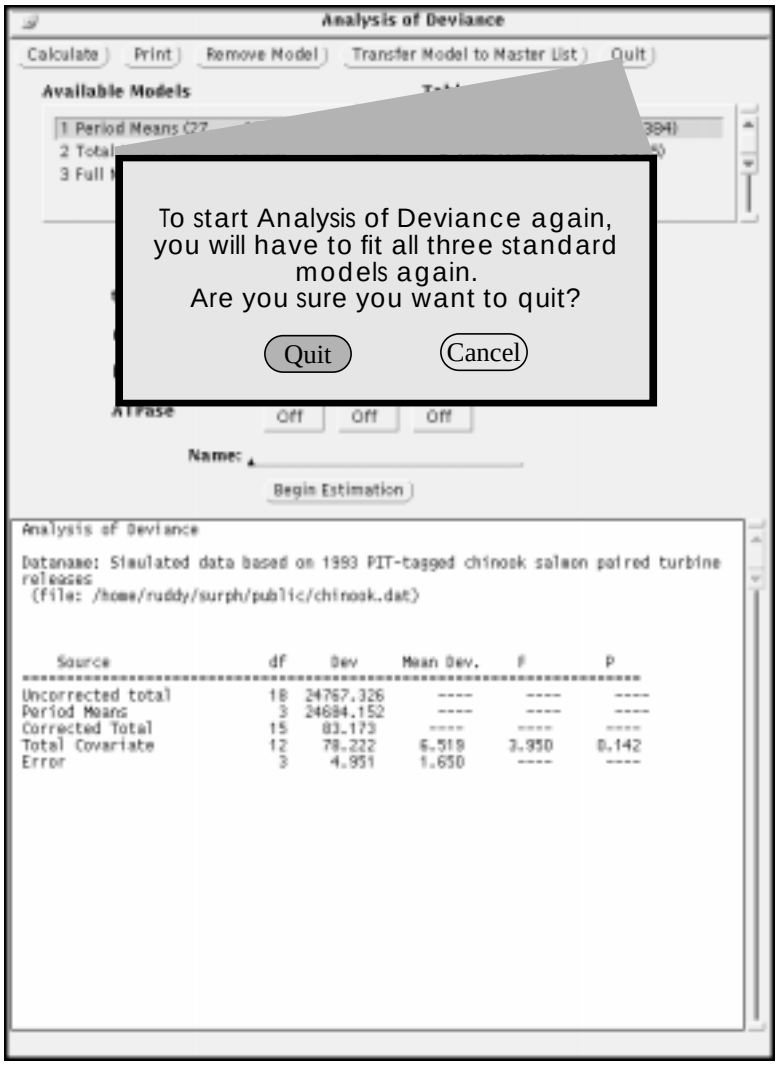

When you attempt to quit the ANODEV window, a pop-up message informs you that the three standard models will be lost if ANODEV is quit. As the estimation of the three standard models can take several minutes, you may wish to reconsider.

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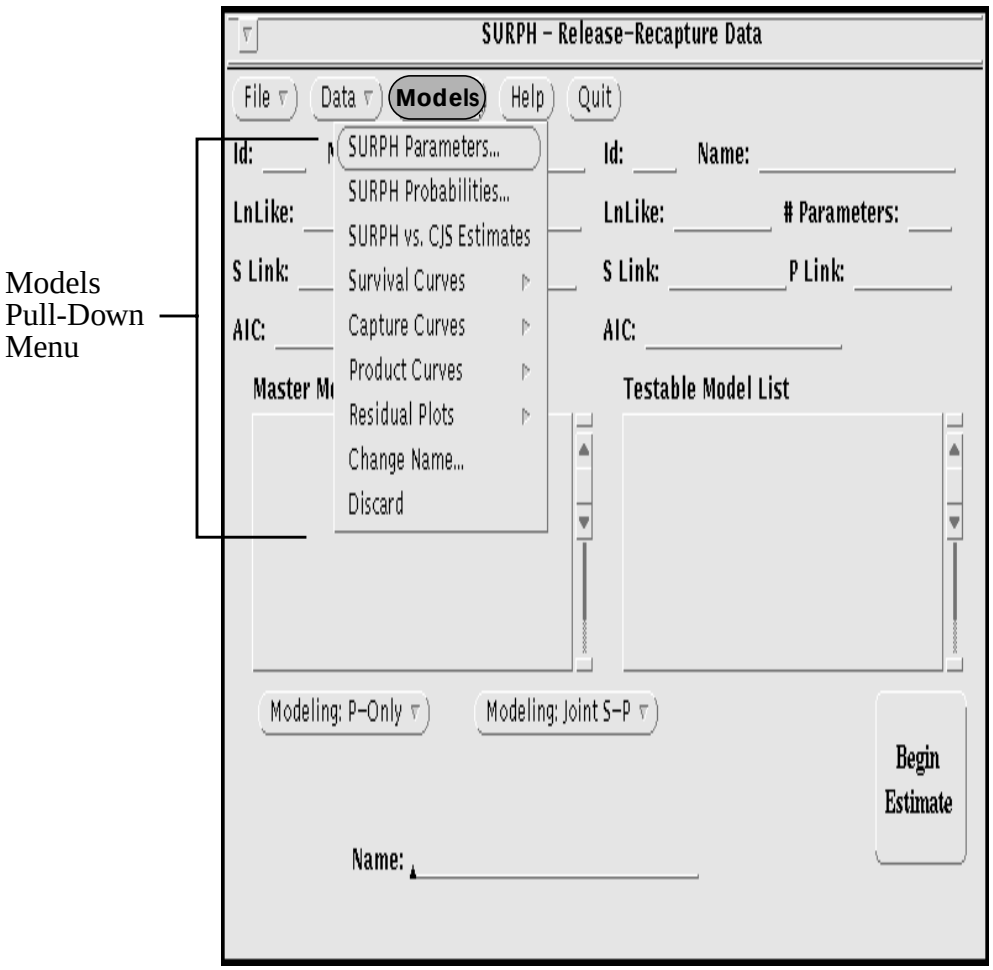

This is the pull-down menu accessed by right-clicking on the **Models Button**. The Model Pull-Down Menu has choices to display SURPH survival and capture estimates, view graphics that illustrate group and individual covariate effects on survival and capture probabilities, view residual plots to investigate goodness-of-fit, change model names, and discard models. All actions pertain to the model currently selected in the **Master Model List**.

SURPH Parameters - Display text window with estimated parameter values, standard errors of parameter values, and the variance-covariance matrix for the model currently selected in the **Master Model List** (see SURPH Parameters).

Estimates are displayed on the scale on which they are estimated by SURPH (e.g., $\underset{\sim}{\beta}$ in the expression $S^{exp(\underset{\sim}{X}'\underset{\sim}{\beta})}$), rather than as probabilities.

SURPH Estimates - Displays text window with "integrated probability estimates" for the model currently selected in the **Master Model List**. Estimates are displayed on the probability scale (e.g., $\hat{S}_{ik} = S^{exp(\underset{\sim}{X}'_{ik}\underset{\sim}{\beta})}$ (see SURPH Probabilities).

SURPH vs. CJS Estimates - Displays plot of integrated probability estimates of capture and survival probabilities versus the corresponding Cormack/Jolly-Seber estimates (see SURPH vs. CJS Estimates).

Survival Curves - Displays graphical representations of group and individual covariate effects on survival probabilities or on relative risk (see Survival Graphics and Relative Risk Graphics).

Capture Curves - Displays graphical representations of group and individual covariate effects on capture probabilities (see Capture Graphics).

Product Curves - Displays graphical representations of group and individual covariate effects on the final period product (Survival x Capture) probabilities (see Product Graphics).

Residual Plots - Displays graphical representations of model residuals from two perspectives, a) Residuals vs. Capture History, or b) Normal Q-Q Plot (see Residual Plot or Quantile-Quantile Plot).

Change Name	-	Changes the name of the currently selected model in the **Master Models List** (see Change Model Name).
Discard	-	Discards the currently selected model in the **Master Model List**. Models that are discarded are no longer accessible to you and have to be recomputed if needed again(see Confirm Discard Dialog Box).

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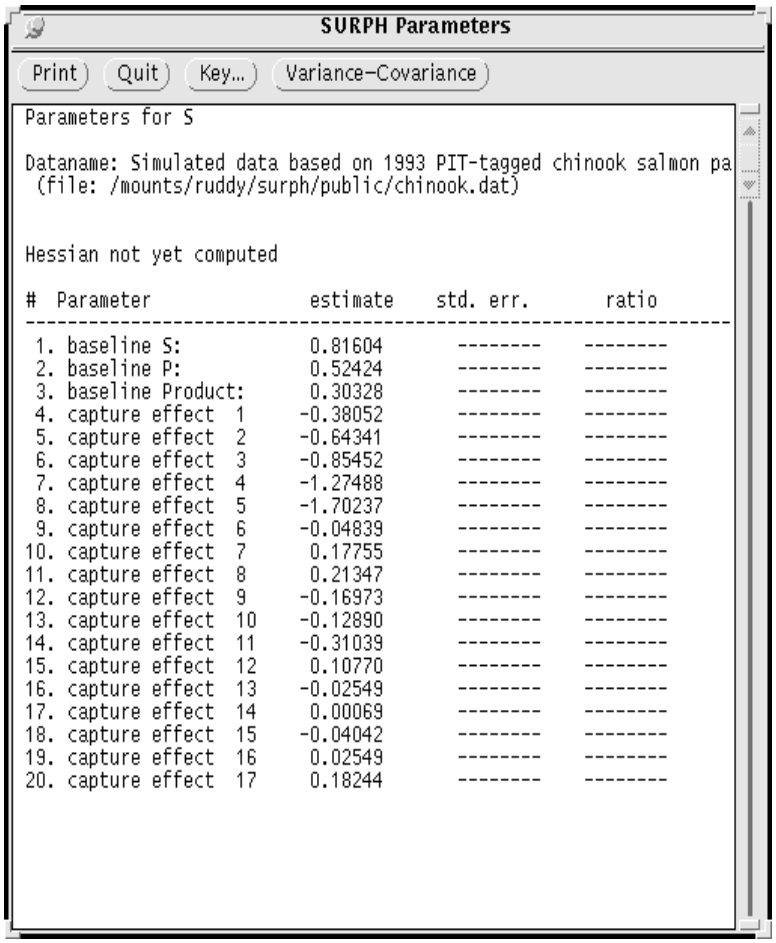



```
Parameters for S

Dataname: Simulated data based on 1993 PIT-tagged chinook salmon pa
 (file: /mounts/ruddy/surph/public/chinook.dat)


Hessian not yet computed

#  Parameter                 estimate    std. err.       ratio
-----------------------------------------------------------------
 1. baseline S:              0.81604       --------    --------
 2. baseline P:              0.52424       --------    --------
 3. baseline Product:        0.30328       --------    --------
 4. capture effect  1       -0.38052       --------    --------
 5. capture effect  2       -0.64341       --------    --------
 6. capture effect  3       -0.85452       --------    --------
 7. capture effect  4       -1.27488       --------    --------
 8. capture effect  5       -1.70237       --------    --------
 9. capture effect  6       -0.04839       --------    --------
10. capture effect  7        0.17755       --------    --------
11. capture effect  8        0.21347       --------    --------
12. capture effect  9       -0.16973       --------    --------
13. capture effect  10      -0.12890       --------    --------
14. capture effect  11      -0.31039       --------    --------
15. capture effect  12       0.10770       --------    --------
16. capture effect  13      -0.02549       --------    --------
17. capture effect  14       0.00069       --------    --------
18. capture effect  15      -0.04042       --------    --------
19. capture effect  16       0.02549       --------    --------
20. capture effect  17       0.18244       --------    --------
```

This text window displays values of the estimated parameters for the model currently selected in the **Master Models List** (**Models -> SURPH Parameters**). Estimates are displayed on the scale on which they are estimated by SURPH (e.g., “capture effect 1” may be the second period effect (ρ_2) such that the capture probability in period 2 is $P^{exp(\rho_2)}$.

There are also columns for estimated standard errors and the ratios of parameters to standard errors. The first time the SURPH parameters text window is displayed for a particular model, these columns are blank because the variance-covariance matrix is not calculated until you left-click on the **Variance-Covariance Button**. The numerical procedure to estimate the variance-covariance matrix can take several minutes or more on some computers, and you will sometimes find it handy to view the parameter estimates alone, without waiting for the variance-covariance computation.

Print Button	-	Left-click to send a copy of this text window information to the printer.
Quit Button	-	Left-click to dismiss this text window.
Key Button	-	Left-click to view the key to the parameter list and two distinct cross-references.
Variance-Covariance Button	-	Left-click to calculate and display the estimated Variance-Covariance Matrix of the parameter estimates.

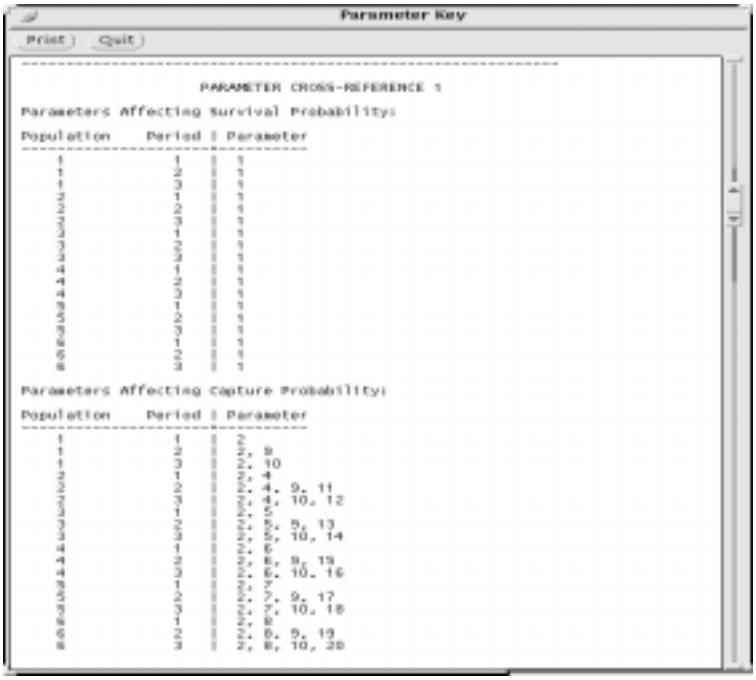
A

This text window (**Models -> SURPH Parameters -> Key**) provides a key to the survival and capture parameter list for the model that is currently selected in the **Master Model List**. Buttons across the top row allow you to **Print** the information contained within this window or allow you to **Quit** (dismiss) this window.

There are three portions to the key. You move from one portion to the next by scrolling through the text pane. The first portion of the key (top, A) displays the Model Name (“S” in this case), Dataname (chinook.dat) and the Survival, Capture and Product Link Functions. This is followed by a listing of the estimated parameters, their numeric designations and their definitions. In the example text window (top), parameter 2 is the Capture Intercept Parameter, whereas parameter 9 is the 2nd period effect on capture.

The second portion of the key (middle, B) displays the Parameter Cross-Reference 1. This listing indicates, by population and period, which parameters (by numeric designation) are involved in the estimation of capture, survival, and product probabilities. In the example text pane (middle), notice that survival for all populations and periods is affected solely by the 1st parameter (Survival Intercept). This is because the **Model S** (see Survival Modeling - Examples) was used to estimate survival probabilities. However, since the **Model Pst** was used to estimate capture probabilities,

each population and period has a unique suite of capture parameters. For example, for the 2nd population in the 2nd period, the capture parameters used to estimate the capture probability are parameters 2 (Capture Intercept), 4 (effect of the 2nd population on capture), 9 (effect of the 2nd period on capture), and 11 (interaction of the 2nd population and 2nd period effects on capture).



Parameter Key

Print Quit

PARAMETER CROSS-REFERENCE 1

Parameters Affecting Survival Probability:

Population	Period	Parameter
1	1	1
1	2	1
1	3	1
2	1	1
2	2	1
2	3	1
3	1	1
3	2	1
3	3	1
4	1	1
4	2	1
4	3	1
5	1	1
5	2	1
5	3	1
6	1	1
6	2	1
6	3	1

Parameters Affecting Capture Probability:

Population	Period	Parameter
1	1	2
1	2	2, 9
1	3	2, 10
2	1	2, 4
2	2	2, 4, 9, 11
2	3	2, 4, 10, 12
3	1	2, 5
3	2	2, 5, 9, 13
3	3	2, 5, 10, 14
4	1	2, 6
4	2	2, 6, 9, 15
4	3	2, 6, 10, 16
5	1	2, 7
5	2	2, 7, 9, 17
5	3	2, 7, 10, 18
6	1	2, 8
6	2	2, 8, 9, 19
6	3	2, 8, 10, 20

B

The final portion of the key (bottom, C) displays the Parameter Cross-Reference 2. This display, rather than being organized by populations and periods, is organized by Design, Group, and Individual Effects on Survival, Capture and Product Probabilities. This portion of the key is used to understand the Design, Group Covariate, and Individual Covariate Effects on Populations and Periods. For example, for the 2nd population in the 2nd period, the capture parameters used to estimate the capture probability are the Capture Intercept, which is included in all capture probabilities (parameter 2), the Design Effect on Capture of the 2nd population (parameter 4), the Design Effect on Capture of the 2nd period (parameter 9), and the Design Effect on Capture of the 2nd population and 2nd period interaction (parameter 11). All Group and Individual Covariate Effects on capture are zero, which indicates that the fitted model (“Pst”) did not include these effects.

C

Parameter Key

Print Quit

```
-----------------------------------------------------------------
Design Effects on Capture Probability

 Population      |   1   2   3   4   5   6
-----------------+-------------------------
 Parameter       |   0   4   5   6   7   8

 Period          |   1   2   3
-----------------+------------
 Parameter       |   0   9  10

                     Period
 Interactions    |   1   2   3
-----------------+------------
 Population    1 |   0   0   0
               2 |   0  11  12
               3 |   0  13  14
               4 |   0  15  16
               5 |   0  17  18
               6 |   0  19  20


Group Covariate Effects on Capture Probability

 Period          |   1   2   3
-----------------+------------
 treatment       |   0   0   0
 mid_releas      |   0   0   0
 late_relea      |   0   0   0
 ATPase          |   0   0   0

Individual Covariate Effects on Capture Probability

                     Period
 length          |   1   2   3
-----------------+------------
 Population    1 |   0   0   0
               2 |   0   0   0
               3 |   0   0   0
               4 |   0   0   0
               5 |   0   0   0
               6 |   0   0   0
```

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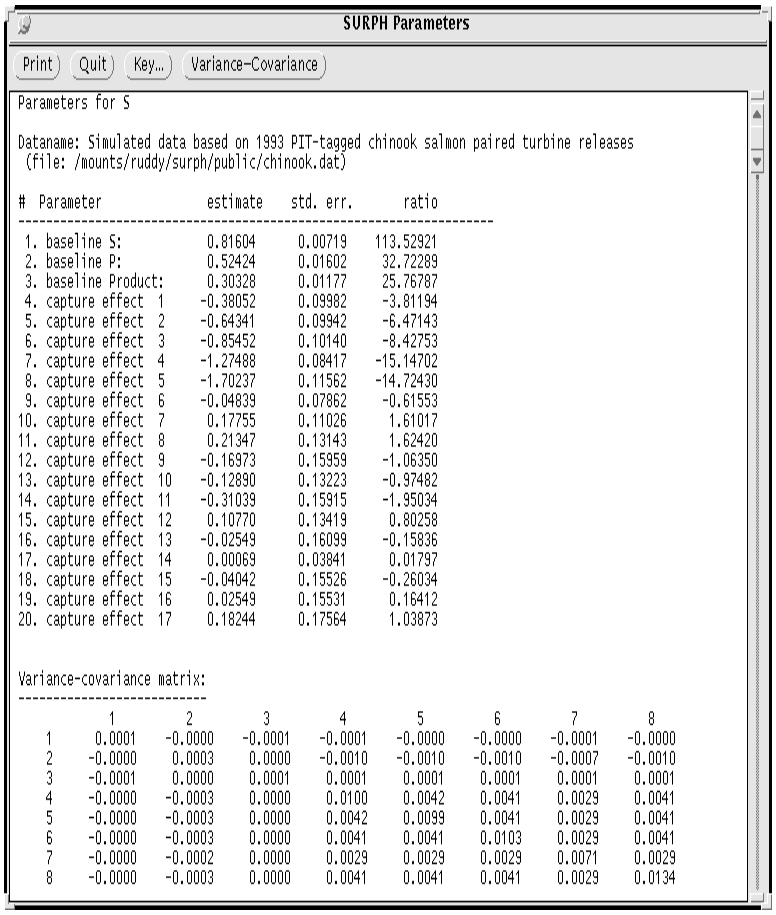


SURPH Parameters

Print Quit Key... Variance-Covariance

```
Parameters for S

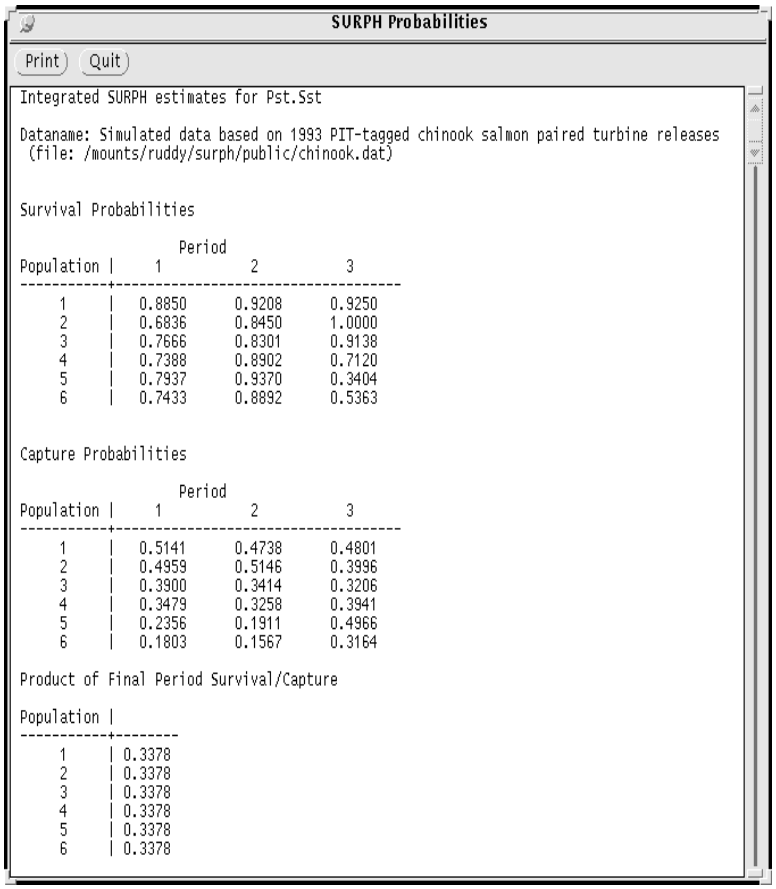
Dataname: Simulated data based on 1993 PIT-tagged chinook salmon paired turbine releases
 (file: /mounts/ruddy/surph/public/chinook.dat)

#  Parameter              estimate   std. err.      ratio
-----------------------------------------------------------------
 1. baseline S:           0.81604     0.00719   113.52921
 2. baseline P:           0.52424     0.01602    32.72289
 3. baseline Product:     0.30328     0.01177    25.76787
 4. capture effect  1    -0.38052     0.09982    -3.81194
 5. capture effect  2    -0.64341     0.09942    -6.47143
 6. capture effect  3    -0.85452     0.10140    -8.42753
 7. capture effect  4    -1.27488     0.08417   -15.14702
 8. capture effect  5    -1.70237     0.11562   -14.72430
 9. capture effect  6    -0.04839     0.07862    -0.61553
10. capture effect  7     0.17755     0.11026     1.61017
11. capture effect  8     0.21347     0.13143     1.62420
12. capture effect  9    -0.16973     0.15959    -1.06350
13. capture effect  10   -0.12890     0.13223    -0.97482
14. capture effect  11   -0.31039     0.15915    -1.95034
15. capture effect  12    0.10770     0.13419     0.80258
16. capture effect  13   -0.02549     0.16099    -0.15836
17. capture effect  14    0.00069     0.03841     0.01797
18. capture effect  15   -0.04042     0.15526    -0.26034
19. capture effect  16    0.02549     0.15531     0.16412
20. capture effect  17    0.18244     0.17564     1.03873


Variance-covariance matrix:
---------------------------
            1         2         3         4         5         6         7         8
    1     0.0001   -0.0000   -0.0001   -0.0001   -0.0000   -0.0000   -0.0001   -0.0000
    2    -0.0000    0.0003    0.0000   -0.0010   -0.0010   -0.0010   -0.0007   -0.0010
    3    -0.0001    0.0000    0.0001    0.0001    0.0001    0.0001    0.0001    0.0001
    4    -0.0000   -0.0003    0.0000    0.0100    0.0042    0.0041    0.0029    0.0041
    5    -0.0000   -0.0003    0.0000    0.0042    0.0099    0.0041    0.0029    0.0041
    6    -0.0000   -0.0003    0.0000    0.0041    0.0041    0.0103    0.0029    0.0041
    7    -0.0000   -0.0002    0.0000    0.0029    0.0029    0.0029    0.0071    0.0029
    8    -0.0000   -0.0003    0.0000    0.0041    0.0041    0.0041    0.0029    0.0134
```

This illustration (**Models -> SURPH Parameters -> Variance-Covariance**) shows the SURPH Parameters text window as it appears after left-clicking on the **Variance-Covariance Button**. It is sometimes necessary to expand the window to view the matrix elements. This estimated variance-covariance is based upon the Cramer-Rao Lower Bound (Hogg and Craig 1978) under Maximum Likelihood theory. Each element on the diagonal of the matrix is the estimated variance for the associated parameter (e.g. the estimated variance for parameter #3 - baseline Product - is the element (3,3) of the Variance-Covariance Matrix, whose value is 0.0001). Off-diagonal elements are the estimated covariance between the two associated parameters (e.g., the estimated covariance between parameters #3 and #1 - baseline Product and baseline S - is the element (3,1) of the Variance-Covariance Matrix, whose value is -0.0001). All diagonal elements should be non-negative, as variances are strictly non-negative. Off-diagonal elements may be negative or positive.

Once the variance-covariance matrix has been estimated, the standard error and the ratio of the estimate to its standard error is displayed in the upper region of the text pane. The ratio of $\hat{\theta}/(\sqrt{var(\hat{\theta})})$ is asymptotically distributed as a standard normal deviate (i.e., N(0,1)).



SURPH Probabilities

Print Quit

```
Integrated SURPH estimates for Pst.Sst

Dataname: Simulated data based on 1993 PIT-tagged chinook salmon paired turbine releases
 (file: /mounts/ruddy/surph/public/chinook.dat)


Survival Probabilities

                    Period
Population |     1          2          3
-----------+-------------------------------------
     1     |   0.8850     0.9208     0.9250
     2     |   0.6836     0.8450     1.0000
     3     |   0.7666     0.8301     0.9138
     4     |   0.7388     0.8902     0.7120
     5     |   0.7937     0.9370     0.3404
     6     |   0.7433     0.8892     0.5363


Capture Probabilities

                    Period
Population |     1          2          3
-----------+-------------------------------------
     1     |   0.5141     0.4738     0.4801
     2     |   0.4959     0.5146     0.3996
     3     |   0.3900     0.3414     0.3206
     4     |   0.3479     0.3258     0.3941
     5     |   0.2356     0.1911     0.4966
     6     |   0.1803     0.1567     0.3164

Product of Final Period Survival/Capture

Population |
-----------+--------
     1     | 0.3378
     2     | 0.3378
     3     | 0.3378
     4     | 0.3378
     5     | 0.3378
     6     | 0.3378
```

This text pane (**Models -> SURPH Estimates**) provides survival and capture probability estimates for the model that is currently selected in the **Master Model List**. These probabilities are calculated from the SURPH parameters for the effects modeled. When the selected SURPH model does not include individual-based covariates, the probabilities are computed from the formula:

$$S_{ik} = S^{exp(\pi_i + \rho_k + (\pi\rho)_{ik} + \underset{\sim}{X}_{ik}\underset{\sim}{\beta}_k)}$$

where S_{ik} is the survival probability for population *i* in period *k*;

S is the intercept parameter for survival;

π_i is the effect for population *i*;

ρ_k is the effect for period *k*;

$(\pi\rho)_{ik}$ is the effect for the population *i*/period *k* interaction;

$\underset{\sim}{X}_{ik}$ is the vector of group covariates for population *i* in period *k*; and

$\underset{\sim}{\beta}_k$ is the vector of slope parameters for group covariates in period *k*.

When the selected model includes individual-based covariates, the probabilities are “integrated” across all individuals according to the formula:

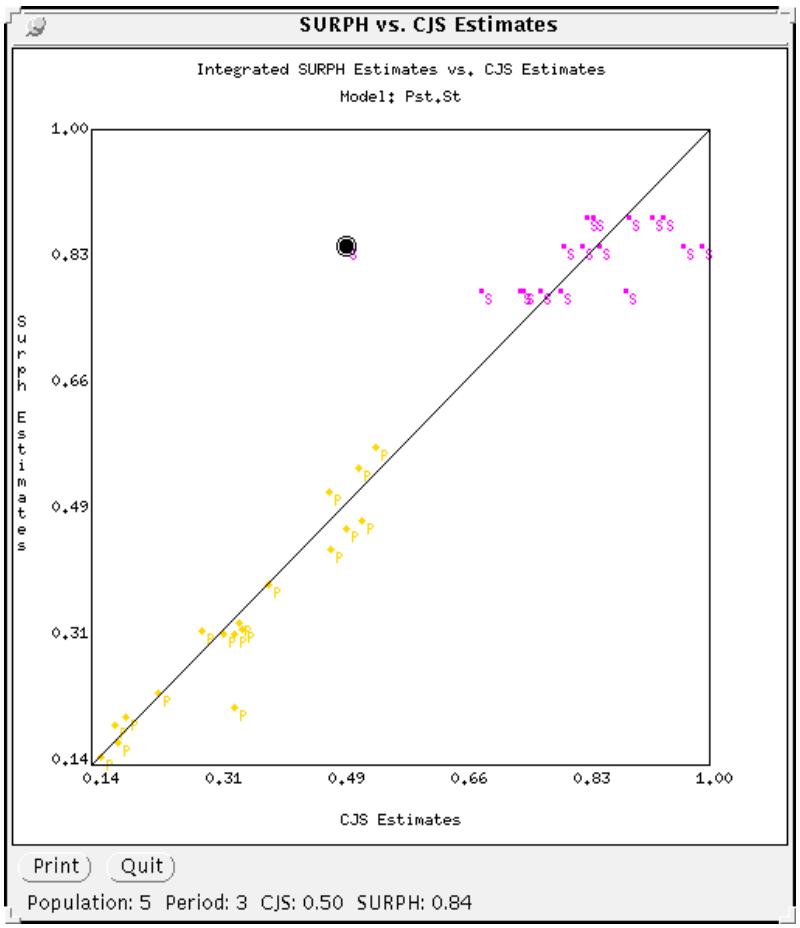
$$S_{ik} = \frac{\sum_{l=1}^{n_{ik}} S^{exp(\pi_i + \rho_k + (\pi\rho)_{ik} + \underset{\sim}{X}_{ik}\underset{\sim}{\beta}_k + \underset{\sim}{Y}_{il}\underset{\sim}{\gamma}_{ik})}}{n_{ik}}$$

where n_{ik} is the number of animals at risk in population *i* in period *k*;

$\underset{\sim}{Y}_{il}$ is the vector of individual covariates for individual *l* in population *i*;

and $\underset{\sim}{\gamma}_{ik}$ is the vector of slope parameters for the individual covariates for population *i* in period *k*.

Buttons in the control panel at the top of the window allow you to **Print** the information contained within this window or allow you to **Quit** this window.



This window (**Models -> SURPH vs. CJS**) provides a graphical display of the "integrated" SURPH probability estimates for the model currently selected in the **Master Model List** versus the Cormack/Jolly-Seber (Cormack 1964, Jolly 1965, Seber 1965) estimates. Both Capture ("P's" on the graphic) and Survival ("S's" on the graphic) probabilities are plotted. The control panel along the bottom of the window has buttons to **Print** a copy of this window or to **Quit** (dismiss) this window.

This graphic provides a visual diagnostic for assessing the fit of models that have fewer parameters than the CJS Model. Individual points on the graphic can be selected to identify the period and population they represent. To select a point, move the mouse cursor to that point, then left-click. The point that is displayed above as a small white circle has been selected. The description of the selected point appears in the footer of the window. Here, the selected point is from population 5, period 3. The CJS capture estimate is 0.50, and the SURPH capture estimate is 0.84.

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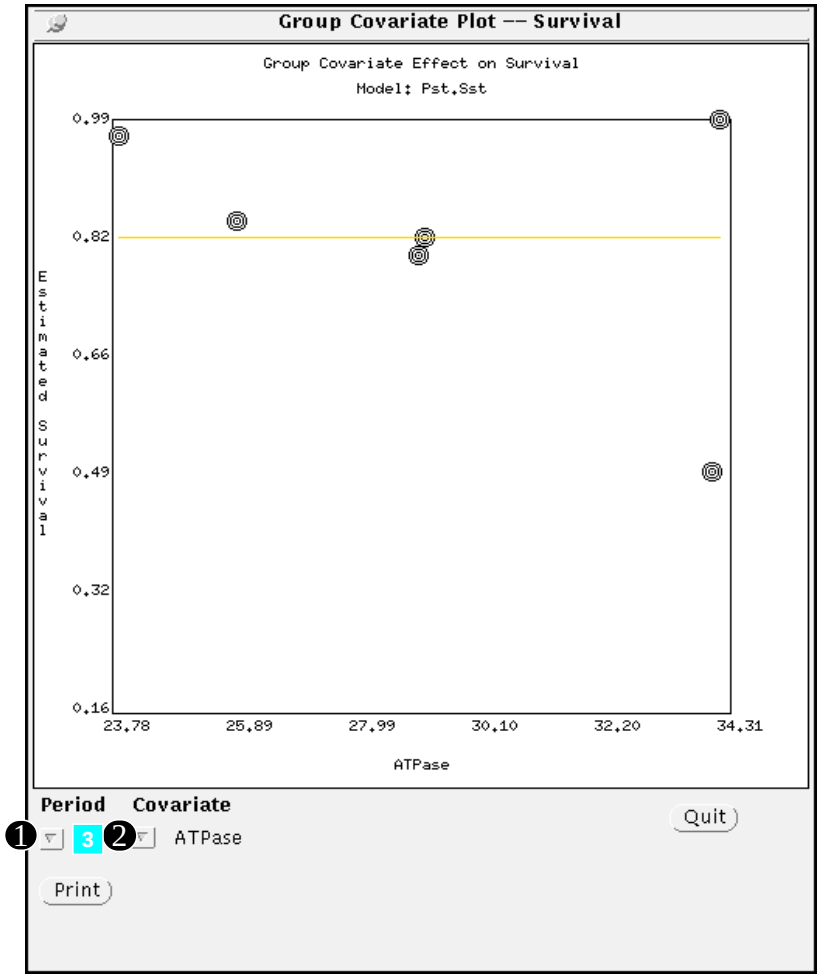

This window (**Models -> Survival Curves -> Group**) provides a graphical display of the estimated SURPH survival curve for a group covariate. The large circular points on the plot represent estimated survival probabilities from the Cormack/ Jolly-Seber (Cormack 1964, Jolly 1965, Seber 1965) model plotted against the group covariate value for each population. The colored line (dashed above) is the fitted survival model as a function of the current group covariate. This graphic, therefore, can be used in conjunction with the SURPH vs CJS graphic to determine how well the SURPH model fits the data. There are two pull-down menus available on the control panel at the bottom of the window:

❶ Period Pull-Down Menu - Determines the sampling period for the diplayed graphic.

❷ Covariate Pull-Down Menu - Determines the group covariate for the displayed graphic.

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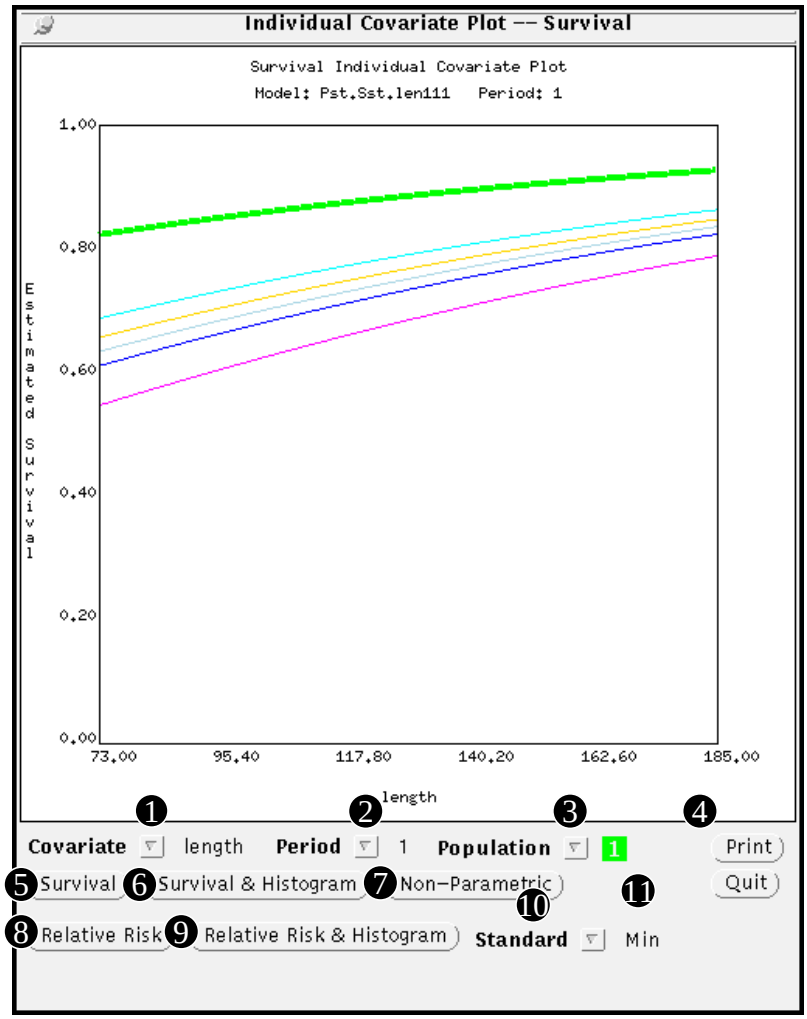

This window (**Models -> Survival Curves -> Individual**) provides graphical displays of the fitted model of survival as a function of individual covariates. Several different graphics can be displayed on the same window. The graphic to be displayed depends upon the combination of choices you make from the control panel at the bottom of the window. The default display, shown when the window is first displayed, and illustrated above, shows the fitted survival curves for all populations. The covariate value is on the horizontal axis, and the estimated survival probability is on the vertical axis. The curve for each population has a distinct color, and the curve for the population currently selected on the Population Pull-Down Menu (see below) is double the thickness of those for the non-selected populations.

User options on the control panel are:

❶ Covariate of Interest - This pull-down menu allows you to select the individual covariate to be displayed. Right-click to access the pulldown menu, then left-click on the desired covariate.

❷ Period of Interest - This pull-down menu allows you to select the period to be displayed. Right-click to access the pull-down menu, then left-click on the desired period.

❸ Population of Interest - This pull-down menu allows you to select the population to be displayed. Right-click to access the pull-down menu, then left-click on the desired population.

❹ **Print** - This button allows you to print the graphic. Left-click on this button to send a copy of the current display to the printer.

❺ **Survival** - Left-click to display fitted survival curves for all populations for the selected covariate and period (default, shown above).

❻ **Survival & Hist** - Left-click to display fitted survival curves for the selected population, superimposed on the histogram of the selected covariate for the period of interest.
See Models: Survival Graphics: Individual Covariate (B) for an example of this display.

❼ **Non-Parametric** - Left-click to display the fitted survival curve for the population, period and covariate of interest, along with a nonparametric analogue.
See Models: Survival Graphics: Individual Covariate (C) for an example of this display.

❽ **Relative Risk** - Left-click to display the fitted relative risk curves for all populations for the selected covariate and period.
See Models: Survival Graphics: Individual Covariate (D) for an example of this display.

❾ **Relative Risk & Hist** - Left-click to display the fitted relative risk curve for the selected population, superimposed on a histogram of the selected covariate for the period of interest.
See Models: Survival Graphics: Individual Covariate (E) for an example of this display.

❿ Standard - This pull-down menu allows you to specify the standard covariate value for calculation of the relative risk. you can specify the risk as relative to either the minimum covariate value, the mean covariate value, or the maximum covariate value. Right-click to access the pull-down menu, then left-click on the desired standard.

⓫ Quit - Left-click to dismiss this window.

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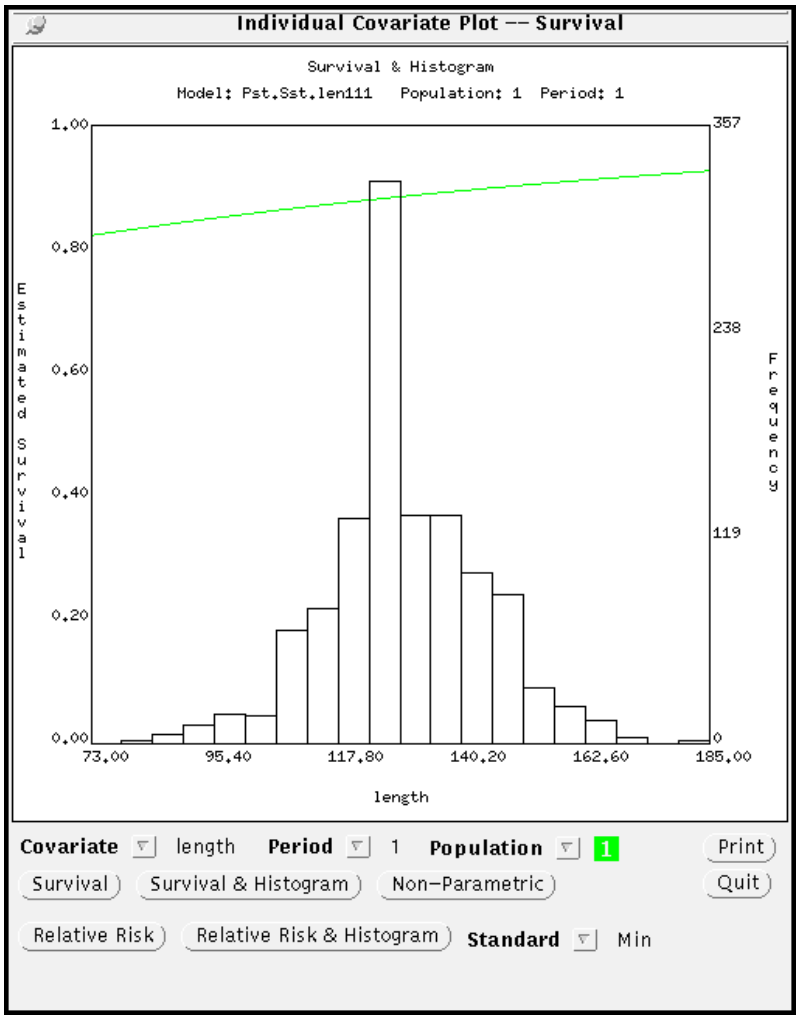

This display (**Models -> Survival Curves -> Individual**) shows the fitted survival curve for the population, covariate, and period of interest, superimposed over a histogram of the covariate for animals known alive at the start of the period displayed. While the "Survival and Histogram" display is active, you have the option of changing the population, covariate, or period of interest using the respective pull-down menus.

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This display (**Models -> Survival Curves -> Individual**) shows the fitted survival curve (smooth) for the population, covariate, and period of interest, superimposed on a nonparametric analogue curve (jagged). For further information concerning the nonparametric curve, see Section 4.6.4. While the “Non-Parametric” display is active, you have the option of changing the population, covariate or period of interest using the respective pull-down menus.

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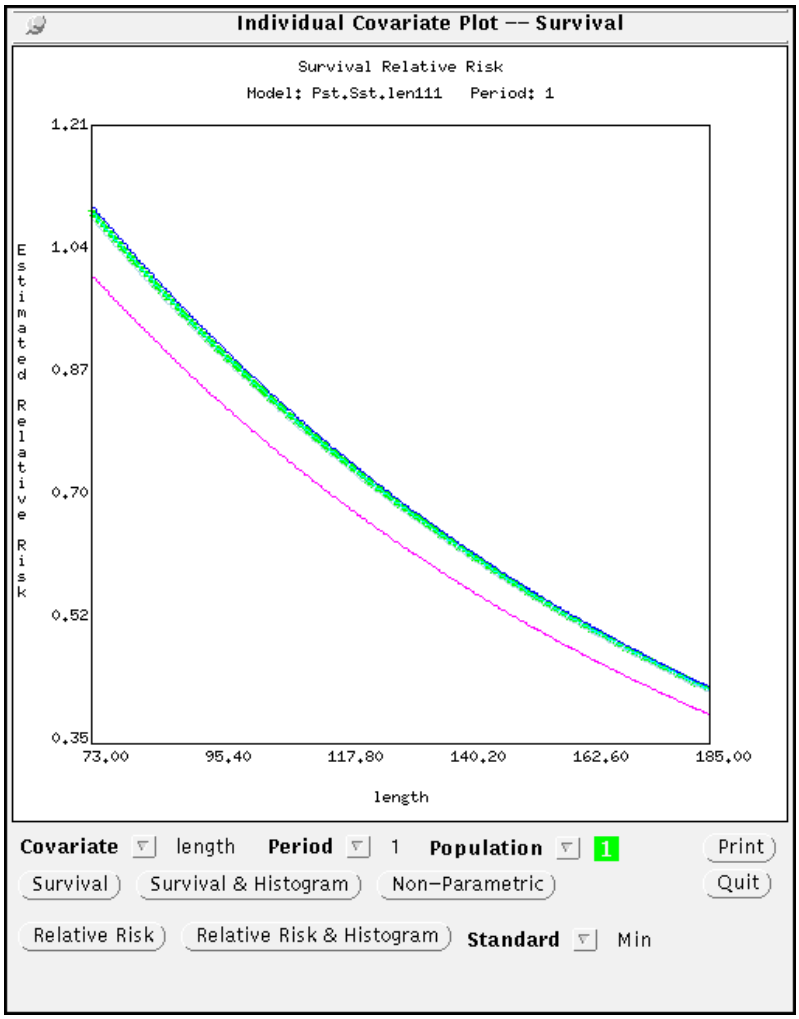

This display (**Models -> Survival Curves -> Individual**) shows the fitted relative risk curves for the covariate and period of interest for all populations. The “standard” covariate value for the risk can be changed so that the risk to the animal with the minimum value of the covariate is set to “1”, the risk to the animal with the mean value of the covariate is set to “1”, or the risk to the animal with the maximum value of the covariate is set to “1”. Because the risk is given in relative terms, changing the standard affects the scale of the curve, but does not affect the shape of the curve, nor the conclusions to be drawn. While the “Relative Risk” display is active, you have the option of changing the population, covariate, or period of interest using the respective pull-down menus.

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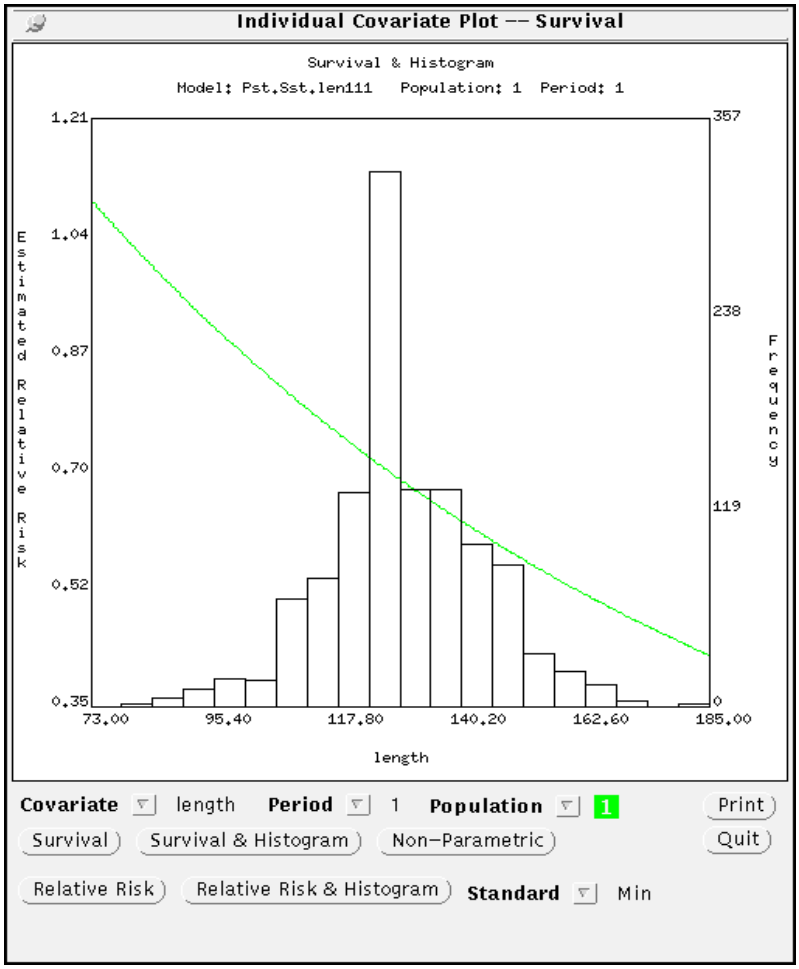

This display (**Models -> Survival Curves -> Individual**) shows the fitted relative risk curve for the population, covariate, and period of interest, superimposed over a histogram of the individual covariate of interest for the population of animals released during the period specified. The "standard" covariate value for the risk can be changed so that the risk for the animal with the minimum value of the covariate is set to 1.0, the risk for the animal with the mean value of the covariate is set to 1.0, or the risk for the animal with the maximum value of the covariate is set to 1.0. Because the risk is given in relative terms, changing the standard affects the scale, but does not affect the shape of the curve, nor the conclusions to be drawn. While the "Survival and Histogram" display is active, you have the option of changing the population, covariate, or period of interest using the respective pull-down menus.

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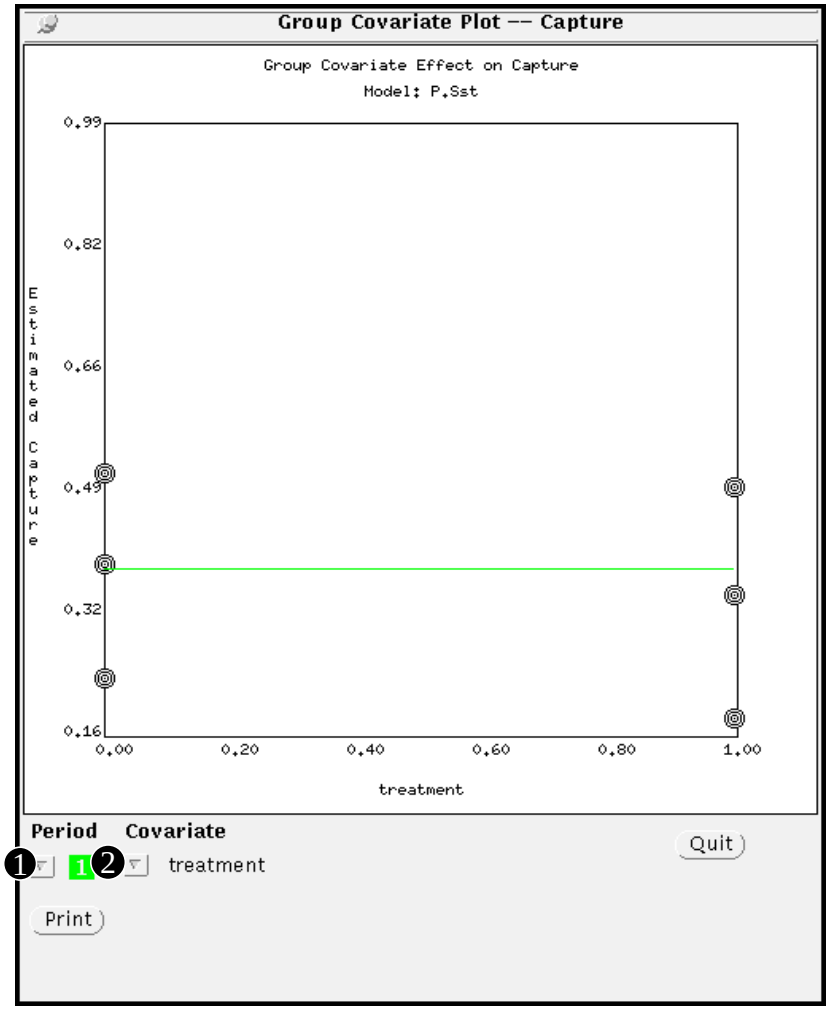

This window (**Models -> Capture Curves -> Group**) provides a graphical display of the estimated SURPH capture curve for a group covariate. The large circular points on the plot represent estimated capture probabilities from the Cormack/Jolly-Seber (Cormack 1964, Jolly 1965, Seber 1965) model plotted against the group covariate value for each population. The colored line (dashed above) is the fitted captured model as a function of the current group covariate. This graphic, therefore, can be used in conjunction with the SURPH vs CJS graphic to determine how well the SURPH model fits the data. There are two pull-down menus available on the control panel at the bottom of the window:

❶ Occasion Pull-Down Menu - Determines the sampling occasion for the diplayed graphic.

❷ Covariate Pull-Down Menu - Determines the group covariate for the displayed graphic.

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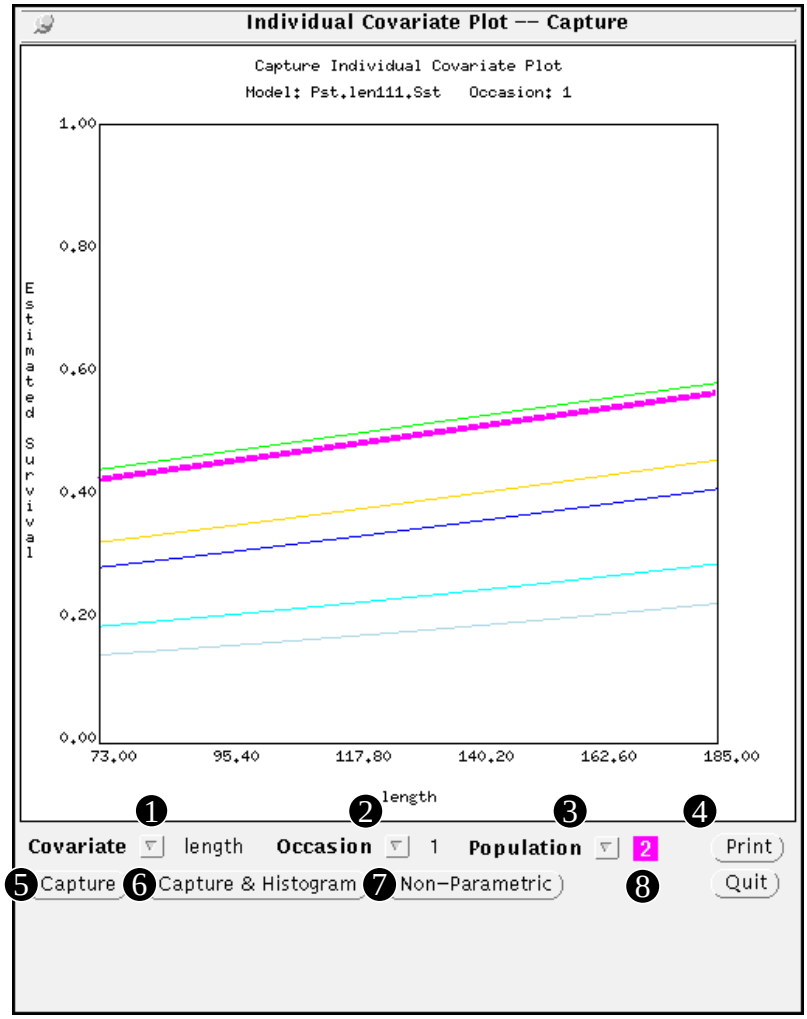


This window (**Models -> Capture Curves -> Individual**) provides graphical displays of the fitted model of capture as a function of individual covariates. Several different graphics can be displayed on the same window. The graphic to be displayed depends upon the combination of choices you make from the control panel at the bottom of the window. The default display, shown when the window is first displayed and illustrated above, shows the fitted capture curves for all populations. The covariate value is on the horizontal axis, and the estimated capture probability is on the vertical axis. The curve for each population has a distinct color, and the curve for the population currently selected on the Population Pull-Down Menu (see below) is double the thickness of those for the non-selected populations.

User options on the control panel are:

❶ Covariate of Interest - This pull-down menu allows you to select the individual covariate to be displayed. Right-click to access the pulldown menu, then left-click on the desired covariate.

❷ Occasion of Interest - This pull-down menu allows you to select the occasion to be displayed. Right-click to access the pull-down menu, then left-click on the desired occasion.

❸ Population of Interest - This pull-down menu allows you to select the population to be displayed. Right-click to access the pull-down menu, then left-click on the desired population.

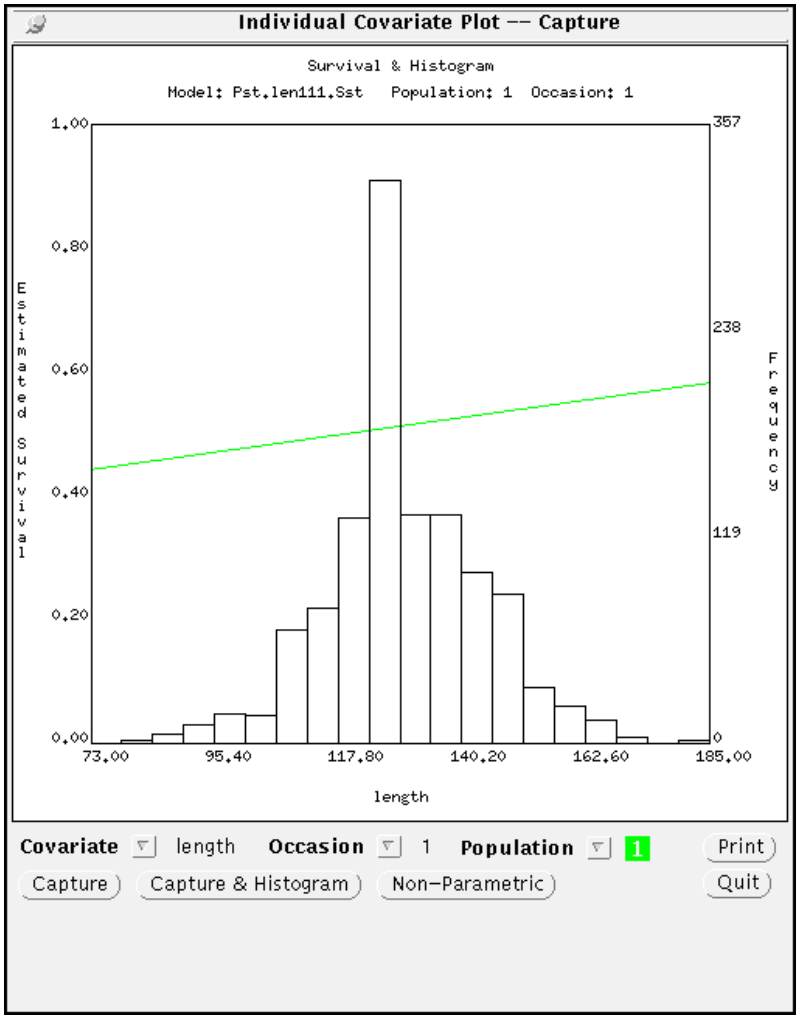
❹ **Print** - This button allows you to print the graphic. Left-click on this button to send a copy of the current display to the printer.

❺ **Capture** - Left-click to display fitted capture curves for all populations for the selected covariate and period (default, shown above).

❻ **Capture & Histogram** - Left-click to display fitted capture curves for the selected population, superimposed on the histogram of the selected covariate for the period of interest.
See Models: Capture Graphics: Individual Covariate (B) for an example of this display.

❼ **Non-Parametric** - Left-click to display the fitted capture curve for the population, period and covariate of interest, along with a nonparametric analogue.
See Models: Capture Graphics: Individual Covariate (C) for an example of this display.

❽ **Quit** - Left-click to dismiss this window.



This display (**Models -> Capture Curves -> Individual**) shows the fitted capture curve for the population, covariate, and occasion of interest, superimposed over a histogram of the covariate for animals known alive at the time of the selected sampling occasion. While the "Capture and Histogram" display is active, you have the option of changing the population, covariate, or occasion of interest using the respective pull-down menus.

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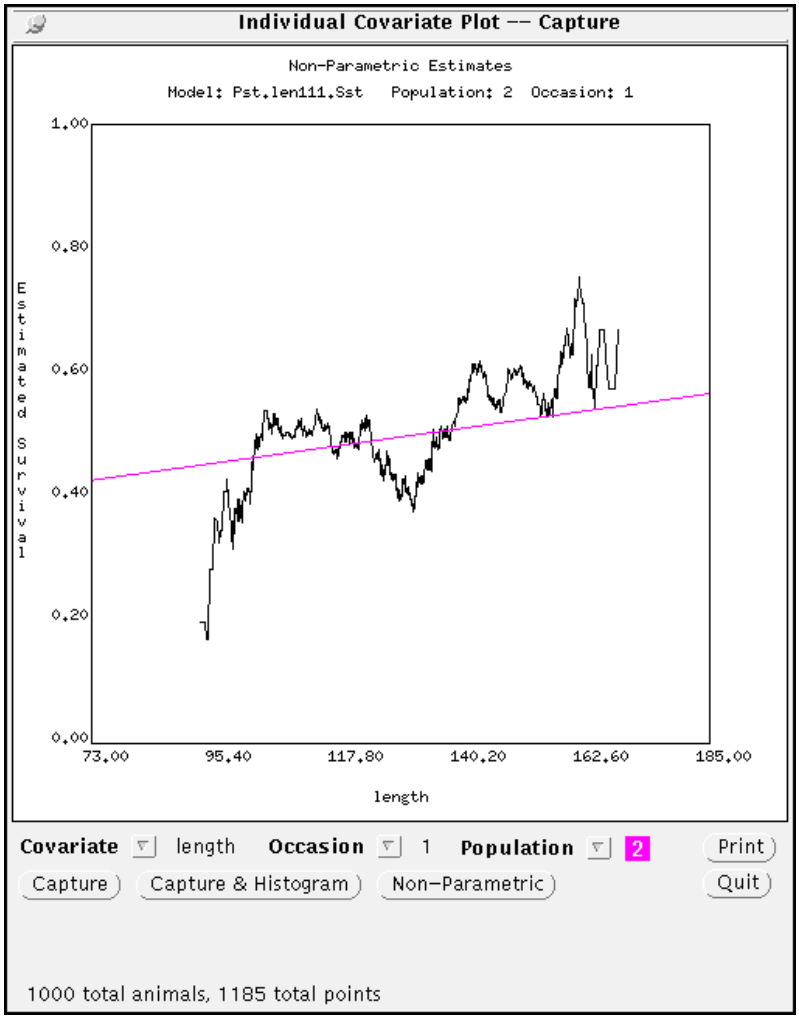

This display (**Models -> Capture Curves -> Individual**) shows the fitted capture curve (smooth) for the population, covariate, and occasion of interest, superimposed on a nonparametric analogue curve (jagged). For further information concerning the nonparametric curve, see Section 4.6.2.5. While the “Non-Parametric” display is active, you have the option of changing the population, covariate or occasion of interest using the respective pull-down menus.

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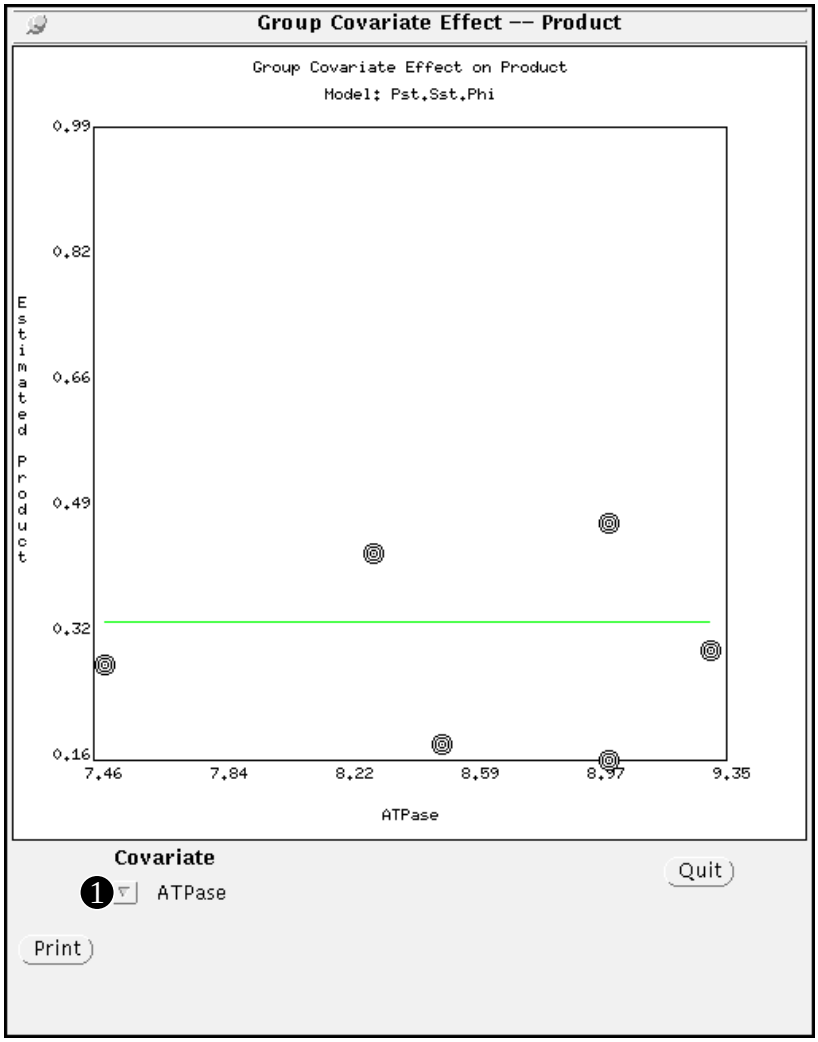

This window (**Models -> Product Curves -> Group**) provides a graphical display of the estimated SURPH product curve for a group covariate. The large circular points on the plot represent estimated product probabilities from the Cormack/Jolly-Seber (Cormack 1964, Jolly 1965, Seber 1965) model plotted against the group covariate value for each population. The colored line (dashed above) is the fitted survival model as a function of the current group covariate. This graphic, therefore, can be used in conjunction with the SURPH vs CJS graphic to determine how well the SURPH model fits the data. There are two pull-down menus available on the control panel at the bottom of the window:

❶ Covariate Pull-Down Menu - Determines the group covariate for the displayed graphic.

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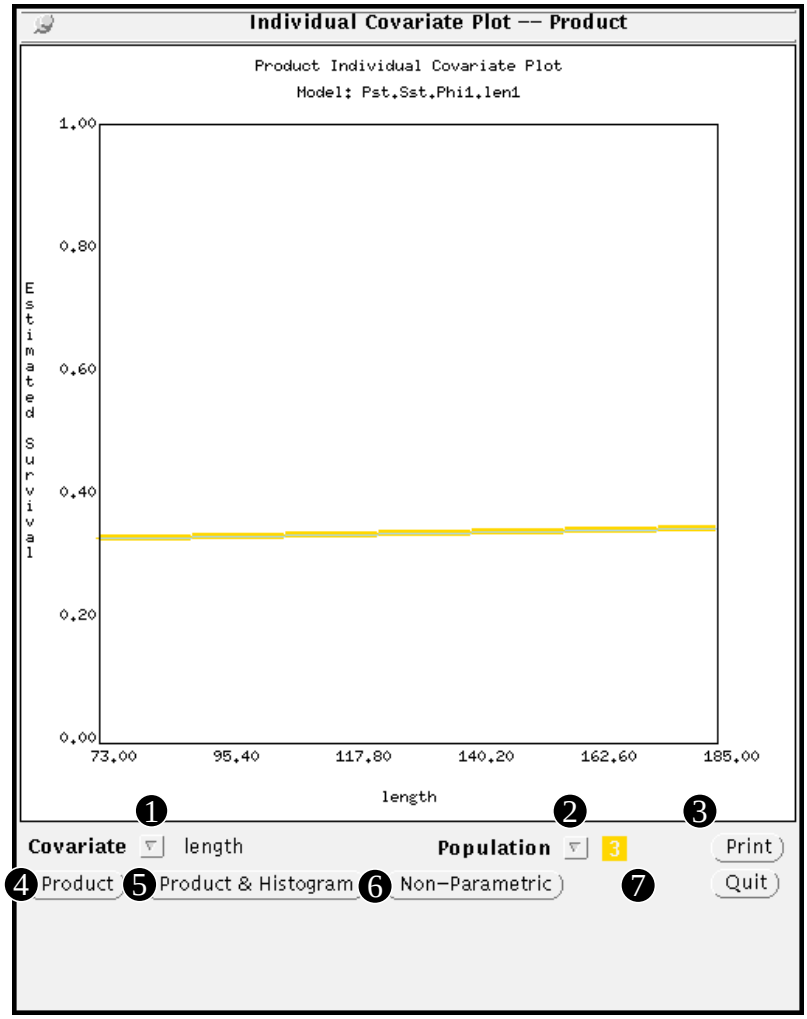


This window (**Models -> Product Curves -> Individual**) provides graphical displays of the fitted model of product as a function of individual covariates. Several different graphics can be displayed on the same window. The graphic to be displayed depends upon the combination of choices you make from the control panel at the bottom of the window. The default display, shown when the window is first displayed, and illustrated above, shows the fitted product curves for all populations. The covariate value is on the horizontal axis, and the estimated product probability is on the vertical axis. The curve for each population has a distinct color, and the curve for the population currently selected on the Population Pull-Down Menu (see below) is double the thickness of those for the non-selected populations.

User options on the control panel are:

❶ Covariate of Interest - This pull-down menu allows you to select the individual covariate to be displayed. Right-click to access the pull-down menu, then left-click on the desired covariate.

❷ Population of Interest - This pull-down menu allows you to select the population to be displayed. Right-click to access the pull-down menu, then left-click on the desired population.

❸ **Print** - This button allows you to print the graphic. Left-click on this button to send a copy of the current display to the printer.

❹ **Product** - Left-click to display fitted product curves for all populations. for the selected covariate (default, shown above).

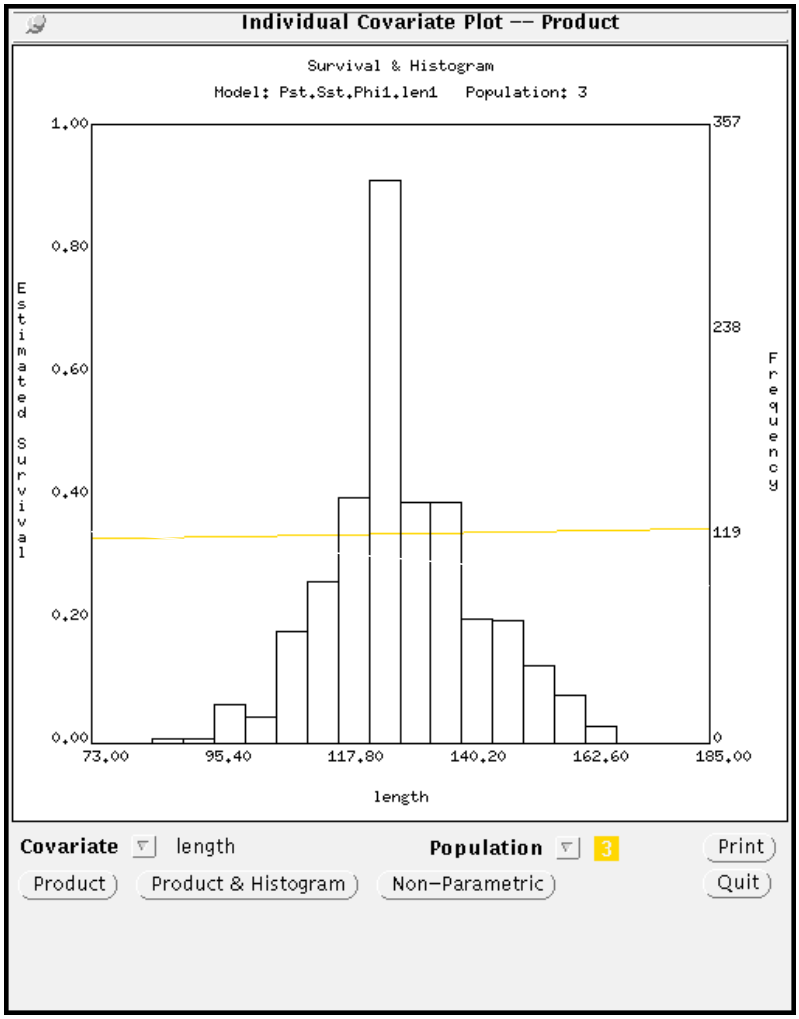
❺ **Product & Histogram** - Left-click to display fitted product curve for the selected population, superimposed on the histogram of the selected covariate of interest.

See Models: Product Graphics: Individual Covariate (B) for an example of this display.

❻ **Non-Parametric** - Left-click to display the fitted product curve for the population and covariate of interest, along with a nonparametric analogue.

See Models: Product Graphics: Individual Covariate (C) for an example of this display.

❼ **Quit** - Left-click to dismiss this window.



This display (**Models -> Product Curves -> Individual**) shows the fitted product curve for the population and covariate of interest, superimposed over a histogram of the covariate for animals known alive during the final period. While the "Product and Histogram" display is active, you have the option of changing the population or covariate of interest using the respective pull-down menus.

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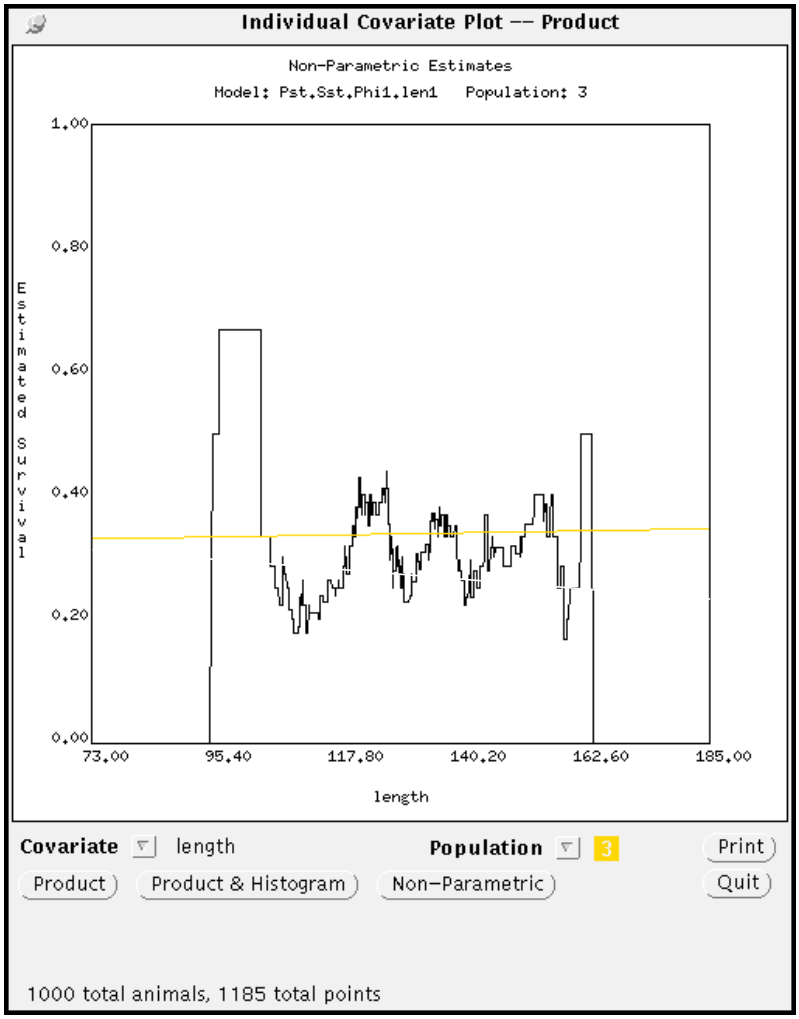

This display (**Models -> Product Curves -> Individual**) shows the fitted product curve (smooth) for the population and covariate of interest, superimposed on a nonparametric analogue curve (jagged). For further information concerning the nonparametric curve, see Section 4.6.2.5. While the “Non-Parametric” display is active, you have the option of changing the population or covariate of interest using the respective pull-down menus.

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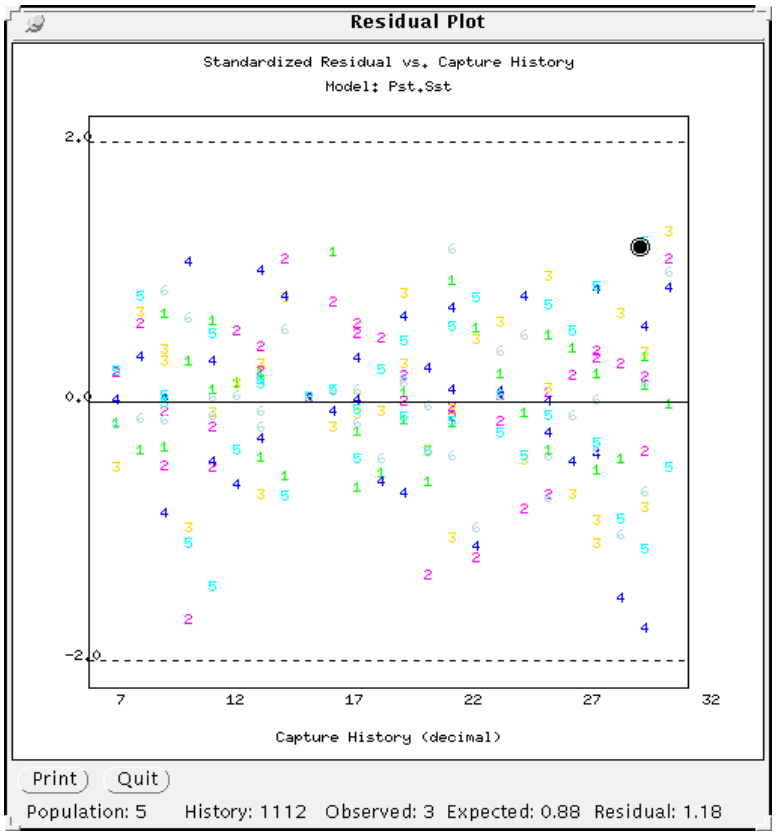

This plot (**Models -> Residual Plots -> vs. Capture Histories**) displays the Anscombe standardized residuals (Anscombe standardized residuals are distributed Assymptotically Normal (0,1); McCullagh and Nelder 1983) versus the capture histories. Buttons in a control panel at the bottom allow you to **Print** a copy of this window or to **Quit** (dismiss) this window. The left mouse button can be used to select individual points on the plot (indicated by the small white circle). When a point is selected, the capture history, the expected value of the capture history and the observed value of the capture history are displayed for the selected point in the window footer. The plotting characters of the points on the plot designate the population from which the residual was calculated. Thus, for each possible capture history, there are *p* points on the plot, where *p* is the the number of populations in the data set.

Recall that capture histories resemble binary numbers (e.g., $10000_2 = 16_{10}$). The x-axis, therefore, displays capture histories converted into decimal equivalents.

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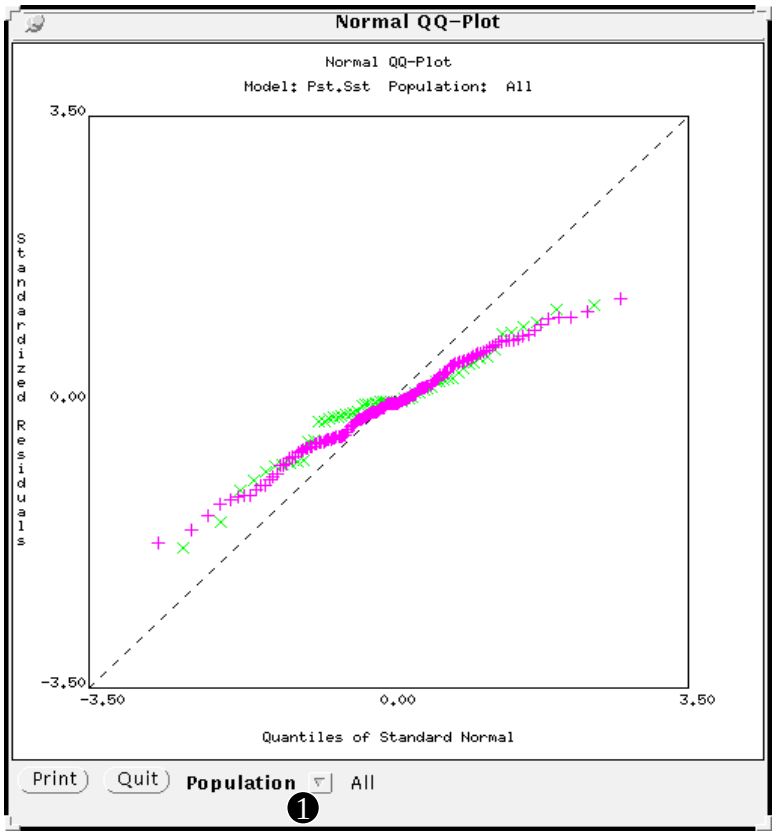

This plot (**Models -> Residual Plots -> QQ-Plot**) displays the Anscombe standardized residuals (McCullagh and Nelder 1983) for the model currently selected in the **Master Model List** versus their expected value under the Normal distribution (Zar 1984). Purple crosses indicate capture histories of removed animals, whereas green x's indicate complete capture histories of tagged animals. Buttons on the control panel at the bottom of this plot allow you to **Print** a copy of this window, or **Quit** (dismiss) this window.

❶ Population - This Pull Down Menu allows you to specify the population from which the residuals will be drawn. You may specify either residuals for an individual population or the residuals for all populations.

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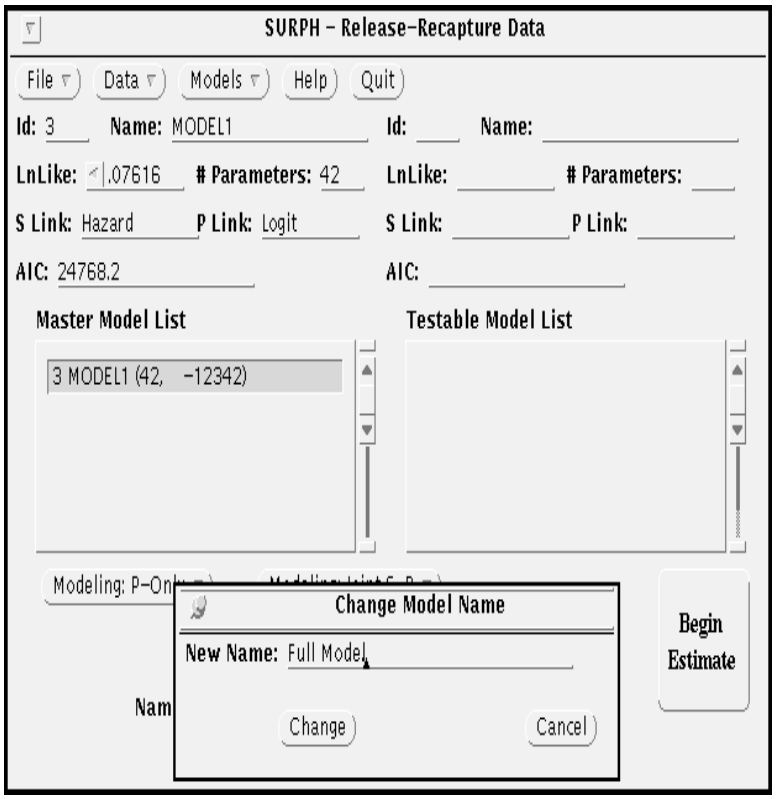

This small pop-up window (**Models -> Change Name**) allows you to change the name of the model currently selected within the **Master Model List**. To change the name of the selected model, left-click on the **New Name Field**, type the new name, then left-click on the **Change Button**. In this example, the model currently named “MODEL 1” will be renamed “Full Model” upon left-clicking the **Change Button**.

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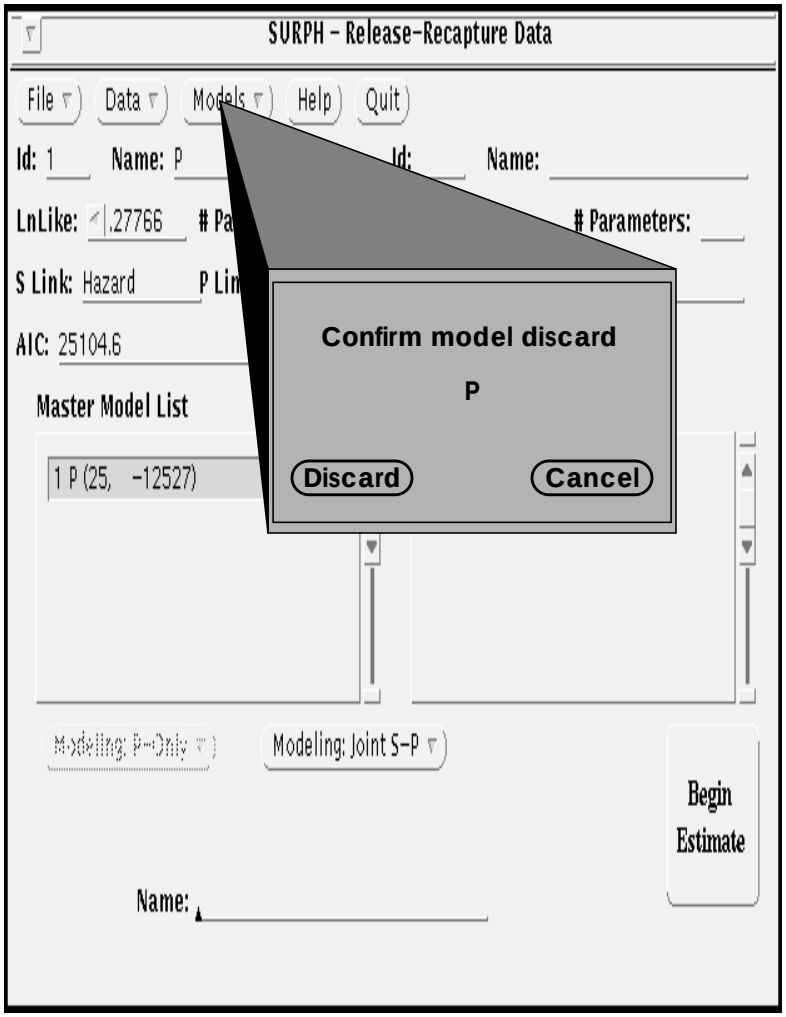

This dialog box (**Models -> Discard**) allows you to remove models that are no longer needed in SURPH. In the **Master Model List**, select the model you wish to delete by left-clicking on the model name. Then go to the Discard Models command (**Models -> Discard**), and depress the left-click on the **Discard** menu option. The **Cancel Button** allows you to exit this command without deleting a model. Once a model has been deleted, it is inaccessible, and cannot be undeleted. The only way you can "retrieve" a model that has been deleted is to estimate a new model that has the exact same parameterization as the one deleted.

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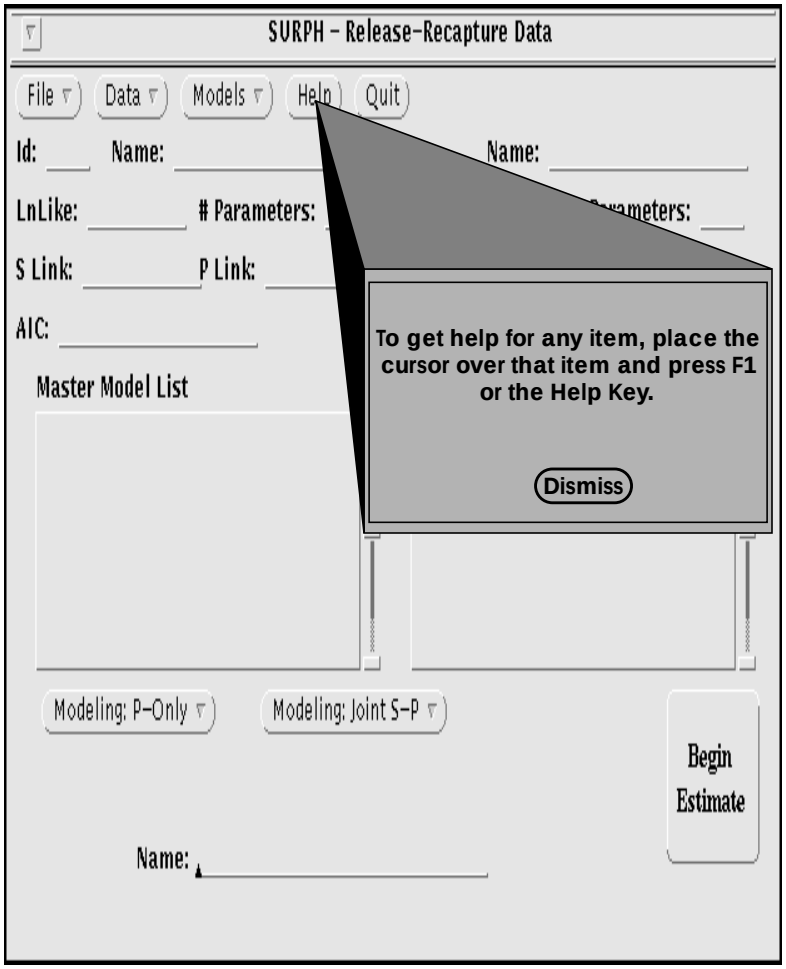

Left-clicking on the **Help Button** summons the Help Dialog Box. This dialog box window tells you how to get help for any item of the SURPH program.

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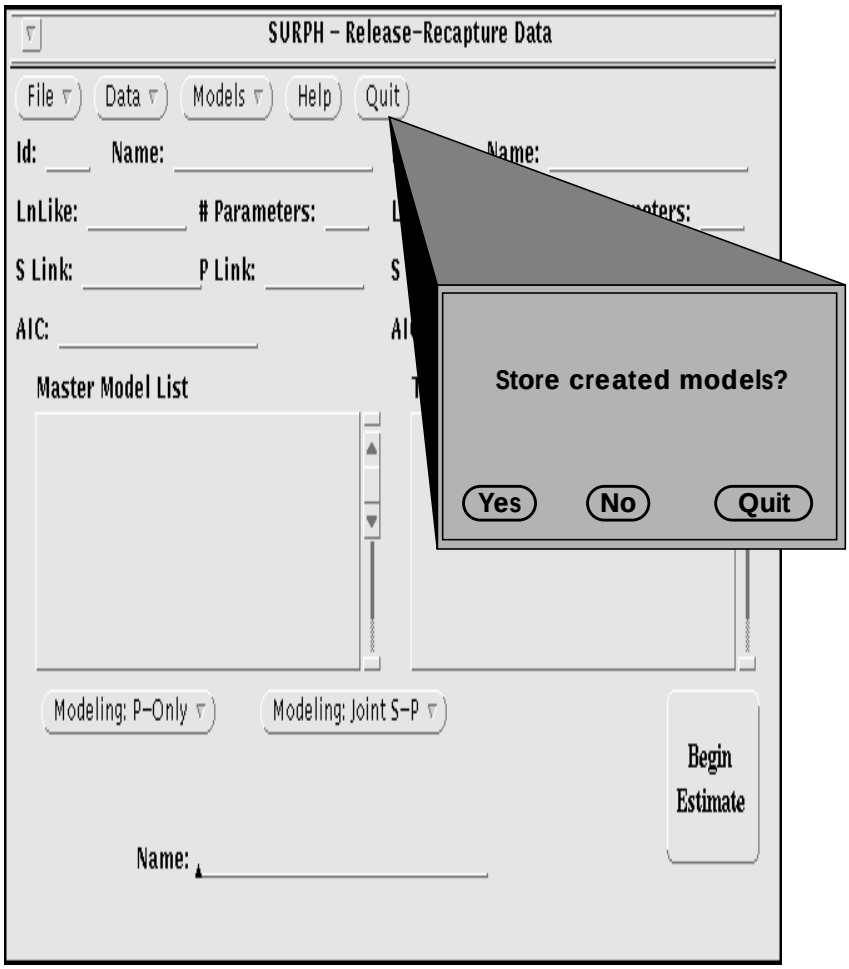

Left-clicking on the **Quit Button** summons the Quit Dialog Box. If models have been created since the most recent Store Models command, you are asked if the models should be saved before quitting the program. To choose an answer, left-click on the answer desired. If you answer "**Yes**", a Store Model Pop-Up window appears (see File: Store Models). You then enter the name of the file in which the models are to be stored. Once the models have been stored, the SURPH session ends. If you answer "**No**", the SURPH session is ended, without storing the estimated models. If you answer "**Cancel**", the dialog box is dismissed and the SURPH session continues.

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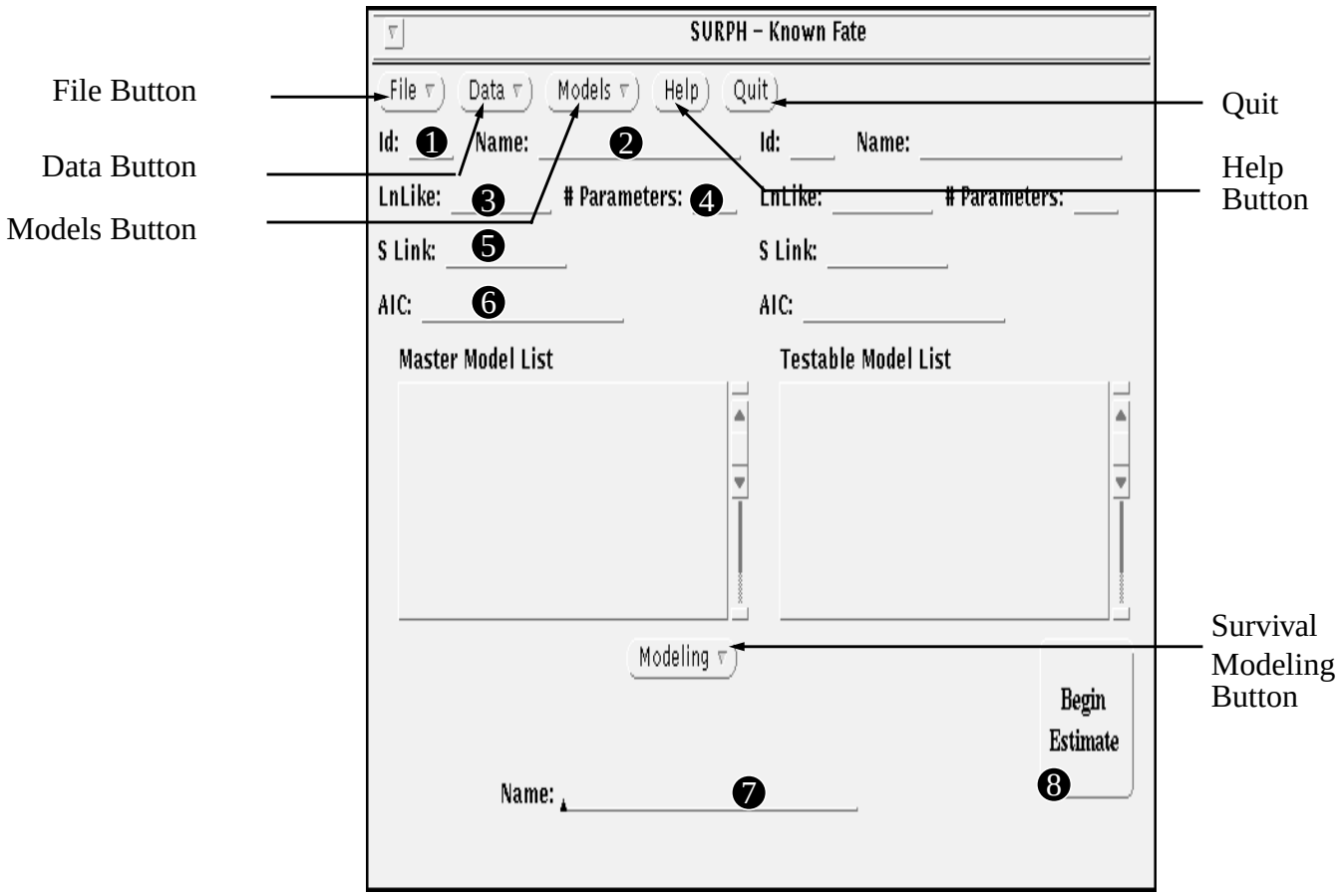


This is the SURPH Base Window for Known-Fate data files, the first window that appears after you select the Known-Fate modeling option from the SURPH Introductory Window. The SURPH Introductory Window appears when the program is started with a command line:

> **surph** *datafile*

All data summaries, modeling operations, graphics, and diagnostics are accessed from the SURPH Base Window.

Overview of Command Buttons

The pull-down menu accessed by the **File Button** is used to load data files, and to load or store model files. The **File** pull-down can also be used to end the SURPH session. Because the data file was specified on the command line, the Load Data command (**File -> Load Data**) is disabled.

The pull-down menu accessed by the **Data Button** has choices for computed Binomial probability estimates and Sampling Summary Statistics; graphical data display; data transformations; and echoing input data to the screen.

The pull-down menu accessed by the **Models Button** allows display of model estimates and graphical displays of model fit. This button also allows you to discard models and change model names.

The **Help Button** explains the use of the various buttons. To see further instructions, left-click on this button.

The **Quit Button** ends the SURPH session.

The **Modeling Button** is used to specify the parameterization of survival models. These buttons have pull-down menus that allow you to model the relationships between factors measured at the population and individual level, and the survival processes. Menu choices under the **Modeling Button** allow you to model the survival processes at the population or individual level, and allow you to specify the link function. For further descriptions of the functions associated with this button, see

Survival Modeling: Pull-Down Menu.

The SURPH Known-Fate Base Window has two lists of estimated models, the **Master Model List** and the **Testable Model List**. The **Master Model List** contains all models that have been estimated during the current SURPH session, and those that have been loaded from previous SURPH sessions. The Testable Model List contains models that can be compared to the model that has been selected from the **Master Model List**. For a model to appear within the **Testable Model List**, either the model within the **Testable Model List** is nested within the model selected from the **Master Model List**, or the model selected from the **Master Model List** is nested within the model in the **Testable Model List** (see Testing Nested Models: Master and Testable Lists).

Numbered Features

The numbered spaces 1-7 refer to attributes of the model selected from the **Master Model List**. Analogous spaces in the upper right-hand portion of the SURPH Base Window refer to attributes of the model selected within the **Testable Model List**.

❶ Displays the Model ID Number of the selected model in the **Master Model List**.

❷ Displays the name of the selected model in the **Master Model List**.

❸ Displays the Log-Likelihood of the selected model in the **Master Model List**.

❹ Displays the number of parameters estimated in the selected model in the **Master Model List**.

❺ Displays the link function for the survival parameters of the selected model in the **Master Model List**.

❻ Displays Akaike's Information Criterion (Akaike 1973) - This is used to help determine the best fitting models when the models are not nested.

The space numbered 7, and the button numbered 8 are used to create new models:

❼ This field allows you to name the model prior to running the estimation procedure. If you does not specify a name for the model, the name "Model 'n'" is assigned, where "n" is the Model ID Number. If you have a model you wish to rename, see the section for the **Models Button**.

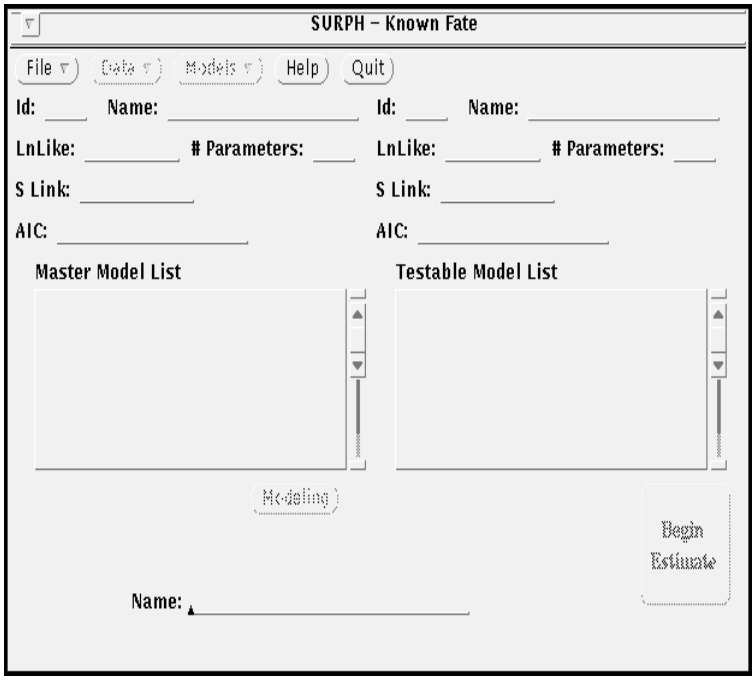
❽ Left-clicking on this button initiates the numerical optimization routine to estimate the parameters of the model specified in the modeling options under **Modeling**.

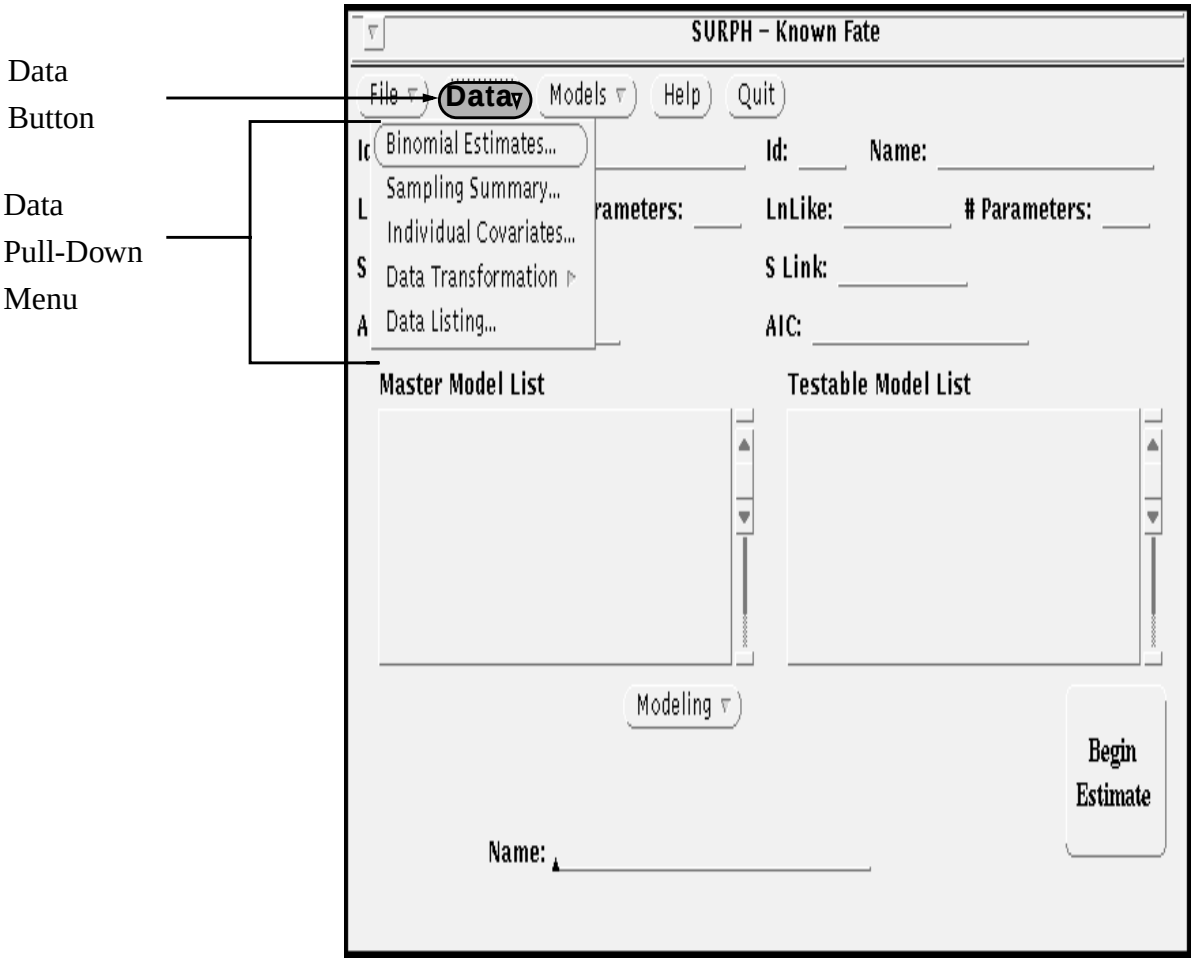
If you start SURPH without specifying an input data file on the command line:

> **surph**

not all buttons are activated (see below). Before these de-activated buttons can be used, data must be loaded. To load data, right-click on the **File Button**. A pull-down menu will appear. Left-click on **Load Data**. The **Load Input File** window will appear. If your data file is in the directory from which you started SURPH, left-click in the **File** text field and type the name of the file that contains your data. If your data is in a different directory, left-click in the **Directory** text

field and change the directory path in the **Directory** field, then left-click in the **File** field and enter the file name in the blank **File** field. Left-click on the **Load Button** in the **Load Input Data** window to load the data.





To access this pull-down menu, right-click on the **Data Button**.

The commands available from this menu specify data summaries and transformations:

Binomial Estimates - Provides the binomial estimates of survival probabilities. For further information, see Data: Binomial Estimates.

Sampling Summary - Provides a summary of the sampling results for each population during each period. For further information, see Data: Sampling Summary.

Individual Covariates - Displays the graphical representation (histograms or cumulative distribution functions) of the data, by covariate, by population, by period. For further information,

see Individual Covariates - Histograms or

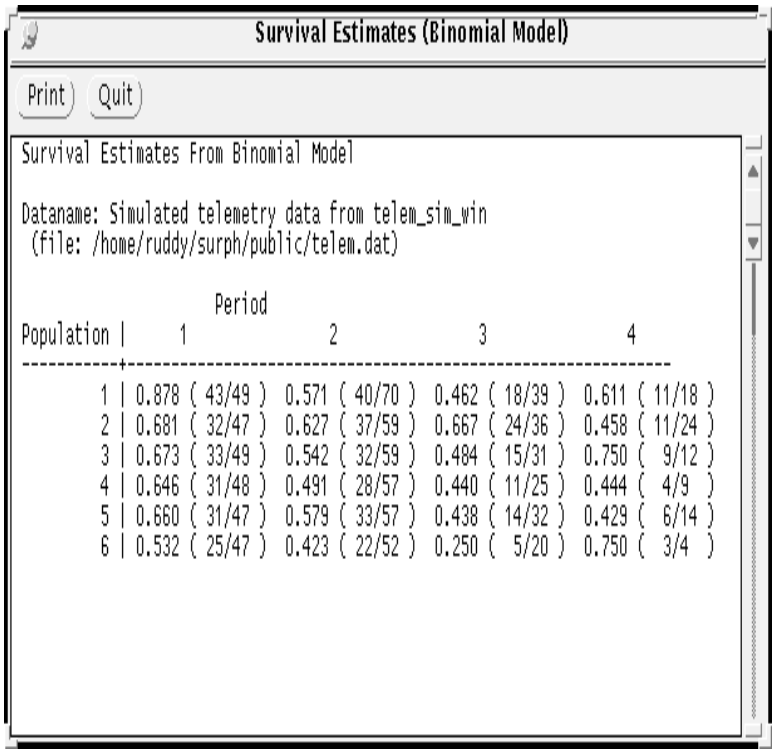
Individual Covariates - CDF Plot

Data Transformation - Allows transformations of covariate data. Examples of transformations are squares, square roots, cross products, reciprocal and natural log. For further information, see

Data Transformations: Group Covariates or

Data Transformations: Individual Covariates

Data Listing - Gives a complete listing of the input data in a formatted display. For further information, see Data Listing .




```
Survival Estimates From Binomial Model

Dataname: Simulated telemetry data from telem_sim_win
 (file: /home/ruddy/surph/public/telem.dat)

                    Period
Population |     1              2              3              4
-----------+-------------------------------------------------------------
         1 | 0.878 ( 43/49 )  0.571 ( 40/70 )  0.462 ( 18/39 )  0.611 ( 11/18 )
         2 | 0.681 ( 32/47 )  0.627 ( 37/59 )  0.667 ( 24/36 )  0.458 ( 11/24 )
         3 | 0.673 ( 33/49 )  0.542 ( 32/59 )  0.484 ( 15/31 )  0.750 (  9/12 )
         4 | 0.646 ( 31/48 )  0.491 ( 28/57 )  0.440 ( 11/25 )  0.444 (  4/9  )
         5 | 0.660 ( 31/47 )  0.579 ( 33/57 )  0.438 ( 14/32 )  0.429 (  6/14 )
         6 | 0.532 ( 25/47 )  0.423 ( 22/52 )  0.250 (  5/20 )  0.750 (  3/4  )
```

This text window (**Data -> Binomial Estimates**) shows the binomial survival probability estimates. The number in parentheses beside each probability estimate show the fraction of the number of animals that were released and that were subsequently detected (the numerator) to the total number of animals released (the denominator) (i.e., For Population 1 in Period 1, the estimated binomial survival probability is 0.878, which is equal to 43/49; 43 of the 49 animals released on the first occasion in the first population were subsequently detected).

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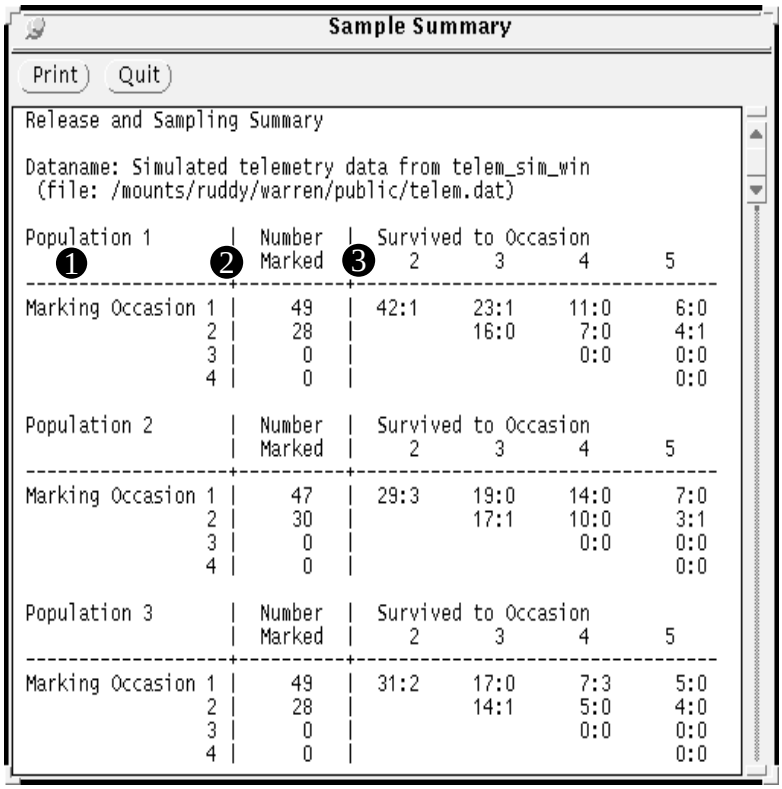

Sample Summary

Print Quit

```
Release and Sampling Summary

Dataname: Simulated telemetry data from telem_sim_win
 (file: /mounts/ruddy/warren/public/telem.dat)

Population 1        |  Number  |  Survived to Occasion
   ❶                ❷ Marked ❸    2       3       4       5
-------------------+----------+-----------------------------------
Marking Occasion 1 |     49   |  42:1     23:1    11:0     6:0
                 2 |     28   |           16:0     7:0     4:1
                 3 |      0   |                    0:0     0:0
                 4 |      0   |                            0:0

Population 2        |  Number  |  Survived to Occasion
                    |  Marked  |    2       3       4       5
-------------------+----------+-----------------------------------
Marking Occasion 1 |     47   |  29:3     19:0    14:0     7:0
                 2 |     30   |           17:1    10:0     3:1
                 3 |      0   |                    0:0     0:0
                 4 |      0   |                            0:0

Population 3        |  Number  |  Survived to Occasion
                    |  Marked  |    2       3       4       5
-------------------+----------+-----------------------------------
Marking Occasion 1 |     49   |  31:2     17:0     7:3     5:0
                 2 |     28   |           14:1     5:0     4:0
                 3 |      0   |                    0:0     0:0
                 4 |      0   |                            0:0
```

This text pane (**Data -> Sampling Summary**) display numbers of animals released and subsequently recaptured. There is one table for each population. The elements of the table for each population are:

❶ Marking Occasion — Occasion when the animal was marked and released.

❷ Number Marked — Number of animals marked and released at this occasion. This total only includes animals released for the first time.

❸ Survived to Occasion — For each marking occasion, the number of animals that survived until each subsequent occasion. The number to the left of the colon is the total number of animals known to have survived and remained at risk in the next period. To the right of the colon is the number “removed” from the sample for occasion “i”, either because they were known to be dead on occasion “i”, or because their radio-tags failed before the next samplng occasion. For example, 47 animals were marked on occasion 1 in population 2. Of these, 29 were detected alive on occasion 2 and were known to have working transmitters. Three animals detected on oocasion 2 were removed from the sample.

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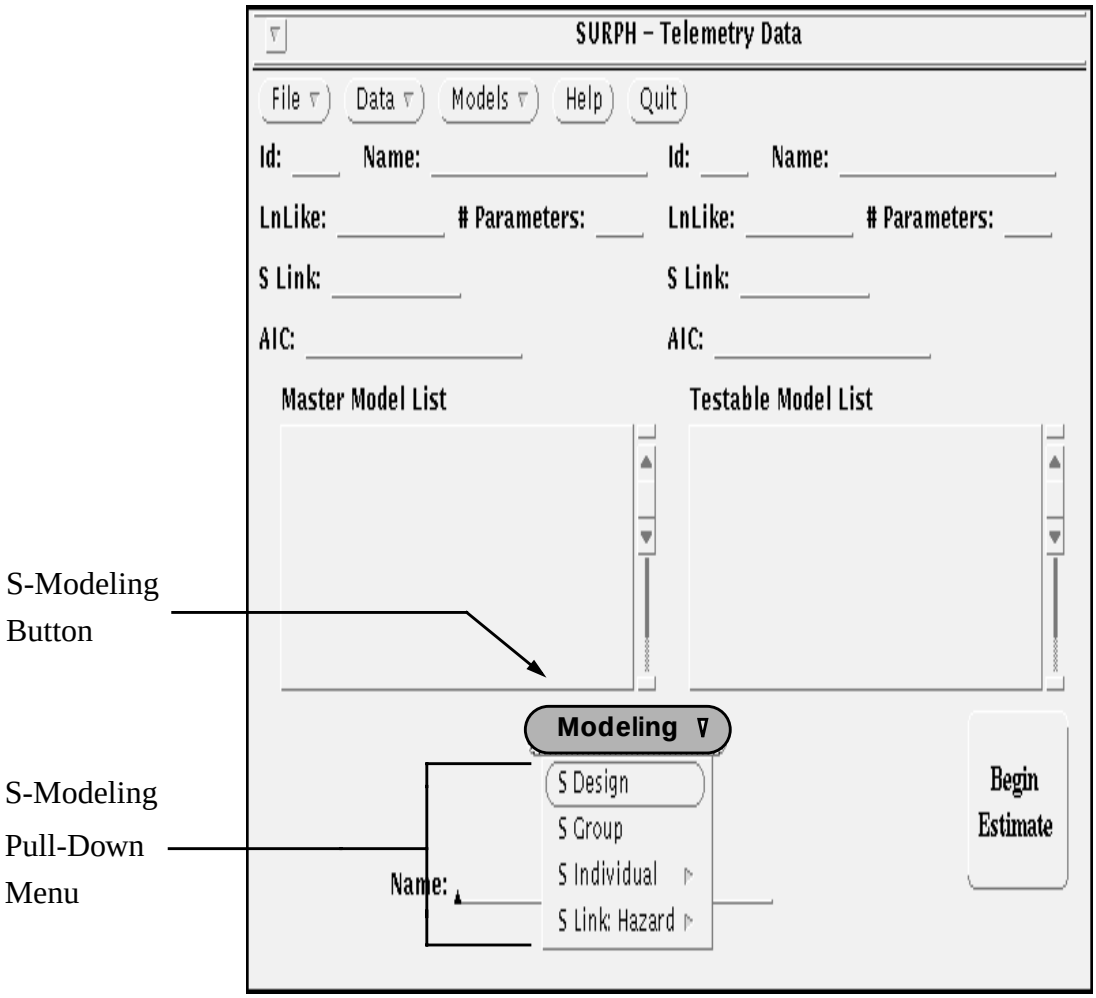


This is the pull-down menu displayed when you right-click on the **Modeling Button**.

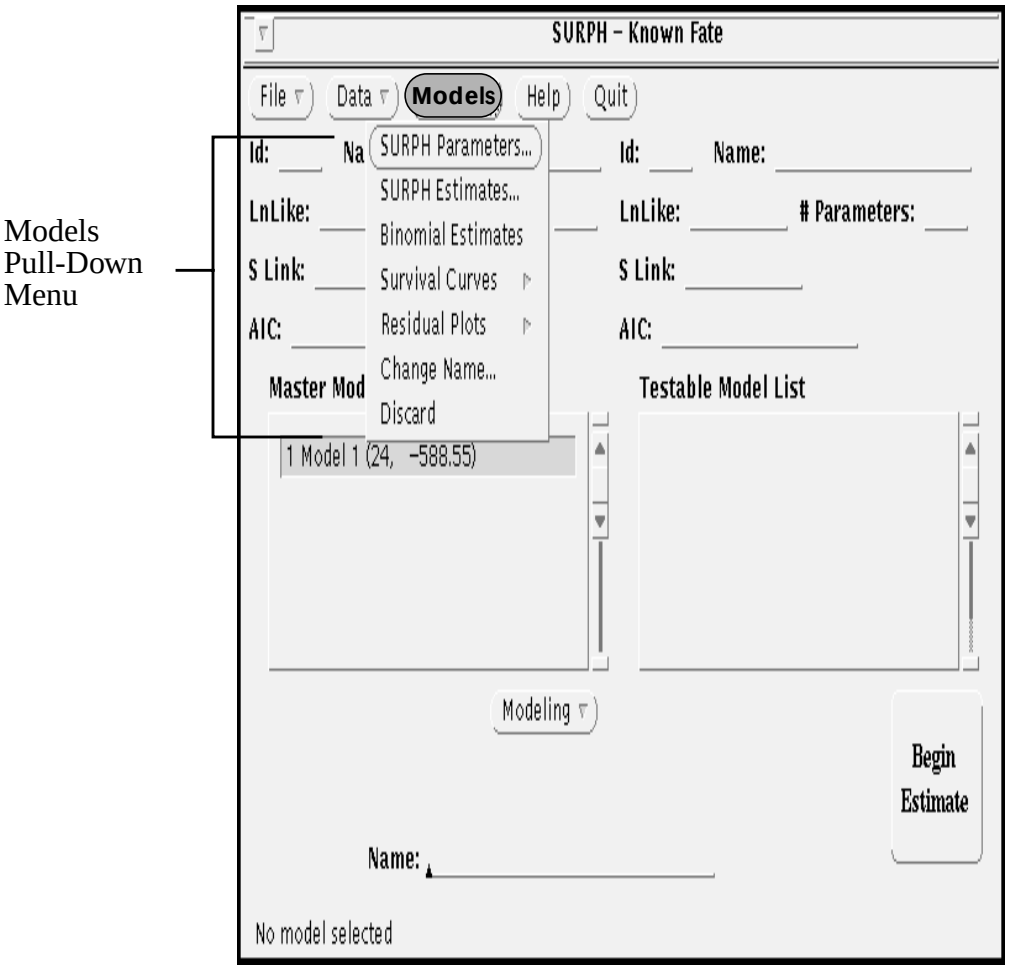
The commands available from this submenu specify models for survival probabilities:

S Design - Specify effects of the experimental design factor on survival probabilities. A Button Pad will appear that allows you to specify period and population-specific effects (see Survival Modeling: Design Pop-Up).

S Group - Specify group covariate effects on survival probabilities. A Button Pad will appear that allows you to specify parameters for period-specific group covariate effects (see Survival Modeling: Group Covariates).

S Individual - Specify individual covariate effects on survival probabilities. For each covariate selected, a Button Pad will appear. This Button Pad allows you to specify parameters for period and population-specific effects (see Survival Modeling: Individual Covariates).

S Link - Specify the function that links covariate effects to survival probabilities. The default link is Hazard. Alternatively, the Logit link function can be specified (see Survival Modeling: Link Function).



This is the pull-down window accessed by right-clicking on the **Models Button** while analyzing known-fate data. The Model Pull-Down Menu has choices to display SURPH survival estimates; view graphics that illustrate group and individual covariate effects on survival probabilities; view residual plots to investigate goodness-of-fit; change model names; and discard models. All actions pertain to the model currently selected in the **Master Model List**.

SURPH Parameters - Displays text window with estimated parameter values, standard errors of parameters, and the variance-covariance matrix for the model currently selected in the **Master Models List**. In addition, this option also provides a legend with a verbal description of the fitted parameters (see SURPH Parameter Estimates). Estimates are displayed on the scale on which they

are estimated by SURPH (e.g., $\underset{\sim}{\beta}$ in the expression $S^{exp(\underset{\sim}{X}'\underset{\sim}{\beta})}$), rather than as probabilities.

SURPH Estimates - Displays text window with "integrated probability estimates" for the model currently selected in the **Master Model List**. Estimates are displayed on the probability scale (e.g., $\hat{S}_{ik} = S^{exp(\underset{\sim}{X}'_{ik}\underset{\sim}{\beta})}$ (see SURPH Probability Estimates).

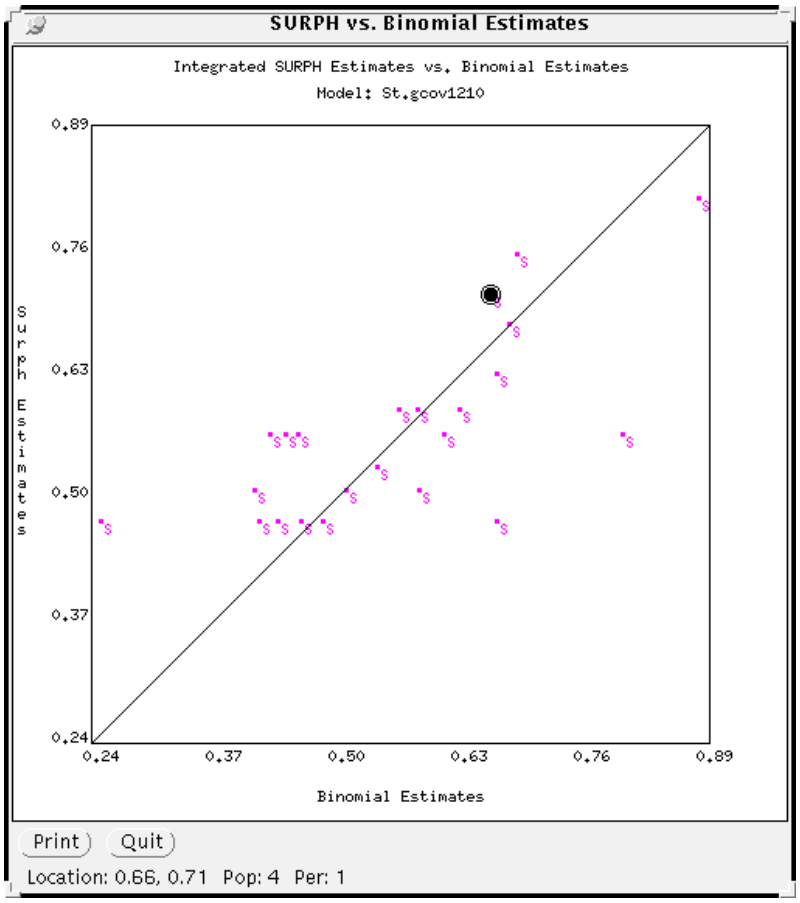
Binomial Estimates - Displays plot of integrated probability estimates of survival probabilities versus the corresponding Binomial Estimates (see Models: Binomial Estimates).

Survival Curves - Displays graphical representations of group and individual covariate effects on survival probabilities or on relative risk (see Survival Graphics and Relative Risk Graphics).

Residual Plots - Displays graphical representation of model residuals from two perspectives, a) Residuals vs. Capture History, or b) Normal Q-Q Plot (see Residual Plot or Quantile-Quantile Plot).

Change Name - Changes the name of the currently selected model in the **Master Models List** (see Change Model Name).

Discard - Discards the currently selected model in the **Master Model List**. Models that are discarded are no longer accessible to the user and have to be recomputed if needed again (see Confirm Discard Dialog Box).



This window (**Models -> Binomial Estimates**) provides a graphical display of the "integrated" SURPH probability estimates for the model currently selected in the **Master Model List** versus the binomial estimates. Survival ("S's" on the graphic) probabilities are plotted. The control panel along the bottom of the window has buttons to **Print** a copy of this window or to **Quit** (dismiss) this window.

This graphic provides a visual diagnostic for assessing the fit of models. Individual points on the graphic can be selected to identify the period and population they represent. To select a point, move the mouse cursor to that point, then left-click. The point that is displayed above as a small white circle has been selected. The description of the selected point appears in the footer of the window. Here, the selected point is from population 4, period 1. The binomial survival estimate is 0.66, while the SURPH survival estimate is 0.71.

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Glossary of Terms

A

Akaike's Information Criterion (AIC) - A criterion used for selecting among non-hierarchical models. It is defined as $-2*L_q + 2q$, where L_q is the maximized log-likelihood under the model fit with "q" parameters. Among competing models, the model with the minimum AIC is selected.

alpha level - The probability of rejecting the null hypothesis when it is true. Also known as a Type I error (α). See also significance level.

alternative hypothesis - Any admissable hypothesis alternative to the one being tested. Typically, the alternative hypothesis is the hypothesis the user wishes to "prove"; the working hypothesis.

analysis of deviance (ANODEV) - A statistical technique that partitions the total deviance associated with a set of observations into the contributions of each independent variable in the model. In SURPH, ANODEV is used to test for the contributions of group covariates. As in analysis of variance, deviance not attributable to independent variables is attributed to the error term.

Anscombe residual - A transformation of a non-normal residual (a Poisson residual in SURPH) to give an approximately normal residual. The transformation used in SURPH is

$$\text{residual} = \frac{(\text{Observed}^{2/3} - \text{Expected}^{2/3})}{\text{Expected}^{1/6}} .$$

anthropogenic - Relating to or resulting from the influence of humans.

apparent survival - a) in known-fate survival estimation models, "survival" probability when individuals lost to follow-up are treated as mortalities; b) in release-recapture models, probability that an individual survives and remains detectable; also known as "persistence."

B

baseline hazard function -The value of the hazard function for an individual or group with all covariates set equal to zero (See hazard function).

Bernoulli trial - An experiment in which the outcome can be coded with a “1” for success with probability *p* or a “0” for failure with probability (*1-p*).

binomial distribution - A discrete distribution for a random variable *X* with probability function

$f(x) = \binom{n}{x} p^x (1-p)^{n-x}$; where f(*x*) is the probability of observing *x* successes in *n* trials. The binomial distribution is derived from a series of independent Bernoulli trials, each with probability of success *p*.

block - In experimental design, the name given to a group of experimental units sharing similar non-experimental conditions. The general purpose of a block is to control for external sources of heterogeneity by having the units within the block as homogenous as possible except for the experimental application.

C

capture-effects model - A statistical model for release-recapture data that explicitly models the relationships between capture probabilities and experimental or environmental conditions.

capture-estimation model - A statistical model that estimates the capture probabilities on sampling occasions, but does not include explicit relationships between capture probabilities and covariates.

capture history - In release-recapture studies, a series of 1’s and 0’s that denote whether an individual was sighted or recorded on a particular sampling event. A “1” indicates that the individual was sighted on that particular sampling event; the “0” indicates the individual was not sighted on that particular sampling event. In SURPH a, “2” is used to denote known removals.

capture parameters - Those parameters of a release-recapture model related to the capture process.

censor - The death time of an individual is not known at the conclusion of the study or death was prematurely caused by the study process itself. In known-fate studies, censoring occurs when an individual leaves the experimental site, is removed from the study during recapture, is killed in the recapture process or the radio-tag stops functioning. In release-recapture studies, censoring occurs when live animals are removed during the study, or handling causes mortalities. These events are coded as 2's in the capture or survival histories.

Chi-Square (χ^2) Distribution - A distribution function for a continuous random variable *X* defined as

$$f(x) = \frac{x^{(k/2)-1} exp(-x/2)}{2^{(k/2)}\Gamma(k/2)} .$$

Among many uses, this distribution is used to test the overall goodness-of-fit between observed and hypothetical frequencies in contingency tables, and is used to test the significance of likelihood ratio tests of hierarchical models.

coefficient of variation - The standard error of an estimate divided by the estimate and multiplied by 100% (i.e. $\text{C.V.} = \frac{\text{SE}(\hat{\theta})}{\hat{\theta}} \times 100\ \%$). It is a measure of the relative precision of the estimate.

coefficient of determination - The square of the product moment correlation (r^2). In ANOVA, it expresses the proportion of the total corrected sum of squares of the dependent variable that is explained by the independent variable(s). It is also known as the "index of determination." In ANODEV, it expresses the ratio of the model deviance to the total corrected deviance; or the amount of total deviance explained by the independent variable(s).

Completely Randomized Design - An experimental design where the treatments are randomly assigned to the experimental units without any constraints imposed on order or placement.

conditional survivor function - Probability an animal will survival in the next time interval, given that it has survived to the current time interval.

$S_k = P(T > t_k | T \geq t_{k-1})$ where T is a random variable defined as the death time for an individual, and k and k-1 indicate sequential sampling events.

contingency table - A table of R-rows for characteristic A and C-columns for characteristic B, where the cells within the table define mutually exclusive and exhaustive class of characteristics. The table is used to test for independence or homogeneity based on the Chi-Square test statistic.

continuous - Measurement scale with an infinite number of subdivisions.

correlation - A measure of dependency between two variates. It is a number between -1 and 1, where 0 indicates no correlation, -1 indicates perfect negative correlation, and +1 indicates perfect positive correlation. It is defined mathematically as

$$\rho = \frac{\mathrm{Covar}(a, b)}{\sqrt{\mathrm{Var}(a) \cdot \mathrm{Var}(b)}} .$$

covariance matrix - The square matrix that summarizes the variance-covariance structure for n variates $x_1,..., x_n$. The diagonal elements are the variances and the off-diagonal elements are the covariances. This matrix is also known as the "Variance-Covariance Matrix."

covariate - A concomitant or independent variable. These can be divided into group-based and individual-based. Group-based covariates are traits that characterize all members of a group (e.g., treatment, control). Individual-based covariates are traits of individual animals (e.g., sex, weight, length).

Cramer-Rao Lower Bound - The asymptotic lower bound of the variance of an unbiased estimator. It is a function of the inverse of the Information matrix.

cumulative density function (cdf) - The cumulative density function (cdf) denoted F(x) of a variate X is the probability that the random variate is less than or equal to a specific value (i.e. $\mathrm{P}(\mathrm{X} \leq x)$). For a continuous random variable

$$\mathrm{F}(x) = \mathrm{P}(\mathrm{X} \leq x) = \int_{u=(-\infty)}^{x} f(u)du \text{ and for a discrete random variable } \mathrm{F}(x) = \sum_{i \leq x} p(i) .$$

cumulative hazard function - Fraction of the population dying by time t (See hazard function and empirical survivor function)

$$F(t) = \int_{T=0}^{t} f(T)\,dt.$$

D

deviance - The quantity 2 times the difference between the maximum log-likelihood attainable and that attained by the model under investigation (i.e. $2[\ln L_1 - \ln L_2]$ for two nested models where L_1 is typically the likelihood of the full model, and L_2 is a specific case of $L_{(full)}$.).

discrete - Measurement scale that is divided into a finite number of subdivisions.

dose-response - A regression relationship relating a dependent variable to a treatment dosage.

E

effect parameters - Parameters that relate the effect of an independent variable to the value of a dependent variable. Effect parameters ("slopes") are analogous to regression coefficients in linear regression.

efficiency - The ratio of variance of an estimator to the Cramer-Rao Lower Bound. If an unbiased estimator has efficiency equal to 1, it is said to be efficient.

empirical survivor function - For the case in which there are no censored individuals, the estimated survival probability defined as the ratio of the number individuals known to be alive at some time beyond time *t* to the total number of individuals released

$$\text{ESF} = \frac{\text{Number alive at time} \geq t}{n}.$$

error variance - The variance associated with the estimate of a parameter $\hat{\theta}$, denoted $\text{Var}(\hat{\theta})$.

experimental control - Experimental units where no treatment is applied, but all other manipulations are undertaken. Under certain situations, the control is also treated,

but it is treated in the manner that is the accepted standard for comparison with treatment conditions.

experimental study - A study where the experimental units are directly manipulated in a controlled and prescribed way, using the tenets of randomization and replication, as opposed to an observational study.

exponential distribution - A distribution for a continuous random variable X defined by the pdf $f(x) = \frac{1}{\theta} exp\left(\frac{-x}{\theta}\right)$. The mean of this distribution is θ, with variance θ^2.

F

F Distribution - The distribution for a continuous random variable X defined as the ratio of two independent Chi-Square random variables. It is also known as the variance ratio distribution. For a random variable X with numerator degrees of freedom m and denominator degrees of freedom k, the pdf is

$$f(x) = \frac{\Gamma((k+m)/2)(m/k)^{m/2}}{\Gamma(k/2)\Gamma(m/2)(1+(mx)/k)^{(k+m)/2}} \cdot x^{(m/2)-1}$$

where $\Gamma(x)$ is the gamma function.

full model - The maximally parameterized model in a sequence of hierarchical models, especially where the sequence is used for analysis of deviance.

G

Gamma distribution - A distribution for a continuous random variable X defined by the probability density function $f(x) = \frac{e^{-x} x^{\lambda - 1}}{\Gamma(\lambda)}$ with parameter λ.

grand mean model - The model that is fit with a single common parameter for all of the observations. This is also known as the null model.

group-based covariate - A trait or characteristic that applies to a group of individuals. Examples of group covariates include environmental factors, treatment conditions or release conditions.

H

handling mortality - An individual within the study is accidentally killed by the capture or release procedure, independent of the experimental treatment.

hazard function - The hazard function measures the probability of dying within the next small interval Δt, given survival to time t. It is given by $h(t) = \frac{f(t)}{\{1 - F(t)\}}$ where f(t) is the probability density function for the survival time distribution, and $F(t) = \int_{-\infty}^{t} f(s)ds$ **,** i.e. F(t) is the cumulative distribution f unction which gives the fraction of the population dying by time t.

hazard link function - See log-log link function.

hierarchical model - A model “B” is nested within model “A” if the model “B” can be derived from model “A” by equating two or more parameters of model “A”, or by omitting one or more parameters of model “A”. These are also known as nested models.

I

identity link function - A link function where the response variable is linearly related to the independent variables. This is also known as the linear link. When this functional form of the link function is specified, $S_k(\underset{\sim}{x}) = \underset{\sim}{x}'\underset{\sim}{\beta}$.

individual-based covariate - A trait or characteristic that applies to an individual animal. Examples of individual covariates include weight, length, hormone level, and disease intensity.

information matrix - The matrix consisting of the negative expected values of all second derivatives and all mixed partial second derivatives of a log-likelihood function. The ij^{th} element of the information matrix is

$$-\mathrm{E}\left[\frac{\partial^2}{\partial\theta_i\partial\theta_j} lnL(\underset{\sim}{\theta})\right]$$

instantaneous relative risk - A version of the relative risk where the time span between successive measures, in the limit, goes to zero; i.e. the ratio of two individuals' hazard functions (See also Relative Risk)

$$\mathrm{IRR}(\underset{\sim}{x}_1, \underset{\sim}{x}_2) = \frac{\lambda(t;\underset{\sim}{x}_1)}{\lambda(t;\underset{\sim}{x}_2)} .$$

J

Jolly-Seber Model - A release-recapture model that estimates animal abundance, birth rates, survival and capture probabilities for an open population survey.

K

Kaplan-Meier estimate - A non-parametric estimate of the survivor function. If there is no censoring, the Kaplan-Meier estimate of survival is the empirical survivor function. If there is censoring, the Kaplan-Meier estimate of survival is defined as

$$\hat{S}(t) = \prod_{i \in t_i < t} \frac{n_i - d_i}{n_i}$$

where t_i is the set of observed death times, n_i is the number of individuals at risk at time t_i (n_i = number known alive at time t_{i-1} minus those individuals known dead or censored at time t_{i-1}), and d_i is the number of individuals known dead at time t_i.

known-fate - Tag-release survival study that has 100% capture success on each sampling event.

known removal - An individual that is purposefully removed from the survival study before the study is completed or an individual that dies in the recapture process as a consequence of handling ("handling mortality").

L

Latin Square Design - An experimental design that is blocked in two directions (rows and columns) to control for two sources of extraneous error. Experimental treatments are applied randomly under the constraint that each treatment must appear once in each row and each column of the blocking scheme. For *k* treatments, a *k*x*k* square is defined.

life expectancy - The expected value for the life time of an individual within a population, i.e. E(T)=$\int tf(t)dt$.

likelihood function - The probability density function that relates the data and the parameters of the sampling process. In the likelihood function, the data are considered fixed and the parameters are permitted to vary.

likelihood ratio test - A test of the null hypothesis (with *n* parameters) against an alternative hypothesis (with *m* parameters) based on the ratio of the likelihoods $\left(\lambda = \frac{L_n}{L_m}\right)$ derived from the competing hypotheses. The quantity, $-2ln\lambda$, is distributed as a Chi-Square random variable, with *m*-*n* degrees of freedom.

linear-link function - A link function where the response variable is linearly related to the independent variables. This is also known as the identity link. When this functional form of the link function is specified, $S(\underset{\sim}{x}) = \underset{\sim}{x}'\underset{\sim}{\beta}$.

linear predictor - A linear function of the independent variables and the effect parameters ($\underset{\sim}{x}'\underset{\sim}{\beta}$).

link function - A function *f(x)* that relates the expected value (E(*y*)) of the response variable to the linear predictor such that *f*(E(*y*)) = $\underset{\sim}{x}'\underset{\sim}{\beta}$.

logistic-link function - Link function where the linear predictor is related to the following function of the response variable: $ln\left(\frac{S(\underset{\sim}{x})}{1 - S(\underset{\sim}{x})}\right) = \underset{\sim}{x}'\underset{\sim}{\beta}$. When this functional form of the link function is specified, survival probability is $S_k(\underset{\sim}{x}) = \frac{exp(\underset{\sim}{x}'_k\underset{\sim}{\beta})}{1 + exp(\underset{\sim}{x}'_k\underset{\sim}{\beta})}$.

logistic regression - A statistical model that relates observed proportions p to the linear predictor through the following function: $ln\left(\frac{p(\underset{\sim}{x})}{1-p(\underset{\sim}{x})}\right) = \underset{\sim}{x}'\underset{\sim}{\beta}$.

log-likelihood - The natural (napierian) logarithm of the likelihood function. Maximizing the log-likelihood is often more tractable than maximizing the likelihood, although the parameter estimates will be identical.

log-link function - Link function where the dependent variable is related to the linear predictor through a log transform such that $ln(S(\underset{\sim}{x})) = \underset{\sim}{x}'\underset{\sim}{\beta}$. When this functional form of the link function is specified, survival is parameterized as: $S_k(\underset{\sim}{x}) = S \cdot exp(\underset{\sim}{x}'_k\underset{\sim}{\beta})$. This link function has the property of proportional hazards.

log-log link function - Link function where the linear predictor is related to the following function of the response variable $ln(ln(S(\underset{\sim}{x}))) = \underset{\sim}{x}'\underset{\sim}{\beta}$. When this functional form of the link function is specified, survival is parameterized as: $S(\underset{\sim}{x}_k) = S^{exp(\underset{\sim}{x}'_k\underset{\sim}{\beta})}$.

lost to follow-up - An individual's fate is unknown before the conclusion of the study as a result of tag loss or other technical problems. In SURPH, the capture history is truncated on the occasion when the individual was last known to be alive.

M

maximum likelihood estimates (MLE's) -The values for the parameters that maximize the likelihood for a specific set of observed data. MLE's are asymptotically unbiased, normally distributed, and efficient.

maximum likelihood method - The method of parameter estimation where the parameter estimates are computed by maximizing the likelihood function of the parameters given the observed data.

multinomial distribution - The discrete distribution associated with events that have more than two mutually exclusive and exhaustive outcomes. The multinomial distribution is a generalization of the binomial distribution.

multiple bernoulli trial - A multinomial sample with n=1 (Also see Bernoulli trial).

N

nested models - See hierarchical models.

Newton-Raphson method - A numerical optimization method that uses the first and second derivatives of a function to find maxima/minima.

nonparametric - Another name for distribution-free methods. Nonparametric techniques do not depend upon the form of the underlying distribution.

normal distribution - A distribution for a continuous random variable X defined by the probability density function $f(x) = \frac{1}{\sigma\sqrt{2\pi}} exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right)$ with mean μ and variance σ^2.

null hypothesis - The hypothesis one wishes to nullify. This hypothesis has fewer parameters than the alternative hypothesis.

null model - The minimally-parameterized model in a hierarchical sequence, especially as related to ANODEV. For multiple-population studies in SURPH, the null model is the Period Means Model, where separate survival probabilities are estimated for each interval, common to all populations within that period. For single-population studies in SURPH, the null model fits a common survival probability for all intervals.

numerical optimization - A mathematical technique that searches throughout the parameter space Θ to find the values of the parameters that minimize or maximize the objective function.

O

objective function - A function that relates the data and the parameters through some criteria. The goal of the optimization is to maximize/ minimize the value of this function. For example, in Maximum Likelihood Estimation, the objective function is the likelihood, and the goal is to maximize the value of the likelihood function.

observational study - A study where the treatment levels are not prespecified nor randomly assigned to the treatment units, but instead the treatment levels are self-assigned through some process outside the control of the investigator.

observed information matrix - The information matrix evaluated at the maximum likelihood estimates.

odds ratio - The odds ratio compares the odds of success for one individual to that of a second. It measures how much more likely a success is for the first individual than for the second. It is defined as

$$OR(\underset{\sim}{x}_1, \underset{\sim}{x}_2) = \frac{P(A|\underset{\sim}{X} = \underset{\sim}{x}_1)/(1-P(A|\underset{\sim}{X} = \underset{\sim}{x}_1))}{P(A|\underset{\sim}{X} = \underset{\sim}{x}_2)/(1-P(A|\underset{\sim}{X} = \underset{\sim}{x}_2))} \quad \text{where}$$

$P(A|\underset{\sim}{X} = \underset{\sim}{x}_i)$ is the probability of event A under conditions $\underset{\sim}{x}_i$.

P

Paired Design - A special case of the randomized block design where two treatment levels are randomly assigned to two experimental units within each block.

parameter - An unknown quantity that characterizes the distribution of a random variable. For example, in simple linear regression, y is related to x through the slope parameter β and the intercept parameter α as $y = \alpha + \beta x$.

parametric distribution - A frequency distribution (discrete or continuous) that has a defined relationship between the parameters and the probability of observing a particular value of a random variable.

parsimony - The quality of choosing a model that fits an hypothesis while using the fewest number of possible parameters.

Pearson's χ^2 goodness-of-fit test - A statistical test that is used to determine whether the data fit an assumed distribution. The calculated statistic is

$$\text{TS} = \sum_{i=1}^{n} \frac{(\text{Observed}_i - \text{Expected}_i)^2}{\text{Expected}_i} \quad \text{where } n = \text{number of observations.}$$

Under the null hypothesis, the calculated statistic (TS) has an asymptotic Chi-Square distribution with degrees of freedom equal to {n - 1 - (number of estimated parameters)}.

PIT (Passive Interrogated Transponder)-tag - A small electronic tag (10mm) that can be inserted into an individual and that responds with a unique electronic signal when the tag is passed through an interrogating device.

population - A distinct group of individuals that share the same levels of all group covariates. This definition is specific to SURPH when used in this manual, and differs from the typical ecological or biological definition of population.

power - The probability that a statistical test rejects the null hypothesis when the alternative hypothesis is true ($1 - \beta$, where β is the probability of a Type II error).

precision - a) Measure of relative dispersion for an estimate about the true parameter value. b) Probability of discrepancy between $\hat{\theta}$ and θ. expressed as

$$P(|\hat{\theta}-\theta| < \varepsilon) = 1-\alpha \quad \text{or} \quad P\left(\left|\frac{\hat{\theta}-\theta}{\theta}\right| < \varepsilon\right) = 1-\alpha$$

probability density function (pdf) - A function that gives the probability of observing a specified value of a random variable *X* for a discrete distribution as a function of *x*. For example, with a binomial random variable, the probability density function is given as $f(x) = \binom{n}{x} p^x (1-p)^{n-x}$.

For a continuous random variable, the probability density function is the height of the function at a specified value of X, such that $\int_{-\infty}^{x} f(x)dx = P(X \le x)$ provides the cumulative distribution function.

probability distribution - Any function that maps an observation *x* with its probability of occurrence.

product-limit estimate - See Kaplan-Meier estimate.

product term - In a release-recapture model, the product of the final capture and survival probabilities. The final capture and survival probabilities are confounded.

Although it is not possible to estimate either the capture or the survival probability separately, it is possible to estimate the product of the two probabilities.

proportional hazards - A model that assumes that factors affecting survival have a multiplicative effect on the hazard function (or equivalently, an additive effect on the log hazard function) so that individuals with different covariates have proportional survival.

Q

Quasi-Newton method - Numerical optimization methods that find maxima or minima based on numerical estimates of first and second derivatives rather than using actual functional forms of the first and second derivatives.

R

radiotelemetry - The process of locating tagged individuals via radio frequencies emitted by the tag.

randomization - The process of allocating treatments in a random, probabilistic order to experimental units.

Randomized Block Design - An experimental design where each block contains one replicate of each treatment level. The treatments are randomly allocated to the experimental units within each block.

random variable - An observable quantity that may take on a range of values with a specified relative frequency or probability.

regression coefficient - The coefficient of an independent variable in a regression equation (e.g. the β parameters in the linear equation $y_i = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i}$.). Also known as “slope”.

relative risk - If death within an interval is denoted by the event $\bar{A}$, the *relative risk* of death $(RR(\underset{\sim}{x}_1, \underset{\sim}{x}_2))$ between two individuals with covariate vectors $\underset{\sim}{x}_1$ and $\underset{\sim}{x}_2$ is:

$$RR(\underset{\sim}{x}_1, \underset{\sim}{x}_2) = \frac{P(\bar{A} | \underset{\sim}{X} = \underset{\sim}{x}_1)}{P(\bar{A} | \underset{\sim}{X} = \underset{\sim}{x}_2)}$$

The $(RR(\underset{\sim}{x}_1, \underset{\sim}{x}_2))$ is a measure of how much more likely it is for an animal with covariate vector $\underset{\sim}{x}_1$ to die in the interval than for an animal with covariate vector $\underset{\sim}{x}_2$.

release group - The collection of animals within a population marked and released for the first time on a particular sampling event. Note that this definition differs from that used by Burnham et al. (1987) where a release group is defined to be the collection of animals captured and released at a particular sampling event, including previously-marked individuals.

release-recover - A subset of tag-release studies where the individuals are captured, tagged and released. The marked animals are subsequently resighted at most once, usually upon death

release-recapture - A subset of tag-release studies where the individuals are tagged with a uniquely-coded band or ring and released. Resampling is the recapture of tagged individuals while still alive. This allows the possibility of recapture multiple times, rather than only once as in release-recover studies.

replication - The application of similar treatment conditions to two or more experimental units. Replication accomplishes three major objectives: (1) It allows the experimenter to show that the treatment effect is repeatable; (2) it allows estimation of experimental error or error variability; and (3) it leads to a more precise estimate of treatment effects.

residual - The difference between the observation and the predicted model value $(y_i - \hat{y}_i)$.

response curve - The functional form of the relationship between the response variable and the independent variables.

response variable - The dependent variable of interest. In SURPH, the response variable is either the capture probability or the survival probability.

risk - Risk is the probability of a negative response (e.g., death) given present conditions.

S

sampling event - An occasion in time or a location in space when individuals are recaptured or queried to determine the status of tagged individuals. Survival status is determined in known-fate studies and recapture efforts are made in release-recapture studies.

sampling interval - The time or distance between two sampling events.

sampling location - Location in space when individuals are recaptured or queried to determine the survival status of tagged individuals

sampling occasion - A point in time when individuals are recaptured or queried to determine the survival status of tagged individuals.

sampling period - The span of time between two sampling events.

sampling segment - The distance between two sampling events.

saturated model - A model that has as many parameters as observations. This model will fit the data exactly. Also known as the full model.

score vector - The values of the first derivatives for the set of log-likelihood equations under a given parameterization. This vector is used during iterative numerical optimization procedures to solve the likelihood equations.

single-entry - A study design where tagged individuals are introduced into the study only on the first sampling event.

Split-Plot Design - An experimental design where subsidiary treatments are introduced by dividing each whole plot into two or more portions and randomly assigning the split plot treatments to the individual portions.

staggered-entry - A study design where tagged individuals are introduced into the study on more than one release occasion.

standardized residual - A transformed residual that is approximately normally distributed, with mean=0 and variance=1.

survival-effects model - A statistical model that explicitly models the relationships between survival probabilities and covariates.

survival-estimation model - A statistical model that estimates the survival probabilities between sampling occasions, but does not include explicit relationships between survival probabilities and covariates.

survival history - In known-fate studies, a series of 1's and 0's that denote whether an animal was alive or dead on a particular sampling event. A "1" indicates that the animal was alive on that particular sampling event; a "0" indicates the animal was found dead on that sampling event. A "2" indicates the animal was removed from the study, or was killed during the sampling process. A "3" indicates the animal was alive, but was lost to follow-up as a result of radio-telemetry failure.

survival parameters - Parameters that account for effects of covariates on the survival process.

survival probability - The probability of an individual surviving an interval. The realization of the survivor function for a specific interval.

survivor function - The function that describes the probability distribution that an animal survives to at least time t: $S(t) = P(T \geq t), \ 0 < t < \infty$.

T

tag-release study - Any study where individuals are marked in a manner that allows future identification, then released back into the population. Subsequent sampling is used to recapture marked individuals to evaluate demographic parameters. Tag-release studies are used to estimate a variety of population parameters including survival, abundance, density, and births.

time-invariant covariate - A covariate that does not change with time or space throughout the duration of the study. Examples of time-invariant covariates include gender, genotype, and treatment designation.

time-variant covariate - A covariate whose value changes significantly with time or space sometime during the study. Examples of time-variant covariates include age, body size and average temperature.

total corrected deviance - See total discrepancy.

total discrepancy - The deviance associated with the difference between the full model and the null model (Also termed “total corrected deviance”). The fit of an intermediate model can be assessed by examining the proportion of the total discrepancy it “explains”, taking into account the number of parameters required to achieve the reduction in deviance.

treatment - In experimentation, a stimulus that is applied in order to observe a response. In practice, a treatment may be a physical substance, a procedure or anything capable of controlled application according to the requirements of the experiment.

Type I error - Rejecting the null hypothesis when it is true. The probability of committing a Type I error is called the alpha level (α) or the significance level.

Type II error - Failure to reject the null hypothesis when it is false. The probability of committing a Type II error is called the beta level (β) .

U

unbiased estimator - An estimator whose expected value is equal to the parameter it is estimating (i.e. $E(\hat{\theta}) = \theta$.).

V

Variance-Covariance Matrix - See covariance matrix.

W

Weibull distribution - A distribution for a continuous random variable *X* of the form: $f(x) = \alpha\lambda x^{\alpha-1} exp(-\lambda x^{\alpha})$. This distribution can be used to describe lifetimes and fatigue tests. The mean of this distribution is $\lambda^{-1/\alpha}\Gamma(1+\alpha^{-1})$. A special case of the Weibull is the exponential distribution.

X-Z

z-distribution - A normal distribution with mean=0 and variance=1.

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Glossary of Symbols

Listed below are the algebraic symbols used in Chapters 2-8, along with their definitions. The symbols are listed in alphabetical order first for the English alphabet, capitals before lower case, and then the Greek alphabet, capitals before lower case.

I = total number of replicate populations.

K = number of sampling events.

P = baseline, or intercept parameter for capture probabilities.

P_{ik} = probability that a previously marked animal in population i that is alive at the time of the kth sampling event is detected on that event (group-based models) (i = 1,2,..., I; k = 2,3,..., K-1). Subscript i is dropped for single-population studies.

P_{ikj} = detection probability on sampling event k for jth animal known to be alive in population i on event k (individual-based models). Subscript i is dropped for single-population studies

S = baseline, or intercept parameter for survival probabilities.

S_{ik} = the probability that a marked animal in population i, alive immediately after sampling event k, survives to event k+1 (group-based models) (i = 1,..., I; k = 1,..., K-1). Subscript i is dropped for single-population studies

S_{ikj} = detection probability in interval k for jth animal known to be alive in population i just after event k-1 (individual-based models). Subscript i is dropped for single-population studies.

a_{ik} = number of previously marked animals in population i detected alive on sampling event k (i = 1,..., I; k = 2,..., K; a_{i1} = 0). Subscript i is dropped for single-population studies.

b_{ik} = number of previously unmarked animals in population i that are marked and released on sampling event k (i = 1, 2,..., I; k = 1, 2,..., K - 1). Subscript i is dropped for single-population studies.

c_{ik} = number of individuals in population i detected for the last time on event k (i = 1, 2,..., I; k = 1, 2,..., K – 1). Subscript i is dropped for single-population studies.

g_{ik} = number of animals marked before sampling event k that were detected both on event k and on at least one later event (i = 1,2,..., I; k = 2,3,..., K-1). Subscript i is dropped for single-population studies.

h_{ik} = number of animals marked before sampling event k that were not detected on event k, but were detected on at least one later event (i = 1,2,..., I; k = 2,3,..., K-1). Subscript i is dropped for single-population studies.

r_{ik} = total number of animals detected in population i on event k ($r_{ik} = a_{ik} + b_{ik}$) (i = 1,2,..., I; k = 1,2,..., K). Subscript i is dropped for single-population studies.

t_{ik} = total number of animals in population i detected on event k and on a later event ($t_{ik} = r_{ik} - c_{ik}$) (i=1, 2,..., I; k = 1, 2,..., K-1). Subscript i is dropped for single-population studies.

v_{ik} = number of individuals marked on or prior to event k in population i known to be alive at the time of event k + 1 (i = 1, 2,..., I; k = 1, 2,..., K - 1). Subscript i is dropped for single-population studies.

$\underset{\sim}{w}_{ik}$ = vector of group covariates in interval k for population i (i = 1, 2,..., I; k = 1, 2,..., K - 1). Subscript i is dropped for single-population studies.

$\underset{\sim}{x}_{ikj}$ = vector of individual-based covariates for the jth animal released on the kth sampling event in population i. Subscript i is dropped for single-population studies.

β_{ikl} = regression parameter for the relationship between the lth (l = 1,..., L) individual-based covariate and survival probability in the kth interval (k= 1,..., K-1) for the ith population (i = 1,..., I). These parameters are also referred to as selection parameters. Subscript i is dropped for single-population studies.

γ_j = regression parameter for the relationship between capture probabilities and the jth event-specific (group-based) covariate (j=1,..., J) (single-population models).

γ_{kj} = regression parameter describing the relationship between capture probabilities on the kth event (k= 2,..., K) and the jth (j = 1,..., J) environmental covariate measured for all populations on the kth event (multiple-population models).

δ_{ikl} = regression parameter describing the relationship between the lth (i = 1,..., L) individual-based covariate and capture probability on the kth event (k= 2,..., K) for the ith population (i = 1,..., I). Subscript i is dropped for single-population studies.

η_k = regression parameter describing the difference from the baseline capture probability for event k (k = 3,..., K).

λ = baseline, or intercept parameter for product term (product of final-interval survival and final-event capture probabilities).

ν_i = regression parameter describing the difference from the baseline capture probability

for population i (i = 2,..., I).

$(\nu\eta)_{ik}$ = regression parameter describing the interaction between population and event effects on baseline capture probability (i = 2,..., I) and (k = 3,..., K).

π_i = regression parameter describing the difference from the baseline survival probability for population i (i = 2, 3,..., I).

$(\pi\rho)_{ik}$ = regression parameter describing the interaction between population and interval effects on baseline survival probability (i = 2, 3,..., I) and (k = 2, 3,..., K-1).

φ_i = regression parameter describing the difference from the baseline product term for population i (i = 2, 3,..., I).

ρ_k = regression parameter describing the difference from the baseline survival probability for interval k (k= 2, 3,..., K-1).

τ_j = regression parameter for the relationship between survival probabilities and the jth interval-specific environmental (group-based) covariate (j=1,..., J) (single-population models).

τ_{kj} = regression parameter describing the relationship between survival probabilities in the kth interval (k= 1,..., K-1) and the jth (j = 1,..., J) environmental (group-based) covariate measured for all populations in the kth interval (multiple-population models).

χ_{ik} = probability that a marked animal in population i is detected for the last time on event k (i = 1, 2,..., I; k = 1, 2,..., K - 1). Subscript i is dropped for single-population studies.

χ_{il} = regression parameter for the relationship between the *l*th (*i* = 1,..., *L*) individual-based covariate and product term for the *i*th population (*i* = 1,..., *I*). Subscript *i* is dropped for single-population studies.

ω_j = regression parameter describing the relationship between product terms and the *j*th (*j* = 1,..., *J*) population-specific environmental covariate measured on the *K*th (final) event.