

CHAPTER 12

Jolly-Seber models in MARK

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The original Jolly-Seber (JS) model (Jolly, 1965; Seber, 1965) was primarily interested in estimating abundance. Since then, the focus of many mark-recapture experiments changed to estimating survival rates (but not abundance) using the Cormack-Jolly-Seber (CJS) models (Cormack, 1964; Jolly, 1965; Seber, 1965) particularly with the publication of Lebreton *et al.* (1992). In previous chapters concerning analysis of live encounter data, we have focussed exclusively on CJS models. In recent years, however, interest has returned to estimating parameters related to abundance such as population growth (λ_i), recruitment (f_i), as well as abundance (N_i).*

Much of the theory about estimating population growth, recruitment, and abundance can be found in Williams *et al.* (2002).

12.1. Protocol

The protocol for JS experiments is very similar to that of CJS experiments. In each of K sampling occasions, animals are captured. Unmarked animals are tagged with individually identifiable tags and released. Previous marked animals have their tag numbers read and are again released.[†] The key difference between JS and CJS experiments is the process by which unmarked animals are captured and marked. In CJS experiments, no assumptions are made about how newly marked animals are obtained. The subsequent process of recovering marked animals in CJS models is conditional upon the animal being released alive at first encounter, and survival and catchability refer only to these marked animals.[‡]

In JS experiments, the process by which unmarked animals are newly captured to be marked and released is crucial – the assumptions about this process allows the experimenter to estimate recruitment and population sizes. In particular, it is assumed that unmarked animals in the population have the same probability of capture as marked animals in the population, i.e., that newly captured unmarked animals are a random sample of all unmarked animals in the population.

* One of the reasons for preferring estimation of population growth is that estimates of population growth are fairly robust against heterogeneity in catchability (Schwarz 2001), and tag loss (Rotella & Hines 2005).

[†] Losses on capture are possible at every sampling occasion and are ignored in the discussion that follows.

[‡] Of course, we hope that the survival of the marked subset of animals tells us something about the remaining unmarked animals in the population at large.

This assumption of equal catchability for marked and unmarked animals is needed to estimate abundance or recruitment or population growth and is required for the Pradel, Link-Barker, POPAN, and Burnham JS formulations in MARK...

Other assumptions about the experiment are similar to those for the CJS model:

- Animals retain their tags throughout the experiment.*
- Tags are read properly.
- Sampling is instantaneous.
- Survival probabilities are the same for all animals (marked and unmarked) between each pair of sampling occasions (homogeneous survival).
- Catchability is the same for all animals (marked and unmarked) at each sampling occasion (homogeneous catchability). This is the most crucial assumption for JS models.[†]
- The study area is constant. If the study area changes over time, then the population size may change with the changing size of the study area.

There are generally two sources of non-closure in any particular study. Animals may leave the population through death or permanently emigrate. Conversely, animals may enter the study area from outside (immigration) or be recruited from within the study area (e.g. fish growing into the catchable portion of the population). Specific tests for closure have been developed (e.g., Stanley and Burnham, 1999), but more often tests for closure are performed by fitting models with no apparent mortality ($\varphi = 1$), or no apparent recruitment ($f = 0$, $\lambda = \varphi$, or $b = 0$), or both and letting the AIC_c indicate the appropriate weight for such simpler models.

12.2. Data

The basic unit of analysis is the capture history, a sequence of 0's and 1's that indicates when a particular animal was seen in the experiment. The JS models in **MARK** use the 'LLLLL' capture history format. For example, the history ('011010') indicates that an animal was captured for the first time at sampling occasion 2, was seen again at sampling occasion 3, not seen at sampling occasion 4, seen at sampling occasion 5, and not seen after sampling time 5.[‡] Either individual or grouped capture histories may be used.

In many papers, the list of capture histories is too long to publish, and so a series of summary statistics are commonly used (Table 12.1; see also the reduced and full m -array descriptions in Chapter 5). For example, the history (011010) would contribute a count of 1 to n_2 , n_3 , n_5 , u_2 , m_3 , m_5 , R_2 , R_3 , R_5 , r_2 , r_3 , and z_3 .

* Refer to Cowen & Schwarz (2006) for dealing with tag loss in JS experiments.

[†] Refer to Pledger and Efford (1998) for details on dealing with heterogeneity in JS models.

[‡] Again losses on capture are ignored for now but are handled in the same way as elsewhere in **MARK**.

Table 12.1: Summary statistics often used for JS experiments. Losses-on-capture are found as $n_i - R_i$.

Statistics	Definition
n_i	Number of animals captured at occasion (i), both marked and unmarked. $n_i = m_i + u_i$.
u_i	Number of unmarked animals captured at occasion (i).
m_i	Number of previously marked animals captured at occasion (i).
R_i	Number of animals released alive at occasion (i^+), i.e., just after sampling occasion (i).
r_i	Number of animals from R_i that are subsequently captured after occasion (i).
z_i	Number of animals seen before (i), seen after occasion (i), but not seen at occasion (i).

While these summary statistics form the sufficient statistics for the Jolly-Seber probability model, their use has fallen out of favor in place of the raw histories used by **MARK** for two reasons. First, the use of individual covariates will require the individual capture history vectors (see Chapter 2, and Chapter 11).

Second, it is difficult to compute goodness-of-fit statistics (i.e., the RELEASE suite of tests; Chapter 5) from the summary statistics.* If only summary statistics are available, it is possible to work ‘backwards’ and create a set of histories that will reproduce these summary statistics that can be used with **MARK** to fit various models. One problem in using these pseudo-histories is that goodness-of-fit tests are nonsensical – the goodness-of-fit tests require the full capture history of each animal.

12.3. Multiple formulations of the same process

There are a number of formulations used in **MARK** to estimate abundance and related parameters, e.g., the *POPAN*; the Link-Barker and Pradel-recruitment; and the Burnham JS and Pradel- λ formulations. All of these models are slightly different parameterizations of the underlying population processes, and all are (asymptotically) equivalent in that they should give the same estimates of abundance and related parameters.

The two main differences among the various formulations are

1. the way in which they parameterize new entrants to the population
2. if estimation is conditional upon the animals actually seen in the study (refer to Sanathanan 1972, 1977).

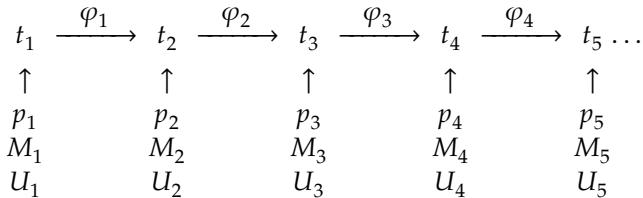
All of the formulations model the recapture of marked animals in the same way. In this section, several of these models will be examined and contrasted.

* Indeed, if the summary statistics are used by themselves, the fully time-dependent JS models will be ‘perfect’ fit to the summary statistics regardless if the model overall is a good fit.

12.3.1. The Original Jolly-Seber formulation

In the original JS formulation of Jolly (1965) and Seber (1965), the population process can be modeled as shown in Figure 12.1. The parameters p_i and φ_i are similar, but not identical to those in the CJS models. The parameter p_i is the probability of capture of both unmarked and marked animals that are alive at occasion (i) (the CJS models referred only to marked animals); the parameter φ_i refers to the survival probabilities of both marked and unmarked animals between occasions (i) and ($i + 1$) (the CJS models referred only to marked animals).

Figure 12.1: Original process model for JS experiments. p_i represents the probability of capture at occasion (i); φ_i represents the probability of an animal surviving between occasions (i) and ($i + 1$); and M_i and U_i represent the number of marked and unmarked animals alive at occasion (i). Losses-on-capture are not modeled here, but are easily included.



The number of marked animals in the population just before occasion ($i + 1$) is found as $M_{i+1} = (M_i + u_i)\varphi_i$ where u_i is the number of newly unmarked animals captured and subsequently marked.

The number of *net* new entrants to the population was *defined* as

$$B_i = U_{i+1} - \varphi_i(U_i - u_i).$$

The B_i values refer to the *net* number of new entrants to the population between sampling occasions (i) and ($i + 1$). The reference to '*net*' number of new entrants implies that animals that enter between two sampling occasions but then die before being subject to capture at occasion ($i + 1$) are excluded.* As in the CJS models, the term *survival* refers to *apparent* survival – permanent emigration is indistinguishable and treated the same as mortality. Similarly, the term *births* refers to any new animals that enter the study population regardless if *in situ* natural births or immigration from outside the study area.

The likelihood function consists of three parts. The first part models *losses-on-capture* using a simple binomial distribution as in the CJS models. The second part models the *recapture of marked animals* in exactly the same way as in the CJS model. Finally, the third part models the *number of unmarked animals captured at occasion (i)* as a binomial function of the number of unmarked animals in the population, i.e., u_i is $\text{Bin}(U_i, p_i)$.

The estimates of p_i and φ_i are found in exactly the same way as in the CJS models. The estimated unmarked population sizes were estimated as $\hat{U}_i = u_i/\hat{p}_i$. The estimated number of births was found by substituting in the estimates in the previous definition and does not form part of the likelihood. Finally, estimates of population size at each time point are found by adding the estimates of U_i and M_i .

* The term *gross* number of entrants would include these deaths prior to the next sampling occasion. Refer to Schwarz *et al.* (1993) for details on the estimation of these *gross* births.

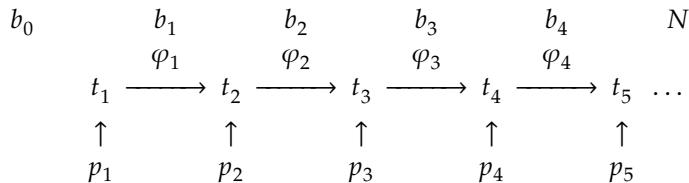
12.3.2. POPAN formulation

Schwarz & Arnason (1996) adopted a slightly different parameterization, for a number of reasons:

- The parameters B_i never directly entered into the likelihood function. The number of entrants must be non-negative, but it was difficult to enforce $\hat{B}_i \geq 0$ and negative estimates of births were often obtained.
- Because the B_i did not appear in the likelihood, how could these be forced to be equal across groups following the Lebreton *et al.* (1992) framework?
- How could death-only models (e.g., all B_i known to be zero) or birth-only models (all $\varphi_i=1$) or closed models be obtained by constraining the likelihood function.

In their parameterization, first implemented in the computer package *POPAN* and now a sub-module of **MARK**, they postulated the existence of a *super-population* consisting of all animals that would ever be born to the population, and parameters b_i which represented the probability that an animal from this hypothetical super-population would enter the population between occasion (i) and ($i + 1$) as shown in Figure 12.2.*

Figure 12.2: Process model for POPAN parameterization of JS experiments. p_i represents the probability of capture at occasion (i); φ_i represents the probability of an animal surviving between occasions (i) and ($i + 1$); and b_i represents the probability that an animal from the super-population (N) would enter the population between occasions (i) and ($i + 1$) and survive to the next sampling occasion ($i + 1$). Losses-on-capture are assumed not to happen, but are easily included.



Now the expected number of *net* new entrants is simply found as $E[B_i] = Nb_i$. If B_0 represents the number of animals alive just prior to the first sampling occasion, then

$$N = B_0 + B_1 + B_2 + \cdots + B_{K-1}$$

In other words, the total number of animals that ever are present in the study population. The parameters b_i are referred to as *PENT* (Probability of Entrance) probabilities in **MARK**. Notice that $b_0 + b_1 + \cdots + b_{K-1} = 1$. This will have consequences later when the models are fitted using **MARK**. Even though the number of new animals is not modeled in the process, modeling the entrance probabilities and a super-population size is equivalent.

* The super-population approach was first described by Crosbie and Manly (1985) where distribution functions (e.g. a Weibull distribution) was used to model survival time once an animal had entered the population. To our knowledge, there is no readily available computer code for the Crosbie & Manly (1985) model.

Under this parametrization,

$$\begin{aligned} E[N_1] &= Nb_0 \\ E[N_2] &= E[N_1]\varphi_1 + Nb_1 \\ &\vdots \end{aligned}$$

The probability of any capture history can be expressed using these parameters. For example, $\text{Pr}[(01010)]$ is found as:

$$\text{Pr}[(01010)] = [b_0(1-p_1)\varphi_1 + b_1] p_2\varphi_2(1-p_3)\varphi_3p_4[1-\varphi_4 + \varphi_4(1-p_5)].$$

As in the CJS models, the fate of the animal after the last capture is unknown – either it died, or it survived and was not seen at occasion 5. In a symmetrical fashion, the fate of the animal before the first time it is captured is also unknown. Either it was present in the population prior to sampling occasion 1 and wasn't seen at occasion 1 and survived to occasion 2, or it entered the study population between sampling occasions 1 and 2 and survived to sampling occasion 2 where it was captured for the first time. The likelihood function is again a multinomial function over all the observed capture histories. Schwarz & Arnason (1996) showed that it could be factored into three parts:

$$\mathcal{L} = \text{Pr}(\text{first capture}) \times \text{Pr}(\text{subsequent recaptures}) \times \text{Pr}(\text{loss on capture}),$$

where the second and third components are identical to the CJS models. It turns out that similar to CJS models, not all parameters are identifiable and only functions of parameters can be estimated in the fully time-dependent model. The set of non-identifiable parameters is given in Table 12.2. In particular, the final survival and catchability parameters are confounded (as in the CJS models), and symmetrically the initial entrance and catchability are confounded. This impacts three other sets of parameters, in particular N_1 and N_K cannot be clearly estimated, nor can b_1 and b_{K-1} . If confounding takes place, the estimated super-population number may be suspect, so some care must be taken in fitting appropriate models. For example, models with equal catchability over sampling occasions make all parameters identifiable.

This confounding implies that careful parameter counting may have to be done when fitting POPAN models. The fully time-dependent model $\{p_t, \varphi_t, b_t\}$ has K parameters for catchability, $(K-1)$ parameters for survival, K parameters for the PENTs, and 1 parameter for the super-population size for a total of $3K$ parameters. However, not all are identifiable and the PENTs must sum to one. Only the products b_0p_1 and $\varphi_{K-1}p_K$ can be estimated, and one of the PENTs is not 'free' (as the sum must equal 1), leaving $(3K - 3)$ parameters that can be estimated for each group.

Furthermore, as indicated in Table 12.2 (top of the next page), the b_1 and b_{K-1} parameters are affected (the estimates reflect the combination of parameters as listed in the table) which further affect N_1 and N_K . While the latter parameter combinations are 'estimable', they seldom represent anything biologically useful. The actual number of parameters reported by MARK in the results browser should be checked carefully.

Once estimates of p, φ, b , and N are obtained, the estimated number of births is obtained as $\hat{B}_i = \hat{N}\hat{b}_i$. The estimated population sizes are obtained in an iterative fashion:

$$\begin{aligned} \hat{N}_1 &= \hat{B}_0 \\ \hat{N}_2 &= \hat{N}_1\varphi_1 + \hat{B}_1 \\ &\vdots \end{aligned}$$

Table 12.2: Confounded parameters in the POPAN parameterization in the fully time-dependent model. In order to resolve this confounding, the models must make assumptions about the initial (p_1) and final (p_K) catchabilities. For example, a model may assume that catchabilities are equal across all sampling occasions.

Function	Interpretation
$\varphi_{K-1}p_K$	Final survival and catchability.
b_0p_1	Initial entrance and catchability.
$b_1 + b_0(1 - p_1)\varphi_1$	Entry between first and second occasions cannot be cleanly estimated because initial entrance probability cannot be estimated. MARK (and other programs) will report an estimate for this complicated function of parameters but it may not be biologically meaningful.
b_{K-1}/φ_{K-1}	Entry prior to last sampling occasion cannot be cleanly estimated because final survival probability cannot be estimated. MARK (and other programs) will report an estimate for this complicated function of parameters but it may not be biologically meaningful.

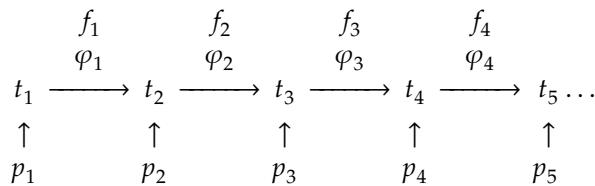
If losses on capture occur, they are removed before the population size at occasion (i) is propagated to occasion ($i + 1$).

The likelihood does not contain any terms for B_i or N_i – these are derived parameters and standard errors for these estimates are found using the Delta method (see Appendix 2).

12.3.3. Link-Barker and Pradel-recruitment formulations

The Link-Barker (2005) and Pradel-recruitment* (1996) formulations are conceptually the same and the process model is shown in Figure 12.3. The parameters for survival (φ_i) and catchability (p_i) are standard. The parameter f_i is interpreted as a *per capita* recruitment probability, i.e., how many net new animals per animal alive at occasion (i) enter the population between occasion (i) and ($i + 1$)?

Figure 12.3: Process model for Link-Barker and Pradel-recruitment parameterization of JS experiments. p_i represents the probability of capture at occasion (i); φ_i represents the probability of an animal surviving between occasions (i) and ($i + 1$); and f_i represents the net recruitment probability, i.e., the *per capita* number of new animals that enter between occasions (i) and ($i + 1$) and survive to the next sampling occasion ($i + 1$) per animal alive at occasion (i). Losses-on-capture are assumed not to have happened, but are easily included.



* There are three different Pradel models and ‘recruitment’ refers to the Pradel models parameterized using f_i terms

Unlike the *POPAN* formulation, the Link-Barker formulation conditions upon an animal being seen somewhere in the experiment. This eliminates the necessity of estimating the super-population size, but also means that abundance cannot be directly estimated. Any probability of a history must be normalized by the probability of being a non-zero history.

For example, $\text{Pr}[(01010)|\text{animal seen}]$ is proportional to:

$$\text{Pr}[(01010)|\text{animal seen}] \propto [(1 - p_1)\varphi_1 + f_1] / p_1 \times p_2\varphi_2 (1 - p_3) \varphi_3 p_4 [1 - \varphi_4 + \varphi_4 (1 - p_5)],$$

where the constant of proportionality is related to the probability of seeing an animal somewhere in the experiment. As in the CJS models, the fate of the animal after the last capture is unknown – either it died, or it survived and was not seen at occasion 5. In a symmetrical fashion, the fate of the animal before the first time it is captured is also unknown – either it was present among animals seen in the experiment at time 1, was not seen, and survived to time 2, or it entered between times 1 and 2. The likelihood function is a multinomial function over all the observed capture histories conditional upon an animal being seen somewhere in the experiment.

The implementation of the Link-Barker model differs from the Pradel-recruitment formulation in a number of ways. First, Link-Barker partitioned the likelihood in a similar fashion to the *POPAN* formulation which made it easier to implement in the Bayesian context of their paper. Second, Link-Barker explicitly modeled the confounded parameters (but the **MARK** implementation leaves the confounded parameters separate and it is the user's responsibility to understand the confounding). Third, losses on capture are handled differently between the two formulations and this affects the interpretation of the recruitment parameters.

The Link-Barker model also differs from the *POPAN* formulation as there is no need to postulate the existence of a super-population – the model is fit conditional upon the observed number of animals in the experiment.* Section 12.3.5 outlines the equivalences between the Link-Barker parameters and those of other formulations.

As in the *POPAN* formulation, the fully time-dependent Link-Barker and Pradel-recruitment models have a number of parameter confoundings as listed in Table 12.3.

Table 12.3: Confounded parameters in the Link-Barker parameterization in the fully time-dependent model.

In order to resolve this confounding, the models must make assumptions about the initial (p_1) and final (p_K) catchabilities. For example, a model may assume that catchabilities are equal across all sampling occasions.

Function	Interpretation
$\varphi_{K-1}p_K$	Final survival and catchability
$(\varphi_1 + f_1)/p_1$	Initial recruitment and survival
$f_{K-1}p_K$	Final recruitment and catchability cannot be cleanly estimated. MARK (and other programs) will report an estimate for this complicated function of parameters but it may not be biologically meaningful.

* The implementation of Schwarz & Arnason (1996) in the *POPAN* package also estimates parameters conditional upon being seen, and then adds another step to estimate the super-population size.

On the surface, the fully time-dependent model $\{p_t \varphi_t f_t\}$ has K catchability parameters, $(K - 1)$ survival parameters, and $(K - 1)$ recruitment parameters for a total of $(3K - 2)$ parameters. However, only the product $\varphi_{K-1} p_K$ and the ratio (f_1/p_1) can be estimated, leaving a net of $(3K - 4)$ parameters. The estimate for f_{K-1} estimates are functions of other parameters as shown in Table 12.3.

The abundance at each sampling occasion and the absolute number of new entrants cannot be estimated even as derived parameters because of the conditioning upon animals seen at least once during the experiment.

12.3.4. Burnham JS and Pradel- λ formulations

The final formulations to be considered in this chapter model new entrants to the population indirectly by modeling the rate of population growth (λ) between each interval where population growth is the net effect of survival and recruitment. If φ_i is the decrease in the population per member alive at time (i), and f_i is the increase in the population per member alive at time (i), then the sum of their contributions is the net population growth:

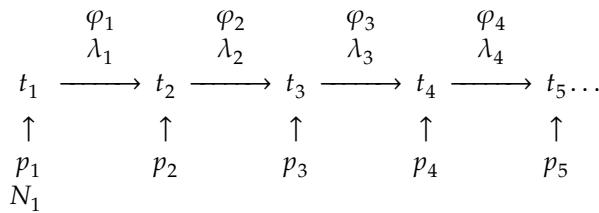
$$\lambda_i = N_{i+1}/N_i = \varphi_i + f_i$$

. These formulations were developed by Burnham (1991) and Pradel (1996).

The key difference between the two parameterizations is that the Pradel- λ approach is conditional upon animals being seen during the study, while the Burnham JS formulation is not. Therefore, the Burnham Jolly-Seber formulation also includes a parameter for the population size at the start of the experiment. This enables the estimation of the population size at each subsequent time point.

However, in practice, it is often difficult to get the Burnham-JS model to converge during the numerical maximization of the likelihood. Although the implementation of this model has been thoroughly checked and found to be correct, **MARK** has some difficulty obtaining numerical solutions for the parameters because of the penalty constraints required to keep the parameters consistent with each other.* For this reason, only the Pradel- λ formulation will be discussed further in this section (and treated in depth in Chapter 13). The process model is shown in Figure 12.4. The parameters for survival (φ_i) and catchability (p_i) are standard. The parameter λ_i is interpreted as the ratio of successive population abundances.

Figure 12.4: Process model for Burnham and Pradel- λ parameterization of JS experiments. p_i represents the probability of capture at occasion (i); φ_i represents the probability of an animal surviving between occasions (i) and ($i + 1$); and λ_i represents the rate of population change. The population size at time 1, N_1 is used by the Burnham formulation, but not by the Pradel- λ formulation. Losses-on-capture are assumed not to happen, but are easily included.



* This convergence problem disappears for some models if simulated annealing is used for the numerical optimization. –J. Laake & E. G. Cooch, *pers. obs.*

Unlike the POPAN and Burnham formulations, the Pradel- λ formulation conditions upon an animal being seen somewhere in the experiment. This eliminates the necessity of estimating the population sizes at any sampling occasion. But, the probability of a history must now be normalized by the probability of being a non-zero history. For example, $\text{Pr}[(01010)|\text{animal seen}]$ is proportional to:

$$\text{Pr}[(01010)|\text{animal seen}] \propto [\lambda_1 - p_1 \varphi_1] \times p_2 \varphi_2 (1 - p_3) \varphi_3 p_4 [1 - \varphi_4 + \varphi_4 (1 - p_5)],$$

where the constant of proportionality is related to the probability of seeing an animal somewhere in the experiment.

As in the CJS models, the fate of the animal after the last capture is unknown – either it died, or it survived and was not seen at occasion 5. In a symmetrical fashion, the fate of the animal before the first time it is captured is also unknown – either it was present at the initial sampling occasion and not seen, or was part of the population growth (over and above survival from the first sampling occasion). The likelihood function is a multinomial function over all the observed capture histories conditional upon an animal being seen somewhere in the experiment.

Section 12.3.5 outlines the equivalences between the Pradel- λ parameters and those of other formulations.

As in the POPAN formulation, the fully time-dependent Pradel- λ formulation has a number of parameter confoundings as listed in Table 12.4. On the surface, the fully time-dependent model $\{p_t, \varphi_t, \lambda_t\}$ has K catchability parameters, $(K - 1)$ survival parameters, and $(K - 1)$ growth parameters for a total of $3K - 2$ parameters. However, only the product $\varphi_{K-1} p_K$ and the function $\lambda_1 - \varphi_1 p_1$ can be estimated, leaving a net of $(3K - 4)$ parameters. Furthermore, the estimate for λ_{K-1} estimates a function of other parameters and may not be interpretable.

The abundance at each sampling occasion and the absolute number of new entrants cannot be estimated even as derived parameters because of the conditioning upon animals seen at least once during the experiment.

Table 12.4: Confounded parameters in the Pradel- λ parameterization in the fully time-dependent model. In order to resolve this confounding, the models must make assumptions about the initial (p_1) and final (p_K) catchabilities. For example, a model may assume that catchabilities are equal across all sampling occasions.

Function	Interpretation
$\varphi_{K-1} p_K$	Final survival and catchability
$\lambda_1 - \varphi_1 p_1$	Initial growth and survival
$\lambda_{K-1} p_K$	Final recruitment and catchability cannot be cleanly estimated. MARK (and other programs) will report an estimate for this complicated function of parameters but it may not be biologically meaningful.

Because population growth (λ) is a function both of survival and recruitment (i.e., $\lambda_i = \varphi_i + f_i$), the modeler should be careful about fitting simpler models that restrict population growth but leave survival time-dependent. For example the model $\{p_t \varphi_t \lambda_t\}$ would imply that recruitment varies in a time dependent fashion to exactly balance changes in survival to keep population growth constant. This may not be a sensible biological model.

Another potential problem with the Pradel- λ model is that no constraints are imposed in **MARK** that population growth must exceed the estimated survival probability. Consequently (as seen in the examples that follow), it is possible to get estimated survival probabilities of 80% while the estimated population growth rate is only 70%. This logically cannot happen, and is often an indication that recruitment did not occur in that interval – the illogical estimates are artifacts of the estimation process. Under these circumstances, models that separate recruitment from population growth may be preferred.

12.3.5. Choosing among the formulations

All of the formulations use the same input file in the same format. Which JS formulation should be used for a particular experiment? There are two considerations.

First, only certain of the formulations can be used in **MARK** if losses-on-capture occur in the experiment.

Secondly, and more importantly, different formulations give you different types of information and can be used to test different hypotheses. All of the formulations should give the same estimates of survival and catchability, as all formulations estimate these from recaptures of previously marked animals using a CJS likelihood component. Even though all the models give different types of estimates for growth or recruitment or births, it is always possible to transform the estimates from one type to another by simple transformation and the standard errors can be found using the Delta method.

The major equivalents are between NET births, recruitment, and population growth parameters. Recruitment parameters are the net number of new animals that enter the population between occasions (i) and ($i + 1$) per animal present in the population at occasion (i)

$$f_i = \frac{B_i}{N_i} = N \frac{b_i}{N_i}.$$

Population growth is the proportionate increase in abundance between occasions (i) and ($i + 1$):

$$\lambda_i = \frac{N_{i+1}}{N_i} = \frac{N_i \varphi_i + B_i}{N_i} = \varphi_i + f_i.$$

Actual estimates from fitted models may not follow these exact relationships for several reasons.

First, certain estimates (e.g., apparent survival) should be constrained to lie between 0 and 1. If an estimated survival hits against this boundary, estimates of survival prior to and after this sampling occasion will also be affected. If the *identity* link of **MARK** is used, estimates are allowed to fall outside these ‘normal’ boundaries, and usually the exact relationships above then hold true among the estimates as well.

Second, losses on capture complicate the equivalences among parameters. For example, Link & Barker (2005) indicate that their f_i should be interpreted as the number of new animals that enter between occasions (i) and ($i + 1$) per hypothetical animals alive at occasion (i) in the absence of losses on capture, while the Pradel-recruitment f_i is the number of new animals after losses on capture have been taken into account.

Lastly, **MARK** does **not** impose constraints that estimated population growth parameters must be at least as great as estimated survival probabilities. Consequently, it is possible (as seen in the examples) that the estimated population growth rate is less than the estimated survival probability which would imply a negative recruitment. In my opinion, formulations that model recruitment and survival as separate processes are preferred in these case – the estimated population growth rate can always be derived from these alternative models.

It cannot be emphasized too strongly, that **all of the formulations require the same careful attention to study design** – in particular the study area must remain a consistent size, and the probability of capturing an unmarked individual must be the same as a marked individual at each sampling occasion. A Cormack-Jolly-Seber experiment where marked animals are captured and released haphazardly, should not be analyzed using any of the formulations of the Jolly-Seber model discussed in this chapter.

Table 12.5: Summary of criteria to choose among the different JS formulations

formulation	losses on capture	estimates available for			
		abundance	net births	recruitment	λ
POPAN	yes	yes	yes	no	no
Link-Barker	yes	no	no	yes	yes
Pradel-recruitment	no	no	no	yes	yes
Burnham JS	yes	yes	yes	no	yes
Pradel- λ	yes	no	no	no	yes

- The implementation of Burnham's JS model in **MARK** often does not converge, and is not recommended (although convergence problems may be minimized for some models if simulated annealing is used for the numerical optimization. – J. Laake & E. G. Cooch, *pers. obs.*)
- The standalone package of *POPAN* will estimate recruitment, and population growth as derived parameters

12.3.6. Interesting tidbits

There have been a number of queries in the **MARK** forum (<http://www.phidot.org/forum>) about the use of *POPAN* and other models to estimate abundance. This section will try to answer some of these queries in more detail.

Deviance of 0 in *POPAN*

The following query was received in the **MARK** forum (<http://www.phidot.org/forum>, 2006-04-07) which asked:

'I read on one of the other posts that getting a deviance of zero was possible using the robust design model because the saturated model hadn't been computed yet and some constants were left out for faster computation. Is something along these lines at play in POPAN also because when I run a particular set of data, I get a deviance of zero?'

The deviance of models is often computed as the negative of twice the difference in the log-likelihood between the current model and a 'saturated' model. The usual saturated model in CJS and other models that condition upon an animal's first capture, is to have a separate probability for each observed history, i.e., if ω is a capture history (e.g., '010011') then the $\text{Pr}(\omega)$ under the saturated model is found as $\text{Pr}(\omega) = \frac{n_\omega}{n_{obs}}$ where n_ω is the number of animals with capture history ω , and n_{obs} is the total number of animals observed.

In such cases, the log-likelihood of the saturated model (ignoring constants) is then

$$\sum n_\omega \log(p_\omega) = \sum n_\omega \log\left(\frac{n_\omega}{n_{obs}}\right).$$

However, this doesn't work for models where abundance is estimated because you need to include the animals with history ('000000....'), i.e., those animals not observed. This can only be computed if the population size is estimated which cannot be estimated under the saturated model. Hence a 'deviance' cannot be directly computed.

However, the likelihood can be portioned as shown earlier into components representing the probability of first capture, the probability of subsequent recapture given the animal has been captured, and the probability of losses-on-capture given that an animal is captured. Schwarz & Arnason (1996) and Link & Barker (2005) showed that the first component is essentially non-informative about the capture, survival, and loss-on-capture rates.

This suggests that an approximate deviance could be computed using only the latter two components, i.e., by conditioning upon animals that are seen at least once in the experiment. The difference between the two likelihoods would be based only on the part representing animals seen at least once.

In practice, we would suggest that you compute a deviance based on conditioning on the observed animals. The easiest way is to use the Link-Barker model (which doesn't estimate abundance) but is 'equivalent' to the POPAN model. So if you fit a $\{p_t \varphi_t b_t\}$ model in POPAN look at the deviance of the $\{p_t \varphi_t f_t\}$ model in Link-Barker formulation. This could be used to estimate a variance-inflation factor to adjust reported standard errors.

12.4. Example 1 – estimating the number of spawning salmon

After spending several years at sea, coho salmon (*Oncorhynchus kisutch*) return to spawn in the Chase River, British Columbia. The normal life cycle of coho salmon is to return at age 3 as adults to spawn and die. But, some precocious males return earlier at age 2 to spawn and die. One question of interest is if the distribution of salmon that return to spawn at different parts in the spawning period the same for regular adult and precocious males?

As fish return to the Chase River, they are captured using electrofishing gear. If they are unmarked they are given a unique tag number and released. If they were previously marked, the tag number is read. The experiment took place over a 10 week period in 1989, but the data from weeks 1 and 2, and weeks 9 and 10 were pooled and labeled as weeks 1.5 and 9.5. Approximately the same amount of effort was expended in each week of sampling. More details of this experiment are found in Schwarz *et al.* (1993).

The data file is given in the **chase_both.inp** file, and a portion of it is reproduced in Figure 12.5 (top of the next page). This study has two groups, the regular adult males and the precocious males (called jacks). Notice that a separate capture history is used for *each* tagged fish – unfortunately, this implies that the residual plots and deviance plots in MARK cannot be used to assess goodness of fit.

Figure 12.5: Portion of the data for the Chase 1989 experiment

```

/* Estimating salmon numbers returning to spawn in Chase River 1989 */
/* These are the male salmon with two groups. */
/* Group1 = adults . group2=jacks */
/* Survey conducted over 10 weeks. Weeks 1 & 2 pooled. weeks 9 & 10 pooled */
11000000 -1 0 ; /* tagnum=1 */
10000000 0 1 ; /* tagnum=3 */
10000000 0 1 ; /* tagnum=4 */
10000000 0 1 ; /* tagnum=6 */
11000000 0 1 ; /* tagnum=8 */
10110000 0 1 ; /* tagnum=9 */
10000000 0 1 ; /* tagnum=10 */
10000000 1 0 ; /* tagnum=11 */
... additional histories follow ....

```

Summary statistics for this experiment are presented in Table 12.6:

Table 12.6: Summary statistics for the Chase 1989 experiment

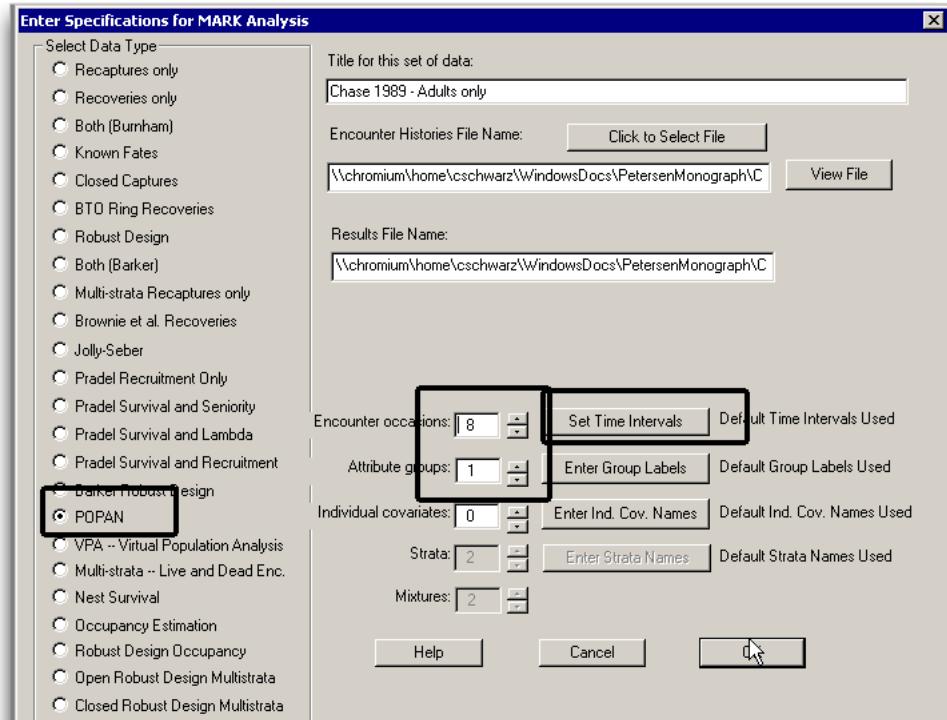
statistics for adults							statistics for jacks						
t_i	n_i	m_i	u_i	R_i	r_i	z_i	t_i	n_i	m_i	u_i	R_i	r_i	z_i
1.5	37	0	37	37	12	0	1.5	67	0	67	62	21	0
3.0	22	6	16	21	13	6	3.0	28	9	19	25	7	12
4.0	52	7	45	41	19	12	4.0	46	6	40	44	9	13
5.0	56	17	39	54	26	14	5.0	47	12	35	45	5	10
6.0	46	26	20	38	8	14	6.0	25	9	16	24	3	6
7.0	28	16	12	20	2	6	7.0	16	6	10	12	1	3
8.0	22	3	19	16	2	5	8.0	7	1	6	5	1	3
9.5	10	7	3	0	0	0	9.5	7	4	3	0	0	0

Because $n_i > R_i$ for some sampling occasions, this indicates that some losses-on-capture occurred. For example, there was one adult loss-on-capture in week 3; 11 adults lost in week 4, etc.

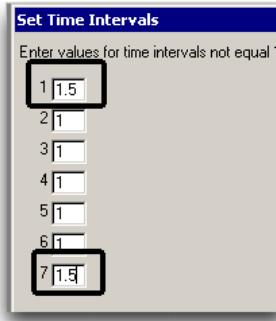
12.4.1. POPAN formulation

The POPAN super-population is a natural way to think of this experiment – a pool of fish is returning to spawn. During each week, a certain fraction of these returning fish decide to enter the spawning areas.

Let us begin by fitting a model **only** to the regular adults (use the input file **chase_adult.inp**), i.e., to the first group. Later models will be fit to both groups (and will require the **chase_both.inp** file). Launch **MARK**. Select the **POPAN** data type, enter the number of sampling occasions and the number of attribute groups, as shown at the top of the next page.



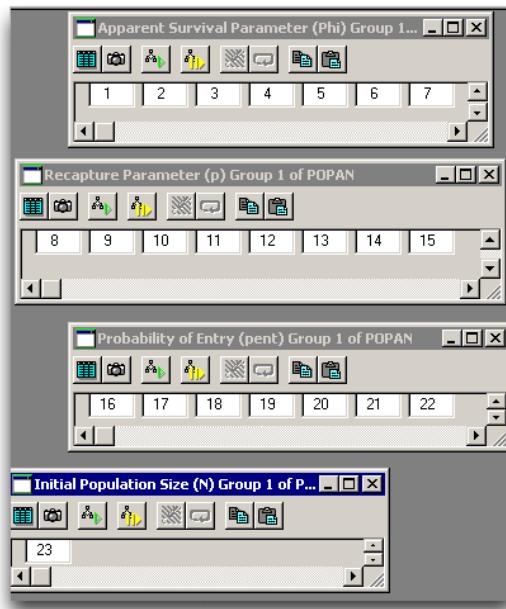
Don't forget to set the intervals between sampling occasions. As weeks (1 and 2) were pooled and labeled as week 1.5, the interval between the first and second sampling occasion is 1.5 weeks. Similarly weeks (9 and 10) were pooled and so the last interval is also longer.



Start by fitting a fully-time dependent model $\{p_t \varphi_t b_t\}$ (using an obvious notation extension from CJS models). In this model there are 8 sampling occasions which give rise to 8 capture probabilities, 7 apparent survival probabilities, 8 probability of entry probabilities, and 1 super-population parameter.

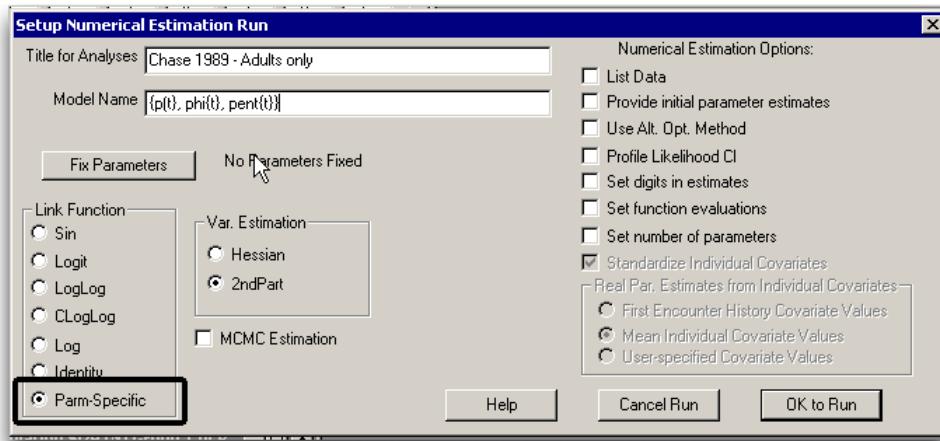
Note that **MARK** does *not* allow the user to specify the parameter b_0 (the proportion of the population available just before the first sampling occasion) and so only presents 7 *PENT* parameters in the PIM and output corresponding to b_1, \dots, b_7 .*

* In the stand alone *POPAN* package, the user has access to all of the *PENT*'s.



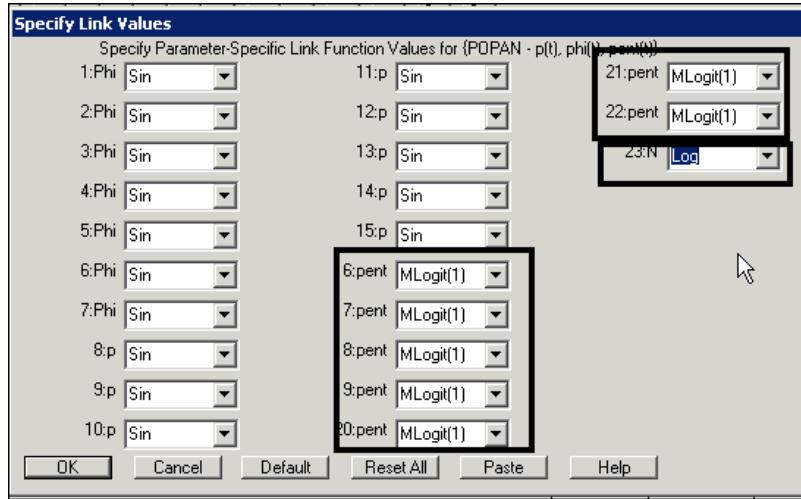
Note that *unlike* the CJS models, we assume a single set of survival and catchability parameters, regardless of when previously captured. The super-population size has its own parameter.

Because $b_0 + b_1 + \dots + b_{K-1} = 1$, a special link-function must be specified for the *PENT* parameters. This is done using the '**Parameter specific link function**' radio button:



The *sin* or *logit* or any of the other link functions can be used for the p and φ parameters. In order to specify that a set of parameters must sum to 1, the *Multinomial Logit* link function (called **Mlogit** in **MARK**) must be used (the multinomial logit (**Mlogit**) link was introduced in some detail in Chapter 10). If there are several groups, each set of *PENTs* must independently sum to 1, so **MARK** provides several sets of **Mlogit** link functions. As there is only one group, the **Mlogit(1)** link-function is used for the *PENTs*. It is possible to specify that some of the *PENTs* are zero if, for example, the experimenter knew that no new animals entered the study population during this interval.

Also notice, that a log or *identity* link should be used for the super-population size as it is not restricted to lie between 0 and 1:



Now run **MARK**. If we look at the *REAL* estimates, we must keep in mind that not all parameters are identifiable:

Chase 1989 Adults Only		
Real Function Parameters of {p(t), phi(t)}		
Parameter	Estimate	Standard Error
1:Phi	0.5717376	0.0977208
2:Phi	0.9999994	0.6125507E-03
3:Phi	0.7191576	0.1175738
4:Phi	1.0000000	0.0000000
5:Phi	0.7826687	0.4727436
6:Phi	0.2822160	0.2337353
7:Phi	0.9975084	2.0560912
8:p	0.9999993	0.0133128
9:p	0.3751059	0.1375089
10:p	0.2346356	0.0392107
11:p	0.3697123	0.0623328
12:p	0.3077557	0.0556362
13:p	0.2146932	0.1361140
14:p	0.2651052	0.1474306
15:p	0.1303810	0.4117473
16:pent	0.1366109	0.0612740
17:pent	0.5259542	0.0936811
18:pent	0.1648277E-11	0.3260178E-12
19:pent	0.1648277E-11	0.3260178E-12
20:pent	0.0631742	0.0777153
21:pent	0.1553686	0.0804563
22:pent	0.1648277E-11	0.3260178E-12
23:N	311.75769	38.375642

In particular, the final survival and catchability are confounded as in the CJS model. The initial entrance and catchability parameters are also confounded (only the product $b_0 p_1$ can be estimated) – however, **MARK** does **not** report b_0 so the first PENT reported here refers to b_1 which cannot be estimated separately (refer to Table 12.2). This non-identifiability can often be recognized by the large standard errors for certain estimates, or by estimates tending to the value 1.0. Also notice, that because the intervals are unequal size, the survival probabilities are given on a *per week basis*, so that the survival probability for the initial 1.5 week interval is found as $0.57^{1.5} = 0.43$.

The estimates of population size and net births are found under the derived parameter section:

Grp.	Occ.	B-hat	Standard Error
1	1	42.654354	10.772958
1	2	163.97026	29.66556
1	3	0.5138632E-09	0.7960027E-10
1	4	0.5138632E-09	0.7960027E-10
1	5	19.695050	25.021000
1	6	48.437357	28.200096
1	7	0.5130032E-09	0.7960027E-10
Population Estimates of {p(t)}.			
Grp.	Occ.	N-hat	Standard Error
1	1	37.000665	5.7316095
1	2	58.650105	20.302137
1	3	221.62033	26.690452
1	4	151.46921	21.665511
1	5	149.46921	21.665511
1	6	130.41856	80.203341
1	7	82.985839	44.256052
1	8	76.698288	241.27819

Again, not all parameters are identifiable. The derived parameters also include estimates of gross births – these are explained in more detail in Schwarz *et al.* (1993).

Goodness-of-fit can be assessed using the RELEASE suite as in CJS models (see Chapter 5 for details on RELEASE). The results are shown below.

Summary of TEST 3 (Goodness of fit) Results					
Group	Component	Chi-square	df	P-level	Sufficient Data
1	3.SR2	0.2652	1	0.6065	No
1	3.SR3	0.0000	1	1.0000	No
1	3.SR4	0.0903	1	0.7638	Yes
1	3.SR5	0.0000	1	1.0000	No
1	3.SR6	0.3434	1	0.5579	No
1	3.SR7	0.0000	0	1.0000	No
Group 1	3.SR	0.6989	5	0.9830	
1	3.Sm2	0.0000	1	1.0000	No
1	3.Sm3	0.0000	1	1.0000	No
1	3.Sm4	0.1848	1	0.6673	Yes
1	3.Sm5	0.0000	1	1.0000	No
1	3.Sm6	0.0000	0	1.0000	No
Group 1	3.Sm	0.1848	4	0.9960	
Group 1	TEST 3	0.8837	9	0.9997	
Summary of TEST 2 (Goodness of fit) Results					
Group	Component	Chi-square	df	P-level	Sufficient Data
1	2.C2	0.1942	1	0.6594	Yes
1	2.C3	6.1651	2	0.0458	Yes
1	2.C4	0.4521	1	0.5013	Yes
1	2.C5	0.2399	1	0.6244	Yes
1	2.C6	2.5951	1	0.1071	No
Group 1	TEST 2	9.6463	6	0.1404	
Goodness of Fit Results (TEST 2 + TEST 3) by Group					
Group	Chi-square	df	P-level		
1	10.5300	15	0.7851		

There is some evidence of potential lack-of-fit as indicated by **Test2** in component **C3**, but a detailed investigation of that table shows it is not serious. Unfortunately, because individual capture histories were used, residual plots are not useful.

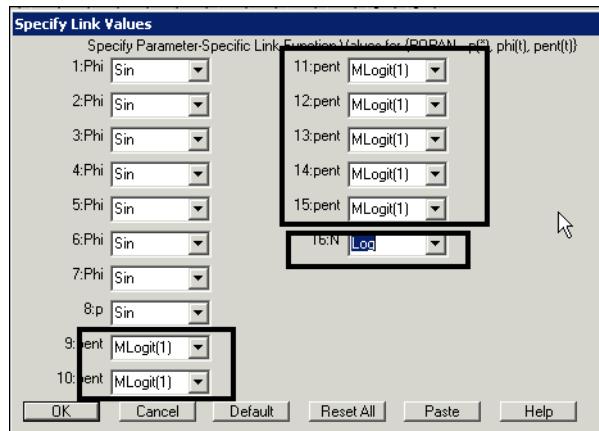
Because of parameter confounding, it is important to count the actual number of estimable parameters. On the surface there are 24 parameters composed of 8 capture parameters, 7 survival parameters, 8 PENT parameters and 1 super-population parameter. However, the PENTS must sum to 1, and Table 12.2

indicates that two parameters are lost to confounding which leaves a net of 21 actual identifiable parameters. Check that the results browser shows 21 parameters for this model.

The original sampling experiment has approximately equal effort at all sampling occasions. Perhaps a model with constant catchability over time is suitable, i.e., model $\{p, \phi_t, b_t\}$. This model is specified in the PIM in the usual fashion:



None of the other PIM's need to be respecified. The model is run, and again the parameter specific link functions must be specified for the PENTS (use the **MLogit(1)** link function) and for the super-population size (use the log link function):



Now all parameters are identifiable (shown below):

Chase 1989 Adults Only			
Real Function Parameters of {p(*)}, phi(t)			
Parameter	Estimate	Standard Error	
1:Phi	0.5843217	0.1007203	
2:Phi	0.9264539	0.1759781	
3:Phi	0.7973302	0.1328374	
4:Phi	0.9216908	0.1312724	
5:Phi	0.5792390	0.1372571	
6:Phi	0.3306517	0.1258056	
7:Phi	0.6180676	0.1405468	
8:p	0.3153771	0.0422789	
9:pent	0.0449635	0.0506509	
10:pent	0.3325037	0.0718152	
11:pent	0.1107655	0.0718261	
12:pent	0.1742893E-06	0.1128910E-03	
13:pent	0.0279008	0.0411325	
14:pent	0.1313499	0.0355726	
15:pent	0.2496515E-06	0.7215834E-04	
16:N	331.99832	29.077189	

Population Estimates of {p(*)}.			
Grp.	Occ.	N-hat	Standard Error
1	1	14.927808	16.774252
1	2	110.39068	25.706697
1	3	36.773956	23.491246
1	4	0.5786375E-04	0.0374800
1	5	9.2630338	13.603729
1	6	43.607953	12.918315
1	7	0.8288389E-04	0.0239567
Population Estimates of {p(*)}.			
Grp.	Occ.	N-hat	Standard Error
1	1	117.03475	23.994394
1	2	67.202663	15.042773
1	3	171.72480	28.778965
1	4	164.92468	22.812181
1	5	150.16623	25.907957
1	6	91.611254	19.255066
1	7	71.254152	16.093113
1	8	31.707588	10.775021

The results show $\hat{b}_1 = 0.044$, $\hat{b}_2 = 0.33$, etc. These are interpreted as 4.4% of adult returning salmon return between weeks 1.5 and 3; about 33% of adult returning salmon return to spawn between weeks

4 and 5, etc. The value of $\hat{b}_0 = 0.352$ is obtained by subtraction ($\hat{b}_0 = 1 - \hat{b}_1 - \hat{b}_2 - \dots - \hat{b}_{K-1}$). This is interpreted as 35% of adults returning salmon has returned to spawn before sampling began in week 1.5.

The total number of salmon returning to spawn (the super-population) is estimated to be $\hat{N} = 332$ (SE=29) fish. The derived birth parameters are found as $\hat{B}_i = \hat{N}\hat{b}_i$. For example, $\hat{B}_1 = \hat{N}\hat{b}_1 = (332 \times 0.044) = 14.9$. This is interpreted as about 15 adult fish returned to spawn between weeks 1.5 and 3. $\hat{B}_0 = \hat{N}\hat{b}_0 = (332 \times 0.352) = 117$ fish are estimated to be present before the first sampling occasion.

The derived estimates of population size are found iteratively and must account for losses-on-capture and the unequal time intervals (which affects the survival terms).

$$\hat{N}_1 = \hat{B}_0 = 117.03.$$

$$\hat{N}_2 = (\hat{N}_1 - loss_1)\hat{\phi}_1^{1.5} + \hat{B}_1 = (117.03 - 0)0.584^{1.5} + 14.92 = 67.2.$$

$$\hat{N}_3 = (\hat{N}_2 - loss_2)\hat{\phi}_2^{1.0} + \hat{B}_2 = (67.2 - 1)0.926^{1.0} + 110.39 = 171.72$$

⋮

The number of identifiable parameters for this model is 16 composed of 1 capture parameters, 7 survival parameters, 8 PENT parameters and 1 super-population parameter less the restriction that the PENTs must sum to 1. The number of parameters reported in the browser may have to be manually adjusted to indicate the correct number of parameters.

Another sub-model can also be fit where the apparent survival probability (per unit time) is constant over all intervals, i.e., model $\{p, \varphi, b_t\}$. It is fit in the same fashion by adjusting the PIMs:



This model would have 10 parameters composed of 1 capture parameter, 1 survival parameter, 8 PENT parameters, and 1 super-population parameters with 1 restriction that the PENTs sum to 1.

The final results table (after making sure that the number of parameters is correct):

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance
{POPAN - p("), phi(t), pent(t)}	524.530	0.0000	0.85726	1.0000	16	0.0000
{POPAN - p("), phi("), pent(t)}	528.270	3.7401	0.13212	0.154	10	0.0000
{POPAN - p(t), phi(t), pent(t)}	533.311	8.7814	0.01062	0.012	21	0.0000

shows not much support for this final model. If model averaging is to be used, some care must be taken as not all parameters are identifiable in all models. For example, most models with a p_t structure, will be unable to estimate abundance at the first (N_1) or last (N_K) sampling occasion; nor can recruitment be estimated for the first (b_1 , or B_1) or last (b_{K-1} or B_{K-1}) interval.

Other models could be fit, e.g., an equal fraction of the super-population returns to spawn in each week, but in this example is highly unlikely biologically and was not fit.

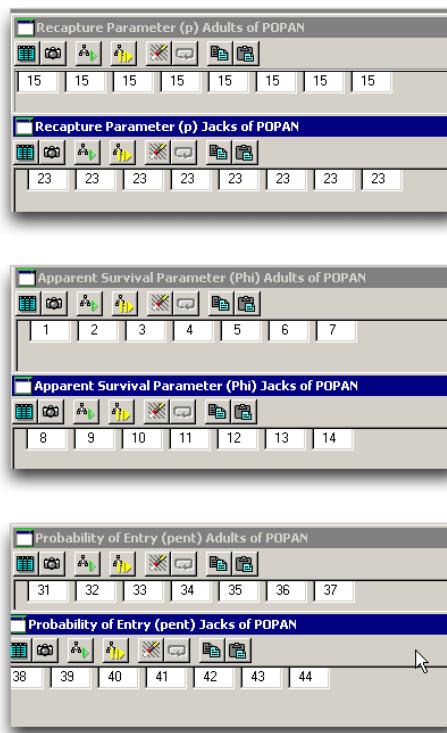
Now let us return to the real question of interest – do jacks and adults have the same return pattern? This is now a two group problem and is handled in a similar fashion to the ordinary CJS model.

Start a new project, using **chase_both.inp**, and this time specify **two** groups (regular adults and jacks) rather than a single group. Also specify the names of the two groups.



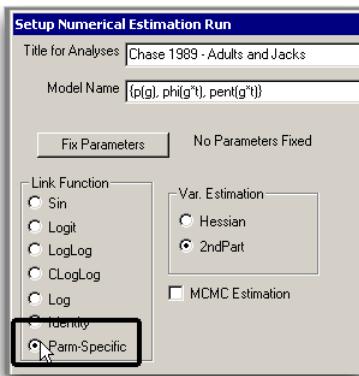
Now each parameter can vary over sampling occasions (intervals) and/or groups. The full model fit will be specified by a triplet of specifications.

In the previous example, a model with equal catchability over sampling occasions was tenable, but adults and jacks may have different catchabilities. Survival probabilities varied by time, so perhaps start with a fully time- and group-dependent model for φ . Also start with a full group and time dependence for the *PENTs*. This would correspond to model $\{p_g \varphi_{g*t} b_{g*t}\}$ with the following PIMs.

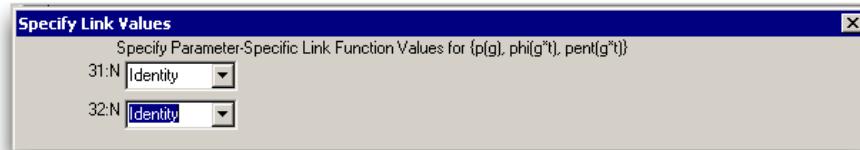
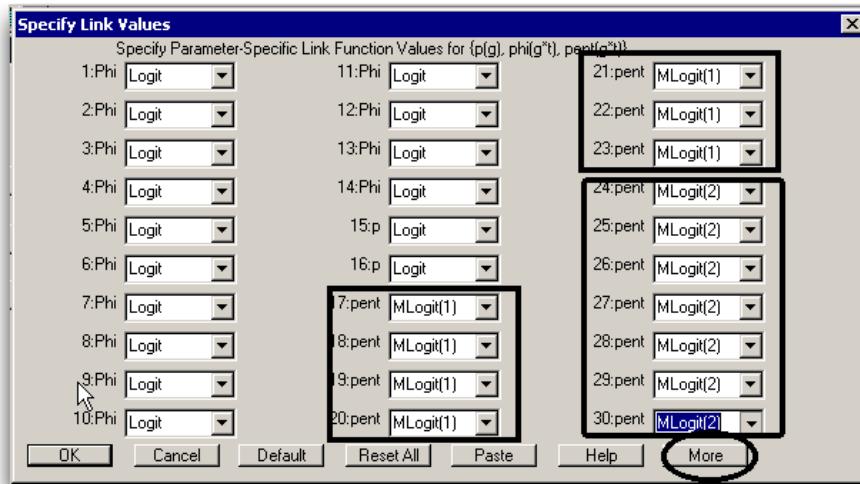


The two PIMs for the super-population size of the adults and jacks (respectively) are not shown.

Request that **MARK** fit this model. As before, we must indicate to **MARK** that the *PENTs* sum to 1, for each group using the parameter specific link functions.



There are a total of 8 sampling occasions, 8 *PENTs* per group, but MARK only shows the last seven (b_0 for each group is implicitly assumed). Use the *MLogit(1)* link function for the first seven *PENTs* (belonging to group 1) and the *MLogit(2)* link function for the last seven *PENTs* (belonging to group 2). Notice that only 30 parameters are displayed per window, so the 'More' button must be used to scroll to the next page:



Don't forget to specify that the two super-population parameters should have the identity or log link function.

Run the model and add it to the results browser. Then, run and fit the models $\{p_g \varphi_t b_{g*t}\}$ and $\{p_g \varphi_t b_t\}$.*

* The option to 'Initial → Copy 1 PIM to another PIM' is helpful here.

Count parameters carefully. All of the models have a simple structure for the p 's so there is no problem with confounding. The model $\{p_g \varphi_t b_{g*t}\}$ has 2 catchability parameters, 7 survival parameters, 16 PENTs, and 2 super-population sizes. However, each set of PENTs must sum to 1, leaving 25 free parameters. The model $\{p_g \varphi_t b_t\}$ has 2 catchability parameters, 7 survival parameters, 8 PENTs (but these must sum to 1), and 2 super-population parameters for a total of 18 parameters. The model $\{p_g \varphi_{g*t} b_{g*t}\}$ has 2 catchability parameters, 14 survival parameters, 18 PENTs (but each of the two groups of PENTs must sum to 1), and 2 super-population sizes for a total of 32 parameters.

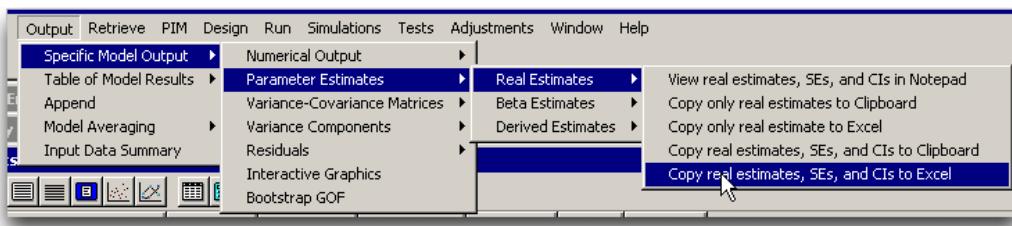
The final results window looks like (after adjusting for the number of parameters)

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance
{POPAN 2 groups ({p(g), phi(t), pent(g*t)})	933.4122	0.0000	0.95057	1.0000	25	0.0000
{POPAN 2 groups ({p(g), phi(t), pent(t)})	940.5470	7.1348	0.02683	0.0282	18	0.0000
{POPAN 2 groups ({p(g), phi(g*t), pent(g*t)})	940.8910	7.4788	0.02259	0.0238	32	0.0000

The final models of interest are a comparison between model $\{p_g \varphi_t b_{g*t}\}$ and $\{p_g \varphi_t b_t\}$ (why?). The ΔAIC_c shows very little support for the model where the jacks enter in the same distribution as the adults. In particular, examine the estimates of the PENTs for the $\{p_g \varphi_t b_{g*t}\}$ model:

10:pent	0.0333328	0.0457877
11:pent	0.3268064	0.0685035
12:pent	0.1307572	0.0752736
13:pent	0.0011528	0.0591666
14:pent	0.0410032	0.0386589
15:pent	0.1214374	0.0324185
16:pent	0.1719801E-08	0.0000000
17:pent	0.9631933E-11	0.1043234E-11
18:pent	0.2276932	0.0835763
19:pent	0.0362517	0.0864785
20:pent	0.1635956E-09	0.0000000
21:pent	0.0056390	0.0455758
22:pent	0.0368692	0.0266959
23:pent	0.5456831E-06	0.4850133E-03

Recall that even though there are 8 PENT parameters per group that MARK does not let you specify the b_0 parameter in the PIMs – this value is obtained by subtraction from 1. Further manipulations can be done by copying the real parameter values to an Excel spreadsheet:



You will find that about 34% ($1 - 0.033 - 0.326 - \dots - 0.000$) of adults were in the stream prior to the first sampling occasion, while about 69% ($1 - 0.000 - 0.227 - 0.036 - \dots - 0.000$) of jacks were in the stream prior to the first sampling occasion. So it appears that precocious males tend to return earlier (for this stream and year) than regular adults.

In this example, it is vitally important that catchability be approximately constant across all sampling occasions so that a model with p_g could be fit; any model where catchability varied across time (a p_t or p_{g*t} model) would have the first *PENT* parameter hopelessly confounded with the first catchability parameter and in many cases, makes it difficult if not impossible to do sensible model comparisons. This again illustrates the need for careful study design with JS models.

begin sidebar

The multinomial logit link and the POPAN model

In situations where you want to constrain estimates from a set of 2 or more parameters to sum to 1, you might use the multinomial logit link (MLogit), which was introduced in some detail in Chapter 10 with respect to multi-state models (where the transitions from a given stratum must logically sum to 1.0).

While specifying the MLogit link in **MARK** is straightforward, you need to be somewhat careful. Consider the following set of parameters in a PIM for the probability of entry (*pent*) in a POPAN model:

61 62 63 64 65 66 67 68 69 70

The parameter-specific link would be selected in the ‘**Setup Numerical Estimation Run**’ window, and the **MLogit(1)** link would be applied to parameters 61 → 70 to force these 10 estimates to sum to ≤ 1 . But suppose that you wanted to force *all* of the 10 entry probabilities to be the same, and have the sum of all 10 be ≤ 1 ? You might be tempted to specify a PIM such as

61 61 61 61 61 61 61 61 61 61

(i.e., simply use the same index value for all the parameters in the PIM), but that would be incorrect. Changing the PIM and selecting the MLogit link for parameter 61 would result in parameter 61 alone summing to ≤ 1 (i.e., just like a logit link), but would not force the sum of the 10 values of parameter 61 to sum to ≤ 1 .

To implement the proposed model, the PIM should not be changed from the top example (i.e., it should maintain the indexing from 61 → 70), and the design matrix should be used to force the same estimate for parameters 61 → 70:

Parameter	Design Matrix
61	1
62	1
63	1
64	1
65	1
66	1
67	1
68	1
69	1
70	1

Then the **MLogit(1)** link should be specified for the 10 parameters 61 → 70. The result is that now all 10 parameters have the same value, and 10 times this value is ≤ 1 .

Another example – suppose you wanted parameters 61 and 62 to be the same value, 63 to 66 the same, 67 and 68 the same, and 69 and 70 the same, but the sum over all parameters to be ≤ 1 . Again you would use the PIM

61 62 63 64 65 66 67 68 69 70

but again use the design matrix to implement the constraints. The following design matrix is one example that would produce such a set of constraints.

Parameter Design Matrix

61	1	1	0	0
62	1	1	0	0
63	1	0	1	0
64	1	0	1	0
65	1	0	1	0
66	1	0	1	0
67	1	0	0	1
68	1	0	0	1
69	1	0	0	0
70	1	0	0	0

The key point with these examples is that the PIM *cannot* be used to constrain parameters if you want the entire set of parameters to sum to ≤ 1 . Rather, the design matrix has to be used to make the constraints, with each of the entries in the PIM given the same **MLogit(x)** link. Further examples of the MLogit link are discussed in Chapter 10.

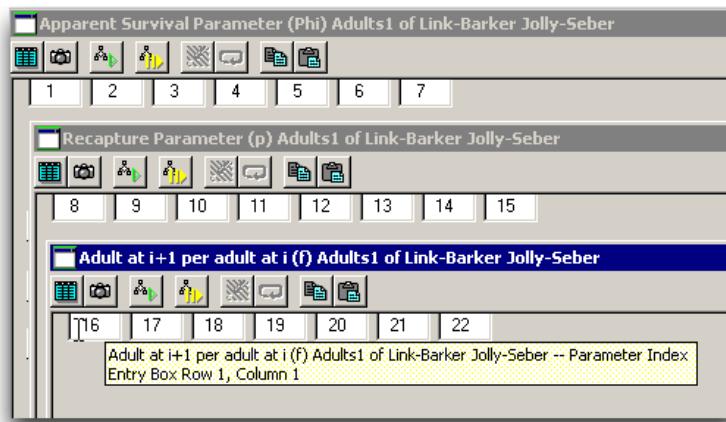
end sidebar

12.4.2. Link-Barker and Pradel-recruitment formulations

The Link-Barker or Pradel-recruitment formulation can be conveniently obtained by switching data types from any of the JS formulations. We will illustrate the use of the Link-Barker formulation; that for the Pradel-recruitment is similar, but in this case cannot be used because of losses-on-capture.

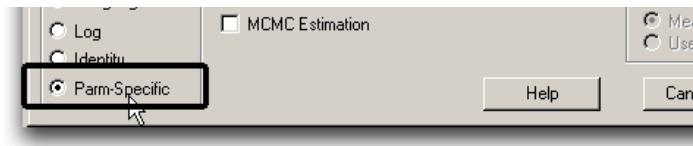
Let us begin with a time dependent model for all parameters, i.e., $\{p_t \varphi_t f_t\}$. The number of groups and sampling intervals would have been entered as seen in the POPAN formulation. The survival and catchability PIMs mimic those for the POPAN formulation.

In the Link-Barker formulation, there are $(K - 1) = 7$ recruitment parameters with a standard PIM:

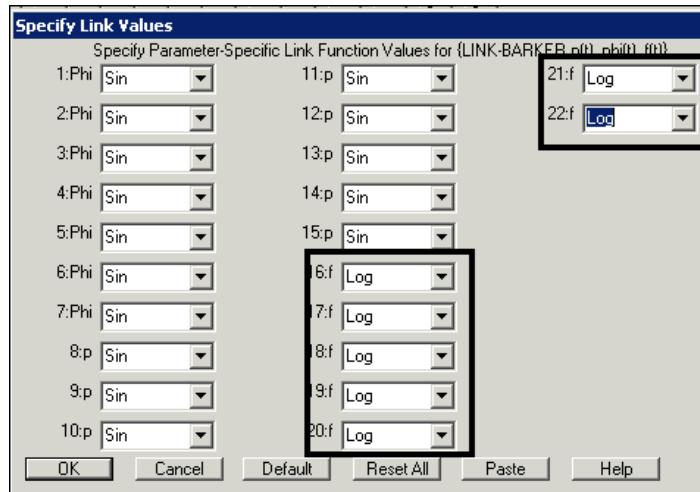


Because the population recruitment value is **not** limited to lie between 0 and 1 (for example, the recruitment value could exceed 1), the '**Parameter Specific Link**' functions should be specified when models are run:^{*}

* An undocumented feature of **MARK** is that it will use the log link for the recruitment parameter if you specify a *logit* or *sin* link in the radio buttons.



Any of the link functions can be used for the catchability and survival parameters (although the *logit* and *sin* link are most common), but either the *log* or the *identity* link function should be used for the population recruitment parameters. There are no restrictions that the recruitment parameters sum to 1 over experiment so the *Mlogit* link should **not** be used.



Run the model and append it to the browser.

As in the POPAN formulation, both the fully time-dependent Link-Barker and Pradel-recruitment formulations suffer from confounding. If you examine the β parameter estimates, and the estimated SE (below), there are several clues that confounding has taken place:

Chase 1989 - Adults (Group 1) c PARM-SPECIFIC Link Function Parameters of {LINK}		
Parameter	Beta	Standard Error
1:Phi	0.2941125	0.4008748
2:Phi	63.626154	0.2371159E-07
3:Phi	0.8990273	0.5629100
4:Phi	29.911114	0.3114257E-07
5:Phi	50.818396	0.0000000
6:Phi	-1.2029741	0.8224589
7:Phi	36.399168	0.0000000
8:p	2.2179782	371.53733
9:p	-0.5156723	0.5868032
10:p	-1.1910425	0.2189992
11:p	-0.5259468	0.2662951
12:p	-0.8037093	0.2600251
13:p	-1.6006708	0.2852519
14:p	-1.0678417	0.7797062
15:p	-1.9459115	0.7559225
16:f	0.3732777E-03	34.850271
17:f	1.0326275	0.4631279
18:f	-12.670864	719.29324
19:f	-21.666706	3987.8326
20:f	-1.8117237	1.1636719
21:f	-1.3234632	0.6606008
22:f	-18.040081	873.33896

As in the *POPLAN* formulation, survival in the last interval and catchability at the last sampling occasion are confounded. The corresponding β parameters are very large on the logit scale with standard errors that are either zero or very large. Similarly, p_1 cannot be estimated and its β standard error is very large.

Finally, because the first and last catchabilities cannot be estimated, neither can 'population size' (despite population size not being explicitly in the model) and so the recruitment parameter (the f_i values) based on occasion 1 (f_1) or terminating with occasion K (f_{K-1}) cannot be estimated either. We notice that the standard errors for these recruitment parameters are nonsensical.

Chase 1989 – Adults (Group 1) only				
Parameter	Estimate	Standard Error	95% Confidence Interval	
			Lower	Upper
1:Phi	0.5730026	0.0980823	0.3795162	0.7464613
2:Phi	1.0000000	0.3293066E-18	1.0000000	1.0000000
3:Phi	0.7107496	0.1157256	0.4491078	0.8810416
4:Phi	1.0000000	0.4325081E-18	1.0000000	1.0000000
5:Phi	1.0000000	0.0000000	1.0000000	1.0000000
6:Phi	0.2309466	0.1460771	0.0565193	0.6008590
7:Phi	1.0000000	0.0000000	1.0000000	1.0000000
8:p	0.9919521	32.006593	0.1976126E-09	1.0000000
9:p	0.3738648	0.1373647	0.1589841	0.6535005
10:p	0.2330725	0.0391460	0.1651661	0.3182547
11:p	0.3714627	0.0621741	0.2596314	0.4989979
12:p	0.3092326	0.0555434	0.2119254	0.4270102
13:p	0.1678879	0.0398501	0.1034223	0.2608458
14:p	0.2558137	0.1484351	0.0693920	0.6131049
15:f	0.1340000	0.0036700	0.0214464	0.2050655
16:f	1.0003733	24.063393	67.231662	69.232400
17:f	2.8084353	1.2967330	0.2668385	5.3500321
18:f	0.3141329E-05	0.0022595	0.4362674E-16	0.9999956
19:f	0.3892862E-09	0.1552408E-05	-0.3042331E-05	0.3043110E-05
20:f	0.1633723	0.1901117	0.0126231	0.7489145
21:f	0.2662118	0.1758597	0.0585004	0.6793057
22:f	0.1463161E-07	0.1277036E-04	0.2032000E-10	0.9990517

The user must be *very* careful to count parameters carefully and to see if **MARK** has detected the correct number of parameters. There are 8 sampling occasions. The fully time-dependent model has, on the surface, 8 capture parameters, 7 survival parameters, and 7 recruitment parameters for a total of 22 parameters. However, as shown in Table 12.3, there are two parameters lost to confounding which gives a total of 20 parameters that can be estimated. The number of parameters reported in the results browser may have to be modified manually.

As in the *POPLAN* formulation, models where constraints are placed on the initial and final catchabilities can resolve this confounding. Because roughly the same effort was used in all sampling occasions, the model $\{p_*, \varphi_t, f_t\}$ seems appropriate.

Adjust the PIM for the recapture probabilities to be constant over time, re-run the model (don't forget to use the '**Parameter Specific Link**' function option),* and append the results to the browser. Let's look at the parameter estimates (top of the next page). The number of parameters that can be estimated is now 15 being composed of 1 capture parameter, 7 survival parameters, and 7 recruitment parameters.

If you compare the estimates of p and φ between the Link-Barker formulation and the *POPLAN* formulation they are identical (except for rounding errors). Note that because of unequal time intervals, estimates of φ_i are on a per-unit basis. The actual survival in the first and last interval must be obtained by raising the reported φ 's to the 1.5th power (corresponding to the 1.5 week interval).

* CAUTION: When we ran this model with the *logit* link for the φ 's, one φ converged to a value of 1; we would recommend that the *sin* link be used.

Chase 1989 - Adults (Group 1) only					
Parameter	Estimate	Standard Error	95% Confidence Interval		
			Lower	Upper	
1:Phi	0.5833992	0.1006706	0.3834096	0.7592529	
2:Phi	0.9279969	0.1765803	0.0676519	0.9995634	
3:Phi	0.7970321	0.1330251	0.4393349	0.9516419	
4:Phi	0.9221987	0.1316963	0.2450770	0.9976947	
5:Phi	0.5800559	0.1375482	0.3135128	0.8068629	
6:Phi	0.3308433	0.1259074	0.1395454	0.6011657	
7:Phi	0.6190726	0.1399812	0.3367479	0.8387623	
8:p	0.3137171	0.0420822	0.2375970	0.4013852	
9:f	0.2521580	0.2045257	0.0386820	0.7385912	
10:f	1.6441301	0.5502536	0.5656329	2.7226273	
11:f	0.2114983	0.1593520	0.0395904	0.6357435	
12:f	0.2728460E-07	0.6223856E-04	0.3789270E-18	0.9994913	
13:f	0.0571923	0.0884807	0.0024271	0.6019896	
14:f	0.4270444	0.1464334	0.1874095	0.7066338	
15:f	0.1160248E-04	0.0108513	0.1611365E-15	0.9999988	

The PENTs from POPAN and the f 's from the Link-Barker are not directly comparable. However, the following equivalents are noted:

$$(\hat{f}_1^{LB})^{1.5} = 0.252^{1.5} = 0.127 = \frac{\hat{B}_1^{PO PAN}}{\hat{N}_1^{PO PAN}} = \frac{14.92}{117.034}$$

$$\hat{f}_2^{LB} = 1.644 = \frac{\hat{B}_2^{PO PAN}}{\hat{N}_2^{PO PAN}} = \frac{110.39}{67.20}$$

$$\hat{f}_3^{LB} = 0.211 = \frac{\hat{B}_3^{PO PAN}}{\hat{N}_3^{PO PAN}} = \frac{36.77}{171.72}$$

...

Similarly, estimates of population growth are also equivalent:

$$(\hat{f}_1^{LB})^{1.5} + (\hat{\phi}_1^{LB})^{1.5} = 0.583^{1.5} + 0.252^{1.5} = 0.571 = \frac{\hat{N}_2^{PO PAN}}{\hat{N}_1^{PO PAN}} = \frac{67.20}{117.03} = 0.574$$

$$\hat{f}_2^{LB} + \hat{\phi}_2^{LB} = 1.644 + 0.928 = 2.57 = \frac{\hat{N}_3^{PO PAN}}{\hat{N}_2^{PO PAN}} = \frac{171.72}{67.20} = 2.55$$

...

If you examine the results browser (after any changes for the actual number of parameters that are estimated):

Results Browser: Link-Barker Jolly-Seber						
Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance
{LINK-BARKER p(*), phi(t), f(t)}	1204.4444	0.0000	0.98096	1.0000	15	169.0603
{LINK-BARKER p(*), phi(*), f(t) - indiv sin link}	1212.8183	8.3739	0.01490	0.0152	9	186.3137
{LINK-BARKER p(t), phi(t), f(t)}	1215.3806	10.9362	0.00414	0.0042	20	166.0108

you will also see that the ΔAIC_c values between these two models matches very closely with the

difference in the *POPAN* formulation. The differences in ΔAIC_c between the two formulation are artifacts of the different number of parameters estimated and the small sample correction applied to the AIC. If the actual AIC values from the two formulations are compared, the difference in AIC are nearly identical because the two formulations are simply re-parameterizations of the same models for modeling the marked animals and only differ in estimating the super-population size.

As Sanathanan (1972, 1977) showed, the conditional approach of Link & Barker (2005) is asymptotically equivalent to the full likelihood approach of Schwarz & Arnason (1996). For example, in the table shown below, the log-likelihood and AIC (before small sample corrections are applied) were extracted from the model outputs. The differences in the log-likelihoods and the AIC among the models in different formulations are nearly the same.

POPAN formulation				Link-Barker formulation			
Model	$-2 \times \log \mathcal{L}$	# parms	AIC	Model	$-2 \times \log \mathcal{L}$	# parms	AIC
$\{p_{..}, \varphi_t, b_t\}$	489.94	16	521.94	$\{p_{..}, \varphi_t, f_t\}$	1176.74	15	1206.74
$\{p_{..}, \varphi_{..}, b_t\}$	507.25	10	527.25	$\{p_{..}, \varphi_{..}, f_t\}$	1193.99	9	1211.99
$\{p_t, \varphi_t, b_t\}$	486.80	21	528.80	$\{p_t, \varphi_t, f_t\}$	1173.69	20	1213.69

The two group case can be fit in a similar fashion as seen in the *POPAN* example. However, it is not clear exactly which models should be compared because the f_i parameters in the Link-Barker formulation depend both upon the *NET* number of new births, but also upon the population size at occasion (i) which depends upon the pattern of previous births and survival probabilities. Consequently, even if the same birth pattern occurred between the two groups, differences in survival probabilities could result in differences in patterns of the f 's. Fortunately, it appears the survival probabilities are roughly constant between groups, so a comparison of models $\{p_g \varphi_t f_{g*}\}$ vs $\{p_g \varphi_t f_t\}$ is a valid test of the hypothesis of equal return patterns for adults and jacks.

Fitting these two models to the two groups is left as an exercise for the reader.

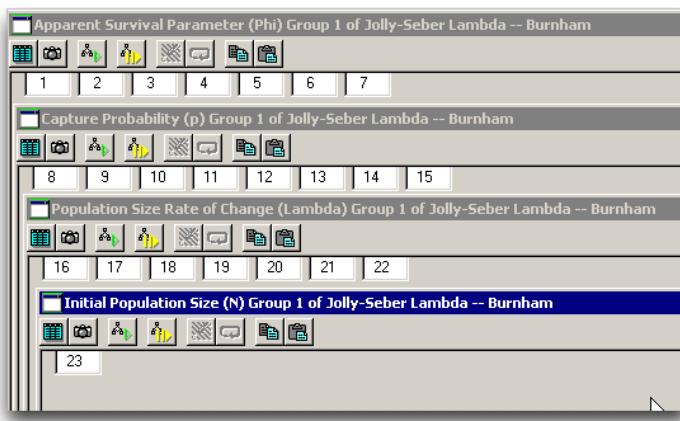
12.4.3. Burnham Jolly-Seber and Pradel- λ formulations

The Burnham model

The Burnham JS model does not model entrants directly, but rather parameterizes changes in population size using population growth. In the case of the spawning salmon, this would correspond to the increase in the number of spawning salmon at occasion ($i + 1$) relative to occasion (i).

The Burnham JS model is selected using the Jolly-Seber radio button. The same data file as for *POPAN* can be used. Again let us start with fitting a model just to the adults over 8 sampling occasions with unequal sampling intervals (see the screen shots in section 12.4.1 for details). Again, start by fitting the fully time-dependent model (PIM structure shown at the top of the next page).

As in *POPAN* (and all JS formulations) there are $(K - 1) = 7$ survival parameters, $K = 8$ capture probabilities. In the Burnham model, there is a single initial population size parameter per group and $(K - 1) = 7$ population growth parameters.



We were unable to get the Burnham Jolly-Seber model to converge for any of the models considered in this chapter. The **MARK** help files state that

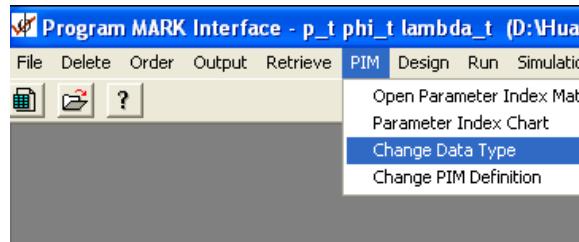
'This model can be difficult to get numerical convergence of the parameter estimates. Although this model has been thoroughly checked, and found to be correct, the program has difficulty obtaining numerical solutions for the parameters because of the penalty constraints required to keep the parameters consistent with each other.'

Bummer... *†

The Pradel- λ model

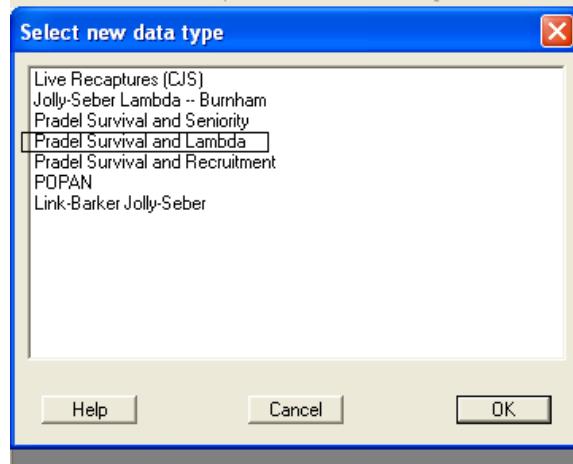
The Pradel- λ formulation (considered in much more detail in Chapter 13) can be conveniently obtained by switching data types from any of the JS formulations (or can be entered directly from the initial screen of **MARK** as discussed in Chapter 12). The number of groups and sampling intervals would have been entered as seen in the *POPAN* formulation.

Let us begin by modeling only the adult salmon.

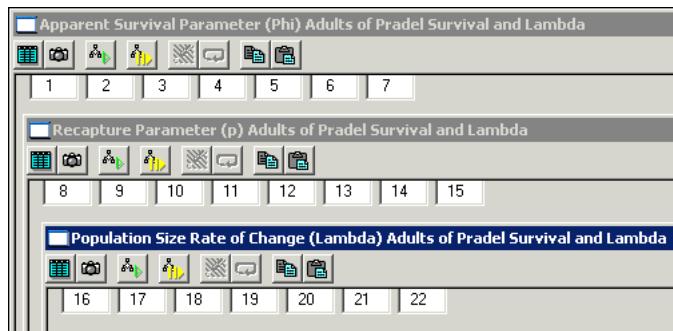


* ...dude. C. Schwarz has clearly spent too much time on the 'wet coast' – E. G. Cooch, *pers. obs.*

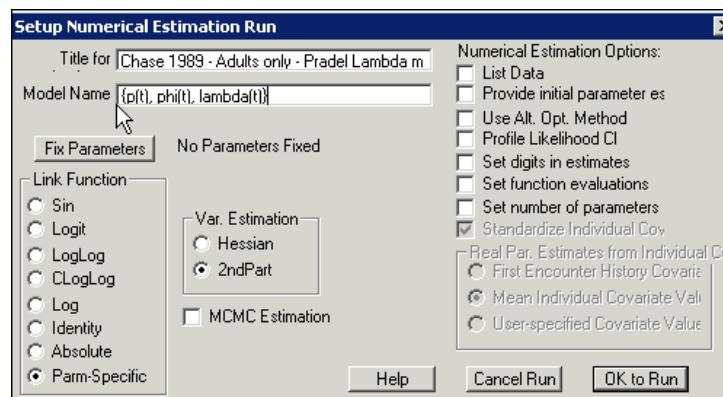
† As noted earlier, this convergence problem disappears for some models if simulated annealing is used for the numerical optimization. – J. Laake & E. G. Cooch, *pers. obs.*



Begin by fitting a fully time-dependent model. The PIMs for survival and catchability mimic those seen in earlier sections; the PIM for the population growth parameter has ($K - 1$) = 7 entries:



Because the population growth parameter is **not** constrained on the interval [0, 1] (i.e., the growth rate could exceed 1), the '**Parameter Specific Link**' option should be selected:^{*}



^{*} A hidden feature of MARK is that it will use the log link for the growth parameter if you specify a *logit* or *sin* link in the radio buttons.

Any of the link functions can be used for the catchability and survival parameters (although the *logit* and *sin* link are most common), but either the *log* or the *identity* link function should be used for the population growth parameters (this is discussed in detail in Chapter 13). There are no restrictions that the growth parameters sum to 1 over experiment so the *Mlogit* link should **not** be used. Because there are more than 20 parameters, we need to press the '**More**' button to specify the link function for the two remaining λ values.

Run the model and append it to the browser.

As in the *POPAN* formulation, the fully time-dependent Pradel- λ formulation suffers from confounding. If you examine the parameter estimates,

Parameter	Beta	Standard Error
1:Phi	0.1489727	0.2001108
2:Phi	1.5708030	1.2446909
3:Phi	0.4566342	0.2760231
4:Phi	1.5707948	1.2177449
5:Phi	0.6248334	1.2075918
6:Phi	0.0750629	1.0102702
7:Phi	-0.0363473	0.0000000
8:p	-0.3956357	222.99293
9:p	-0.2574645	0.2845365
10:p	-0.5821609	0.1860761
11:p	-0.2786746	0.1834005
12:p	-0.3900425	0.1223032
13:p	-0.6174397	0.3359732
14:p	-1.0361815	0.2510108
15:p	-0.2552837	0.0000000
16:Lambda	-0.4751846	223.19723
17:Lambda	1.3852116	0.4381791
18:Lambda	-0.2710648	0.3930451
19:Lambda	-0.0194197	0.2020118
20:Lambda	-0.0422955	0.6444539
21:Lambda	0.9034860	1.0964706
22:Lambda	-1.5696863	0.0000000

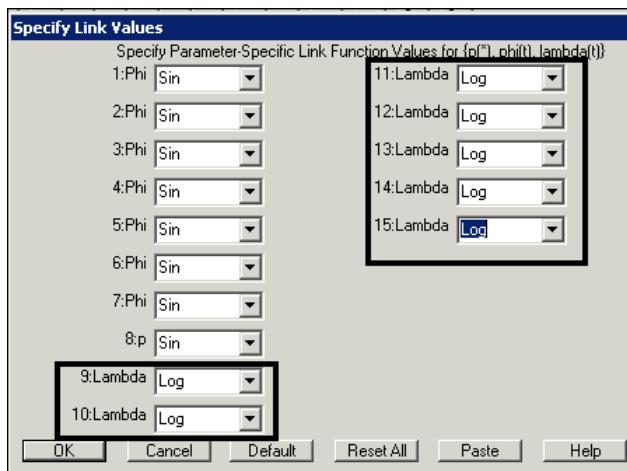
there are several clues that confounding has taken place. The standard errors for some parameters are enormous or the standard error are zero. Survival in the last interval and catchability at the last sampling occasion are confounded. Similarly, λ_1 is confounded with p_1 .

Consequently, not all of the real parameter estimates are usable:

Chase 1989 - Adults only - Pradel La		
Real Function Parameters of {p(t), phi(t)}		
Parameter	Estimate	Standard Error
1:Phi	0.5742111	0.0989472
2:Phi	1.0000000	0.4141439E-05
3:Phi	0.7204648	0.1238711
4:Phi	1.0000000	0.9443671E-06
5:Phi	0.7924811	0.4897150
6:Phi	0.5374962	0.5037127
7:Phi	0.1010001	0.0000000
8:p	0.3673620	102.66338
9:p	0.3726853	0.1375789
10:p	0.2250849	0.0777125
11:p	0.3624592	0.0881625
12:p	0.3098861	0.0565587
13:p	0.2105253	0.1369701
14:p	0.0697675	0.0639462
15:p	0.9797401	0.0000000
16:Lambda	0.6017702	120.77740
17:Lambda	3.9956711	1.7508194
18:Lambda	0.7625671	0.2997233
19:Lambda	0.9807677	0.1981267
20:Lambda	0.9585865	0.6177647
21:Lambda	2.4681924	2.7063005
22:Lambda	0.2001105	0.0000000

The user must be very careful to count parameters carefully and to see if MARK has detected the correct number of parameters. There are 8 sampling occasions. The fully time-dependent model has, on the surface, 8 capture parameters, 7 survival parameters, and 7 growth parameters for a total of 22 parameters. However, there are two parameters lost to confounding which gives a total of 20 parameters that can be estimated. The number of parameters reported in the results browser may have to be modified manually.

As in the POPAN formulation, models where constraints are placed on the initial and final catchabilities can resolve this confounding. Because roughly the same effort was used in all sampling occasions, the model $\{p, \varphi_t, \lambda_t\}$ seems appropriate. Adjust the PIM for the recapture probabilities to be constant over time, re-run the model (don't forget to use the 'Parameter Specific' link functions or let MARK automatically use the log link for the λ parameters).



This gives the final estimates:

Chase 1989 - Adults only - Pradel Lamb		
Real Function Parameters of {p(*), phi(t)}		
Parameter	Estimate	Standard Error
1:Phi	0.5927220	0.1035234
2:Phi	0.9458309	0.1859415
3:Phi	0.8060015	0.1339392
4:Phi	1.0000000	0.5549465E-06
5:Phi	0.5814686	0.1347157
6:Phi	0.2866269	0.1147553
7:Phi	0.8592311	0.2203514
8:p	0.2841406	0.0397731
9:Lambda	0.6810920	0.1085847
10:Lambda	2.6302703	0.5865236
11:Lambda	1.1418285	0.1849586
12:Lambda	0.8602454	0.1113947
13:Lambda	0.6768354	0.1320030
14:Lambda	0.8865846	0.2281068
15:Lambda	0.6158796	0.1298563

The number of parameters that can be estimated is now 15 being composed of 1 capture parameter, 7 survival parameters, and 7 λ parameters.

Note that because of unequal time intervals, estimates of φ_i are on a per-unit basis. The actual survival in the first and last interval must be obtained by raising the reported φ 's to the 1.5th power (corresponding to the 1.5 week interval).

Compare the estimates from the Pradel- λ formulation to those from the POPAN or Link-Barker formulation. Estimates of survival are similar at sampling occasions 1,2, and 3 differing only by roundoff error.

However, the estimate of φ at sampling occasion 4 differs considerably among the models. Indeed, the Pradel- λ formulation is not even consistent as $\hat{\lambda}_4 = 0.86 < \hat{\varphi}_4 = 1.0$! The POPAN formulation estimated that there was **no** recruitment between sampling occasion 4 and 5 (it was constrained so that estimates of recruitment cannot be negative); the Link-Barker model also estimated the recruitment parameter to be 0 (it is also constrained so that it cannot be negative). However, there are **no** constraints in the Pradel- λ model that λ must be at least as great as survival.

The estimates of λ also don't appear to be consistent with the results from POPAN when estimates of population size are compared. However, this discrepancy is explained by the different ways in which losses-on-capture are incorporated into the estimates of population size and growth between the two formulations.

The model $\{p, \varphi, \lambda_t\}$ can also be fit and the results appended to the results browser. The estimates from this model are:

Chase 1989 - Adults only - Pradel Lamb		
Real Function Parameters of {p(*), phi(*)}		
Parameter	Estimate	Standard Error
1:Phi	0.7139171	0.0404565
2:P	0.2979816	0.0435415
3:Lambda	0.7209730	0.1028197
4:Lambda	2.3847961	0.4978027
5:Lambda	1.1183694	0.1788025
6:Lambda	0.7287425	0.1076054
7:Lambda	0.7852352	0.1201662
8:Lambda	1.2179330	0.2103186
9:Lambda	0.5872715	0.0644242

Again, the estimates are not internally consistent as the population growth rate estimates sometimes fall below the common survival probability. These would indicate that there was little or no recruitment in these intervals.

The results browser

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance
{p(t)}. phi(t), lambda(t)}	1179.3052	0.0000	0.89171	1.0000	15	139.3552
{p(t)}. phi(t), lambda(t)}	1184.4159	5.1107	0.06925	0.0777	9	157.9112
{p(t). phi(t), lambda(t)}	1185.5627	6.2575	0.03903	0.0438	20	133.8098

tells the same story as in the other formulations – strong support for the model with constant catchability and time varying survival and population growth.

The two group models can also be fit in similar fashion as in the other formulations. However, there is again the question of which models comparisons are a sensible choice. Because the λ values are population growth on a per capita basis and include both survival and recruitment, models with group- and time-dependence in λ may not be indicative of changes in recruitment between the two groups.

12.5. Example 2 – Muir's (1957) female capsid data

This second example uses the Muir (1957) data on a population of female black-kneed capsid (*Blepharidopterus angulatus*) that was originally analyzed by Jolly (1963)* and Seber (1965).

According to the British Wildlife Trust website[†] a black-kneed capsid is a green insect about 15 mm long that lives on orchard trees (particular apples and limes). It is a predatory insect that is beneficial to orchard owners as it feeds on red spider mites which cause damage to fruit trees. It apparently makes a ‘squawk’ by rubbing the tip of its beaks against its thorax and will stab people with its beak if handled.

Thirteen successive samples at alternating 3- and 4-day intervals were taken. The population is open as deaths/emigration and births/immigration can occur.

The raw history data is located in the file **capsid.inp**. A portion of the histories appears below:

```
000000000001 47;
000000000010 36;
000000000011 12;
0000000000100 30;
0000000000101 8;
...

```

There is only one group (females) and the individual histories have been grouped.[‡]

* The data were subsequently reanalyzed in Jolly (1965)

[†] <http://www.wildlifetrusts.org>

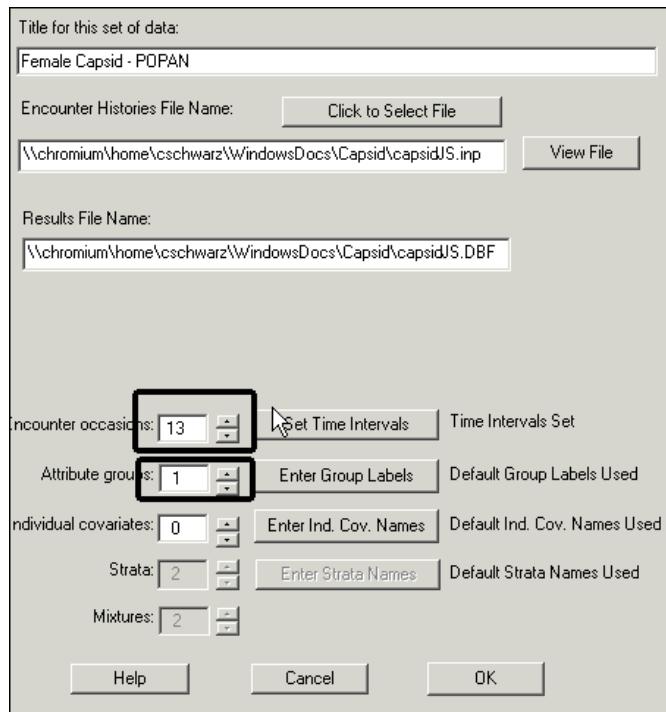
[‡] We suspect that it was impossible to attach individually numbered tags to these small insects and some sort of batch marking scheme (e.g., color dots) was used. This batch marking scheme would enable the history of each insect to be followed, but individuals with the same history cannot be separately identified

The summary statistics are:

<i>Occasion</i>	<i>t_i</i>	<i>n_i</i>	<i>m_i</i>	<i>u_i</i>	<i>R_i</i>	<i>r_i</i>	<i>z_i</i>
1	0	54	0	54	54	24	0
2	3	144	10	134	143	83	14
3	7	166	39	127	166	71	58
4	10	203	56	147	202	71	73
5	14	186	54	132	185	76	90
6	17	197	66	131	196	92	100
7	21	231	97	134	230	102	95
8	24	164	75	89	164	95	122
9	28	161	101	60	160	69	116
10	31	122	80	42	122	55	105
11	35	118	74	44	117	44	86
12	38	118	70	48	118	35	60
13	42	142	95	47	142	0	0

There are a few losses on capture at some of the sampling occasions where $n_i \neq R_i$.

The data are input into MARK in the usual fashion. The time intervals are set to three and four day intervals in the usual fashion:



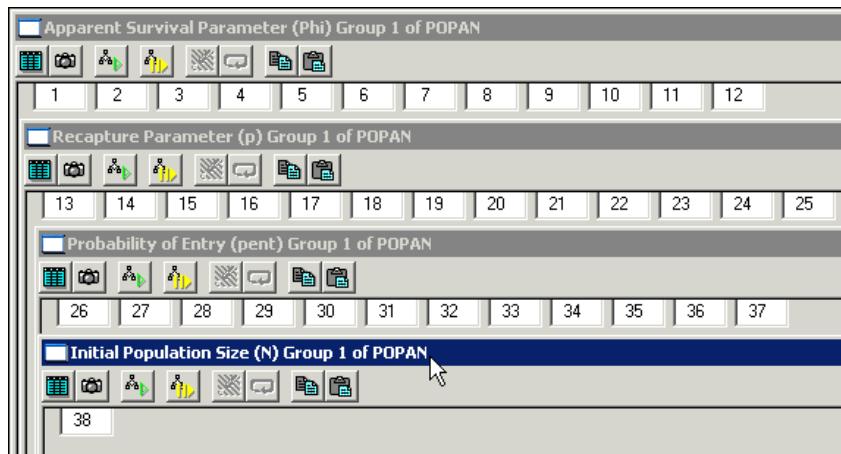
Set Time Intervals

Enter values for time intervals not equal 1

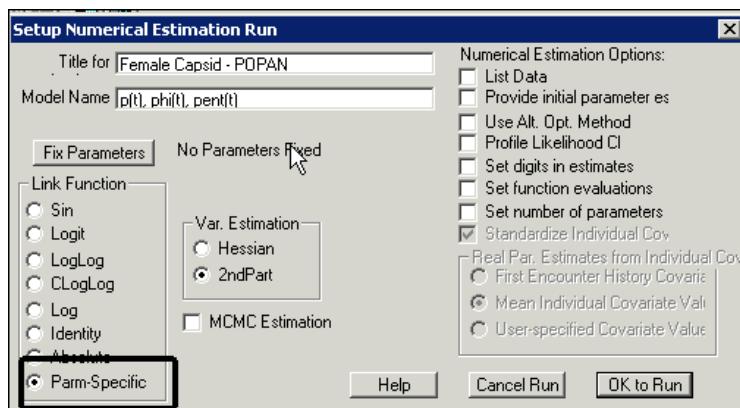
1 3	11 3
2 4	12 4
3 3	
4 4	
5 3	
6 4	
7 3	
8 4	
9 3	
10 4	

12.5.1. POPAN formulation

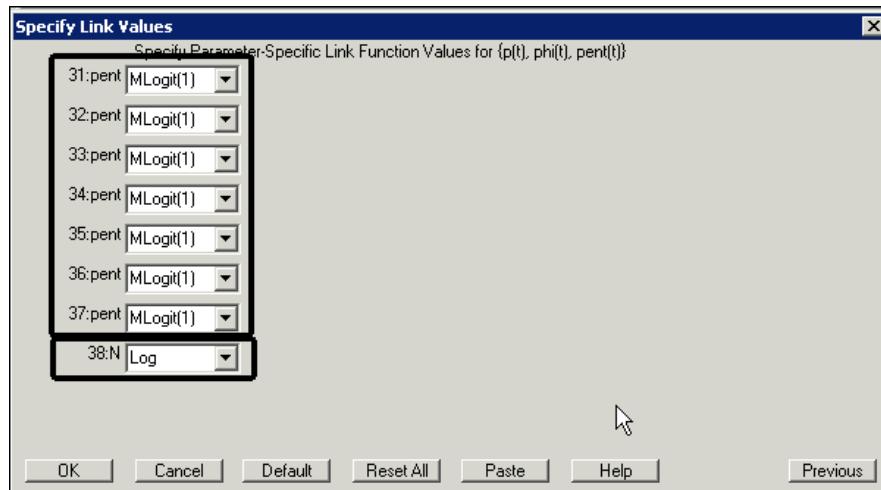
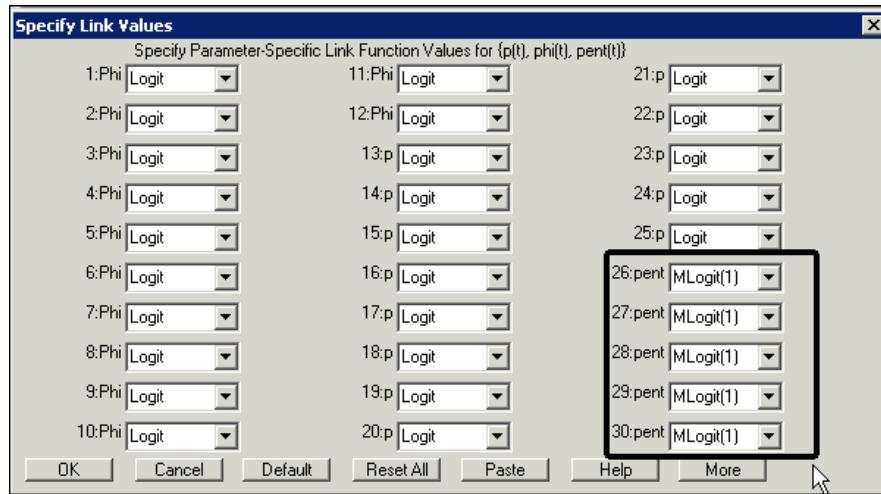
We begin by fitting the fully time-dependent model $\{p_t \varphi_t b_t\}$ in the usual fashion using PIMs:



The model is run, again selecting the 'parameter-specific link' functions:



and specifying the Mlogit(1) link-function for the *PENT* parameters, and the log link-function for the super-population size (*N*).



The resulting model output is:

Results Browser: POPAN						
Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance
{p(t), phi(t), pent(t)}	4887.3189	0.0000	1.00000	1.0000	30	0.0000

There are a total of 36 parameters (13 capture probabilities; 12 survival probabilities; 13 entry probabilities,* and 1 super-population size; less 2 confounded parameters at the start and end of the experiment

* Don't forget that MARK will show only the later 12 *PENTs* in the PIM and output because it never allows you to do anything with the b_0 parameter.

and less 1 restriction that the *PENTs* must sum to 1). The results browser only shows 30 parameters because some of the estimated *PENTs*, p 's and φ 's are estimated to be 0 or 1.*

Female Capsid – POPAN		
Real Function Parameters of {p(t)}, phi(t)		
Parameter	Estimate	Standard Error
1:Phi	0.8759658	0.0465782
2:Phi	→ 0.9999811	0.0012121
3:Phi	0.9848373	0.0352664
4:Phi	→ I 0.8964579	0.0270228
5:Phi	0.8837811	0.0319407
6:Phi	0.9340079	0.0222983
7:Phi	0.8608085	0.0238331
8:Phi	→ 0.9999158	0.0000000
9:Phi	0.8986399	0.0305926
10:Phi	0.9609593	0.0333374
11:Phi	0.9283424	0.0507824
12:Phi	0.7380753	0.0261399
13:p	→ 1.0000000	0.0000000
14:p	0.2089550	0.0288577
15:p	0.2412468	0.0325530
16:p	0.1605427	0.0204321
17:p	0.2279459	0.0305639
18:p	0.2366837	0.0317329
19:p	0.3117792	0.0347702
20:p	0.2721393	0.0249714
21:p	0.2672511	0.0244000
22:p	0.2556812	0.0340349
23:p	0.2445398	0.0366121
24:p	0.2466021	0.0361598
25:p	→ 0.9999997	0.2690778E-03
26:pent	0.3212350	0.0412185
27:pent	→ 0.3690163E-12	0.5151544E-13
28:pent	0.2987720	0.0555976
29:pent	→ 0.3690163E-12	0.5151544E-13
30:pent	0.1327342	0.0447622
31:pent	0.0532585	0.0379329
32:pent	0.0643018	0.0218833
33:pent	→ 0.3690163E-12	0.5151544E-13
34:pent	0.0200259	0.0170383
35:pent	0.0372219	0.0196549
36:pent	0.0458797	0.0162436
37:pent	→ 0.5333631E-11	0.3349635E-08
38:N	2032.3055	77.751562

The number of parameters in the results browser should be reset to 36 in the usual fashion.

Because of the differing time intervals, the estimated survival rates (φ 's) are the survival probabilities *per day*. They also differ from the estimates found in Jolly (1965) because they are also constrained to lie between 0 and 1. For example, Jolly (1965) estimated that the survival probability between the second and third sampling occasion was 1.015.

The estimated population sizes (shown at the top of the next page) are found in the *derived parameters* (accessed using 'Output | Specific Model Output | Parameter Estimates | Derived Estimates'). Because of confounding and non-identifiability at the start and the end of the experiment in the fully time-dependent model, some estimates cannot be used.

* This may be clearer if the β estimates table is also examined.

Grp.	Occ.	B-hat	Standard Error
1	1	652.84767	81.621614
1	2	0.7499538E-09	0.1006871E-09
1	3	607.19604	125.09334
1	4	0.7499538E-09	0.1006871E-09
1	5	269.75648	90.067270
1	6	108.23747	76.909351
1	7	130.68098	43.889423
1	8	0.7499538E-09	0.1006871E-09
1	9	40.698819	34.610264
1	10	75.646247	39.965283
1	11	93.241473	33.179645
1	12	0.1006871E-09	0.1006871E-09
Population Estimates of {p(t)}.			
Grp.	Occ.	N-hat	Standard Error
1	1	34.000348	7.2499813
1	2	689.14354	83.094564
1	3	688.09163	83.139594
1	4	1264.4599	140.58165
1	5	815.98298	98.463291
1	6	832.33436	101.29087
1	7	740.90849	75.248160
1	8	602.63272	43.239669
1	9	602.42969	42.391208
1	10	477.15631	54.867008
1	11	482.53967	64.003556
1	12	478.50392	61.863016
1	13	141.99999	11.492725
Gross Population Estimates of {p(t)}			

Model with constant p and/or constant φ per day may also be tenable and are fit in the usual way using the PIMs. Models with constant b 's don't really have any sensible biological interpretation and should not be fit. A model for the emergence curve may be more sensible and this could result in predictions about the number of new entrants over time that has an early peak and tends to tail off over time. The number of parameters estimated by MARK should be checked and adjusted.

The final results table is:

Results Browser: POPAN						
Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance
{p(t)}, phi(t), pent(t)}	4885.3623	0.0000	0.99924	1.0000	26	0.0000
{p(t)}, phi(t), pent(t)}	4899.7316	14.3693	0.00076	0.0008	36	0.0000
{p(t)}, phi(t), pent(t)}	4918.0136	32.6513	0.00000	0.0000	15	0.0000
{p(t)}, phi(t), pent(t)}	5030.7102	145.3479	0.00000	0.0000	26	0.0000

It appears that virtually all support lies on the model $\{p_0, \varphi_t, b_t\}$. Because the capture probabilities are constant over time, there is no longer any problem with confounding or non-identifiability at the start or end of the experiment.

The final estimates of the basic parameters and the derived parameters are:

Real Function Parameters of {p(*)}, phi(t)		
Parameter	Estimate	Standard Error
1:Phi	0.8659472	0.0446034
2:Phi	0.9999992	0.1192227E-03
3:Phi	0.9392834	0.0254753
4:Phi	0.8934778	0.0202990
5:Phi	0.8956639	0.0249028
6:Phi	0.9594416	0.0187148
7:Phi	0.8503712	0.0180554
8:Phi	0.9997195	0.0000000
9:Phi	0.8953121	0.0186997
10:Phi	0.9556066	0.0232709
11:Phi	0.9533796	0.0303663
12:Phi	0.9999994	0.1128867E-03
13:p	0.2517871	0.0103360
14:pent	0.2425867	0.0208929
15:pent	0.3197505E-11	0.0000000
16:pent	0.1531475	0.0266547
17:pent	0.1220156	0.0280397
18:pent	0.1183510	0.0281414
19:pent	0.1003467	0.0292821
20:pent	0.0465839	0.0195714
21:pent	0.1570017E-06	0.6592920E-04
22:pent	0.0153315	0.0149972
23:pent	0.0350747	0.0161199
24:pent	0.0383922	0.0169404
25:pent	0.0217577	0.0167637
26:N	2014.6912	60.532767

Grp.	Occ.	B-hat	Standard Error
1	1	488.73722	43.307200
1	2	0.6441985E-08	0.0000000
1	3	308.54501	55.178680
1	4	245.82374	56.941222
1	5	238.44074	56.685513
1	6	202.16764	59.840812
1	7	93.852150	39.113762
1	8	0.3163099E-03	0.1328281
1	9	30.888278	30.180443
1	10	70.664776	32.448409
1	11	77.348430	34.059597
1	12	43.835065	34.099976
Population Estimates of {p(*)}.			
Grp.	Occ.	N-hat	Standard Error
1	1	214.38793	30.097406
1	2	627.94845	40.703996
1	3	626.94640	40.704221
1	4	828.08666	57.929862
1	5	772.91542	54.495706
1	6	793.07278	54.416236
1	7	873.34802	57.400075
1	8	630.28498	29.287469
1	9	629.57830	13.944050
1	10	481.99858	38.455100
1	11	472.60577	39.367002
1	12	486.02212	40.529796
1	13	529.85603	40.558755

The estimated super-population size is interpreted as the total number of capsids ever present in the experiment and does not represent the number present at any particular point in time. The population seems to peak at about sampling occasion 4, and then gradually tapers off because of deaths/emigration and fewer new insects entering the population of interest.

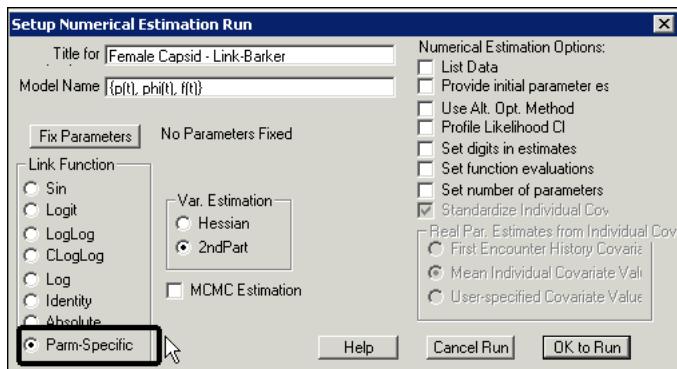
12.5.2. Link-Barker and Pradel-recruitment formulations

Both the Link-Barker and Pradel-recruitment parameterize new entrants to the population using the f_i parameter representing the numbers of new recruits in the interval per member of the population alive at time (i). Because this dataset includes losses-on-capture, the Pradel-recruitment model cannot be used, and the Link-Barker formulation will be used. Don't forget to set the alternating 3- and 4-day time intervals.

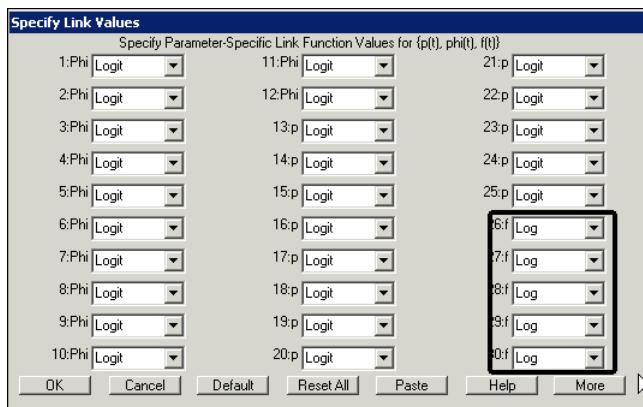
The fully time-dependent model $\{p_t \varphi_t f_t\}$ is fit using PIMs in the usual fashion:

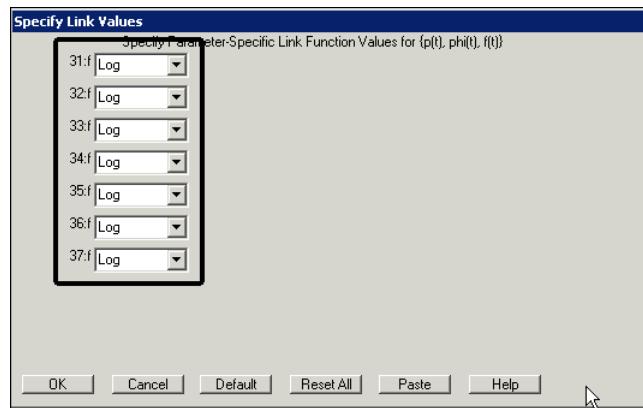


This model is run in the usual fashion.



The recruitment parameter should have a log link-function specified as this parameter can exceed 1.





The results table is:

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance
{p(t), phi(t), f(t)}	10666.1657	0.0000	1.00000	1.0000	35	758.2293

There are 35 parameters (13 capture probabilities; 12 survival probabilities; 12 recruitment probabilities; less 1 non-identifiable parameter at the end of the sampling chain where $\varphi_{12}p_{13}$ can only be estimated; and less 1 non-identifiable parameter at the start of the sampling chain). If the number of parameters in the results table differs, it should be changed in the usual fashion.

The estimates from this model are shown at the top of the next page. The estimated survival probabilities and recruitment parameters are on a *per day* basis. The estimates of p and φ are comparable to the POPAN estimates except for some minor differences at the start of the sampling chain. These are artifacts of the different confounding at the start of the sampling chain between the two formulations. The estimated recruitment parameters indicate the number of new recruits per member of the population. Estimates of the actual population size are not available.

Simpler models for p and φ can be fit in the usual fashion. It may be actually biologically sensible to fit a model with constant f over time as this is the recruitment per existing member. Even if the population is declining over time, perhaps the recruitment is constant over time.

The results table for these models is:

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance
{p(t), phi(t), f(t)}	10657.4228	0.0000	0.98752	1.0000	25	770.1116
{p(t), phi(t), f(t)}	10666.1657	8.7429	0.01248	0.0126	35	758.2293
{p(t), phi(t), f(t)}	10683.1907	25.7679	0.00000	0.0000	14	818.3268
{p(t), phi(t), f(t)}	10783.0539	125.6311	0.00000	0.0000	25	895.7421
{p(t), phi(t), f(t)}	10806.0321	148.6093	0.00000	0.0000	15	939.1373

Virtually all support again lies with the model with constant catchability $\{p, \varphi, f_t\}$. Because capture

Real Function Parameters of {p(t)}		
Parameter	Estimate	Standard Err
1:Phi	1.0000000	0.0000000
2:Phi	0.9830163	0.0259774
3:Phi	0.9562097	0.0394007
4:Phi	0.9035631	0.0277166
5:Phi	0.8838988	0.0319599
6:Phi	0.9339469	0.0223125
7:Phi	0.8616390	0.0255083
8:Phi	0.9976477	0.0229306
9:Phi	0.9003750	0.0355637
10:Phi	0.9609894	0.0333523
11:Phi	0.9235196	0.0512547
12:Phi	0.7372046	0.0261540
12:p	0.1023237	0.0000000
14:p	0.1821002	0.0056901
15:p	0.2241029	0.0371545
16:p	0.2123710	0.0337424
17:p	0.1977410	0.0306743
18:p	0.2365201	0.0317549
19:p	0.3116825	0.0347872
20:p	0.2714373	0.0259713
21:p	0.2689865	0.0305414
22:p	0.2556698	0.0340466
23:p	0.2444797	0.0366274
24:p	0.2570973	0.0431501
25:p	1.0000000	0.0000000
26:f	0.0006197	0.0000000
27:f	0.2533830	0.0000000
28:f	0.7462776	0.1289553
29:f	0.7508969	0.0936962
30:f	0.5802783	0.1278921
31:f	0.6000752	0.1197371
32:f	0.5603289	0.0761922
33:f	0.0648895	1.6747656
34:f	0.4088284	0.1210313
35:f	0.6304078	0.0917065
36:f	0.5477003	0.1062975
37:f	0.3357953	0.1732492

probabilities were constant over time, all parameters are now estimable.

The final estimates are:

Female Capsid - Link-Barker		
Real Function Parameters of {p(*)}, phi		
Parameter	Estimate	Standard Error
1:Phi	1.0000000	0.1128761E-04
2:Phi	0.9727813	0.0207076
3:Phi	0.9401501	0.0285802
4:Phi	0.8934947	0.0203122
5:Phi	0.8957113	0.0249229
6:Phi	0.9594949	0.0187335
7:Phi	0.8502892	0.0208828
8:Phi	0.9999810	0.0000000
9:Phi	0.8952598	0.0238415
10:Phi	0.9556793	0.0232962
11:Phi	0.9535965	0.0304135
12:Phi	0.9999999	0.2860069E-04
13:p	0.2512138	0.0105578
14:f	1.2010867	0.0924535
15:f	0.7083365	0.0831203
16:f	0.7377478	0.0654526
17:f	0.7378570	0.0477018
18:f	0.6751899	0.0600519
19:f	0.7101521	0.0579573
20:f	0.4743710	0.0711472
21:f	0.0486908	1.7038972
22:f	0.3648598	0.1219773
23:f	0.6180099	0.0748742
24:f	0.5460166	0.0851689
25:f	0.5476497	0.1116569

The estimates of p and φ are comparable to those from the POPAN formulation except at the start of the sampling chain. This may be an artifact of convergence to a local minimum by MARK. The estimates of recruitment can be matched to that from POPAN. For example,

$$\hat{f}_{12}^{LB} = 0.54765, \hat{B}_{12}^{PO PAN} = 43.83, \text{ and } \hat{N}_{12}^{PO PAN} = 486.02.$$

Now

$$\frac{\hat{B}_{12}^{PO PAN}}{\hat{N}_{12}^{PO PAN}} = \frac{43.83}{486.02} = 0.090 = (\hat{f}_{12}^{LB})^4 = 0.548^4 = 0.090$$

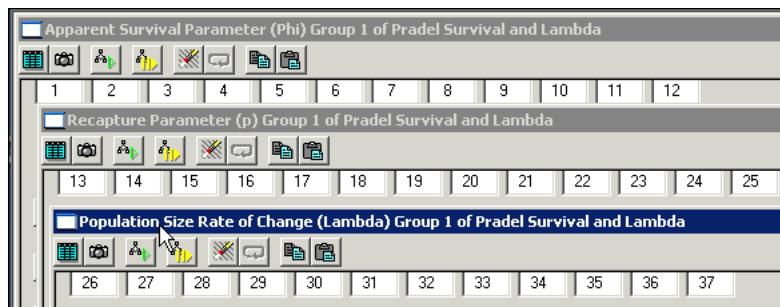
12.5.3. Burnham Jolly-Seber and Pradel- λ formulations

The Burnham-Jolly-Seber and the Pradel- λ formulations parameterize new recruits to the population indirectly by estimating population growth (λ) representing the population size at time ($i + 1$) relative to the population size at time (i). The growth process is the net effect of both survival and recruitment.

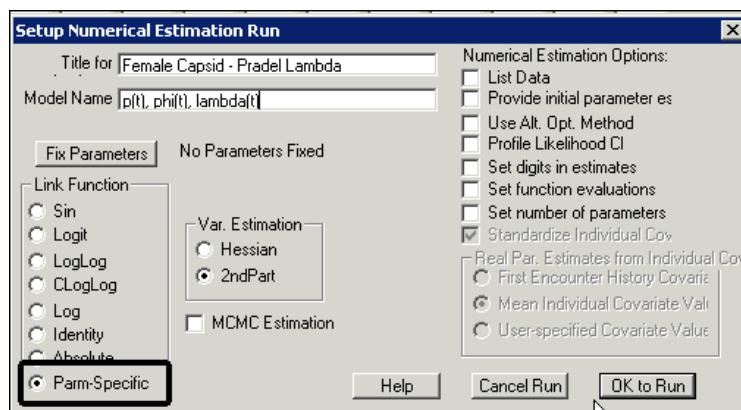
The data are entered in the usual fashion – don't forget to set the alternating 3- and 4-day intervals.

The Burnham-Jolly-Seber formulation again has difficulty in convergence for this example and so is not run against this data.

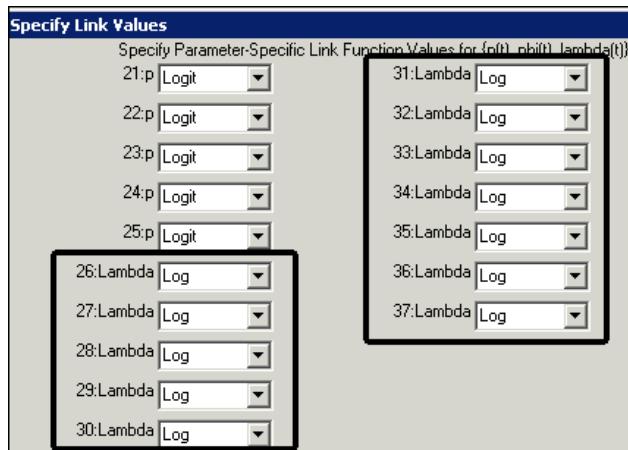
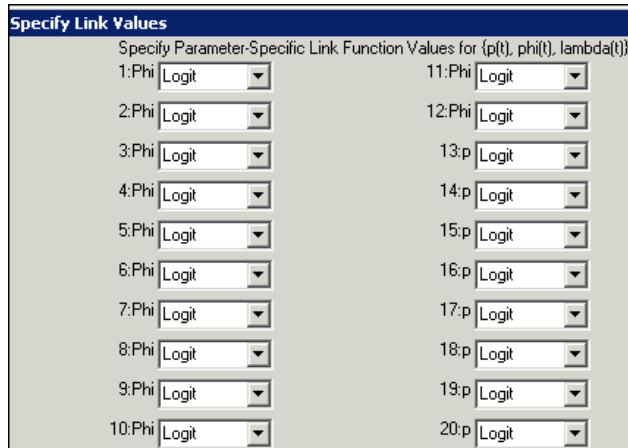
The fully time-dependent Pradel- λ model $\{p_t \varphi_t \lambda_t\}$ is fit using PIMs in the usual fashion:



This model is run in the usual fashion.



The population growth parameter should have a log link-function specified as this parameter can exceed the value of 1.



The results table is:

Results Browser: Pradel Survival and Lambda						
Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance
{p(t), phi(t), lambda(t)}	10643.4100	0.0000	1.00000	1.0000	33	739.6157

There are 35 parameters (13 capture probabilities; 12 survival probabilities; 12 growth rates; less 1 non-identifiable parameter at the end of the sampling chain where $(\varphi_{12}p_{13})$ can only be estimated; and less 1 non-identifiable parameter at the start of the sampling chain). If the number of parameters in the results table differs, it should be changed in the usual fashion.

The estimates from this model are:

Parameter	Estimate	Standard Error
1:Phi	0.8622702	0.0475434
2:Phi	0.9999994	0.1468950E-03
3:Phi	0.9637049	0.0349087
4:Phi	0.9035631	0.0277154
5:Phi	0.8838963	0.0319597
6:Phi	0.9339488	0.0223132
7:Phi	0.8630991	0.0259921
8:Phi	0.9968961	0.0242281
9:Phi	0.9001734	0.0360752
10:Phi	0.9609885	0.0333552
11:Phi	0.9235251	0.0512570
12:Phi	0.9397936	4.5124526
13:p	0.9997664	11.198037
14:p	0.2888521	0.0857385
15:p	0.2326688	0.0332320
16:p	0.2123706	0.0337403
17:p	0.1977443	0.0306722
18:p	0.2365221	0.0317525
19:p	0.3116810	0.0347862
20:p	0.2625937	0.0311958
21:p	0.2729863	0.0324555
22:p	0.2556655	0.0340469
23:p	0.2444797	0.0366279
24:p	0.2570829	0.0431528
25:p	0.2423040	17.196892
26:Lambda	1.1036600	15.502255
27:Lambda	1.0952552	0.0833055
28:Lambda	1.1023949	0.0713553
29:Lambda	0.9965351	0.0509409
30:Lambda	0.9608886	0.0594949
31:Lambda	0.9716717	0.0377260
32:Lambda	0.9450045	0.0445205
33:Lambda	0.9857956	0.0341077
34:Lambda	0.9323707	0.0460851
35:Lambda	1.0027807	0.0421602
36:Lambda	0.9839781	0.0645604
37:Lambda	0.9901150	4.5004712

The estimated survival probabilities and growth rates are on a *per day* basis. The estimates of p and φ are comparable to the POPAN estimates except for some minor differences at the start of the sampling chain. These are artifacts of the different confounding at the start of the sampling chain between the two formulations. The estimated growth parameters indicate ratio of the estimated population size at successive sampling intervals on a per unit time basis. Estimates of the actual population size are not available directly, but as illustrated in previous examples can be derived if needed.

Simpler models for p and φ can be fit in the usual fashion. It may be actually biologically sensible to fit a model with constant λ over time if the population is roughly constant over time. Because the growth rate includes both survival and recruitment, models where growth is constant over time, but survival is not, are not usually fit as it is difficult to believe that changes in recruitment will exactly balance changes in survival to keep the population at a constant level. The results table for these simpler models is:

Results Browser: Pradel Survival and Lambda						
Model	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par.	Deviance
{p(t), phi(t), lambda(t)}	10637.3658	0.0000	0.99386	1.0000	25	750.0546
{p(t), phi(t), lambda(t)}	10647.5518	10.1860	0.00610	0.0061	35	739.6157
{p(t), phi(t), lambda(t)}	10657.6359	20.2701	0.00004	0.0000	25	770.3246
{p(t), phi(t), lambda(t)}	10674.0657	36.6999	0.00000	0.0000	14	809.2009

Virtually all support again lies with the model with constant catchability $\{p, \varphi_t \lambda_t\}$. Because capture rates were constant over time, all parameters are now estimable.

The final estimates are:

Parameter	Estimate	Standard Error
1:Phi	0.8651740	0.0445676
2:Phi	0.9999729	0.0000000
3:Phi	0.9384308	0.0253764
4:Phi	0.8932861	0.0202472
5:Phi	0.8954453	0.0248346
6:Phi	0.9591061	0.0186605
7:Phi	0.8500244	0.0208551
8:Phi	0.9999927	0.7759302E-03
9:Phi	0.8947431	0.0238164
10:Phi	0.9554366	0.0231951
11:Phi	0.9525612	0.0302881
12:Phi	0.9999997	0.7881691E-04
13:p	0.2533691	0.0105643
14:Lambda	1.3830550	0.0698444
15:Lambda	1.0451863	0.0241858
16:Lambda	1.0717819	0.0299564
17:Lambda	0.9835025	0.0204745
18:Lambda	1.0093050	0.0276135
19:Lambda	1.0248589	0.0198782
20:Lambda	0.9043622	0.0240825
21:Lambda	0.9899406	0.0162655
22:Lambda	0.9204955	0.0258054
23:Lambda	0.9949499	0.0237861
24:Lambda	1.0095378	0.0321254
25:Lambda	1.0219978	0.0171985

The estimates of p and φ are comparable to those from the POPAN formulation. There are only a few sampling occasions where the estimates of population growth are inconsistent with estimates of survival, but the differences are minor.

The estimates of population can be matched to that from POPAN . For example, $\hat{\lambda}_{12}^{PL} = 1.0219978$, $\hat{N}_{12}^{POPAN} = 486.02$, and $\hat{N}_{13}^{POPAN} = 529.86$.

Now

$$\begin{aligned}\frac{\hat{N}_{13}^{POPAN}}{\hat{N}_{12}^{POPAN}} &= \frac{529.86}{486.02} = 1.09 \\ &= (\hat{\lambda}_{12}^{PL})^4 = (1.0219978)^4 = 1.09\end{aligned}$$

12.6. Final words

While many researchers think of population numbers and recruitment in terms of actual animals entering populations, the JS model can be extended in a number of ways:

- Manske & Schwarz (2000) used a Jolly-Seber model to estimate stream residence times of salmon. This extended the work of Schaub *et al.* (2001) who used mark-recapture methods to estimate stop-over times of migrating birds. In both methods, the population is transient with new animals arriving and departing on regular basis and the average time at the sampling location is of interest. The key difference between the two approaches is that the methods of Schaub *et al.* (2001) assume that the day the animal is marked is the first day of residence while Manske & Schwarz (2000) did not make this assumption.
- Schwarz & Arnason (2000) and Manske *et al.* (2002) showed how to use the POPAN parametrization to estimate age-specific breeding proportions, i.e., what fraction of animals enter the breeding population at each age.

While current implementations of the JS model allow for multiple groups (e.g., males and females), animals are not allowed to change groups during the experiment. The Cormack-Jolly-Seber (CJS) model has been extended to a multi-state version where animals are allowed to change states during the experiment (e.g., geographical movement) and this is discussed in detail in Chapter 10. Recently, Dupuis & Schwarz (2007) have extended the Jolly-Seber model to allow multiple states. In their example, they modeled a fish population that spawned at various locations around a lake and moved among spawning location during the multiple years of the study. Estimates of abundance at each spawning location and recruitment to spawning locations were obtained.

This stratified Jolly-Seber model can also be used to model stratified closed populations and the Jolly-Seber age-structured model.

The examples in this chapter did not use covariates. System-wide covariates that affect all animals at a particular time point (e.g., temperature) are easily implemented using design matrices. One particular area that requires further work is the use of individual covariates. Individual covariates take two forms – those that vary among individuals, but are fixed for the individual for the study, and individual time-varying covariates. There are two major difficulties. First, even if the covariates are fixed for each animal for the entire study, the value of the covariate is unknown if the animal is not seen. Second, if the individual covariates can change values during the experiment, the value of the covariate is also unknown when an animal is not recaptured after being captured for the first time.

McDonald & Amstrup (2001) used a Horvitz-Thompson type estimator to incorporate individual fixed covariates and were able to estimate population sizes. However, this approach does not have a likelihood basis and so multi-group methods where restrictions on parameters are placed across groups are not easily implemented. Bonner & Schwarz (2006) recently developed methods for the CJS model for individual time-varying covariates, but this has not been extended to JS models. Stay tuned for developments over the next few years.

12.7. References

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