

7.2

EXPLORING ECOLOGICAL RELATIONSHIPS IN SURVIVAL AND ESTIMATING RATES OF POPULATION CHANGE USING PROGRAM MARK

ALAN B. FRANKLIN

Colorado Cooperative Fish and Wildlife Research
Unit, Colorado State University, Fort Collins, CO
80523, USA, alanf@cnr.colostate.edu

Abstract: Recent advances in the theory and application of Cormack-Jolly-Seber capture–recapture models include incorporating individual covariates into the capture–recapture modeling process, and estimating finite rates of population change (λ) from a single capture–history matrix. Program MARK, a software package, incorporates both of these features to allow examination of ecological mechanisms affecting life history traits and how populations change over time. Individual covariates are variables associated with individual capture histories and are modeled in MARK using design matrices. The use of individual covariates in MARK are described with an example examining the effects of physical condition and parasitism on female survival in a fictitious avian species. Individual covariates also can be extended to habitat relationships—at least for territorial species—where individual covariates are habitat variables associated with territories where individuals reside. In program MARK, population rates of change (λ) based on capture–recapture data can be modeled with time-dependency, as a function of external covariates (such as weather) or with individual covariates.

Key words: capture–recapture, individual covariates, program MARK, rate of population change, recruitment rate, survival

In addition to correct parameter estimation, the mechanisms behind variation in parameters over time and space is important in understanding animal population dynamics. Individual covariates are variables associated with individuals, such as indicators of physical condition, size, genetics, and even habitat conditions where individuals reside. They present an avenue for investigating ecological mechanisms in population dynamics, such as individual fitness, competition, and habitat quality. In the simplest case, logistic regression is a feasible tool for examining the effects of individual covariates on survival (White 1983), but only where animals with measurable individual covariates are tracked over time with complete detectability (e.g., through radiotelemetry). However, when detectability

of animals is incomplete (e.g., in band recovery or capture–recapture studies), then nuisance parameters, such as recapture probability, must be incorporated into the analysis. The inclusion of nuisance parameters complicates the estimation of parameters and their sampling variances and covariances. Until recently (see Smith et al. 1994), it was not feasible to examine how individual covariates affected survival estimated from band recovery or capture–recapture data. The reasons behind this recent development were advances in computing power and increased understanding of maximum likelihood estimators. However, given the ability to estimate population parameters with individual covariates, construction of likelihoods that included individual covariates was extremely complicated because of the need to embed logistic equations within the cell probabilities of the likelihood formulation (see White 1983).

In addition to understanding how ecological factors affect life-history parameters, such as survival, a primary concern in understanding and managing animal and plant populations is the estimation of population trends over time and what factors may affect the variation in population growth rates. A useful measure of interest is the finite rate of population change (λ) that can be expressed in its simplest form as:

$$\lambda = \frac{N_t + 1}{N_t} \quad (1)$$

where N is population size and t is the time period when each N is measured. A general question of interest here is whether populations are increasing ($\lambda > 1$), stationary ($\lambda = 1$), or decreasing ($\lambda < 1$) and at what annual rate. Finite rates of population change have traditionally been estimated from estimates of age-specific survival and fecundity using a Leslie projection matrix (Caswell 1989, Noon and Sauer 1992, McDonald and Caswell 1993). Estimates from this method represent averages of λ across some time period when the survival and fecundity were estimated. Hence, this approach has little utility in assessing factors that directly affect λ or in estimating temporal variation in λ . What was needed was an estimator that could estimate λ on a periodic basis (e.g., on an annual basis) with appropriate estimates of sampling variances and covariances. A simplistic approach to dealing with this problem would be to count individuals within some defined area (a census) each t period (e.g., each year t), and estimate λ_t based on Equation (1). However, this approach is invalid for a number of reasons. First, Nichols (1992) provides the relevant philosophical and statistical arguments as to why a census is rarely achieved in wild animal populations because of incomplete detectability and variation in detectability of animals over time. Thus, there are sampling variances associated with each estimate of population size (N) in each period. Second, there are also sampling

covariances between N 's estimated for each sampling period that reflect the inherent lack of independence between N 's (animals in 1 period are also present in preceding and succeeding periods).

In this paper, I present 2 features of program MARK (White and Burnham 1999) that allow (1) the incorporation of individual covariates into estimation of life-history parameters, and (2) a recent method (Pradel 1996) for estimating period-specific λ directly from capture–recapture data. Both these features allow for more meaningful examination of ecological mechanisms that affect life-history traits, how populations change over time, and the underlying factors that may be responsible for those changes.

INDIVIDUAL COVARIATES

Individual covariates are variables associated with individual capture histories (termed “encounter histories” in program MARK). For example, a 6-year study is conducted to examine the effects of physical condition and parasitism on female survival in an avian species. Each year, individual females were captured, weighed, a feather sample taken, checked for parasite loads, color-marked, and then released. Physical condition in terms of nutritional stress was assessed using stable nitrogen isotope ratios ($\delta^{15}\text{N}$ ratios) from feather samples (Mizutani et al. 1990, Hobson et al. 1993), while parasite loads were estimated as the number of hippoboscids (a blood-sucking parasitic fly) found during 10 minutes of combing through the feathers (Young et al. 1993). In subsequent years (encounter occasions), females were re-encountered by resighting their color marks. These are capture–recapture data (the “Recaptures Only” data type in MARK) and the input file for program MARK might look like:

```
111101 1 7.8 0;
101001 1 6.3 1;
101000 1 6.6 0;
001001 1 5.9 3;
001010 1 6.8 1;
001100 1 7.0 1;
001100 1 6.2 4;
010001 1 7.3 0;
010010 1 6.0 6;
010100 1 7.6 1;
100000 1 7.1 0;
001100 1 5.8 5;
.
.
.
000010 1 7.2 0;
```

where the first 6 digits represent the individual's encounter history, the next digit represents the frequency of that encounter history (in this case, frequency is always 1), and the following 2 sets of numbers represent the individual's stable nitrogen isotope value and the

number of hippoboscid flies found. When this file was entered into MARK, the number of individual covariates was specified as 2 and the names NITRO, and FLIES were specified as the individual covariate names in the “Enter Specifications for MARK Analysis” window.

Both group effects on individuals and individual covariates can be modeled together in MARK. Although categorical variables (e.g., sex) can be used as individual covariates, they are generally better considered as group effects on individuals (i.e., male and females separated as groups in the input file). Although all the same analyses can be performed with the group effect treated as an individual covariate, individual covariates are much less efficient of computer time than the group approach. In general, categorical groups are better handled as such rather than as discrete individual covariates. In addition, individual covariates that are continuous should be used as individual covariates and not binned into multiple groups because of the loss in efficiency.

Modeling Individual Covariates in MARK

From the previous example of female condition and parasite loads, the Parameter Index Matrices (White and Burnham 1999) for this particular analysis in MARK are structured as time-dependent for both ϕ and constant for p (merely for the sake of simplicity). Thus, there are 6 parameters in all (5 for ϕ and 1 for p). The simplest structure on N that included 1 of the individual covariates (say, NITRO) would be $\{\phi(\text{NITRO}), p(\cdot)\}$, where survival of individuals is a linear function of their stable nitrogen isotope values. In the “Design Matrix” of MARK, such a model would be constructed as:

1	NITRO	0
1	NITRO	0
1	NITRO	0
1	NITRO	0
1	NITRO	0
0	0	1

From this model, ϕ for an individual i with a given stable nitrogen isotope value can be estimated (using a logit link function) as:

$$\text{logit}(\hat{\phi}_i) = \hat{\beta}_0 + \hat{\beta}_1 \times \text{NITRO} \quad (2)$$

or alternatively as:

$$\hat{\phi}_i = \frac{1}{1 + \exp[-(\hat{\beta}_0 + \hat{\beta}_1 \times \text{NITRO})]} \quad (3)$$

where the estimates of β can be obtained from the output of MARK for this particular model. If $\hat{\beta}_1$ is positive, then a graph of Equation (2) might appear as in Fig. 1a; individual survival is a simple linear function of its stable nitrogen isotope value at initial capture. The manner in which MARK computes the log-likeli-

and ϕ for individuals would be estimated using Equation (6) except that it also would include the interaction terms between year and NITRO.

The preceding examples of models that incorporate individual covariates are analogous to an analysis of covariance (ANCOVA) approach. Models also can be viewed in the framework of multiple regression where multiple continuous variables are examined. For example, the following design matrix in MARK:

```

1 NITRO FLIES 0
1 NITRO FLIES 0
1 NITRO FLIES 0
1 NITRO FLIES 0
1 NITRO FLIES 0
0 0 0 1

```

denotes model $\{\phi(\text{NITRO} + \text{FLIES}), p(\cdot)\}$ where ϕ is estimated as:

$$\hat{\phi}_i = \frac{1}{1 + \exp[-(\hat{\beta}_0 + \hat{\beta}_1 \times \text{NITRO} + \hat{\beta}_2 \times \text{FLIES})]} \quad (8)$$

Currently, interactions between individual covariates cannot be directly constructed in the Design Matrix by multiplying columns together but must be entered as individual covariates with the input file. For example, if the interaction between NITRO and FLIES was included in a potential model, then this variable must be included in the input file as a separate individual covariate and named when the input file is first incorporated into MARK. Thus, interaction terms have to be created and included in the encounter histories file and cannot be created in the Design Matrix from existing individual covariates. Another limitation in MARK is that interactions between continuous cohort-level (i.e., year- or age-specific) covariates—such as weather, effort, etc.—cannot be constructed with individual covariates.

The idea of individual covariates also can be extended to habitats that individuals occupy. Franklin et al. (2000) used habitat covariates on 95 territories occupied by northern spotted owls (*Strix occidentalis caurina*) to examine multiple hypotheses about the effects of landscape habitat configuration on apparent survival (ϕ). In this case, territory-specific covariates were attached to encounter histories for individuals occupying those territories. Thus, more than 1 individual shared the same covariate values. This analysis in MARK also could have been constructed with territories as groups (rather than individual covariates) with the territory-specific covariates used as constraints in the design matrix. However, this would have been unwieldy and inefficient because of the large (95 × 95) size of the design matrix.

Scaling Issues

When the mean value of individual covariates is very large or small or the range of the covariate is over sev-

eral orders of magnitude, the numerical optimization algorithm in MARK may fail to find the correct parameter estimates. To prevent this, the values of individual covariates can be scaled, or standardized. This can be done to each covariate in the input file by dividing each covariate by some number (e.g., 10, 100, etc.) to reduce the magnitude of the covariate before bringing the input file into MARK. Alternatively, the “Standardize Covariate” option can be used in the “Setup Numerical Estimation Run” window in MARK. This option is set as the default and computes the mean (\bar{x}) and standard deviation (SD) of the individual covariate. Then, each value is standardized by the transformation:

$$\text{standardized covariate} = \frac{x - \bar{x}}{\text{SD}}$$

The mean of the standardized covariate is now 0, and the range is roughly from -3 to +3. The range size for the standardized covariates also can be used as a rough rule of thumb when scaling the covariates manually prior to bringing the input file into MARK. One advantage of manually scaling the individual covariates, rather than using the Standardize Covariate option, is that the resulting β s and $s\hat{e}\beta$ s can be easily back-transformed to make predictions from the resulting equation. When the “Standardize Covariate” option is used, back-transformation of the $s\hat{e}\beta$ s requires additional calculations based on the delta method.

RATES OF POPULATION CHANGE AND RECRUITMENT

Pradel (1996) introduced a reparameterization of the Jolly-Seber model (Jolly 1965, Seber 1965) that permitted estimation of λ_t , the annual finite rate of population change at time t in addition to local apparent survival (ϕ_t), recapture probability (p_t), and seniority probability (γ_t ; the probability that an animal at time t had not entered the population between time t and $t - 1$). These parameters can be estimated for demographically open populations; thus, immigration, emigration, births, and deaths are allowed. In addition to the above parameters, a third parameter of interest is recruitment rate (f_t ; the number of new animals in the population at time t per animal in the population at time $t - 1$). The full birth and death model for population change can be accounted for by estimating ϕ and f using the Pradel models. The basic birth and death model for a single age-class that explains changes in a population from 1 time period to another can be written as:

$$N_{t+1} = s_t N_t + b_t N_t + i_t N_t - e_t N_t \quad (9)$$

where s is true survival probability, b is birth rate, i is immigration rate, and e is emigration rate. Equation (9) can be rewritten in terms of Equation (1) as:

$$\lambda_t = s_t + b_t + i_t - e_t.$$

Because the reciprocal of apparent survival (ϕ) includes both mortality and emigration, and recruitment rate (f) includes both birth and immigration, λ_t can be expressed in terms of these 2 parameters:

$$\lambda_t = \phi_t + f_t.$$

Other relationships between the parameters estimated in the Pradel models are shown in Table 1.

Four parameterizations of capture–recapture data are available in program MARK: Pradel Recruitment Only, Pradel Survival and Seniority, Pradel Survival and Lambda, and Pradel Survival and Recruitment. In addition to the ability to obtain time-specific estimates of ϕ , γ , f , and λ , the models implemented in MARK also allowed for constraints by time—such as linear or nonlinear time parameterizations of λ —and by external covariates, such as weather. This can be done with proper consideration of the sampling variances and covariances because estimates of the parameters are included directly in the likelihood rather than through derived parameters, such as recruitment or ϕ .

Underlying Model Assumptions

The 2 parameters obtainable from the Pradel models that have the most interest for population biologists are recruitment rate (f) and λ . A number of design and statistical considerations need to be accounted for before estimation of these parameters can be valid.

First, these models require that the study area size and boundary configurations remain unchanged through time. A common situation is that study areas expand or contract either as investigators become more skilled and experienced in trapping and marking animals or as funding levels increase and decrease. In such cases, the results from the Pradel models in terms of f and λ make no biological sense because the population to which the inferences are being made also is expanding or contracting. Thus, to obtain valid estimates of recruitment or rate of population change, the population must not be altered by adjusting the config-

uration of the study area. Even if study area configuration remains constant, animals can be missed in the first years of the study when observers were first learning their respective study areas. In this case, λ estimates for those initial years will be biased high. If there is a learning curve in the first years of a study, then it would be appropriate to eliminate those years before conducting the analysis.

Second, all animals within the study area must have some probability of being recaptured throughout the study. Consider a study area that has some inaccessible portion where trapping does not occur in the first 2 years but then funding levels allow access for trapping in subsequent years. Individuals captured in the inaccessible portion of the study area will suddenly become new recruits to the population even though they had been present—but not available for sampling—in previous years. This situation is analogous to an internal expansion of the study area.

The sampling situations presented here do not produce bias, in the sense that the estimator of λ is not performing as it was intended. Instead, the area being sampled is increasing, so the estimated population change is the result of 2 conceptually distinct processes. The first process involves expansion of the study area and the increase in number of animals exposed to sampling that result from this expansion. The second process involves changes in the number of animals on the sampled area; this is the change of interest and the 1 to which we would like estimates of λ to apply.

Third, permanent trap response in capture probability can bias estimates of λ (see Appendix D by J. D. Nichols and J. E. Hines in Franklin et al. 1999). Trap response occurs when animals respond positively or negatively to being captured (Seber 1982) and reflects a difference in capture probability between animals that have, and have not, been captured previously and marked. Permanent trap response in the standard Cormack-Jolly-Seber models induces no bias in survival estimates (Pollock et al. 1990) because survival estimates are conditional on animals that are captured, so all modeled capture probabilities correspond to marked animals. Estimates of population size under the Jolly-Seber model, however, are biased in the face of permanent trap response, as the difference in capture probability between marked and unmarked animals causes predictable problems (Nichols and Hines 1984). This same bias also applies to estimates of λ . Nichols and Hines (Appendix D in Franklin et al. 1999) found that bias was positive in the presence of a trap-happy response and negative in the presence of trap-shy responses. This bias was not substantial for small levels of trap responses but could be substantial if levels of trap response were high. If trap response changed over time, then misleading trends in λ could result.

Fourth, heterogeneous capture probabilities can cause bias in estimates of λ . Heterogeneous capture probabilities occur when individuals, or classes of indi-

Table 1. Interrelationship of parameters (γ , λ , and f from models developed by Pradel (1996) and estimated in program MARK.

Parameter	Alternative relationships with other parameters	
γ_{t+1}	$\frac{\phi_t}{f_t + \phi_t}$	$\frac{\phi_t}{\lambda_t}$
λ_t	$\frac{\phi_t}{\gamma_{t+1}}$	$f_t + \phi_t$
f_t	$\lambda_t - \phi_t$	$\phi_t \left(\frac{1 - \gamma_{t+1}}{\gamma_{t+1}} \right)$

viduals, have different capture probabilities. Heterogeneity in capture probabilities results in a negative bias in N (Nichols and Hines 1984). As such, some bias in estimates of λ can be expected because of the inherent relationship with N (see Equation 1), although treating N s as a ratio in Equation (1) should remove some of the bias. However, Nichols and Hines (Appendix D in Franklin et al. 1999) found that heterogeneous capture probabilities did not bias estimates of λ when a single estimate of λ was modeled over a given time period (a $\{\lambda\}$ model). Small bias (from -0.05 to 0.05) did occur when estimating time-specific λ (a $\{\lambda_t\}$ model). However, this bias was not as substantial a problem as that resulting from permanent trap response.

Additional Considerations

The Pradel models implemented in MARK do not allow for age effects because the likelihood is conditioned on the entire encounter history, not just the portion following first capture as when estimating ϕ under the Cormack-Jolly-Seber model. For example, MARK conditions on the full encounter history "001101" to estimate f and λ , whereas it conditions on only the "1101" portion to estimate ϕ and p . Therefore, age cannot be included because age cannot be estimated back to the initial zeros of the encounter history. If age-specific likelihoods are desired, groups of animals can be created based on age.

Another consideration is that of confounded estimates under the full model where all parameters are time-dependent. For example, under model $\{\phi_r, p_r, \lambda_r\}$ the first and last λ are unestimable because ϕ_1 is confounded with p_1 and ϕ_{k-1} is confounded with p_{k-1} (for k encounter occasions). However, when constraints are placed on either ϕ or p , some of the variation in these parameters is taken up by λ , γ , or f . Because λ , γ , and f are the parameters of biological interest in the Pradel models, it is often best to model ϕ and p as completely time-dependent (e.g., as ϕ_r, p_r) and apply constraints of interest on λ , γ , or f .

DISCUSSION

While program MARK provides the capabilities to explore ecological relationships by incorporating individual covariates into estimates of demographic parameters, inferences to those relationships are still limited by the original design of the study. For example, inferences from a study that is observational in nature are more limited than a study that was designed as a true experiment. Program MARK can analyze data from both designs, but the inferences made from the analysis still depends on the original design of the study.

The Pradel models are powerful for analyzing rates of population change solely from a single capture–recapture data set. Combined with the ability to include individual covariates into such an analysis, the Pradel models in MARK form a starting point for

unifying the analysis of demographic parameters (ϕ and f) from an individual standpoint and examining the factors affecting those individual characteristics from a population standpoint in terms of rates of population change. Thus, MARK provides an analytical bridge between individual processes and population processes.

A limitation of the current Pradel models in MARK is that recruitment from in situ reproduction cannot be distinguished from immigration. Thus, changes in recruitment are a function of either fecundity, survival of young to the age when they can be first sampled in the population, immigration, or a combination of all 3. Study areas with estimates of $\lambda \approx 1$ could reflect self-sustaining stationary populations, populations requiring substantial immigration to maintain stability (the "rescue" effect; Gotelli 1991), or a combination of both. For the same reason, source and sink populations (Pulliam 1988) cannot be distinguished based on λ alone as estimated from the Pradel models; other information—such as fecundity, immigration, and emigration rates—needs to be considered as well. Thus, λ estimated from matrix models using age-specific survival probabilities and fecundities address the question: "were the individuals in the population replacing themselves?" However, λ estimated from the Pradel models addresses the question: "had the individuals in the population been replaced?" The latter estimate becomes similar to the first only when immigration and emigration become negligible.

LITERATURE CITED

- BURNHAM, K. P. 1993. A theory for combined analysis of ring recovery and recapture data. Pages 199–213 in J.-D. Lebreton and P. M. North, editors. *Marked individuals in the study of bird populations*. Birkhäuser Verlag, Basel, Switzerland.
- CASWELL, H. 1989. *Matrix population models*. Sinauer Associates, Sunderland, Massachusetts, USA.
- FRANKLIN, A. B., D. R. ANDERSON, R. J. GUTIÉRREZ, AND K. P. BURNHAM. 2000. Climate, habitat quality and fitness in northern spotted owl populations in northwestern California. *Ecological Monographs* 70:539–590.
- , K. P. BURNHAM, G. C. WHITE, R. J. ANTHONY, E. D. FORSMAN, C. SCHWARZ, J. D. NICHOLS, AND J. HINES. 1999. Range-wide status and trends in northern spotted owl populations. U.S. Geological Survey, Colorado Cooperative Fish and Wildlife Research Unit, Fort Collins, and Oregon Cooperative Fish and Wildlife Research Unit, Corvallis, USA.
- GOTELLI, N. J. 1991. Metapopulation models: the rescue effect, the propagule rain, and the core-satellite hypothesis. *American Naturalist* 138:768–776.
- HOBSON, K. A., R. T. ALISAUSKAS, AND R. G. CLARK. 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. *Condor* 95:388–394.
- JOLLY, G. M. 1965. Explicit estimates from capture–recapture data with both death and immigration—stochastic model. *Biometrika* 52:225–247.
- MCDONALD, D. B., AND H. CASWELL. 1993. *Matrix methods*

- for avian demography. Pages 139–185 in D. M. Power, editor. *Current ornithology*. Volume 10. Plenum Press, New York, New York, USA.
- MIZUTANI, H., M. FUKUDA, Y. KABAYA, AND E. WADA. 1990. Carbon isotope ratio of feathers reveals feeding behavior of Cormorants. *Auk* 107:400–403.
- NICHOLS, J. D. 1992. Capture–recapture models: using marked animals to study population dynamics. *Bio-science* 42:94–102.
- , AND J. E. HINES. 1984. Effects of permanent trap responses in capture probability on Jolly-Seber capture–recapture model estimates. *Journal of Wildlife Management* 48:289–294.
- NOON, B. R., AND J. R. SAUER. 1992. Population models for passerine birds: structure, parameterization, and analysis. Pages 441–464 in D. R. McCullough and R. H. Barrett, editors. *Wildlife 2001 populations*. Elsevier Scientific Publishers Limited, London, United Kingdom.
- POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE, AND J. E. HINES. 1990. Statistical inference for capture–recapture experiments. *Wildlife Monographs* 107:1–97.
- PRADEL, R. 1996. Utilization of capture–mark–recapture for the study of recruitment and population growth rate. *Biometrics* 52:703–709.
- PULLIAM, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- SEBER, G. A. F. 1965. A note on the multiple recapture census. *Biometrika* 52:249–259.
- . 1982. *Estimation of animal abundance and related parameters*. Macmillan, New York, New York, USA.
- SMITH, S. G., J. R. SKALSKI, J. W. SCHLECHTE, A. HOFFMAN, AND V. CASSEN. 1994. *Statistical survival analysis of fish and wildlife tagging studies: SURPH.1*. Center for Quantitative Studies, University of Washington, Seattle, USA.
- WHITE, G. C. 1983. Numerical estimation of survival rates from band-recovery and biotelemetry data. *Journal of Wildlife Management* 47:716–727.
- , AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46(suppl.):S120–S139.
- YOUNG, K. E., A. B. FRANKLIN, AND J. P. WARD. 1993. Infestation of northern spotted owls by hippoboscids (Diptera) flies in northwestern California. *Journal of Wildlife Diseases* 29:278–283.