

Investigations of potential bias in the estimation of λ using Pradel's (1996) model for capture-recapture data

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ABSTRACT *Pradel's (1996) temporal symmetry model permitting direct estimation and modelling of population growth rate, λ_i , provides a potentially useful tool for the study of population dynamics using marked animals. Because of its recent publication date, the approach has not seen much use, and there have been virtually no investigations directed at robustness of the resulting estimators. Here we consider several potential sources of bias, all motivated by specific uses of this estimation approach. We consider sampling situations in which the study area expands with time and present an analytic expression for the bias in $\hat{\lambda}_i$. We next consider trap response in capture probabilities and heterogeneous capture probabilities and compute large-sample and simulation-based approximations of resulting bias in $\hat{\lambda}_i$. These approximations indicate that trap response is an especially important assumption violation that can produce substantial bias. Finally, we consider losses on capture and emphasize the importance of selecting the estimator for λ_i that is appropriate to the question being addressed. For studies based on only sighting and resighting data, Pradel's (1996) $\hat{\lambda}'_i$ is the appropriate estimator.*

1 Introduction

Much of the estimation of parameters based on capture-recapture data from open populations can be viewed as conditional on particular entries in each capture history. Survival rate is estimated by conditioning on the initial captures of animals and modelling the capture history with respect to subsequent sampling periods (e.g. Cormack, 1964; Lebreton *et al.*, 1992). Reverse-time modelling conditions

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on the final capture of an individual and models of the prior capture history can provide information about the recruitment of new animals into the population (Pollock *et al.*, 1974; Pradel, 1996). Specifically, the proportion of the population that is 'old' (also members of the population in the previous sampling period) is the reverse-time analogue of survival rate, and is termed the 'seniority parameter' by Pradel (1996). In addition to reverse-time modelling, Pradel (1996) introduced a likelihood for open-population capture-recapture data that models the entire capture history and is based on the temporal symmetry of capture-recapture data. Standard-time and reverse-time approaches are combined in the same likelihood, permitting inference about population growth rate ($\lambda_i = N_{i+1}/N_i$, where N_i denotes abundance at time i), a parameter that integrates recruitment and survival.

Pradel's (1996) paper is relatively recent, and his proposed estimation methodology has not seen a great deal of use, at least until this particular conference. In addition to being only sparsely used, Pradel's (1996) development has not led to the sorts of investigations of estimator robustness (e.g. Carothers, 1973, 1979; Gilbert, 1973) that followed the publication of the Jolly-Seber model (Jolly, 1965; Seber, 1965). We have limited experience with Pradel's (1996) temporal symmetry approach to estimating λ_i , but we have used it with capture-recapture data for northern spotted owls, *Strix occidentalis caurina* (Franklin *et al.*, 1999), meadow voles, *Microtus pennsylvanicus* (Nichols *et al.*, 2000), and roseate terns, *Sterna dougallii* (Nichols & Hines, this issue), and with capture-resighting data for snail kites, *Rostrhamus sociabilis* (Dreitz *et al.*, this issue). In two of these studies (Franklin *et al.*, 1999; Dreitz *et al.*, this issue), concerns about the possibility of obtaining biased estimates of λ_i led us to investigate possible bias resulting from various sources. Here, we report the results of these investigations. Although the investigations are tailored to the specific sampling situations that motivated them, we believe that most of the results are of general interest and should be relevant to other users of this estimation approach.

2 Assumptions

The following assumptions are typically listed for the Jolly-Seber model (e.g. Seber, 1982; Pollock *et al.*, 1990) and are required for reasonable estimates of abundance, N_i .

- (1) Every animal (marked and unmarked) present in the population at sampling period i has the same probability p_i of being captured or sighted.
- (2) Every marked animal present in the population immediately following the sampling in period i has the same probability φ_i of survival until sampling period $i + 1$.
- (3) Marks are neither lost nor overlooked, and are recorded correctly.
- (4) Sampling periods are instantaneous (in reality they are very short periods) and recaptured animals are released immediately.
- (5) All emigration from the sampled area is permanent.
- (6) The fate of each animal with respect to capture and survival probability is independent of the fate of any other animal.

Pradel's (1996) temporal symmetry approach also assumed homogeneity with respect to the reverse-time parameters, γ_i , the probability that an animal present in the sampled population at period i is an 'old' animal that was also present in period $i - 1$.

3 Consequences for $\hat{\lambda}_i$ of assumption violations

3.1 Expansion of study area over time

3.1.1 Background. When Pradel's (1996) approach is parameterized with λ_i , and when interest is focused on the rate of change in population size, then biological interpretations of resulting estimates depend on aspects of study design. For example, one potential problem that arose during consideration of spotted owl sampling involves expansion of some of the study areas over time (Franklin *et al.*, 1999). The sampling situation envisioned begins with a well-defined study area. However, while sampling the study area, investigators may locate birds near the defined study area, yet slightly beyond study area boundaries. As such birds are detected, they are added to the marked sample, and recapture efforts in subsequent years include visits to these particular territory locations, despite the fact that they lie outside the initial study area boundaries. Thus, the investigators are essentially sampling a larger area, and the additional owls within this additional area, as the study progresses.

This sampling situation does not produce bias, in the sense that the estimator of λ_i is not performing as it was intended. Instead, the area being sampled is increasing, so the estimated population change is the result of two conceptually distinct processes. The first process involves changes in the number of birds in the sampled area; this is the change of interest and the one to which we would like $\hat{\lambda}_i$ to apply. The second process involves expansion of the study area and the increase in the number of birds exposed to sampling that results from this expansion.

3.1.2 Bias expressions. If we view the change in the number of birds in the originally defined study area as the true quantity of interest, then we can consider the 'bias' in $\hat{\lambda}_i$ associated with study area expansion. Let N_i denote the number of animals exposed to sampling efforts in the original study area. Then, the true parameter of interest is $\lambda_i = N_{i+1}/N_i$. Let N'_i be the number of birds exposed to sampling efforts during year i that were not exposed to sampling efforts during year $i - 1$ (these birds are associated with the new area sampled in year i). If we view $\hat{\lambda}_i$ as the rate of increase estimated from sampling efforts, then we should be able to approximate relative bias in $\hat{\lambda}_i$ as:

$$\text{Bias}(\hat{\lambda}_i) = E(\hat{\lambda}_i) - \lambda_i \approx \frac{N_{i+1} + N'_{i+1}}{N_i} - \frac{N_{i+1}}{N_i} = \frac{N'_{i+1}}{N_i} \quad (1)$$

If we define relative bias as the ratio of bias to the true parameter value, then relative bias in $\hat{\lambda}_i$ is given by:

$$\text{Rbias}(\hat{\lambda}_i) = \frac{E(\hat{\lambda}_i) - \lambda_i}{\lambda_i} \approx \frac{N'_{i+1}}{N_{i+1}} \quad (2)$$

The interpretation of (2) is that the relative bias of $\hat{\lambda}_i$ is given by the proportional increase in the number of birds exposed to sampling efforts resulting from the expansion of study area in time $i + 1$, relative to the area sampled in time i .

3.2 Permanent trap response in capture probability

3.2.1 Background. Spotted owl sampling also motivated an investigation of possible bias in $\hat{\lambda}_i$ induced by permanent trap response. A standard approach to

owl sampling involves a change in sampling once a territorial bird has been encountered for the first time. In all years following initial location and capture, investigators return to the specific territory (sometimes multiple times) ensuring that capture probability is very high for marked birds. However, it is likely that capture probability for birds that have not been previously marked will be lower, perhaps substantially so. The term 'trap response' was originally intended to apply to an animal's response to being captured (e.g. Seber, 1982), whereas application of the term here applies to a change in capture probability induced by investigator behaviour, rather than bird behaviour. We retain the terminology, because it reflects a difference in capture probability between birds that have, and have not, been previously marked, and this difference in capture probability is the quantity of relevance here. With regard to this investigation, the important point is that the inferences about bias depend only on the differences between capture probabilities of marked and unmarked animals and not on the reasons underlying the differences.

The influence of permanent trap response in the standard Cormack-Jolly-Seber modelling context has been investigated and shown to induce no bias in survival estimates (Nichols *et al.*, 1984). This absence of bias is easily explained, as survival estimates are conditional on animals that are captured, so all modelled capture probabilities correspond to marked birds. 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 causes predictable problems (e.g. see Nichols *et al.*, 1984).

Our initial intuition about this problem led us to believe that $\hat{\lambda}_i$ would likely be positively biased in the face of trap response. The suggestion emerges from a consideration of the natural parameterization of the temporal symmetry model using the γ_i parameter defined above (Pradel, 1996). The relationship between the λ -parameterization and the γ -parameterization can be written as:

$$\lambda_i = \frac{\varphi_i}{\gamma_{i+1}} \quad (3)$$

where these parameters have been defined above (see discussion in Section 4.1). Although the survival estimate under the Cormack-Jolly-Seber model is unbiased in the face of permanent trap response, we believe that the $\hat{\gamma}_i$ are likely to be negatively biased.

As noted above, the $\hat{\gamma}_i$ estimate the fraction of animals present at i that were also present at time $i - 1$. One way to estimate the actual number of animals caught in period i that were present in period $i - 1$ is to divide the number observed in both periods by the estimated capture probability at time $i - 1$, \hat{p}_{i-1} (note that the maximum likelihood estimation does not actually work in this way, but this is an ad hoc estimation approach that can perhaps provide insight into the process). However, most of the information for estimating \hat{p}_{i-1} comes from recaptures and not from new captures of unmarked animals. If recapture probability is really larger than capture probability of unmarked animals, then the \hat{p}_{i-1} will apply approximately to animals marked before $i - 1$ (M_{i-1}) but not to the remainder of animals available for capture at $i - 1$ (the $N_{i-1} - M_{i-1}$ unmarked animals available at $i - 1$). When \hat{p}_{i-1} is too large for some fraction of the animals present at $i - 1$, the estimated number of these animals will be too small, as will the estimates of γ_i . Because of the relationship in equation (3), the $\hat{\lambda}_i$ will show positive bias.

3.2.2 Methods of bias approximation. We examined the influence of permanent trap response on estimates of λ_i using both large-sample analytic approximations and computer simulation (e.g. Nichols *et al.*, 1981; Burnham *et al.*, 1987). The large-sample approximations were obtained by computing the expected value of each observable capture history under a specified set of parameter values. We considered the situation of ten sampling periods. We used 100 000 or 200 000 animals as a population size in order to ensure sufficiently large numbers of animals exhibiting each capture history to permit a reasonable approximation (because we submitted integer numbers to the data-analytic program, MARK, see White & Burnham, 1999). Expected population size was constant over time (i.e. we assumed true $\lambda_i = 1$), and this was accomplished by adding to the population each time period a number of new unmarked animals equal to the number of expected deaths (additions equalled $N(1 - \varphi)$, where N is the population size and φ is the local survival probability). We used a survival rate of $\varphi = 0.85$ for all approximations. The expected values of the capture histories were submitted as data to program MARK, and the resulting parameter estimates are approximations to $E(\hat{\lambda}_i)$. We approximated $E(\hat{\lambda}_i)$ under three different models, model (φ_t, p, λ) , model $(\varphi_t, p, \lambda_t)$, and model $(\varphi_t, p_t, \lambda_t)$, where the subscript t denotes temporal variation and the '.' subscript indicates a parameter that is constant over time.

In addition to these large-sample approximations, we used computer simulation to approximate $E(\hat{\lambda}_i)$ for small population and sample sizes similar to those encountered in spotted owl studies. In these simulations we generated capture history data with individual survival and capture both treated as stochastic processes (Bernoulli trials). For most simulations, we used 100 as a population size. Additions of new animals were treated in a deterministic (rather than stochastic) manner, as we added the number of individuals each time period needed to compensate for the expected number of deaths ($N(1 - \varphi)$, where N is the initial population size). Again, a survival rate of $\varphi = 0.85$ was used in all simulations, and $E(\lambda) = 1$. For each scenario, we conducted 100 iterations and estimated the expected value of $\hat{\lambda}_i$ as the mean of the 100 different parameter estimates. We approximated $E(\hat{\lambda}_i)$ in this manner for two models, model (φ_t, p, λ) , and model $(\varphi_t, p_t, \lambda_t)$. As in the large-sample approximations, we considered the case of ten sample periods.

We investigated several different scenarios for trap response by specifying different values for the capture probabilities of unmarked (p) and previously marked (c) birds. We set the capture probability for previously marked birds as $c = 0.8$ in all scenarios. We investigated values for capture probability of unmarked birds ranging from $p = 0.1$ to 0.9 in increments of 0.1 . These different scenarios included extreme levels of 'trap-happy' response (e.g. $p = 0.1$, $c = 0.8$) as well as an example of a 'trap-shy' response ($p = 0.9$, $c = 0.8$), in order to include the situation of marked owls avoiding capture efforts.

3.2.3 Results of bias approximations. The values of $E(\hat{\lambda}_i)$ obtained using large-sample approximations and computer simulation showed good agreement both for the case of no trap response (underlying model assumptions were met, Fig. 1) and substantial trap-happy response (Fig. 2). Because of this agreement, we present primarily large-sample approximations. As predicted, $E(\hat{\lambda})$ under model (φ_t, p, λ) shows a positive bias in the presence of a trap-happy response. The approximate relative bias of $\hat{\lambda}$ ranged from about 0.10 for $p = 0.1$ and $c = 0.8$ to < 0.01 for $p = 0.7$ and $c = 0.8$. The trap-shy response of $p = 0.9$ and $c = 0.8$ yielded a small negative bias in $\hat{\lambda}$.

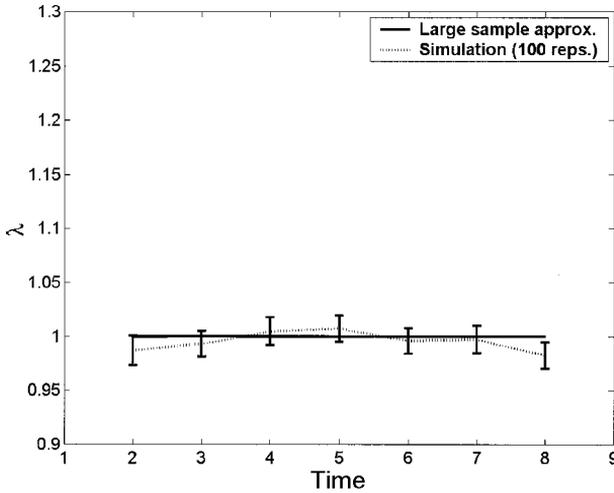


FIG. 1. Comparison of computer simulation (based on 100 iterations) and large-sample approximations for $E(\hat{\lambda}_t)$ under model (φ, p, λ) in the situation where model assumptions are met. Approximations correspond to the following underlying parameter values: $\lambda = 1$, $\varphi = 0.85$, $p = 0.8$. There were ten sample periods, and population size in the simulations was 100 birds.

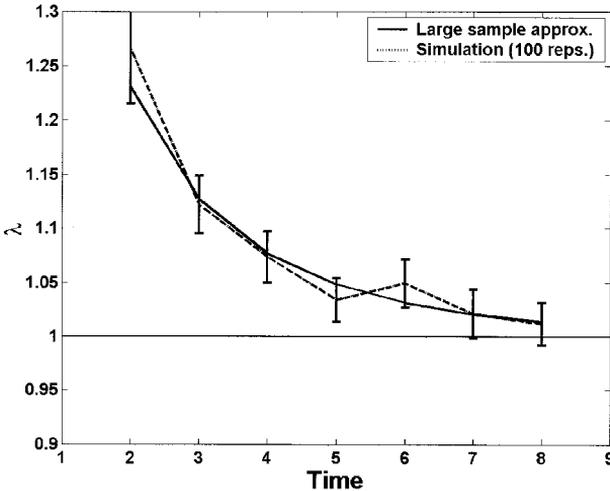


FIG. 2. Comparison of computer simulation (based on 100 iterations) and large-sample approximations for $E(\hat{\lambda}_t)$ under model (φ, p, λ) in the case of trap response. Approximations correspond to the following underlying parameter values: $\lambda = 1$, $\varphi = 0.85$, $p = 0.2$, $c = 0.8$. There were ten sample periods, and population size in the simulations was 100 birds.

The time-specific approximations for $E(\hat{\lambda}_t)$ showed an interesting (and potentially misleading) temporal trend, as $E(\hat{\lambda}_t)$ decreased over time (Fig. 3). $E(\hat{\lambda}_t)$ was largest in sampling period 2 (relative bias of approximately 0.28 for $\hat{\lambda}_2$ in the case of $p = 0.1$ and $c = 0.8$) and decreased monotonically to values near 1 for later sampling periods (Fig. 3). As was the case for the constant-parameter model, bias was not substantial for small levels of trap response, although some evidence of a trend was present for all degrees of trap response investigated. The trend in $E(\hat{\lambda}_t)$ was positive in the case of a trap-shy response.

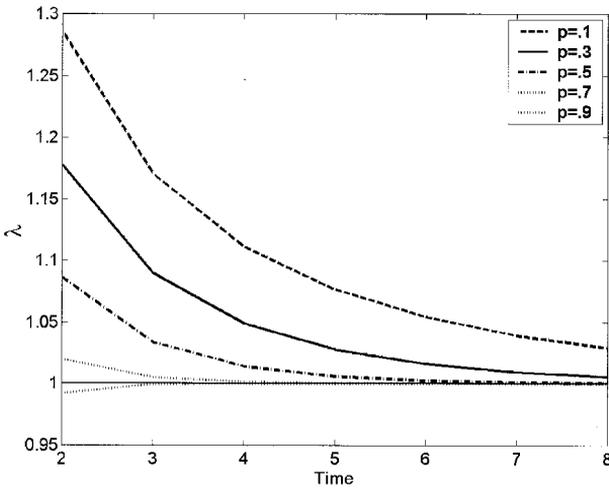


FIG. 3. Large-sample approximations for $E(\hat{\lambda}_i)$ under model $(\varphi_i, p_i, \lambda_i)$ in the case of trap response with ten sample periods. Approximations correspond to the following underlying parameter values: $\lambda = 1$, $\varphi = 0.85$, $c = 0.8$, $p = (0.1, 0.2, \dots, 0.9)$.

An *a posteriori* explanation for the trend in $E(\hat{\lambda}_i)$ involves changes in the relative numbers of marked and unmarked animals in the population through time. The intuitive explanation about the expectation of positive bias in $\hat{\lambda}_i$ under a trap-happy response involved the inappropriate application of capture probability parameters that were based primarily on recaptures to unmarked animals. Unmarked animals comprise a larger proportion of the population in the early periods, whereas marked animals come to dominate the later periods. The greater bias in the earlier time periods is consistent with this line of reasoning.

3.3 Heterogeneous capture probabilities

3.3.1 Background. One of the first problems investigated for the Jolly-Seber model estimators involved heterogeneous capture probabilities among individuals (Carothers, 1973, 1979; Gilbert, 1973). In this situation, different individuals have different capture probabilities, violating assumption 1 underlying the Jolly-Seber model. Although we had no strong intuition about the likely effects of heterogeneous capture probabilities on estimates of λ_i , we guessed that effects might be relatively minor. Our reasoning was that although heterogeneity produces substantial negative bias in individual estimates of population size, parameters (such as λ_i) reflecting ratios of population size should not be badly affected. This prediction is consistent with the results of Skalski & Robson (1992) about estimates of relative abundance based on Lincoln-Petersen estimates of population size.

3.3.2 Methods of bias approximation. As with the numerical investigations of trap response, we used both large-sample approximations and computer simulation to investigate $E(\hat{\lambda}_i)$. We modelled heterogeneity using a simple 2-group distribution (e.g. see Carothers, 1973). The large-sample approximations were computed in the same general manner as for trap response. Instead of having different capture probabilities corresponding to marked/unmarked status, we generated expected

numbers of animals in the different capture histories using one capture probability (p^1) for a constant population of 100 000 birds and a different capture probability (p^2) for a different population of 100 000 birds. These capture probabilities remained the same for birds throughout their lives and did not change with mark status, for example. The number of additions to the population each year was set equal to the expected number of deaths ($N(1 - \varphi)$), so the entire population of 200 000 birds remained approximately constant over time ($\lambda = 1$). These analyses were patterned loosely after spotted owl populations, so a survival rate of $\varphi = 0.85$ was used for these approximations, just as for the trap response investigations. The capture histories for the two groups were combined to yield expected capture histories with heterogeneous capture probabilities for the total population of 200 000 birds. We again considered studies with ten annual sample periods. As in the investigation of trap response, we approximated $E(\hat{\lambda}_t)$ under three different models, model $(\varphi_t, p_., \lambda_.)$, model $(\varphi_t, p_., \lambda_t)$, and model $(\varphi_t, p_t, \lambda_t)$.

In the computer simulation approach, we used 50 birds in each of the two groups (the groups defined by capture probabilities p^1 and p^2) and treated individual survival and capture as Bernoulli trials. For each subgroup, we added new individuals to equal the expected number of deaths in the group each time period ($N(1 - \varphi)$), so $E(\lambda) = 1$. The capture histories for the two groups were combined to yield the data for a heterogeneous population of 100 birds. We estimated λ under two models, $(\varphi_t, p_., \lambda_.)$ and $(\varphi_t, p_t, \lambda_t)$.

We investigated different scenarios reflecting different degrees of heterogeneity. We retained $p^1 = 0.9$ for the high- p group in all scenarios, and we set $p^2 = 0.1, 0.2, \dots, 0.9$, for the low- p group. We first compared the computer simulation and large-sample approximations of $E(\hat{\lambda}_t)$ for the scenario of $p^1 = 0.9, p^2 = 0.2$ under model $(\varphi_t, p_t, \lambda_t)$. The approximations using these two alternative approaches showed good agreement with a positive bias (~ 0.05) in time 2 and a negative bias (~ 0.05) in time 8.

3.3.3 Results of bias approximations. Large-sample approximations for $E(\hat{\lambda})$ under model $(\varphi_t, p_., \lambda_.)$ showed no evidence of bias (i.e. $E(\hat{\lambda}) = 1.00$), indicating no influence of heterogeneous capture probabilities on estimates of λ under this model. However, the time-specific estimates of λ under model $(\varphi_t, p_t, \lambda_t)$ did show evidence of bias, with approximations of bias ranging from -0.05 to 0.05 for the time-specific $\hat{\lambda}_t$ (Fig. 4). Interestingly, the time-specific approximations for $E(\hat{\lambda}_t)$ showed a temporal trend, as $E(\hat{\lambda}_t)$ decreased over time (Fig. 4). The magnitude of bias was dependent on the degree of heterogeneity, although the greatest bias was not observed for the largest degree of heterogeneity. Instead, the greatest bias was associated with the scenario of $p^1 = 0.9, p^2 = 0.3$, whereas the scenario of $p^1 = 0.9, p^2 = 0.1$ showed smaller bias. An *a posteriori* explanation for this difference, is that when the low- p group has a sufficiently low capture probability, these birds provide a small contribution to the capture history data, leaving most data corresponding to birds in the high- p group.

Heterogeneous capture probabilities do not appear to present as substantial a problem as does permanent trap response in capture probabilities. Bias in $\hat{\lambda}$ appears to be negligible under model $(\varphi_t, p_., \lambda_.)$, and bias in the $\hat{\lambda}_t$ under model $(\varphi_t, p_t, \lambda_t)$ is relatively small, yet showed evidence of a temporal trend in bias of $\hat{\lambda}_t$. Clearly, these inferences are restricted to the exact situations that we investigated, and we encourage additional work with different scenarios.

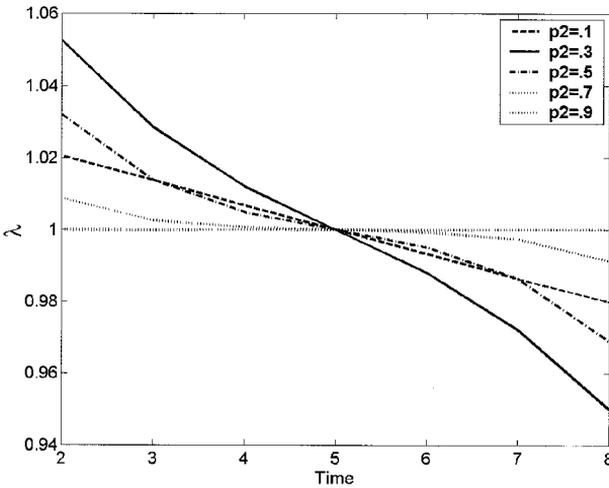


FIG. 4. Large-sample approximations for $E(\hat{\lambda}_i)$ under model $(\varphi_t, p_t, \lambda_t)$ in the case of heterogeneous capture probabilities with ten sample periods. Approximations correspond to the following underlying parameter values: $\lambda = 1$, $\varphi = 0.85$, $p^1 = 0.9$, $p^2 = (0.1, 0.2, \dots, 0.9)$.

3.4 Combined effects of trap response and heterogeneity

It is certainly possible that permanent trap response and heterogeneity could be operating simultaneously in a sampled population. Thus, we investigated a small number of possible scenarios, again based loosely on spotted owls. Specifically, we envisioned two groups of birds (1 and 2) with different capture probabilities for unmarked (p^1, p^2) and marked (c^1, c^2) birds within each group. We investigated this possibility using large-sample approximations as described above. We retained a constant population of 100 000 in each group of birds and used annual survival probabilities of 0.6, 0.7, 0.8 and 0.9. We computed approximations for $E(\hat{\lambda}_i)$ under models $(\varphi_t, p_t, \lambda_t)$, $(\varphi_t, p_t, \lambda_t)$ and $(\varphi_t, p_t, \lambda_t)$.

We left capture probabilities for group 2 the same for all scenarios at $p^2 = 0.4$, $c^2 = 0.9$. We then defined different scenarios using the following capture probabilities for members of group 1: $p^1 = 0.1, c^1 = 0.6$; $p^1 = 0.2, c^1 = 0.7$; $p^1 = 0.3, c^1 = 0.8$; $p^1 = 0.4, c^1 = 0.9$; and $p^1 = 0.45, c^1 = 0.95$. Large-sample approximations for $E(\hat{\lambda})$ under model $(\varphi_t, p_t, \lambda_t)$ show a positive bias of approximate magnitudes 0.05 to 0.06 for survival of 0.85, similar to those observed under some degrees of trap response (Fig. 5). Large-sample approximations for $E(\hat{\lambda}_i)$ under model $(\varphi_t, p_t, \lambda_t)$ show a temporal trend with decreases over time (Fig. 6). Estimates of survival were slightly positively biased, while estimates of seniority were more negatively biased, which would explain the positive bias in λ .

4 Consequences for $\hat{\lambda}_i$ of ignoring losses on capture

4.1 Background

All animals are not always released following capture in capture-recapture studies. Reasons for failure to release an animal vary and can involve trap death, handling death, or removal by the investigator for experimental reasons. In resighting studies that focus on abundance estimation, unmarked animals must be counted at each

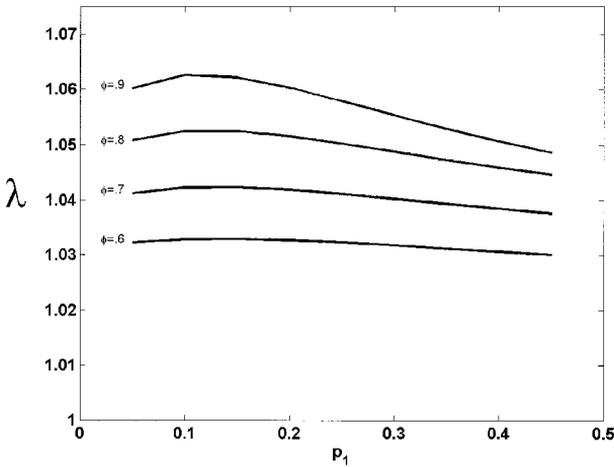


FIG. 5. Large-sample approximations for $E(\hat{\lambda})$ under model $(\varphi_1, p_1, \lambda)$ in the case of simultaneous trap response and heterogeneity with ten sample periods. Approximations correspond to the following underlying parameter values: $\lambda = 1$, $\varphi = (0.9\text{-top line, } 0.8, 0.7, 0.6\text{-bottom line})$. Group 2 capture probabilities remained the same for each scenario at $p^2 = 0.4$, $c^2 = 0.9$, and capture probabilities for members of group 1 were $p^1 = (0.55 - 0.95)$, $c^1 = p^1 + 0.5$.

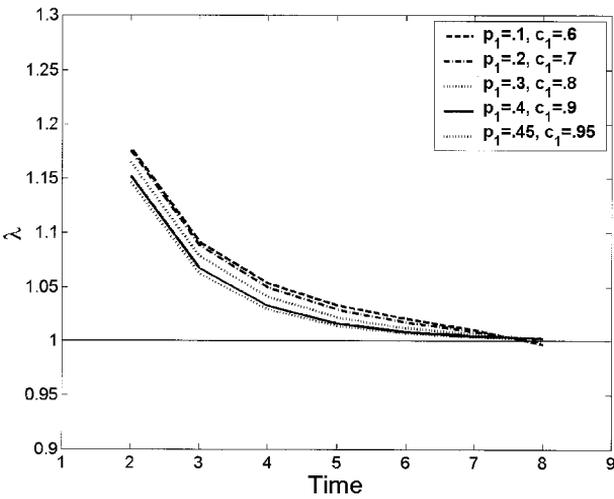


FIG. 6. Large-sample approximations for $E(\hat{\lambda}_t)$ under model $(\varphi_t, p_t, \lambda_t)$ in the case of simultaneous trap response and heterogeneity with ten sample periods. Approximations correspond to the following underlying parameter values: $\lambda = 1$, $\varphi = 0.85$. Group 2 capture probabilities remained the same for each scenario at $p^2 = 0.4$, $c^2 = 0.9$, and capture probabilities for members of group 1 were $p^1 = 0.1$, $c^1 = 0.6$; $p^1 = 0.2$, $c^1 = 0.7$; $p^1 = 0.3$, $c^1 = 0.8$; $p^1 = 0.4$, $c^1 = 0.9$; and $p^1 = 0.45$, $c^1 = 0.95$.

sampling occasion but must be treated as not released, as the investigator has no opportunity to identify them in subsequent periods. The study of Dreitz *et al.* (this issue) used resighting data on snail kites to estimate both abundance and population growth rate and motivated our interest in this topic. Specifically, we were interested in estimating λ_t using the temporal symmetry modelling approach of Pradel (1996).

Consideration of animals that are not released requires that we distinguish

between the moments just before and just following sampling in each period i . Define N_i^- and N_i^+ respectively as abundance just before and after sampling period i . Defining d_i as the number of animals that are caught at i and not released back into the population following sampling, we can write $N_i^+ = N_i^- - d_i$. We denote as η_i the probability that an animal captured in period i survives trapping and handling and is released back into the population. The relationship between N_i^- and N_i^+ can be written as:

$$N_i^+ = N_i^- [1 - p_i(1 - \eta_i)] \quad (4)$$

Equation (4) simply indicates that a member of N_i^- must survive the possibility of being caught and removed from the population in order to become a member of N_i^+ .

Expressions for population growth rate can be obtained by considering two alternative ways of writing the expected number of animals alive in two successive sampling occasions. Based on forward-time and reverse-time modelling, we can write this expectation as $N_i^+ \varphi_i \approx N_{i+1}^- \gamma_{i+1}$ (see Pradel, 1996). Solving this approximate equality yields the expression for population growth rate presented in equation (3):

$$\begin{aligned} \lambda_i &= N_{i+1}^- / N_i^+ \\ &\approx \varphi_i / \gamma_{i+1} \end{aligned} \quad (5)$$

Equation (5) is relevant to biological changes in the population occurring between the two sampling periods, but does not account for animals that are captured and not released back into the population. To account for animals not released, Pradel (1996) suggests the following modified rate of population change (λ'_i) that also incorporates losses of animals during sampling:

$$\begin{aligned} \lambda'_i &= N_{i+1}^- / N_i^- \\ &= \lambda_i (N_i^+ / N_i^-) \\ &= \frac{\varphi_i (1 - p_i [1 - \eta_i])}{\gamma_{i+1}} \end{aligned} \quad (6)$$

The numerator of equation (6) represents the probability of surviving all mortality sources (including those associated with trapping and handling), and the λ'_i defined in equation (6) reflects the actual growth in the presence of sampling and trap mortality.

In the case of a resighting study designed to estimate λ_i , the unmarked data are treated as losses on capture, as noted above. Under such a design, the usual parameter denoting the probability that a captured bird survives the capture process, η_i , now denotes the probability that a randomly selected bird from all those sighted at time i is a marked bird. Stated differently, $\hat{\eta}_i$ estimates the proportion of marked birds among the entire sample of sighted birds. The usual estimator of λ_i from equation (5) now estimates nothing of interest, whereas the estimator (equation (6)) developed to deal with losses on capture (denoted as λ'_i) estimates the growth rate for the population. Note that the η_i are likely to be relatively small in such resighting studies, leading to potentially large differences between λ_i and λ'_i .

The objective of this investigation was to assess the magnitude of bias resulting from use of inappropriate estimators for λ_i in cases where not all animals are

released following capture. Program MARK (White & Burnham, 1999) computes the estimator for λ_i that does not allow for losses on capture. However, because of the many nice features of MARK, it would be tempting to use this program to estimate λ_i even in the presence of losses on capture, if the resulting bias was likely to be small. Thus, one objective was to examine the magnitude of bias in $\hat{\lambda}_i$ produced by MARK, in the presence of losses on capture. The second objective was to examine the difference between growth rate estimates produced by the different estimators of equations (5) and (6) in order to assess the importance of the proper choice of estimators.

4.2 Methods of bias approximation

As with the investigations of assumption violations (Section 3), we used large-sample approximations to investigate the consequences of losses on capture for the three estimators of λ_i : the estimators of equations (5) and (6), and the estimator used in the current version of MARK (White & Burnham, 1999). We used a population size of 100 000, with constant expectation over the six sampling periods. Survival rate and capture/resighting probability were constant over time at 0.70 and 0.40, respectively. We investigated various values of η_i (probability of being released, conditional on capture/sighting) ranging from 0.2 to 1.0. New unmarked animals were added to the population each year in order to replace expected deaths [$N(1 - \varphi)(1 - p(1 - \eta))$]. Thus, the true growth rate of the population (λ'_i) had expectation 1, whereas the growth rate resulting from only biological processes and not sampling (λ_i) was > 1 . Specifically,

$$\lambda_i = \frac{\lambda'_i}{1 - p_i(1 - \eta_i)} = \frac{1}{1 - p_i(1 - \eta_i)}$$

The expected numbers of animals in all possible capture histories were input as data to program MARK and to a GAUSS program written by Hines to compute $\hat{\lambda}_i$, $\hat{\lambda}'_i$ (see Pradel, 1996).

4.3 Results of bias approximations

Results of large-sample approximations for the entire range of η_i values show that all three estimators yield the same, unbiased estimate of $\hat{\lambda}_i = 1$ for the case of all animals released following capture, $\eta_i = 1$ (Fig. 7). Pradel's (1996) $\hat{\lambda}_i$ and $\hat{\lambda}'_i$ provide unbiased estimates of their respective parameters, as expected when sample sizes are larger and all model assumptions are met. Smaller values of η_i lead to greater divergence in the three estimates, as expected. In cases where non-release of animals is a consequence of trap death or handling mortality, we expect η_i to be large and to approach 1.

In the case of true losses on capture, the investigator may be interested in either $\hat{\lambda}_i$ (equation (5)) or $\hat{\lambda}'_i$ (equation (6)), depending on the question(s) being posed. However, in the case of a resighting study, then only $\hat{\lambda}'_i$ is of interest. The substantial difference between Pradel's (1996) $\hat{\lambda}_i$ and $\hat{\lambda}'_i$ for the case of small to moderate values of η_i expected to result from resighting studies emphasizes the importance of focusing on the appropriate estimator $\hat{\lambda}'_i$. The point estimates of η_i computed for snail kites by Dreitz *et al.* (this issue) ranged from 0.13 to 0.17, and the bias resulting from incorrect use of $\hat{\lambda}_i$ in that situation would be substantial (Fig. 7).

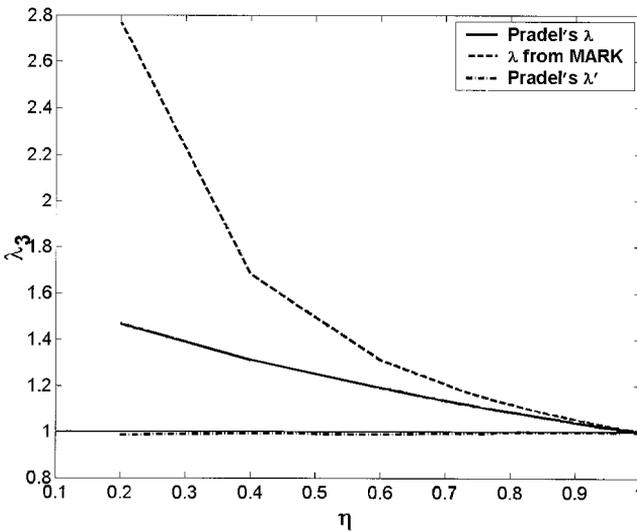


FIG. 7. Large-sample approximations for $E(\hat{\lambda}_2)$ based on estimator developed for use with no losses on capture, and both estimators ($\hat{\lambda}_1, \hat{\lambda}'_1$) of Pradel (1996) accounting for losses on capture, where η_i (probability of being released given capture) ranges from 0.2 to 1.0. Approximations correspond to the following parameter values: $\lambda' = 1, \Phi = 0.7, p = 0.4$.

5 Discussion

The bias investigations that were focused on consequences of assumption violations (Section 3) lead to several inferences. The expressions presented in Section 3.1 lead to the simple recommendation to restrict use of this approach for λ_i estimation to sampling situations where study area expansion is negligible. In situations where this expansion has occurred, it may be possible to restrict analyses to a subset of the data. Perhaps the important thing to remember about this means of estimating λ_i is that it estimates the rate of change in abundance of birds exposed to sampling efforts. If this quantity reflects population dynamics of birds, then it will likely be of interest to us, whereas if it reflects both population dynamics and changes in sampling (e.g. area expansion), then biological interpretation may be more difficult.

The investigations presented in Sections 3.2, 3.3 and 3.4 concerned violations of the assumption of homogeneous capture probabilities. A general observation is that inferences based on forward-time modelling should not be assumed necessarily to apply to reverse-time or temporal symmetry approaches. Our specific numerical investigations lead to a greater concern for trap response in capture probabilities than for heterogeneity. Of particular relevance to the modelling of population growth is the temporal trend in $\hat{\lambda}_i$ that can be generated by these violations of the assumption of equal capture probabilities (both trap response and heterogeneity). Because of this tendency, we believe it prudent to omit from our model set models that incorporate temporal trends in λ_i . In many cases, we believe it will be wise to focus on full time-specific models (e.g. $[\varphi_t, p_t, \lambda_t]$ and on models with time-invariant population growth (e.g. $[\varphi_t, p, \lambda]$ and $[\varphi_t, p_t, \lambda]$). In the case of models with time-specific parameters, it may also be wise to view the initial estimate of population growth (usually $\hat{\lambda}_2$) with caution, as this estimate is likely to exhibit substantially greater bias than any subsequent estimates.

In Section 4, we considered losses on capture and the need to select the

appropriate estimator for λ_i when faced with such losses. It is important that analysts using pre-written software devote adequate thought to the design and objectives of their studies in order to make informed decisions about computing and estimation. In the case of sampling designs based solely on sighting and resighting data, it is especially important to use the appropriate estimator, $\hat{\lambda}'_i$. (The GAUSS program to compute $\hat{\lambda}_i$ in the presence of losses on capture can be obtained from JEH.)

We conclude with the obvious recommendation that investigators devote substantial thought to the design and analysis of studies aimed at estimation of λ_i . The investigations reported here were tailored to specific sampling situations and provided results that were useful to us in our own work. We believe that the results may be useful to others as well (hence this manuscript), but we also urge others to consider similar exercises aimed at their specific studies. As the collective scientific community becomes more familiar with direct estimation of population growth rate, perhaps the need for these types of simulation studies will diminish, but we have certainly not approached such a level of familiarity yet.

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