ROBUSTNESS OF CLOSED CAPTURE–RECAPTURE METHODS TO VIOLATIONS OF THE CLOSURE ASSUMPTION

WILLIAM L. KENDALL[1]

USGS Patuxent Wildlife Research Center, 11510 American Holly Drive, Laurel, Maryland 20708-4017 USA

Abstract. Closed-population capture–recapture methods have been used extensively in animal ecology, both by themselves and within the context of Pollock's robust design and multistate models, to estimate various parameters of population and community dynamics. The defining assumption of geographic and demographic closure (i.e., no births, deaths, immigration, or emigration) for the duration of sampling is restrictive and is likely to be violated in many field situations. I evaluated several types of violations of the closure assumption and found that completely random movement in and out of a study area does not introduce bias to estimators from closed-population methods, although it decreases precision. In addition, if capture probabilities vary only with time, the closed-population Lincoln-Petersen estimator is unbiased for the size of the superpopulation when there are only births/immigration or only deaths/emigration. However, for other cases of nonrandom movement, closed-population estimators were biased when movement was Markovian (dependent on the presence/absence of the animal in the previous time period), when an animal was allowed one entry to and one exit from the study area, or when there was trap response or heterogeneity among animals in capture probability. In addition, the probability that an animal is present and available for capture (e.g., breeding propensity) can be estimated using Pollock's robust design only when movement occurs at a broader temporal scale than that of sampling.

Key words: breeding propensity; capture–recapture; closed populations; emigration; immigration; multistate models; Lincoln-Petersen method; Pollock's robust design; species richness; temporary emigration.

INTRODUCTION

Closed-population capture–recapture methods have a long history of development and use in the study of animal populations, dating back to Petersen (1896). The defining assumption of these methods is that the population is closed to additions (births or immigration) and deletions (deaths or emigration) for the duration of the study, thus requiring a short time frame. These methods have been used to estimate the size of populations from various taxa, including reptiles (Magnusson et al. 1978), nesting birds (Grier et al. 1981), fish (Schwarz and Dempson 1994), terrestrial mammals (Nichols et al. 1984, Karanth and Nichols 1998), and marine mammals (Packard et al. 1985). Recently, they have also been applied to plants (Alexander et al. 1997).

Several authors have used closed-population methods in long-term studies, within the context of Pollock's robust design (1982), to estimate survival (Kendall and Pollock 1992), the proportion of white-footed mice (*Peromyscus leucopus*) in torpor (Kendall et al. 1997), breeding propensity and natal philopatry of Pacific Black Brant (*Branta bernicla orientalis*) (Lindberg et al. 1998; J. S. Sedinger, M. A. Lindberg, and N. Chel-

gren, *unpublished manuscript*), weight class transition probabilities for meadow voles (*Microtus pennsylvanicus*) (Nichols et al. 1992), and both immigration and in situ reproduction of meadow voles (Nichols and Pollock 1990). M. A. Lindberg, W. L. Kendall, J. E. Hines, and M. G. Anderson (*unpublished manuscript*) combined the robust design with band recoveries to simultaneously estimate breeding propensity and fidelity to breeding site of Canvasback ducks (*Aythya valisineria*). A slightly different use of closed-population models has been in the estimation of species richness (Burnham and Overton 1979, Bunge and Fitzpatrick 1993, Nichols and Conroy 1996, Boulinier et al. 1998) and community dynamics (Nichols et al. 1998*a*, *b*).

All of these methods are based on the closure assumption, that the population is static for the duration of the study or within a primary period for the robust design. Otis et al. (1978:66) presented a test for closure, which has been incorporated into program CAPTURE (White et al. 1982, Rexstad and Burnham 1991). However, this test is overly sensitive to behavioral response to capture and insensitive to temporary emigration that occurs in the middle of the closed study period (Otis et al. 1978:67). Stanley and Burnham (1999), building on the efforts of Pollock et al. (1974), have developed a composite test for closure that complements the test just described, but suffers from low power to detect some types of closure violations.

When closure violations cannot be reliably detected, what are the implications of using closed-population methods in the face of these violations? Seber (1982: 59) discussed the implications of specific types of violations of this assumption for the two-sample Lincoln-Petersen (L-P) estimator (Petersen 1896, Lincoln 1930). The purpose of this paper is to more fully evaluate the robustness of closed-population estimation methods to violations of the closure assumption, including when there are more than two capture occasions. I focus on the case in which there is completely random movement in and out of the study area during the time when closure is assumed. I consider this case for various scenarios in which closed-population models are used in animal ecology: short-term studies, longer term studies in which Pollock's robust design is used, especially estimation of temporary emigration, and estimation of species richness and community dynamics. I also consider the effect of other types of closure violations on the estimators: (1) Markovian movement, in which the probability of being in the study area at sampling occasion j depends on whether the animal was in or out of the area at sampling occasion $j - 1$; (2) animals leave the study area throughout the primary sampling period; (3) individual animals arrive in the study area throughout the primary sampling period; (4) individual animals arrive once and leave once throughout the primary sampling period; and (5) capture itself affects movement outside the study area before the end of the primary sampling period.

An exhaustive evaluation of all possible types of violation of closure and their severity is neither possible nor necessary here. My intent is to consider the types of bias one might expect under various realistic scenarios, and thereby comment on where an investigator should be concerned. The investigator could then use simulation to evaluate the potential bias in more detail.

COMPLETELY RANDOM IMMIGRATION AND EMIGRATION

Closed-population models: general

With closed-population studies, we assume that there are N animals in the study area at the first sampling occasion, and we assume that those same animals are there for all sampling occasions. Estimation is easily demonstrated in the two-sample case, in which a sample of n_1 animals is captured, marked, and released. After a short period of time, a second random sample of n_2 animals is captured, m_2 of which are marked. Assuming that (1) the population is closed to additions and deletions between sampling occasions 1 and 2, (2) at each occasion j, each animal present in the study area (i.e., members of the population) has the same probability of capture p_j, and (3) no marks are lost and all marks are reported, one would expect the ratio of

the proportion of marked animals in the second sample to approximately equal the proportion of marked animals in the population:

$$\frac{m_2}{n_2} \approx \frac{n_1}{N}. \tag{1}$$

This leads to the following estimators:

$$\hat{N} = \frac{n_1 n_2}{m_2} \qquad \hat{p}_1 = \frac{n_1}{\hat{N}} \qquad \hat{p}_2 = \frac{n_2}{\hat{N}}. \tag{2}$$

What are the implications if, in reality, those animals move in and out of the study area in a completely random fashion when closure is assumed? In other words, the N_j animals that are in the study area (and thus vulnerable to capture) at capture occasion j are a random sample drawn from a superpopulation of N^0 animals, where each animal is drawn with probability τ_j. In this case, $E(N_j|N^0) = N^0\tau_j$, so the size of the population in the study area is not necessarily constant during the study. Without loss of generality, the use of the L-P estimator again makes the point:

$$E(n_1|N^0) = N^0\tau_1 p_1 \qquad E(n_2|N^0) = N^0\tau_2 p_2$$
$$E(m_2|N^0) = N^0\tau_1 p_1 \tau_2 p_2 \tag{3}$$

implying that

$$E(\hat{N}) \approx \frac{E(n_1|N^0)E(n_2|N^0)}{E(m_2|N^0)} = \frac{(N^0\tau_1 p_1)(N^0\tau_2 p_2)}{N^0\tau_1 p_1 \tau_2 p_2}$$
$$= N^0 \tag{4}$$

and

$$E(\hat{p}_1) = \tau_1 p_1, \qquad E(\hat{p}_2) = \tau_2 p_2. \tag{5}$$

The τ_j and p_j are simply confounded, forming an effective probability of capture for those in the superpopulation (i.e., $p_j^0 = \tau_j p_j$). Therefore, these estimators are biased for the group of animals in the study area at a given capture occasion j, but unbiased for the superpopulation. This is consistent with Seber's (1982: 59) comment that concurrent movement in and out would positively bias $\hat{N}$. His frame of reference was the study area, not the superpopulation. In this case of animals moving in and out in the short term, the superpopulation will often be of more ecological interest than the number of animals in the study area.

The L-P estimator is a special case of the Darroch (1958) estimator (model M_t in Otis et al. 1978) for an arbitrary number of samples, where capture probability varies only with time. When the closure assumption is violated, but by completely random movement in and out of the area, and the superpopulation is *completely* closed during the study, model M_t is still appropriate, although the capture probability estimates again apply to the superpopulation (i.e., expected value of $\tau_j p_j$). Therefore, the only effect of this type of closure violation is to lower the effective capture probability for each animal in the superpopulation.

This result for the estimator under model M_t can be extended to estimators under any models from Otis et al. (1978), which in addition to time, allow for trap response (M_b), heterogeneity among animals (M_h), or any combination of these three sources of variation in capture probabilities. We can evaluate this by considering the effective probability of capture ($p^0 = \tau p$) of a given animal under various scenarios, and note that any subscripting of p^0 is dependent on the subscripting of τ and p. We have already evaluated the case where both τ and p depend only on time (t), and concluded that model M_t is the appropriate model. If τ is constant over time and p is time dependent, or vice versa, then model M_t is still appropriate. If both are constant over time, then $p^0 = \tau p$ and M_0 is the appropriate model.

If there is time variation in neither τ nor $p,$ but there is a trap response in either τ (marked animals have a different probability ψ of being in the study area than unmarked) or p (of those present in the study area, marked animals have a different probability of capture c than unmarked), or both, then $p^0 = \tau p$ for unmarked animals and $c^0 = \psi p$, or $c^0 = \tau c$, or $c^0 = \psi c$, depending on the scenario. These three scenarios cannot be distinguished by the data. However, model M_b is appropriate in any case and its estimator $\hat{N}_b$ (Zippin 1956, Otis et al. 1978:29) is unbiased for superpopulation size N^0.

We can create a parallel argument for the case of heterogeneity among animals. Again assuming constancy over time, we consider the effective capture probability p_a^0 for animal a, where $a = 1, 2, \ldots, N^0$. If either τ, or p, or both, are unique for each animal in the study area, then $p_a^0 = \tau_a p$, or $p_a^0 = \tau p_a$ or $p_a^0 = \tau_a p_a$, respectively. In each case, the effective probability of capture is unique for each animal, but is neither time dependent nor based on previous capture, so model M_h is appropriate. Nevertheless, keep in mind that estimators under model M_h, and other models that include heterogeneity, tend to be biased to some extent, with the severity of the bias depending on the variation in capture probabilities among animals (Otis et al. 1978, Lee and Chao 1994, Norris and Pollock 1996). Therefore, movement that increases variation in capture probabilities, as well as decreasing average capture probability, will tend to exacerbate that bias.

Many additional combinations are possible using this approach. For example, if each animal has a unique conditional capture probability and there is time variation in the probability of being in the study area, then $p_{ta}^0 = \tau_t p_a$, and model M_{th} is appropriate. In general, the appropriate model and associated estimator is the one that incorporates each source of variation in τ and p into p^0. Table 1 lists all of the possibilities when there is one source of variation in τ.

In summary, closed-population models as described in Otis et al. (1978) are still valid when there is movement in and out of the study area of the type(s) just described. However, this phenomenon lowers effective

TABLE 1. Appropriate closed-populaton model from Otis et al. (1978) resulting from combining indicated sources of variation in the probability of being in the study area (τ) and the probability of capture, given that the animal is in the study area (p).

	Sources of variation in τ			
Sources of variation in p	None	Time	Behavior	Heterogeneity
None	M_0	M_t	M_b	M_h
Time	M_t	M_t	M_{tb}	M_{th}
Behavior	M_b	M_{tb}	M_b	M_{bh}
Heterogeneity	M_h	M_{th}	M_{bh}	M_h
Time, behavior	M_{tb}	M_{tb}	M_{tb}	M_{tbh}
Time, heterogeneity	M_{th}	M_{th}	M_{tbh}	M_{th}
Behavior, heterogeneity	M_{bh}	M_{tbh}	M_{bh}	M_{bh}
Time, behavior, heterogeneity	M_{tbh}	M_{tbh}	M_{tbh}	M_{tbh}

capture probabilities, and thus reduces precision in every case. This could cause severe practical problems, especially if the capture probabilities are lowered so far that the numerical routine that produces estimates, such as by program CAPTURE (White et al. 1982, Rexstad and Burnham 1991), becomes unstable, or a large proportion of the superpopulation becomes effectively uncatchable. In addition, if the source(s) of variation in τ are not identical to the source(s) of variation in $p,$ then the appropriate model will be more complex than if $\tau \equiv 1$. Finally, under models M_h, M_{th}, M_{bh}, and M_{tbh}, where realistic maximum likelihood estimators are not currently available, a resulting increase in heterogeneity in p^0 will tend to increase bias in available estimators (Rexstad and Burnham 1991, Lee and Chao 1994, Norris and Pollock 1996).

The validity of these models is dependent on the assumption that the superpopulation is completely closed during the study. In addition, although there can be variation in τ_j among animals, it cannot be 0 (i.e., in each period, each animal must have a non-negligible chance of being available for capture), and it cannot be explicitly dependent on whether the animal was in or out of the study area in sample $j - 1$ (e.g., Markovian movement). I will briefly consider the effect of these two possibilities in subsequent sections.

All of the previous discussion for closed-population models applies directly to each primary period of the robust design as well. I will discuss the implications for estimating temporary emigration under the robust design in the next section.

Estimating temporary emigration under the robust design

Kendall et al. (1997) presented methods for estimating demographic parameters when temporary emigration occurs between primary periods, using data collected under Pollock's robust design (1982). Under the robust design, there are k primary periods. For each primary period i (e.g., a year) there are l_i capture occasions (e.g., trapping days). The study area is assumed
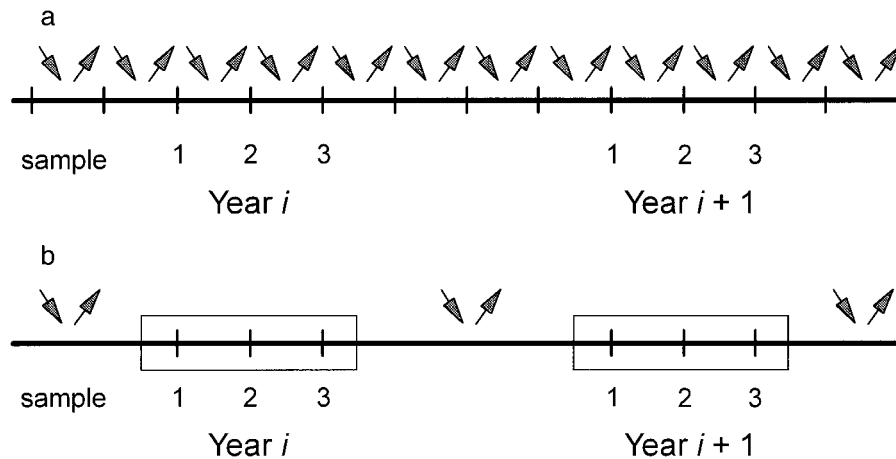
FIG. 1. An illustration of two types of movement in and out of the study area. In (a), movement occurs between each sampling occasion in each year. In (b), movement occurs only between, not within, primary sampling periods.

to be closed to additions and deletions within each primary period. Consequently, if an animal is alive and in the superpopulation, but absent from the study area at any time during primary period i (with probability γ_i), then it is assumed to be absent for the entire primary period, and vice versa. Therefore, to be a temporary emigrant is to be a member of the superpopulation but unavailable for capture in a given primary period.

What are the implications for estimating temporary emigration when this assumption is violated by animals moving in and out randomly between each sampling occasion within a primary period, as described in the last section? If temporary emigration from the study area is defined solely by this process, then $\theta_i = \Pi_{j=1}^{l_i} (1 - \tau_{ij})$ is the probability of being outside the study area for the entire primary period. However, θ_i is not equivalent to γ_i, as defined in Kendall et al. (1997), because each animal outside the study area in sample j of primary period i has a nonzero probability of being in the study area in sample $j + 1$. I present an example of incorporating this type of temporary emigration into a robust design model, using the case in which there is only time variation in either τ or p. First, define ϕ_1 as the probability that an animal alive and in the superpopulation in primary period 1 survives and remains in the superpopulation in primary period 2; R_1 is the total number of individual animals marked and released during primary period 1; m_{12} is the number of animals from R_1 that are recaptured in primary period 2; and X_{12}^{11} is the number of the m_{12} animals that are captured in both samples in primary period 2. Therefore, representative expected cell frequencies from the multinomial model, where there are two capture occasions in each primary period, are:

$$E(m_{12}|R_1) = R_1\phi_1[1 - (1 - \tau_{21}p_{21})(1 - \tau_{22}p_{22})]$$

$$E(X_{12}^{11}|m_{12}) = m_{12}\frac{\tau_{21}p_{21}\tau_{22}p_{22}}{1 - (1 - \tau_{21}p_{21})(1 - \tau_{22}p_{22})}. \quad (6)$$

Under this model, the τ_{ij} are found in both the between- and within-primary-period parts of the model. As in the previous section, τ_{ij} and p_{ij} are completely confounded. By reparameterizing the model, replacing their product with $p_{ij}^0 = \tau_{ij}p_{ij}$, the τ_{ij} drop out of the model and, as in the previous section, we are left with reduced effective capture probabilities.

The implication is that, in order to estimate the probability that an animal in the superpopulation is available for capture, movement in and out of the study area must occur at a coarser temporal scale than sampling. That is, there must be closure to that movement for more than one sample. This can be illustrated in Fig. 1. In Fig. 1a, there are three capture occasions in each year, but the arrows indicate movement in and out of the study area between each occasion. In this case, the probability of being in the study area is at best confounded with capture probability. In Fig. 1b, movement occurs only between primary sampling periods (annual set of three samples), and therefore the probability of availability for capture could be estimated (Kendall et al. 1997).

The case of breeding colonies brings up a situation in which there could be two types of movement, the rate of one of which could be estimated and the other could not. For example, if only breeders were found at a colony site in a given season, then the scenario in Fig. 1b would apply and breeding propensity $(1 - \gamma_i)$ could be estimated. However, there could also be random movement in and out of the area where traps or observers are located within the sampling season, with probability of presence τ_{ij}. This would be similar to Fig. 1a, and therefore τ_{ij} would be unestimable. I anticipate that γ_i is probably of greater ecological interest than τ_{ij} in this case.

Estimation of species richness and community dynamics

This idea of estimation when the population is not closed can be extended to the case in which the number

of species, instead of the number of animals, is of interest. Several authors have used closed-population models to estimate species richness (Burnham and Overton 1979, Bunge and Fitzpatrick 1993, Boulinier et al. 1998). In this case, capture usually refers not to individual animals, but to whether or not any member of a species is captured. In addition, capture occasions can be temporally separated, spatially separated, or consist of independent observers visiting the same site (see review by Nichols and Conroy 1996).

Consider the case in which an investigator defines a geographic area containing a target community consisting of S species. This area is often too large to survey exhaustively, making sampling (e.g., quadrats) necessary. If each species is not distributed uniformly throughout the area containing the community (e.g., the distribution is clustered), there is a chance that a given species will be absent from a selected quadrat. In this case, one has a better chance of accounting for all species by sampling multiple quadrats. More specifically, assume that the area occupied by the target community can be broken into a grid of Q quadrats, each of which could be surveyed by some combination of methods (Fig. 2). A completely random sample of q of these plots is then surveyed, perhaps using various taxa-appropriate methods. For a given species s ($s = 1, 2, \ldots, S^0$), there is a probability $\tau_{js} > 0$ that sample plot j will fall into habitat occupied by the species. Given that species s is present in the sample plot, its probability of detection is p_{js}. Therefore, under this completely random sampling scheme, the effective probability of detection for species s is $p_{js}^0 = \tau_{js} p_{js}$. This form is identical to the form described in previous sections, and therefore the models of Otis et al. (1978), especially M_h or M_{th}, can still be used to estimate the number of species in the community (i.e., the closure assumption is effectively not violated). An additional requirement here is that the sampling of plots must be done with replacement. Otherwise, τ_{js} could be 0 for some sample (i.e., if previous samples exhausted the distribution of the species within the community).

These results also apply to the case of estimating parameters of community dynamics, such as local extinction and turnover rate (Nichols et al. 1998a, b), where Pollock's robust design is employed to estimate open-population parameters as a function of closed-population estimators computed from subsamples collected across multiple points in time or space.

Nonrandom Violations of Closure

The implications when movement is not completely random depend on the nature of the movement process. I briefly consider five general types: (1) Markovian, where the probability of movement in period j is dependent on whether the animal is in or out of the study area in period $j - 1$; (2) emigration only, where the first sample is taken when the entire population is present, but they begin emigrating (e.g., as in a yearly migration) before the last period of sampling; (3) immigration only, the converse of the preceding scenario, where the population is still arriving when sampling begins and all are present by the last sample; (4) where animals potentially enter the study area once and leave it once during the course of sampling (e.g., as in a migration stopover or in a breeding area where individuals arrive in a staggered fashion and remain only long enough to breed); and (5) where capture itself increases the probability that an animal will subsequently be outside the study area.

Markovian movement

Movement is Markovian when the probability that an animal is present in the study area in period j depends on whether the animal was present (τ_j'') or absent (τ_j') in period $j - 1$. When this movement occurs at the same temporal scale as sampling, estimates of capture probability and population size will be biased. However, in this case, there is no simple confounding between availability for capture and capture probability. Based on simulation, neither the magnitude nor direction of the bias is completely predictable, but is a function of the relationship between τ_j'' and τ_j', the change in this relationship over time, and the proportion of the population that is in the study area immediately prior to the study.

Emigration only

When studying migratory animals at their breeding or wintering grounds, the case could arise in which sampling begins when all animals are present, but during the course of sampling, they begin moving out of the study area (e.g., to staging areas in preparation for migration). Seber (1982) considered the effect of this emigration between capture occasions on the two-sample L-P estimator. If both marked and unmarked animals leave with the same probability, and the other assumptions of model M_t still hold, then the L-P estimator remains unbiased for the population size at the time of the first capture occasion. If there are more than two samples, even when there is only time variation in capture probabilities, the estimator for N from model M_t (Darroch 1958, Otis et al. 1978:25) will be negatively biased. However, by pooling all but the first sample into one and using the L-P approach (as in Menkins and Anderson 1988), the bias is removed. In this context, this estimator is identical to the abundance estimator based on the open-population, deaths-only model of Darroch (1959). However, the variance estimators for these estimators are not identical (Seber 1982:60, Jolly 1965), and neither is consistently less biased, based on a bootstrapped variance estimate.

Assuming that capture probabilities vary only with time, this approach of pooling all but the first capture occasion is also valid within the context of the robust design. Estimators for survival rate and temporary emigration (completely random or Markovian) between
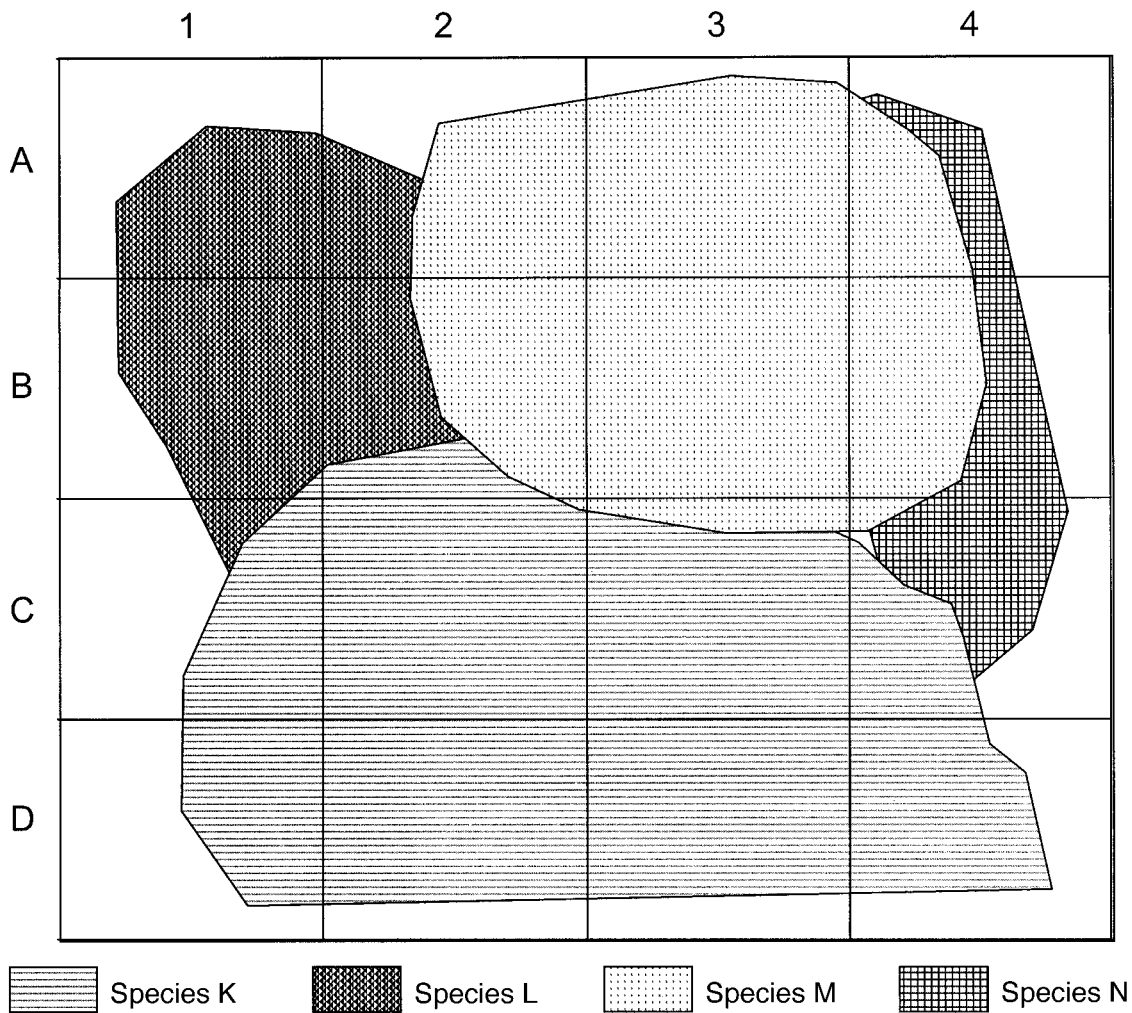
FIG. 2. A hypothetical community of four species, heterogeneously distributed across 16 quadrats. If quadrat C2 is sampled, the probability of detection for species K is positive ($p_{C2,K} > 0$), whereas if quadrat A1 is selected, $p_{A1,K} = 0$.

primary periods remain unbiased, because the estimator for p_i^*, the probability that an animal present at the beginning of the primary period is captured at some point during the period, remains unbiased.

None of this is true when there is trap response or individual heterogeneity in capture probabilities. When there is trap response, the decrease in new captures over time is more severe than expected under the trap response model M_b (Zippin 1956, Otis et al. 1978:29), thus producing a negative bias in $\hat{N}_b$. When there is heterogeneity in capture probability among individuals, emigration affects the bias of the jackknife estimator (Burnham and Overton 1979, Otis et al. 1978) of N, but the nature of this effect is not easily predictable. Pooling capture occasions and using the L-P estimator will not remove the bias in either the trap response or the heterogeneity case.

Immigration only

The converse of the previous scenario could occur, in which only part of a migratory population has arrived at a study site by the time sampling begins, but the entire population is there by the last capture occasion. Again assuming that capture probability varies only with time, Seber (1982) considered the case of two samples. When animals enter the population between samples, the L-P estimator is unbiased for population size in the second period. For more than two samples, the Darroch (1958; Otis et al. 1978:25) estimator is biased, but the bias is removed by pooling all but the last sample into one capture occasion and using the L-P estimator. This approach is equivalent to the births-only model of Darroch (1959).

When there is trap response or heterogeneity in capture probabilities in the case of immigration, the result is similar to the case of emigration. For trap response, $\hat{N}_b$ (Zippin 1956) will be positively biased in the face of immigration. Immigration also has an effect on the bias of the jackknife estimator when there is heterogeneity in capture probability, but this effect is not easily predictable. Again, pooling capture occasions and using the L-P estimator will not remove the bias.

TABLE 2. Effect of various types of closure violations and variation in capture probability on the estimator for abundance of the superpopulation, and alternative approaches where bias is introduced.

Type of closure violation	Source of variation in capture probability	Bias in $\hat{N}$ for superpopulation	Alternative methods
Completely random temporary emigration	time	no	
	trap response	no	
	heterogeneity	maybe†	
Markovian temporary emigration	time	yes	
	trap response	yes	
	heterogeneity	yes	
Emigration only	time	yes	Pool periods 2, 3, ..., 1, use Lincoln-Petersen method; Darroch's deaths-only method.
	trap response	yes	
	heterogeneity	yes	
Immigration only	time	yes	Pool periods 1, 2, ..., $1-1$, use Lincoln-Petersen method; Darroch's births-only method.
	trap response	yes	
	heterogeneity	yes	
One entry, one exit	time	yes	Open-population methods (e.g., Schwarz and Stobo 1997).
	trap response	yes	
	heterogeneity	yes	

† The estimator tends to be biased even when all assumptions are satisfied. Any increase in variation in capture probabilities will tend to increase bias.

One entry and one exit

When an animal enters and leaves the study area once during the course of sampling, no closed-models approach will give an unbiased estimate of abundance (Seber 1982). An open-population approach is more appropriate. In this scenario, which could involve a migration stopover, or a breeding area where an animal enters the area only long enough to breed, the measure of abundance that is often of interest is the total number of individuals that were present during the course of sampling in season *i*. In this case, a superpopulation approach (Crosbie and Manly 1985, Schwarz et al. 1993, Schwarz and Arnason 1996) is more useful, although it requires other assumptions. Schwarz and Stobo (1997) showed how this approach could be used within the context of Pollock's robust design to estimate the breeding proportion of a population of grey seals (*Halichoerus grypus*). These open-population models assume that capture probabilities vary only with time.

Trap response in movement

In some cases, the negative experience of being trapped might increase the probability that an animal will subsequently be absent from the study area. Estimators from models that include trap response in capture probability (Otis et al. 1978) can be used here if one can assume no additional heterogeneity among animals. Kendall and Nichols (1995) presented a model for this phenomenon when it lasts into the next primary period (e.g., year) of the robust design.

DISCUSSION

Closed-population capture–recapture models generally provide estimators that are robust to variation in capture probabilities and, when used within the context of Pollock's robust design, permit the estimation of more parameters than is possible with open-population models alone. This second advantage includes the estimation of (1) basic demographic parameters (i.e., abundance, survival rate, recruitment) for more time periods than open-population models allow, and (2) Markovian temporary emigration that occurs at a coarser temporal scale than sampling. Therefore, it would be advantageous if these estimators were robust even when the closure assumption, which is often difficult to achieve completely, is violated.

Table 2 summarizes the effect of various types of closure violations on the estimator for superpopulation abundance. I have shown here that when members of a superpopulation move in and out of the study area completely randomly, estimators remain unbiased (excluding the case of heterogeneity among individuals), and represent the entire superpopulation. This should not cause an investigator to become complacent, however, because if only a small proportion of the superpopulation uses the study area at any given time, or there is great heterogeneity among individuals in their probability of using the area, the resulting effective capture probabilities could be so low or heterogeneous that additional bias is introduced anyway. Certainly precision will suffer when temporary emigration occurs.

This argument also applies where these methods are used to estimate species richness or community dynamics. If the area occupied by the community is to be subsampled spatially, then temporary emigration is defined not by species moving in and out of a fixed study area, but by moving the study area randomly, where some species might be absent for a given sample. If the samples are selected randomly and with replacement, then temporary emigration will be a random process and closed-population models will still be appropriate for estimation. However, if the distribution of species across the landscape is such that either the probability of selecting an area where a given species is

located, or the probability of detecting it when it is extant, is very low, then the effective probability of detection could be low or heterogeneous enough to cause problems with bias and precision.

Finally, although completely random temporary emigration does not introduce bias to estimators for parameters associated with the superpopulation, the probability of temporary emigration is confounded with capture probability if it occurs at the same temporal scale as sampling. If some facet of temporary emigration occurs at a coarser temporal scale, then that facet can be estimated. I reiterate the example of a breeding population in which nonbreeders are absent from the study area for the entire season (i.e., they are not part of the within-season superpopulation), but breeders randomly move in and out of the study area during the season. One could estimate the breeding propensity, but not the proportion of breeders in the study area at a given time within the season.

When closure is violated only by emigration from the study area, or only by immigration into the study area, and capture probabilities vary only by time, closed models can still be used without bias by pooling all but the first period, or all but the last period, respectively, and using the L-P method. Alternative approaches include Darroch's (1959) deaths-only or births-only open-population methods, respectively. When each animal can enter and leave the study area only once, closed-population models will produce biased estimates. However, with additional assumptions, open-population models can be used in this case (e.g., Schwarz and Stobo 1997).

If the closure violation is based on Markovian movement, closed-population estimators will be biased, as will open-population models. This is also true in the emigration-only or immigration-only cases where there is trap response or heterogeneity in individual capture probabilities. In this case, I suggest that the investigator simulate the sampling process with a range of parameters that seems realistic for the population of interest, to assess whether the resulting bias is acceptable.

I have shown that the nature of both the closure violation and variability in capture probabilities will determine if and to what extent closed-population estimators will be biased. In any case, this violation will reduce precision. This has design implications, a trade-off for a fixed level of sampling effort. Concentrating effort over a small area will increase both conditional capture probability and the probability of animals being absent. Diluting effort over a larger area will decrease both temporary emigration and conditional detection probability. The practitioner should strive to determine both the requisite minimum total effort (e.g., total number of trap days), as well as its optimal allocation over space (e.g., trap grid size and density) and time (how many trapping occasions). Given the complexity of this task, simulation is the only practical approach to completing it in most cases.

LITERATURE CITED

Alexander, H. M., N. A. Slade, and W. D. Kettle. 1997. Application of mark–recapture models to estimation of the population size of plants. Ecology **78**:1230–1237.

Boulinier, T., J. D. Nichols, J. R. Sauer, J. E. Hines, and K. H. Pollock. 1998. Estimating species richness to make inference in community ecology: the importance of heterogeneity in species detectability as shown from capture–recapture analyses of North American Breeding Bird Survey data. Ecology **79**:1018–1028.

Bunge, J., and M. Fitzpatrick. 1993. Estimating the number of species: a review. Journal of the American Statistical Association **88**:364–373.

Burnham, K. P., and W. S. Overton. 1979. Robust estimation of population size when capture probabilities vary among animals. Ecology **60**:927–936.

Crosbie, S. F., and B. F. J. Manly. 1985. Parsimonious modelling of capture–mark–recapture studies. Biometrics **41**:385–398.

Darroch, J. N. 1958. The multiple-recapture census: I. Estimation of a closed population. Biometrika **45**:343–359.

———. 1959. The multiple-recapture census: II. Estimation when there is immigration or death. Biometrika **46**:336–351.

Grier, J. W., J. M. Gerrard, G. D. Hamilton, and P. A. Gray. 1981. Aerial-visibility bias and survey techniques for nesting bald eagles in northwestern Ontario. Journal of Wildlife Management **45**:83–92.

Jolly, G. M. 1965. Explicit estimates from capture–recapture data with both death and immigration–stochastic model. Biometrika **52**:225–247.

Karanth, K. U., and J. D. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology **79**:2852–2862.

Kendall, W. L., and J. D. Nichols. 1995. On the use of secondary capture–recapture samples to estimate temporary emigration and breeding proportions. Journal of Applied Statistics **22**:751–762.

Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture–recapture data with Pollock's robust design. Ecology **78**:563–578.

Kendall, W. L., and K. H. Pollock. 1992. The robust design in capture–recapture studies: a review and evaluation by Monte Carlo simulation. Pages 31–43 *in* D. R. McCullough and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier, London, UK.

Lee, S.-M., and A. Chao. 1994. Estimating population size via sample coverage for closed capture–recapture models. Biometrics **50**:88–97.

Lincoln, F. C. 1930. Calculating waterfowl abundances on the basis of banding returns. U.S. Department of Agriculture, Circular 118.

Lindberg, M. S., J. S. Sedinger, D. V. Derksen, and R. F. Rockwell. 1998. Natal and breeding philopatry in a Black Brant *Branta bernicla nigricans* metapopulation. Ecology **79**:1893–1904.

Magnusson, W. E., G. J. Caughley, and G. C. Grigg. 1978. A double-survey estimate of population size from incomplete counts. Journal of Wildlife Management **42**:174–176.

Menkins, G. E., Jr., and S. H. Anderson. 1988. Estimation of small-mammal population size. Ecology **69**:1952–1959.

Nichols, J. D., T. Boulinier, J. E. Hines, K. H. Pollock, and J. R. Sauer. 1998*a*. Estimating rates of local species extinction, colonization, and turnover in animal communities. Ecological Applications **8**:1213–1225.

Nichols, J. D., T. Boulinier, J. E. Hines, K. H. Pollock, and J. R. Sauer. 1998*b*. Inference methods for spatial variation in species richness and community composition when not all species are detected. Conservation Biology **12**:1390–1398.

Nichols, J. D., and M. J. Conroy. 1996. Estimation of species richness. Pages 226–234 *in* D. E. Wilson, F. R. Cole, J. D. Nichols, R. Rudran, and M. Foster, editors. Measuring and monitoring biological diversity. Standard methods for mammals. Smithsonian Institution Press, Washington, D.C., USA.

Nichols, J. D., and K. H. Pollock. 1990. Estimation of recruitment from immigration versus in situ reproduction using Pollock's robust design. Ecology **71**:21–26.

Nichols, J. D., K. H. Pollock, and J. E. Hines. 1984. The use of a robust capture–recapture design in small mammal population studies: a field example with *Microtus pennsylvanicus.* Acta Theriologica **29**:357–365.

Nichols, J. D., J. R. Sauer, K. H. Pollock, and J. B. Hestbeck. 1992. Estimating transition probabilities for stage-based population projection matrices using capture–recapture data. Ecology **73**:306–312.

Norris, J. L., III, and K. H. Pollock. 1996. Nonparametric MLE under two closed capture–recapture models with heterogeneity. Biometrics **52**:639–649.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference for capture data on closed animal populations. Wildlife Monographs, Number 62.

Packard, J. M., R. C. Summers, and L. B. Barnes. 1985. Variation of visibility bias during aerial surveys of manatees. Journal of Wildlife Management **49**:347–351.

Petersen, C. G. J. 1896. The yearly immigration of young plaice into the Limfjord from the German Sea. Report of the Danish Biological Station 1895 **6**:1–77.

Pollock, K. H. 1982. A capture–recapture design robust to unequal probability of capture. Journal of Wildlife Management **46**:757–760.

Pollock, K. H., D. L. Solomon, and D. S. Robson. 1974. Tests for mortality and recruitment in a K-sample tag–recapture experiment. Biometrics **30**:77–87.

Rexstad, E., and K. P. Burnham. 1991. User's guide for interactive program CAPTURE. Colorado Cooperative Fish and Wildlife Research Unit, Fort Collins, Colorado, USA.

Schwarz, C. J., and A. N. Arnason. 1996. A general methodology for the analysis of open-model capture–recapture experiments. Biometrics **52**:860–873.

Schwarz, C. J., R. E. Bailey, J. R. Irvine, and F. C. Dalziel. 1993. Estimating salmon spawning escapement using capture–recapture methods. Canadian Journal of Fisheries and Aquatic Sciences **50**:1181–1191.

Schwarz, C. J., and J. B. Dempson. 1994. Mark–recapture estimation of a salmon smolt population. Biometrics **50**: 98–108.

Schwarz, C. J., and W. T. Stobo. 1997. Estimating temporary migration using the robust design. Biometrics **53**:178–194.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Macmillan, New York, New York, USA.

Stanley, T. R., and K. P. Burnham. 1999. A closure test for time-specific capture–recapture data. Environmental and Ecological Statistics **6**:197–209.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture–recapture and removal methods for sampling closed populations. Los Alamos National Laboratory LA-8787-NERP, Los Alamos, New Mexico, USA.

Zippin, C. 1956. An evaluation of the removal method of estimating animal populations. Biometrics **12**:163–189.