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Using Open Robust Design Models to Estimate Temporary Emigration from Capture–Recapture Data

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SUMMARY. Capture–recapture studies are crucial in many circumstances for estimating demographic parameters for wildlife and fish populations. Pollock’s robust design, involving multiple sampling occasions per period of interest, provides several advantages over classical approaches. This includes the ability to estimate the probability of being present and available for detection, which in some situations is equivalent to breeding probability. We present a model for estimating availability for detection that relaxes two assumptions required in previous approaches. The first is that the sampled population is closed to additions and deletions across samples within a period of interest. The second is that each member of the population has the same probability of being available for detection in a given period. We apply our model to estimate survival and breeding probability in a study of hawksbill sea turtles (*Eretmochelys imbricata*), where previous approaches are not appropriate.

KEY WORDS: Breeding probability; Detection probability; *Eretmochelys imbricata*; Hawksbill sea turtles; Mark–recapture; Open populations; Survival.

1. Introduction

The purpose of most capture–recapture studies in animal ecology is to estimate parameters that are important to the dynamics of a particular biological population or meta-population. Nevertheless, in some cases, certain members of that population might be unavailable for capture (here detection and identification of an individual) at a given sampling occasion. This could simply be due to home ranges of individuals extending beyond the study area. In other cases, this temporary emigration might have an ecologically meaningful interpretation. For example, in some studies of breeding birds, only breeders are available for capture/resighting. Among birds that have reached a sufficient age to be recruited into the breeding population (see Clobert et al., 1994; Pradel, 1996; Pradel and Lebreton, 1999; Schwarz and Arnason, 2000), being a temporary emigrant is equivalent to being an adult nonbreeder (e.g., Kendall and Nichols, 1995; Lindberg et al., 2001). If a mammal were in hibernation or torpor when sampling is being conducted, this too would be equivalent to temporary emigration (Kendall, Nichols, and Hines, 1997). In general, we equate a temporary emigrant with an

individual member of the population that is not available for detection (and unique identification) in a given period.

Neither closed-population models (Otis et al., 1978) nor classic open-population models (Seber, 1982; Pollock et al., 1990; Lebreton et al., 1992) explicitly permit temporary emigration. The former assume a static population, whereas the latter allow for one entry and one exit from the study area. Burnham (1993) showed that, for an open population, where every animal has the same probability γ_i^* of being in the study area (and therefore available for capture) in period i , standard estimators of capture probability actually estimate the product of availability for capture and conditional probability of capture p_i^* . Therefore,

$$E\left(\hat{p}_i^{\text{CJS}}\right) = \gamma_i^* p_i^*, \quad (1)$$

where \hat{p}_i^{CJS} is the Cormack–Jolly–Seber (Cormack, 1964; Jolly, 1965; Seber, 1965) (CJS) estimator for p_i^* . The implication is that, under these conditions, CJS estimators are unbiased in the face of completely random temporary emigration when

applied to the entire population of interest but not specifically to the study area.

Another source of information is required to separately estimate γ_i^* and p_i^* . In the absence of directly monitoring the population outside of the study area (see Arnason, 1973; Brownie et al., 1993; Schwarz, Schweigert, and Arnason, 1993b; Barker, 1995; Powell et al., 2000), Pollock's robust design (Pollock, 1982) provides that second source of information. Here sampling for each primary period of interest (e.g., year) consists of a series of subsamples (e.g., trapping days). The essential assumption is that, to be considered a temporary emigrant for primary period i , an animal must be unavailable for detection for the entire series of subsamples within period i . In the case of breeding probability, we generally assume an animal is either a breeder in a given season or it is not. Kendall and Nichols (1995) and Kendall et al. (1997) developed models for estimating temporary emigration when complete closure is assumed for the study area for all samples within primary period i . These models include temporary emigration as (1) completely random; (2) Markovian, where the probability of being available for detection in primary period i depends on whether the animal was available (γ_i'') or unavailable (γ_i') for detection in primary period $i-1$; or (3) temporarily trap dependent, where the probability of being available for detection in primary period i depends on the length of time since the animal was last trapped (Kendall and Nichols, 1995). Barker (1995) found that Markovian movement could be estimated under constrained models if incidental tag recoveries or observations from the entire range of the population were available.

Schwarz and Stobo (1997) addressed a problem where closure within a primary period was completely untenable. The population of interest consisted of breeding grey seals (*Halichoerus grypus*), where individuals arrived in the study area in a staggered fashion, remained long enough to breed, and then departed. They relaxed the closure assumption, allowing for one entry and one exit from the study area. Therefore, they developed a robust design model consisting of an open-population model within an open-population model, with changes within primary periods consisting only of arrivals and departures (no mortality or natality). Although they relaxed the closure assumption, their method requires that temporary emigration be a completely random process.

Kendall (1999) showed that, if violation of closure within primary periods is limited to either immigration only or emigration only, the methods of Kendall et al. (1997) could still be used to estimate temporary emigration. This assumes that capture probability varies only by time or as a function of static group covariates (e.g., sex), not due to trap response or individual heterogeneity in capture probabilities.

The purpose of this article is to present a method for estimating temporary emigration and survival where neither closure within primary periods nor completely random temporary emigration are reasonable assumptions. We apply this method to a study of a breeding population of hawksbill sea turtles (*Eretmochelys imbricata*). Sea turtles arrive and depart from their breeding sites in a staggered fashion, similar to the case of seals presented by Schwarz and Stobo (1997). However, a turtle that breeds in a given year has a low probability of breeding in the following year (Hirth, 1980; Witzell, 1983). Therefore, the assumption of completely random temporary emigration is grossly violated. We combine the meth-

ods of Kendall et al. (1997) and Schwarz and Stobo (1997) to construct a Markovian temporary emigration model under the open robust design. We relax the assumption of geographic closure to allow one entry and one exit from the study area within each primary period but preclude deaths or recruitment to the population (i.e., retain demographic closure) within each primary period. The notation defined in Tables 1 and 2 builds on the notation of these two papers in addition to that of Schwarz and Arnason (1996).

2. The Models

2.1 Completely Random Temporary Emigration

We begin with the case of completely random temporary emigration, using the following conditional product multinomial likelihood: $L = L_1 \times L_2 = L_1 \times L_{2a} \times L_{2b} \times L_{2c}$, where

$$\begin{aligned} L_1 &= P(\{m_{hi}^*\} | \{R_i^*\}, \{p_i^*\}, \{\phi_i^*\}, \{\gamma_i^*\}), \\ L_{2a} &= P(\{u_{ij}^* | \{n_i^*\}, \{\psi_{ij}^*\}, \{p_{ij}^*\}), \\ L_{2b} &= P(\{d_{ij}^* | \{n_{ij}^*\}, \{\nu_{ij}^*\}), \\ L_{2c} &= P(\{m_{ihj}^* | \{R_{ih}^*\}, \{\phi_{ij}^*\}, \{p_{ij}^*\}). \end{aligned} \quad (2)$$

The full likelihood function is presented in detail in Appendix 1. L_1 conditions on the number of animals released in a given primary period (R_i^*) and describes the sampling process across primary sampling periods. It is taken from Kendall et al. (1997) and can be considered an extension of the CJS model as parameterized by Brownie, Nichols, and Hines (1986). Our focus here is not on estimating population size, so L_1 ignores the sampling process for unmarked animals. L_2 describes the sampling process across secondary samples within each primary period, conditioning on the total number of individuals detected during the primary period ($u_i^* + m_i^* = n_i^*$). We relax the assumption of closure within a primary period, taking the form of this part of the likelihood largely from the Schwarz and Arnason (1996) parameterization of the Jolly-Seber model, also used by Schwarz and Stobo (1997). L_{2a} describes the probability of being detected for the first time within a given primary period, L_{2b} describes the probability that a detected animal is released to the population (i.e., deals with losses on capture), and L_{2c} describes the probability that a released animal is detected again within the same primary period. We include L_{2b} for completeness, but it is unnecessary for computing estimators of interest, so we will disregard it for the remainder of the article. Using this model, which we call $(\phi_i^*, \gamma_i^*, \psi_{ij}^*, p_{ij}^*, \nu_{ij}^*, \beta_{ij}^*)$, we numerically obtain conditional maximum likelihood estimators (MLEs) for all identifiable parameters, including γ_i^* .

Schwarz and Stobo (1997) estimated most parameters in the same way but estimated γ_i^* as a function of estimates derived from the MLEs. They assumed uniform arrival times between sampling occasions, allowing for some breeders to arrive and depart before the next sample and thereby being unavailable for detection in that breeding season. Therefore, they had to adjust their MLEs from a likelihood conditioned on detection to account for these other breeders (also see Crosbie and Manly, 1985; Schwarz et al., 1993a; Schwarz and Arnason, 1996). This is not necessary for our sea turtle example because intensive sampling is conducted nightly and

Table 1
Definitions of parameters and statistics at the secondary sampling level

Notation	Definition
u_{ij}	number of individuals detected in sample j of primary period i that were not detected previously within period i , $i = 1, 2, \dots, k$; $j = 1, 2, \dots, l_i$
m_{ihj}	number of individuals detected in sample j of primary period i that, within period i , were last detected in sample h , $i = 1, 2, \dots, k$; $h = 1, 2, \dots, l_i - 1$; $j = 2, 3, \dots, l_i$; $m_{i \cdot j} = \sum_{h=1}^{l_i-1} m_{ihj}$; $r_{ih} = \sum_{j=k+1}^{l_i} m_{ihj}$
d_{ij}	number of individuals detected in sample j of primary period i that are removed from the population at that point (e.g., trap deaths), $i = 1, 2, \dots, k$; $j = 1, 2, \dots, l_i - 1$
n_{ij}	total number of individuals detected in sample j of primary period i ($u_{ij} + m_{i \cdot j}$), $i = 1, 2, \dots, k$; $j = 1, 2, \dots, l_i$
R_{ij}	number of n_{ij} animals that are rereleased to the population ($n_{ij} - d_{ij}$), $i = 1, 2, \dots, k$; $j = 1, 2, \dots, l_i - 1$
p_{ij}	probability that an animal is detected in secondary sample j of primary period i , given that it is alive and available for detection at that time, $j = 1, 2, \dots, l_i$; $i = 1, 2, \dots, k$
ν_{ij}	probability that an animal detected in secondary sample j of primary period i is rereleased to the population at that point (e.g., does not die in the trap), $i = 1, 2, \dots, k$; $j = 1, 2, \dots, l_i - 1$
ϕ_{ij}	probability that an animal in the study area in sample j of primary period i is still available for detection in sample $j + 1$, $j = 1, 2, \dots, l_i - 1$; $i = 1, 2, \dots, k$
β_{ij}	proportion of animals present in the study area in primary period i that enter the study area after sample j is taken but prior to sample $j + 1$ and are present during sample $j + 1$, $j = 0, 1, 2, \dots, l_i - 1$; $i = 1, 2, \dots, k$ (β_{i0} is the proportion that enter just prior to sample 1); $\sum_{j=0}^{l_i-1} \beta_{ij} = 1$ for each primary period i
χ_{ij}	probability that an animal detected and released in sample j of primary period i is not detected in a subsequent sample within period i , $i = 1, 2, \dots, k$; $j = 1, 2, \dots, l_i$; $\chi_{ij} = 1 - \phi_{ij}[1 - (1 - p_{i,j+1})\chi_{i,j+1}]$, $j = 1, 2, \dots, l_i - 1$; $\chi_{il_i} = 1$
ψ_{ij}	probability that an animal present during primary period i enters the study area prior to sample j , remains available for detection until sample j is taken, but is not detected before sample j , $i = 1, 2, \dots, k$; $j = 1, 2, \dots, l_i$; $\psi_{i1} = \beta_{i0}$, $\psi_{i,j+1} = \psi_{ij}(1 - p_{ij})\phi_{ij} + \beta_{ij}$

turtles tend to return to lay multiple clutches of eggs. Therefore, our approach is equivalent to assuming first arrival (i.e., within-season recruitment) occurs immediately before sampling (Schwarz et al., 1993a).

Schwarz and Stobo's (1997) assumption of uniform arrival times between secondary sampling periods can be accommodated in our approach (Appendix 2) but only with an ad-

ditional assumption. The probability of emigrating from the study area for the remainder of the primary period, given that an animal has arrived in the study area, must be constant across samples ($\phi_{ij} \equiv \phi_i$ for all i).

If demographic closure were assumed within primary periods (Kendall, Pollock, and Brownie, 1995), L_2 would involve only the p_{ij} , each of which would be identifiable. Because we

Table 2
Definitions of parameters, statistics, and unknown random variables for primary periods

Notation	Definition
u_i^*	number of animals captured during primary period i that were unmarked prior to period i , $i = 2, 3, \dots, k$
m_{hi}^*	number of animals detected in primary period i that were last detected in primary period h , $h = 1, 2, \dots, i - 1$; $i = 2, 3, \dots, k$; $m_{i \cdot}^* = \sum_{h=1}^{i-1} m_{hi}^*$; $r_h^* = \sum_{i=h+1}^k m_{hi}^*$
n_i^*	total number of individuals detected in primary period i ; $n_i^* = u_i^* + m_{i \cdot}^*$; $i = 1, 2, \dots, k$
R_i^*	number of n_i^* individuals released with marks during primary period i (excludes trap deaths), $i = 1, 2, \dots, k - 1$
p_i^*	probability that an animal is detected in at least one of the l_i secondary samples of primary period i , given that the animal is available for detection in at least one of the samples during period i , $i = 1, 2, \dots, k$; $p_i^* = \sum_{j=1}^{l_i} \psi_{ij} p_{ij}$
ϕ_i^*	probability that an animal alive and in the population during primary period i survives and is in the population in period $i + 1$, $i = 1, 2, \dots, k - 1$
γ_i''	probability that an animal is available for detection in primary period i , given that it was available for detection in period $i - 1$, $i = 2, 3, \dots, k$
γ_i'	probability that an animal is available for detection in primary period i , given that it was not available for detection in period $i - 1$, $i = 2, 3, \dots, k$
χ_i^*	probability that an animal alive in primary period i is never detected again after period i under the completely random model of temporary emigration, $i = 1, 2, \dots, k - 1$; $\chi_i^* = 1 - \phi_i\{1 - (1 - \gamma_{i+1}^* p_{i+1}^*)\chi_{i+1}^*\}$ for $i = 1, 2, \dots, k - 1$; $\chi_k^* = 1$

relax the closure assumption, we must constrain some parameters to obtain an MLE for p_i^* .

Unidentifiable parameters can be divided into two groups. First, β_{i0} and p_{i1} are confounded and β_{i1} is also unidentifiable. By estimating any one of these three through constraints, the other two can be estimated. Similarly, ϕ_{il-1} and p_{il} are confounded and β_{il-1} is unidentifiable. By estimating any one of these three through constraints, the other two can be estimated (unless $\beta_{il-1} = 0$). For the purposes of estimating p_i^* , which leads directly to our main objective of estimating γ_i^* , it is sufficient to estimate the product $\phi_{il-1}p_{il}$ and $\beta_{i,l-1}$. The latter can be eliminated (i.e., $\beta_{i,l-1} = 0$) by extending sampling effort sufficiently long that there are no new arrivals between sample $l_i - 1$ and l_i (Schwarz and Stobo, 1997).

2.2 Markovian Temporary Emigration

Kendall et al. (1997) established that temporary emigration cannot be estimated in an *ad hoc* fashion under the Markovian emigration model, where the probability of being available for detection in primary period i is dependent on whether or not the animal was available for detection in period $i - 1$. Therefore, the approach of Schwarz and Stobo (1997) does not lend itself to estimation under this model. However, we can extend the approach we presented above to the Markovian case. We create model $(\phi_i^*, \gamma_i'', \gamma_i', \phi_{ij}, p_{ij}, \beta_{ij})$ by generalizing L_1 above to L'_1 , taken from Kendall et al. (1997). We illustrate L'_i by including selected expected cell frequencies:

$$\begin{aligned} E(m_{12}^*) &= R_1^* \phi_1^* \gamma_2'' p_2^*, \\ E(m_{13}^*) &= R_1^* \phi_1^* \phi_2^* p_3^* [(1 - \gamma_2'') \gamma_3' + \gamma_2'' (1 - p_2^*) \gamma_3''], \quad (3) \\ E(m_{23}^*) &= R_2^* \phi_2^* \gamma_3'' p_3^*. \end{aligned}$$

In $E(m_{13}^*)$, the expression in brackets is split into one term for animals outside the study area in primary period 2 and another term for those in the study area but not captured in period 2. As the number of primary periods becomes larger, cell probabilities become more complex. Appendix 3 contains a fuller treatment of this model (now $L' = L'_1 \times L_{2a} \times L_{2b} \times L_{2c}$) for an arbitrary number of primary periods using matrix notation.

Estimation under this model requires additional constraints on γ_i'' and γ_i' , such as $\gamma_k'' = \gamma_{k-1}'$, $\gamma_k' = \gamma_{k-1}'$. With these constraints, γ_i'' is identifiable for $i = 2, 3, \dots, k$ and γ_i' is identifiable for $i = 3, 4, \dots, k$. γ_2' is not identifiable because there are no marked animals in the population in primary period 2 that were not in the sampled area in period 1.

The model in Appendix 3 assumes that all new arrivals within a primary period are there long enough to be accessible by the sampling process. The case of uniform arrival time and constant within-period departure probability developed in Appendix 2 can also be applied in the Markovian case. In Appendix 3, replace γ_i'' with $\gamma_i''(\phi_i - 1)/\log(\phi_i)$ and γ_i' with $\gamma_i'(\phi_i - 1)/\log(\phi_i)$ (as ϕ_i approaches 1.0, the need for this adjustment is removed because $\log(\phi_i)/(\phi_i - 1)$ approaches 1). In this way, the methods of Schwarz and Stobo (1997) are extended to allow estimation of Markovian temporary emigration probabilities while assuming uniform arrival times between secondary sampling occasions. The price of this extension is that the conditional probability of leaving the

study area permanently (i.e., for the rest of the primary period) must be constant within a primary period.

2.3 Assumptions

Our emphasis in this article is on relaxing the usual robust design assumption of closure within primary periods. We have already discussed the relative assumptions with respect to temporary emigration required by the completely random and Markovian temporary emigration models, respectively. Another key assumption is that survival probability ϕ_i^* is the same for all animals in the population regardless of whether they enter the study area in a given primary period.

Other assumptions are typical of multinomial capture–recapture models under the robust design: detection probability is the same for all animals that are in the sampled area during sample j in primary period i ; although animals can arrive and depart once during a primary period, we assume no deaths or true immigration to the population during that time; each animal behaves independently with respect to presence/absence in the study area, mortality, detection, arrival, departure, immigration, and permanent emigration; and tags are not lost and are recorded correctly.

3. Example

Hawksbill sea turtles (*Eretmochelys imbricata*) include in their range the warmer waters of the Atlantic Ocean, Gulf of Mexico, and Caribbean Sea. The data from several localities, including the western Atlantic, suggest that hawksbills have an extended breeding season, as some nesting takes place throughout the entire year (Groombridge, 1982). However, most nesting activity occurs between June and November (Richardson, Bell, and Richardson, 1999). The female crawls onto the beach mostly between dusk and dawn, excavates a nest in the sand above the tidal zone, deposits her clutch of eggs, and then returns to the surf. She usually repeats this process approximately five times, each occasion separated by approximately 14 days (Ryder et al., 1989). While on the beach, she is accessible for either capture and marking with a uniquely coded tag clipped onto her front flipper (the shell is also notched, providing a double-marking scheme) or observation if she already has a tag. This period of egg deposition is often the only time in the life history that a substantial sample of these turtles is accessible unless they are fitted with telemetry devices. Therefore, this is an important opportunity not only to study reproduction but population dynamics in general, at least that of adult females.

A capture–recapture study of a breeding population of these turtles is ongoing on Long Island, a small island several kilometers offshore of the island of Antigua in the eastern Caribbean. A team of observers combs the beaches nightly from dusk to dawn from June to December. Any unmarked turtles are marked and the tag number for previously marked animals is recorded (Hoyle and Richardson, 1993).

Individual turtles arrive and depart in a staggered fashion over this period. Departure from the beach falls under one of three categories: (1) The female returns to the surf after laying, remaining in the near-shore zone until it is time to lay the next clutch of eggs. Therefore, she could be absent during any particular night of sampling. This represents within-season temporary emigration from the study area. (2) After

Table 3
Recapture array at the primary sampling period level for data collected from breeding hawksbill sea turtle (Eretmochelys imbricata) females at Jumby Bay, Long Island, Antigua, West Indies, 1987–1996

Release year	Number released (R_h^*)	Number recaptured (m_{hi}^*) in year i								
		1988	1989	1990	1991	1992	1993	1994	1995	1996
1987	22	0	17	4	0	0	0	0	0	0
1988	38		0	11	15	4	0	1	0	0
1989	30			0	13	9	3	1	0	0
1990	21				0	12	4	1	1	0
1991	34					0	13	7	4	0
1992	31						0	11	9	1
1993	27							0	15	7
1994	32								0	8
1995	37									0

she lays her last clutch, she does not return to the beach until the next year that she breeds again at this site. This represents within-season permanent emigration, but she remains part of the local breeding population. (3) After laying her last clutch, she leaves the local breeding population altogether, moving either permanently or temporarily to another breeding population outside the study area.

We applied the methods developed above (Appendices 1 and 3) to these data for the years 1987–1996. Because turtles were sought nightly, we believe each breeding turtle was at least exposed to sampling effort. We included observations from June 15 to November 15, breaking the nightly observations into 10 half-month periods. This approximates the periodicity of a given female’s arrival to lay a given clutch of eggs. As suggested by Schwarz and Stobo (1997), we included observations beyond the date by which the last female should have laid her first clutch in order to be able to fix $\beta_{i9} = 0$. Table 3 contains recapture data pooled within year.

Applying our Markovian model, we could not get numerical convergence for the model that allowed for time variation in all parameters, probably because of some lack of identifiability due to the data (i.e., only 123 marked animals in the study). The most general model we could fit was $\{\phi^*, \gamma_i'' = 0, \gamma_i', \phi_i, p_i, \beta_{ij}\}$, which fit reasonably well ($\chi^2 = 134, 155$ d.f., $P = 0.89$) based on Pearson’s goodness-of-fit (GOF) test, pooling cells with low expected frequencies (White, 1983). Although the power of this test has not been fully evaluated for this class of model, experience with similar models has shown that the Type I error rate tends to be high (Hines and Nichols, unpublished data).

We compared models based on Akaike Information Criteria (AIC) corrected for small-sample bias (Hurvich and Tsai, 1989). There is some debate over what should be considered the effective sample size for a multinomial capture–recapture model. Table 4 contains ΔAIC_c values (i.e., AIC_c for model m minus the minimum AIC_c over the candidate models) under

Table 4
Akaike’s Information Criterion (AIC) for selected models fit to capture–resight data collected from breeding hawksbill sea turtle (Eretmochelys imbricata) females at Jumby Bay, Long Island, Antigua, West Indies, 1987–1996

Model	No. of Parameters	ΔAIC_c		
		$n_{\text{eff}} = 1050$	$n_{\text{eff}} = 272$	$n_{\text{eff}} = 123$
$\{\phi^*, \gamma_i'' = 0, \gamma_i', \phi_{..}, p_{..}, \beta_{..}\}^a$	11	0	0	0
$\{\phi_i^*, \gamma_i'' = 0, \gamma_i', \phi_{..}, p_{..}, \beta_{..}\}$	11	3.41	3.41	3.41
$\{\phi^*, \gamma_i'' = 0, \gamma_i', \phi_{..}, p_{..}, \beta_{ij}\}$	91	3.44	78.23	523.97
$\{\phi^*, \gamma_i'' = 0, \gamma_i', \phi_{..}, p_{..}, \beta_{..}\}$	4	5.32	4.67	3.50
$\{\phi^*, \gamma_i'' = 0, \gamma_i', \phi_{..}, p_{..}, \beta_{ij}\}$	84	6.28	67.09	365.15
$\{\phi^*, \gamma_i'' = 0, \gamma_i', \phi_{..}, p_i, \beta_{ij}\}$	100	8.88	104.96	903.65
$\{\phi^*, \gamma_i'' = 0, \gamma_i', \phi_{..}, p_i, \beta_{ij}\}$	93	12.39	91.57	594.88
$\{\phi^*, \gamma_i'' = 0, \gamma_i', \phi_i, p_i, \beta_{ij}\}$	109	27.60	149.35	1844.57
$\{\phi^*, \gamma_i'' = 0, \gamma_i', \phi_i, p_i, \beta_{ij}\}$	102	30.73	132.12	1057.02
$\{\phi^*, \gamma_i'' = \gamma_i', \phi_{..}, p_{..}, \beta_{..}\}$	12	223.81	223.96	224.22
$\{\phi^*, \gamma_i'' = \gamma_i', \phi_i, p_i, \beta_{ij}\}$	110	251.52	376.43	2258.39

^a Because $\sum_{j=0}^9 \beta_{ij} = 1$, models including $\beta_{..}$ imply that β_{ij} is fixed. In this case, we fix $\beta_{i9} = 0$ and $\beta_{ij} = 0.111111$ for $j = 0$ to 8.

Table 5
Comparison of parameter estimates from breeding hawksbill sea turtle (Eretmochelys imbricata) females at Jumby Bay, Long Island, Antigua, West Indies, 1987–1996, under model allowing Markovian breeding probability $\{\phi^, \gamma_i'' = 0, \gamma_i', \phi_{..}, p_{..}, \beta_{..}\}$ with estimates under model allowing only completely random breeding probability $\{\phi^*, \gamma_i'' = \gamma_i', \phi_{..}, p_{..}, \beta_{..}\}$*

Parameter	Markovian ^a		Completely random	
	Estimate	SE	Estimate	SE
ϕ^*	0.95	0.013	1.00	0.015
γ_{89}'	0.80	0.098	0.29	0.060
γ_{90}'	0.41	0.083	0.21	0.049
γ_{91}'	0.60	0.075	0.36	0.057
γ_{92}'	0.68	0.084	0.30	0.053
γ_{93}'	0.50	0.083	0.23	0.047
γ_{94}'	0.46	0.079	0.22	0.046
γ_{95}'	0.60	0.087	0.27	0.049
γ_{96}'	0.34	0.079	0.14	0.035

^a γ_i'' fixed at 0; $\hat{\phi}_{..} \equiv 0.80$ (SE = 0.013); for all i , $\beta_{ij} = 0.1111111$, $j < 9$; $\beta_{ij} = 0$ (for $j = 9$); $\hat{p}_{..} \equiv 0.90$ (SE = 0.015), implies $\hat{p}^* \approx 1.0$.

three values for effective sample size for 11 models. The first is based on the number of releases that can result in recaptures, $n_{\text{eff}} = \sum_{i=1}^9 \sum_{j=1}^{10} R_{ij} + \sum_{j=1}^9 R_{10,j} = 1050$, as in Burnham, Anderson, and White (1994). We believe, given the independence assumption inherent in these multinomial models, that this is a reasonable approach. However, we have also included two other approaches in Table 4 for comparison. The most conservative approach is $n_{\text{eff}} = 123$, the number of individual animals released in the study. Another approach, based on the number of releases that are used to estimate the parameters of interest, γ_i' and ϕ_i^* , is to use $n_{\text{eff}} = \sum_{i=1}^9 n_i^* = 272$.

We found that model $\{\phi^*, \gamma_i'' = 0, \gamma_i', \phi_{..}, p_{..}, \beta_{..}\}$ was the most parsimonious based on any of the three approaches. Dots in the subscript denote constancy over time. Therefore, under this model, probabilities of arrival, detection, and leaving the site for the year were constant within and among seasons. At the primary level, breeding probability in year i for non-breeders in year $i - 1$ varied by year but survival probability did not. Breeding probability for those that were breeders in year $i - 1$ was fixed at zero because no females at this nesting beach were ever found breeding two years in a row. Detection probability for each secondary sample was very high (0.90, SE = 0.012), producing an effective detection probability for a given year of virtually 1.0. As expected, comparable models assuming completely random breeding probability did not fit nearly as well (Table 4). Table 5 compares estimates of ϕ^* and γ_i' for the most parsimonious Markovian model with its counterpart that assumes completely random breeding probability. For these sea turtles, which never breed two years in a row, the result for breeding probability is not surprising. It is intuitive that estimates of γ_i' would be larger than under the completely random emigration model. Nevertheless, the differences are striking and demonstrate the need for the Markovian emigration model in this case.

Estimates of survival probability also differ between the Markovian and completely random emigration models ($\hat{\phi}^* = 0.94$ versus $\hat{\phi}^* \approx 1.0$). Estimated survival probability was also

virtually 1.0 when we fit the CJS model to the resightings pooled within year (i.e., ignoring the within-season information provided in the robust design). This is consistent with the point demonstrated by Kendall et al. (1997) that ignoring Markovian temporary emigration can produce bias in other parameters that, due to covariances among estimators, goes beyond simple confounding.

We computed estimates using a modification of program SURVIV (White, 1983) called ORDSURV (www.mbr-pwrc.usgs.gov/software.html). Because $\sum_{j=0}^{l_i-1} \beta_{ij} = 1.0$, to avoid numerical problems, we set $\hat{\beta}_{is} = 1 - \sum_{j \neq s} \hat{\beta}_{ij}$ for some sample s in each primary period i . Computationally, it is desirable in these cases to let the parameter with the value farthest from zero be estimated by subtraction (Hines, 1994). We varied our choice by primary period based on a crude estimator u_{ij}/u_i^* .

Sampling continued within a breeding season for five months. Despite the fact that we relax the closure assumption, we relax it only for movement out of the area, not for mortality. Mortality that occurs during the sampling period can bias estimates of survival (Smith and Anderson, 1987) due to heterogeneity in the interval of observed survival (e.g., one animal is seen early in a sampling period one year and late in a sampling period of another year or vice versa). Although the potential for this problem exists in this case, it should not be as severe as it first appears. When a turtle returns to the breeding site, its arrival time within season is extremely consistent from year to year. Therefore, the elapsed time between first observations for an individual is approximately divisible by 12 months. If bias is introduced, we claim that it would not be a result of the five-month sampling period but the potential for mortality during the two months that an individual female tends to remain in the area to renest.

4. Discussion

Motivated by breeding populations such as sea turtles, our intent in this article was to extend the methods of Kendall et

al. (1997) and Schwarz and Stobo (1997) to permit estimation under Markovian temporary emigration while relaxing the closure assumption of the robust design in a systematic way. We derived these estimators for temporary emigration directly from the likelihood function, and therefore models that constrain temporary emigration over time or as a function of covariates are easily accommodated. We have shown that, even when we allow for animals that enter the area during a primary period to leave again without being exposed to the sampling process, Markovian temporary emigration can still be estimated if that probability of departure is constant within a primary period.

The study of hawksbill sea turtles we have described provided a good candidate for the use of these methods. Intense sampling effort raised the detection probability to virtually 1.0 for a given year and also made it unlikely that an animal would arrive and leave without being exposed to sampling effort. Because these animals never breed two years in a row, a model that requires breeding to be a completely random process is simply not useful here.

These methods should also be useful in the study of other taxa that enter and leave an area in a staggered fashion over the duration of a study period. This occurs most frequently in migratory populations and could apply to wintering and stopover locations in addition to breeding areas.

The focus of our discussion has been on the dynamics of a population between primary periods, with parameters within primary periods treated as incidental. However, the approach we have taken from Schwarz and Arnason (1996) to parameterize the within-primary period part of the model could be used to consider questions about arrival and departure probabilities and make comparisons across periods. This would be similar to the treatment by Pradel et al. (1997).

The assumption that both breeders and nonbreeders have the same annual survival probability is a strong one for these turtles, or any species, and it is unfortunate that it is not testable under this sampling design. That would require sampling in other areas, in which case the multistate models of Arnason (1973) and Brownie et al. (1993) could be used. Despite this potential problem, there was no indication that fit was poor, and the estimate for survival rate was high. Kendall and Jennelle (unpublished manuscript) studied the expected bias in survival rate and breeding probability when survival rate is different for breeders and nonbreeders. They found that, for cases like the turtle example (e.g., $\gamma_i'' \equiv 0$ and $\phi_i \equiv 0.9$ for breeders), percent bias in $\hat{\phi}_i^*$ (with respect to the average survival probability for the entire population) and $\hat{\gamma}_i'$ never exceeded 8% when $\phi_i \geq 0.72$ for nonbreeders. It is also not clear to what extent true mortality within a primary period would bias $\hat{\phi}_i^*$ or $\hat{\gamma}_i'$ versus $\hat{\phi}_{ij}$, which deserves further attention.

The assumption that tags are not lost would normally be a strong assumption for such a long-term study of sea turtles, tending to underestimate survival probabilities. However, because the shell is also notched, tag loss was not a problem here. Where tag loss is a problem, a model that combines robust design and multistrata (e.g., retains two tags, one tag, etc.) data could be employed to adjust for that loss.

The strongly Markovian breeding process in the turtle example made it easy to distinguish it from a completely random process. Kendall and Nichols (1995) found that power

to detect Markovian temporary emigration is still reasonable for other cases where detection and survival probability are smaller and where the Markovian nature of temporary emigration is weaker.

The methods presented here extend or modify previous approaches (Kendall and Nichols, 1995; Kendall et al., 1997; Schwarz and Stobo, 1997) to estimating movement in and out of a single study site as well as achieving unbiased estimates of survival. This is accomplished under relatively mild assumptions by the extra information on detection probability available from the secondary samples of Pollock's robust design. We recommend this design wherever possible because of this and other previously discussed (Kendall and Pollock, 1992) advantages. If the ecologist can also identify and devote substantial sampling effort to other areas where a mobile population (or meta-population) is extant, then multistate models (Arnason, 1973; Brownie et al., 1993) provide for direct estimation of differential movement and survival probabilities.

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RÉSUMÉ

Les études de capture-recapture sont essentielles en diverses circonstances pour l'estimation des paramètres démographiques d'espèces sauvages et en halieutique. Le schéma robuste de Pollock, mettant en jeu plusieurs échantillonnages par période étudiée, dispose de plusieurs avantages sur les approches classiques. Il inclut ainsi la capacité d'estimer la probabilité de présence et d'accessibilité à la détection, ce qui dans certains cas équivaut à la probabilité de reproduction. Nous présentons un modèle pour estimer la disponibilité de détection qui ne dépend plus de deux hypothèses nécessaires dans les approches précédentes. La première est que la population échantillonnée est fermée aux adjonctions et suppressions entre échantillons pendant la période étudiée. La seconde est que chaque individu de la population a la même probabilité d'être accessible à la détection pendant une période donnée. Nous appliquons notre modèle à l'estimation de la survie et de la probabilité de reproduction dans l'étude de tortues de mer (*Eretmochelys imbricata*) pour laquelle les approches antérieures n'étaient pas appropriées.

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APPENDIX 1

The following product-multinomial likelihood function, $L = L_1 \times L_2 = L_1 \times L_{2a} \times L_{2b} \times L_{2c}$, describes the sampling process under the robust design where temporary emigration is completely random and closure within primary periods is not assumed (i.e., each animal is allowed one entry to and one exit from the study area in a given primary period):

$$L_1 = \prod_{i=1}^{k-1} \binom{R_i^*}{m_{i,i+1}^*, \dots, m_{i,k}^*} (\phi_i^* \gamma_{i+1}^* p_{i+1}^*)^{m_{i,i+1}^*} \times (\phi_i^* (1 - \gamma_{i+1}^* p_{i+1}^*) \phi_{i+1}^* \gamma_{i+1}^* p_{i+2}^*)^{m_{i,i+2}^*} \dots \times (\phi_i^* (1 - \gamma_{i+1}^* p_{i+1}^*) \dots \times \phi_{k-2}^* (1 - \gamma_{k-1}^* p_{k-1}^*) \phi_{k-1}^* \gamma_k^* p_k^*)^{m_{i,k}^*} \times (\chi_i^*)^{R_i^* - r_i^*}, \quad (\text{A1.1})$$

$$L_{2a} = \prod_{i=1}^k \binom{n_i^*}{u_{i1}, u_{i2}, \dots, u_{il_i}} \prod_{j=1}^{l_i} \left(\frac{\psi_{ij} p_{ij}}{\sum_{j=1}^{l_i} \psi_{ij} p_{ij}} \right)^{u_{ij}}, \quad (\text{A1.2})$$

$$L_{2b} = \prod_{i=1}^k \prod_{j=1}^{l_i} \binom{n_{ij}}{d_{ij}} (1 - \nu_{ij})^{d_{ij}} (\nu_{ij})^{n_{ij} - d_{ij}}, \quad (\text{A1.3})$$

$$L_{2c} = \prod_{i=1}^k \prod_{j=1}^{l_i-1} \binom{R_{ij}}{m_{ij,j+1}, \dots, m_{ij,l_i}} (\phi_{ij} p_{i,j+1})^{m_{ij,j+1}} \times (\phi_{ij} (1 - p_{i,j+1}) \phi_{i,j+1} p_{i,j+2})^{m_{ij,j+2}} \dots$$

$$\times (\phi_{ij} (1 - p_{i,j+1}) \dots \times \phi_{i,l_i-2} (1 - p_{i,l_i-1}) \phi_{i,l_i-1} p_{il_i})^{m_{ij,l_i}} \times (\chi_{ij})^{R_{ij} - r_{ij}}. \quad (\text{A1.4})$$

Recall that $p_i^* = \sum_{j=1}^{l_i} \psi_{ij} p_{ij}$. The form of L_{2c} is easiest to implement in our modification of program SURVIV (White, 1983). An alternative is the conditional independent binomial approach used by Schwarz and Arnason (1996).

APPENDIX 2

The methods we use here assume that animals arrive in the study area immediately prior to sampling (i.e., the probability that an animal arrives and leaves again before having the opportunity to be detected is zero). Schwarz and Stobo (1997) assumed that breeders arrive uniformly between sampling occasions and that therefore they could breed and leave without being exposed to sampling. Schwarz et al. (1993) discussed various options for modeling arrival.

For the case where animals can leave before exposure to detection, we partition breeders (those that use the study area) based on availability for detection. The expected number of breeders in period i would be $E(N_i^{\text{breed}} | N_i) = N_i \gamma_i^*$. The expected number of breeders available for detection would be

$$E(N_i^{\text{available}} | N_i^{\text{breed}}) = N_i^{\text{breed}} \alpha_i^* = N_i \gamma_i^* \alpha_i^*, \quad (\text{A2.1})$$

where α_i^* is the probability of availability for detection, given presence in the breeding area, and N_i is the total number of animals in the population of interest (e.g., breeding and non-breeding adult females) in primary period i . The expected number of animals detected in primary period i can then be expressed as $E(n_i^*) = N_i \gamma_i^* \alpha_i^* p_i^*$. If we replaced γ_i^* with $\gamma_i^* \alpha_i^*$ throughout (A1.1), thus modeling availability directly and breeding indirectly, the two parameters would be apparently confounded. Under the options for arrival distribution presented by Schwarz et al. (1993), α_i^* is a function of the ϕ_{ij} but not one that can be extracted cleanly at the primary period level, with the exception of the special case described below.

Briefly, Schwarz and Stobo (1997) adjusted their calculations of breeding probability for this phenomenon. They derived a net number of arrivals for each secondary sampling session as $\hat{B}_{ij} = \hat{\beta}_{ij} n_i^* / \hat{p}_i^*$. Based on a uniform distribution of arrivals, the gross number of arrivals for each sampling session is $\hat{B}_{ij}^{\text{gross}} = \hat{B}_{ij} (\log \hat{\phi}_{ij}) / (\hat{\phi}_{ij} - 1)$. The total number of breeders is then $\hat{N}_i^{\text{breed}} = \hat{B}_{i0} + \sum_{j=1}^{l_i-1} \hat{B}_{ij}^{\text{gross}}$ (the number of new arrivals before the first sampling session (B_{i0}) is treated as a separate case). Using $E(\hat{N}_i^{\text{js}}) \approx N_i$, where \hat{N}_i^{js} is the Jolly–Seber estimator for N_i ignoring within-season capture information, breeding probability is estimated as $\hat{\gamma}_i^* = \hat{N}_i^{\text{breed}} / \hat{N}_i^{\text{js}}$. This is thus a moment-type estimator derived outside of the modeling process.

Based on the following development, we can estimate all parameters numerically directly from the likelihood. If we (1) assume $\phi_{ij} \equiv \phi_i$ constant within a primary period and (2) consider those that arrived and left before the first sample of period i , then $\hat{N}_i^{\text{breed}} = \sum_{j=0}^{l_i-1} \hat{B}_{ij} (\log \hat{\phi}_i) / (\hat{\phi}_i - 1) = (\log \hat{\phi}_i) /$

Table A

Year of release	Number released	Year of recapture			
		2	3	4	5
Recapture array (m_{hi}^*)					
1	R_1^*	m_{12}^*	m_{13}^*	m_{14}^*	m_{15}^*
2	R_2^*		m_{23}^*	m_{24}^*	m_{25}^*
3	R_3^*			m_{34}^*	m_{35}^*
4	R_4^*				m_{45}^*
Multinomial cell probabilities					
1		$\phi_1^* \gamma_2'' p_2^*$	$\phi_1^* f_2'' \phi_2^* a_3 p_3^*$	$\phi_1^* f_2'' \phi_2^* G_3 \phi_3^* a_4 p_4^*$	$\phi_1^* f_2'' \phi_2^* G_3 \phi_3^* G_4 \phi_4^* a_5 p_5^*$
2			$\phi_2^* \gamma_3'' p_3^*$	$\phi_2^* f_3'' \phi_3^* a_4 p_4^*$	$\phi_2^* f_3'' \phi_3^* G_4 \phi_4^* a_5 p_5^*$
3				$\phi_3^* \gamma_4'' p_4^*$	$\phi_3^* f_4'' \phi_4^* a_5 p_5^*$
4					$\phi_4^* \gamma_5'' p_5^*$

$(\hat{\phi}_i - 1) \sum_{j=0}^{i-1} \hat{B}_{ij} = (\log \hat{\phi}_i) / (\hat{\phi}_i - 1) \hat{N}_i^{\text{available}}$. From (A2.1), in this case, we can define $\alpha_i^* = (\phi_i - 1) / \log \phi_i$, γ_i^* in (A1.1) could be replaced by $\gamma_i^* (\phi_i - 1) / \log(\phi_i)$, and estimates could be computed from the resulting likelihood.

APPENDIX 3

The capture process across primary periods under the Markovian temporary emigration model and hence the likelihood that describes it (L_1') are complex. However, matrix notation makes it more tractable. Let $q_i^* = 1 - p_i^*$ and

f_i'', f_i' = row vectors of probabilities an animal in the population in primary period i is not available for detection (column 1) or is available but not captured (column 2), given that it is or is not, respectively, available for detection in primary period $i - 1$ and survives from period $i - 1$ to i , i.e.,

$$\begin{aligned} f_i'' &= [(1 - \gamma_i'') \quad \gamma_i'' q_i^*], \\ f_i' &= [(1 - \gamma_i') \quad \gamma_i' q_i^*], \end{aligned}$$

G_i = a transition matrix of probabilities that an animal is unavailable for detection (column 1) or available but not captured (column 2) in primary period i , given that it is unavailable (row 1) or available (row 2) for detection in primary period $i - 1$, survives to period i , and is in the population in both periods, i.e.,

$$= \begin{bmatrix} (1 - \gamma_i'') & \gamma_i'' q_i^* \\ (1 - \gamma_i') & \gamma_i' q_i^* \end{bmatrix},$$

a_i = a vector of probabilities of being available for detection in primary period i , given an animal is unavailable (row 1) or available (row 2) for detection in period $i - 1$ and survives to period i , i.e.,

$$= [\gamma_i' \quad \gamma_i'']^T.$$

Note that we can then describe the probabilities of any multinomial cell from L_1' as in Table A.

The probability that an animal detected in primary period i is never detected in subsequent primary periods can be computed by subtracting the row sum above, as is done in program SURVIV. Alternatively, this probability can be written recursively. Let

$$\chi_i = [\chi_i' \quad \chi_i'']^T,$$

where χ_i'' is the probability that an animal alive and in the study area in primary period i is never seen again after period i under the Markovian temporary emigration model,

$$\chi_i'' = \begin{cases} 1, & i = k, \\ 1 - \phi_i^* \gamma_{i+1}'' p_{i+1}^*, & i = k - 1, \\ 1 - \phi_i^* (1 - f_{i+1}'' \chi_{i+1}), & i = 1, 2, \dots, k - 2, \end{cases}$$

and χ_i' is an intermediate quantity; the probability that an animal alive, in the population but not in the study area, is never seen again after period i is

$$\chi_i' = \begin{cases} 1, & i = k, \\ 1 - \phi_i^* \gamma_{i+1}' p_{i+1}^*, & i = k - 1, \\ 1 - \phi_i^* (1 - f_{i+1}' \chi_{i+1}), & i = 1, 2, \dots, k - 2. \end{cases}$$

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