

## CAPTURE-RECAPTURE ESTIMATION OF PREBREEDING SURVIVAL RATE FOR BIRDS EXHIBITING DELAYED MATURATION

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**Abstract.**—Many species of seabirds exhibit delayed maturity and do not return to the natal colony to breed for several years after fledging. Capture-recapture studies are frequently conducted at such breeding colonies and often include marking of young birds. However, because of the absence of these birds from the natal colony during the first few years after banding, the data do not fit neatly into existing capture-recapture models. Here we present a method for estimating prebreeding survival rate from capture-recapture studies on species exhibiting such patterns of delayed maturation. We illustrate the method using data from a capture-recapture study of Roseate Terns (*Sterna dougallii*) on Falkner Island, Connecticut. The method appears to work well and emphasizes the potential to tailor capture-recapture models to specific field situations.

### ESTIMADO DE LA TASA DE SOBREVIVENCIA DE AVES PRE-REPRODUCTIVAS QUE EXHIBEN MADURACIÓN TARDÍA A BASE DE DATOS TOMADOS POR EL MÉTODO CAPTURA-RECAPTURA

**Sinopsis.**—Muchas especies de aves marinas exhiben maduración tardía y no regresan a sus colonias natales a reproducirse hasta pasados varios años. Con frecuencia se conducen estudios en estas colonias utilizando el método captura-recaptura. Sin embargo, debido a la ausencia de estas aves que son marcadas como pichones pero que luego no aparecen en las colonias por varios años, los datos tomados en estos grupos no se ajustan debidamente a los modelos existentes de captura-recaptura. En este trabajo, presentamos un método para estimar la sobrevivencia de aves pre-reproductivas que exhiben maduración tardía a base de datos tomados en una colonia de *Sterna dougallii* en la Isla Falkner, Connecticut. El método parece trabajar bien y enfatiza en el potencial de ajustar el método de captura-recaptura a situaciones específicas.

In this paper we present a method for estimating prebreeding survival rate for birds exhibiting delayed maturation. During the past 15 yr, models have become available for use in estimating survival rates of young birds from both band-recovery (Brownie and Robson 1976, Brownie et al. 1985) and capture-recapture (Brownie et al. 1986, Pollock 1981, Stokes 1984) data. When used in conjunction with an annual sampling period, these models require the annual release of both young and adult birds and annual recaptures or recoveries of birds of both ages (here we refer to the simple case of only two age classes, young and adult, although extension to three or more classes is possible). These methods have proven extremely useful and have provided the first good estimates of annual survival rates of young birds (e.g., see review of waterfowl estimates by Johnson et al., in press).

Recently we encountered a situation that did not fit neatly into any of the above models. Spendelow has been engaged in a capture-recapture study of Roseate Terns, *Sterna dougallii*, on Falkner Island, Connecticut,

since 1978, and we recently used these data to estimate adult survival rates (Spendelov and Nichols 1989). These capture-recapture efforts included annual bandings of fledglings, and we became interested in using these data, together with subsequent recaptures, to estimate survival rates of young birds. However, Roseate Terns exhibit delayed maturation, and birds released as fledglings typically do not return to Falkner Island to breed until at least 3 yr later. Releases of fledglings in year  $i$  are thus usually followed by 2 yr ( $i + 1, i + 2$ ) of no information, with the first recaptures occurring in year  $i + 3$ . Clearly, such data will not permit estimates of annual survival rates of young birds during each of the 3 yr before they return to the island, but the data do permit estimation of the probability of surviving the entire 3-yr period.

Others have encountered similar problems in dealing with situations of this sort (e.g., see Weimerskirch and Jouventin 1987). Delayed maturation, coupled with failure to return to the natal colony until the first breeding attempt, is common among seabirds. Thus, we believe that a method for estimating survival rate in such situations would be of general use.

Here, we present a method for estimating survival rates of young birds that exhibit delayed maturation and that cannot be sampled for one or more years following release. We illustrate the method with capture-recapture data for Roseate Terns on Falkner Island.

#### THE METHOD

Our method can be viewed as a special extension of the Jolly-Seber cohort approach presented by Loery et al. (1987, also see Buckland 1982, Pollock et al. 1990). Let  $j$  be the number of years between hatching and first return to the breeding colony, and define the following capture-recapture statistics:

- $R_i$  = the number of young birds banded and released in year  $i$ .
- $m_{i+j}$  = the number of  $R_i$  that are recaptured (or resighted) in year  $i + j$ .
- $r_{i+j}$  = the number of  $m_{i+j}$  that are recaptured (or resighted) at least once in some subsequent year ( $> i + j$ ).
- $z_{i+j}$  = the number of  $R_i$  that are not recaptured (or resighted) in year  $i + j$ , but that are recaptured (or resighted) in some subsequent year ( $> i + j$ ).

Define the following model parameters:

- $\phi_i$  = the probability that a young bird will survive the  $j$ -year period ( $i$  to  $i + j$ ) following release and return to its natal colony.
- $p_{i+j}$  = the probability that a bird marked as young in year  $i$  and alive at the breeding colony in year  $i + j$ , is recaptured (or resighted) during year  $i + j$ .
- $\chi_{i+j}$  = the probability that a bird marked as young in year  $i$  and alive at the breeding colony in year  $i + j$ , is never recaptured (or resighted) again after  $i + j$ .

Note that the complement of survival probability  $(1 - \phi_i)$  includes both mortality and permanent emigration to other breeding colonies. Also note that  $\chi_{i+j}$  can be written as a function of all annual survival and capture probabilities for periods following  $i + j$ , although these individual probabilities cannot be separately estimated. Finally, define the following random variable to be estimated from the data:

$M_{i+j}$  = the number of birds marked as young in year  $i$  and alive and in the natal colony in year  $i + j$ .

For a specific group of birds released as young ( $R_i$ ), we first estimate the number still alive and at the natal colony  $j$  years later using the following bias-adjusted Jolly-Seber estimator:

$$\hat{M}_{i+j} = \frac{(m_{i+j} + 1)z_{i+j}}{r_{i+j} + 1} + m_{i+j} \tag{1}$$

We can then estimate  $\phi_i$  as:

$$\hat{\phi}_i = \hat{M}_{i+j}/R_i \tag{2}$$

The variance of  $\hat{\phi}_i$  can be estimated as shown in Seber (1982:202). Capture probability and its variance can be estimated as in Pollock et al. (1990).

The above estimator (2) is adequate for a single group of released young. If several such groups are released in different years, then it would be desirable to test for temporal variation in survival and/or capture probabilities and, if no such variation is detected, to combine data from all groups to obtain an overall estimate with better precision than the individual estimates. We can accomplish this testing and estimation using program SURVIV (White 1983). We simply treat each group of released young as a different cohort and model the fates of individuals within each group with a multinomial distribution. Each multinomial contains four possible fates: (1) birds seen at  $i + j$  and also seen later ( $r_{i+j}$ ), (2) birds seen at  $i + j$  and not seen later ( $m_{i+j} - r_{i+j}$ ), (3) birds not seen at  $i + j$  but seen later ( $z_{i+j}$ ), and (4) birds not seen after release ( $R_i - m_{i+j} - z_{i+j}$ ). We can write the expected values for these statistics, conditional on  $R_i$ , as follows:

$$\begin{aligned} E(r_{i+j}) &= R_i \phi_i p_{i+j} (1 - \chi_{i+j}), \\ E(m_{i+j} - r_{i+j}) &= R_i \phi_i p_{i+j} (\chi_{i+j}), \\ E(z_{i+j}) &= R_i \phi_i (1 - p_{i+j}) (1 - \chi_{i+j}). \end{aligned} \tag{3}$$

The expected value for the number of young never seen after release is obtained by subtracting the above three expectations from  $R_i$ .

The most general model we consider uses the parameterization of (3) with different parameters for each cohort of released chicks. Under this model, SURVIV produces estimates very similar to those obtained using (2). The estimates based on (2) differ because they contain the bias-adjustment terms recommended by Seber (1982), whereas the estimates from SURVIV represent unadjusted maximum likelihood estimates. We

also consider reduced-parameter models with survival rates constant regardless of calendar year, capture probabilities constant regardless of calendar year, and both survival and capture probabilities constant regardless of calendar year. Likelihood ratio tests between models and model goodness-of-fit tests are used to select the most reasonable model for a given data set. A copy of the SURVIV input for these different models is available from the authors.

#### EXAMPLE

Descriptions of the Falkner Island tern colony site, located at 41°13'N, 72°39'W, in Long Island Sound about 5 km south of Guilford, New Haven Co., Connecticut, and the habitats used as nest sites by Roseate Terns breeding there are given in Spendelow (1982). Descriptions of the methods used to mark nests, band young chicks, and trap adult Roseate Terns are given in Spendelow and Nichols (1989). From 1978–1983, most active Roseate Tern nest sites were closely monitored for only about 5 d following the hatching and banding of the last chick. More intensive searches of the areas surrounding the nest sites to locate older chicks have been made since the initiation of growth studies of the chicks in 1984. With the possible exception of no more than two individuals in any given year, all Roseate Tern chicks hatched on Falkner Island since 1978 that have survived to fledging have been banded, usually before 3 d of age. Chicks that survived at least 5 d after hatching and were not found dead later in that same nesting season were presumed to have fledged and were incorporated in the  $R_t$ .

Capture-recapture summary statistics are presented in Table 1. Although at least 100 fledglings were released in each year, the number of these birds captured as breeding adults in subsequent years was relatively small. Estimates of survival and capture probability are presented in Table 2, together with the proportion of released fledglings seen in any subsequent years (this value is commonly equated with survival, and provides a lower bound for survival rate). Annual estimates of surviving the 3-yr period following hatch and not permanently emigrating to another colony were computed using (2) and ranged from 0.059 to 0.270. Annual estimates of capture probability of the surviving birds ranged from 0.109 to 0.430.

All three reduced-parameter models fit the data acceptably well ( $P > 0.05$ ). The likelihood ratio test between the general model and the model with both survival and capture probabilities constant over calendar year did not indicate rejection of the reduced-parameter model ( $\chi^2_{14} = 23.2$ ,  $P = 0.06$ ). We conclude that we have no strong evidence of temporal variation in either survival or capture probabilities, despite the variation among point estimates. Our best estimate of the probability of surviving the 3 yr following fledging and returning to the natal breeding colony is thus 0.156 (SE = 0.018). Note that this estimate is about 50% larger than the naive estimate based on proportion of fledglings ever recaptured.

Our estimate of the average annual survival rate of breeding adult

TABLE 1. Capture-recapture summary statistics through 1989 for Roseate Terns banded as chicks from 1978–1985 on Falkner Island, Connecticut.

Year of hatch ( <i>i</i> )	Fledglings released ( $R_i$ )	Caught at $i + 3$ ( $m_{i+3}$ )	Caught at $i + 3$ and at some period $> i + 3$ ( $r_{i+3}$ )	Not caught at $i + 3$ but caught subsequently ( $z_{i+3}$ )
1978	202	12	8	11
1979	184	5	3	6
1980	101	1	1	5
1981	241	11	5	22
1982	152	6	4	8
1983	204	6	2	21
1984	259	15	6	12
1985	209	9	7	10

Roseate Terns for 1978–1987 under the assumption that survival rates did not vary significantly from year to year (Spendelov and Nichols 1989) was 0.738 (SE = 0.016). An estimated survival rate of an adult for a 3-yr period, therefore, would be 0.402. Our best estimate of the probability of surviving from fledging to first breeding is only 0.156, indicating that the prebreeding survival rate for a 3-yr period of an immature bird is about 40% that of an adult.

The results of our earlier study (Spendelov and Nichols 1989) produced strong evidence of year-to-year variation in capture probabilities and weak evidence of year-to-year variation in survival rates of breeding adults. Assuming that there is no age-specific variation in wintering ground location (Nisbet 1981), it is not surprising that the results of this

TABLE 2. Estimates of capture probability and survival rate based on the Roseate Tern data in Table 1.<sup>a</sup>

Year of hatch ( <i>i</i> )	Proportion of fledglings recaptured <sup>b</sup>	Survival rate		Capture probability	
		$\hat{\phi}_i$	$\widehat{SE}(\hat{\phi}_i)$	$\hat{p}_i$	$\widehat{SE}(\hat{p}_i)$
1978	0.114	0.138	0.032	0.430	0.114
1979	0.060	0.076	0.030	0.357	0.162
1980	0.059	0.059	0.024	0.167	0.152
1981	0.137	0.228	0.073	0.200	0.079
1982	0.092	0.113	0.037	0.349	0.139
1983	0.132	0.270	0.150	0.109	0.072
1984	0.104	0.164	0.048	0.354	0.114
1985	0.091	0.103	0.025	0.419	0.120
All years	0.103	0.156	0.018	0.268	0.038

<sup>a</sup> Annual estimates of survival rate, capture probability and their variances are based on equation (2) and on Pollock et al. (1990). The estimates for all years were computed by SURVIV under the model assuming that both survival and capture probability were constant over calendar year.

<sup>b</sup> Computed as  $(m_{i+3} + z_{i+3})/R_i$ .

study produced no strong evidence of significant variation in survival probabilities of fledglings from different cohorts, because extreme winter conditions that might cause low survival from year  $i$  to year  $i + 1$  would affect three cohorts (birds banded in years  $i - 2$ ,  $i - 1$ , and  $i$ ). In other words, a cohort from year  $i$  would be subjected to the same winter conditions for 2 yr with cohorts from years  $i - 1$  and  $i + 1$ , and to similar conditions for 1 yr with cohorts from years  $i - 2$  and  $i + 2$ .

#### DISCUSSION

The methods presented here provide a means of estimating prebreeding survival rate for species that exhibit delayed maturation and are not exposed to sampling efforts (band recovery, recapture, resighting) until the year of first breeding. This situation is typical among seabirds, many of which leave breeding colonies as fledglings and return several yr later to breed. Estimation in this case can be handled using this straightforward extension of the cohort-based Jolly-Seber approach (Loery et al. 1987, Pollock et al. 1990).

As with all estimation methods, the survival rate estimator in (2) and the related estimators from the reduced-parameter models require some assumptions. First, we assume that all birds released at time  $i$  have the same probabilities of surviving to time  $i + j$  ( $\phi_i$ ), being recaptured or resighted at time  $i + j$  ( $p_{i+j}$ ), and being recaptured or resighted sometime after  $i + j$  ( $1 - \chi_{i+j}$ ). Second, we assume that marks (bands) are not lost or overlooked. Third, we assume that samples (captures or resightings) are instantaneous and that releases follow immediately after sampling. Fourth, we assume that all emigration is permanent. Fifth, we assume that all birds initiate breeding at exactly  $j$  yr after hatching. The general model underlying equation (2) is fully parameterized and standard goodness-of-fit tests are not possible. Such tests can be conducted for the reduced-parameter models, however, and these tests have some ability to detect violation of assumptions (1), (4), and (5).

Certain specific kinds of assumption violations will not result in biased estimates. For example, assume that most of the Roseate Terns in our example returned to Falkner Island at age 3, but that some birds did not return until age 4. This scenario is a clear violation of assumption (5). However, if both groups of birds (those "programmed" to return to Falkner after 3 and 4 yr, respectively) had the same probability of surviving until age 3 ( $\phi_i$ ) and of being recaptured or resighted after year 3 ( $1 - \chi_{i+3}$ ), then survival estimates based on (2) should be unbiased. However, if the difference in breeding status and migration pattern for these two groups of birds in year  $i + 3$  results in differing survival probabilities, then our estimates will be biased, although this bias may not be large (see Carothers 1973, 1979).

If we are willing to make additional assumptions about age-specificity of survival, then we can obtain more efficient estimators than those given in (1) and (2). For example, assume that all adult birds (age  $> j$ ) exhibit the same survival rates and capture probabilities in any calendar year,  $i$ ,

regardless of their exact age. In this case, we can rewrite equation (1) as:

$$\hat{M}_{i+j} = \frac{(R_{i+j} + 1)z_{i+j}}{r_{i+j} + 1} + m_{i+j} \quad (4)$$

where statistics are as defined before except that  $R_{i+j}$  denotes all adult birds captured and released in period  $i + j$  (this includes, but is not restricted to, birds banded as chicks in year  $i$ ), and  $r_{i+j}$  now refers to the number of individuals in  $R_{i+j}$  that are recaptured (or resighted) in any period following year  $i + j$ . This use of data from additional adult birds (not just those banded as chicks in year  $i$ ) yields a more precise estimate of  $M_{i+j}$ , which results in a better estimate of  $\phi_i$  using (2).

Finally, we believe that many people who consider using capture-recapture models, discard them when they discover that the models do not fit their specific application exactly. However, a variety of capture-recapture models are now available (Burnham et al. 1987, Pollock et al. 1990), and these models can often be tailored to specific applications with little difficulty. Flexible programs such as SURVIV permit estimation under virtually any multinomial model, even in cases where closed-form estimators do not exist. The method presented in this paper provides a convenient example of a situation that did not fit neatly into previously-developed capture-recapture applications, but that required only a minor modification of existing estimators. We urge those involved in capture-recapture studies to consider such tailoring of available estimators to their specific applications before discarding formal models in favor of *ad hoc* estimators.

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