

Estimation by capture-recapture of recruitment and dispersal over several sites

J. D. Lebreton, J. E. Hines, R. Pradel, J. D. Nichols and J. A. Spindelov

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Dispersal in animal populations is intimately linked with accession to reproduction, i.e. recruitment, and population regulation. Dispersal processes are thus a key component of population dynamics to the same extent as reproduction or mortality processes. Despite the growing interest in spatial aspects of population dynamics, the methodology for estimating dispersal, in particular in relation with recruitment, is limited. In many animal populations, in particular vertebrates, the impossibility of following individuals over space and time in an exhaustive way leads to the need to frame the estimation of dispersal in the context of capture-recapture methodology. We present here a class of age-dependent multistate capture-recapture models for the simultaneous estimation of natal dispersal, breeding dispersal, and age-dependent recruitment. These models are suitable for populations in which individuals are marked at birth and then recaptured over several sites. Under simple constraints, they can be used in populations where non-breeders are not observed, as is often the case with colonial waterbirds monitored on their breeding grounds. Biological questions can be addressed by comparing models differing in structure, according to the generalized linear model philosophy broadly used in capture-recapture methodology. We illustrate the potential of this approach by an analysis of recruitment and dispersal in the roseate tern *Sterna dougallii*.

J. D. Lebreton and R. Pradel, CEFÉ CNRS, 1919 Route de Mende, FR-34 293 Montpellier Cedex 5, France (lebreton@cefe.cnrs-mop.fr). – J. E. Hines, J. D. Nichols and J. A. Spindelov, Patuxent Wildlife Research Center, US Geological Survey, Laurel, MD 20708, USA.

In vertebrates, the on-set of reproduction is fairly well defined at the species level, since most species have a clear-cut age at which reproduction first becomes physiologically possible (Gaillard et al. 1989, Bradley and Wooller 1991). However, at the individual level, many different constraints may delay recruitment: acquire enough energy, find a mate, establish a territory, etc. (Coulson 1968). Such factors and their interactions influence the age at first reproduction of any particular individual, such that recruitment of an individual into the breeding part of the population is best viewed as a random variable. However, for any cohort of young animals, the fraction of individuals that have been recruited as breeders will increase with age, such that

accession to reproduction (recruitment into the breeding part of the population; we will shorten this phrase and refer to this event as recruitment) is progressive at the population level.

In many animals, accession to reproduction involves dispersal from the birth site by some proportion of the population (Duncan and Monaghan 1977). Attempting to recruit at the natal site, or dispersing to become a breeder at another site, are indeed alternative strategies molded by various selective pressures, in relation to the constraints at the individual level mentioned above and with habitat heterogeneity (Greenwood 1980, Danchin et al. 1991, Lidicker and Stenseth 1992, Béchichon et al. 1996). As a consequence, accession to reproduction and

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dispersal are intimately linked. In general, “natal dispersal”, i.e. dispersal between birth and the first reproductive event, occurs with greater probability than “breeding dispersal”, i.e. dispersal between successive breeding attempts (Greenwood and Harvey 1982). This pattern is especially well known in seabirds (Bradley and Wooller 1991).

Heterogeneity in habitat quality (Fretwell 1972) and attractiveness (Boulinier and Danchin 1997) induces differences in density and demographic performance between habitats. As a consequence, recruitment and dispersal are also intimately linked with population regulation in a large variety of organisms, including birds (Chabryk and Coulson 1976, Coulson et al. 1982), marine invertebrates (Sutherland 1990), small mammals (Krebs et al. 1973, Hestbeck 1986), and plants (Hatfield and Chesson 1989). These links have received considerable theoretical attention both from the proximate demographic point of view (Brown 1969, Kot and Schaffer 1986, Pulliam 1988, Davis and Howe 1992, Murdoch 1994, Rodenhouse et al. 1997) and from the ultimate evolutionary perspective (McPeck and Holt 1992, Doncaster et al. 1997). Even in the absence of local extinctions and re-colonizations typical of metapopulations *sensu stricto* (Levins 1969, 1970), there is thus considerable interest in the dynamics of dispersal and recruitment in subdivided populations (Hanski 1991, Cooke and Francis 1993, Lebreton 1997). With the emergence of long-term research programs on various vertebrate species, many data sets exist to address questions dealing with the interplay of dispersal, accession to reproduction, population regulation and habitat heterogeneity. This is in particular the case for colonial birds (Coulson and Butterfield 1986, Jouventin and Weimerskirch 1991, Coulson and Nève de Mévergnies 1992, Spindelov et al. 1995), which constitute a straightforward example of sub-divided populations.

Despite this promising context, there are nearly no demographic tools to estimate and model dispersal-recruitment patterns (Conroy et al. 1996), and to test biological hypotheses concerning these patterns. But for the rare case of certainty of detection (Aars and Ims 1999), such tools must account for the practical impossibility of detecting every marked individual at every sampling occasion and should thus be developed in a capture-recapture context (Lebreton et al. 1992, Nichols 1992). The existing capture-recapture approaches dealing with recruitment are concerned with the estimation of local immature survival (Rothery 1983, Nichols et al. 1990), which is basically the product of an immature survival probability and a probability of returning to, or remaining within, a study area. As noted above, in many species it is necessary to account for the spread of accession to reproduction over several age classes, a process that can be modeled in terms of age-specific recruitment proba-

bilities (Lebreton et al. 1990, Clobert et al. 1994, Pradel and Lebreton 1999). Capture-recapture models incorporating dispersal must thus consider some age-dependence in parameters (Pollock 1981) and must be developed in a multisite setting (Arnason 1973, Hestbeck et al. 1991).

Based on these premises, multistate capture-recapture models (reviewed by Lebreton and Pradel 2002) can be used to estimate transitions between reproductive states defined as “breeder” and “non-breeder” provided both breeders and non-breeders are observable or catchable, even if not at the same rate (Nichols et al. 1994, Cam et al. 1998). Such multistate approaches could also be generalized to a multisite context by considering states combining reproductive state and sites. We consider here such a model for accession to reproduction that generalizes the capture-recapture recruitment model of Clobert et al. (1994) to several sites. In this model, the basic data consist of recaptures or resightings as breeders of animals marked as young (at birth or hatch). We treat non-breeders as non-observable, i.e. they have a probability of capture equal to 0, as this situation cannot be handled using existing models and generates specific restrictions to the analysis. However, as mentioned above, more powerful approaches can be easily derived from our model when non-breeder individuals are observable as well. Our model is thus well adapted to the study of colonial waterbirds, in which breeders are commonly followed over several breeding sites. Between the first age when reproduction becomes possible and the age at which all animals show adult breeding probability, age classes represent a mixture of breeders, which show some non-zero capture probability, and non-breeders. The resulting overall probability of capture in these age classes is lower than that for older age classes, which are composed of individuals having reached a typical adult breeding propensity. This difference in probabilities of capture makes it possible to estimate age-specific proportions of breeders relative to the adult breeding probability (Lebreton et al. 1990, Clobert et al. 1994), hereafter called relative age-specific breeding proportions. As in Clobert et al. (1994), the impossibility of estimating adult breeding propensity and thus absolute age-specific proportions of breeders is a direct consequence of the non-observability of non-breeders, a situation once again typical of colonial waterbirds.

The models presented can be viewed as direct generalizations of the models of Clobert et al. (1994) parameterized as in their multistate version in Pradel and Lebreton (1999). They can be used to estimate several quantities of interest in studies of meta-populations for which non-breeders are not observable in sampling efforts. Specifically, the modeling approach permits estimation of (1) location-specific pre-breeding survival probabilities, (2) location-specific annual survival probabilities for breeders, (3) location-specific natal disper-

sal probabilities, (4) location-specific breeding dispersal probabilities, (5) location- and relative age-specific probabilities of breeding for animals that have not bred previously, and (6) location-specific detection probabilities for breeding adults. We apply our models to recapture data obtained at three breeding colonies of roseate tern *Sterna dougallii* (Spendelow and Nichols 1989, Spendelow 1991, Spendelow et al. 1995). We then use these models to test a priori hypotheses about (1) relative magnitudes of natal and breeding dispersal probabilities, (2) age-specific variation in recruitment probabilities, and (3) variation in age-specific survival probabilities associated with a powerful hurricane.

The model

The basic ideas underlying our approach to multisite capture-recapture modeling are:

- We use multisite capture-recapture models (Hestbeck et al. 1991) as multistate models (Lebreton and Pradel 2002), with specific non-observable states for non-breeders (Lebreton et al. 1999).
- Age-dependence in the parameters of these models is considered (Pollock 1981, Buckland 1982, Loery et al. 1987). Model fitting and estimation can be handled by programs MARK (White and Burnham 1999), MSSURVIV (Hines 1994), and M-SURGE (Choquet et al. in prep.).
- We combine these ideas to rewrite the model of Clobert et al. (1994) as a multistate model (Pradel and Lebreton 1999, Spendelow et al. 2002).
- The approach is expanded to incorporate several geographical sites.

For the sake of simplicity, we consider below the specific case of the roseate tern example. More general model structures are straightforward. The basic assumptions and notation are as follows.

- There are s sites. The $s = 3$ sites in the particular case presented are denoted as site A, site B and site C.
- There are K occasions of capture, 11 in our roseate tern example, corresponding to successive breeding seasons. In the case of birth pulse populations (Caswell 2001), the captures occur over a short period of time (e.g. 6–8 weeks in our example) when compared to the interval between two occasions (one year in our example), as commonly requested for capture-recapture models (Nichols 1992).
- Breeding cannot start before a specified age at first breeding $c = 2$ (the second breeding season following the season of hatch). This assumption is not restrictive, as any initial breeding age, c , can be used.
- There is an age m at which full adult breeding propensity is reached; here $m = 6$.
- In each site, the status of an animal of age v , where $c \leq v < m$, can be either breeder (states denoted as A,

B, C, respectively for the three sites) or non-breeder (states denoted as a, b, c, for the 3 sites). As noted in the previous two points, all animals of age $v < c$ are non-breeders, and all animals of age $v \geq m$ have reached adult breeding propensity, i.e. have recruited. The combination of $s = 3$ sites and two states for reproductive status yields six states (Table 1).

- As in Clobert et al. (1994), an animal which has started to breed (i.e. which has moved from a, b, or c into A, B, or C) is assumed to remain at adult breeding propensity for the rest of its life, i.e. to remain in A, B, or C. This does not imply that the individual will reproduce every year, but simply that it exhibits the same probability of breeding as all other adults. If some reproductive events are skipped, this will be accounted for in the probability of capture which may be well below the probability of capture of an animal present on the site concerned (Blondel et al. 1992, Kendall et al. 1997). Treating non-breeders as “not observable” is appropriate for our example study of roseate tern breeding colonies because of our interest in estimating age-specific breeding probabilities. However, the assumption may be easily relaxed when non-breeders are observable, in which case non-breeders and breeders may even have different probabilities of detection (Nichols et al. 1994, Cam et al. 1998).
- The demographic parameters of animals recruited (i.e. animals in states A, B or C) do not depend on age. This makes it possible to consider animals of unknown age marked as breeders in addition to those marked as young. If we consider only animals marked as young, then it is possible to incorporate age-specific survival differences after recruitment.

The described model reduces to a particular case of an age-dependent multistate capture-recapture model and can be fit using software such as MARK (White and Burnham 1999).

Recruitment dispersal, i.e. “natal dispersal” in the terminology of Greenwood and Harvey (1982), is applied immediately after age 0 and does not depend on age. It is thus modeled as a pre-breeding dispersal (3×3 transition sub-matrix from a, b, c to a, b, c).

Table 1. States considered in the multisite recruitment model over three sites.

State number	Reproductive status	Site	Notation
1	Breeder	Site A	A
2	Breeder	Site B	B
3	Breeder	site C	C
4	Non-breeder	Site A	a
5	Non-breeder	Site B	b
6	Non-breeder	Site C	c

Note that this application of dispersal immediately after age 0 reflects a convention useful for computation, and does not represent a strong biological assumption. Basically, we have limited or no observations of animal location between the initial marking and the first observation as a breeder and thus no basis for inference about multiple movements occurring during the pre-breeding period. Instead, we can estimate the probability n_{ij} that an individual from birthplace j first breeds at location i , given that the individual survives to breed. Even if multiple movements during the pre-breeding period were estimable, it is only the compound parameters n_{ij} that influence the dynamics of the population, and could be used, for instance, in a multi-site Leslie matrix model (Lebreton 1996). Reproductive dispersal, i.e. “breeding dispersal” in the terminology of Greenwood and Harvey (1982), corresponds to transitions from A, B, C to A, B, C (3×3 transition sub-matrix). The progressive accession to reproduction occurs after recruitment dispersal from ages 2 to 6, with no further pre-recruitment dispersal (3×3 diagonal transition sub-matrices, from a to A, b to B, c to C, respectively). For the sake of robustness, we consider thus that breeding dispersal has no direct relation to recruitment. More complex assumptions reflecting relationships between site-specific recruitment and reproductive dispersal probabilities could be easily considered and modeled, but would likely be difficult to address with real data.

The basic data are based on individuals marked at birth in each of the three sites (as non-breeders), later observable as breeders in the same sites over several occasions of recapture. Using the codes for states in Table 1, typical recapture histories may be:

- 0a0AA0, for an animal marked as young at occasion 2 in Site A, recaptured (or resighted) as a breeder in site A at occasions 4 and 5 and not observed at occasions 3 and 6;
- 00b000, for an animal marked as young at occasion 3 in site B and never recaptured or resighted again.

Reproducing adults of unknown age may be marked and recaptured in parallel with the young and will exhibit histories such as AB0CC0. On the contrary, the initial capture for animals marked at birth (i.e. at age 0) can never be in A, B, or C (states 1, 2, 3), since all

animals marked at birth are non-breeders. In addition, recaptures can never be in a, b, or c (states 4, 5, 6) since non-breeders are not observable following year of birth; i.e. all recapture probabilities for these states equal 0. This structure implies that some transitions are impossible (e.g. B to b) and never observed. The corresponding transition probabilities must be considered as fixed to 0. This will imply further constraints on parameters to make parameters identifiable, as a consequence of the non-observability of non-breeders, as already noted by Clobert et al. (1994).

Among several possible choices, the survival-transition matrix from age 0 to age 1 is parameterized here as a function of:

- Probabilities of local immature survival in the 3-site study system (Site A \cup Site B \cup Site C), denoted as Φ_{1A} , Φ_{1B} , and Φ_{1C} , respectively, conditional on the site of birth and marking. Permanent emigration at the immature stage out of Site A \cup Site B \cup Site C is confounded with death before reproduction. These survival probabilities correspond to the entire period between birth and the first possible age of breeding (in our example, $c = 2$ years).
- Probabilities of natal dispersal n_{ij} , represented as a 3×3 stochastic sub-matrix (i.e. with column sums equal to 1) having at most 6 identifiable parameters. Once again, in this version of the model, recruitment dispersal probabilities are independent of the age at recruitment.

The entries in the lower right 3×3 sub-matrix of the survival transition matrix are the products of natal dispersal probabilities and pre-breeding survival probabilities (Table 2). We use this parameterization for computational reasons as neither pre-breeding survival nor natal dispersal probabilities correspond exactly to the transition between ages 0 and 1. Instead the dispersal parameters n_{ij} correspond to the probability that animals from birthplace j first breed in location i , and require no assumptions about the timing or number of prebreeding movements. Similarly, the survival probabilities of young correspond to the entire period between birth and the first age at which animals can reproduce. Further variation (e.g. time dependence), or constraints (e.g. the equality of immature survival irre-

Table 2. Survival-transition matrix from age 0 to age 1 (see Table 1 and text for notation). The upper left sub-matrix applies to breeders of unknown age captured in parallel to non-breeders aged 0.

to/from	A	B	C	a	b	c
A	$\Phi_A b_{AA}$	$\Phi_B b_{AB}$	$\Phi_C b_{AC}$	0	0	0
B	$\Phi_A b_{BA}$	$\Phi_B b_{BB}$	$\Phi_C b_{BC}$	0	0	0
C	$\Phi_A b_{CA}$	$\Phi_B b_{CB}$	$\Phi_C b_{CC}$	0	0	0
a	0	0	0	$\Phi_{1A} n_{AA}$	$\Phi_{1B} n_{AB}$	$\Phi_{1C} n_{AC}$
b	0	0	0	$\Phi_{1A} n_{BA}$	$\Phi_{1B} n_{BB}$	$\Phi_{1C} n_{BC}$
c	0	0	0	$\Phi_{1A} n_{CA}$	$\Phi_{1B} n_{CB}$	$\Phi_{1C} n_{CC}$
Sum	Φ_A	Φ_B	Φ_C	Φ_{1A}	Φ_{1B}	Φ_{1C}

Table 3. Survival–transition matrix after age 6 (see text for notation).

to/from	A	B	C	a	b	c
A	$\Phi_A b_{AA}$	$\Phi_B b_{AB}$	$\Phi_C b_{AC}$	0	0	0
B	$\Phi_A b_{BA}$	$\Phi_B b_{BB}$	$\Phi_C b_{BC}$	0	0	0
C	$\Phi_A b_{CA}$	$\Phi_B b_{CB}$	$\Phi_C b_{CC}$	0	0	0
a	0	0	0	0	0	0
b	0	0	0	0	0	0
c	0	0	0	0	0	0
Sum	Φ_A	Φ_B	Φ_C	0	0	0

spective of the site of birth $\Phi_{1A} = \Phi_{1B} = \Phi_{1C}$) can be considered as needed.

If breeders are considered in parallel, the transition probabilities from A, B, or C to A, B, or C are based on breeding dispersal parameters b_{ij} , which are the probabilities that a breeder in site j this year that is alive next year is then in site i , and a location-specific survival probability Φ_i independent of age (upper left 3×3 transition sub-matrix in Table 2). When animals marked as young have recruited, the same sub-matrix will apply to them. The transition matrix after age 6 is straightforward, since all individuals have recruited and the only transitions are among states A, B, and C (Table 3).

The transition matrix between age 1 and c ($c = 2$ for the roseate tern example) represents a particular case. To force the survival probabilities in the transition matrix between age 0 and 1 to represent survival over the whole immature period (0–2 years), the survival probabilities between age 1 and 2 are constrained to be equal to 1. In the absence of observations at age 1, these probabilities are at any rate not identifiable separately from first-year survival probabilities. The transition matrices from age k to $k + 1$ for $c - 1 < k < m - 1$ (in the roseate tern case, $k = 2, 3, 4$) are more involved. Individuals that have already reproduced may exhibit breeding dispersal, with the same probabilities (parameters b_{ij}) as above. Individuals that are still non-breeders recruit at age k with probabilities depending on their age and on their site, a_{kA} , a_{kB} and a_{kC} . In the following survival–transition matrices from age k to $k + 1$ (Table 4), non-breeders (states a, b, c) are supposed to have the same survival probabilities as animals already recruited in the corresponding states (A, B, C). The survival–

Table 5. Survival–transition matrix from ages 5 to 6 (see text for notation).

to/from	A	B	C	a	b	c
A	$\Phi_A b_{AA}$	$\Phi_B b_{AB}$	$\Phi_C b_{AC}$	Φ_A	0	0
B	$\Phi_A b_{BA}$	$\Phi_B b_{BB}$	$\Phi_C b_{BC}$	0	Φ_B	0
C	$\Phi_A b_{CA}$	$\Phi_B b_{CB}$	$\Phi_C b_{CC}$	0	0	Φ_C
a	0	0	0	0	0	0
b	0	0	0	0	0	0
c	0	0	0	0	0	0
Sum	Φ_A	Φ_B	Φ_C	Φ_A	Φ_B	Φ_C

transition matrix from age 5 to 6 is simpler, because full adult reproductive propensity is assumed at age $m = 6$ (i.e. $a_{5A} = a_{5B} = a_{5C} = 1$), i.e. all surviving pre-breeders are recruited between age 5 and 6 (Table 5).

A key feature of this class of recruitment models is that non-breeders have a probability of recapture equal to 0. Hence all vectors of capture probabilities are of the type:

$$\begin{matrix} p_A \\ p_B \\ p_C \\ 0 \\ 0 \\ 0 \end{matrix}$$

The likelihood can be calculated, based on the parameter matrices, from the general formula for multi-state capture-recapture models provided by Brownie et al. (1993). Time-dependence in the parameters can be added to the intrinsic age-dependence needed to model accession to reproduction. A generalized linear model philosophy can be applied, as in Cormack-Jolly-Seber models (Lebreton et al. 1992), to model specific biological hypotheses with as much parsimony as possible. However, the degree of flexibility attainable heavily depends on software availability. By allowing age-dependence in multistate models, programs MS-SURVIV (Hines unpubl.), M-SURGE (Choquet et al. unpubl.) and MARK (White and Burnham 1999), make it possible to fit various models of the type described above. Computations for our example analysis were done in MARK, because of its wide availability and of its user-friendliness.

Table 4. Survival–transition matrix from age k to age $k + 1$ ($k = 2, 3, 4$) (see text for notation).

to/from	A	B	C	a	b	c
A	$\Phi_A b_{AA}$	$\Phi_B b_{AB}$	$\Phi_C b_{AC}$	$\Phi_A a_{kA}$	0	0
B	$\Phi_A b_{BA}$	$\Phi_B b_{BB}$	$\Phi_C b_{BC}$	0	$\Phi_B a_{kB}$	0
C	$\Phi_A b_{CA}$	$\Phi_B b_{CB}$	$\Phi_C b_{CC}$	0	0	$\Phi_C a_{kC}$
a	0	0	0	$\Phi_A(1 - a_{kA})$	0	0
b	0	0	0	0	$\Phi_B(1 - a_{kB})$	0
c	0	0	0	0	0	$\Phi_C(1 - a_{kC})$
Sum	Φ_A	Φ_B	Φ_C	Φ_A	Φ_B	Φ_C

Dispersal and recruitment in the roseate tern *Sterna dougallii*

We used data obtained over $K = 11$ years (1988–1998) on the population of roseate tern breeding from Long Island Sound, between Connecticut and New York east to Buzzards Bay, Massachusetts along the Atlantic coast of North America. The three sites considered were breeding colonies established respectively on Falkner Island (A), Bird Island (B), and Great Gull Island (C). Descriptions of the colony sites, the distances among them, and the techniques used to mark, recapture, and resight marked adult terns at them are given by Spendelow et al. (1995), and references therein). From 1988 to 1998, the estimated number of breeding adult roseate terns at these sites varied from 240–380, 2140–3560, and 2200–3700, respectively, at A, B, and C (Spendelow et al. 1995; USFWS 1998; Spendelow, Nisbet, and Hays, unpubl.).

Hypotheses and predictions

The general modeling approach described above was used to test several hypotheses about the population dynamics and movement of roseate terns in the Buzzards Bay-Long Island Sound system. Natal dispersal is thought to be more prevalent than breeding dispersal in many bird species (Greenwood and Harvey 1982), including seabirds (Bradley and Wooller 1991). Thus, we predicted that the probability of moving from one colony to another would be greater for pre-breeders than for breeders, i.e. that $n_{ij} > b_{ij}$, for all pairs of colony sites, i and j .

Based on information about the relative sizes and demographic histories of the three study sites, we also made a specific prediction about the relative magnitudes of dispersal/fidelity for the three colonies. Site A has been the least successful of the three sites over the last decade, and the size of this colony has decreased slowly over the time of the study (Spendelow et al. 2002). We thus predicted that the probability of returning to the same breeding colony (not dispersing) would be lower for site A than for the other two sites for both new recruits ($n_{AA} < n_{CC}$, n_{BB}) and experienced breeders ($b_{AA} < b_{CC}$, b_{BB}). Similarly, we predicted that the probability of moving from another site to site A would be smaller than the corresponding probability of moving to the other available colony site both before ($n_{AB} < n_{CB}$, $n_{AC} < n_{BC}$) and after recruitment ($b_{AB} < b_{CB}$, $b_{AC} < b_{BC}$). We had no evidence to suggest predictions of relative differences in fidelity or dispersal probabilities between sites B and C. However, it seems reasonable that determinants of the attractiveness of a colony are similar for adults and young. Some evidence exists for similarity of dispersal probabilities for experienced breeders and new recruits in the kittiwake *Rissa tri-*

dactyla, and this pattern is believed to result from prospecting individuals of both groups gathering information on breeding success (Boulinier and Danchin 1997). Thus, we included in the model set a model to test this prediction formally, using the constraint $\text{logit } b_{ij} = u + \text{logit } n_{ij}$ ($i \neq j$). In this constraint, the parameter u characterizes the relationship between breeding and natal dispersal (see Lebreton et al. 1992 for the general use of linear constraints in capture-recapture models). We expect u to be negative, to reflect the prediction $n_{ij} > b_{ij}$.

The importance of age at first reproduction to fitness and population growth is well known (Cole 1954, Charnov and Schaffer 1973). If all other vital rates are equal, an animal that begins breeding at an earlier age will exhibit greater fitness than an animal beginning reproduction at a later age. This fact does not lead to specific predictions about exact ages at first reproduction in roseate terns, because we do not understand the factors that result in delayed reproduction in this species (e.g. cost of early reproduction in subsequent mortality or reproduction; physiological constraint). However, because of the importance to fitness of early recruitment into the breeding population, probabilities of recruitment should increase monotonically with age, as considered in our models.

We made two straightforward predictions about tern survival. The first prediction was that annual survival of pre-breeders would be lower than that of breeders ($\sqrt{\Phi_{1t}} < \Phi_t$; the square root is needed to convert the 2-year pre-breeder survival rate to an annual time period). Such age-specificity is believed to be common in birds (Ricklefs 1973, Loery et al. 1987), especially when capture-recapture estimates are compared, as the complement of survival in capture-recapture estimation includes both death and permanent emigration out of the study system. As with natal dispersal to other locations in the study system, any permanent emigration is also suspected to be greater for pre-breeders than breeders. We also made specific predictions about the effects on survival of a hurricane in August 1991 (Hatch et al. 1997), which passed over the major premigratory staging areas for this population (Trull et al. 1999). Specifically, we predicted that survival would be lower in 1991 than other years for both hatch-year birds and adults.

Data analysis and modeling

For the purpose of estimating age-specific breeding probabilities, the data analyzed for model development were restricted to those individuals identified at nests by trapping at all three sites and by resighting at site A; we did not include any resighting data from sites B or C because breeding status could not be confirmed. Because relatively little trapping was done late in the

breeding season at site B, the youngest age classes (2- and 3-yr-olds) that tended to breed later in the season may be under-sampled at this site each year.

The models used to analyze these data follow the general presentation above. In particular, for the sake of robustness, we considered time-independent breeding (b_{ij}) and natal (n_{ij}) dispersal probabilities. Similarly, the breeding propensities (a_{ki}) were considered as depending on age k and site i , but not on time. However variation over time and between sites in survival and capture probabilities was kept in this general model, on the basis of one-site capture-recapture analysis results. The deviance for this model was 20074.437, for 105 estimable parameters.

The goodness-of-fit of this model was impossible to check in a straightforward way in the absence of canonical goodness-of-fit contingency table tests similar to those developed by Pollock et al. (1985) for the Cormack-Jolly-Seber model (see however Pradel et al. 2003, for time-dependent multistate models). We used in a preliminary step the adult data classified by site in the following way: we suppressed the first capture for the individuals marked as chicks; keeping thus only the captures as breeders. We then classified the data according to the site of first capture as an adult, keeping nevertheless all further captures as breeders of every individual, whether in the site or origin or not. The three one-site data sets obtained in that way were submitted to the usual goodness-of-fit tests for the Cormack-Jolly-Seber model. The goodness-of-fit test in Release (Burnham et al. 1987) indicated a strong lack-of-fit, in particular for Falkner Island (A), where a strong immediate trap-dependence (Pradel 1993) was apparent (Spendlow et al. 2002). The cumulative results over the three sites led to a lack-of-fit coefficient χ^2/df equal to 4.1116. Although the use of a multistate

model in which capture probabilities may differ between sites was expected to eliminate some causes of lack-of-fit, it seemed impossible to use the Akaike Information Criterion $AIC = deviance + 2 \times np$ for the selection of multistate recruitment models. We tentatively used an AIC corrected for lack-of fit as $QAIC = deviance/\hat{c} + 2 \times np$, with $\hat{c} = 4.1116$. Although this correction cannot be interpreted as a correction for over-dispersion, since structural causes for lack-of-fit were present as apparent from the preliminary analysis, it has the advantage of putting the emphasis on models with fewer parameters. This strategy is conservative with respect to detection of structural features in the data, in accordance with the general philosophy of statistical tests and with a hypothetico-deductive attitude, i.e. the approach limits the risk of falsely rejecting null hypotheses.

The a priori model set included various effects on “young” survival (the probability of surviving the first 2 years, Φ_{1i}), “adult” survival (the annual survival probability following age 2, Φ_i), probability of capture, rate of movement, and rate of accession to reproduction. Model selection is summarized in Table 6. The variation in recapture probabilities was much stronger between sites than over time, and this was reflected in the final model. The various attempts to simplify the structure of accession to reproduction did not improve noticeably the fit. It is worth noting that the preferred model would be the same for any value of \hat{c} greater than 2.58. In the absence of more detailed procedures for checking the fit of the various models considered, the final model with a reasonably small number of parameters seemed to us a good compromise between precision and bias. Moreover the point estimates of dispersal and recruitment parameters were remarkably stable in all models considered.

Table 6. Selection of multisite recruitment models for the roseate tern, based on corrected Quasi-AIC (QAICc), with lack-of-fit coefficient $c = 4.1116$. Columns: p = probability of recapture, b = breeding dispersal, n = natal dispersal, a_{ik} = probabilities of accession to reproduction. Notation for effects: s = site, t = time, a = age, A = age (quantitative), h = before/during/after hurricane, $-$ = constant.

Young survival	Adult survival	p	b	n	a_{ik}	Delta QAICc	Number of param.	Deviance
t × s	t	s	-	-	a × s	0.00	66	20270.593
S	s	s	-	-	a × s	2.88	35	20538.353
-	-	t × s	-	-	a × s	6.31	33	20568.957
S	s	t × s	-	-	a × s	7.14	61	20341.258
S	-	s	-	-	a × s	13.87	60	20377.181
t × s	t × s	t × s	-	-	a × s	15.76	87	20161.668
t × s	t × s	t × s	-	-	a × s	29.79	104	20078.540
t × s	t × s	t × s	-	-	a × s	36.86	108	20074.437
t × s	t × s	t × s	≡	≡	a × s	41.08	109	20083.502
t × s	t × s	t × s	-	-	A × s	41.89	105	20120.013
t × s	t × s	t × s	h	h	a × s	59.40	126	20017.760
t × s	t × s	t × s	h	-	a × s	80.22	137	20012.006
t × s	t × s	t × s	-	-	A	204.28	100	20829.136
s	t	t × s	-	-	a × s	1114.0	67	24842.860

≡ logit transformed b_{ij} and n_{ij} parallel.

Results

The results of the final model are as follows. The estimates of breeding and natal dispersal are shown in Tables 7 and 8, respectively. As expected, natal dispersal was stronger than breeding dispersal for all three sites. The fidelity probability estimates ranked the three sites in the same order for both types of dispersal ($B > C \gg A$). The probability of movement was the highest from A to C in both cases. These results are quite consistent with previous results (Spendelov et al. 1995), and with the fact that site A has been less successful than the other two sites, with colony size decreasing slowly over the time of the study (Spendelov et al. 2002). Site C is closer to site A than is site B and may have attracted the largest proportion of emigrants. Obviously these results cannot take into account potential emigration out of the three study sites. As noted above, the relative parallelism in dispersal intensity of young and adults may imply that the attractiveness of a colony is determined similarly for adults and young. However the model with logit $b_{ij} = u + \text{logit } n_{ij}$ ($i \neq j$) was less favored in terms of QAIC than the general model (Table 6), although, as expected, the estimate of u was negative (-1.433 ± 0.054).

The estimates of age-specific probabilities of accession to reproduction are shown in Table 9. Breeding at age 2 remained anecdotal. It concerned mainly males, and led in general to breeding failure (Spendelov and Nisbet, unpubl.). The rate of accession to reproduction estimated here in a non-cumulative way showed acceleration with age, as predicted. Breeding propensity at age 5 in site A was close to the adult rate since the estimate under the final model was $\hat{a}_5 = 0.9125$ (but see Spendelov et al. 2002) with a wide confidence interval (0.0256, 0.9998) suggesting that the pattern of accession to reproduction might well have been the same over the three sites, with full recruitment at age 5. Our results provide thus some evidence for full recruitment at age 5. Cumulative accession to reproduction, calculated using the formulas given in Pradel and Lebreton (1999 p. 79) from the estimates of the a_{ik} is represented in Fig. 1.

The estimates of survival probabilities in our final model (Table 10) were consistent with prior knowledge (Spendelov et al. 1995, Hatch et al. 1997). The annual adult survival probability was higher than the corresponding probability for the first two years of life, as predicted. The effect of the hurricane in August 1991 was apparent. The average value of adult survival over

Table 7. Estimates of breeding dispersal probabilities (\pm s.e.; roseate tern, final model).

Next breeding site	Breeding site		
	A	B	C
A	0.8852*	0.0009 \pm 0.0007	0.0069 \pm 0.0023
B	0.0232 \pm 0.0136	0.9847*	0.0128 \pm 0.0073
C	0.0916 \pm 0.0239	0.0144 \pm 0.0088	0.9812*

* Fidelity probability obtained as $1 - \text{sum of movement probabilities}$. s.e. not given by Mark, would have to be obtained by the delta-method.

Table 8. Estimates of natal dispersal probabilities (\pm s.e.; roseate tern, final model).

First breeding site	Birth site		
	A	B	C
A	0.5824*	0.0044 \pm 0.0036	0.0197 \pm 0.0088
B	0.0468 \pm 0.0596	0.9132*	0.0824 \pm 0.0376
C	0.3708 \pm 0.1304	0.0824 \pm 0.0423	0.8979*

* Fidelity probability obtained as $1 - \text{sum of movement probabilities}$. s.e. not given by Mark, would have to be obtained by the delta-method.

Table 9. Estimates of age-specific probabilities of accession to reproduction (\pm s.e.; roseate tern, final model).

Breeding site	Age				
	2	3	4	5	6
A	0.0104 \pm 0.0121	0.5146 \pm 0.0852	0.6197 \pm 0.1448	0.9125 \pm 0.2438	1*
B	0.0459 \pm 0.0358	0.6742 \pm 0.1806	1.0000 ⁺	–	1*
C	0.0190 \pm 0.0227	0.4475 \pm 0.1593	0.6682 \pm 0.4107	1.000 ⁺	1*

* Constrained to 1 (adult breeding propensity).

⁺ No standard error estimate available (parameter on a boundary).

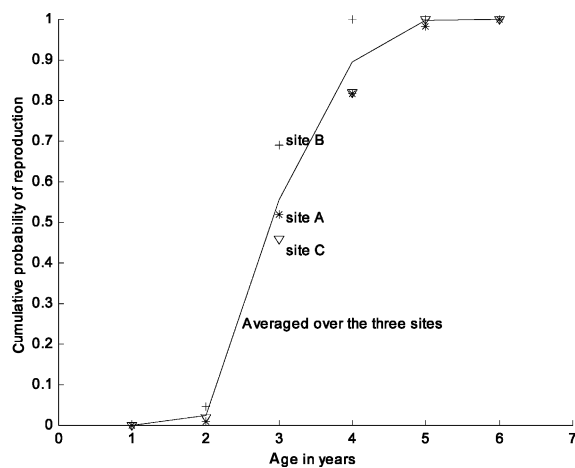


Fig. 1. Cumulative age-specific probability of breeding (final model, roseate tern example).

Table 10. Estimates of adult survival probabilities (roseate tern, final model).

Time period	Estimate
1988–1989	0.6420 ± 0.0758
1989–1990	0.8548 ± 0.0641
1990–1991	0.9333 ± 0.0548
1991–1992 (hurricane year)	0.6658 ± 0.0553
1992–1993	0.9840 ± 0.0511
1993–1994	0.9073 ± 0.0540
1994–1995	0.7648 ± 0.0632
1995–1996	0.8765 ± 0.0636
1996–1997	0.8355 ± 0.0598
1997–1998	0.8525 ± 0.0695

sites and years (without the hurricane year), equal to 0.8501, was comparable to earlier estimates based on four-site capture recapture approaches (most average annual estimates fall in the range 0.81–0.84, Spendelov et al. 1995). Survival over the first two years of life averaged 0.3762, with a marked effect of the hurricane year, more pronounced in site A (Table 11). The estimated recapture-resighting probabilities (Table 12) differed widely among sites. Site A was submitted to intense resighting and recapture pressures, and this leads to an estimated recapture probability equal to

Table 11. Estimates of local immature (over 2 years) survival probabilities (roseate tern, final model).

Time period	Site		
	A	B	C
1988–1990	0.3104 ± 0.1114	0.3255 ± 0.0870	0.3516 ± 0.1472
1989–1991	0.3204 ± 0.1477	0.3400 ± 0.0900	0.5054 ± 0.1653
1990–1992	0.3356 ± 0.1272	0.3781 ± 0.0884	0.4904 ± 0.1444
1991–1993 (hurricane year)	0.0629 ± 0.0571	0.1853 ± 0.0950	0.0649 ± 0.0445
1992–1994	0.5932 ± 0.2267	0.7476 ± 0.2045	0.4964 ± 0.1658
1993–1995	0.5470 ± 0.1725	0.2754 ± 0.1090	0.4980 ± 0.1590
1994–1996	0.3544 ± 0.1541	0.4149 ± 0.1497	0.5451 ± 0.2184
1995–1997	0.4070 ± 0.2494	0.0456 ± 0.0663	0.4338 ± 0.2593

Table 12. Estimates of recapture-resighting probabilities (roseate tern, final model).

Site	A	B	C
Estimate	0.8930 ± 0.0191	0.0597 ± 0.0077	0.0545 ± 0.0079

0.8930, much higher than in sites B and C, for which only physical recaptures were used for the sake of unambiguous determination of breeding (Table 12). An additional model exploring the role of the hurricane with three levels of dispersal (before, during, and after the hurricane years) did not lead to an improvement in fit, at least as judged by the rough model selection procedure used (Table 6). Further models exploring more specific biological questions will be examined in other papers (Spendelov et al. 2002).

Discussion

Roseate tern biology

This study is of special interest in permitting inference about natal dispersal and accession to reproduction, two processes about which few strong inferences exist for any bird species. The estimated probabilities of young birds dispersing to a colony site other than the natal site was 2–6 times higher than the probability of breeders dispersing to breed at another site. This result is consistent with widely-held belief (Greenwood and Harvey 1982), yet this is the first study of which we are aware to estimate natal dispersal in a manner that accounts for different sampling intensities at different breeding locations. In this 3-colony system, it is noteworthy that natal and breeding dispersal probabilities were highest for departing the colony site (A) that exhibited declines over much of the study period. This result suggests that movement, and not simply survival and reproduction, have contributed to the decline of the Falkner Island breeding colony.

Strong inferences about age-specific recruitment into the breeding population are also rare in the literature of avian ecology. The age-specific breeding probabilities were estimated at 1% to 4.5% for 2-year-old birds and

increased to 100% by age 5 or 6. The monotonic increase in conditional breeding probability for birds that have not previously been recruited as breeders is consistent with expectations based on evolutionary theory and likely reflects strong selective pressure to breed as early as physiologically possible, or at least at the first age at which fitness costs are not prohibitively high.

Good survival rate estimates for young seabirds are also rare in the avian literature. Most of the cohort-specific estimates for the first two years of life ranged from about 0.3 to 0.5. Estimates for the 1991 cohort were substantially lower, ranging from 0.06 to 0.19 and likely reflecting the predicted effects (Hatch et al. 1997) of a hurricane that passed over Long Island Sound and the main pre-migratory staging area for this species (Trull et al. 1999) on Cape Cod, Massachusetts, in August 1991. Estimates of adult survival probability were also substantially lower for the period 1991–1992 (about 0.67) than for other years (average of about 0.85), although another as yet unexplainably low estimate was obtained for year 1989–1990. Despite the strong belief in the potential importance of dramatic environmental events such as hurricanes to avian fitness, this study provides some of the first strong inferences about such effects on survival (Spendelov et al. 2002).

Statistical modeling

The models presented here provide a canonical approach to the analysis of recruitment over several sites in a population where individuals are marked at birth. They make it possible to estimate simultaneously age-dependent accession to reproduction, natal dispersal, and breeding dispersal. Under the assumptions described above, the parameters characterizing the three biological phenomena above can be estimated efficiently even when only reproducing individuals are recaptured or resighted. The two main assumptions, which are that an animal that has started reproducing continues to exhibit adult breeding probability in the future, and that non-breeders past the age at which first breeding takes place in the population have the same survival as breeders, can easily be relaxed when non-reproducing individuals are recaptured as well (Nichols et al. 1994). In this case the probability of capture of non-breeders can well be different from that of breeders.

The model structure is simple enough, with a single natal dispersal matrix and a single breeding dispersal matrix, to be fairly robust. The precision and stability of estimates of parameters of dispersal and recruitment in the roseate tern example are quite satisfying, despite a strong imbalance among the different study sites in recapture pressure. In our experience with some simulated data sets, the parsimonious representation of dis-

persal is a key feature for the robustness of the analysis. Accession to reproduction is represented as a directional process, with, as noted above, the assumption that an animal that breeds continues to exhibit adult breeding probability. As noted by Lebreton et al. (1990), it seems reasonable to think of stabilization at some adult breeding propensity. The age-specific breeding probabilities that can be deduced from the probabilities of accession to reproduction (Pradel and Lebreton 1999) are then relative to this adult breeding propensity (Lebreton et al. 1990). Annual breeding probabilities for adults can be estimated under two different sampling situations. As noted above, when non-breeders are detectable, then multistate models based on breeding state can be used to estimate breeding probabilities (Nichols et al. 1994). When non-breeders are truly not observable, then use of the robust design (with secondary capture periods each breeding season) permits estimation of breeding probabilities (Kendall et al. 1997, Schwarz and Stobo 1997). Whenever possible, it is thus recommended to sample non-breeders. However care should be taken with the potential heterogeneity of non-breeders. In particular, it is common in colonial waterbirds to have a large proportion of the birds not yet recruited absent from the breeding grounds. Recaptures among the small proportion present on the study sites will not make it possible to adequately estimate the proportion of breeders. Neglecting the recaptures or resightings of non-breeders, and using the type of models developed here would then be preferable, unless more complex multistate models are developed.

The models proposed pertain to the wide class of product-multinomial models for individual histories. Within this large class, they are a particular case of age-dependent multistate capture-recapture models. As such, they are quite flexible and can be generalized easily in case of need, as shown with the roseate tern example. Biological questions can be addressed by comparing models, and model selection based on information criteria (Burnham and Anderson 1998) can proceed as usual.

The degree of flexibility attainable opens the way to further reflections on relevant modeling of dispersal and recruitment by appropriate model structures. The test of parallelism of natal and breeding dispersal in the roseate tern is an example of this potential. However, as for many complex product-multinomial models, progress is needed on several statistical issues for greater efficiency in analysis (Lebreton and Pradel, 2002). The absence of interpretable and detailed goodness-of-fit tests for age-dependent multistate models is a first major pending problem. The use of an over-dispersion or lack-of-fit coefficient obtained from simulated data to correct model selection and standard error estimates would be a safer approach to model selection, given the present state of the art, than that used here. In relation

with this, progress is expected in the automatic detection of identifiability problems (Viallefont et al. 1998, Reboulet et al. 1999), the number of identifiable parameters being needed for the calculation of information criteria. Lastly, user-friendly software that includes dispersal–recruitment models as standard structures, and faster estimation algorithms will facilitate the use of capture–recapture dispersal models by population biologists. These statistical models can in turn serve to feed multisite Leslie matrix models (Lebreton 1996) for (meta)population projections. We expect that the analysis of recruitment and dispersal will become an integral part of empirical demographic analysis in animal populations.

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