

# Modelling postfledging survival and age-specific breeding probabilities in species with delayed maturity: a case study of Roseate Terns at Falkner Island, Connecticut

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**ABSTRACT** *We modelled postfledging survival and age-specific breeding probabilities in endangered Roseate Terns (*Sterna dougallii*) at Falkner Island, Connecticut, USA using capture-recapture data from 1988-1998 of birds ringed as chicks and as adults. While no individuals bred as 2-year-olds during this period, about three-quarters of the young that survived and returned as 3-year-olds nested, and virtually all surviving birds had begun breeding by the time they reached 5 years of age. We found no evidence of temporal variation age of first breeding of birds from different cohorts. There was significant temporal variation in the annual survival of adults and the survival over the typical 3-year maturation period of prebreeding birds, with extremely low values for both groups from the 1991 breeding season. The estimated overwinter survival rate (0.62) for adults from 1991-1992 was about three-quarters the usual rate of about 0.83, but the low survival of fledglings from 1991 resulted in less than 25% of the otherwise expected number of young from that cohort returning as breeding birds; this suggests that fledglings suffered a greater proportional decrease in survival than did adults. The survival estimates of young from 1989 and 1990 show that these cohorts were not negatively influenced by the events that decimated the young from 1991, and the young from 1992 and 1993 had above-average survival estimates. The apparent decrease since 1996 in development of fidelity of new recruits to this site is suspected to be due mainly to nocturnal disturbance and predation of chicks causing low productivity.*

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## 1 Introduction

As a step in further investigating the population dynamics (Spendelow *et al.*, 1995) of the endangered Northwest Atlantic breeding population of Roseate Terns (*Sterna dougalli*), new models have been developed to estimate directly postfledging survival and age-specific breeding. These models also allow estimation of  $\tau$  (Pradel *et al.*, 1997), a parameter related to the proportion of first-time breeders at a site that are transient and emigrate to other colony sites after this breeding attempt, and the proportion that develop colony-site fidelity. The general modelling approach described here should prove useful in studies of other seabirds and species with similar life-history schedules; i.e. species that do not necessarily return to the breeding area the year after birth, such as sea turtles (e.g. Crouse *et al.*, 1987; Crowder *et al.*, 1994), anadromous fish (e.g. Schaffer & Elson, 1975), some amphibians (e.g. Bell, 1977; Gill, 1978), and some marine mammals such as seals (e.g. Chapman, 1964; Schwarz & Stobo, 1997).

The estimation of postfledging survival and recruitment of first-time breeders of migratory species with delayed maturation is a difficult problem that has received much attention in recent years (Rothery, 1983; Lebreton *et al.*, 1990, 1992; Nichols *et al.*, 1990; Cooke & Francis, 1993; Clobert *et al.*, 1994). A factor contributing to the difficulty of making such estimates is that individuals of some species may not mature simultaneously, and may delay first breeding over a span of many years (Wooller *et al.*, 1990; Bradley & Wooller, 1991). For example, young of many colonial bird species depart the natal colony site following fledging and may not return (or may travel to other colony sites) for several subsequent breeding seasons until they are ready to breed (Duncan & Monaghan, 1977; Greenwood & Harvey, 1982).

For those interested in analysing life-history strategies (Roff, 1992), the age at which an individual begins breeding is of great importance since fitness and lifetime reproductive success are quite sensitive to changes in this trait. As noted by Stearns (1992), 'changes in age at maturity and in juvenile survival have large impacts on fitness across a wide range of types of life histories'. Age at first breeding is also an important variable influencing population dynamics and is thus relevant to the management of animal populations (Jouventin & Weimerskirch, 1991). The age at which first breeding occurs may be influenced by many factors including physiological maturity, getting a territory and mate, acquiring foraging skills sufficient to feed offspring, etc. (Chabryk & Coulson, 1976; Wooller & Coulson, 1977; Danchin *et al.*, 1991). In addition, some studies of seabirds suggest that age of first breeding may be lower in newly-formed colonies than in established ones (Williams & Joanen, 1974), or may decrease following a major decrease in population breeding size or density (Coulson *et al.*, 1982). Whereas first-breeding may occur over a wide range of years in longer-lived species such as albatrosses and shearwaters (Bradley & Wooller, 1991), the relatively high mortality rate of adult Roseate Terns (Spendelow & Nichols, 1989; Spendelow *et al.*, 1995) and a knowledge of trade-offs in life-history theory (Stearns, 1992) led us to suspect that there would be a narrow range of years of first breeding for this species relative to other seabirds with higher adult survival rates.

The nesting population of Roseate Terns in the New York-Connecticut-Massachusetts area has grown fairly steadily from 1988 to 2000 except for a decrease of about 17% between 1991-1992 (Nisbet & Spendelow, 1999). The most likely cause of the 1991-1992 decrease was Hurricane Bob (Hatch *et al.*,

1997), which passed over the terns' main premigratory staging area on Cape Cod, MA (Trull *et al.*, 1999) on 19 August 1991. While nesting populations at most other major colony sites increased (USFWS, 1998; Nisbet & Spendelow, 1999), the Roseate Tern nesting population at the Falkner Island Unit of the US Fish and Wildlife Service's Stewart B. McKinney National Wildlife Refuge, Guilford, CT, after only partially recovering from the hurricane-induced decline, declined again in the late 1990s with the onset in 1996 of nocturnal disturbance and predation of tern chicks by Black-crowned Night-Herons (*Nycticorax nycticorax*) (Zingo, 1998; Grinnell & Spendelow, 2000).

Most 1- and 2-year-old Roseate Terns do not return north to the breeding colonies (Nisbet, 1984), so we did not expect that Hurricane Bob would have had much impact on the survival and recruitment to the breeding population of young from the 1989 and 1990 cohorts. Although the unequal sex ratio in the adult breeding population (Nisbet & Hatch, 1999) may limit the ability of some younger females to form a seasonally-permanent pairbond with a male (thereby delaying first-breeding for those females), the overall growth of the regional population and decrease in the local nesting population during the study suggest that density-dependent factors probably were not playing a major role in limiting the age of first breeding for Roseate Terns at this site.

Using the Roseate Tern capture-recapture data from Falkner Island, we wanted to use the new models to address several *a priori* hypotheses about temporal variation in three types of demographic parameters: (a) survival probabilities; (b) age-specific breeding probabilities; and (c) transiency versus the development of fidelity. In particular, we wanted to compare survival of fledglings from the 1989-1993 cohorts and adult birds with regard to the impact of Hurricane Bob. We also wanted to determine if first-time breeders at Falkner Island since 1996 would be less likely to develop colony-site fidelity and more likely to emigrate than first-time breeders in the preceding years.

We list our predictions concerning the parameters of most interest below with brief explanations of why these predictions seemed biologically plausible. The biological plausibility of our choices of how to model or constrain other parameters is discussed in the following sections.

## 2 Predictions

- (1) We predicted low survival of adults between the 1991-1992 breeding seasons as a result of the impact of Hurricane Bob (Hatch *et al.*, 1997).
- (2) Lacking another major storm and other factors being equal, we expected there might be above-average overwinter survival of adults following the 1992 breeding season because presumably only 'higher quality' individuals survived the hurricane, and also because there might be less competition than usual for resources by the new recruits to the breeding population in 1992.
- (3) We predicted a much greater negative impact of Hurricane Bob on the survival of fledglings from 1991 compared to the survival of breeding adults that year because recent fledglings have not perfected their foraging skills enough to become self-sufficient and are still dependent on one or both parents for food (Watson & Hatch, 1999).
- (4) We predicted little, if any, impact on the survival over the usual minimum 3-year maturation period of young from the 1989 and 1990 cohorts because

most of them probably were not present in the Cape Cod area (Nisbet, 1984) when Hurricane Bob passed over it.

- (5) We thought there might be above-average survival of young from the 1992 breeding season in part because most of these young would be produced by the 'high quality' survivors noted in Prediction 2 above.
- (6) With regard to age-specific breeding probabilities, although we could not predict actual values for the proportion of individuals that first breed at a particular age, we suspected that many, if not most, individuals would begin to breed as soon as physiologically capable of doing so. Also, we expected the proportion of young birds recruiting to the breeding population to increase with age until virtually all healthy surviving members of a cohort were breeding.
- (7) We did not expect to find much temporal variation in age-specific breeding probabilities among the fledgling cohorts (even for the 1989 and 1990 cohorts expected to begin breeding in 1992 and 1993, the two years following the regional population decline) because we suspected that first-time breeding Roseate Terns are limited more by physiological constraints in attaining maturity than by density-dependent factors.
- (8) With regard to the development of fidelity to this site by first-time breeders, we had no *a priori* predictions regarding the impacts of Hurricane Bob. However, we predicted that first-time breeding adults from the 1996 and 1997 breeding seasons would be less likely to develop fidelity to this site (and more likely to show transiency) than birds from the preceding years because beginning in 1996 there has been considerable disturbance and predation of young tern chicks by Black-crowned Night-Herons resulting in almost complete reproductive failure of late-nesting first-time breeders (Nisbet *et al.*, 1998; Zingo, 1998; Grinnell & Spendelow, 2000).

### 3 Methods

#### 3.1 Study site

Data were collected as part of a long-term study (since 1978) of Roseate Terns conducted on the breeding colony at Falkner Island, Connecticut (now part of the US Fish and Wildlife Service's Stewart B. McKinney National Wildlife Refuge), in Long Island Sound. Detailed descriptions of the study site and fieldwork methods (including methods for estimating the number of nesting pairs and productivity) used in prior years have been given in Spendelow (1982, 1991), Spendelow & Nichols (1989), Spendelow *et al.* (1994, 1995), and Nisbet *et al.* (1995, 1998). Data from chicks and adults ringed and/or encountered from 1988-1998 were used in this analysis (Table 1).

#### 3.2 Ringing and colour-ringing

From 1988-1993, adult Roseate Terns were given unique 4-ring combinations (two rings on each tarsometatarsus) of a metal incoloy U.S. Bird Banding Laboratory (BBL) ring and three Darvic plastic colour-rings for long-term, long-distance identification. From 1988-1990 chicks were given a BBL ring on one leg and a single orange plastic colour-ring on the other leg, but because of loss of colour-rings (Spendelow *et al.*, 1994), we did not use them on chicks in 1991. Since 1992

TABLE 1.  $m_{ij}^{(v)}$ —array for Roseate Terns captured and released as both young (Y,  $v = 0$ ) and adult breeders (A,  $v = 3+$ ) and then recaptured in subsequent breeding seasons, 1988-1998, at Falkner Island, Connecticut

Age $v$	Release year, $i$	Mark status	Number released $R_i$	Next encountered in year $j =$										
				1989	90	91	92	93	94	95	96	97	98	
Y	1988	U	206	0	0	17	9	3	0	0	0	0	0	0
	1989	U	136		0	0	9	6	3	0	0	0	0	0
	1990	U	142			0	0	9	7	3	2	0	0	0
	1991	U	158				0	0	3	0	2	0	0	0
	1992	U	103					0	0	17	4	4	1	
	1993	U	189						0	0	26	14	7	
	1994	U	186							0	0	15	8	
	1995	U	122								0	0	10	
	1996	U	82									0	0	0
1997	U	97											0	
A	1988	U	160	57	20	3	0	2	0	0	0	0	0	0
	1989	U	136		78	9	1	0	1	1	0	0	0	0
	1989	M	57		37	4	1	0	0	0	0	0	0	0
	1990	U	108			73	7	0	2	0	0	0	0	0
	1990	M	135			100	3	0	2	0	1	0	1	
	1991	U	72				37	4	3	1	0	0	0	0
	1991	M	206				115	7	0	1	1	0	1	
	1992	U	31					16	1	0	0	0	0	0
	1992	M	182					158	6	2	0	0	0	0
	1993	U	72						28	1	0	0	0	0
	1993	M	205						177	5	1	0	0	0
	1994	U	29							11	4	1	0	
	1994	M	233							182	3	1	0	
	1995	U	21								7	2	2	
	1995	M	224								175	15	0	
	1996	U	39									9	1	
	1996	M	226									173	7	
1997	U	23											5	
1997	M	234											176	

\*U denotes previously unmarked. M denotes previously marked.

we have ringed all chicks with a BBL ring on one leg and a special field-readable (FR) incoloy ring with a 4-character complex (two upper and two lower characters stamped twice on the circumference for quick identification by observation at distances up to about 25 m) on the other leg. The growth and fate of virtually all chicks from hatching to death or fledging was recorded (Nisbet *et al.*, 1995, 1998). Since 1994, each adult has received a unique 6-ring combination consisting of a lower metal ring (one leg BBL, the other FR) and two plastic celluloid colour-rings (one on the tarsometatarsus, one on the tibiotarsus) on each leg.

### 3.3 Identification of marked birds

Individuals were (re)identified either by being trapped at a nest or as a result of having FR rings and/or colour-ring combinations read by an observer in one of seven hides that overlook the six Roseate Tern subcolonies at this site. While several immature (mostly 2-year-old) non-breeders were seen at this colony site

each year, only known breeders were used in this analysis, so the estimation problem is the same as if non-breeders were completely absent.

Even though not all adults identified each year actually were captured (trapped), hereafter we use the terms ‘encountered’ and ‘released’ for birds identified at a nest site, but continue to use the term ‘capture probability’ when referring to our general modelling. If a chick is designated as age = 0, then few birds return to the colony site as breeders until age 3 years, and some are not seen again until ages 6 and 7. The data are summarized in  $m_{ij}$ -array format in Table 1, where  $m_{ij}^{(v)}$  denotes the number of birds of age  $v$  released at period  $i$  that are next encountered in period  $j$ . Birds ringed as chicks (designated as young = Y, age = 0) are all unmarked when captured (i.e. not marked in previous years). Note that the first non-zero entries in the array for young are for  $m_{i,i+3}^{(0)}$ , reflecting the fact that very few birds breed before age 3 (Spendelow, 1991). Releases of adult birds are divided into two categories, previously unmarked (not captured or identified as breeding previously on Falkner Island during this study period) and marked. This categorization is useful for models that include certain types of encounter-history dependence.

### 3.4 General modelling approach

Prebreeders of age  $> 0$  can be viewed as temporary emigrants with no probability of being captured or observed prior to their first breeding attempt. One modelling approach to dealing with temporary emigration of this sort involves the use of the robust design (Pollock, 1982; Kendall *et al.*, 1997). The other approach is to use standard open-model capture history data, but to develop a model structure that accommodates the absence of prebreeders. Here we focus on the latter approach. Rothery (1983) and Nichols *et al.* (1990) considered estimation in the situation where all birds begin breeding at the same age. Clobert *et al.* (1990, 1994) considered the more general situation where animals may begin breeding at different ages. This approach will be described here, with the understanding that the models of Rothery (1983) and Nichols *et al.* (1990) represent a special case of the Clobert *et al.* (1994) approach.

Our approach can be viewed as a hybrid similar in some respects to the age-specific models of Pollock (1981) and the cohort models of Buckland (1980, 1982) and Loery *et al.* (1987). Birds are marked at age 0 on the breeding grounds, and their subsequent age is known because of this knowledge of the year of hatching. However, the adult or breeder stage is treated as in the age-specific models of Pollock (1981), in the sense that age is considered to be no longer relevant once a bird begins breeding. Thus, releases each year can consist of both young birds (age 0) and adult breeders of unknown age (sometimes the minimum age of adults is known). The time separating successive sample periods must equal the time required to make the transition from one age class to the next. This requirement corresponds well to the annual sampling of terns during the breeding season.

Capture-recapture data for this modelling can be summarized either as encounter histories or in  $m_{ij}^{(v)}$ -array format. The number of birds exhibiting each encounter history carries a superscript denoting the age at initial encounter and release. Young birds are denoted as age  $v = 0$ , and birds first encountered as breeding adults will be indicated as  $v = k +$ , where age  $k$  is the first age at which birds can become breeders (we assume that  $k$  is known). In this Roseate Tern example, the first age of breeding is age 3. Then  $x_{100101}^{(0)}$  denotes the number of birds released as young (age 0) during the first year of the study that are subsequently encountered

in years 4 and 6 (at ages 3 and 5, respectively). Note that in this case all birds released as young have two 0s following the initial release. This corresponds to the fact that the Roseate Terns essentially do not breed until age 3 at the earliest (Spendlow, 1991). The birds displaying the above encounter history attempted to breed and were observed in year 4, were not observed in year 5, but were encountered again in year 6. The statistic  $x_{010110}^{(3+)}$  denotes the number of birds first encountered as adult breeders (hence at least 3 years old) in year 2, not observed in year 3, and encountered again in years 4 and 5, but not 6.

As shown in Table 1, the data can also be summarized in  $m_{ij}^{(v)}$ -array form. Note that all  $m_{ij}^{(0)} = 0$  for ages  $j - i$ , such that  $j - i < k$  (i.e. for all ages less than the age of first possible breeding). Birds released at age 0 can appear only in a single  $m_{ij}^{(0)}$  statistic. The young are re-encountered only as breeders, and breeders are released following encounter as age  $k +$ . Birds may appear in a number of releases ( $R_i^{(k+)}$ ) and re-encounters ( $m_{ij}^{(k+)}$ ) as breeding adults.

### 3.5 Model structure

We have modified the approach of Clobert *et al.* (1994) to permit direct estimation and modelling of breeding probability parameters. Clobert *et al.* (1994) recognized that under a standard capture-recapture modelling approach parameterized by survival and capture probabilities, the information about non-breeding and temporary emigration is incorporated into the capture probability estimates. They estimated age-specific breeding probabilities as functions of these capture probability estimates. We have applied a direct estimation approach here because (1) we believe it is more easily understood, and (2) it provides interesting possibilities for modelling age-specific breeding probabilities.

We define the following threshold ages:

$k$  = first possible age at which a young bird can breed, and thus first possible age at which a bird marked as young ( $R_i^{(0)}$ ) can be exposed to encounter efforts and possibly re-encountered;

$m$  = age by which all birds are assumed to be breeding; i.e. first age at which breeding probability is known to be 1 (or at asymptotic adult rate, see below).

We also define the following model parameters:

$p_i^{(k+)}$  = probability that a marked breeder (denoted as age  $k +$ ) alive and in the study population at sampling period  $i$  is captured or observed during period  $i$ ;

$\varphi_i^{(k+)}$  = probability that a marked bird of age  $\geq k$  (regardless of breeding status) that is alive at sampling period  $i$ , survives until period  $i + 1$  and remains in the population;

$\varphi_i^{(0)}$  = probability that a young bird (age 0) released at sampling period  $i$  survives until sampling period  $i + k$  (hence, until age  $k$ );

$\alpha_i^{(v)}$  = probability of breeding for a bird of age  $v$  at sampling period  $i$  that has not previously bred;

$\tau$  = probability that an unmarked bird is a transient and only breeds once at this site (see Pradel *et al.*, 1997).

Capture probability is defined as conditional on being a breeder (hence, exposed to sampling efforts), so a corresponding parameter is needed only for breeders. Prebreeders are assumed to have capture (encounter) probabilities equal to 0.0. The adult or breeder survival parameter,  $\varphi_i^{(k+)}$  is equivalent to the  $\varphi_i^{(l+1)}$  in Pollock's

(1981) model in that it applies to all birds above a threshold age. The young survival parameter,  $\varphi_i^{(0)}$  differs from survival parameters in standard capture-recapture models (e.g. Pollock, 1981; Lebreton *et al.*, 1992), because it corresponds to the time interval separating multiple sampling periods. No inference can be drawn about time-specific survival probability of prebreeders before age  $k$ , because the birds cannot be sampled during this interval. Inferences about average annual survival probability of young prebreeders can be obtained by focusing on  $(\varphi_i^{(0)})^{(1/k)}$ , which can be thought of as an ‘annualized’ (constant) rate over the prebreeding period. Finally, we note that  $\alpha_i^{(v)}$  is only needed (and estimated) for ages  $v = k, k + 1, \dots, m - 1$ . Breeding probability before age  $k$  is assumed to be 0.0, and breeding probability after age  $m - 1$  is assumed to be 1.0 (or at least is assumed to be at some asymptotic adult level). In addition, it is assumed that following the initial breeding attempt, a bird breeds with probability 1.0, or again at least with adult probability.

Consider a situation where the first possible age of breeding is  $k = 3$  and the age at which all birds breed is  $m = 5$ . Consider encounter history 100011 for both young (age 0) and adult breeder (age 3+) releases. The probability associated with this encounter history for young birds can be modelled as:

$$\begin{aligned} & \Pr\{100011 \mid \text{released at period 1 as marked young}\} \\ &= \varphi_1^{(0)} [\alpha_4^{(3)} (1 - p_4^{(3+)}) \varphi_4^{(3+)} p_5^{(3+)} \varphi_5^{(3+)} p_6^{(3+)} + (1 - \alpha_4^{(3)}) \varphi_4^{(3+)} \alpha_5^{(4)} p_5^{(3+)} \varphi_5^{(3+)} p_6^{(3+)}] \end{aligned} \tag{1}$$

The first survival term,  $\varphi_1^{(0)}$  corresponds to the survival of the birds from release in year 1 until sampling in year 4. The large term in brackets consists of the sum of two different products of probabilities, each product corresponding to a different path or sequence of events. In the first component of the sum, the bird breeds in the first available year (year 4) at age 3, but is not encountered during that breeding season. The bird then survives and is encountered during each of the next two breeding seasons. The breeding probability parameter is only needed in year 4, because once the bird breeds for the first time, breeding probability is 1.0 for subsequent years. In the second component of the sum, the bird does not begin breeding in year 4; hence no encounter parameter is needed for this year (because prebreeders are not exposed to sampling efforts). The bird survives and then does breed in year 5, and is encountered at that time. The bird then survives until year 6 and is observed again.

If we dissect the sequence of 1s and 0s that comprise the encounter history, we see that the ‘0’s in periods 2 and 3 are required by the restriction that  $k = 3$ . The ‘0’ in period 4 causes uncertainty, as there are two possibilities: the bird bred in period 4 but was not observed, or the bird did not breed. The sum in the above probability statement reflects this uncertainty, with each side of the sum representing a path associated with one of these possibilities. Given the ‘1’ in period 5, there was no uncertainty associated with the modelling for the final ‘1’.

The probability associated with this same encounter history for adults is modelled as:

$$\begin{aligned} & \Pr\{100011 \mid \text{released at period 1 as marked adult}\} \\ &= \varphi_1^{(3+)} (1 - p_2^{(3+)}) \varphi_2^{(3+)} (1 - p_3^{(3+)}) \varphi_3^{(3+)} (1 - p_4^{(3+)}) \varphi_4^{(3+)} p_5^{(3+)} \varphi_5^{(3+)} p_6^{(3+)} \end{aligned} \tag{2}$$

This modelling is more straightforward, as there is only one possible path and hence no uncertainty requiring a sum of two probabilities. All survival probabilities from period 1 through period 5 are required. Capture probabilities are used for



the periods when the bird was encountered, and the complements of capture probabilities are used for time periods of no observation. This modelling for adults, therefore, is identical to that for the standard Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965).

The probabilities associated with the different encounter histories follow multinomial distributions conditional on the releases of previously unmarked birds of both ages (young [0] and breeding adults [3+]). These product multinomials are of the same basic form as the multiple-age models of Pollock (1981).

The probability distribution for this model can also be based on the  $m_{ij}^{(v)}$ -array summary statistics of Table 1. Writing out the expected values or cell probabilities for the entire table would be tedious, so we present only two examples below. As with the modelling of encounter history data, the probabilities for birds released as young are more complicated than those for birds released as adults. Assume the same age thresholds as above ( $k = 3, m = 5$ ) and consider the birds released in period 1 as young and next seen in period 6 as breeders:

$$\Pr\{m_{16}^{(0)} | R_1^{(0)}\} = \varphi_1^{(0)} [\alpha_4^{(3)}(1 - p_4^{(3+)})\varphi_4^{(3+)}(1 - p_5^{(3+)})\varphi_5^{(3+)}p_6^{(3+)} + (1 - \alpha_4^{(3)})\varphi_4^{(3+)}\alpha_5^{(4)}(1 - p_5^{(3+)})\varphi_5^{(3+)}p_6^{(3+)} + (1 - \alpha_4^{(3)})\varphi_4^{(3+)}(1 - \alpha_5^{(4)})\varphi_5^{(3+)}p_6^{(3+)}] \tag{3}$$

The above probability includes the sum of three terms inside the brackets. The first term corresponds to a bird that began breeding in the first possible year (4) and was simply not encountered until year 6. The second term corresponds to the possibility that the bird began breeding in year 5, and the third term reflects the possibility of not breeding for the first time until year 6. No parameter for breeding probability is needed for period 6 even in this last component of the sum, because all birds are assumed to breed at age  $m = 5$ .

The corresponding probability for birds released as adults in period 1 and not encountered again until period 6 is given by:

$$\Pr\{m_{16}^{(3+)} | R_1^{(3+)}\} = \varphi_1^{(3+)}(1 - p_2^{(3+)})\varphi_2^{(3+)}(1 - p_3^{(3+)})\varphi_3^{(3+)}(1 - p_4^{(3+)})\varphi_4^{(3+)}(1 - p_5^{(3+)})\varphi_5^{(3+)}p_6^{(3+)} \tag{4}$$

The above is again equivalent to the probability under the standard CJS model. The bird survives and is not observed for three consecutive sampling periods, and then survives and is finally encountered at period 6.

### 3.6 Model assumptions

The age-specific model for breeding adults described above uses standard open-model capture-recapture data and permits estimation of a kind of temporary emigration associated with prebreeding birds. The ability to estimate these temporary emigration probabilities (actually, their complements, the age-specific breeding probabilities) comes at the cost of some potentially restrictive assumptions:

- (1) The age of first possible breeding,  $k$ , is known;
- (2) All birds become breeders by age  $m$ , at the oldest;
- (3) Every young bird released at age 0 in sampling period  $i$  has the same probability of survival until sampling period  $i + k$ ,  $\varphi_i^{(0)}$ ;
- (4) Every marked bird aged  $\geq k$  in sampling period  $i$ , regardless of breeding status, has the same probability of survival until sampling period  $i + 1$ ,  $\varphi_i^{(k+)}$ ;

- (5) Every marked breeding bird present in the population at sampling period  $i$  has the same probability of being recaptured or resighted,  $p_i^{(k+)}$ ;
- (6) Every marked prebreeding bird of age  $> 0$  in any sampling period is not exposed to sampling efforts and has probability 0.0 of being encountered in that period;
- (7) Every marked prebreeding bird of age  $v$ , where  $m > v \geq k$ , in sampling period  $i$  has the same probability of initiating breeding and becoming a breeder in  $i$ ,  $\alpha_i^{(v)}$ ;
- (8) Every marked bird that attempts to breed for the first time in period  $i$ , breeds with probability 1.0 (or with asymptotic adult breeding probability) at all sampling periods after  $i$ ;
- (9) Marks are not lost or overlooked and are recorded correctly;
- (10) Sampling periods are instantaneous (in reality they are very short periods) and encountered birds are released immediately;
- (11) The fate of each bird with respect to capture and survival probability is independent of the fate of any other bird.

If age of first breeding is not known *a priori* (Assumption 1), the investigator may simply set  $k$  equal to the first age at which birds are observed to return and breed. Assumption 2 will typically be made in practice for reasons of parsimony, but is not actually required for estimation. It is most easily met when all birds of age  $m$  and greater breed with probability 1.0. As noted above, however, use of this model is still probably reasonable when all birds do not have to be assumed to breed with probability 1.0, but instead breed with some asymptotic adult probability. In this case, the age-specific breeding probability estimates are no longer absolute probabilities but should instead reflect age-specific breeding proportions expressed relative to those for adults. Although estimation under a particular model is conditional on *a priori* knowledge of  $m$ , it is possible to fit models incorporating different values of  $m$ , and then to use likelihood ratio (LR) tests or, especially, AIC (Burnham & Anderson, 1998) to select the most reasonable model, and therefore the most reasonable value of  $m$ .

Assumptions 3 and 4 deal with homogeneity of survival probability within an age class. Of particular potential importance is the assumption that survival probability of birds of age  $\geq k$  is the same regardless of whether or not the bird has become a breeder. It does not appear that relaxation of this assumption is possible with single-state, open-model data.

Assumption 5 of homogeneous capture probabilities is required in most open-population capture-recapture models. Assumption 6 of capture probability of 0.0 for prebreeders is assumed for this model. However, if prebreeders are available for sampling on the breeding grounds, then multistate modelling can be used, even if prebreeders (or even non-breeding adults) have different capture probabilities than breeding adults (see Nichols *et al.*, 1994; Cam *et al.*, 1998).

Assumption 7 deals with homogeneity of age-specific breeding probabilities for birds that have not previously bred. Discussions of heterogeneity of rate parameters for the CJS model are relevant to this parameter as well (e.g. see Williams *et al.*, in press). Assumption 8 represents another strong hypothesis about the underlying process of accession to reproduction. The assumption basically states that following recruitment into the breeding population, all birds have the same probability of breeding each year. If this probability is 1.0, then the  $\hat{\alpha}_i^{(v)}$  estimate breeding probabilities for young birds, age  $v$ . If the breeding probability for adults is  $< 1.0$ , then  $\hat{\alpha}_i^{(v)}$

estimates the ratio of breeding probability for a young bird of age  $v$  to that of an adult breeder. We describe designs in Section 5.5 that permit relaxation of this assumption.

### 3.7 Estimation

Clobert *et al.* (1994) used maximum likelihood estimation to estimate survival and capture probability parameters for this underlying model. However, the parameterization of Clobert *et al.* (1994) did not include  $\alpha_i^{(v)}$  parameters. Instead, estimates of breeding probabilities were obtained as functions of capture probabilities of young birds (the complements of their  $\hat{p}_i^{(v)}$  include the probability of not breeding and therefore of not being exposed to sampling efforts) and adult breeders (the complements of the  $\hat{p}_i^{(v)}$  of Clobert *et al.* (1994) include both failure to observe and adult non-breeding for  $k \leq v < m$ ). We have implemented this model more directly using program SURVIV (White, 1983), as this approach permits direct estimation and flexible modelling of the age-specific breeding probabilities. We have recently implemented it as a multistate model in program MARK (White & Burnham, 1999), and this should facilitate use of the model.

As with the CJS and other multiple-age models, capture probabilities cannot be estimated for age class 0. In addition, capture probabilities for the initial sampling period cannot be estimated even for adults, and the final capture and survival probabilities can only be estimated as products. Additional information on estimable parameters is provided by Clobert *et al.* (1994) and Williams *et al.* (in press).

### 3.8 Alternative modelling

Models such as those described above can be designated as models  $(\varphi_i^{(0)}, \varphi_i^{(3+)}, p_i^{(3+)}, \alpha^{(3,4)})$  and  $(\varphi_i^{(0)}, \varphi_i^{(3+)}, p_i^{(3+)}, \alpha^{(3,4,5)})$  where the superscripts for the  $\alpha$  parameter specify the age classes for which breeding probability is to be estimated. These are general models with time-specific survival probabilities for both young and adults and time-specific capture probabilities. Breeding probabilities frequently will be difficult to estimate, so we thought it useful and reasonable to assume these to be constant over time. Time constraints can also be placed on capture or survival probability parameters.

The above model structure is fairly general in some respects, and we note that constraints on this model can produce the models considered by Rothery (1983) and Nichols *et al.* (1990). In particular, they considered the case in which  $k = m$ . Birds released as young (age  $v = 0$ ) in year  $i$  do not return to the breeding grounds until year  $i + k$ , but breeding probability at age  $k$  is 1.0 (or at least the same as that of adults). So  $\alpha_i^{(k-1)} = 0$  and  $\alpha_i^{(k)} = 1$  both by assumption, and the breeding probability parameters are simply removed from the general age-specific breeding model to produce the simple model in which all individuals begin breeding at the same age.

Both previous experience modelling portions of these data and knowledge of the breeding ecology of Roseate Terns led us to consider additional parameters dealing with movement to and from Falkner Island. A transient parameterization,  $(\tau)$ , of the above models (designated as model  $(\varphi_i^{(0)}, \varphi_i^{(3+)}, \tau_i^{(3+)}, p_i^{(3+)}, \alpha^{(3,4)})$ ) was implemented by rewriting survival for unmarked adults allowing for some proportion of transients (see Pradel *et al.*, 1997). We could also have applied this transient probability to birds marked as young and seen for the first time as adults. However, we suspected that such birds would have a higher probability (than unmarked birds) of being 'residents', so did not implement this other parameterization. We

also considered models (e.g.  $(\varphi_i^{(0)}, \varphi_i^{(3+)}, p_i^{(3+)}, p^{(3+)'}, \alpha^{(3,4)})$ ) in which birds encountered in the previous sampling period had different capture probabilities than birds not encountered in the previous period (see Pradel, 1993; Williams *et al.*, in press). Modified models with age-specific breeding probabilities, a transient response in adult survival probability, and a first-order Markovian response in capture probabilities also were developed (e.g.  $(\varphi_i^{(0)}, \varphi_i^{(3+)}, \tau_i^{(3+)}, p_i^{(3+)}, p^{(3+)'}, \alpha^{(3,4)})$ ).

We had *a priori* reason to suspect the need for parameters related to prior breeding experience. Specifically, the two forms of ‘trap-dependence’ included in the model set (the transient and encounter-history response parameterizations) could deal with permanent and temporary emigration from Falkner Island to other breeding colonies in the New York-Connecticut-Massachusetts region. Emigration from Falkner Island is known to occur (Spendelov *et al.*, 1995). Some is permanent, whereas some can be viewed as Markovian temporary emigration (see Kendall *et al.*, 1997) in that birds emigrate, stay at the other colony site for some time, and then return to Falkner Island. Thus, the need for ‘trap-dependent’ models is attributed to the movement of birds among the breeding colonies of the study system. We did not include in the model set additive models in which the two types of capture probabilities (for birds that were and were not detected the previous period) were modelled as time-varying but parallel. Our reasoning was that we believe that different processes (e.g. movement and conditions on other breeding areas for birds not detected the previous period and conditions on Falkner for birds detected the previous period) are primarily responsible for the temporal variation in the different capture probabilities. The best way to deal with movement is via multistate modelling with multiple sampling sites (Spendelov *et al.*, 1995), and we are making progress on extending such models to deal with age-specific breeding probabilities (Lebreton *et al.*, in review).

In addition to these model generalizations, we considered various constrained models. We investigated models with young survival  $(\varphi^{(0)}, \varphi_i^{(3+)}, \tau_i^{(3+)}, p_i^{(3+)}, p^{(3+)'}, \alpha^{(3,4)})$  and adult survival  $(\varphi_i^{(0)}, \varphi^{(3+)}, \tau_i^{(3+)}, p_i^{(3+)}, p^{(3+)'}, \alpha^{(3,4)})$  constant over time. Breeding probabilities also are hypothesized to increase monotonically with age under many reasonable scenarios, and it will be useful to model these probabilities as linear-logistic functions of age; e.g. as:

$$\alpha_i^{(v)} = \frac{e^{(\gamma_i + \beta v)}}{1 + e^{(\gamma_i + \beta v)}}$$

thus

$$\ln \left[ \frac{\alpha_i^{(v)}}{(1 - \alpha_i^{(v)})} \right] = \gamma_i + \beta v \quad (5)$$

where  $\gamma_i$  is a parameter associated with year effects and  $\beta$  is the linear-logistic slope parameter (expectation is that  $\beta > 0$ ). Recall that  $\alpha_i^{(v)}$  is estimable for ages  $v = k, k + 1, \dots, m - 1$ , and is defined to be 0.0 for  $v < k$  and 1.0 for  $v > (m - 1)$ . We constructed model  $(\varphi_i^{(0)}, \varphi_i^{(3+)}, \tau_i^{(3+)}, p_i^{(3+)}, p^{(3+)'}, \alpha^{(L)})$  in which age-specific breeding probability was modelled as a linear-logistic function of age (years + 1) for ages 3–5.

Pearson goodness-of-fit tests computed by SURVIV (White, 1983) were used to assess the fit of the various models to the data. For these tests, cells are pooled when expected values are small. Model selection was based on Akaike’s Information Criterion modified for small sample sizes,  $AIC_c$  (e.g. Burnham & Anderson, 1998). We report  $\Delta AIC_c$  values reflecting the difference in  $AIC_c$  between the model in question and the low- $AIC_c$  model.

#### 4 Results

The basic models parameterized as in Clobert *et al.* (1994) and Williams *et al.* (in press) with no transient parameters or trap dependence did not provide good fit to the data of Table 1, as indicated by large  $\chi^2$  goodness-of-fit test statistics (Table 2). Examinations of residuals led to the conclusion that some sort of transient behaviour of first-time breeders at this site was important in the data set. The residuals also provided some evidence of trap-dependence.

Three general models containing both the transient parameterization and Markovian trap-dependence exhibited the smallest AIC<sub>c</sub> values. Comparison of the AIC<sub>c</sub> values of these three models with those of the other models provided strong evidence of the need for both the transient and the trap-dependent parameterizations (Table 2). The low-AIC<sub>c</sub> model ( $\varphi_i^{(0)}, \varphi_i^{(3+)}, \tau_i^{(3+)}, p_i^{(3+)}, p^{(3+)/}, \alpha^{(3,4)}$ ) had breeding probability parameters only for ages 3 and 4. Another model that described the data well contained parameters for age-specific breeding probability for ages 3, 4 and 5 ( $\varphi_i^{(0)}, \varphi_i^{(3+)}, \tau_i^{(3+)}, p_i^{(3+)}, p^{(3+)/}, \alpha^{(3,4,5)}$ ). The other model that performed well modelled age-specific breeding probability for ages 3-5 as a linear-logistic ( $\varphi_i^{(0)}, \varphi_i^{(3+)}, \tau_i^{(3+)}, p_i^{(3+)}, p^{(3+)/}, \alpha^{(L)}$ ).

Estimates were very similar for the two low-AIC<sub>c</sub> models that did not contain the linear-logistic model, and we present estimates from model ( $\varphi_i^{(0)}, \varphi_i^{(3+)}, \tau_i^{(3+)}, p_i^{(3+)}, p^{(3+)/}, \alpha^{(3,4)}$ ), which contains time-specific parameters for young and adult survival and for the proportion of transients among unmarked adults. The adult capture probability for birds encountered in the previous period is time-specific, whereas the capture probability for birds not observed in the previous period was constrained as a constant over time. This latter constraint is required for parameter identifiability in this model as for the simpler CJS-type models (see Sandland & Kirkwood, 1981; Pradel, 1993). The age-specific breeding probabilities were modelled as constant over time. We did fit a model with time-specific  $\alpha_i^{(v)}$  but encountered some numerical problems as many  $\alpha_i^{(v)}$  were estimated near the boundary of 1.0. The Pearson  $\chi^2$  goodness-of-fit statistic for the three low-AIC<sub>c</sub> models indicated reasonable fit (Table 2) and provided no reason for quasi-likelihood adjustments (see Lebreton *et al.*, 1992; Burnham & Anderson, 1998).

The estimated number of nesting pairs, productivity, parameter estimates for

TABLE 2.  $\Delta$ AIC<sub>c</sub> values and Pearson  $\chi^2$  goodness-of-fit test statistics for several age-specific breeding probability models fit to the Falkner Island Roseate Tern capture-recapture data of Table 1. Model notation is specified in the text

Model	Number of parameters	$\Delta$ AIC <sub>c</sub>	Goodness-of-fit*		
			$\chi^2$	df	P
$(\varphi_i^{(0)}, \varphi_i^{(3+)}, \tau_i^{(3+)}, p_i^{(3+)}, p^{(3+)/}, \alpha^{(3,4)})$	39	0.00	24.8	25	0.47
$(\varphi_i^{(0)}, \varphi_i^{(3+)}, \tau_i^{(3+)}, p_i^{(3+)}, p^{(3+)/}, \alpha^{(L)})$	39	0.78	25.4	25	0.44
$(\varphi_i^{(0)}, \varphi_i^{(3+)}, \tau_i^{(3+)}, p_i^{(3+)}, p^{(3+)/}, \alpha^{(3,4,5)})$	40	2.15	24.8	24	0.41
$(\varphi_i^{(0)}, \varphi_i^{(3+)}, \tau_i^{(3+)}, p_i^{(3+)}, p^{(3+)/}, \alpha^{(3,4)})$	32	33.14	68.9	33	< 0.01
$(\varphi_i^{(0)}, \varphi_i^{(3+)}, \tau_i^{(3+)}, p_i^{(3+)}, \alpha^{(3,4)})$	38	82.03	29.8	17	0.03
$(\varphi_i^{(0)}, \varphi_i^{(3+)}, \tau_i^{(3+)}, p_i^{(3+)}, p^{(3+)/}, \alpha^{(3,4)})$	30	82.74	122.1	35	< 0.01
$(\varphi_i^{(0)}, \varphi_i^{(3+)}, p_i^{(3+)}, p^{(3+)/}, \alpha^{(3,4)})$	30	159.38	225.3	33	< 0.01
$(\varphi_i^{(0)}, \varphi_i^{(3+)}, p_i^{(3+)}, \alpha^{(3,4,5)})$	30	239.00	237.9	27	< 0.01
$(\varphi_i^{(0)}, \varphi_i^{(3+)}, p_i^{(3+)}, \alpha^{(3,4)})$	29	240.23	239.1	28	< 0.01

\*Pearson  $\chi^2$  goodness-of-fit with cell pooling for low expected cell values computed by program SURVIV (White, 1983).

survival probability of adults and young from the different cohorts, the probability that a previously unmarked adult exhibits fidelity and becomes a resident, and capture probability for adult breeders encountered the previous breeding season at Falkner Island are shown in Table 3. The relatively low productivity of fledglings for 1996 and 1997 was due in large part to the nocturnal activities of predatory Black-crowned Night-Herons (Nisbet *et al.*, 1998; Grinnell & Spendelow, 2000).

The parameter estimates are generally consistent with biological knowledge and *a priori* predictions. With the exception of the 1989 estimate, the capture probabilities for individuals encountered the prior breeding season at Falkner Island ( $p_i^{(v)}$ ) are above 0.8, suggesting a relatively high degree of colony-site fidelity for experienced residents. The estimated capture probabilities for birds not encountered the previous period,  $p^{(v)}$  was smaller than those for birds that were encountered the previous period,  $p_i^{(v)}$ .

#### 4.1 Survival probabilities

Similar to what was found in previous analyses (Spendelow *et al.*, 1995), most of the estimated annual survival probabilities for adults fell in the interval from 0.78–0.89. The 1991 estimate (0.62) was lower, and the 1992 and 1993 estimates were higher than the others.

The annualized survival probabilities for immature prebreeders mostly fell in the interval from 0.53 to 0.57. As with the breeding adults, the estimate (0.33) for the 1991 cohort was significantly lower, and estimates for the 1992 and 1993 cohorts (0.67, 0.68) were significantly higher than the others.

#### 4.2 Age-specific breeding probabilities

In addition to survival, the parameters of primary interest were the age-specific breeding probabilities. The most appropriate model from this group was the one for which  $m = 5$ . This model yielded estimates of about 0.77 ( $\hat{SE} = 0.081$ ) for the probability that a young bird of age 3 would breed at that age ( $\alpha^{(3)}$ ) and about 0.66 ( $\hat{SE} = 0.251$ ) for the probability that a bird that had not bred by age 4 would breed at that age ( $\alpha^{(4)}$ ) (Table 3). The estimate for age 4 was imprecise. The probabilities of breeding for birds older than 4 years that had not previously bred were then 1.0 by assumption. The point estimate of  $\alpha^{(5)}$  under Model ( $\varphi_i^{(0)}, \varphi_i^{(3+)}, \tau_i^{(3+)}, p_i^{(3+)}, p^{(3+)'}, \alpha^{(3,4,5)}$ ) was also 1.0. The linear-logistic model expressing breeding probabilities as a function of age yielded estimates based on this relationship of  $\hat{\alpha}^{(3)} = 0.85$ ,  $\hat{\alpha}^{(4)} = 0.90$ ,  $\hat{\alpha}^{(5)} = 0.94$ .

#### 4.3 Proportion of unmarked first-time breeders that became residents

The estimated proportions of residents that developed fidelity among unmarked birds ( $1 - \hat{\tau}_i^{(3+)}$ ) varied substantially. Estimates for 1989–1991 were greater than, or equal to, 0.9, most estimates for the next four years were between 0.6–0.7, and estimates for 1996–1997 were considerably lower, around 0.3.

## 5 Discussion

### 5.1 Capture probabilities

Capture probabilities for birds encountered the previous period at Falkner Island were predicted to be larger than those for birds not encountered the previous period under a hypothesis of first-order Markovian temporary emigration to other colony sites. This prediction held true (Table 3).

TABLE 3. Parameter estimates\* for annualized survival probability of young ( $\phi_i^{(0)}$ ), annual survival probability of adults ( $\phi_i^{(3+)}$ ), probability that an unmarked adult becomes a resident ( $1 - \tau_i^{(3+)}$ ), and capture probability for adult breeders encountered the previous period ( $\hat{p}_i^{(3+)}$ ) for Roseate Terns at Falkner Island, Connecticut

Year ( $t$ )	Estimated # nesting pairs	Productivity (fledglings per pair)	$\phi_i^{(0)}$	( $\hat{SE}$ )	$\phi_i^{(3+)}$	( $\hat{SE}$ )	$1 - \tau_i^{(3+)}$	( $\hat{SE}$ )	$\hat{p}_i^{(3+)}$	( $\hat{SE}$ )
1988	190	1.08	0.57	(0.033)	0.59**	(0.050)	—**	—	—	—
1989	165	0.82	0.53	(0.039)	0.78	(0.063)	0.90	(0.090)	0.61	(0.060)
1990	170	0.84	0.55	(0.037)	0.83	(0.039)	0.96	(0.068)	0.82	(0.038)
1991	180	0.88	0.33	(0.049)	0.62	(0.034)	> 0.99	(0.109)	0.86	(0.031)
1992	130	0.79	0.67	(0.038)	0.92	(0.022)	0.60	(0.099)	0.88	(0.027)
1993	160	1.18	0.68	(0.030)	0.91	(0.022)	0.45	(0.065)	0.94	(0.019)
1994	140	1.33	0.56	(0.037)	0.81	(0.027)	0.69	(0.118)	0.96	(0.016)
1995	130	0.94	0.56	(0.059)	0.89	(0.028)	0.62	(0.130)	0.94	(0.019)
1996	150	0.50	—	—	0.84	(0.032)	0.32	(0.088)	0.86	(0.029)
1997	150	0.65	—	—	—	—	0.29	(0.115)	0.91	(0.030)

\*Time-invariant parameter estimates for breeding probability at age  $v(\alpha^v)$  and adult capture probability for animals not caught the previous period:  $\hat{\alpha}^{(v-3)} = 0.00$ ,  $\hat{\alpha}^{(3)} = 0.77$  ( $\hat{SE} = 0.081$ ),  $\hat{\alpha}^{(4)} = 0.66$  ( $\hat{SE} = 0.251$ ),  $\alpha^{(v-4)} = 1.00$ ,  $\hat{p}^{(3+)} = 0.60$  ( $\hat{SE} = 0.043$ ).

\*\*Initial adult survival probability represents the product  $\phi_i^{(3+)}(1 - \tau_i^{(3+)})$ , as the parameter cannot be separated the first year of marking.

## 5.2 Survival probabilities

Prediction 2.1 clearly held true, as shown by the low survival estimate of breeding adults from the 1991 breeding season (Table 3). The probable cause of the low survival estimates of adults and young after the 1991 breeding season was the passage of Hurricane Bob over the major premigratory staging area for these terns on Cape Cod, MA, on 19 August 1991 (Hatch *et al.*, 1997). The complement of the survival estimates (which includes mortality and permanent emigration) of adults at Falkner Island between the 1991-1992 breeding seasons was about twice as high as typical, and this unusually high loss of breeding adults was not fully compensated for by new recruits from the 1989 and 1988 cohorts in the 1992 breeding season, resulting in a major decline in the Roseate Tern breeding population not only at this site, but throughout the New York-Connecticut-Massachusetts region (USFWS, 1998).

Our prediction (2.2) that there might be above-average overwinter survival of adults following the 1992 breeding season also held true, and overwinter survival of adults following the 1993 breeding season was similarly high. The average loss rate (about 0.09, again, the complement of the survival estimates) of breeding birds for these two years was only about half the typical loss rate of about 0.17.

We predicted (2.3) that there would be a greater negative impact on the survival of fledglings from 1991 compared with the impact on the survival of breeding adults from that year, because the recent fledglings were not self-sufficient and were still dependent on at least one parent for food (Watson & Hatch, 1999). Therefore, if a parent providing care for a fledgling had died, that fledgling would also probably have died. Prediction 2.3 held true although the magnitude of the impact may not be obvious at first based on our presentation of the survival estimates of young in Table 3 as annualized rates  $(\varphi_{i,i+3}^{(0)})^{1/3}$  (corresponding to constant average survival over the 3-year maturation period following release as fledglings). We presented these as annualized rates because we could not divide survival over the entire 3-year period into separate yearly rates. However, we do not believe that 'constant survival' over this period is likely, and note that evidence given in more detail below indicates that the extremely low survival of the 1991 cohort of young was due mainly to forces acting in just one year of the 3-year maturation period. Regardless of when most losses actually occurred, we estimated that less than 4% (or only about 25% of the otherwise typically-expected number) of the fledglings from the 1991 cohort survived to become breeding birds.

Our prediction (2.4) that there would be little impact of Hurricane Bob on the survival of young from the two preceding years also was confirmed. Virtually no young from 1990 and relatively few from 1989 were expected to have been present around Cape Cod in August 1991 (Nisbet, 1984), and these two cohorts show no sign of less than typical survival.

Our prediction (2.5) that there might be above-average survival of fledglings from the 1992 breeding season (despite the low productivity of young that year) was also confirmed. We were somewhat surprised, though, by the magnitude of the survival estimates for both the 1992 and 1993 cohorts, as the annualized survival estimates for these cohorts were about 20% higher than estimates for the 1988-1990 and 1994-1995 cohorts (Table 3). These translate into 3-year survival rates of about 30% for the fledglings from 1992 and 1993, and about 17% for the fledglings from the other five cohorts, respectively. We will not know to what extent this apparent higher local survival-and-return of young from the 1992 and 1993



cohorts was due to a possible reduction in the emigration of first-time breeders to other sites until a detailed multisite recruitment analysis is done.

The survival of the cohorts of fledglings from the two years immediately after the hurricane is higher than normal, ruling out severe conditions over the winters of 1992 and 1993 as playing an important role in the low survival of the 1991 cohort of young. All these factors in combination indicate that the extremely low survival estimate for young from 1991 was due mostly to recent fledglings being very strongly affected by an event occurring after the 1991 breeding season but before the terns reached their wintering areas.

### 5.3 Age-specific breeding probabilities

We expected (Prediction 2.6) to find a narrow range of years for Roseate Terns recruiting to the breeding population, and our modelling results confirmed this with more than three-quarters of the surviving young first breeding by age 3, and virtually all surviving birds breeding by age 5. Although a few cases of Roseate Terns nesting as 2-year-olds have been reported in the past (Donaldson, 1971; Spendelow, 1991), none was detected in this study. Given the amount of intercolony movement by adults that takes place between this site and nearby Great Gull Island, NY (Spendelow *et al.*, 1995), it seems most likely that birds found first nesting at Falkner Island when six or more years old probably really began nesting elsewhere first (Spendelow, 1991).

Our modelling process led to the selection of models with time-invariant age-specific breeding probabilities, so we found no strong evidence (Prediction 2.7) of temporal variation in breeding probabilities. All cases of nesting 2-year-olds that have been reliably sexed have been males (Spendelow *et al.*, unpublished data), suggesting that it is the females' physiological maturity and development of the capability to produce eggs that may be the major factor limiting further reduction in the age at first breeding for this species.

### 5.4 Proportion of unmarked first-time breeders that became residents

The high estimated proportions of residents among unmarked adults ( $1 - \hat{\tau}_i^{(3+)}$ ) for 1989-1991 (Table 3) are thought to be an artefact because many individuals classified as 'unmarked' (i.e. not previously encountered) in the first two years of this particular study period actually had been encountered as breeding adults before 1988, but needed to be retrapped and colour-ringed for inclusion in the metapopulation study (Nisbet & Spendelow, 1999). We think that the estimates for the period 1992-1995 are probably more typical and that usually between  $\frac{1}{2}$  to  $\frac{2}{3}$  of the first-time breeders at this colony site remain as 'residents'. Prediction 2.8 that relatively fewer unmarked first-time breeders from 1996 and 1997 would become residents after experiencing severe nocturnal disturbance, predation, and low productivity (Table 3) caused by Black-crowned Night-Herons (Zingo, 1998; Grinnell & Spendelow, 2000), was also borne out by the low fidelity estimates for 1996 and 1997 in Table 3.

### 5.5 Conclusions

We believe that this direct modelling and estimation approach to the model developed by Clobert *et al.* (1994) should be useful to animal population ecologists.

A number of species exhibit this type of life history in which young prebreeders are not available for sampling conducted on breeding grounds and are not recruited into the breeding population at a single predetermined age. As described above, it is possible to estimate these age-specific recruitment probabilities directly and to model them, for example, as an increasing function of age.

Other sampling designs are also useful for such species, but alternative sampling is not always possible. For example, if prebreeders are available for sampling, then it will generally be best to use multistate models. Transition probabilities from the prebreeder to the breeder state can be estimated, as with the approach presented here, but without the potentially restrictive assumption that all prebreeders exhibit breeder survival beginning at the first age at which recruitment can occur. If a robust design (Pollock, 1982) is possible, then the modelling approach of Kendall *et al.* (1997) permits estimation of breeding probabilities of adult breeders. The approach of Kendall *et al.* (1997) could be combined with the approach presented above to estimate directly recruitment probabilities of prebreeders, rather than recruitment probabilities expressed relative to breeding probabilities of adult breeders.

The magnitudes of age-specific recruitment probability estimates for Roseate Terns are of interest, as such estimates are not available for many species. It also is interesting that these probabilities approach 1.0 at age 5. Although other seabirds may postpone breeding longer, the relatively lower survival probabilities of Roseate Terns were expected to be associated with shorter prebreeding intervals.

The survival rates of young terns returning to their natal site reported here, although slightly higher than those reported by Spendelow (1991), are quite low, but it must be recalled that the complements of these estimates include permanent emigration. We are working on a multistate version of this model that will permit estimation of true survival rates, and we expect these estimates to be somewhat larger for young birds than those presented here.

Of particular interest was the dramatic influence of a severe hurricane on survival of young and adult birds. Despite the general perception that extreme weather events influence animal survival, relatively few conclusive demonstrations of such influence exist in the scientific literature. The reductions in tern survival were large for a bird with this life history and emphasize the potential importance of such chance events. However, equally interesting were the apparently compensatory changes in survival probabilities of both young and adults that occurred in the two years immediately following the hurricane. We believe that long-term demographic studies, combined with continued efforts to develop estimation models appropriate to the sampling situations, will continue to provide useful insights into animal population ecology.

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