



Age-dependent breeding dispersal and adult survival within a metapopulation of Common Terns *Sterna hirundo*

ANDRÉ R. BRETON,^{1*} IAN C. T. NISBET,² CAROLYN S. MOSTELLO³ & JEREMY J. HATCH^{4†}

¹Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, 201 Wagar Building, Fort Collins, CO 80523-1484, USA

²I. C. T. Nisbet & Company, 150 Alder Lane, North Falmouth, MA 02556, USA

³Massachusetts Division of Fisheries and Wildlife, 100 Hartwell St., West Boylston, MA 01583, USA

⁴Department of Biology, University of Massachusetts, Harbor Campus, Boston, MA 02125, USA

Dispersal is increasingly recognized as a process of fundamental importance in population dynamics and other aspects of biology. Concurrently, interest in age-dependent effects on survival, including actuarial senescence, has increased, especially in studies of long-lived seabirds. Nevertheless, datasets necessary for studying dispersal and age-dependent effects are few, as these require simultaneous data collection at two or more sites over many years. We conducted a 22-year capture-mark-recapture study of Common Terns *Sterna hirundo* at three breeding colonies 10–26 km apart in Buzzards Bay, Massachusetts, USA. All birds in the study were of known age (range 2–28 years, median 7 years, $n = 3290$) and 77% were of known sex. Estimates of adult recapture, survival and breeding dispersal rates were obtained for all age-classes from 2 to 20 years. The model that acquired 100% of the QAIC_c (Akaike's Information Criterion adjusted for small sample size and overdispersion) weight in our analysis included age-specificity in all parameters but no relationship with sex. Our study may be the first to demonstrate age-specificity in recapture, survival and breeding dispersal rates simultaneously, using a single model. Annual rates of breeding dispersal ranged from <0.01 to 0.27, with a population-weighted mean of 0.065; they decreased with increasing distance between colony sites and, unexpectedly, increased with age. Breeding dispersal did not increase consistently after years with predation on adults or after an attempt to displace birds from an oiled site. Survival rates did not vary among sites or years. Annual adult survival increased from 0.80 in 2-year-old birds to a maximum of approximately 0.88 around age 8 years and then declined to 0.76 at age 20 years, yielding strong evidence for actuarial senescence. The peak annual survival rate of 0.88 is at the low end of other estimates for Common Tern and in the lower part of the range recorded for other terns, but total numbers in the three colonies increased seven-fold during the study. This was part of a slower increase in the regional population, with net immigration into the study colonies. Our results demonstrate the biological significance of breeding dispersal in local population dynamics and age-related effects on survival and dispersal from a metapopulation of a long-lived seabird.

Keywords: actuarial senescence, Buzzards Bay, capture-mark-recapture, immigration, movement rates, predation, program MARK, program U-CARE.

†Present address: Lower Dibbe, South Tawton, Devon EX20 2LQ, UK.

*Corresponding author.
Email: andre.breton@colostate.edu

Dispersal is a process of fundamental importance in population biology, with implications for local and large-scale population dynamics, metapopulation structure and source-sink dynamics, population synchrony, gene flow and genetic structure, colonization and range expansion (Greenwood

1980, Pulliam 1988, Johnson & Gaines 1990, Kot *et al.* 1996, Bohonak 1999, Colbert *et al.* 2001, Matthiopoulos *et al.* 2005). Although dispersal was formerly regarded as being of little importance in local population dynamics (Elton 1927, Nicholson 1933, Lack 1954), recent studies have shown that it significantly influences local population dynamics in many species of birds (e.g. Hestbeck *et al.* 1991, Lebreton *et al.* 2003, Breton *et al.* 2006). Nonetheless, dispersal remains a difficult demographic process to study, especially in continuous habitats, because it requires sampling at multiple locations. Dispersal is somewhat easier to study in discontinuous metapopulations, such as those formed by colonial seabirds nesting on islands, but it still requires data collection at several sites, and large samples at each site may be required if rates of dispersal are low.

Dispersal may take place either before the animal has bred for the first time (natal dispersal) or after it has bred one or more times (breeding dispersal). Although natal dispersal generally takes place at higher rates than breeding dispersal (Greenwood & Harvey 1982, Paradis *et al.* 1998), the latter may be disproportionately important because individuals that survive to breed for the second time are generally believed to survive better and breed more successfully thereafter than first-time breeders. Because adults show higher site-fidelity than young birds, it might be predicted that rates of breeding dispersal would decline with age after the first breeding attempt. However, there have been few studies of the dependence of breeding dispersal on age (Serrano *et al.* 2001).

In recent years, multistate capture-recapture (CMR) models have been developed that can yield estimates of dispersal among multiple sites (Lebreton *et al.* 2003, 2009, Kendall & Nichols 2004). These models also yield estimates of survival, reducing the downward bias that inevitably results if only one site is studied (Frederiksen *et al.* 2005). To date, several studies have used these models to estimate adult survival and breeding dispersal in seabirds (e.g. Cam *et al.* 2004, Hénau *et al.* 2007, Devlin *et al.* 2008, Ratcliffe *et al.* 2008, Spindel *et al.* 2008, Gauthier *et al.* 2010); relatively few seabird studies have estimated pre-breeding survival and natal dispersal together (Lebreton *et al.* 2003, Breton *et al.* 2006).

Seabirds are long-lived and have age-structured populations, so that full characterization of their populations requires that chicks are ringed for

many years and that studies of adults are continued over periods comparable with the birds' lifespans. Several studies of seabirds undertaken at single sites have revealed that survival varies with age, typically increasing during the first few years of breeding, levelling off in middle age, and sometimes declining again (actuarial senescence) among the older age-classes (e.g. Pugesek *et al.* 1995, Cam & Monnat 2000, Sidhu *et al.* 2007). However, there have been no CMR studies of the age-dependence of breeding dispersal, except for a two-site study by Nisbet and Cam (2002) which yielded only single-year estimates of dispersal rates. Simultaneous estimation of age-dependent survival, dispersal and recapture rates in an actively dispersing species over multiple sites and years involves complex models with many estimable parameters, and consequently requires large datasets. Despite the wide use of multistate models, no seabird study has, to our knowledge, assessed the effect of age on recapture, survival and dispersal probabilities simultaneously, using a single model.

Here, we report a CMR study of a metapopulation of Common Terns *Sterna hirundo* comprising three breeding colonies 10–26 km apart. All birds included in the study were of known age. We obtained estimates of adult survival and breeding dispersal; estimation of juvenile survival and natal dispersal is deferred to a subsequent analysis. The study was conducted for 22 years (1983–2004), but many birds had been ringed as chicks earlier and consequently were of known age at the outset. Total numbers increased rapidly and two of the breeding sites were recolonized during the study period, so that we could document movements among sites during and after the recolonizations. Our objectives were to estimate rates of adult survival and breeding dispersal, to test for dependence of these rates on sex and age, including actuarial senescence, to test for variations among years, and to test for the effects of predation and other covariates likely to influence breeding dispersal and survival rates.

METHODS

Study sites and field methods

Our study was conducted at three sites in Buzzards Bay, Massachusetts, USA: Bird Island (hereafter, BI; 41°40'N, 70°43'W), Ram Island (RI; 41°37'N, 70°48'W) and Penikese Island (PI;

41°27'N, 70°55'W) between 1983 and 2004. These sites are separated by 10 km (BI–RI), 16 km (RI–PI) and 26 km (BI–PI; Fig. 1).

Nisbet (1973) summarized historical information on Common Terns at these sites; we have conducted censuses in each year since 1973 (Table S1). BI has been occupied continuously since at least 1935: numbers reached a minimum of about 200 pairs in 1969, increased steadily to 720 pairs in 1983 and 1879 pairs in 1988, and remained more or less constant at about 1800 pairs thereafter until 2004. Terns were displaced from RI by gulls *Larus* spp. in 1973; they recolonized the site in 1992 and numbers increased rapidly to 2938 pairs in 2004. Terns were displaced from PI by gulls in the 1950s; they recolonized the site in 1992; numbers were low and variable until 1999, then increased to 661 pairs in 2003 and 631 pairs in 2004. Recolonization at RI and PI followed programmes to control and displace the gulls (Harlow 1995). Total numbers at the three sites increased more than seven-fold during the study period (Table S1). In the period 1996–2004, some of the changes in numbers at BI and RI were thought to be attributable to intermittent predation by Great Horned Owls *Bubo virginianus* and to 'hazing' of terns at RI in 2003 (using systematic harassment

and pyrotechnics) in an attempt to displace them to other sites following an oil spill (Nisbet *et al.* 2013a).

Terns have been marked with durable rings (incoloy: Nisbet & Hatch 1989) as chicks at all sites in Buzzards Bay, when occupied, and at several other sites within 80 km of Buzzards Bay from 1975 to 2002 ($n = 81\,633$). Adult terns were sampled by trapping at BI from 1983 to 2004, at RI from 1994 to 2004 and at PI from 1999 to 2004. Total numbers of birds encountered at each site in each year are listed in Table S1. From 1995 to 1997, Common Terns were trapped using stratified random sampling designed to sample 45% of the birds at BI and 20% of those at RI in each year (Nisbet & Cam 2002). Sampling in other years was not rigorously randomized, but trapping was uniform in space and time at all three sites in 1999 and at BI and RI in 2002 (Nisbet *et al.* 2002, 2007, Apanius & Nisbet 2003, 2005, Tims *et al.* 2004); in all other sites and years, trapping was designed to sample all parts of each colony throughout the main peak of nesting in May and the first half of June. However, little trapping was done after about 10 June in all years except 1995–97, 1999 and 2002; this would have resulted in under-sampling of birds aged 2–4 years in the

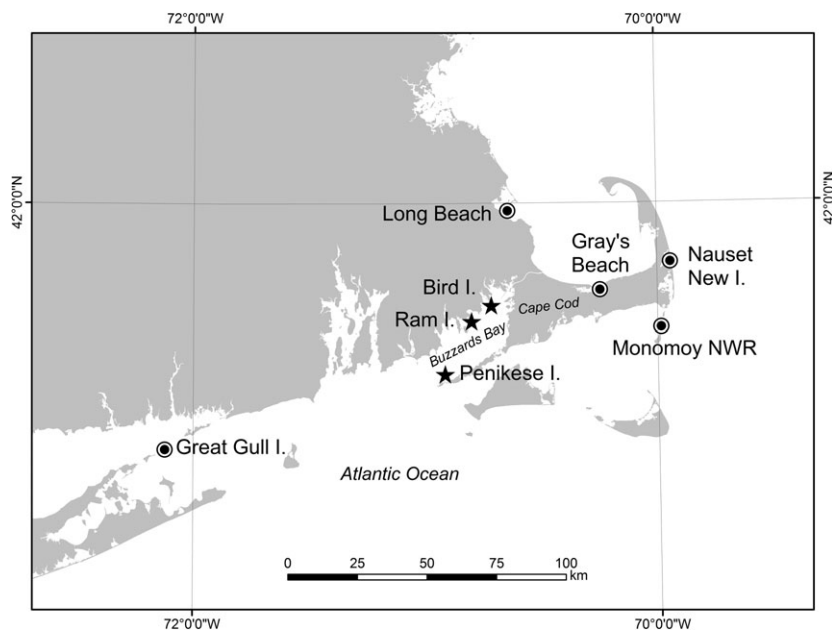


Figure 1. Coastline of Massachusetts, Rhode Island and eastern New York, showing the three study sites in Buzzards Bay (stars) and the five large contiguous colonies of Common Terns to the north (Long Beach), east-northeast (Gray's Beach, Nauset New Island), east (Monomoy National Wildlife Refuge) and west-southwest (Great Gull Island; circles).

remaining 17 years (Nisbet *et al.* 1984). Terns were trapped using treadle traps set over nests with eggs, usually during morning hours (07:00–11:00 h). Most birds were released within 15 min after trapping and resumed normal incubation within about 20 min. All activities were conducted under appropriate state and federal permits.

All Common Terns included in this study had been ringed as chicks and hence were of known age (range 2–28 years, median 7 years). Terns were sexed genetically ($n = 94$), by being seen to lay an egg ($n = 3$), by the presence or absence of a palpable egg in the oviduct or distended cloacae when trapped during egg-laying ($n = 193$), by body-mass during egg-laying ($n = 371$), by observation of copulation or repeated courtship-feeding ($n = 218$), by head length ($n = 1225$), by the same characters recorded in previous or subsequent years ($n = 1070$), and/or from the sex of their mates in one or more years ($n = 432$); most terns were sexed using two or more of these characters. Through these combined approaches, 2518 (77%) of the 3290 birds in the study were sexed; the remainder were treated as being of unknown sex.

The three breeding colonies in Buzzards Bay are thought to comprise a discrete group (Nisbet & Cam 2002) but are located within a larger metapopulation of Common Terns along the Atlantic coast of North America, with other large colonies 40–130 km away (Fig. 1; Table S2). Sampling in 1999 indicated that some terns breeding at BI, many at RI and most at PI had been ringed at sites outside Buzzards Bay, either as chicks or as adults, demonstrating high rates of immigration into our study area (Tims *et al.* 2004). To estimate rates of emigration, we compiled records of birds that had been ringed as adults in our study area and subsequently retrapped at contiguous sites, using data supplied by the Bird Banding Laboratory and by ringers at the other sites (Appendix S1).

Statistical methods

We assessed two datasets. The first ($n = 2518$) comprised all birds of known sex and age that were encountered as breeding adults in one of the years of the study, 1983–2004. The second ($n = 3290$) also included birds of known age but unknown sex. CMR data were analysed using programs MARK (version 6.2, White & Burnham 1999, White *et al.* 2001) and U-CARE (version 2.3.2, Choquet *et al.* 2009). Analysis proceeded in

six stages. In stage one, we conducted a goodness-of-fit (GOF) assessment of the global model for dataset one, using tests WBWA, 3G.SR, 3G.Sm, M.ITEC and M.LTEC in U-CARE. Results of these tests were used to calculate a dispersion parameter (\hat{c}) which was used in stage two. Data limitations, and possibly a lack of time-variation in survival (see Results), precluded the inclusion of interactions between sites and years in the survival and movement portions of the global model (these models did not converge). Survival, encounter and movement probabilities prior to the first study years at RI (1994) and PI (1999) were fixed to zero in all models, as were movement probabilities from PI to BI. The latter were essentially zero, too low to be estimated given the data.

In stage two, we used MARK to assess the relationship of sex with survival, encounter and movement probabilities. We compared the global model (with time and space variation in each parameter) with models in which one parameter also varied with sex. In all model selection stages (stages two, four to six), support for competing models was determined by QAIC_c (Akaike's Information Criterion adjusted for small sample size and overdispersion) and QAIC_c weights (Burnham & Anderson 2002). In cases involving model selection uncertainty, we examined effect sizes and their 95% confidence intervals and excluded models in which these confidence intervals included zero. In one case, we integrated a likelihood ratio test (White & Burnham 1999).

Finding no consistent relationship of sex with any parameter (see Results), we used the larger dataset that included birds of unknown sex in all subsequent analyses. In stage three, we assessed GOF in the same way as in stage one, and calculated a dispersion parameter (\hat{c}) for use in subsequent analyses. In stage four, we assessed site and year effects by comparing the global model with sets of reduced models in which one parameter was constrained to be equal over various combinations of site and year. This comparison was made separately for each parameter while maintaining full time and space variability in the other two. At this stage we tested two hypotheses: (1) that survival would have been lower in 1991–92 than in all other years, based on the finding by Lebreton *et al.* (2003) and Spindelov *et al.* (2008) that survival of Roseate Terns *Sterna dougallii* that bred at BI in 1991 was markedly reduced by a hurricane that passed through a post-breeding staging area

also used by Common Terns; and (2) that movement probabilities would have been higher following incidents of predation or hazing (see above).

In stage five, we assessed the dependence of each model parameter on age. We constructed a model combining the preferred structures for each parameter from stage four, and compared this with models in which one parameter varied with age. For survival, we assessed seven age structures: ages 2–3, 4+ years; 2–4, 5+ years; 2–3, 4, 5+ years; 2–3, 4, 5, 6+ years, fitting linear, quadratic and cubic terms. For encounter, we assessed three age structures: ages 2–4, 5+ years, fitting linear and quadratic terms. For movement, we assessed linear, quadratic and cubic age terms. We used functions of individual covariates in program MARK to implement linear, quadratic and cubic age effects (Frederiksen *et al.* 2004).

In stage six, we combined preferred site, year and age structures from stages four and five into a single model. This model was then compared with top models from stage five (assessment of age effects) and the global model from stage four (assessment of site and year effects); this 'combined age-structure model' acquired 100% of the QAIC_c weight. Thus, it was not necessary to use model averaging (Burnham & Anderson 2002).

Finally, we combined estimates of movement probability for each combination of site, year and age with the age-structure of the breeding population to calculate age-weighted mean movement probabilities. We multiplied these movement probabilities by twice the number of breeding pairs to yield estimates of the number of adult terns leaving each site in each year, and hence net inflows or outflows from each site during the period when the colonies at RI and PI were growing rapidly.

RESULTS

Assessment of GOF and effect of sex

A dispersion parameter estimate (\hat{c}) of 1.07 was obtained based on five multi-site tests for dataset one (known age and sex; Table 1). Group-specific tests revealed that the source of the overdispersion was birds that entered the sample at age 4 years: Test M.ITEC: $\chi^2_5 = 16.57$, $P = 0.005$. Among the four models used to assess the effect of sex, the QAIC_c weights were 0.41 for the global model and 0.40, 0.14 and 0.05 for the models with sex-dependence in encounter, survival and move-

Table 1. Goodness-of-fit results in stages one and three (see Methods). Estimates of the dispersion parameter were obtained by summing the χ^2 values and dividing this sum by the number of degrees of freedom (df; Choquet *et al.* 2009). Dataset one included only birds of known sex, while dataset two included birds of unknown sex.

Test	Dataset one			Dataset two		
	χ^2	df	P-value	χ^2	df	P-value
WBWA	3.84	3	0.28	5.89	3	0.12
3G.SR	35.76	32	0.30	64.37	32	0.001
3G.Sm	82.48	79	0.37	84.77	82	0.40
M.ITEC	7.01	7	0.43	6.22	8	0.62
M.LTEC	4.54	4	0.34	16.10	4	0.003

ment probabilities, respectively. However, ΔQAIC_c was >2 for both the survival and the movement models, and confidence limits on the effect of sex on encounter probability widely bounded zero (-0.035 , 0.224 , logit scale). A likelihood ratio test yielded a P -value of 0.15 ($\chi^2_1 = 2.04$), consistent with a spurious effect of sex. Given the weak evidence for a relationship with any parameter, sex was dropped from further consideration.

Assessment of site, year and age effects

The dispersion parameter estimate (\hat{c}) for dataset two was 1.38 based on five multi-site tests (Table 1). Group-specific tests suggested that lack of fit stemmed from Test M.LTEC: birds aged 7+ years on release $\chi^2_3 = 11.12$, $P = 0.011$; birds aged 4 years on release $\chi^2_3 = 11.46$, $P = 0.075$. Group-specific tests did not reveal the source of the significance for Test 3G.SR when groups were pooled (Table 1), which suggests that incorporating age into our MARK models accounted for this source of heterogeneity. Nevertheless, we applied 1.38, probably a conservative overestimate, as an adjusted variance inflation factor for all remaining analysis stages.

In our assessment of site and year effects (stage four), the QAIC_c weight of the constant survival model was 0.43 (Table 2). Three models had $\Delta\text{QAIC}_c < 3$, with QAIC_c weights of 0.12–0.27. However, none of the effect sizes in these models (1991–92; site) was statistically significant. For example, the 1991–92 effect from model S(1991–92) was -0.468 (95% CI: -1.239 , 0.304 ; logit scale); and the site effects from model S(site) were: RI (-0.454 [-0.973 , 0.064]); and PI (-0.539 [-1.986 , 0.908]). Models including

Table 2. Assessment of site and year effects on survival, encounter and movement probabilities (stage four). The global model within each model set is shown in bold font. #Par indicates the number of parameters in each model.

Model	ΔQAIC_c	QAIC_c weight	#Par	Deviance
Survival^a				
S(.)	0.00	0.43	50	12 958.14
S(1991–92)	0.96	0.27	51	12 957.06
S(site)	1.78	0.18	52	12 955.84
S(site + 1991–92)	2.58	0.12	53	12 954.60
S(site + year)	12.46	0.00	71	12 927.62
S(year)	12.76	0.00	69	12 932.03
Encounter^b				
p(site * year)	0.00	1.00	71	12 927.62
p(site + year)	19.40	0.00	59	12 971.62
p(year)	75.61	0.00	57	13 031.92
p(site)	549.60	0.00	39	13 542.59
p(.)	564.25	0.00	37	13 561.29
Movement^c				
ψ (site_s + site_e + year)	0.00	0.55	71	12 927.62
ψ (site_e)	2.77	0.14	62	12 948.85
ψ (site_e + year)	2.99	0.12	69	12 934.72
ψ (site_s + year)	3.50	0.10	69	12 935.23
ψ (year)	5.73	0.03	67	12 941.56
ψ (site_s + site_e)	6.30	0.02	64	12 948.28
ψ (site_s + site_e + owl)	7.92	0.01	65	12 947.86
ψ (site_s + site_e + disturbance)	8.23	0.01	65	12 948.17
ψ (site_s + site_e + owl + hazing)	8.26	0.01	65	12 948.19
ψ (site_s + site_e + hazing)	9.40	0.01	66	12 947.28
ψ (.)	40.15	0.00	60	12 990.32
ψ (site_s)	43.44	0.00	62	12 989.52

^aTop model $\text{QAIC}_c = 13\ 059.11$. Encounter and movement model structure for all models:

$$P_{\text{year}(\text{int})}^s \psi_{\text{year}(\text{add})}^{\text{rs}}$$

^bTop model $\text{QAIC}_c = 13\ 071.57$. Survival and movement model structure for all models:

$$S_{\text{year}(\text{add})}^r \psi_{\text{year}(\text{add})}^{\text{rs}}$$

^cTop model $\text{QAIC}_c = 13\ 071.57$. Survival and encounter model structure for all models:

$$S_{\text{year}(\text{add})}^r P_{\text{year}(\text{int})}^s$$

categorical year effects acquired no support (Table 2). In conclusion, there was no evidence that year or site contributed to variation in survival; hence, only the constant survival model was used in subsequent stages.

In the encounter parameter model set, the model with year, site and interactions had QAIC_c weight = 1.00; all other models were dropped from further consideration (Table 2). In the movement parameter model set, the model with origin site (labeled site_s in models), destination site (labeled site_e in models) and categorical year effects had QAIC_c weight = 0.55 (Table 2). Three other models acquired substantial QAIC_c weights (0.10–0.14), but these were dropped from further consideration because most of the confidence limits for site and year effects widely bounded zero. Models with different movement parameters for years following predation, hazing or both were not supported (Table 2).

In stage five, the model with survival fitted as a cubic function of age had QAIC_c weight = 0.85 and the quadratic model had QAIC_c weight = 0.15 (Table 3). All of the age effects in the top two models were significant. Effect sizes from the cubic model were: age: 0.513 (95% CI: 0.230, 0.796); age²: -0.038 (-0.063, -0.013); age³: 0.0008 (0.0001, 0.0014). The quadratic model yielded survival estimates virtually identical to the cubic model except for more rapid decline beyond age 16, and was dropped from further consideration. The model with encounter probability fitted as a quadratic function of age had QAIC_c weight = 1.00; all other models in this set were dropped from further consideration (Table 3). In the movement parameter model set, the top model had QAIC_c weight = 0.44; in this model, movement was a linear function of age. Two additional models had significant QAIC_c weights (Table 3): quadratic and cubic. However, 95% confidence limits on the effects widely bounded zero: quadratic model; age: -0.048 (95% CI: -0.222, 0.125); age²: 0.004 (-0.002, 0.011); cubic model; age: -0.215 (-0.716, 0.287), age²: 0.019 (-0.023, 0.060), age³: -0.0004 (-0.001, 0.0007). In contrast, the linear age effect from the best model was statistically significant: 0.061 (0.017, 0.106). The linear model was retained and all others were dropped.

In stage six, the model that combined the best site, year and age structures from stages four and five had QAIC_c weight = 1.00 (Table 3). ΔQAIC_c values for the top age models from the stage five survival, encounter and movement model sets were 17.39, 17.58 and 47.24, respectively, and for the global model from stage four, 52.3 (Table 3).

Table 3. Assessment of age effects on survival, encounter and movement probabilities (stage five) including top model structures from our assessment of site and year effects shown in bold font (stage four). In the fourth model set, we compare (stage six) top models from our assessments of site, year and age with a model that includes the best age structures fitted to all parameters from stage five. #Par indicates the number of parameters in each model.

Model	ΔQAIC_c	QAIC_c weight	#Par	Deviance
Survival^a				
S(age + age ² + age ³)	0.00	0.85	53	12 929.57
S(age + age ²)	3.62	0.14	52	12 935.23
S(age(2-3))	11.18	0.00	51	12 944.83
S(age(2-3, 4, 5+))	13.04	0.00	52	12 944.65
S(age(2-3, 4-5, 6+))	13.19	0.00	52	12 944.80
S(age(2-4))	14.45	0.00	51	12 948.10
S(age)	19.96	0.00	51	12 953.61
S(.)	22.45	0.00	50	12 958.14
Encounter^b				
p(site × year + age + age ²)	0.00	1.00	73	12 888.78
p(site × year + age(2-4))	17.10	0.00	72	12 907.94
p(site × year + age)	21.52	0.00	72	12 912.36
p(site × year)	34.72	0.00	71	12 927.62
Movement^c				
ψ (site_s + site_e + year + age)	0.00	0.44	72	12 920.50
ψ (site_s + site_e + year + age + age ²)	0.51	0.34	73	12 918.95
ψ (site_s + site_e + year + age + age ² + age ³)	2.10	0.15	74	12 918.49
ψ (site_s + site_e + year)	5.06	0.04	71	12 927.62
Top model structures combined (stage six)^d				
S(age + age ² + age ³) p(site × year + age + age ²) ψ (site_s + site_e + year + age)	0.00	1.00	56	12 906.06
S(age + age ² + age ³) p(site × year) ψ (site_s + site_e + year)	17.39	0.00	53	12 929.57
S(site + year) p(site × year + age + age ²) ψ (site_s + site_e + year)	17.58	0.00	73	12 888.78
S(site + year) p(site × year) ψ (site_s + site_e + year + age)	47.24	0.00	72	12 920.50
S(site + year) p(site × year) ψ (site_s + site_e + year)	52.30	0.00	71	12 927.62

^aTop model $\text{QAIC}_c = 13\ 036.66$. Encounter and movement model structure for all models:

$$p_{\text{year (add)}}^s \psi_{\text{year (add)}}^{rs}$$

^bTop model $\text{QAIC}_c = 13\ 036.85$. Survival and movement model structure for all models:

$$S_{\text{year (add)}}^r \psi_{\text{year (add)}}^{rs}$$

^cTop model $\text{QAIC}_c = 13\ 036.51$. Survival and encounter model structure for all models:

$$S_{\text{year (add)}}^r p_{\text{year (int)}}^s$$

^dTop model $\text{QAIC}_c = 13\ 019.27$.

Parameter estimates

Parameter estimates from the top model in stage six are presented in Table 4 and Figure 2(a-c), and more fully in Tables S3 and S4. Few birds were encountered after age 20 years (Fig. 3); for this reason we report survival, encounter and movement probabilities for birds aged 2–20 years but not older to avoid extrapolation errors. Average values of the five movement parameters for each site in each year were derived from the top model by weighting the age-specific values by the proportions of each age-class in the sample (Table 4). Values for years with owl predation or hazing (see Methods) are marked

in bold. Average values over all years are presented in the last line of Table 4. Finally, we estimated the numbers of birds that moved from one site to another in each year (Table 5) by multiplying the year-specific movement rates in Table 4 by twice the number of pairs provided in Table S1.

Emigration to sites outside the study area

Based on the retrapping data and calculations presented in Appendix S1, we estimate that the average rate of emigration of adult Terns from the study population in Buzzards Bay to sites outside

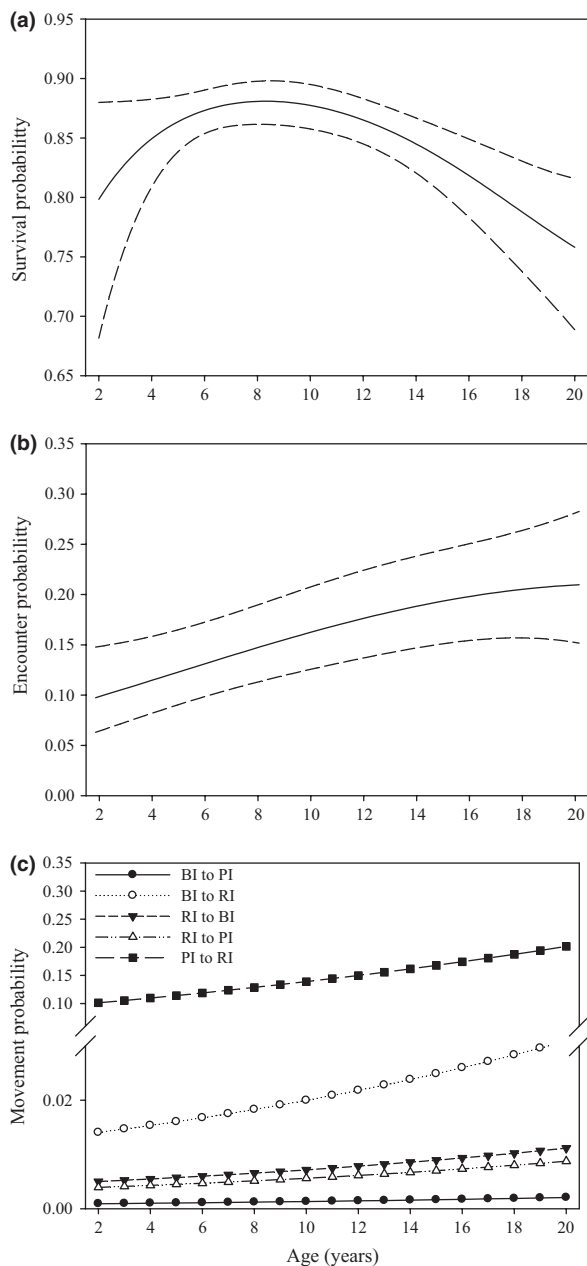


Figure 2. Parameter estimates from the top model. (a) Age-specific survival probabilities (solid line) with 95% confidence intervals (dashed lines) for all sites. (b) Age-specific encounter probabilities with 95% confidence intervals for Bird Island in 2000. The same increase in encounter probability with age applies to other years and sites (Table S3). (c) Age-specific movement probabilities in 2000–01 (note change in vertical scale). The same increase with age applies to other years (Table S4). Movement rates from PI to BI were very low and were fixed to zero.

the area was probably <0.01 per year (Table S5A, B). Some of this emigration was not permanent, because several birds that were encountered at

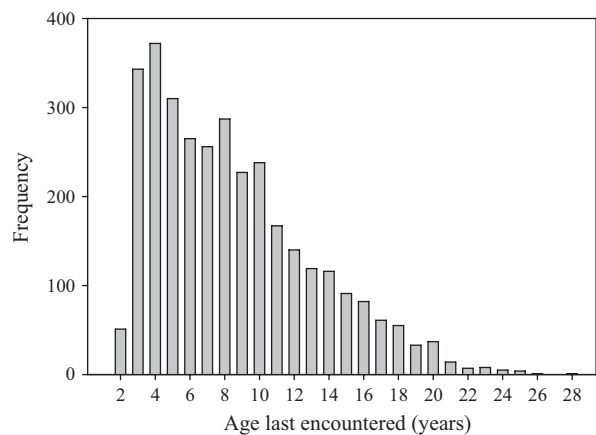


Figure 3. Frequency distribution of the age at last encounter for all birds ($n = 3290$). Thirty-seven birds were encountered for the last time at age 20 years. Relatively few were encountered after age 20. To avoid extrapolation errors, parameter estimates for birds >20 years are not reported.

other sites were subsequently retrapped at one of the Buzzards Bay sites (Appendix S1).

DISCUSSION

Our results demonstrate age-related effects on survival and dispersal from a metapopulation of a long-lived seabird. Following significant advances in theory and statistical methods, notably the concept of metapopulations (Hanski 1998) and the development of multi-state mark-recapture models (Lebreton *et al.* 2003, 2009), respectively, dispersal is now widely viewed as being of fundamental importance in population dynamics (Colbert *et al.* 2001). The biological significance of age has been demonstrated by a broad spectrum of effects on phenotypic, physiological and behavioural traits of individual animals, and on populations through vital rates including survival and dispersal (Pardo *et al.* 2013).

Our finding of age-dependence in recapture probability (Fig. 2b) contributes to the already extensive literature on sources of heterogeneity in recapture probabilities of marked animals, further reinforcing the need for careful modelling of this 'nuisance' parameter in CMR analyses (Seber 1982, Williams *et al.* 2002, Amstrup *et al.* 2005). Our finding of age-dependence in survival, including actuarial senescence (Fig. 2a), contributes to the already extensive literature on this topic (Jones *et al.* 2008). It is noteworthy that previous studies of Common Terns (Nisbet & Cam 2002, Jones

Table 4. Estimates of movement probabilities by site of origin, site of destination and year. Each entry in the table is the weighted mean of the year- and age-specific movement probabilities tabulated in Table S4, weighted by the proportion of each age-class in the birds sampled at the site of origin. The last line gives population-weighted means for each site over all years; the population-weighted mean for all sites was 0.065. Values in bold indicate years when emigration was predicted to be above average based on predation. Note that predation at RI in 1997 took place prior to and during settlement, so that the predicted effects would have been recorded as emigration after 1996. Predation in other sites and years occurred after egg-laying, so that the predicted effects would have been recorded as emigration after the year when predation occurred.

Years	Sites of origin and destination						
	BI to RI	BI to PI	BI to both	RI to BI	RI to PI	RI to both	PI to RI
1994–95	0.072		0.072	0.032		0.032	
1995–96	0.061		0.061	0.027		0.027	
1996–97	0.100		0.100	0.043		0.043	
1997–98	0.174		0.174	0.083		0.083	
1998–99	0.065	0.005	0.069	0.029	0.018	0.047	
1999–2000	0.024	0.002	0.026	0.011	0.007	0.017	0.152
2000–01	0.018	0.001	0.019	0.008	0.005	0.012	0.115
2001–02	0.027	0.002	0.029	0.012	0.007	0.019	0.166
2002–03	0.113	0.008	0.121	0.052	0.033	0.085	0.476
Weighted mean			0.075		0.041		0.192

Table 5. Estimated numbers of adult Terns changing sites within the Buzzards Bay metapopulation each year. Estimates were derived by multiplying the movement rates from Table 4 by twice the number of pairs at the site of origin from Table S1. Numbers in bold indicate years in which emigration was predicted to be high following predation.

Years	Number of birds moving					Net inflow		
	BI to RI	BI to PI	RI to BI	RI to PI	PI to RI	BI	RI	PI
1994–95	260		10			–250	250	
1995–96	193		23			–170	170	
1996–97	357		95			–262	262	
1997–98	709		155			– 554	554	
1998–99	246	17	122	47		–141	77	64
1999–2000	89	6	65	25	31	–30	30	0
2000–01	67	4	51	19	29	–20	26	–6
2001–02	115	8	72	28	92	– 51	107	–56
2002–03	385	28	381	151	266	–32	119	–87
Totals	2421	64	975	270	417	–1510	1595	–85

et al. 2008) failed to find evidence of actuarial senescence. The reason for this discrepancy may have been our use of a time-varying individual covariate to implement the effect of age in our models (Frederiksen *et al.* 2004); other factors that may have caused the discrepancy include our relatively large sample size and careful control of confounding factors in the other parameters (recapture; dispersal) in our models. Our novel findings include relatively high rates of breeding dispersal among our three closely spaced breeding colonies (confirming the earlier result of Nisbet & Cam 2002 but running contrary to the prevailing view that seabirds exhibit high site-fidelity) and

increasing rates of breeding dispersal with age. An increasing rate of breeding dispersal with age was opposite to our prediction, which we based on the fact that rates of natal dispersal in birds are generally thought to be higher than rates of breeding dispersal (Paradis *et al.* 1998). We found little evidence for differences between males and females in any recapture, survival or dispersal parameter. This is a strong negative result given our long time-series and ability to control for site and age effects. Becker *et al.* (2008) reported that natal dispersal in Common Terns is female-biased, but we know of no previous information on breeding dispersal in this species.

Breeding dispersal probabilities

Breeding dispersal probabilities varied greatly by sites of origin and destination, age and year (Table S4). Unexpectedly, they increased with age (Fig. 2c). It is generally believed that seabird colonies are founded by young birds (Kharitonov & Siegel-Causey 1988) but this may result primarily from natal dispersal, which occurs at higher rates than breeding dispersal in most or all species, including terns (Lebreton *et al.* 2003). Within our study, Common Terns breeding in 1999 at PI (soon after its recolonization) and RI (during its period of rapid growth) were much younger than those at BI (Tims *et al.* 2004). Most of these birds at PI and many of those at RI were immigrants from outside Buzzards Bay (Tims *et al.* 2004); within Buzzards Bay, movements of adults from BI to RI and from RI to PI were more frequent among older birds as early as 1995 and 1999, respectively (Table S4). We know of no other study in which age-specific breeding dispersal rates between seabird colonies have been estimated. Within colonies, Danchin *et al.* (1998) found that Black-legged Kittiwakes *Rissa tridactyla* were more likely to move to another cliff within a large colony after breeding for the first time than after subsequent breeding attempts. Kim *et al.* (2007) found that young (ages 5–8 years) and old (12–16 years) Blue-footed Boobies *Sula nebouxii* dispersed farther than middle-aged (9–11 years) birds, but dispersal distances were only 10–25 m. Neither of these findings is directly comparable with our finding of age-dependent breeding dispersal between islands 10–26 km apart. In the Lesser Kestrel *Falco naumanni*, a colonial raptor, rates of breeding dispersal to colonies at other locations (median dispersal distance 1.6 km) declined with age but were related more closely to the number of years that a bird had bred in the source colony than to age per se (Serrano *et al.* 2001).

Averaged over all years, about 7.6% of all birds that bred at BI changed sites in the following year, mainly to RI (Table 5). This high rate of breeding dispersal probably reflected the availability of nesting space at RI, as well as the consistently lower breeding success at BI (Tims *et al.* 2004). It is more surprising that about 4.4% of all birds that bred at RI changed sites in the following year, of which two-thirds moved to BI (Table 5), in spite of the availability of nesting space in the rapidly growing colony at PI. The very high rate of

movement from PI to RI (averaging 19% of breeders per year) was unexpected because breeding productivity and food availability were high at PI (Tims *et al.* 2004). High rates of emigration from PI were also detected among Roseate Terns in the same years (J. Spindelow unpubl. data). These high rates of emigration may have been caused by the abundance of Garter Snakes *Thamnophis sirtalis* at PI: although the snakes infrequently take eggs or chicks, the adult terns may perceive them as threats to themselves.

Estimates of the numbers of adult terns that moved from site to site in each year (Table 5) indicate that there was net movement from BI to RI throughout the study period, although this slowed markedly after 1999. By 1999, this net movement totalled about 1400 birds, more than one-third of the numbers breeding at RI in that year, although numbers breeding at BI had not changed (Table S1). More surprisingly, there was net movement of adults from PI to RI in each year from 2000 onwards, in spite of the rapid increase in numbers breeding at PI during that period. Because birds raised as chicks at RI and PI would not have returned to breed there early enough in the season to have been included in the nest counts until 1999 and 2003, respectively, when they were 4 years old (see footnote to Table S1), most of the increases in numbers at RI and PI must have resulted from natal dispersal of birds raised at BI and RI (which we did not measure), from immigration from outside the study area, or both (Tims *et al.* 2004). Movement rates among the Buzzards Bay colonies declined with distance (BI→RI > BI→PI, RI→BI > RI→PI and PI→RI > PI→BI; Table 4; Table S4). Similar differences according to distance have been reported in several previous studies of seabirds, including Spindelow *et al.* (1995), Lebreton *et al.* (2003), Cam *et al.* (2004), Hénaux *et al.* (2007) and Ratcliffe *et al.* (2008). Our estimates of emigration rates to more distant sites conformed to this pattern, being lower than all the movement rates among the Buzzards Bay colonies, except for the near-zero rate from PI to BI (Table 4; Appendix S1). Thus, the pattern of breeding dispersal within this large metapopulation combines high rates of dispersal at short ranges with lower rates at long ranges. This is consistent with results from Paradis *et al.* (1998) but their analysis did not account for important sources of variation in recovery probabilities including species, years and geographical locations.

Although we had expected that emigration rates would have been higher following incidents of predation or hazing at RI and BI (see Methods), models incorporating such differences were not supported (Table 2). However, two of the values in Table 4 were the highest for each site. Movement rates from RI following hazing were slightly lower than those in other years (Table 4), opposite to our prediction, although the difference was not significant (Table 2). Numbers of breeding pairs declined after each incident of predation and hazing (Table S1); our findings suggest that these declines resulted from lower rates of recruitment rather than from emigration of adults. Oro and Pradel (2000) reported increased emigration, but no reduction in recruitment to a colony of Audouin's Gulls *Ichthyaetus audouinii* following a predation incident. Despite there being no clear pattern in our results regarding the effect of hazing and predation on breeding dispersal rates, time variation was supported in all of our top breeding dispersal models (Table 3) and annual variation in rates of dispersal between colonies, such as BI to RI, was biologically significant (Table 4).

Survival probabilities

Given the evidence for high rates of breeding dispersal within Common Tern metapopulations (this study, and Appendix S2), estimates of survival based on data for single sites are inevitably biased downwards. Studies conducted over multiple sites are less subject to downward bias, but require more extensive fieldwork and much more complex modelling (Frederiksen *et al.* 2005). Our study adds to a small but increasing number of multi-site CMR studies of survival and dispersal in seabirds (Danchin & Monnat 1992, Nisbet & Cam 2002, Cam *et al.* 2004, Breton *et al.* 2006, Devlin *et al.* 2008, Ratcliffe *et al.* 2008, Spindelov *et al.* 2008, Braby *et al.* 2012).

We found that annual survival rates of Common Terns increased from about 0.80 in 2-year-old birds to a peak of about 0.88 around age 8 years and then declined to about 0.76 at age 20 years. The upper confidence limits on the estimates of annual survival rate for all ages ≥ 16 years were lower than the lower confidence limit at the peak (Fig. 2a). Note that the trends shown in Fig. 2(a) have been controlled for the age-specific dispersal among colonies shown in Table S4. If we had used data from only one site, our estimates of

survival would have shown an even greater decline among the older age-classes. This illustrates the importance of conducting multi-site studies of species with relatively high rates of adult dispersal.

Reduced survival among birds aged ≤ 4 years has been reported in two previous studies of Common Terns (Nisbet & Cam 2002, Szostek & Becker 2012). However, declining survival among older Common Terns (actuarial senescence) had not been demonstrated in earlier studies (Nisbet & Cam 2002, Jones *et al.* 2008, Szostek & Becker 2012), although Nisbet and Cam (2002) found weak evidence for it in a subset of the data used in this study. These earlier studies used smaller sample sizes (both numbers of birds and study years). However, a major reason for the difference is probably that we incorporated age into our models as a time-varying individual covariate, which increased modelling efficiency (Frederiksen *et al.* 2004). Only 9.4% (308/3290) of the birds in this study lived to ≥ 16 years (Fig. 3), so their lower survival has only minor demographic significance. However, actuarial senescence is an important concept in evolutionary biology and has been demonstrated in most animal species for which sufficient data exist (Jones *et al.* 2008).

We found no evidence for differences in survival between sexes or among sites: this is consistent with previous studies of Common Terns (Nisbet & Cam 2002, Szostek & Becker 2012). We had predicted that survival would not differ among sites because most mortality of Common Terns is thought to take place on migration or in the winter quarters (Nisbet 2002).

We found only weak evidence for differences in survival rates among years (Table 2). In contrast, Szostek and Becker (2012) found marked changes in many demographic parameters of Common Terns at a site in Germany, associated with a decrease in food availability during the breeding season. However, in that study changes in survival rates were most pronounced among birds prior to breeding for the first time; changes in annual adult survival rates were relatively minor and associated confidence intervals overlapped widely (0.90 ± 0.06 in 2002–09 vs. 0.92 ± 0.08 in 1992–2001). We had predicted that survival of our terns would have been reduced in 1991–92, based on the finding by Lebreton *et al.* (2003) and Spindelov *et al.* (2008) that survival of Roseate Terns that bred at BI in that year was markedly reduced by a hurricane that passed through a staging area used by

both species. We found some evidence for this difference, in that models with a lower survival rate in that year had QAIC_c weights of up to 0.27 (Table 2), but the magnitude of the difference in survival (1991–92 vs. other years) was lower for Common Terns (age-weighted -0.052 based on our top S(1991–92) model; Table 2) than for adult Roseate Terns (-0.091 based on model averaging from the top two models from Spendlow *et al.* 2008).

Our estimate of the maximum annual survival rate of 0.88 for middle-aged birds (Fig. 2a) is at the low end of the range of previous estimates for Common Terns (0.88–0.92; see Appendix S2). It is also in the lower part of the range of CMR estimates for other terns, although higher than those for Roseate Terns (Table S6). Our estimates take into account movements among the three breeding sites within the Buzzards Bay metapopulation, but they are subject to downward bias because emigration to sites outside Buzzards Bay is known to occur. However, available evidence indicates that the rate of emigration to other sites was probably below 0.01 (Appendix S1), which is insufficient to bring our estimate of the true survival rate as high as Szostek and Becker's (2012) estimates of local survival. However, confidence limits overlapped widely, so there is no clear evidence for a difference.

Our estimate of 0.88 is also unexpectedly low given that the population was increasing rapidly (Table S1). This was part of a steady increase in the regional population along the Atlantic coast (Nisbet 2002, Nisbet *et al.* 2013b), but the rate of increase was much higher within our study area (mean about 0.10/year vs. 0.01–0.02/year in the regional population), indicating a high rate of net immigration. Immigrants were drawn from a wide area and included birds ringed as adults as well as birds ringed as chicks (Nisbet & Cam 2002, Tims *et al.* 2004). However, it is not yet possible to assess the relative contribution of natal dispersal, breeding dispersal and local recruitment to the observed changes in numbers. Although we have data on productivity at each site in each year of our study, there are no firm estimates of pre-breeding survival for our population (Nisbet 2002), so that we cannot estimate rates of recruitment of locally raised birds. This is a significant knowledge gap that we intend to fill with a future analysis of juvenile survival and natal dispersal using our dataset on birds ringed as chicks.

CONCLUSION

Our study, the first to our knowledge to demonstrate age-specificity in recapture, survival and movement probabilities simultaneously using a single model, illustrates the value of long-term, multi-site studies of known-aged birds. It adds to other recent studies which have revealed substantial rates of breeding dispersal of several seabird species, especially terns (Appendix S2), with important implications for metapopulation dynamics and population genetics. We encourage others with similar datasets on species that exhibit breeding dispersal to use them to investigate the age-dependence of both survival and dispersal, and to account carefully for any age-related effects on encounter probabilities in their analyses.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Numbers of breeding pairs and numbers of birds encountered by trapping at each site in each year of the study.

Table S2. Numbers of pairs of terns in five large breeding colonies surrounding and contiguous to the Buzzards Bay colonies, 1984–2012.

Table S3. Parameter estimates for survival and encounter probabilities from the top model in stage six.

Table S4. Parameter estimates for breeding dispersal probabilities from the top model in stage six.

Table S5. (A) Estimated emigration rates of adults from the Buzzards Bay colonies to Monomoy National Wildlife Refuge. (B) Estimated emigration rates of adults from the Buzzards Bay colonies to Great Gull Island.

Table S6. Estimates of annual adult survival rates of Terns.

Appendix S1. Estimating rates of emigration from the study area to contiguous sites.

Appendix S2. Published data on survival and breeding dispersal in Terns.

Data S1. References for Supporting Information.