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Roseate Tern breeding dispersal and fidelity: responses to two newly restored colony sites

Jeffrey A. Spendelow,[1] David Monticelli,[2,†] James D. Nichols,[1] James E. Hines,[1] Ian C. T. Nisbet,[3]
Grace Cormons,[4] Helen Hays,[5] Jeremy J. Hatch,[6,‡] and Carolyn S. Mostello[7]

[1]*USGS Patuxent Wildlife Research Center, Laurel, Maryland 20708 USA*
[2]*Marine and Environmental Sciences Centre, Departamento de Ciências da Vida, Faculdade de Ciências e Tecnologia, Universidade de Coimbra, 3004-517 Coimbra, Portugal*
[3]*I.C.T. Nisbet & Company, 150 Alder Lane, North Falmouth, Massachusetts 02556 USA*
[4]*26201 Dennis Road, Parksley, Virginia 23421 USA*
[5]*Great Gull Island Project, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024 USA*
[6]*Department of Biology, University of Massachusetts, Boston, Massachusetts 02125 USA*
[7]*Massachusetts Division of Fisheries and Wildlife, Westborough, Massachusetts 01591 USA*

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Abstract. We used 22 yr of capture–mark–reencounter (CMR) data collected from 1988 to 2009 on about 12,500 birds at what went from three to five coastal colony sites in Massachusetts, New York, and Connecticut, United States, to examine spatial and temporal variation in breeding dispersal/fidelity rates of adult Roseate Terns (*Sterna dougallii*). At the start of our study, Roseate Terns nested at only one site (Bird Island) in Buzzards Bay, Massachusetts, but two more sites in this bay (Ram and Penikese Islands) were subsequently recolonized and became incorporated into our CMR metapopulation study. We examined four major hypotheses about factors we thought might influence colony-site fidelity and movement rates in the restructured system. We found some evidence that colony-site fidelity remained higher at long-established sites compared with newer ones and that breeding dispersal was more likely to occur among nearby sites than distant ones. Sustained predation at Falkner Island, Connecticut, did not result in a sustained drop in fidelity rates of breeders. Patterns of breeding dispersal differed substantially at the two restored sites. The fidelity of Roseate Terns at Bird dropped quickly after nearby Ram was recolonized in 1994, and fidelity rates for Ram soon approached those for Bird. After an oil spill in Buzzards Bay in April 2003, hazing (deliberate disturbance) of the terns at Ram prior to the start of egg-laying resulted in lowering of fidelity at this site, a decrease in immigration from Bird, and recolonization of Penikese by Roseate Terns. Annual fidelity rates at Penikese increased somewhat several years after the initial recolonization, but they remained much lower there than at all the other sites throughout the study period. The sustained high annual rates of emigration from Penikese resulted in the eventual failure of the restoration effort there, and in 2013, no Roseate Terns nested at this site.

Key words: breeding dispersal; colony-site fidelity; metapopulation dynamics; multistate capture–recapture models; Roseate Tern; spatial variation; *Sterna dougallii;* temporal variation.

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‡ Deceased.
† **E-mail:** monticelli.david@gmail.com

INTRODUCTION

Most seabird species aggregate in discrete colonies (patches) during their breeding periods at which time their population dynamics can be viewed in a metapopulation context (sensu Hanski and Simberloff 1997, Sanderlin et al. 2012), that is, a spatially structured system in which individuals may be faithful to the same colony site between two successive breeding events (site fidelity) or move to a different colony site from the previous one (breeding dispersal) (Clobert et al. 2001). In the latter case, individuals may either decide to settle at an active (already used) colony site or to colonize a new breeding site (e.g., in expanding populations; Clobert et al. 2001). In metapopulation theory, dispersal of individuals between connected patches is primarily related to interpatch distance (Hanski and Gilpin 1997, Matthiopoulos et al. 2005) with, for instance, the recent modeling of empirical data sets collected from small mammals suggesting an inverse relationship between dispersal probability and distance (Sanderlin et al. 2012). This relationship, however, has been more difficult to validate in studies involving seabird metapopulations (e.g., Spendelow et al. 1995, Oro and Pradel 1999, Fernandez-Chacon et al. 2013), presumably because colonially breeding seabirds are extremely mobile and can easily move over large distances, which overall render this physical factor less influential (Oro and Pradel 1999, Fernandez-Chacon et al. 2013). Also, while it might be expected that all available/suitable patches should be occupied relatively quickly in a seabird metapopulation, given the high level of mobility of individuals, behavioral traits typically exhibited by seabirds such as a high degree of site tenacity (Aebischer and Coulson 1990) and the importance of social cues (e.g., conspecific attraction) in the recruitment of new breeders (Reed et al. 1999) may decrease the propensity for individuals to disperse and slow down the colonization of available breeding sites (Kildaw et al. 2005, Matthiopoulos et al. 2005).

The study of metapopulation dynamics in long-lived seabirds is not easy, as some questions require either data sets of individually marked birds collected over a long time period and at multiple sites over a large geographic area (Spendelow et al. 1995, 2008, Lebreton et al. 2003, Cam et al. 2004, Fernandez-Chacon et al. 2013), or detailed genetic data across the entire focal system (Munilla et al. 2016). Most existing studies of seabird movement dynamics among multiple colony sites have focused on systems for which the set of sites sampled remains unchanged throughout the course of the study. Studies in which one or more colony sites are abandoned and/or become available during the course of the research are rare in the literature (but see Oro and Ruxton 2001, Martinez-Abrain et al. 2003, Breton et al. 2014). In many ways, however, systems experiencing transient dynamics far from equilibrium offer the greatest possibilities for learning when using non-experimental (observational) methods (e.g., Yackulic et al. 2014).

Fidelity to the breeding site allows individuals in long-lived species to improve knowledge of their local environment, thereby maximizing foraging efficiency and predator defense (Greenwood and Harvey 1982). Many colonially breeding seabirds have evolved a strong level of site tenacity with most individuals repeatedly breeding at the same location. Density-dependent processes such as increasing competition for access to a suitable nest site in expanding populations, nevertheless, can enhance the pool of non-breeding individuals, which may lead to the formation of new colonies (Coulson 2001). Dispersal of individuals to a different colony site also may increase following breeding failures (Massey and Fancher 1989, Palestis and Hines 2015), often linked to the deteriorating conditions at the previous colony site due to the presence of predators, poor food availability/foraging conditions, or changes in the quality of the nesting habitat (Greenwood 1980, Bried and Jouventin 2001, Kildaw et al. 2005).

In this study, we exploited the restoration and recolonization of two additional colony sites within an existing metapopulation system to address several questions about bird movements within the restructured system. Roseate Terns *Sterna dougallii* breeding in coastal areas along the Northwest Atlantic Ocean form a metapopulation with >90% of the total numbers from 1988 to 2013 typically nesting at five colony sites with a distance of 170 km between the two most widely separated sites in the warmwater areas (sensu Nisbet and Spendelow 1999) of Massachusetts, New York, and Connecticut (MA-NY-CT) in the northeastern United States: Bird Island, MA (BD; 41°40′ N, 70°43′ W), Ram Island, MA (RM; 41°37′ N, 70°48′ W), Penikese Island, MA (PK; 41°27′ N, 70°56′ W), Great Gull Island, NY (GG; 41°12′ N, 72°07′ W), and Falkner Island, CT (FI; 41°13′ N, 72°39′ W; Table 1). The first three of these sites form a cluster 10–26 km apart in Buzzards Bay and are separated by ≥100 km from the other

Table 1. Estimated "peak period†" numbers of Roseate Tern nests‡ at the five study sites and other colony sites in the warmwater group§ in the northeastern United States, 1988–2013.

	Site						
Year	Falkner Island	Great Gull Island	Penikese Island	Ram Island	Bird Island	Other sites	Total
1988	147	1004	–	–	1572	137	2860
1989	96	960	–	–	1473	155	2684
1990	150	1026	–	–	1547	137	2860
1991	149	1204	–	–	1728	178	3259
1992	107	964	–	–	1375	144	2590
1993	130	1040	–	–	1319	109	2598
1994	123	1138	–	76	1238	128	2703
1995	125	1056	–	197	1250	289	2917
1996	135	1064	–	719	996	70	2984
1997	136	1455	–	253	1179	100	3123
1998	115	1690	–	543	1113	162	3623
1999	110	1747	–	630	1148	76	3711
2000	110	1762	–	988	1130	32	4022
2001	95	1562	–	626	1062	84	3429
2002	65	1505	–	952	505	161	3188
2003	45	1613	251	557	904	178	3548
2004	37	1352	9	936	554	289	3177
2005	44	1195	76	724	680	137	2856
2006	62	1227	48	463	1111	133	3044
2007	54	1546	102	661	919	222	3504
2008	32	1288	66	566	747	30	2729
2009	28	1413	43	588	708	29	2809
2010	45	1303	37	584	735	14	2718
2011	48	1439	34	377	937	4	2839
2012	36	1596	9	439	814	1	2895
2013	26	1543	0	535	772	1	2877

† All counts are of nests initiated during the main peak of nesting at each colony (usually the first 23–27 d of the season). At most sites in most years, additional nests (usually 5–20% of the total) were initiated after the peak. These nests were attended by young birds (2- to 4-yr old) or pairs re-laying after early failures.

‡ A few nests (1.5–2.5% of the total) were attended by three or more birds (Nisbet and Hatch 1999).

§ The warmwater group includes all sites known to have been occupied by Roseate Terns in Connecticut, New York, and Massachusetts south and west of Cape Cod.

two sites, which are 45 km apart in Long Island Sound (Fig. 1). This population has been intensively studied since 1988, with capture–mark–reencounter (CMR) studies yielding estimates of survival of both adults and juveniles through 2004, as well as estimates of breeding and natal dispersal rates among three of the sites through 1998 (Spendelow et al. 1995, 2002, 2008, Lebreton et al. 2003, Nichols et al. 2004). Bird, Great Gull, and Falkner were established breeding colony sites for decades before 1988; Ram and Penikese were the sites of former colonies that had been overrun by gulls *Larus* spp. in the 1950s and 1970s, respectively, and were re-occupied by Roseate Terns in 1994 (Harlow 1995) and 2003 (Tims et al. 2004), respectively, after their initial recolonization by Common Terns (*S. hirundo*). Here, we extend our previous CMR studies to investigate changes in dispersal rates of adults during the period in which Ram and Penikese were re-occupied. We also document the consequences to adult movements of two disruptive events during the study period: a prolonged period of predation at Falkner that started in the mid-1990s and an oil spill in Buzzards Bay in April 2003 following which terns were hazed (deliberately disturbed) in an attempt to discourage them from settling at Ram during cleanup operations there and to induce them to move to other sites. These events provided us with a unique opportunity to examine several questions about movements of adult Roseate Terns to and from new and existing colony sites, with a particular focus on the differences in the

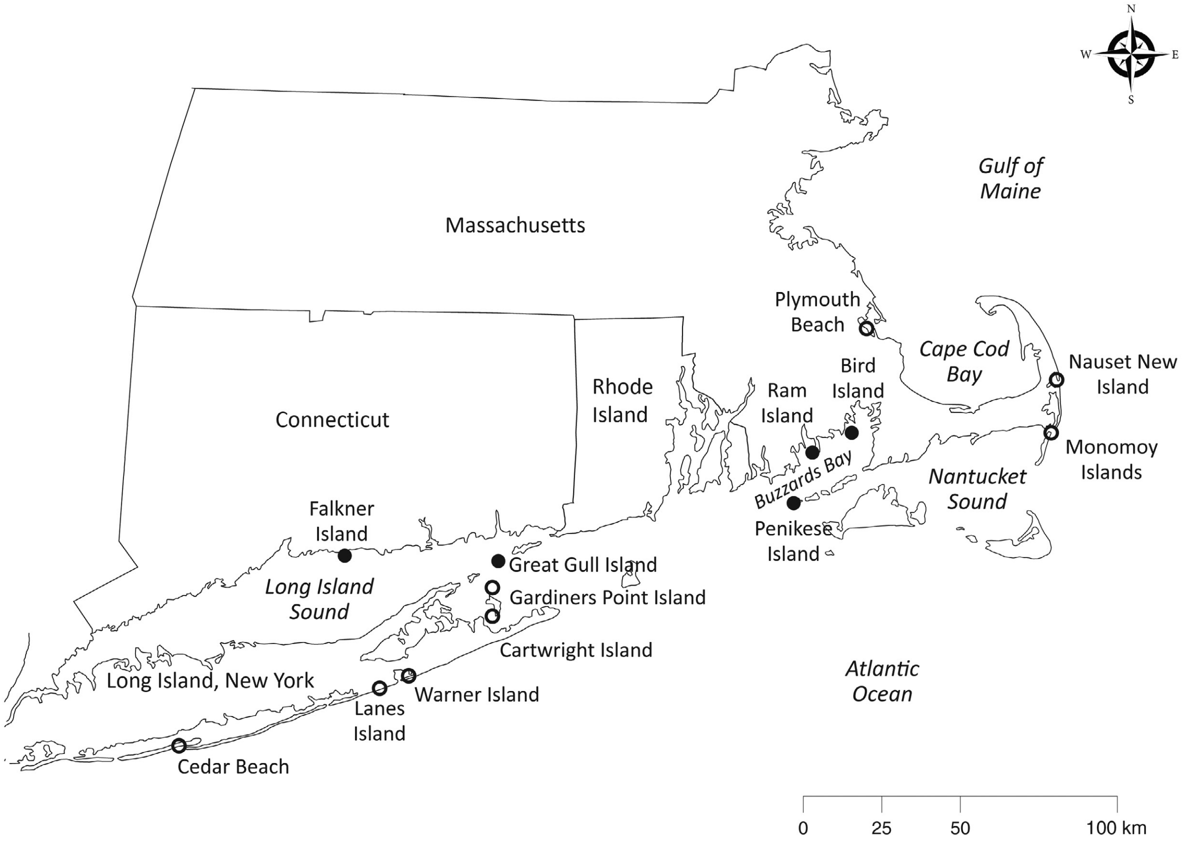

Fig. 1. Location of study colonies (filled circles) and other colony sites (open circles) used by Roseate Terns 1988–2013 in the MA-NY-CT area of the northeastern United States.

recolonization processes at the two new sites as the study progressed. Determining the effects of these factors on survival (Lebreton et al. 2003, Spendelow et al. 2008) and breeding dispersal/fidelity rates (this study) should lead to a better understanding of the ways in which management actions may affect overall recovery of this and other metapopulations and species with similar life-history attributes.

Hypotheses and predictions

Based on the available literature and prior information, we formulated four hypotheses about intercolony movements and colony-site fidelity of breeding adults. Each hypothesis leads to predictions that can be tested using CMR methodology:

Hypothesis 1.—The repeated use of a colony site by breeding individuals may indicate high habitat quality, and colony-site fidelity may be expected to be higher at long-established colonies than at newly established ones (Martinez-Abrain et al. 2003). The prediction is that site fidelity during 1994–2008 should have been lower at the "new" colony sites Ram and Penikese than at the long-established colonies at Bird, Great Gull, and Falkner. Fidelity would be expected to have been lowest during the first few years of settlement at Ram and Penikese and to have increased progressively thereafter.

Hypothesis 2.—The hazing at Ram in 2003 was successful in displacing previous breeders to other sites and reducing movements to this site by previous breeders. The prediction is that fidelity at Ram from 2002 to 2003 should have been lower than that in earlier and later years, with increased dispersal to other (likely nearby) sites as was intended by the management action.

Hypothesis 3.—Dispersal rates may increase following predation on eggs, chicks, and/or adults (Massey and Fancher 1989). The specific events investigated here are predation of chicks and eggs at Falkner by Black-crowned Night-herons (*Nycticorax nycticorax*) from 1996 through the mid-2000s (Spendelow et al. 2002, 2008). Predation at this colony site was classified as moderate from 1996 to 2001, acute from 2002 to 2003, and moderate after 2003 (U.S. Fish and Wildlife Service [USFWS] 2010); hence, the prediction is that emigration rates should have increased progressively across the periods 1988–1995, 1996–2001, 2002–2003 and decreased again in 2004–2008.

Hypothesis 4.—An individual leaving one colony site is more likely to settle at a nearby site than at a more distant one (the "distance" hypothesis: Hanski 1998, Grosbois and Tavecchia 2003). The predictions are that dispersal rates among the three sites in Buzzards Bay (Bird, Ram, and Penikese) and those between the two sites in Long Island Sound (Great Gull and Falkner) should have been higher than those between the Buzzards Bay sites and the two more distant Long Island Sound sites.

METHODS

Study population, area, sites, and period

Our study population was comprised of the adult Roseate Terns occurring in the coastal areas of MA-NY-CT (Fig. 1) during the breeding period from late May to mid-July from 1988 to 2009. Counts or estimates of breeding pairs at each of the five study sites where CMR data were collected, and at the other sites within the study area where CMR data were not collected, are shown in Table 1. Total numbers increased steadily from 1988 to 2000, except for a decline from 1991 to 1992 attributed to a hurricane (Spendelow et al. 2008), mostly decreased from 2000 to 2010, then increased slightly from 2011 to 2013. The study site population comprised 90–99% of the warmwater segment (Nisbet and Spendelow 1999, USFWS 2010) of the regional population throughout the study period. Up to 300 pairs of Roseate Terns nested at several other sites within Gardiners Bay and on the south shore of Long Island to the south and west of our study sites (Fig. 1) sporadically during the study period, but CMR studies at two of these sites revealed little interchange with those in our study area (Spendelow et al. 1995; authors' *unpublished data*) and <30 nested at those sites after 2009 (Table 1). A partially discrete population of 200–300 pairs of Roseate Terns breeds in the coldwater region in the Gulf of Maine and Nova Scotia (USFWS 2010), but breeding dispersal of adults from the warmwater group to the coldwater group appears to be infrequent (Spendelow et al. 2010). Hence, rates of permanent emigration of prior breeders from our study sites are thought to be low.

Study design and fieldwork methods

Study design.—We designed this study to produce combinations of recapture and resighting encounters at each study site that were representative of the Roseate Terns present during the main peak of the nesting season. We marked individuals with various combinations of metal bands and plastic colorbands, and we resampled them by a combination of trapping at nests and resighting by spotting scopes (Spendelow et al. 2008, for details, see Appendix S1). Although there may have been some heterogeneity in resighting rates of birds marked with different types of band combinations, we pooled all trappings and resightings to estimate a single "encounter rate" for each site-year (Table 2).

Estimates of nesting population size.—Estimates of the "peak season" numbers of pairs nesting at the five study sites and at the other "warmwater sites" from 1988 to 2013 are given in Table 1. Even though CMR data were not collected at all study sites after 2009, we have included the nesting population data for the next 4 yr because they provide information relevant to some of our predictions about trends in colony-site fidelity.

Identification of banded terns.—After their initial banding, adult terns could be re-encountered and identified by being trapped, caught by hand, or resighted via a spotting scope. A few banded Roseate Terns found dead were not counted as being identified in the year they were found dead. We considered use of these birds found dead in our modeling but concluded that the small numbers did not justify the added modeling complexity. Resightings were made at all sites in most years and resighting efforts were designed to sample the Roseate Terns in all parts of each study site except at Great Gull, where logistic constraints prevented this. Trapping was

Table 2. Adult Roseate Tern colony-site encounters (captures and resightings: see text for details) at the five study sites in the northeastern U.S. warmwater group, 1988–2009.

	Site				
Year	Falkner Island	Great Gull Island	Penikese Island	Ram Island	Bird Island
1988	160	247	–	–	207
1989	201	203	–	–	327
1990	256	188	–	–	431
1991	286	338	–	–	502
1992	229	237	–	–	571
1993	291	359	–	–	631
1994	276	330	–	31	994
1995	279	266	–	41	872
1996	305	161	–	193	809
1997	295	205	–	134	781
1998	243	201	–	332	770
1999	220	125	–	291	736
2000	223	203	–	290	725
2001	176	211	–	151	692
2002	145	216	–	307	515
2003	105	226	285	343	550
2004	63	259	12	907	619
2005	48	227	112	641	552
2006	20	201	61	360	705
2007	0	269	124	542	700
2008	28	205	98	537	928
2009	0	223	56	533	794

terminated and resighting efforts were reduced at Falkner after 2003. We used only trapping data from Great Gull, but combined trapping and resighting data from the other sites. This difference was readily handled in the CMR modeling, as we used different encounter probabilities for each site and year. Resightings of individuals made before 1 June in Buzzards Bay and those made after 16 July at all sites were excluded from the analysis unless those "early" or "late" birds were recorded as being associated with a nest.

Modeling approach and goodness-of-fit testing

Our CMR data set incorporated marked adult Roseate Terns that nested at least once during the study period in our five-site system with the modeling and parameter estimation strategy being similar to that given in Spendelow et al. (2008). For terns first banded as nestlings, the initial capture or resighting as a breeding adult at a nest was the initial encounter used in our modeling. Briefly, as a result of prior modeling done for our study of temporal variation in survival rates (Spendelow et al. 2008), our most general model (Arnason-Schwarz model [Brownie et al. 1993] accounting for the presence of transients [Pradel et al. 1997]; see M8 in Table 3) has the following structure, $S^{r}_{t\times\tau}, \psi^{rs}_{t}, P^{r}_{t}$, where S refers to survival probability, ψ to transition (movement) probability, and P to recapture probability. Subscripts t and τ denote "time" (year) and the transient effect, respectively, with $t \times \tau$ indicating an interaction between these two factors. The term "transient" applies to the situation in which some unknown fraction of new (i.e., not previously detected as breeding) birds has a near-zero chance of returning to the study system (Pradel et al. 1997). The transient effect was implemented with different survival parameters during any year t for new adults caught and marked for the first time and for previously marked birds, the latter parameter reflecting survival of adult members of the studied metapopulation. Superscripts r and s correspond to the site of release in year t and to the site of recapture or resighting in year t+1, respectively. Thus for each year, this five-state model incorporates 20 transition parameters corresponding to movement probabilities among sites. Five transition parameters corresponding to "site

Table 3. Set of candidate models used to address several hypotheses about intercolony movements (ψ^{rs}) and site fidelity (ψ^{rr}) of Roseate Tern adults breeding at five locations (Bird Is., BD; Falkner Is., FI; Great Gull Is., GG; Penikese Is., PK; Ram Is., RM) in the northeastern United States (1988–2009).

Model	Notation	ΔQAIC$_c$	QAIC$_c$ weight	No. Par	Deviance
M1	$S^{r}_{(88-99,91,00-08)\times\tau},\psi^{\mathrm{rs}}_{88-92,93,94-01,02,03-08},P^{s}_{t}$	0	0.556	173	89754.30
M2	$S^{r}_{(88-99,91,00-08)\times\tau},\psi^{\mathrm{rs}}_{88-92,93,94-00,01,02,03-08},P^{s}_{t}$	0.577	0.417	185	89701.24
M3	$S^{r}_{(88-99,91,00-08)\times\tau},\psi^{\mathrm{rs}}_{88-92,93,94-95,96-01,02,03-05,06-08},P^{s}_{t}$	6.101	0.026	205	89632.15
M4	$S^{r}_{(88-99,91,00-08)\times\tau},\psi^{\mathrm{rs}}_{88-92,93,94-01,02,03-05,06-08},P^{s}_{t}$	13.543	0.001	193	89694.37
M5	$S^{r}_{(88-99,91,00-08)\times\tau},\psi^{\mathrm{rs}}_{88-92,93,94-01,02,03,04-05,06-08},P^{s}_{t}$	24.338	0	213	89628.21
M6	$S^{r}_{(88-99,91,00-08)\times\tau},\psi^{\mathrm{rs}}_{88-92,93,94-00,01,02,03,04,05-08},P^{s}_{t}$	25.789	0	225	89577.14
M7	$S^{r}_{(88-99,91,00-08)\times\tau},\psi^{\mathrm{rs}}_{88-92,93,94-95,96-01,02,03,04-05,06-08},P^{s}_{t}$	29.384	0	225	89585.28
M8	$S^{r}_{t\times\tau},\psi^{\mathrm{rs}}_{t},P^{s}_{t}$	791.457	0	921	88158.39

Main predictions† for ψ^{rs} under different models:

M1: Site fidelity constant among years both at RM following recolonization in 1994 (94–01) and at PK following recolonization in 2003 (03–08)

M2: Same model as M1 but with site fidelity decreasing at FI‡ after 2000 due to predation in 2001 (01) which became even more acute in 2002

M3: Site fidelity lower at RM for first two years (94–95) following recolonization in 1994 and site fidelity at PK lower for first three years (03–05) following recolonization in 2003; Site fidelity decreasing progressively at FI after 1995 (96–01) due to predation from 1996 onwards

M4: Site fidelity at RM constant among years (same as M1) and site fidelity at PK lower for first three years (03–05) following recolonization in 2003

M5: Site fidelity at RM constant among years (same as M1) and site fidelity at PK lower for first year following recolonization (03), then progressively increasing (04–05, 06–08)

M6: Same as M2 but with site fidelity at PK lower for first year following recolonization (03), then progressively increasing (04, 05–08)

M7: Site fidelity lower at RM for first two years (94–95) following recolonization and site fidelity at PK lower for first year (03) following recolonization, then progressively increasing (04–05, 06–08); Site fidelity decreasing progressively at FI after 1995 due to predation from 1996 onwards (96–01)

M8: Arnason-Schwarz model with transient effect on survival

Notes: Site specificity in survival (*S*), movement (ψ^{rs}), and recapture (*P*) probabilities is denoted by superscripts *r, s*, and the subscripts *t* and τ stand for year and the transient effect, respectively. Reduced-parameter models (M1–M7) are obtained by combining specific sets of years for *S* and ψ^{rs}. As an example of notation, model M1 has a survival component estimated separately over the following three periods: 1988–1990/1992–1999, 1991, 2000–2008. QAIC$_c$ values are based on a variance inflation factor $\hat{c} = 2.27$ according to the GOF test performed on M8 (Arnason-Schwarz model with transient effect on survival; see *Methods*). No. Par is the number of parameters estimated.

† In all models, both 1993 and 2002 transition probabilities were necessarily modeled separately from all other years (see *Methods*).

‡ 2001 was a transition year between a period of increasing (1992–2000) and decreasing (2001–2009) population trend. The breeding population at FI declined by about 30% between 2001 and 2002.

fidelity" probabilities (i.e., probability of an individual breeding at one of the study sites in year *t* breeding at the same site the next year *t*+1) are subsequently estimated for any particular site as "1-sum of movement probabilities to the other sites."

The set of candidate models was developed by simplifying the parameterization of this general model, with the new emphasis on testing hypotheses related to movement of individuals among sites. Model structure for both survival and recapture rates followed Spendelow et al. (2008). Thus, models with time- and site-specificity in recapture probabilities were fitted, while for the survival component we used specific sets of years corresponding to the periods of increasing (1988–1990 + 1992–1999) and decreasing (2000–2009) population trends, and the year (1991) of passage of Hurricane Bob.

Transition probabilities were modeled to account for the fact that not all five sites were available for sampling during the entire study period. Only Bird, Great Gull, and Falkner were used by Roseate Terns during the earliest study years (1988–1993), while Ram and Penikese were re-occupied by Roseate Terns from the 1994 and 2003 breeding seasons onwards, respectively. The incorporation of more sites in the CMR data set as the study progressed required that 1993 and 2002 transition probabilities be examined separately from those of all other years due to the fact that movements from Ram and Penikese to other

Table 4. Transition probabilities (ψ^{rs}), conditional on survival, for five Roseate Tern colony sites in the northeastern United States monitored from 1988 to 2009.

ψ^{rs}	Study period				
	1988–1992	1993	1994–2001	2002	2003–2008
(a) Intercolony movements between FI and GG					
FI → GG	0.077 (0.012)	0.047 (0.017)	0.080 (0.010)	0.097 (0.040)	0.062 (0.021)
GG → FI	0.022 (0.004)	0.026 (0.007)	0.016 (0.002)	0.004 (0.004)	0.006 (0.002)
(b) Intercolony movements among the three sites in Buzzards Bay (BD, RM, PK)					
BD → RM	–	0.009 (0.004)	0.211 (0.014)	0.114 (0.021)	0.145 (0.008)
RM → BD	–	–	0.234 (0.014)	0.228 (0.030)	0.197 (0.010)
BD → PK	–	–	–	0.101 (0.013)	0.035 (0.004)
PK → BD	–	–	–	–	0.315 (0.027)
RM → PK	–	–	–	0.100 (0.015)	0.029 (0.004)
PK → RM	–	–	–	–	0.384 (0.030)
(c) Intercolony movements between any of the three sites in Buzzards Bay and FI					
FI → BD	0.015 (0.004)	0.078 (0.018)	0.010 (0.003)	0.000	0.012 (0.007)
BD → FI	0.004 (0.001)	0.000	0.002 (0.001)	0.003 (0.002)	0.000
FI → RM	–	0.004 (0.004)	0.009 (0.003)	0.000	0.007 (0.006)
RM → FI	–	–	0.001 (0.001)	0.000	0.001 (0.001)
FI → PK	–	–	–	0.017 (0.012)	0.000
PK → FI	–	–	–	–	0.007 (0.005)
(d) Intercolony movements between any of the three sites in Buzzards Bay and GG					
GG → BD	0.037 (0.005)	0.064 (0.013)	0.014 (0.002)	0.011 (0.006)	0.007 (0.002)
BD → GG	0.021 (0.005)	0.000	0.011 (0.002)	0.004 (0.007)	0.011 (0.003)
GG → RM	–	0.012 (0.005)	0.014 (0.003)	0.012 (0.008)	0.015 (0.003)
RM → GG	–	–	0.018 (0.004)	0.004 (0.004)	0.013 (0.003)
GG → PK	–	–	–	0.016 (0.006)	0.008 (0.002)
PK → GG	–	–	–	–	0.026 (0.011)

Notes: Parameter estimates (±SE) are derived according to the best QAIC$_c$-ranked model (model M1 in Table 3), in which transition rates were estimated over five periods (1988–1992, 1993, 1994–2001, 2002, 2003–2008). Abbreviation codes for the five colony sites are BD = Bird Is., FI = Falkner Is., GG = Great Gull Is., PK = Penikese Is., RM = Ram Is. As an example, the parameter noted "FI → GG" for 1993 refers to the probability of movement from Falkner to Great Gull over the 1993–1994 time interval. Two colony sites were unused by the birds until 1994 (RM) and 2003 (PK), with notation "–" indicating that no parameter estimate is available (i.e., for transitions that cannot occur).

sites could not occur during their initial year of recolonization (Table 4).

As an example of model notation, the following model structure $\{S^r_{(88-99,91,00-08)\times\tau}, \psi^{rs}_{88-92,93,94-00,01,02,03-08}, P^r_t\}$ has (1) site-specific survival rates estimated separately over three periods (1988–1990 + 1992–1999, 1991, 2000–2008; see above for the rationale), (2) site-specific transition probabilities estimated separately for six subsets of years (including years of recolonization of Ram in 1994 and Penikese in 2003), and (3) fully time-dependent and site-specific recapture–resighting probabilities (see Table 3). Our set of reduced-parameter models was built by combining specific sets of years for transition probabilities to allow us to test predictions 1, 2, and 3. A goodness-of-fit test was developed for our most general (Arnason-Schwarz with transient effects) model, and the resulting chi-square statistic and degrees of freedom were used to compute a variance inflation factor ($\hat{c}$), which, in turn, was used to compute QAIC$_c$ values of our candidate models (also see Pradel et al. 2003, Spendelow et al. 2008). Candidate models were compared using QAIC$_c$ weights, which provide a relative measure of how well a model is supported by the data compared with other models (Burnham and Anderson 2002). The final model was the one with the lowest QAICc value as it provides the best explanation of the processes that generated the data, and the parameter estimates of this best $\mathrm{QAIC_c}$-ranked model provided further means to assess the validity of our predictions. All analyses were conducted with program M-SURGE (Choquet et al. 2004).

RESULTS

Model fit and selection

The goodness-of-fit test for our most general model (Arnason-Schwarz model with transient effect on survival) yielded $\hat{c} = 2.27$, and this value was used to compute $\mathrm{QAIC_c}$ values and to inflate model-based variance estimates. This model was poorly ranked by $\mathrm{QAIC_c}$ when compared to most reduced-parameter models in which specific sets of years were pooled (model M8 vs. models M1–M7; Table 3). The best $\mathrm{QAIC_c}$-ranked models were those with survival parameters (with transient effect) modeled separately over three periods (1988–1990 + 1992–1999; 1991; 2000–2008) and with both full time- and site-specificity retained for the re-encounter (recapture and resighting) parameters (see Table 3 and also Appendices S2 and S3 for survival/recapture parameter estimates).

Based on this starting structure for survival and detection parameters, our set of competing models was further developed by focusing on various parameterizations of ψ^{rs} according to the specific predictions being tested (see *Introduction*). In general, models in which transition probabilities during the first 2–3 yr of recolonization of the new sites were modeled separately from those of subsequent years did not perform well according to $\mathrm{QAIC_c}$ ranking (models M3–M7), suggesting the absence of a progressive long-term increase in site fidelity as recolonization progressed. For example, models M7 and M3 in which site fidelity at Ram during the first two recolonization years (1994–1995) differed from that of later years (combined $\mathrm{QAIC_c}$ weights of 0.026) were much less supported than the two models M1 and M2 in which site fidelity was constant among those years (combined $\mathrm{QAIC_c}$ weights of 0.973, Table 3). Similarly, models in which site fidelity at Penikese during the first three recolonization years (2003–2005; because few of the individuals that nested at Penikese in 2003 returned in 2004, we allowed an extra year for adults with prior breeding experience to start developing fidelity to this site) differed from that of later years (models M1 and M2 vs. M3 and M4) also were less supported by the data (combined $\mathrm{QAIC_c}$ weights of 0.973 vs. 0.027, Table 3). Several variants of M3 and M4 also were developed by pooling different subsets of years based on a priori hypotheses (M5–M7), but none of those more highly parameterized models performed better. In fact, the best $\mathrm{QAIC_c}$-ranked models (M1 and M2) were those where transition probabilities were modeled with the smallest number of parameters possible (i.e., model M1 only used five subsets of years: 1988–1992, 1993, 1994–2001, 2002, 2003–2008). However, we note that these transition parameters are typically small and difficult to estimate, so it is always possible that more complicated models would have been better supported with larger sample sizes.

Estimates of site fidelity

Site fidelity estimates derived from the best $\mathrm{QAIC_c}$-ranked model (M1) suggested that fidelity remained high (i.e., >0.87) for the duration of the study at the two established colony sites in Long Island Sound, Great Gull, and Falkner (Fig. 2). Estimated fidelity to the other established site, Bird, was very high (>0.97) prior to Ram becoming available (1994) and then dropped to 0.77–0.81 (Fig. 2, Table 4). Estimated fidelity differed for the new colony sites, with estimates for Ram being somewhat lower than estimates for Bird during years with no hazing and substantially greater than estimated fidelity for Penikese (Fig. 2, Table 4). Ram had low estimated fidelity from 2002 to 2003 ($\hat{\psi}_{2002}^{\mathrm{RM,RM}} = 0.67$), consistent with the hypothesis of an effect of the hazing done early in 2003 while the terns were deciding where to nest. For all five subsets of years, site fidelity estimates for all three long-established colonies (Bird, Great Gull, and Falkner) were higher than those for the newly established colonies (Ram, Penikese; Fig. 2). Site fidelity estimates at Ram quickly approached those for Bird, but this did not happen at Penikese which was nearly abandoned the year following its initial recolonization.

Contrary to expectations, we found no evidence of a decrease in site fidelity at Falkner following the first year (1996) when moderately

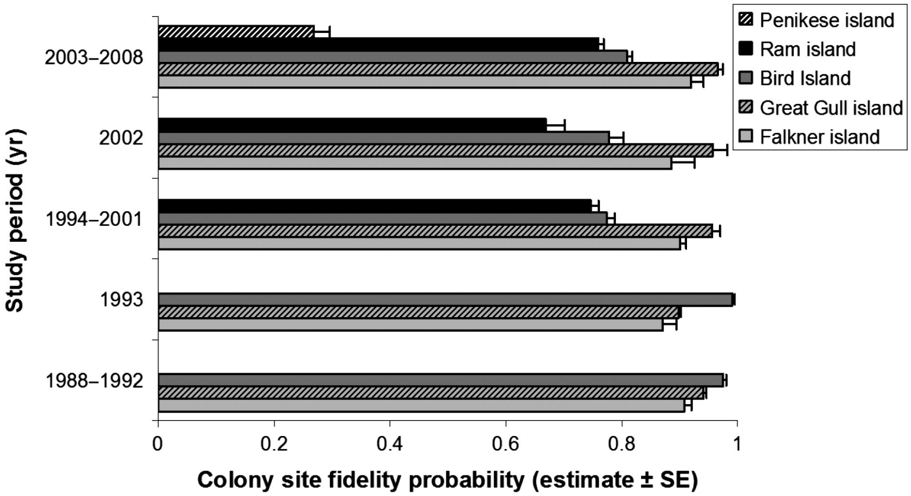

Fig. 2. Site fidelity (ψ^{rr}) probabilities at five Roseate Tern colony sites in the northeastern United States over five periods (1988–1992, 1993, 1994–2001, 2002, and 2003–2008). Two colony sites were unused by these terns until 1994 (Ram Island) and 2003 (Penikese Island). Parameter estimates (±SE) are derived according to the best $QAIC_c$-ranked model (model M1 in Table 3).

high rates of nest predation depressed breeding success. Despite the population decline that occurred after 1998 at Falkner, fidelity at that site by prior breeders was fairly stable over the entire study period, with the highest estimates observed during the 2003–2008 time interval (estimated site fidelity = 0.92; Fig. 2) following the 2 yr (2002–2003) when nest predation was particularly acute.

Intercolony movements

The 20 transitions probabilities derived from our best $QAIC_c$-ranked model (M1) are presented in Table 4, which comprises eight pairs of intercolony movement rates between nearby colony sites (Table 4a, b) and 12 pairs of intercolony movement rates between distant ones (Table 4c, d). For each of five periods (1988–1992, 1993, 1994–2001, 2002, and 2003–2008), movement rates of breeding adults between colonies were averaged (mean ± SE) separately between pairs of distant sites and pairs of nearby sites. Overall, there was a strong tendency for nearby sites to exchange individuals at a much higher rate compared with the more distant sites (Fig. 3). In addition, the estimates presented in Table 4 suggest that movement between the two colony sites in Long Island Sound was asymmetric, with consistently greater rates from the smaller colony at Falkner to the large colony at Great Gull than vice versa. Adults from both Falkner and Great Gull moved to the Buzzards Bay colony sites at estimated annual rates <0.08 and usually <0.04. In more recent years (>1993), estimated annual rates of movement between Falkner or Great Gull and Bird, Ram, and Penikese were <0.02 (Table 4). Adults from all three established colony sites contributed to the colonization of Ram and Penikese as they became available. However, the estimated rate of movement of adults from nearby Bird to Ram and Penikese was much larger for most years than rates of movement to Ram and Penikese from the other two sites. Rates of movement of adults among sites within Buzzards Bay were high, with estimates consistently greater from the new sites to Bird than vice versa (Table 4). Ram adults showed greater estimated rates of movement to Bird (0.20–0.23) than to Penikese (0.03–0.10). Penikese adults, however, showed substantial estimated movements (>0.30) to both Bird and Ram.

Finally, based on colony size data (Table 1), transition probabilities were used to crudely estimate the number of breeding adults moving annually between colonies during each of the five study periods (Table 5). The most apparent trend was a negative net colony gain (i.e., a loss) associated with movement for the large Great Gull

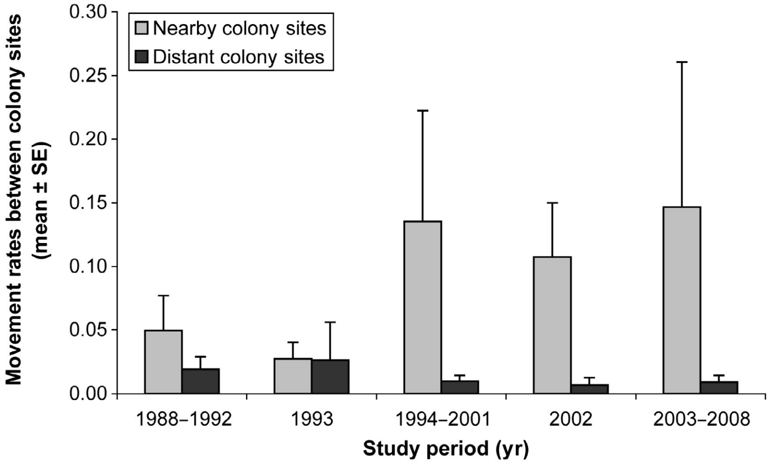

Fig. 3. Movement rates (mean ± SE) between pairs of nearby colony sites (eight pairs of rates; cf. Table 4a, b) and distant colony sites (12 pairs of rates; cf. Table 4c, d) over five periods (1988–1992, 1993, 1994–2001, 2002, and 2003–2008).

colony ("source colony") and positive net colony gain from movement for Falkner ("sink colony") throughout the course of this study (Table 5). For the three sites in Buzzards Bay, Bird was an important "source colony" during the initial recolonization process of Ram, while the latter colony site was, in turn, a major "source colony" during the initial colonization of Penikese (Table 5).

Discussion

We developed multistate models to examine movement probabilities of breeding adults (and their complements—site fidelity) based on a 22-yr CMR data set involving the largest subpopulation units of the northeastern U.S. Roseate Tern metapopulation. Of particular interest was the fact that two colony sites became available to the terns as the study progressed, allowing us to test four a priori hypotheses regarding dynamics of the recolonization process. These predictions and associated evidence are discussed below based on our modeling results.

Prediction 1: Colony-site age hypothesis

Our first prediction that site fidelity would be higher at long-established colonies compared with newly available ones was supported by the

Table 5. Estimated numbers of Roseate Tern breeding adults moving annually among five colony sites of the northeastern United States metapopulation.

Study period	Birds moving from					Birds moving to					Net colony gain from movement†				
	FI	GG	BD	RM	PK	FI	GG	BD	RM	PK	FI	GG	BD	RM	PK
1988–1992	24	122	76			58	84	80			34	−38	4		
1993	34	212	24			54	12	154	50		20	−200	130	50	
1994–2001	24	126	510	256		50	62	278	524		26	−64	−232	268	
2002	14	130	224	632		16	24	468	152	152	2	−106	244	−480	152
2003–2008	8	98	312	312	134	16	28	334	280	118	8	−70	22	−32	−16

Notes: Estimates are the product of movement rates (cf. Table 4) and the estimated numbers of breeding individuals (2× nest number data in Table 1) averaged during each of five periods (1998–1992, 1993, 1994–2001, 2002, 2003–2008). "Bird moving from" (= emigration) refers to the estimated total number of breeding adults emigrating annually from a given site to the other four colony sites, while "Birds moving to" (= immigration) corresponds to the estimated total number of breeding adults immigrating annually to a particular site from the other four colony sites. Abbreviation codes for the five colony sites are FI = Falkner Is., GG = Great Gull Is., BD = Bird Is., RM = Ram Is, PK = Penikese Is.

† Negative "gain" indicates net loss of breeding adults.

data to a degree, suggesting the potential importance of colony-site age (old vs. new) to an individual's decision to switch colony sites between two successive seasons. However, we noted a substantial reduction in fidelity at one established colony (Bird) soon after nearby Ram became available. The initial colonization of Ram resulted from only small movement rates of prior nesters from the three established colony sites at Bird, Great Gull, and Falkner. Subsequent breeding dispersal rates to Ram from Falkner and Great Gull continued to be small, but movement rates from Bird to Ram increased quickly and substantially with estimates exceeding 0.20 for the period 1994–2001 and continuing >0.10 for the remainder of the study. Because of the close proximity of Bird and Ram, and possibly as a result of intermittent predation by owls and mammals at both sites in different years, the drop in fidelity at Bird really was not that surprising as some terns moved back and forth repeatedly between these two sites. We also expected site fidelity at the newly established colony sites to increase progressively with time. However, Ram showed a fairly quick increase rather than a sustained trend in estimated fidelity in the 15 yr following colonization. Movement rates from Ram to Bird were relatively large and variable, but estimated fidelity of adults to Ram for years without hazing was about 0.75, only slightly smaller than that for Bird. These latter results do not support the prediction that colony age is the most important determinant of fidelity and movement. The fidelity results at Bird and Ram are more consistent with previous work reporting that seabird movement dynamics were relatively unaffected by the number of years of site occupation and are influenced more by other factors (e.g., Martinez-Abrain et al. 2003).

Prediction 2: Responses to hazing at Ram Island

Our second prediction concerned the effectiveness of the hazing conducted prior to the start of the 2003 breeding season at Ram, leading to a predicted reduction in fidelity to the latter site from 2002 to 2003. Consistent with this prediction, estimated fidelity at Ram from 2002 to 2003 was 0.67, compared with 0.75–0.76 during years before and after. The estimated rate of movement from Ram to Bird from 2002 to 2003 ($\hat{\psi}^{RM,BD}_{2002}$) was >0.20, consistent with earlier years (Table 4), but 2002 Ram adults also showed an estimated probability of 0.10 of moving to Penikese in 2003. The overall combined movements and the first breeding of Roseate Terns at Penikese for many decades are believed to have resulted from the hazing efforts at Ram. Also, the estimated movement rate from Bird to Ram from 2002 to 2003 was 0.11, only about half of what it had been (0.21) in the preceding period, suggesting that the hazing also reduced movements to Ram substantially. The effect of the hazing was successful, but appeared to be short-lived as the fidelity and movement rates of the Roseate Terns at Bird and Ram soon returned to their "prehazing" levels. This suggests that this sort of management activity would have to be repeated for several years to drive individuals away "permanently."

Prediction 3: Response to sustained nocturnal predation at Falkner Island

Contrary to our previous expectations (see Spendelow et al. 2002), our estimates provided no evidence that site fidelity of breeders decreased substantially at Falkner following predation by Black-crowned Night-herons, which began in 1996 and resulted in sustained low productivity through 2007 (USFWS 2010). This lack of response by breeders to predation and resulting low chick productivity resulted in some adults continuing to breed in successive years at the same familiar location despite the apparent decreasing quality of that site ("ecological trap": Gates and Gysel 1978). However, depredation and nocturnal disturbance by night-herons may have lowered recruitment, probably resulted in a decrease in the development of site fidelity by first-time breeding terns (Spendelow et al. 2002), and likely was an important factor causing the decline in breeding pairs at this site that began in the late 1990s while the overall nesting population in our study area was still increasing (Table 1).

Prediction 4: Breeding dispersal rates are influenced by intercolony distances

Despite the substantial movement capabilities of Roseate Terns (they can migrate several thousands of kilometers between reproductive and wintering quarters), we found some evidence that breeding dispersal within our system of five sites was influenced by distance, with intercolony movements occurring more commonly among nearby sites than among more distant sites. The recolonization of two colony sites within Buzzards Bay led to larger estimates of between-colony movement than we had ever seen before for adult Roseate Terns, sometimes exceeding 0.20 and even 0.30. As a result, the warmwater-breeding component of the overall metapopulation can be viewed as spatially segregated into two subunits containing Great Gull and Falkner in one cluster where breeding dispersal was relatively low, and the three Buzzards Bay sites in the other cluster where breeding dispersal among Bird, Ram, and Penikese was much greater. Despite the relevance of spatial proximity to movement rates, the initial colonization of Ram by prior breeders involved small rates of movement from all three established sites, Falkner, Great Gull, and Bird. However, following the initial establishment of Roseate Terns at Ram, subsequent contributions of prior breeders to Ram were primarily from Bird. In contrast, the initial recolonization of Penikese involved small rates of movement from Falkner and Great Gull, but larger rates of movement from Ram and Bird Islands following the hazing done at Ram. Overall, these results showing high movement rates among the three sites in Buzzards Bay parallel results from a study of Common Terns based on trapping data from only those three sites (Breton et al. 2014).

Some seabird metapopulation studies found distance to be an important explanatory factor influencing breeding dispersal (e.g., Hénaux et al. 2007 in Great Cormorants [*Phalacrocorax carbo*]; Péron et al. 2010 in Black-headed Gulls [*Chroicocephalus ridibundus*]; Devlin et al. 2008 in Arctic Terns [*S. paradisaea*]), whereas other studies of Roseate Terns (Spendelow et al. 1995, Lebreton et al. 2003) and other species (e.g., Fernandez-Chacon et al. 2013 in Audouin's Gulls [*Larus audounii*]) did not, suggesting that the role of this factor in explaining breeding dispersal in seabird species is not yet fully understood and/or may differ according to the study species (Paradis et al. 1998) and local conditions. A common element in all these non-experimental studies of metapopulation dynamics is the existence of many potentially important "hidden covariates" or colony-specific factors not included in analyses but still potentially important drivers of dispersal (e.g., population size, nest density, average productivity, habitat quality). Thus, distance alone is likely never the sole driver of intercolony movement, and its role might be indirectly related to other factors. For example, long dispersal distances have been related to behavioral costs associated with a loss of familiarity with the breeding environment (Péron et al. 2010). This pattern may apply to our study species because adults are known to forage within close range of the colony site (range 1–25 km; Heinemann 1992, Rock et al. 2007) when nesting, so that it may be more advantageous for an individual leaving one of the Buzzard Bay colony sites to resettle at a nearby site rather than moving to the more distant sites of Long Island Sound (Great Gull and Falkner).

Roseate Terns, however, also can gain familiarity with more distant colony sites during the "postbreeding dispersal period" from mid-July to mid-September when young hatch-year (HY) individuals of this species and their caregiving parents from the warmwater MA-NY-CT breeding sites have been seen at colony sites in southern Maine (Shealer and Kress 1994), and HYs and adults from the Gulf of Maine have been seen as far west as Long Island Sound at Great Gull (H. Hays, *unpublished data*) and Falkner (J. A. Spendelow, *unpublished data*) before they begin migration to South America. Visiting distant colony sites during this period probably provided the opportunity for some individuals to learn about foraging areas near those sites and likely facilitated the switch in breeding regions that was done by a small number of adults (Spendelow et al. 2010).

Conclusions and management implications

Relative to our a priori predictions, this study provided evidence that fidelity tended to be at least somewhat higher at long-established colonies compared with newer colonies. However, fidelity estimates for one new colony site (Ram) approached those of the three older colony sites rather rapidly. The establishment of a breeding colony at Ram, and later Penikese, led to two new inferences about Roseate Terns in this system. First, after Ram was colonized, estimated rates of breeding dispersal to it from nearby Bird were higher than we had ever observed for birds in this system (approximately 0.1–0.2), and reciprocal rates (Ram to Bird) were even higher at about 0.2 and above (Table 4). Estimated rates of breeding dispersal from Penikese to Bird were higher still, at >0.3. Second, these high rates of breeding dispersal did not occur between the Buzzards Bay sites and the Long Island Sound sites at Falkner and Great Gull, with estimates always <0.1 and most <0.02. So while distance may not be an important determinant of breeding dispersal probability at one scale (e.g., >45 km; Spendelow et al. 1995), such dispersal can be much greater at small, local scales (e.g., <26 km). Some of the explanations for high fidelity at breeding colony sites include familiarity with such factors as feeding grounds and likely predators. It may be that the distances moved by dispersers within Buzzards Bay were sufficiently short that birds could retain this familiarity, despite their movements.

Although we had no a priori hypotheses about variation between newly colonized sites, the recolonization of Ram and Penikese by Roseate Terns offered an interesting contrast. The fidelity to Ram was relatively high, whereas a high degree of fidelity did not develop at Penikese and by 2013 no Roseate Terns nested there (Table 1). It is reasonable to hypothesize that this variation was associated with some aspects of site quality, but our study was not focused on such differences.

One aspect of site quality that we did identify a priori was the deteriorating conditions at Falkner due to sustained predation in later years of the study. However, we found no evidence that emigration from Falkner to other sites increased in response to the predation, a pattern consistent with the concept of an ecological trap.

A management attempt to initiate dispersal of breeding birds from Ram via hazing appeared to be successful in the short term by inducing movement from that site and reducing movement to it, and the large increase in breeding dispersal from Ram also resulted in the establishment of a new Roseate Tern colony at a site (Penikese) that had been recolonized by Common Terns several years earlier. This ability to increase breeding dispersal and even catalyze colonization of a nearby site is a potentially important tool for managers interested in seabird conservation. The inference that hazing effects on dispersal were temporary, with fidelity to Ram increasing to prehazing levels in the years following hazing, is important as well. This inference should reduce concerns that hazing activities during a single season would result in permanent abandonment of a colony site.

Future work

Examination of changes in natal dispersal/fidelity rates (see Lebreton et al. 2003) resulting from the creation or restoration of new colony sites, and the inclusion of data on the age composition and length of prior breeding experience of the first colonists at new sites were beyond the scope of this study of breeding dispersal of adults. However, these are important factors that may have influenced the different outcomes seen at Ram and Penikese, and they merit further study in the future.

Finally, we note the importance of consistent sampling efforts at Roseate Tern nesting colony sites within this metapopulation system. Matrices of movement and fidelity estimates such as those in Table 4 are rare in the ecological literature, yet contribute substantially to our knowledge of dispersal dynamics. The ability to draw inferences about movements to and from newly established colony sites is even rarer, but was possible in this situation because of the sustained intensive CMR field efforts in our system through 2009. The type of analysis described here could be applied to similar studies of intercolony movements of the other part of our endangered Roseate Tern metapopulation nesting further north in New Hampshire, Maine, and Nova Scotia.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1510/supinfo