

ENCOUNTER, SURVIVAL, AND MOVEMENT PROBABILITIES FROM AN ATLANTIC PUFFIN (*FRATERCULA ARCTICA*) METAPOPOPULATION

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Abstract. Several weaknesses in our understanding of long-lived animal populations have persisted, mainly due to a prevalence of studies of a single local population at the expense of multisite studies. We performed a multisite capture–mark–resight analysis using 2050 Atlantic Puffins (*Fratercula arctica*) banded as chicks on four islands (colonies) over 24 years in the Gulf of Maine, USA and Canada. Within program MARK, encounter, apparent survival, pre-breeding movement (PBM; annual movements between colonies prior to breeding), and natal dispersal (ND) probabilities were modeled as functions of age, colony, and several covariates. Information-theoretic model selection criteria and estimated model effect sizes were used to identify important effects and select models to estimate parameters. Encounter probabilities were extremely variable (0.10–0.95) and declined annually starting six years after bands were applied, due to changes in resighting effort, and band wear, respectively. Colony-dependent survival probabilities increased to a peak at age six years; arithmetic means from all colonies were: 0.70 for age 0–3, 0.78 for age 4, 0.81 for age 5, and 0.84 for age 6–8 years. Low adult survival (age ≥ 5 years) may reflect inclusion of breeding and nonbreeding adults in our sample or a bias due to band loss and illegibility. Consistent with a density-dependent prediction, the effect of colony size on survival was negative and acquired strong AIC_c support. However, this effect was inconsistent with strata effects in competing top models; the latter suggest that survival was lowest on the smallest island. The effects of origin and destination colony and origin colony size in PBM and ND probabilities resulted in important variation in these parameters. As few as 8% and as many as 57% of the puffins that we marked may have bred away from their natal colony, a signal of highly variable philopatry. Consistent with the conspecific attraction hypothesis, ND and PBM probabilities declined as the size of the origin colony increased. PBM probabilities were highest in the age 0–3 period, and these declined quickly with age thereafter. Strong colony and age effects in ND and PMB probabilities identify movement as a critical contributor to local population dynamics at our four study sites.

Key words: *Atlantic Puffin; dispersal; Fratercula arctica; Gulf of Maine islands; K-selected; local population; movement; multistrata; natal; seabird; subadult; survival.*

INTRODUCTION

Three persistent weaknesses in our understanding of the demography of long-lived seabirds have been identified: (1) very few data on movement patterns and processes (Greenwood and Harvey 1982, Clobert and Lebreton 1991, Coulson 1991, Wooller et al. 1992, Brownie et al. 1993, Walters 2000, Weimerskirch 2002, Lebreton et al. 2003); (2) few rigorous estimates of subadult survival probabilities (Weimerskirch 2002, Lebreton et al. 2003); and (3) sparse evidence for density-dependent population regulation (Croxall and Rothery 1991, Wooller et al. 1992, Weimerskirch 2002) in these so-called *K*-selected species (MacArthur and Wilson 1967). Estimates of movement between sites require

overcoming the challenge of monitoring two or more local populations simultaneously. Because long-lived seabirds often delay maturation by three or more years, estimates of subadult survival require a long-term commitment to collect data. Additionally, because dispersal by pre-breeding birds (natal dispersal) is much more common than dispersal by established breeders (Greenwood and Harvey 1982, Lebreton et al. 2003), investigators interested in estimating subadult survival probabilities must monitor several local populations simultaneously or risk reporting negatively biased estimates.

Researchers often monitor a single local population for a few years, often less than the life span of the focal species. In contrast, multisite and long-term studies are extremely rare; however, considerable challenges often preclude initiation or completion of these studies (Wooller et al. 1992). In addition, necessary statistical theory (Arnason 1972, 1973, Schwarz et al. 1993, Lebreton et al. 2003) and relatively easy-to-use computer software for running required multisite, or strata, models have been developed only recently (see review in

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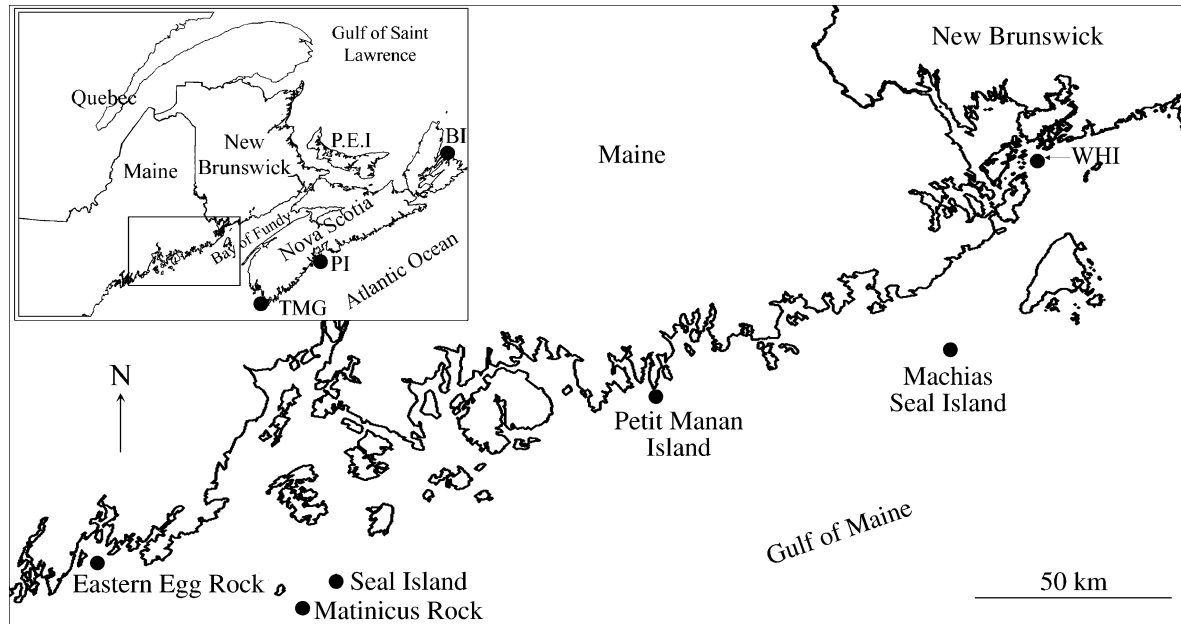


FIG. 1. Study sites in the Gulf of Maine and Bay of Fundy, USA and Canada. Additional colonies mentioned in the text are also shown: White Horse Island (WHI), Tusket and Mud Island Groups (TMG; these include Green and Noddy Islands respectively), Pearl Island (PI) and the Bird Islands (BI).

Lebreton and Pradel [2002]). Importantly, these multisite models, and other mark–encounter type models, include encounter probabilities; the lack of these is a crippling source of bias in earlier methods for estimating demographic parameters (Pollock et al. 1990, Lebreton et al. 1992). Studies that have overcome these challenges and produced rigorous estimates of subadult survival and/or movement are rare (Hestbeck et al. 1991, Spindel et al. 1995, Lindberg et al. 1998, Grosbois and Tavecchia 2003, Lebreton et al. 2003, Cam et al. 2004, Doherty et al. 2004, Oro et al. 2004, Schreiber et al. 2004). Consequently, knowledge of factors driving local population dynamics within metapopulations (Hanski and Gilpin 1991) remains limited (Walters 2000, Weimerskirch 2002, Lebreton et al. 2003).

In the Gulf of Maine (GOM; Fig. 1), including the Bay of Fundy, eight currently active Atlantic Puffin (*Fratercula arctica* Linnaeus; Charadriiformes: Alcidae) breeding colonies are known (Lowther et al. 2002; J. Nocera, *personal communication*). Three nonmanaged colonies represent <5% of the regional breeding population (Fig. 1; Lowther et al. 2002; J. Nocera, *personal communication*). The remaining 95% (see Fig. 1) nest at five managed colonies: Eastern Egg Rock (EER), Matinicus Rock (MR), Seal Island (SI), Petit Manan (PM), and Machias Seal Island (MSI). At these five colonies, resident summer observers have monitored puffins through capture–mark–resight/recapture since the 1980s. In 2000, through a cooperative agreement among the three managing agencies, mark–resight/recapture data from all five colonies were made available for multisite analyses.

We report here on a multisite capture–mark–resight (CMR) analysis using Atlantic Puffins banded as chicks at four colonies in the GOM. Breton et al. (2005) report adult survival estimates from breeders nesting on EER and SI over 11 years. Here we expand coverage to 24 years of data (1980–2003), to subadult as well as adult survival, and from two islands to four (MR, SI, PM, and MSI); EER contributed too few chicks ($n = 12$) to justify inclusion in the analysis. Using CMR models, we performed several exploratory and hypothesis-driven tests to (1) identify important structure in the data and (2) produce estimates of three demographic parameters and encounter probabilities. Demographic parameters measured here were: apparent survival (White and Burnham 1999); pre-breeding movement (annual inter-island movements prior to first breeding); and natal dispersal (a single transition from colony of birth to nesting colony at age five years; Greenwood and Harvey 1982). We distinguish between nonexplanatory, or structural, factors (such as age and colony); and explanatory factors, such as resighting effort and distance between colonies, which involve a specific cause–effect relationship. Our exploratory tests involve non-explanatory factors, whereas explanatory factors are reserved for hypothesis-driven tests. Tests and hypotheses were prepared prior to analysis of data and were guided mainly by the weaknesses just described. In addition, by simultaneously measuring two sources of movement between colonies as well as survival, our analysis provided a rare opportunity to determine the relative influence of these parameters in local population dynamics.

STUDY AREA AND METHODS

Study sites and data collection

Study sites.—Island descriptions are available in Kress and Nettleship (1988; Matinicus Rock (MR) and Eastern Egg Rock (EER)), Breton et al. (2005; Seal Island (SI)), Anderson and Devlin (1999; Petit Manan (PM)), Diamond and Devlin (2003; Machias Seal Island (MSI)). MSI (44°30' N, 67°06' W; Fig. 1) is owned by the Canadian Coastguard, managed by the Canadian Wildlife Service (CWS), and monitored cooperatively by CWS and the Atlantic Cooperative Wildlife Ecology Research Network (ACWERN). Petit Manan (PM; 44°22' N, 67°52' W), SI (44°14' N, 68°44' W) and Matinicus Rock (MR; 43°47' N, 68°51' W) are National Wildlife Refuges owned by the U.S. Fish and Wildlife Service (USFWS) and managed by them and cooperatively by the National Audubon Society's Seabird Restoration Program (Fig. 1). PM (6.5 ha) is located ~3 km south of Petit Manan Point. MR (7 ha) and SI (40.5 ha) are ~45 km south of Rockland, Maine, USA. MSI (9.5 ha) lies 18.9 km west of Grand Manan Island, New Brunswick, Canada (Fig. 1).

Data collection.—All puffins were marked as chicks with two individually engraved leg bands. Each bird received a Monel or Incoloy U.S. Geological Survey (hereafter "federal") band and colored field-readable band on opposite tarsi. Plastic bands were bi-laminar polyvinylchloride (PVC or Darvic; Darvic was rarely substituted) with one to four characters engraved through the top layer; engravings were repeated on the band (e.g., 101 – 101). Each island used a unique color scheme (MR used two).

Banding occurred annually from mid-July to late August. Chicks were captured in burrows (by hand) or (on MSI only) while fledging. Atlantic Puffins "fledge" when they leave their burrows for the ocean at ~6 weeks after hatching (Harris 1984, Lowther et al. 2002). Marked animals were resighted annually, with few exceptions, from mid-May to late August; colored leg bands were read preferentially over the less readable, but more durable, federal bands using spotting scopes (power 25–70×) and occasionally binoculars or naked eye. Observers varied seasonally; each made one observation stint daily to resight puffin leg bands, with stint duration varying between islands and years.

Analysis

Encounter histories and parameter estimates.—CMR data were summarized and then imported into program MARK as individual multistrata or site encounter histories (White and Burnham 1999). Encounter histories (EH) used to model encounter, apparent survival, and pre-breeding movement (PBM) were 24 occasions long (years 1980–2003).

The EH set used to model natal dispersal (ND) probabilities was imported and analyzed in MARK independent of the EH set used to model encounter, ap-

parent survival, and PBM probabilities. These EHs were set up "as if" birds were banded as four-year-olds at their colony of birth, resulting in 20 occasions rather than 24. With EHs modified in this way, we estimated ND as the probability of transitioning from the colony of birth to the location at age five years, i.e., as the first diagonal in the ND parameter index matrices (White and Burnham 1999); justification for the age five cutoff will be given.

Because a few birds did not breed until six, seven, or eight years after fledging, PBMs continued, and were therefore potentially estimable beyond our age five cutoff used to measure ND. In the analysis of encounter, apparent survival, and PBM, we retained the "pre-breeding" description for these age-specific transition probabilities (ages 5–6, 6–7, 7–8) because dispersal by adults has never been observed in Atlantic Puffin (Harris and Wanless 1991).

There were 411 individuals that were seen on more than one island within a summer. In order to set up EHs, which require only one character per occasion (White and Burnham 1999), and measure between summer (annual) movement probabilities and ND, we had to reduce multisite sightings within a summer to a single record. We chose the location at last sighting from each summer.

Parameters reported here are maximum likelihood estimates (Lebreton et al. 1992, White and Burnham 1999); the logit-link and second partial options in program MARK were used to calculate probabilities from model intercepts and offsets (betas) and the variance-covariance matrix, respectively (White and Burnham 1999). Apparent survival (ϕ) and PBM (ψ) are the probabilities of surviving or moving between colonies, respectively, from occasion i (origin colony) to $i + 1$ (destination colony). Encounter probabilities (p) estimate the probability of being resighted on occasion i . Natal dispersal (ψ) is the probability of a permanent movement from first release location (origin colony) to location at age five years (destination colony). In order to separate the probability of surviving (ϕ) and moving (ψ) from occasion i to $i + 1$, multistrata models used in this study condition survival only on location at occasion i , ϕ_i^r , and condition PBM and ND probabilities on surviving from period i to $i + 1$, ψ_i^r , where r is location at time i (origin colony) and s is location at $i + 1$ (destination colony; Spendelov et al. 1995). In addition, movement probabilities for strata- and age-specific cohorts are constrained to sum to 1.0.

Modeling strategy and global model structure.—We used multistrata models developed by Arnason (1972, 1973) and Schwarz et al. (1993; Arnason-Schwarz model). Parameters were modeled in the following order: encounter, apparent survival, PBM, ND. Our global model in the encounter-survival-PBM model set was:

$$p_{\text{age3_8+effort+effort}}^s \phi_{\text{age3_5,}\geq 6}^r \psi_{\text{age3_8}}^s$$

where superscripts represent strata, origin (r) and des-

tion (s) colonies, and subscripts refer to all other model effects. Age 3_8 describes a unique effect for each age 0–3, 4, 5, 6, 7, 8; age 3_5, ≥ 6 describes the effect for each age 0–3, 4, 5, 6–8; effort is a resighting effort covariate. To perform various tests, we built reduced designs of the global model and several models constrained by covariates.

We assumed a constant adult survival probability between ages 6–8 in order to reduce the number of parameters, thereby increasing the precision in those that remained. To avoid bias and loss of precision due to a decreasing sample size from mortality and the accumulating effects of band surface wear, we fixed encounter, survival, and transition probabilities for ages >8 years to zero; consistent with this approach, we also replaced encounters with birds after their eighth year with zeros (not seen) in EHs. Transition probabilities between ages 7–8 were too close to zero to be estimable; these were fixed to zero in all PBM models. Transition parameters beyond age five years (5–6, 6–7, 7–8) in ND models were all fixed to zero.

Atlantic Puffins are rarely seen at colonies in their first summer after fledging; many are seen for the first time as two year olds, and virtually all survivors return by year three (Harris 1984, Gaston and Jones 1998, Lowther et al. 2002; S. W. Kress, *unpublished data*; A. W. Diamond, *unpublished data*). These life-history traits conflict with an important assumption of CMR models: all animals surviving from occasion i to $i + 1$ are available for encounter on occasion $i + 1$; i.e., there is no temporary emigration (Lebreton et al. 1992). To satisfy this assumption, we modeled the age period 0–3 as a single effect, giving a single survival estimate, by fixing age one and two encounter and movement probabilities to zero (not observable) and survival probabilities to one (zero mortality); we also replaced encounters with one- and two-year-old birds with zeros (not seen) in EHs.

Atlantic Puffins recolonized SI and colonized PM in 1992 and 1987, respectively (Drury 1973, Kress 1997, Anderson and Devlin 1999); MSI and MR were occupied throughout the study period. All islands had resident summer observers by 1984 (SI) or much earlier (all others). Prior to recolonization, with the exception of seven native MR chicks seen on SI in 1990 and 1991, native GOM puffins banded as chicks were not seen on either SI or PM. Pre-colonization encounter parameters for SI and PM, 1980–1989 and 1980–1985, respectively, were fixed to zero in all models.

An important limitation was our inability to include time as a factor in our global model due to too few birds being released in most colony-year cohorts (see Appendix A); model interaction terms were also excluded, with one exception, due to sparse data.

Goodness-of-fit (GOF).—We were aware of two statistical tests for assessing the fit of multistrata models: median \hat{c} in program MARK (White and Burnham 1999) and the multiple-test approach proposed by Pra-

del et al. (2003). An important limitation of the multistrata GOF tests proposed by Pradel et al. (2003) and implemented in program U-CARE (Utilities Capture–Recapture; Choquet et al. 2003) was that we could test the fit of our data to only the time-dependent Arnason-Schwarz and JMV models. U-CARE implements several contingency table tests to assess GOF of the Arnason-Schwarz and JMV models; our data produced too many low values (≤ 2) in the expected cells to successfully perform these tests. We considered the option of extensive pooling to increase expected values (Pradel et al. 2003). However, we decided that a test of these extensively pooled data would not give a reliable measure of GOF for our unmanipulated data and global model, a model fitted to an important source of time structure (resighting effort) in encounter probabilities, but not survival or movement. We suspect that limitations of our data were also responsible for complications that we encountered while trying to estimate median \hat{c} , the overdispersion parameter, in program MARK (White and Burnham 1999). These complications left us without a formal way to test for the presence of overdispersion in our data or structural inadequacies in our global model.

Our response was to devise an ad hoc test involving \hat{c} and combine this with (1) and (2) to provide an overall assessment of GOF: (1) we carefully assessed each multistrata model assumption and the potential of our data to uphold them, which led to the addition of four nonbiological factors into our analysis; and (2) the biological tenability of our top model estimates was determined by comparing these to published estimates for the species. For the \hat{c} component, we started by assuming that overdispersion (several sources are provided in our discussion) was not present in our data ($\hat{c} = 1.0$) and went through the process of model building, selection, and inference previously and subsequently described. Following these steps, we applied \hat{c} values of 2.0 and 4.0 to all model sets in order to simulate inference following adjustments for overdispersed data (Burnham and Anderson 2002). An important consequence of adjusting \hat{c} is that sampling variances are inflated, which leads to a lower risk of falsely identifying a model factor as important, i.e., of making a Type I error (Lebreton et al. 2003). After applying each level of \hat{c} , we noted important changes in model support; we report these with other results.

Multistrata model assumptions that were a concern with our data were: there is no heterogeneity in encounter and demographic parameters within strata- or age-specific cohorts; marks remain readable throughout the study; sampling is instantaneous; there is no temporary emigration away from study colonies (Hestbeck et al. 1991). Specific to the Arnason-Schwarz multistrata model is the “memoryless” assumption (Brownie et al. 1993). Failure to meet these assumptions can lead to biased estimates and underestimated sampling

variances (Arnason 1972, 1973, Schwarz et al. 1993, Anderson et al. 1994).

To address the heterogeneity assumption, we included age and colony terms in our models, acknowledging any among-group heterogeneity in the data that we could identify. In place of time effects on encounter probabilities, we tested a time-varying effort covariate (number of observation stints/colony/year) to account for an important source of time dependence in our data. To assess the additivity and linearity assumptions of the effort effect, we tested interaction (site \times effort) and quadratic (effort²) terms, respectively.

The assumption of marks remaining readable was an issue for our study. Breton et al. (2005) showed a reduction in band readability of 70% between the third and fifth year post-application on adult breeding puffins; in the first three years, readability remained high. In our sample of puffins marked as chicks, we predicted that band readability would not decline until age six years, i.e., following two summers at sea and three at colonies accumulating wear. Therefore, we tested a delayed, declining, trend effect, which, if present, would account for a decline in encounter probabilities due to band wear; trends in our analysis were fitted using index values and a single beta in the design matrix of program MARK (White and Burnham 1999, Franklin 2001). Lastly, in an attempt to "shave off" data most affected by band wear, we fixed encounter, survival, and transition probabilities above age eight years to zero in our models; this effectively removes each bird from our analysis at the end of their eighth year.

Sampling all individuals simultaneously cannot be expected in studies requiring resampling of marked animals. However, the concern of this assumption, that mortality occurs only between sampling periods, should be approximately met with our data. In our study, losses of marked or unmarked birds within the summer sampling period have rarely been suspected or documented.

After accounting for the delayed return of young puffins to the colonies, the requirement of no temporary emigration should be approximately met in our data. Exceptions would include birds visiting EER or another island(s) in or outside the GOM exclusively and then returning to our study sites on a subsequent occasion. Although rare, this has probably occurred with EER and other GOM puffin islands. There have been no reports of a native GOM chick visiting or emigrating out of the GOM. The two nearest puffin colonies to those in the GOM, Pearl Island and Bird Islands, NS, are ~220 and ~680 km over water, respectively, from the Tusket and Mud Island Groups (Fig. 1).

A scan of our encounter histories demonstrates that puffins in our study tend to return at occasion i to their location at $i - 1$. However, our data were too sparse to apply the Jolly-movement (JMV) or memory multistrata model from Brownie et al. (1993) in place of the Arnason-Schwarz model; the latter assumes that

"transition probabilities for period i [do not] depend on the stratum occupied at $i - 1$ " (Brownie et al. 1993). With our data, the memory model would require 64 transition probabilities to be estimated per period, or 1472 for all periods (Brownie et al. 1993). This number of parameters is close to the number of animals in our sample.

Model selection.—Information-theoretic model selection criteria (Burnham and Anderson 2002), model effect sizes and their 95% confidence intervals (on the logit scale) were used to determine support for competing models so that we could perform tests and select one or more best models to estimate parameters. Selection criteria that we used were: Akaike's information criterion (AIC) adjusted for small sample size (AIC_c; Anderson et al. 1994); delta (Δ)AIC_c, where (i) is a particular model in the set; AIC_c weights (w_i) for each model (i); and evidence or odds ratios (w_i/w_j) where (i) and (j) are competing models. A Δ AIC_c difference of about 2 is equivalent to an evidence ratio of ~3:1; a difference of four, ~7:1; eight, ~55:1; 10, ~150:1. Strong support is therefore inferred for all models within 0–3 AIC_c units from the top model, considerably less for those between 4–7, and essentially none for models achieving a Δ AIC_c \geq 10 (Burnham and Anderson 2002).

TESTS AND HYPOTHESES

Encounter models.—The process of detecting a marked animal, unlike survival or movement, is partially a function of the behavior of the investigators. Certain bird "states," such as sex or age, and degradation or loss of marks may also influence the detection process. A priori, differences among colonies (including distribution of breeding pairs) and resighting effort were identified as features that would probably contribute to our detection probabilities; age of bird and a delayed decline in band readability from surface wear were also identified as potential contributors. We assessed the assumption of additivity and linearity of the effort effect by testing a site \times effort interaction term ($s \times$ effort) and quadratic term (effort²), respectively.

Estimation problems occurred when the $s \times$ effort interaction term was included in the global model. In order to test the $s \times$ effort term, we fitted the $s \times$ effort interaction term with the declining trend effect in place of the age effects in our global model ($p_{\text{trend+effort+effort}^2+s \times \text{effort}}^s$). Support for this model was then compared to the global model and the trend model without the interaction term ($p_{\text{trend+effort+effort}^2}^s$). We then tested all possible combinations of factors from the best model from this small set.

Apparent survival models.—Acquiring empirical evidence of shared characteristics between discrete local populations, such as seabirds breeding on islands, requires a multisite design and therefore has rarely been provided (see *Introduction*). However, a common assumption made by investigators monitoring migratory

species is that the “isolation” of local groups, e.g., on islands or among forest patches, translates into an independent risk of mortality. Although sample size was small, Breton et al. (2005) failed to detect a biologically important difference in adult survival between two colonies (separated by ~ 42 km); here, we test for a difference in age-specific survival among four colonies (greatest distance between colonies 167 km). No evidence for a biologically important difference in survival would suggest that birds from four discrete colonies share the same risk of mortality. This test was performed in an exploratory way by comparing the global model for this set ($\phi'_{\text{age3}_{5,\geq 6}}$) to a model without colony ($\phi_{\text{age3}_{5,\geq 6}}$); we also considered colony effect sizes from the global model and support for the colony-only design (ϕ').

For long-lived species, differences in survival probabilities between subadult (pre-breeding) and adult (potential breeders) stages are widely recognized (Ricklefs 1973, Hudson 1985, Dobson 1990, Sibley et al. 1997, Gaillard et al. 1998, Loison et al. 1999). However, much of the supporting empirical evidence does not account for encounter probabilities and rarely accounts for dispersal out of a single mark-encounter site (Pollock et al. 1990, Hestbeck et al. 1991, Lebreton et al. 1992, 2003). We tested for age differences in survival by comparing the global and three reduced age-structured models, $\phi_{\text{age3}_{5,\geq 6}}$, $\phi_{\text{age3}_{\geq 4}}$, $\phi_{\text{age3}_{4,\geq 5}}$ and $\phi_{(\cdot)}$, respectively, while accounting for movement between sites and site-specific encounter probabilities; age 3, ≥ 4 provides a unique effect in the model for each age 0–3, 4–8 and age 3–4, ≥ 5 for each age 0–3, 4, 5–8.

We monitored four colonies: three small and one relatively large. Although many factors other than density might explain a survival difference between these colonies, we recognized in our data a rare opportunity to test for a density-dependent response in both survival and movement (pre-breeding and natal dispersal). To set up these tests, we adopted the convention of using abundance (colony size), rather than individuals per unit area, to test for a density-dependent response (Lack 1954). With the exception of SI, we used colony size estimates from 2003: PM (25), SI (231), MR (280) and MSI (2800). Numbers on SI have been increasing rapidly in the last 10 years, while the others have remained relatively constant. To better reflect the majority of the years of the study when numbers of breeding pairs on SI were much lower than in 2003, we used the average number of pairs from 1992 to 2003 for this island: $\hat{\mu}_{\text{SIcol}} = 86$, where the subscript refers to SI colony size. We constrained the top survival model from above with the rescaled colony size covariate; rescaling ($0.0001 \times$ colony size) was necessary to avoid estimation problems in MARK (White and Burnham 1999). Strong support for this model, along with a negative colony size effect, would support a negative density-dependent relationship between source-colony size and survival.

Determining dispersal status.—Before we could perform any tests of ND, we first had to identify the ND status (disperser or nondisperser) of every individual in our sample. The norm in seabird studies is to determine dispersal status based on knowledge of individual breeding histories (e.g., Spindel et al. 1995). Using this approach, marked birds that breed away from their natal colony are dispersers and the remainder are nondispersers. For most of the birds in our study, breeding histories were not known. In place of this information, we determined ND status based on estimates from a PBM model fitted only to a declining age trend (ψ_{trend}). We looked for an age at which most individuals had stopped moving between colonies; this age was then used as an end point to estimate a single transition or ND probability from initial release location.

Movement models.—Opportunities to identify factors controlling the processes of movement among local populations and, consequently, philopatry, have been rare. Here we measure movement in two forms: as short-term PBMs and ND. In contrast, several hypotheses have been proposed to explain directional biases in movement; these include ideal-free distribution (Fretwell and Lucas 1970) and conspecific attraction (Stamps 1988, Serrano and Tella 2003).

Our initial sets (PBM and ND) of tests were purely exploratory: all possible designs of the global PBM ($\psi'_{\text{age3}_{\geq 3}}$) and ND (ψ'^{N}) models were compared. From these models, we hoped to identify the biological importance of the nonexplanatory predictors origin and destination colony, and age. Kress and Nettleship (1988) reported a decline in PBM probabilities with age, starting from a peak at age three years. However, their estimates, based on percentages of birds moving, do not account for birds that were present but not seen. As part of our analysis, we wanted to confirm this important result, which we did by constraining the top PBM model from preceding tests with a declining age trend.

As distance between colonies increases, movement between them is thought to decline as the exploration boundary of the species is reached (MacArthur and Wilson 1967). In both PBM and ND, we tested this hypothesis by comparing support for a model constrained by distance between colonies (in kilometers) to the top model from preceding tests.

Conspecific attraction (Stamps 1988) and ideal-free distribution hypotheses (Fretwell and Lucas 1970) predict two contrasting relationships between destination colony size and movement probability. Conspecific attraction suggests that movers are attracted to conspecifics (Stamps 1988), possibly in greater numbers as the abundance of established conspecifics increases (Serrano and Tella 2003). Here we test the hypothesis discussed by Serrano and Tella (2003), which predicts a positive relationship between destination colony size and movement probability. Ideal-free distribution predicts that animals are “free” to disperse to an “ideal”

TABLE 1. Encounter probability (p) model set ($\hat{c} = 1.0$), including selection criterion and number of parameters (np) for each model A_{en} – Q_{en} referred to in the text.

Model	AIC _c	ΔAIC _c	Akaike weight	np	Model deviance
$A_{en} p_{trend+effort+s \times effort}^s$	13 024.57	0.00	0.684	27	4794.28
$B_{en} p_{trend+effort+effort^2+s \times effort}^s$	13 026.58	2.01	0.250	28	4794.26
$C_{en} p_{trend+effort+effort^2}^s$	13 029.52	4.95	0.057	25	4803.28
$D_{en} p_{age3.8+effort+effort^2}^s$	13 033.35	8.78	0.008	29	4799.00
$E_{en} p_{trend+effort+effort^2}^s$	13 054.08	29.51	0.000	22	4833.91
$F_{en} p_{effort+s \times effort}^s$	13 058.85	34.28	0.000	26	4830.59
$G_{en} p_{effort+effort^2}^s$	13 060.12	35.55	0.000	24	4835.90
$H_{en} p_{effort+effort^2+s \times effort}^s$	13 060.69	36.10	0.000	27	4830.38
$I_{en} p_{trend+effort}^s$	13 063.18	38.61	0.000	24	4838.96
$J_{en} p_{effort+effort^2}^s$	13 084.77	60.20	0.000	21	4866.62
$K_{en} p_{effort}^s$	13 087.74	63.17	0.000	23	4865.54
$L_{en} p_{trend+effort}^s$	13 093.45	68.88	0.000	21	4875.29
$M_{en} p_{effort}^s$	13 118.41	93.84	0.000	20	4902.27
$N_{en} p_{trend}^s$	13 166.21	141.64	0.000	23	4944.02
$O_{en} p^s$	13 178.06	153.49	0.000	22	4957.88
$P_{en} p_{(.)}$	13 515.99	491.42	0.000	19	5301.87
$Q_{en} p_{trend}$	13 517.70	493.13	0.000	20	5301.56

Notes: Models are ordered ascending by AIC_c, and model D_{en} is the global model for this set; pre-breeding movement and survival structure in all models are: $\psi_{age3.8}^s, \phi_{age3.5, \geq 6}^s$.

habitat where competition is relatively low (Fretwell and Lucas 1970). If we assume that, excluding density, all factors that affect suitability of breeding habitat among the islands are equal, an inverse relationship between destination colony size and movement would be expected under the ideal-free distribution hypothesis (Fretwell and Lucas 1970). Although no formal study has been conducted to assess habitat suitability among islands, the assumption that these are equal should be approximately met in this study (see island descriptions and references in *Study sites*).

Conspecific attraction and ideal-free distribution predict different relationships between origin or source colony and movement probability: respectively, the probability of movement away from colonies declines as a function of origin colony size (Serrano and Tella 2003) or movement away increases as a function of colony size (Fretwell and Lucas 1970). We tested the relationship between origin and destination colony size and movement to assess these hypotheses.

RESULTS

Data set.—From 1980 to 2003, 2050 chicks were marked and released from all islands (see Appendix A); these animals were subsequently resighted 17 311 times.

Encounter models.—Three models acquired all of the AIC_c support in this set:

$$p_{trend+effort+s \times effort}^s, p_{trend+effort+effort^2+s \times effort}^s, p_{trend+effort+effort^2}^s$$

(A_{en}, B_{en}, C_{en} , respectively; Table 1). In models B_{en} and C_{en} , the (effort²) quadratic effect was weak and strong, respectively; 95% \hat{CI} values around the (effort²) effect in model B_{en} widely bounded zero (Table 2). None of the interaction effects in model A_{en} bounded zero; however, the PM \times effort interaction effect was highly

imprecise (Table 2). The MSI \times effort and SI \times effort interaction effects in model B_{en} bounded zero; all interaction effects were highly imprecise in this model. About half the time, 95% \hat{CI} around strata effects in these top models (A_{en}, B_{en}, C_{en}) bounded zero (Table 2). The effort and declining age trend effects, respectively, were strongly and weakly positive in models A_{en} (Table 2), B_{en} , and C_{en} ; the effort effect in model B_{en} bounded zero (Table 2). Based on AIC_c support for the interaction and strata effects in models A_{en} and B_{en} (Table 1) and strong positive trend and effort effect sizes, model $p_{trend+effort+s \times effort}^s$ (A_{en} ; Table 1) was maintained in all subsequent survival and movement models.

Apparent survival models.—The models for origin colony size and strata, $\phi_{origincol+age3.5, \geq 6}$ and $\phi_{age3.5, \geq 6}^s$, acquired all of the AIC_c support in this set (models B_s and A_s , respectively, Table 3). Although the fit of the colony size model was slightly poorer than the strata effects model A_s ($\Delta AIC_c = 1.74$), this fit was achieved with two fewer parameters. In model B_s , the colony size effect was strongly negative and its 95% \hat{CI} did not bound zero (Table 2). Strata effects in model A_s were all negative relative to the reference site, MR; the SI effect widely bounded zero (Table 2). Inconsistent with the colony size effect, strata effects in model A_s suggest that survival was lowest on PM ($\hat{B}_{PM} = -0.60 \pm 0.25$, $\hat{B}_{MSI} = -0.33 \pm 0.10$, $\hat{B}_{SI} = -0.12 \pm 0.18$; all values are mean \pm SE; see Table 2). Age effects in models A_s and B_s were all strongly positive, suggesting that survival probabilities were age dependent and that these increased rapidly from the reference age 0–3 to adult ages 6–8 (Table 2).

Given the inconsistency between the colony size and strata effects, and to avoid problems associated with under-fitting (Burnham and Anderson 2002), we use

TABLE 2. Estimates of model effect sizes (β_i) with \widehat{SE} , 95% \widehat{CI} , and references, where appropriate, for effects referred to in the text; estimates are on the logit scale.

Model†	Par‡	Effect	Reference island, age	Effect size (β_i)	\widehat{SE}	95% \widehat{CI}	
						Lower	Upper
A _{en}	En	MSI	MR	-1.0660	0.2559	-0.5645	-1.5674
A _{en}	En	PM	MR	-0.3901	0.4665	-1.3045	0.5243
A _{en}	En	SI	MR	3.3968	1.2732	0.9013	5.8923
A _{en}	En	declining trend		0.4151	0.0631	0.2913	0.5388
A _{en}	En	resighting effort		1.5276	0.2563	1.0252	2.0299
A _{en}	En	MSI × effort	MR	1.1530	0.3834	0.4015	1.9044
A _{en}	En	PM × effort	MR	8.4469	3.1061	2.3589	14.5349
A _{en}	En	SI × effort	MR	-1.6612	0.5179	-0.6462	-2.6763
B _{en}	En	(effort ²)		-0.0972	0.8077	-1.6804	1.4859
B _{en}	En	resighting effort		1.7122	1.5562	-1.3379	4.7623
C _{en}	En	(effort ²)		-0.6808	0.1150	-0.4553	-0.9062
A _s	S	MSI	MR	-0.3344	0.0974	-0.1435	-0.5252
A _s	S	PM	MR	-0.6020	0.2492	-0.1137	-1.0904
A _s	S	SI	MR	-0.1155	0.1756	-0.4597	0.2288
A _s	S	age 4	0-3	0.3496	0.1679	0.0205	0.6788
A _s	S	age 5	0-3	0.5345	0.1749	0.1916	0.8773
A _s	S	age ≥6	0-3	0.7578	0.2204	0.3259	1.1898
B _s	S	origin colony size		-1.0142	0.3420	-0.3439	-1.6846
A _{pbm}	PBM	origin colony, MSI	MR	-1.3262	0.1428	-1.0464	-1.6061
A _{pbm}	PBM	origin colony, PM	MR	0.5229	0.1986	0.1336	0.9121
A _{pbm}	PBM	origin colony, SI	MR	0.4395	0.1949	0.0575	0.8216
A _{pbm}	PBM	destination colony, PM	SI	-1.3089	0.2091	-0.8992	-1.7187
A _{pbm}	PBM	destination colony, MSI	SI	-1.1548	0.2045	-0.7539	-1.5557
A _{pbm}	PBM	destination colony, MR	SI	0.1451	0.1565	-0.1616	0.4518
A _{pbm}	PBM	declining trend		-0.4925	0.0527	-0.3891	-0.5958
B _{pbm}	PBM	age 4	0-3	-0.2560	0.1234	-0.0142	-0.4978
B _{pbm}	PBM	age 5	0-3	-0.8998	0.1767	-0.5535	-1.2460
B _{pbm}	PBM	age 6	0-3	-1.5467	0.2752	-1.0073	-2.0861
B _{pbm}	PBM	age 7	0-3	-2.3248	0.4816	-1.3808	-3.2688
C _{pbm}	S	origin colony size		-1.0193	0.3425	-0.3481	-1.6906
D _{pbm}	PBM	origin colony size		-5.9168	0.4683	-4.9989	-6.8347
A _{nd}	ND	origin colony, MSI	MR	-1.7352	0.2521	-1.2412	-2.2293
A _{nd}	ND	origin colony, PM	MR	0.8000	0.3646	0.0853	1.5147
A _{nd}	ND	origin colony, SI	MR	fixed = 0			
A _{nd}	ND	destination colony, MR	SI	-0.2314	0.3156	-0.8500	0.3871
A _{nd}	ND	destination colony, PM	SI	-1.5430	0.3749	-0.8081	-2.2778
A _{nd}	ND	destination colony, MSI	SI	-3.7511	1.0211	-1.7499	-5.7524
B _{nd}	ND	origin colony size		-7.5203	0.9428	-5.6724	-9.3682

† See Tables 1 (en), 3 (s), 4 (pbm), and 6 (nd).

‡ Identifies the parameter (par) where the constraint (effect) was applied: En, encounter; S, survival; PBM, pre-breeding movement; ND, natal dispersal.

model A_s ($\phi^r_{age3,5,≥6}$) as a starting survival structure in PBM models. The colony size covariate is introduced into the top PBM model following all other tests.

Pre-breeding movement models.—AIC_c exclusively favored the global model in this set (B_{pbm}) over all of its reduced forms (Table 4). Improvement over the

TABLE 3. Apparent survival (ϕ) model set ($\hat{c} = 1.0$), including selection criterion and number of parameters (np) for each model A_s–G_s referred to in the text.

Model	AIC _c	ΔAIC_c	Akaike weight	np	Model deviance	
A _s	$\phi^r_{age3,5,≥6}$	13 024.57	0.00	0.684	27	4794.28
B _s	$\phi^r_{origcol+age3,5,≥6}†$	13 026.31	1.74	0.287	25	4800.06
C _s	$\phi^r_{age3,4,≥5}$	13 032.52	7.95	0.013	23	4810.32
D _s	$\phi^r_{age3,5,≥6}$	13 032.97	8.40	0.010	24	4808.75
E _s	$\phi^r_{age3,≥4}$	13 034.11	9.54	0.006	22	4813.94
F _s	ϕ^r	13 038.72	14.15	0.001	24	4814.5
G _s	$\phi_{(.)}$	13 053.74	29.17	0.000	21	4835.58

Notes: Models are ordered ascending by AIC_c, and model B_s is the global model for this set; model B_s is the same as model A_{en} in Table 1; pre-breeding movement and encounter structure in all models: $\psi^r_{age3,8} \cdot P^s_{trend+effort+s \times effort}$

† Model for origin colony size.

TABLE 4. Pre-breeding movement (ψ) model set ($\hat{c} = 1.0$) including selection criterion and number of parameters (np) for each model $A_{\text{pbm}}-N_{\text{pbm}}$ referred to in the text.

Model	AIC _c	Δ AIC _c	Akaike weight	np	Model deviance
$A_{\text{pbm}} \psi_{\text{trend}}^{\text{rs}}$	13 023.48	0.00	0.385	24	4799.26
$B_{\text{pbm}} \psi_{\text{age3,8}}^{\text{rs}}$	13 024.57	1.09	0.224	27	4794.28
$C_{\text{pbm}} \psi_{\text{trend}}^{\text{rs}} \Phi_{\text{origcol+age3.5,}\geq 6}$	13 024.69	1.20	0.211	22	4804.51
$D_{\text{pbm}} \psi_{\text{origin colony size+age3,8}}^{\text{rs}}$	13 025.00	1.51	0.181	25	4798.76
$E_{\text{pbm}} \psi_{\text{distance+age3,8}}^{\text{rs}}$	13 046.72	23.23	0.000	25	4820.47
$F_{\text{pbm}} \psi_{\text{destination colony size+age3,8}}^{\text{rs}}$	13 068.89	45.40	0.000	25	4842.64
$G_{\text{pbm}} \psi_{\text{age3,8}}^{\text{rs}}$	13 097.08	73.59	0.000	24	4872.86
$H_{\text{pbm}} \psi_{\text{rs}}^{\text{rs}}$	13 130.57	107.09	0.000	23	4908.37
$I_{\text{pbm}} \psi_{\text{age3,8}}^{\text{rs}}$	13 181.04	157.55	0.000	24	4956.82
$J_{\text{pbm}} \psi^{\text{r}}$	13 189.32	165.83	0.000	20	4973.18
$K_{\text{pbm}} \psi_{\text{trend}}^{\text{rs}}$	13 221.16	197.67	0.000	18	5009.06
$L_{\text{pbm}} \psi_{\text{age3,8}}^{\text{rs}}$	13 222.00	198.52	0.000	21	5003.85
$M_{\text{pbm}} \psi^{\text{r}}$	13 273.16	249.68	0.000	20	5057.03
$N_{\text{pbm}} \psi_{(.)}$	13 304.02	280.54	0.000	17	5093.94

Notes: Models are ordered ascending by AIC_c, and model B_{pbm} is the global model for this set; model B_{pbm} is the same as model A_{s} in Table 3; survival and encounter structure unless otherwise written: $\Phi_{\text{age3.5,}\geq 6}^{\text{r}}$, $P_{\text{trend+effort+s}\times\text{effort}}^{\text{r}}$

global model (B_{pbm}) when age effects were substituted by a declining age trend (A_{pbm}) was marginal (Δ AIC_c = 1.09), but the trend model achieved this better fit with three fewer parameters (Table 4). All of the age effects in model B_{pbm} were negative and these increased with age (Table 2); apparently, as with the trend fitted to encounter probabilities, the trend effect (Table 2) in model A_{pbm} adequately captured the age structure in PBM probabilities. With the exception of the SI destination colony effect, none of the strata effects in model A_{pbm} bounded zero (Table 2).

PBM models fitted to destination colony size (F_{pbm}) and distance (E_{pbm}) effects acquired no AIC_c support (Table 4). Consistent with the conspecific attraction hypothesis (Serrano and Tella 2003), the origin colony size effect fitted to PBM was negative and its estimated CI did not bound zero (D_{pbm} ; Table 2). Model C_{pbm} , which included the colony size constraint on survival in place of strata effects in model A_{pbm} , acquired support equal to other top models in this set. The colony size effect fitted to survival was strongly negative. Strata effects fitted to survival in model A_{pbm} were also negative; but as in the survival model set, these suggested that PM survival, rather than MSI, was lowest.

Given the uncertainty as to which model was best (A_{pbm} , B_{pbm} , C_{pbm} , D_{pbm} ; Table 4), we used a form of multimodel inference known as model averaging (Burnham and Anderson 2004) to produce estimates of parameters from all of the models in the PBM set (Figs. 2–3, Table 5; see Appendices B and C). The contribution that each model makes to a model-averaged estimate of a parameter is determined by its AIC_c weight; additional details are available in Burnham and Anderson (2004).

Natal dispersal models.—PBM estimates from model K_{pbm} ($\psi_{\text{trend}}^{\text{rs}}$; Table 4) remain high from age 3–5 years and then decline from age 5–6, suggesting that location at age five is generally maintained (see Appendix D).

Based on these estimates, location at age five was selected as a cutoff to estimate ND probabilities as a single transition from initial release location.

The origin colony size model (B_{nd}) and global model (A_{nd}) acquired exclusive AIC_c support in the ND model set (Table 6). The colony size effect in model B_{nd} was strongly negative and its 95% estimated CI did not bound zero (Table 2). Consistent with the colony size effect, the MSI origin colony effect was negative and PM effect was positive compared to the reference MR site (A_{nd} ; Table 2). All destination colony effects in model A_{nd} were negative, suggesting that movement to SI, the reference effect, was preferred over the other three sites (Table 2). None of the strata effects in model A_{nd} bounded zero (95% CI; Table 2). In order to account for model selection uncertainty in this set, we estimated ND probabilities by model averaging (Table 7) across the full ND model set.

Assessment of goodness of fit: conspecific comparison and \hat{c} .—Harris (1983) monitored the movements of color-banded Atlantic Puffins among several colonies in northeast Scotland from 1972 to the early 1980s. From these data, Harris (1983) estimated survival up to age five years as 39% and natal dispersal as 23%; the method used to estimate immature survival incorporated encounter probabilities and their estimate of natal dispersal. Based on arithmetic means of age 0–3, 3–4, and 4–5 survival from our model-averaged estimates (see “all,” Table 5), survival to age five years is 44%. Based on our model-averaged estimates of ND (Table 7) the probabilities of dispersing from each site were 0.25 (MR), 0.57 (PM), and 0.08 (MSI); and the arithmetic mean of these estimates was 0.30.

An increase in \hat{c} from unadjusted 1.0 to 2.0 in the encounter, PBM, and ND model sets had no effect on our inference. An adjustment to 2.0 in the survival model set resulted in five top models ($A_{\text{s}}-E_{\text{s}}$; Table 3); the colony size and age model (B_{s}) remained best. With

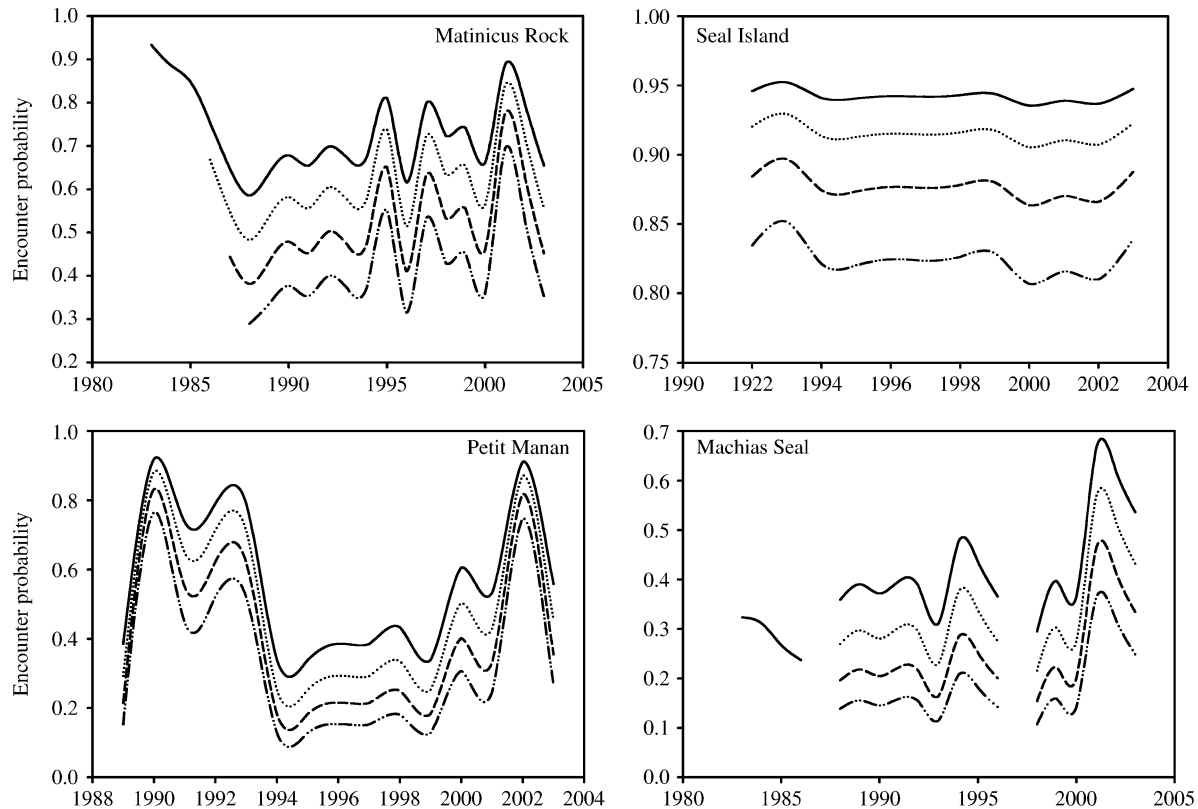


FIG. 2. Modeled averaged encounter probabilities (1983–2003) from the full PBM model set (Table 4) for all islands and bands aged 3–5 (solid line), 6 (dotted), 7 (dashed), and 8 (dashed-dotted) years; \widehat{SE} and 95% \widehat{CI} are provided in Appendix B.

\hat{c} set at 4.0, support for effects in model A_{en} remained strong; and the (effort²) effect acquired unambiguous support. With \hat{c} adjusted to 4.0 in the survival model set, all models were within 5 AIC_c units from the top model, $\phi_{age3,=4}$ (E_s ; Table 3). Model effect sizes and their 95% \widehat{CI} values favored inference from model E_s . Sup-

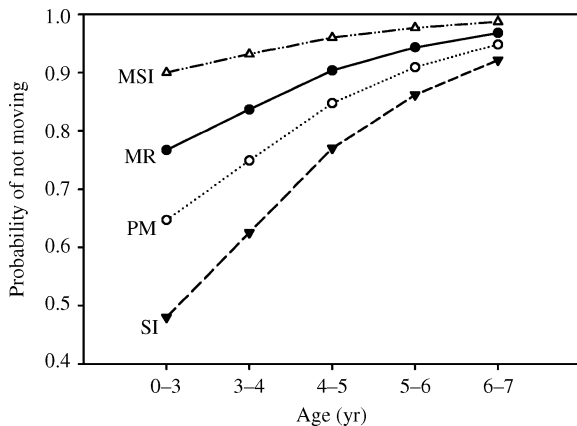


FIG. 3. Model-averaged colony and age-specific probabilities of not moving (e.g., B–B in Appendix C) from the full PBM model set (Table 4); \widehat{SE} and 95% \widehat{CI} are provided in Appendix C.

port for effects in top models did not change when \hat{c} was increased to 4.0 in the PBM set. ND models including distance (D_{nd}) and destination colony size effects (C_{nd}) acquired moderate support when \hat{c} was increased to 4.0; however, the origin colony size (B_{nd}) and strata models (A_{nd}) remained the AIC_c -favored models in this set (Table 6). In summary, with \hat{c} set at 2.0 and 4.0, inference from the encounter, PBM, and ND model sets remained essentially unchanged. Support for colony and age effects in survival remained essentially unchanged in the presence of moderate ($\hat{c} = 2.0$) overdispersion; inference in the presence of severe ($\hat{c} = 4.0$) overdispersion would have favored a reduced age model without strata or colony size effects.

Dispersal to other colonies in the Gulf of Maine.—The following counts of puffins from this study have been confirmed breeding on EER: MR (10), SI (3), PM (1), and MSI (3). On 1 August 2002, two puffins banded on MSI (green plastic leg bands) were observed loafing on Green Island, Nova Scotia (Fig. 1; T. C. D'Eon, *personal communication*). However, neither identity nor breeding status could be determined.

DISCUSSION

Goodness of fit.—In order to compare our estimates to those from Harris (1983), it is important that we can

TABLE 5. Model-averaged age- and colony-specific apparent survival probabilities with SE and 95% CI. Arithmetic means for “all” islands are also provided.

Age	Island	Estimate	SE	95% CI	
				Lower	Upper
0-3	MR	0.7531	0.0200	0.7118	0.7903
4	MR	0.8129	0.0211	0.7679	0.8508
5	MR	0.8383	0.0226	0.7889	0.8779
6, 7, 8	MR	0.8665	0.0241	0.8120	0.9071
0-3	SI	0.7369	0.0329	0.6676	0.7962
4	SI	0.7995	0.0285	0.7380	0.8496
5	SI	0.8264	0.0283	0.7639	0.8751
6, 7, 8	SI	0.8564	0.0261	0.7974	0.9003
0-3	PM	0.6565	0.0683	0.5136	0.7757
4	PM	0.7307	0.0620	0.5941	0.8341
5	PM	0.7638	0.0600	0.6275	0.8613
6, 7, 8	PM	0.8018	0.0558	0.6701	0.8896
0-3	MSI	0.6895	0.0189	0.6514	0.7253
4	MSI	0.7597	0.0234	0.7110	0.8025
5	MSI	0.7906	0.0255	0.7363	0.8362
6, 7, 8	MSI	0.8254	0.0298	0.7591	0.8764
0-3	all	0.7090	0.0221	0.6657	0.7523
4	all	0.7757	0.0188	0.7389	0.8125
5	all	0.8048	0.0170	0.7714	0.8381
6, 7, 8	all	0.8375	0.0148	0.8086	0.8665

demonstrate that the environmental conditions experienced by puffins in our study and those monitored by Harris (1983) were similar. Percentages calculated from our resighting data provide three-year return rates, postfledge, of 75%, 67%, 64%, and 47% for cohorts released from 1980 to 2000 at MR, SI, PM, and MSI, respectively; the anomalous percentage from MSI is due to low resighting effort relative to colony size. Without accounting for encounter probabilities and other structure in our data, these percentages already demonstrate a high immature survival rate. Similarly, counts of puffins at colonies and numbers of breeding pairs have increased in recent years at all colonies (S. W. Kress and A. W. Diamond, unpublished data). These data, which are free from biases due to poor model fit, suggest that environmental conditions experienced by puffins in our study were similar to those reported by Harris (1983), i.e., conducive to high survival and colony expansion.

Also important is assurance that estimates from Harris (1983) are biologically tenable. During the study

by Harris (1983), the number of puffins at the Isle of May “quadrupled.” At another study site, the Farne Islands, the population “doubled in seven years”: from 6800 (in 1969) to 13 600 breeding pairs (in 1975). Although high survival rates alone cannot account for the growth at these colonies, high immature survival must have been at least partially responsible for the observed growth (Harris 1983). Based on these observations and given the complementary estimates of immature survival and natal dispersal from our study and Harris (1983), it seems reasonable to assume that the models we fitted to encounter, survival, and movement probabilities were appropriate for assessing variation in these parameters.

Heterogeneity among individual probabilities (such as survival or encounter) and dependence among individuals (such as flocks or mated pairs with strong pair bonds) are scenarios that can lead to underestimated sampling variances due to a condition in the data known as overdispersion (Anderson et al. 1994). Given what is known about the biology of the Atlantic Puffin (Harris 1984, Lowther et al. 2002) and other members of the Alcidae (Nettleship and Birkhead 1985, Gaston and Jones 1998), we did not expect “dependence” to be an issue with our data. However, heterogeneity in detection and movement probabilities due to aspects of our study design (e.g., varying band colors among islands), not accounting for “memory” in our data, and other sources (e.g., unaccounted heterogeneity from band wear) could produce overdispersion.

In the absence of an estimate of \hat{c} , we applied \hat{c} values of 2.0 and 4.0 in order to determine how much, if any, our inference would have changed if an overdispersion adjustment had been made. Important differences were: weakened support for the colony size covariate, strata effects, and the full age structure (3_5, ≥ 6) in survival probabilities; and increased support for the (effort²) effect fitted to encounter probabilities. We will now incorporate the uncertainty detected here into our inference concerning the importance of effects fitted to our survival probabilities. Although some uncertainty was detected in the ND set, the following inference concerning encounter, PBM, and ND should be robust to even severe ($\hat{c} = 4.0$) amounts of overdispersion in our data.

TABLE 6. Natal dispersal (ψ) model set ($\hat{c} = 1.0$), including selection criterion and number of parameters (np) for each model A_{nd}–G_{nd} referred to in the text.

Model	AIC _c	Δ AIC _c	Akaike weight	np	Model deviance
A _{nd} ψ^{rs}	18 990.45	0.00	0.541	20	14 526.85
B _{nd} $\psi_{\text{origin colony size}}^s$	18 990.79	0.33	0.458	19	14 529.22
C _{nd} $\psi_{\text{destination colony size}}^s$	19 004.40	13.94	0.001	18	14 544.85
D _{nd} ψ_{distance}^s	19 006.54	16.09	0.000	18	14 547.00
E _{nd} ψ^r	19 039.87	49.41	0.000	17	14 582.35
F _{nd} ψ^s	19 059.43	68.98	0.000	18	14 599.89
G _{nd} $\psi_{(.)}$	19 090.30	99.85	0.000	15	14 636.83

Notes: Models are ordered ascending by AIC_c, and model A_{nd} is the global model for this set; survival and encounter structure in all models: $\phi_{\text{age}0,5,\geq 6}^r$, $p_{\text{trend+effort+s}\times\text{effort}}^s$

TABLE 7. Model-averaged natal dispersal probabilities with \widehat{SE} and 95% \widehat{CI} from the full ND set (Table 6).

Age	Transition (km)	Estimate	\widehat{SE}	95% \widehat{CI}	
				Lower	Upper
0–5	B to B	0.7462	0.0299	0.6956	0.8048
0–5	B to C (15)	0.1982	0.0251	0.1536	0.2519
0–5	B to D (102)	0.0499	0.0163	0.0261	0.0934
0–5	B to E (167)	0.0057	0.0057	0.0000	0.0169
0–5	C to B (15)	fixed = 0.0			
0–5	C to C	fixed = 1.0			
0–5	C to D (87)	fixed = 0.0			
0–5	C to E (152)	fixed = 0.0			
0–5	D to B (102)	0.2639	0.0741	0.1450	0.4310
0–5	D to C (87)	0.2968	0.0791	0.1672	0.4701
0–5	D to D	0.4294	0.1339	0.1669	0.6919
0–5	D to E (64)	0.0100	0.0105	0.0000	0.0306
0–5	E to B (167)	0.0335	0.0079	0.0210	0.0529
0–5	E to C (152)	0.0389	0.0082	0.0257	0.0585
0–5	E to D (64)	0.0086	0.0034	0.0019	0.0152
0–5	E to E	0.9190	0.0131	0.8933	0.9447

Notes: Distances (km) between islands are given in parentheses following transition descriptions; all Seal Island (SI) chicks were seen exclusively on SI (or EER, not in analysis) by age five years; for this reason, SI transitions are fixed to zero. Abbreviations: B, Matinicus Rock; C, Seal Island; D, Petit Manan; and E, Machias Seal Island; (A) was reserved for Eastern Egg Rock (islands are labeled ascending from west to east; Fig. 1), but this island was excluded from the CMR analysis due to small sample size.

Encounter effects and probabilities.—Accounting for major factors that contribute to the encounter process (e.g., time, age, effort) has been a primary focus in the development of CMR models (White et al. 1982, Lebreton et al. 1992). However, as demonstrated by recent publications (e.g., Holl et al. 2004, Lin and Batzli 2004), some wildlife biologists remain unconvinced that the process of detecting an animal contributes critical structure to their data. Validity of these studies often hinges on the assumption that detection probabilities are constant across space and time. With data available from 24 years and four islands, our study provided a rare opportunity to test for spatiotemporal variability in encounter probabilities: results identified strong temporal (0.10–0.95) and spatial (MR (0.73), SI (0.94), PM (0.55), MSI (0.40)) variation; the latter are arithmetic means before bands begin to wear. These results emphasize why it is wrong to assume that spatiotemporal variation in encounter probabilities is negligible when estimating demographic parameters.

Strong support for the effect of resighting effort on detection probabilities demonstrates the importance of carefully budgeting banding and reencounter components of CMR studies. Further, our data were too sparse to support a high-dimensional time-dependent encounter model; without the effort covariate, a CMR analysis with our data probably would not have been possible.

Tag loss and wear are recurring problems in mark-encounter studies, causing heterogeneity, and are a major source of bias in estimates (Arnason and Mills 1981, Pollock et al. 1990); therefore, knowledge of the presence and process of wear and ways to avoid potential biases will be valuable for future CMR studies. Breton et al. (2005) show that plastic field-readable bands ap-

plied to adult (breeding) puffins in our region wore rapidly from abrasion against island bedrock and rock piles. To avoid heterogeneity due to band wear, Breton et al. (2005) used double-banded adults monitored intensively at two small puffin colonies; as plastic bands wore out, bias was avoided by resighting the less readable, but more durable, federal band. In the present study, bias may or may not have been avoided by removing birds from the sample eight years after initial marking, prior to the onset of severe wear; and by fitting encounter probabilities to a declining age trend to account for a decline in band readability from surface wear.

Although these ad hoc solutions may have removed or reduced negative effects due to band wear and loss, researchers should keep in mind that rigorous quantitative solutions are also available, such as modeling a band loss rate along with other parameters (Spendlow et al. 1995) or including individual states, such as presence or absence of a highly visible marker, in multistate models (Conn et al. 2004). Application of these solutions often requires a large data set and/or ancillary data, which were both unavailable in our study. We recommend that investigators become familiar with the requirements of these solutions prior to initiating CMR studies.

Apparent survival effects and probabilities.—As *K*-selected species (MacArthur and Wilson 1967), puffins and many other marine birds are expected to maintain their populations near carrying capacity through density-dependent mechanisms; but evidence to support this view is sparse (Wooller et al. 1992). Under the assumption of no ($\hat{c} = 1.0$) and moderate ($\hat{c} = 2.0$) heterogeneity in our data, and using colony size as an

index of density, we detected a biologically important, negative, density-dependent response in survival probabilities. Although support for this result declined under the assumption of severe heterogeneity ($\hat{c} = 4.0$), we suspect that this assumption was unrealistic for our data; and instead favor the assumption of moderate heterogeneity. Similarly, colony effects suggest that individuals from the smallest, rather than the largest, colony experienced the highest mortality. However, our index of density, colony size, did not account for the amount of available breeding habitat. This resource is extremely limited on Petit Manan (Anderson and Devlin 1999) relative to the other three sites (Breton et al. [2005] and references therein). Given this, if a true measure of density had been available, PM may have ranked close to the crowded MSI colony (Diamond and Devlin 2003).

Given the strong support for both the colony size covariate and colony effects, we feel confident that a biologically important colony effect in survival, from density or some other factor(s), contributed to the survival process measured by our data. However, considering complicating factors, including those just described and the important limitation imposed by measuring survival at three small and one relatively large colony (MSI), we recommend that the inverse association between density and survival be regarded as only an exploratory result, and that inference beyond this be reserved for a meta-analysis.

It is often assumed by managers that the fates of discrete breeding colonies are independent; this view, however, may be biased from an abundance of single local population studies and few multisite studies. Breton et al. (2005) did not detect a biologically important difference in adult survival between two colonies. However, their sample included only 148 individuals, and support for the colony effect on survival in their models was equivocal. In the present study, which included a larger sample and 24 years of data from four islands, support for a colony effect was again equivocal, but this time the evidence favored a biologically important difference.

Considering that important mortality in alcids has often been shown to be a winter phenomenon (Harris 1984, Hudson 1985, Gaston and Jones 1998), knowledge of shared demographic characteristics derived from simultaneously monitoring multiple sites may be critical for making reliable management decisions; further, reliable decision making for other long-lived migratory species may require the same insights. For these reasons, we have emphasized in our research the need to identify shared characteristics, if any, among local populations. However, combined results from this study and that of Breton et al. (2005) demonstrate how difficult it will be to achieve this important insight.

It is generally thought that in long-lived organisms, survival is age dependent, especially between subadults and potential breeders (Lack 1954, Ricklefs 1973, Hud-

son 1985, Dobson 1990, Sibley et al. 1997, Gaillard et al. 1998, Loison et al. 1999). After accounting for nearly all dispersers, using multiple sites within a metapopulation, and site-specific encounter probabilities, we found strong evidence for an age effect on survival. The largest mortality occurred in the first few years and probably, as shown by many seabird studies (Hudson 1985, Gaston and Jones 1998), in the first fall–winter–spring period of life. Thereafter, survival increased steadily to age six years, but fell far short of the range of estimates typical for adult Atlantic Puffins and other long-lived seabirds, ~ 0.92 – 0.98 (Breton et al. [2005] and references therein). Failure to reach a high survival rate near the age of first breeding (typically age 4–5; Harris 1984) contrasts with many mammal (Sibley et al. 1997, Loison et al. 1999) and bird (Ricklefs 1973, Wooller et al. 1992, Harris et al. 1997, Harris et al. 2000) studies, across diverse taxa, that report high survival of breeding adults maintained over several years.

Low adult survival probabilities could be due to band loss or illegibility from band wear; an analysis of surface wear accumulated on our plastic bands suggests that severe band wear may have been prevalent enough in adult cohorts to produce these problems (Breton et al., *in press*). Alternatively, high adult survival observed in many studies of long-lived seabirds may, due to sampling design, be consistent with only the breeding segment of the population. Typically, it is the latter that is sampled to measure adult survival (summaries in Spendelov and Nichols 1989, Croxall and Rothery 1991, Jouventin and Weimerskirch 1991, Harris et al. 2000, Breton et al. 2005). In contrast, and consistent with our results, the nonbreeder segment of the adult population, which is typically excluded from such studies, may be experiencing much lower survival. Consequently, adult survival estimates would be misleading (too low for some, too high for others), and a small number of adults would be responsible for producing the majority of the next generation. The latter point is consistent with the findings of many bird studies including long-lived seabirds (Newton 1995). In summary, we do not know whether high adult mortality was a function of failing bands or actual losses of birds in our study.

Movement effects and probabilities.—Coulson (1991) identified studies of dispersal as the “most neglected aspect of avian demography”; these comments certainly apply to studies of PBM as well. Since then, few studies have contributed real-life insights into these demographic processes (Brownie et al. 1993, Walters 2000, Lebreton et al. 2003). Our results move toward a better understanding of ND and PBM and provide rare estimates of these parameters. As in previous studies (Harris 1983, Kress and Nettleship 1988), we found that the prevalence of non-movers increased with increasing age. In addition, we were able to demonstrate that the percentage of non-movers increased

simultaneously at four sites and exceeded 92% between ages 6–7.

Whether or not philopatry is strong or variable represents an old and unresolved issue in ornithology (Greenwood and Harvey 1982, Wooller et al. 1992, Weimerskirch 2002). Origin and destination colony achieved strong AIC_c support, suggesting that characteristics of both factors are important predictors of movement and, hence, philopatry. Similarly, age 0–3 estimates for movers varied from about 10% to 52% (MSI, PM); as few as 8% (MSI) and as many as 57% (PM) of the puffins that we marked may have bred away from their natal colony. Strong variation in ND and age 0–3 PBM summarized here show, without doubt, that philopatry varied considerably across the local populations we sampled.

As predicted by the conspecific-attraction hypothesis discussed by Serrano and Tella (2003), birds marked on (age 0–3) or arriving to (all other ages) the two smallest islands were more likely to shift colonies than those marked on or arriving to MR and MSI. With the exception of the rapidly expanding SI colony (Kress 1997; S. W. Kress, *unpublished data*), natal recruitment ($1 - ND$) probabilities increased as a function of colony size. These results suggest that birds arriving or being born at large colonies (MR, MSI) were more likely to remain there relative to those arriving or being born at small colonies (SI, PM). However, as Cam et al. (2004) point out, the source–sink hypothesis proposed by Pulliam (1988) may also result in a negative relationship between movement and colony size. Future investigators will need to plan carefully in order to isolate evidence for these competing hypotheses.

Consequence of natal dispersal probabilities for genetic mixing.—It is important to recognize, especially for genetic mixing, that ND probabilities reported here do not reflect numbers of dispersing individuals; the number dispersing is a function of both the probability of moving from a particular island and the number of individuals that survive to age five years. Consequently, a low probability of ND away from MSI, by far the largest colony and producer of young in our study, sends out more young than the small SI and PM colonies and possibly MR, even though the latter all demonstrated much higher dispersal probabilities. In summary, movement probabilities and factors tell us something about processes of ND and PBM. Colony size together with probabilities provide an estimate of the contribution of young among islands, which has considerable genetic, as well as purely demographic, consequences.

Local population dynamics.—Traditionally, the contributions of dispersal and short-term exploratory movements, here measured as PBM, to population dynamics were generally thought to be unimportant (Lidicker 1975). The predominance of research on single local populations in the last 20 years suggests that the traditional view is still generally held or is maintained

due to the difficulties of measuring movement between local populations. In our study, strong colony-dependent variation in movement probabilities identifies ND and PBM as key parameters affecting the numbers of individuals at each colony. This important result has been replicated in all other multisite studies of birds known to us (Hestbeck et al. 1991, Spendelov et al. 1995, Lindberg et al. 1998, Grosbois and Tavecchia 2003, Lebreton et al. 2003, Cam et al. 2004, Oro et al. 2004). Many years ago, a minority of authors, including Andrewartha and Birch (1954) and Lidicker (1975) challenged the traditional view by predicting that dispersal would be elevated to vital status in future studies. Recent multisite CMR studies are providing strong support for these predictions; consequently, the validity of studies monitoring a single local population to estimate demographic parameters is surely suspect.

Additional suggestions for improving on our multistrata study design.—Our use of different band color schemes on islands could cause bias in our encounter and survival probabilities by introducing differences in observability and wear rates, respectively. To avoid these potential problems, we suggest a generic metal-type field-readable band for all islands or groups in multisite mark–encounter studies; generic features of these bands should include non-group-specific characters. We do not recommend plastic bands due to their high susceptibility to wear (Breton et al., *in press*).

Our use of location at last sighting results in a loss of information about movement and survival processes for animals that visited more than one site within a summer (see also Spendelov et al. 1995). Also, multiple transitions between occasions violate an implicit assumption of multistrata models: all transitions take place at the end of the survival interval. We know of no solution to account adequately for these problems, but expect that an extension of current multistrata models will be required.

Given the duration of our study and high rate of observer turnover, we were reluctant to remove suspicious sightings, including birds seen one time after an absence of five or more years. However, the cost was likely inclusion of a small percentage of sightings that were not in fact “data,” i.e., information consistent with the process under study (Romesburg 1981, Anderson 2001): in this case, misread bands. Studies like ours that require observers to read engraved marks from a distance should consider a screening method to reduce the number of erroneous sightings. Solutions include requiring two or three sightings of each animal or, alternatively, including only sightings made by more than one observer.

Sparse data on SI and PM and for early cohorts on MSI and MR required that we treat all colony–year cohorts as one age-specific cohort per colony. The obvious solution is to mark an adequate number of chicks on each occasion. However, for small local populations, such as EER and PM, with ~50 and 25 breeding pairs

in 2003, respectively, a large sample is not possible (Pollock et al. 1990). Researchers interested in investigating processes that occur across multiple sites should carefully consider the sample potential of prospective study species and their local populations.

Our approach to estimating ND probabilities required removal of all parameters between release and age five years and loss of information about dispersers that were not seen at age five. Ideally, we would have used an alternative modeling strategy, proposed by Lebreton et al. (2003), which allows state, as well as strata, transitions to be modeled (see also Conn et al. 2004). However, the small numbers of releases previously described could not support the high-dimensional models that this solution requires. Investigators planning dispersal studies should attempt to meet the minimum data requirements of this rigorous method (Lebreton et al. 2003).

Few approaches are available for assessing the goodness of fit of many types of capture–mark–recapture models, including the multistrata models used in this study (Lebreton et al. 2003). The few options that exist are often limited in their ability to assess fit to a few pre-defined models, rather than the global model for a particular study. Until significant progress can be made in these areas, investigators will have to rely, as we have done here, on careful a priori selection of candidate predictor variables and models (see the excellent discussion in Burnham and Anderson [2002:15–19]) in place of formal GOF testing. A comparison of estimates from other studies, such as our use of estimates from Harris (1983), might also contribute valuable evidence for assessing fit. If these alternatives can be carefully applied, and confirmatory inference is reserved for meta-analyses rather than individual studies, we suspect that the importance of formal GOF testing may decline or even become unnecessary.

Conclusion

Our study contributes to accumulating insights into local population dynamics within metapopulations and highlights ways of improving the inferential quality of future CMR multisite studies. CMR data over 24 years from four colonies revealed strong age variation in survival and uncertain support for a colony effect from density or some other factor. Consistent with colony growth and expansion during the study period, immature survival was apparently extremely high. In contrast, our estimates of adult survival were anomalously low, suggesting a bias due to combining breeding and nonbreeding adults in our sample or failure of plastic leg bands. Our estimates of movement show that philopatry varied considerably among islands; and that PBM declines as a function of increasing age. Support for the colony size constraint on movement probabilities provides evidence that PBM and ND varied inversely with colony size. By estimating survival and two sources of movement simultaneously, we were able

to determine the relative contribution of these parameters to local population dynamics: our results suggest that movement plays a much larger role in modifying numbers than established theory would predict. Based on our results and those of others (Hestbeck et al. 1991, Spindel et al. 1995, Lindberg et al. 1998, Grosbois and Tavecchia 2003, Lebreton et al. 2003, Cam et al. 2004, Oro et al. 2004), we recommend long-term regional-scale CMR studies involving simultaneous data collection at several local populations in place of the norm in population research (short-term and single-site data) to estimate parameters accurately and to identify factors driving local population dynamics in long-lived animal species. Otherwise, inference is likely to be misled by many biases, especially unaccounted-for sources of movement among sites.

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APPENDIX A

A table providing colony- and time-specific numbers of Atlantic Puffin (*Fratercula arctica*) chicks banded with individually engraved plastic field-readable and federal leg bands at all study sites from 1980 to 2003 (*Ecological Archives* M076-006-A1).

APPENDIX B

A table providing model-averaged year, colony, and age of band-specific encounter probabilities from the full PBM model set (Table 4) (*Ecological Archives* M076-006-A2).

APPENDIX C

A table providing model-averaged age- and transition-specific pre-breeding movement probabilities from the full PBM model set (Table 4) (*Ecological Archives* M076-006-A3).

APPENDIX D

A table providing age-specific pre-breeding movement probabilities from model ψ_{tend} (K_{pbm} ; Table 4) (*Ecological Archives* M076-006-A4).