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ADULT SURVIVAL ESTIMATES FROM TWO ATLANTIC PUFFIN (*FRATERCULA ARCTICA*) COLONIES IN THE GULF OF MAINE

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ABSTRACT.—We report survival probabilities for 148 breeding adult Atlantic Puffins (*Fratercula arctica*) monitored through capture–mark–resight at two colonies for 11 years (1992–2003). The colonies, Eastern Egg Rock and Seal Island, are ~42 km apart in the Gulf of Maine. Support for competing models in the program MARK suggests constant survival of 0.95 ± 0.01 (SE) that is independent of colony. Our high survival probability is consistent with published estimates for Atlantic Puffins and other long-lived seabirds. No time-variance contrasts with many long-term seabird studies, which often report high survival in most years, broken occasionally by low-survival events. However, a *post-hoc* observation of survival estimates from the time-dependent model suggests that there may have been at least two low-survival events in our time-series; sparse data may have precluded detection by our models. In this study, each bird received an individually engraved, plastic, field-readable leg band, as well as the standard metal band. Using an index of band readability, we show that plastic bands wore rapidly, resulting in accumulating losses of engraved characters through time. Degradation and loss of marks is a common source of overdispersion in capture–mark–re-encounter data and results in underestimated sampling variances. In the presence of a 70% reduction in band readability over eight years, an estimate of the adjusted overdispersion factor ($\hat{c} = 1.14$) identified very little overdispersion in our data. Overdispersion was avoided by double banding and intensively resighting metal bands. Received 2 October 2003, accepted 4 January 2005.

Key words: Atlantic Puffin, band wear, capture–mark–resight/recapture, CMR, *Fratercula arctica*, Gulf of Maine, overdispersion, program MARK, survival.

Estimation de la Survie Adulte de Deux Colonies de *Fratercula arctica* dans le Golfe du Maine

RÉSUMÉ.—Nous présentons les probabilités de survie de 148 adultes de *Fratercula Arctica* reproducteurs issus de deux colonies et suivis par capture-marquage-réobservations pendant 11 ans (1992-2003). Les colonies, Eastern Egg Rock et Seal Island, sont éloignées d'environ 42 km dans le Golfe du Maine. Les deux modèles privilégiés lors de la sélection dans le programme MARK suggèrent une survie constante de $0,95 \pm 0,01$ (SE) indépendante de la colonie. Notre forte probabilité de survie est en accord avec les estimations publiées pour *Fratercula Arctica* et d'autres oiseaux de mer à longue durée de vie. Par contre, l'absence de variation temporelle contraste avec les résultats d'autres études réalisées sur ces espèces. Ces études affichent généralement une survie élevée au cours de la plupart des années, mais peuvent être occasionnellement recoupées par des événements de faible survie.

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Néanmoins, une observation *post-hoc* des estimations de survie issues du modèle dépendant du temps suggère que nos séries temporelles pourraient présenter au moins deux événements de faible survie. La dispersion des données pourrait avoir empêché leur détection par nos modèles. Dans cette étude, chaque oiseau recevait une bague tarsale en plastique, gravée et lisible sur le terrain, ainsi qu'une bague de métal classique. En utilisant un index de lisibilité de bagues, nous montrons que les bagues en plastique se détériorent rapidement, conduisant à l'effacement progressif des caractères inscrits. La dégradation et la perte de marqueurs constituent une source fréquente de surdispersion avec des données de capture-marquage-réobservations et conduisent à des variances d'échantillonnage sous-estimées. En présence d'une réduction de 70% de la lisibilité des bagues en huit ans, l'estimation du facteur de surdispersion ajustée ($= 1.14$) n'a permis d'identifier que très peu de surdispersion dans nos données. La surdispersion a été évitée par un marquage double et des réobservations fréquentes de bagues métalliques.

MOST SPECIES OCCUR as several "local populations, each one intercommunicating and intergrading with the others" (Mayr 1970). Although the truth of this premise remains generally accepted, studies aimed at measuring communication and intergradations between or among local populations remain relatively rare. Instead, sampling of a single local population remains the norm in population research. This represents a bias that may have deep implications for established population theory and, consequently, for management decision-making.

Breeding colonies of Atlantic Puffin (*Fratercula arctica*; hereafter "puffins") are distributed across eight islands in the Gulf of Maine (Lowther et al. 2002, J. Nocera pers. comm.). At five of those colonies and for several years, both adult and juvenile puffins have been monitored through capture-mark-resight/recapture (CMR). The resulting data set provides a rare opportunity for measuring demographic processes simultaneously across two or more local populations.

Our objectives were two-fold: first, we reported survival probabilities from two colonies in the Gulf of Maine, Eastern Egg Rock and Seal Island. Given the high risk of getting spurious results from using only 148 marked birds (Anderson et al. 2001), we limited our CMR analysis to a series of exploratory tests (using models) that looked for differences in survival and resighting probabilities among years and between colonies. In our discussion, we (1) explore two implications of our results concerning differences in survival between two neighboring local breeding

populations, (2) compare survival probabilities from this study with other studies of long-lived seabirds, and (3) draw attention to the regional importance of our survival estimates. Second, we showed that our plastic bands wore rapidly through time and also assessed whether or not band wear led to heterogeneity among individual resighting probabilities; heterogeneity can cause data to become overdispersed, which may lead to underestimated sampling variances in CMR models.

STUDY AREA AND METHODS

Study sites.—Data were collected at two colonies, Seal Island (44°14'N, 68°44'W; 40.5 ha) and Eastern Egg Rock (43°51'N, 69°22'W; 2.9 ha), Maine (Fig. 1; Kress and Nettleship 1988). Seal Island is ~42 km east of Eastern Egg Rock. Restoration efforts, including transplanting chicks from Newfoundland and social attraction (Kress 1997), preceded recent puffin recolonization of both Eastern Egg Rock (Kress and Nettleship 1988) and Seal Island (Kress 1997) in 1981 and 1992, respectively. Since recolonization, the number of puffins breeding has increased to 70 pairs on Eastern Egg Rock and 290 pairs on Seal Island in 2004 (Kress 1978–2004). Both islands are composed of granite bedrock with numerous boulder and rock slab berms; rock crevices within those features are the primary nest sites for puffins in the Gulf of Maine. The nonforested island interiors consist mainly of dense raspberry (*Rubus* sp.) thickets and herbaceous meadow (Kress and Nettleship 1988).

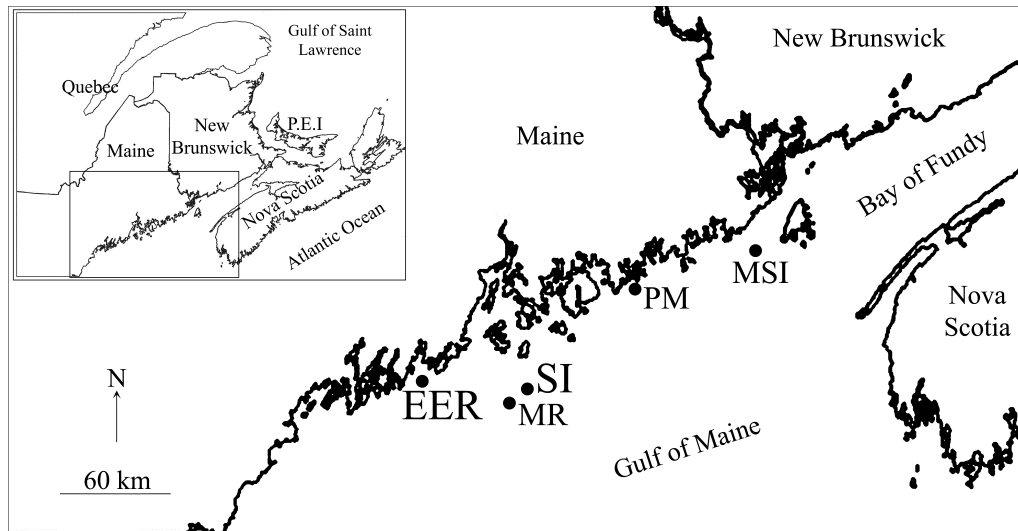


FIG. 1. Locations of managed Atlantic Puffin colonies in the Gulf of Maine and Bay of Fundy: Eastern Egg Rock (EER), Matinicus Rock (MR), Seal Island (SI), Petit Manan (PM), and Machias Seal Island (MSI).

Sampling scheme.—Breeding adults were captured by hand in nesting burrows, with noose mats tied to rocks, with wooden drop boxes, or with swivel-lid boxes. Native chicks were captured in burrows by hand or while fledging (Diamond and Devlin 2003). Each puffin received an individually engraved, plastic or metal (incoloy) field-readable band on one tarsus and a metal federal band on the other. Eight birds included in the CMR analysis received the metal-type field-readable band. However, those were applied in 1999 ($n = 5$) and 2000 ($n = 3$)—that is, near the end of the study. Worn plastic bands were replaced on a small proportion of birds; those few recaptures were excluded because of an abundance of resightings. The federal bands, made of monel or incoloy, were rarely replaced, and all remained legible throughout the study.

Bands, preferably field-readable type, were resighted by blind-concealed observers using binoculars and spotting scopes. Banding and resighting occurred every year from mid- to late May through early to mid-August. That period overlaps with the breeding period for puffins at both colonies (mid-April through late August).

Band wear.—Our plastic field-readable leg bands consist of two layers of darvic (rigid polyvinyl chloride [PVC]) plastic with repeated characters (e.g. U12–U12) engraved on the

surface. In our region, surface wear from abrasion against colony rocks appears to accumulate over time, resulting in gradual losses of engraved characters and a concurrent decrease in plastic band readability. Band degradation is a source of failure of the “individual heterogeneity” assumption common to all CMR data types (White et al. 1982, Burnham et al. 1987, Pollock et al. 1990, Lebreton et al. 1992). When the assumption is violated, data become “overdispersed” (see below), resulting in underestimated sampling variances and inflated confidence in survival estimates (Anderson and Burnham 1994).

Given the generality of the problem of overdispersion, we believed that (1) validation of rapid wear and (2) confirmation of our assumption that detectability was unaffected would provide valuable contributions to the CMR literature. To quantify band wear through time, we developed a band readability curve. To determine whether CMR data were overdispersed, we estimated the adjusted overdispersion factor (\hat{c} ; see below).

Band readability curve and data set.—We fit a quadratic regression line (readability curve) to the mean resighting frequency in each year, divided by the mean frequency in the first year after banding, against age of band in years. Date of banding varied, so we excluded

application year (i.e. year zero). Age-specific sighting counts from 38 plastic bands applied to known breeders on Eastern Egg Rock (14), Seal Island (3), and Matinicus Rock (21) (island substrates do not differ) were used to calculate means. All individuals sampled were detected for at least eight years postbanding on islands where resighting effort does not vary with time. Criteria were developed to maximize sample size, minimize confounding factors, and cover the typical readability lifespan of a plastic band. These sampling criteria being applied, our readability curve should isolate the effects of wear on our ability to read aging bands.

Capture-mark-resight/recapture data set.—Data from adults breeding on Matinicus Rock, Petit Manan, and Machias Seal Island (Fig. 1)—islands where resighting effort has been low in comparison with Eastern Egg Rock and Seal Island—were excluded from the CMR analysis to avoid problems associated with individual heterogeneity resulting from degrading plastic bands. On the basis of counts of hours spent resighting bands, we believed that resighting effort on Eastern Egg Rock and Seal Island would be high enough to compensate for failing bands (S. W. Kress unpubl. data). Nevertheless, we tested this assumption by estimating \hat{c} (see below).

Birds were marked as either breeding adults ($n = 70$) or chicks ($n = 78$); 46 of the chicks had been transplanted from Newfoundland and raised on Eastern Egg Rock or Seal Island in artificial burrows (Kress and Nettleship 1988, Kress 1997). All adults were initially captured and marked on Eastern Egg Rock and Seal Island. Most of the native Gulf of Maine chicks were captured and banded on Matinicus Rock; those remaining were marked on Eastern Egg Rock, Seal Island, Petit Manan, or Machias Seal Island (Fig. 1). Although almost half our sample were initially marked as chicks, including those transplanted from Newfoundland, we analyzed survival only in their adult years here (see below); immature survival and natal dispersal probabilities were analyzed elsewhere (Greenwood and Harvey 1982).

Birds entered and remained in the sample only after their first observed breeding attempt (i.e. as breeding adults); earlier failed nesting attempts may have gone unnoticed. Breeding was confirmed either by watching marked birds deliver fish (puffins carry fish exposed in their

beak back to an awaiting chick; Harris 1984) to a concealed nest, or by observation of an egg and later confirmation of adults moving in and out of that nest site. We found no evidence of breeding dispersal (i.e. adults changing islands between breeding attempts; Greenwood and Harvey 1982); breeding dispersal has not been detected in puffins (Harris and Wanless 1991).

Capture-mark-resight/recapture analysis.—We tested for differences in annual survival and resighting probabilities between colonies and among years by comparing models built in MARK (White and Burnham 1999). We based support for individual models on ΔQAIC_c values and 95% confidence intervals around model effect sizes ($\text{QAIC}_c \equiv \text{Akaike's information criterion [AIC] corrected for overdispersion [Q; using } \hat{c}] \text{ and small sample size [c]; Burnham and Anderson 2002}$). ΔQAIC_c is the QAIC_c difference between the top ranked model, that is, the model with the smallest QAIC_c value (minimum), and a competing model (i), $\equiv \text{QAIC}_{c_{\min}} - \text{QAIC}_{c_i}$. Rules of thumb were adopted from Burnham and Anderson (2002): if ΔQAIC_c is 0–2, that indicates “substantial support” for both models; if ΔQAIC_c is 4–7, that indicates “considerable” support in favor of the top model; and if ΔQAIC_c is >10, that indicates “essentially” no support for the competing model.

Survival and resighting probabilities are maximum-likelihood estimates generated from our best model. The default logit link function was maintained in all models following construction in the design matrix of MARK (White and Burnham 1999). Consistent with Lebreton et al. (1992), we began our analysis by assessing goodness-of-fit (GOF) of our global model: survival and resighting probabilities are time- and colony-dependent but the effect of time on colony is not colony-specific (i.e. the model does not include time * colony interaction terms). Exclusion of interaction terms was required because of the limited data. Following GOF testing, we tested for colony and time dependence in resighting and then survival probabilities by comparing support for the global model with support for nested designs.

Because of the limited data set, assessment of model fit with RELEASE was limited to only the combined chi-square results for tests 2 and 3 (Burnham et al. 1987). We also assessed fit using the parametric bootstrap approach: divide the deviance of the global model by the average

model deviance from 100 bootstraps to produce an adjusted overdispersion factor (\hat{c}). The factor provides an omnibus measure of problematic structure in the data, including individual heterogeneity (Anderson and Burnham 1994). When data fit the model perfectly, $\hat{c} = 1.0$; this is also referred to as unadjusted \hat{c} . Burnham and Anderson (2002) suggest that both AIC_c and estimated sampling variances should be adjusted using \hat{c} only if some “distinct lack of fit has been found.” Given our limited ability to assess fit with RELEASE, we took a conservative approach and applied \hat{c} if \hat{c} were >1.0 . This is “conservative” because applying \hat{c} to both AIC_c and sampling variances causes support for models with fewer parameters and uncertainty in parameter estimates to increase; in effect, our ability to draw inferences about subtle to moderate features of the data declines.

RESULTS

Readability curve.—Fit of a quadratic regression line (readability curve) to our data demonstrates a strong relationship between our readability index and age ($r^2 > 0.96$, $y = -0.0123(x^2) + 0.0068(x) + 1.0254$), including a period of high detectability followed by a rapid decline; between years 3 and 8, readability declined steeply by 70% (Fig. 2).

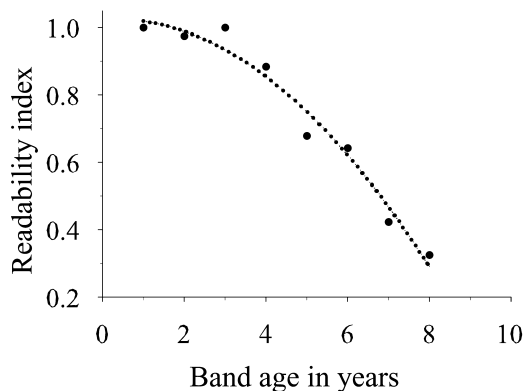


FIG. 2. An index of band readability, mean number of resightings year⁻¹ divided by the mean in year one, against age of band in years ($n = 38$ plastic bands). Data were fit to a line using a quadratic equation resulting in our readability curve ($r^2 > 0.96$, $y = -0.0123(x^2) + 0.0068(x) + 1.0254$).

Capture-mark-resight/recapture analysis.—From 1992 to 2003, 148 adults (59 from Eastern Egg Rock and 89 from Seal Island) were released. Those birds were later resighted 18,376 times. The combined result for tests 2 and 3 in RELEASE was not significant ($\chi^2 = 24.72$, $df = 28$, $P > 0.64$). Our adjusted \hat{c} , global model deviance (188.13) divided by average deviance from 100 bootstraps (164.99), was 1.14. Although those results suggest appropriate fit and little or no heterogeneity, we applied our adjusted \hat{c} to sampling variances and AIC_c prior to running additional models.

Models D–G (Table 1) were compared to determine importance of colony and time in predicting resighting probabilities. In those models, colony and time dependence were maintained in survival probabilities. Models D (resighting probabilities as a function of colony), E (resighting probabilities constant), and F (global model; resighting probabilities as a function of colony and time) acquired nearly equal $\Delta QAIC_c$ support. However, with only one exception, estimated time-effect sizes in model F widely bound zero (e.g. slope coefficient for time effect in 1996: 0.55 ± 1.04 [SE], 95% confidence intervals [CI]: -1.48 to 2.58). Wide confidence intervals demonstrate high uncertainty in regard to the importance of time effects on resighting probabilities, precluding confident inference. By contrast, the colony effect in model D was positive and did not bound zero (1.06 ± 0.48 , 95% CI: 0.13 to 1.99); under certain assumptions, this suggests that the difference in resighting probabilities is a true feature of the sampled colonies. On the basis of $\Delta QAIC_c$ and confidence intervals around model effects, we maintained the colony effect in resighting probabilities and proceeded to test for colony and time dependence in survival (models A–D; Table 1).

Models D and C (survival as a function of time) acquired essentially no support compared with the highly $\Delta QAIC_c$ -favored models A (survival probabilities are constant) and B (survival as a function of colony). Models A and B acquired equal support. However, the confidence intervals around the colony effect in model B bound zero substantially (0.31 ± 0.33 , 95% CI: -0.35 to 0.96); consequently, there is high uncertainty in regard to a colony effect and so the estimated effect size should not be used as a basis for inference. Given the data, $\Delta QAIC_c$

TABLE 1. Competing models ranked by ascending QAIC_c, including model selection criteria.

Model	QAIC _c	ΔQAIC _c	Akaike weight	Model likelihood	K	Model deviance
A { ϕ (.) p (c)}	496.279	0.00	0.65004	1.0000	3	189.611
B { ϕ (c) p (c)}	497.538	1.26	0.34628	0.5327	4	188.852
C { ϕ (t) p (c)}	507.577	11.30	0.00229	0.0035	13	180.491
D { ϕ (c + t) p (c)}	509.072	12.79	0.00108	0.0017	14	179.916
E { ϕ (c + t) p (.)}	511.953	15.67	0.00026	0.0004	13	184.867
F { ϕ (c + t) p (c + t)}	515.162	18.88	0.00005	0.0001	24	165.026
G { ϕ (c + t) p (t)}	523.246	26.97	0.00000	0.0000	23	175.232

Parameter definitions: ϕ = survival parameter, p = resighting parameter, (.) parameter constant, (c) parameter as a function of colony, (t) parameter as a function of time, and (c + t) parameter as a function of colony and time (with no interaction).

and model effects suggest that model A is the overall best model. Estimates from model A are provided in Table 2.

DISCUSSION

Band wear and overdispersion.—Calvo and Furness (1992) reviewed 786 papers on birds and found that 39.6% used engraved or nonengraved plastic color bands. Given the wide use of plastic bands, it seems likely that band wear (as in our study) is common. Therefore, analyses aimed at gaining insights into the process and severity of wear and ensuing biases should be valuable. Plastic bands in our study wore rapidly but did not result in overdispersion; we accomplished this by using both the wear-resistant federal bands and the plastic bands and by intensively resighting birds. We maintained detection of marked animals, because as the plastic bands wore out, we switched our focus to the less-legible federal bands.

It is unlikely that our high resighting probabilities can be accomplished in most studies. Whether or not this is the case, we recommend double-banding and careful selection of band

types, especially if geological substrates in the study area may cause wear. Investigators should keep in mind that resistance qualities of plastics vary and that other nonmetal alternatives exist. In studies experiencing band wear, the investigators should estimate \hat{c} for the data they have acquired to determine whether overdispersion is present. In most cases, it may not be possible to preclude overdispersion by increasing effort; switching to a more durable band may be the only solution.

Survival effects and inference.—Exclusive support for model A suggests that probabilities of resighting and survival were a function of colony and constant, respectively, over the period studied (1992–2003). Consistency in survival between Eastern Egg Rock and Seal Island (~42 km between islands) over 11 years suggests that mortality factors affecting breeding adults were independent of the local breeding population (colony). Shared survival combined with very little evidence of mortality in the breeding period (A. W. Diamond and S. W. Kress unpubl. data) provides evidence that adults from Eastern Egg Rock and Seal Island may exist sympatrically in the nonbreeding period

TABLE 2. Survival and resighting probabilities as maximum-likelihood estimates (MLE) generated in MARK (White and Burnham 1999) from model A { ϕ (.) p (c)}, with survival probabilities constant and resighting probabilities a function of colony.

Colony	Parameter	MLE	SE	95% Confidence limit	
				Lower	Upper
Both	ϕ : All years	0.9500	0.0083	0.9308	0.9641
Eastern Egg Rock	p : All years	0.9816	0.0078	0.9579	0.9920
Seal Island	p : All years	0.9463	0.0129	0.9145	0.9667

Parameter definitions: ϕ = survival parameter, p = resighting parameter.

(fall, winter, spring). That inference, if true, makes an important contribution to our limited knowledge of the winter distribution of western Atlantic Puffins (Lowther et al. 2002).

Managers generally accept and implement the belief that by protecting several spatially discrete local populations, they improve the chances of a species persisting. However, that belief hinges on the critical assumption that adult survival is a local population phenomenon (i.e. independent of neighboring conspecific groups). Obviously, if that assumption fails, several "discrete" local breeding populations could go extinct simultaneously, because of shared high adult mortality. Suggestions for avoiding that scenario are beyond our scope here, but our results clearly suggest that to make confident management decisions, we need to know more about shared characteristics of local populations. The results also demonstrate that our understanding of population dynamics, based mainly on knowledge from single local population research, may in some cases be deficient and misleading.

Survival pattern and comparisons.—Our estimate of adult survival is consistent with published estimates for many long-lived seabirds experiencing conditions conducive to low mortality (see summaries in Spendelow and Nichols 1989, Jouventin and Weimerskirch 1991, Harris et al. 2000). Survival estimates from puffin colonies in the eastern and western Atlantic Ocean (Table 3), again for adults experiencing favorable conditions ($\geq 95\%$), are also consistent with our own. With our small data set, we did not detect biologically important changes in survival over the period studied. High survival in most years broken only occasionally by low survival is a common finding in long-term studies of K-selected seabirds, including the European Shag (*Phalacrocorax aristotelis*), Common Murre (*Uria aalge*), and Razorbill (*Alca torda*) in the Northern Hemisphere (Harris et al. 2000), and the Light-Mantled Sooty Albatross (*Phoebastria palpebrata*) and Sooty Albatross (*P. fusca*) in the Southern (Weimerskirch et al. 1987). Although results from those studies contrast with our

TABLE 3. Annual survival estimates from breeding adult Atlantic Puffins from the eastern and western Atlantic Ocean, including study location and methods.

Study location	Method	Survival estimate (%)	Author(s)
Eastern Atlantic			
British Isles	Ring recoveries	95.5	Mead (1974)
Skomer Island, Wales	Resight (color bands) ^{a, c}	95.0	Ashcroft (1979)
Skomer Island, Wales	Resight (color bands) ^{a, d}	89.0	Hudson (1979)
Isle of May, Scotland	Resight (color bands) ^{a, c}	96.3	Harris (1983), Harris and Wanless (1991), Harris and Bailey (1992)
Isle of May, Scotland	Resight (color bands) ^{b, c}	97.5 (1973–1980) 92.4 (1981–1994) 80.6 (1990)	Harris et al. (1997)
Rost, Norway	Resight (color bands) ^{b, c}	92.7	Erikstad et al. (1998)
Hornoya, Norway	Resight (color bands) ^{b, c}	86.0	Erikstad et al. (1998)
Skomer Wales	Resight (color bands) ^{b, c}	91.3	Poole et al. (1998)
Isle of May, Scotland	Resight (color bands) ^{b, c}	91.6	Harris et al. (2000)
Western Atlantic			
Great Island, Newfoundland	Resight (color bands) ^{a, c}	95.0	Nettleship (1972) and pers. comm. from Hudson (1985)
Eastern Egg Rock, Gulf of Maine	Resight (color bands) ^{a, c}	>95.0	Kress (1978–2004)
Gulf of Maine	Resight (color bands) ^{b, c}	95.0	Present study

^a Survival rate estimated using return rates (i.e. by dividing the number of marked animals encountered in year $i + 1$ by the number marked in year i).

^b Maximum-likelihood method used to estimate survival probabilities following a CMR analysis.

^c Sample consists of known breeders captured at burrows.

^d Breeding status of birds not always known (Gaston and Jones 1998).

own, a *post-hoc* observation of estimates from model C (survival and resighting as a function of time and colony, respectively) suggests that two low-survival events in our data may have eluded detection: 1999–2000 (0.91 ± 0.03) and 2001–2002 (0.92 ± 0.03). Interestingly, those events preceded two of three low estimates of fledging success for the period studied (S. W. Kress and A. W. Diamond unpubl. data). It is not surprising, given our small sample size, that we were unable to detect those potentially important events. Consequently, the time-independent survival probability reported here (0.95 ± 0.01) may be too low for most years.

An unusual survival pattern was documented by Harris et al. (1997) in CMR data from adult puffins monitored at the Isle of May, Scotland. Harris et al. (1997) report a stepped pattern in survival over the period studied, 1973–1990 (Table 3). We speculate that such a stepped pattern may be detectable only in data sets that approach 20 years or more.

Regional contribution.—Survival probabilities presented here are the first for Atlantic Puffins in the western Atlantic to be estimated from competing models using the maximum-likelihood method, and update the last published estimates for the region from 1987 (Kress 1978–2004; Table 3). As shown in Table 3, previously published estimates in the western Atlantic estimated survival from year i to $i + 1$ as return rates given by the estimator (notation varies)

$$\phi_i = r_{i+1} / R_i$$

where R_i is the number of marked animals released at time i and r_{i+1} is the number subsequently encountered in year $i + 1$ (Pollock et al. 1990). Using that estimator, return rates underestimate survival unless the encounter (e.g. resight, recapture, or both) probability at year $i + 1$ is equal to 1.0. Considering major factors that complicate our ability to relocate marked animals, including landscape heterogeneity and observer experience, it seems reasonable to assume that return rates are confounded by encounter probabilities and to use CMR models to estimate survival.

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