The Auk 125(3):723–730, 2008

Printed in USA.

HIGH SURVIVAL OF IMMATURES IN A LONG-LIVED SEABIRD: INSIGHTS FROM A LONG-TERM STUDY OF THE ATLANTIC PUFFIN (*FRATERCULA ARCTICA*)

Hanno Sandvik,[1,3] Kjell Einar Erikstad,[2] Per Fauchald,[2] and Torkild Tveraa[2]

[1]*Centre of Conservation Biology, Department of Biology, Norwegian University of Science and Technology, 7491 Trondheim, Norway; and*
[2]*Division of Arctic Ecology, Polar Environmental Centre, Norwegian Institute for Nature Research, 9296 Tromsø, Norway*

Abstract.—Survival from fledging to maturity is an important life-history parameter in long-lived species such as seabirds. However, because of the long period of unobservability following fledging, few studies have reported reliable estimates of survival rates for immatures. We estimated survival to maturity of two cohorts of Atlantic Puffin (*Fratercula arctica*) fledglings from Hornøya in northern Norway using capture–mark–recapture methodology. By considering only juveniles that actually left their nest burrows, we arrived at unbiased estimates of survival rates for immatures. Contrary to many previous studies, annual survival of immatures was not depressed in relation to adult survival. By the age of five years, more than two-thirds of all fledglings are still estimated to be alive. Averaged over this period, annual survival of immatures is estimated as 0.933 (95% confidence interval: 0.806–0.993). This compares to an annual adult survival of 0.943 (0.909–0.965) during the same period. The survival estimates also imply that the cohorts studied are overwhelmingly philopatric. Dispersal of immatures must be extremely rare or absent. The annual estimates of resighting reveal a clear age-related pattern, including a peak at three years of age and a subsequent minimum at six years of age. Possible biological explanations for this behavior are given. *Received 12 April 2007, accepted 18 February 2008.*

Key words: Atlantic Puffin, capture–mark–recapture, *Fratercula arctica*, immature survival, juvenile survival, philopatry, recruitment rate.

Hohe immature Überlebensraten eines langlebigen Seevogels – Resultate einer Langzeitstudie des Papageitauchers

Zusammenfassung. – Bei langlebigen Arten wie Seevögeln ist die Überlebensrate flügger Junger bis zur Geschlechtsreife eine wichtige Variable des Lebenszyklus. Weil immature Seevögel nach dem Ausfliegen mehrere Jahre lang schwer zu beobachten sind, haben jedoch nur wenige Studien verläßliche Angaben zu ihren Überlebensraten machen können. Wir ermittelten die Überlebensraten zweier Kohorten immaturer Papageitaucher (*Fratercula arctica*) an Hand von Fang–Wiederfang-Studien auf Hornøya in Nordnorwegen. Eine mögliche Fehlerquelle wurde ausgeschlossen, indem wir nur tatsächlich ausgeflogene Junge berücksichtigten. Das Ergebnis vieler früherer Arbeiten, daß immature Überlebensraten deutlich niedriger als die adulten sind, wurde von uns nicht bestätigt: Mehr als zwei Drittel aller ausgeflogenen Jungen erreichten das Alter von fünf Jahren. Dies entspricht einer jährlichen immaturen Überlebensrate von durchschnittlich 0,933 (95%-Konfidenzintervall: 0,806–0,993), während die adulte Rate 0,943 (0,909–0,965) beträgt. Diese Werte bedeuten auch, daß so gut wie alle Jungvögel zum Brüten zu ihrer eigenen Geburtskolonie zurückkehrten. Die jährlichen Beobachtbarkeitsraten folgten einem deutlich altersabhängigen Muster, welches durch ein Maximum im Alter von drei Jahren und ein Minimum im Alter von sechs Jahren gekennzeichnet war. Mögliche biologische Erklärungen für dieses Verhalten werden diskutiert.

In long-lived species, theoretical considerations and population models indicate that survival to maturity may be the single most important life-history parameter after adult survival (Newton 1991, Gaillard et al. 1998, Stahl and Oli 2006). This means that a change in survival rates affects the population growth rate (λ) more than a change of the same relative size in any other demographic parameter (Caswell 2001), or that survival of adults and immatures has high elasticity (Sæther and Bakke 2000). At the same time, the available evidence suggests that survival rates of immatures vary more between years than adult survival rates (Serventy and Curry 1984, Massey et al. 1992, Harris et al. 1994, Weimerskirch et al. 1997, Waugh et al. 1999), which means that variation

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[3]E-mail: hanno@evol.no

The Auk, Vol. 125, Number 3, pages 723–730. ISSN 0004-8038, electronic ISSN 1938-4254. DOI: 10.1525/auk.2008.07059

in survival to maturity may explain a large proportion of the variance in population growth rates (Gaillard et al. 2000). All of this indicates the immense importance of a good understanding of the process of recruitment to the breeding population.

However, in seabirds and other long-lived birds, reliable data on survival of immatures have been notoriously rare (Dunnet and Porter 1991; but see Breton et al. 2006). Although reproductive success is comparatively straightforward to measure and the past years have seen the development of robust methodologies to estimate annual survival (Burnham et al. 1987, White and Burnham 1999), the fate of immatures is inherently difficult to study in the field (but see Pradel et al. 1997). The main reason for this is that large numbers of potential future recruits (i.e., fledglings) need to be marked to obtain reliable estimates of survival for immatures. This problem is especially severe in long-lived species such as seabirds, because these also tend to have high and variable ages at first reproduction (Weimerskirch 2002). Mortality, dispersal, ring wear, and ring loss during this initial non-breeding period, during which the birds are not normally observed, decrease the reliability of survival estimates for immatures.

To date, the "established wisdom" in seabird ecology is that annual survival of immatures is lower than annual adult survival, and that emigration rates are higher than for experienced breeders (e.g., Hudson 1985 and references therein). Accordingly, rates of return to the natal colony are rarely reported to exceed 50% of any given cohort: for auks (Alcidae), the estimated cumulative survival to breeding age falls into the range 0.13–0.56 (Hudson 1985, Harris and Wanless 1991, Gaston et al. 1994, Lyngs 1994, Frederiksen 1999, Breton et al. 2006, Crespin et al. 2006). In the present study, we analyzed the survival from fledging to the mean age at first reproduction of two cohorts of Atlantic Puffin (*Fratercula arctica*; hereafter "puffin") within a capture–mark–recapture framework.

METHODS

Field methods.—The study was carried out on Hornøya (72°22′N, 31°10′E), an island off the northern Norwegian east cost in the southwestern Barents Sea. The breeding population of puffins at Hornøya was ~7,500 pairs in 1994 and had increased to ~11,000 by 2005 (Lorentsen 2006). Puffins lay one egg in earth-dug nesting burrows. Both parents incubate the egg and feed the chick. The duration of the breeding period is normally 77–88 days, which is equally divided between the incubation and brooding periods (Lowther et al. 2002).

In the summers of 1994 and 1995, we marked chicks with metal rings and unique combinations of color rings when they had reached an age of ~30 days. Birds that died between ringing and fledging were removed from the data set. In 1994, 69 ringed chicks fledged, and in 1995, 182 chicks fledged. Chicks in 1994 were part of an experiment that did not affect survival rates of immatures in this cohort (for details, see Erikstad et al. 1997). During all subsequent years, the colony was searched for color-ringed birds using binoculars. All sightings were recorded, but we have no data on the breeding status of individual birds.

Since 1990, 629 breeding adults have been ringed on Hornøya. Adult and immature puffins were incorporated into the same data set and analyses (see below). By "immatures," we refer to all birds between fledging and the average age at first reproduction.

Statistical analysis.—The data were analyzed in a capture–mark–recapture framework, using MARK (White 2004). This enabled us to estimate apparent (or local) survival probabilities (ϕ; hereafter "survival") and resighting probabilities (p; White and Burnham 1999). The analysis methods are described below; see Sandvik et al. (2005) for a more detailed account.

Initial inspection of data was done using Test 2 and Test 3 in RELEASE (cf. Burnham et al. 1987). Test 3 showed that ϕ and p were identical among individuals ($\chi^2 = 16.45$, df = 44, $P = 1.00$), whereas Test 2 revealed that ϕ and p were strongly dependent on prior capture histories ($\chi^2 = 326.84$, df = 58, $P << 10^{-12}$). Because trap dependence is one of the factors that can lead to such resighting heterogeneity, we used the correction suggested by Pradel (1993). Accounting for trap dependence extending over two years was sufficient to remove the resighting heterogeneity (i.e., the overdispersion factor $\hat{c}$ was <1).

Loss of color rings posed a potential problem that was solved in the way explicated by Sandvik et al. (2005)—that is, by ignoring observations of birds starting with the year in which they could have given rise to an observed incomplete color-ring combination (whether or not their specific ring combination was observed later). This procedure reduced the sample size (from an effective sample size of 10,650 to 6,535 bird-years)—though substantially less so than if those birds had been excluded altogether (effective sample size of 2,278 bird-years)—and, more importantly, it is not biased toward keeping birds that were seen more often.

Resighting histories of adults and two cohorts of immatures were incorporated into the same data set as separate attribute groups. In this way, resighting and survival rates of adults and immatures could be estimated separately, up to a specifiable recruitment age. After this age, birds marked as fledglings were treated as equivalent to adult birds. Because we incorporated several models with differing recruitment ages, we were able to estimate the threshold age, rather than assuming it in advance. The initial model assumed that both resighting and survival rates of immatures differ from adult rates for the first 10 years of the potential recruits' lives and that they differ between ages and cohorts of immatures (cf. model 18 in Table 1). We then investigated whether this model could be simplified by replacing multiplicative with additive models; by dropping the effects of age, cohort, or both; and by reducing the range of years during which rates for immatures and adults were estimated separately.

Model simplifications were guided by Akaike's information criterion corrected for small sample sizes (AIC_c). All estimates were derived by model averaging and are given as best estimates, with 95% unconditioned confidence intervals. Having arrived at a final model, we also tested which estimates for immatures differed from the corresponding adult rates. These tests were likelihood ratio tests based on twice the difference between the log likelihoods of the models compared. This measure is distributed as chi squared and tested accordingly, on one degree of freedom. Models compared were the final model and a model that differed only in whether the rates for immatures at the respective age are constrained to equal adult rates or are estimated separately.

TABLE 1. Models of local survival to maturity of Atlantic Puffins at Hornøya. Models shown are the initial model, the final model, and its neighborhood (i.e., the best models that differ from the final model in one characteristic), sorted in order of ascending $\Delta\mathrm{AIC}_c$ values. The columns give a description of the difference between each model and the final one, followed by the model notations (shown only for the parts that deviate from the final model) for survival of immatures (ϕ), resightings of immatures (p), the age until which survival of immatures differs from that of adults (ξ), the age until which resightings of immatures differ from resightings of adults (ζ), the number of parameters (n_P), model deviance (Dev.), $\Delta\mathrm{AIC}_c$, and AIC_c weights (w).

	Description of the model	ϕ	p	ξ	ζ	n_P	Dev.	$\Delta\mathrm{AIC}_c$	w
1.	Final model (see text)	—	$a + c + h2$	0	6	28	37.16	0.00	0.052
2.	Survival differs from adults' during the first four years			4		29	35.53	0.41	0.042
3.	Survival differs from adults' during the first three years			3		29	35.62	0.50	0.040
4.	Survival increases linearly with age during the first six years	A		6		30	34.04	0.96	0.032
5.	Resighting differs from adults' during the first seven years				7	29	36.10	0.98	0.032
6.	Survival increases linearly with age during the first six years, and the intercept differs between cohorts	$A + c$		6		31	32.67	1.63	0.023
7.	Survival differs from adults' and between cohorts during the first three years	c		3		30	34.82	1.74	0.022
8.	Survival is age-dependent and differs from adults' during the first two years	a		2		30	34.98	1.90	0.020
9.	Re-sighting differs from adults' during the first four years				4	26	43.51	2.27	0.017
10.	The cohort effect in re-sighting is multiplicative rather than additive		$a * c + h2$			31	33.67	2.63	0.014
11.	Survival is age-dependent and differs from adults' during the first six years	a		6		33	29.92	2.97	0.012
12.	Survival increases linearly with age during the first six years, and both slope and intercept differ between cohorts	$A * c$		6		32	32.36	3.37	0.010
13.	Resighting does not differ between cohorts		$a + h2$			26	46.12	4.89	0.005
14.	The effect of trap dependence differs between cohorts		$(a + h2) * c$			33	33.54	6.59	0.002
15.	Survival is age-dependent and differs from adults' and (additively) between cohorts during the first three years	$a + c$		3		33	33.72	6.77	0.002
16.	Survival is age-dependent and differs from adults' and (multiplicatively) between cohorts during the first three years	$a * c$		3		34	7.06	6.83	0.001
17.	Resighting is age-independent and differs from adults' during the first two years		$c + h2$		2	22	62.07	12.70	0.000
18.	Initial model (see text)	$a * c$	$(a+ h2) * c$	10	10	59	0.00	26.73	0.000

Abbreviations: — = no effect (constant); a = age; A = linear trend with age; c = cohort; $h2$ = sighting heterogeneity extending for two years after the last sighting. Operators: + additive effect; * multiplicative effect, i.e., main effects + interaction.

RESULTS

Several models obtained low AIC_c values (Table 1). We refer to the model with the lowest AIC_c as the "final model" and use it as a reference for the description of the other models in Table 1. This is accomplished in the following paragraphs by describing the characteristics of the final model and comparing them with the other models (referred to by means of their numbers in Table 1).

Resighting rates of immatures differed between the two cohorts and with age. The cohort effect was additive to the age effect (i.e., resighting rates varied in parallel in both cohorts; Fig. 1). The best models without cohort effect (model 13) and with a multiplicative effect of age and cohort (model 10) were substantially less supported, as was the best model without an age effect (model 17).

Resighting rates for immatures differed from those for adults up to and including the sixth year after fledging (cf. model 9). Beyond that age, differences were less pronounced (model 5), as can also be seen from the overlapping confidence intervals in Figure 1B and Table 2. For the first two years after fledging, resighting rates were low, but above zero (Fig. 1 and Table 2). Immatures three and four years of age, however, had a very high probability of being observed at the colony: at the age of three, a higher proportion of immatures (mean for the two cohorts = 0.867 [0.773–0.939], n = 251) than of adults (mean for the period 1995–2003 = 0.796 [0.765—0.824], n = 484) were resighted, whereas resighting in the fourth year did not differ from adult resighting rates (Table 2). Resighting rates for immatures during the fifth and sixth years of age were again lower than the rates for adults (Fig. 1 and Table 2).

Rates of survival of immatures were high throughout. Cumulative survival from fledging to the seventh season was 0.614 (0.313–0.848; n = 251). Expressed as a yearly average, this is equivalent to an annual survival of 0.933 (0.806–0.993) for immatures, compared with an annual adult survival rate during the same period of 0.943 (0.909–0.965; n = 484). Cumulative survival from fledging to the fifth year was 0.682 (0.341–0.890). Because of low resighting rates, separate estimates of annual survival of immatures were imprecise for the first couple of years of life. In the final model, survival of immatures equaled adult survival at all ages. According to several other models, estimates for immatures differed slightly from those for adults, the tendency being lower-than-adult estimates during the initial years (1–3) and

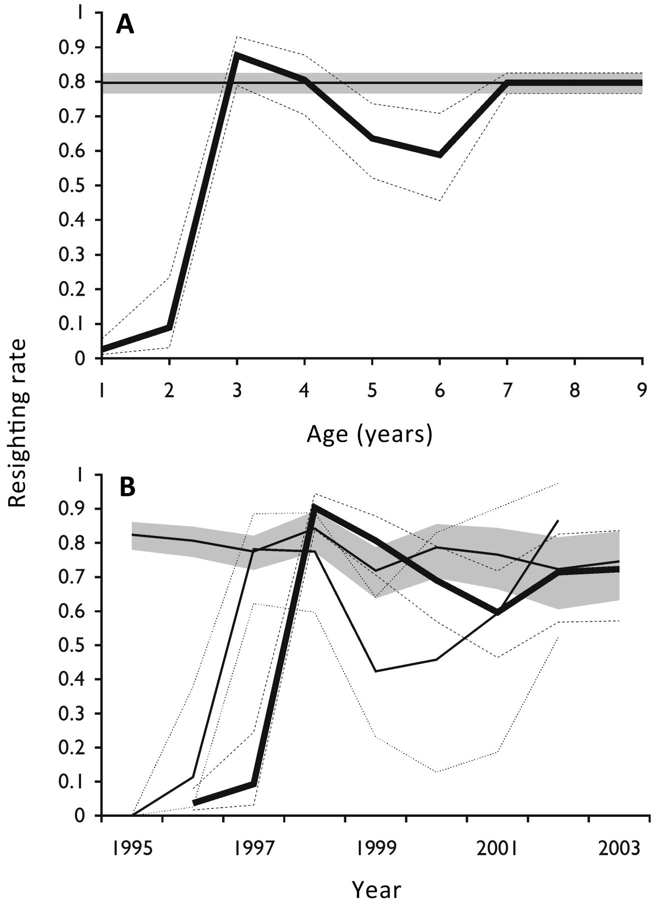

Fig. 1. Rates of resighting of two cohorts of immature Atlantic Puffins at their natal colony. The thin line within the gray bar gives the adult estimates for comparison. All values are mean estimates and 95% confidence intervals. (A) Resighting rates by age, based on the best model without cohort effect {$p(a)$}. (B) Resighting rates by year, based on a model with a multiplicative cohort effect {$p(a * c)$}; the 1994 cohort is shown with thin and dotted lines, the 1995 cohort with bold and broken lines. The final model had an additive cohort effect {$p(a + c)$} and was very similar in shape to A. See Table 1 for explanation of model notation.

Table 2. Estimates of resighting and apparent survival rates of two cohorts of Atlantic Puffins at Hornøya. Estimates are tabulated age- and cohort-wise with mean estimate and 95% confidence intervals (CI). Estimates are based on model averaging, and confidence intervals include model uncertainty. For each age, estimates are compared with the corresponding estimates of adult birds during the same years. The sign of the differences is indicated by (in)equality signs,[a] and significance levels are indicated by asterisks ($0.05 > p^* \geq 0.01 > p^{**} \geq 0.001 > p^{***}$). Tests performed are likelihood ratio tests based on twice the difference between the log-likelihoods (deviance [Dev.]) of the models compared.[b]

	Cohort 1994		Cohort 1995		Difference from adults	
Age	Mean	95% CI	Mean	95% CI	Sign[a]	Dev.[b]
			Resighting			
1	0.000	0.000–0.000	0.037	0.017–0.082	<	304.21***
2	0.057	0.016–0.181	0.105	0.034–0.277	<	111.20***
3	0.805	0.654–0.901	0.890	0.802–0.942	>	5.98*
4	0.704	0.537–0.830	0.823	0.717–0.895	≈	1.85
5	0.506	0.343–0.668	0.666	0.546–0.767	<	12.70***
6	0.439	0.250–0.647	0.593	0.454–0.719	<	5.24*
7	0.740	0.610–0.839	0.741	0.649–0.816	≈	1.06
8	0.742	0.652–0.816	0.750	0.659–0.823	≈	1.10
			Survival			
0–1	0.906	0.281–0.996	0.920	0.742–0.979	≈	0.30
1–2	0.905	0.279–0.996	0.918	0.724–0.980	≈	1.67
2–3	0.908	0.694–0.977	0.916	0.739–0.977	≤	2.31
3–4	0.934	0.834–0.976	0.940	0.865–0.975	≈	0.31
4–5	0.946	0.861–0.980	0.951	0.882–0.980	≈	1.70
5–6	0.948	0.870–0.981	0.952	0.885–0.981	≥	2.08
6–7	0.947	0.899–0.973	0.947	0.899–0.973	≈	0.00
7–8	0.945	0.904–0.969	0.945	0.904–0.969	≈	0.03

[a] (In)equality signs indicate the sign of the difference: rates for immatures may be indistinguishable (≈) from adult rates (i.e., the sign differs between cohorts); may tend to be lower (≤) or higher (≥) than adult rates (i.e., estimates for both cohorts are either lower or higher than for adults, but the test is insignificant); or may be significantly lower (<) or higher (>) than adult rates.

[b] Likelihood ratio tests are based on twice the difference between the log-likelihoods of the models compared (deviance). This measure is distributed as chi squared and tested accordingly, on one degree of freedom. See text for further details.

higher-than-adult estimates during later years (5–7 years of age). None of those differences was significant (Table 2). All estimates are summarized in Table 2.

Discussion

Local survival rates of immatures between fledging and maturity were high, and, by inference, emigration was low or nonexistent. At the age of five years, a mean estimate of age at first breeding (cf. Table 3), more than two-thirds of the fledglings were estimated to have recruited to their natal colony. The annual survival of immature birds averaged over that period (93%), therefore, was indistinguishable from that of adults (94%). Resighting rates showed a prominent age-related pattern (Fig. 1), which is very similar in the two cohorts.

Age-related patterns in resighting.—The temporal pattern in resighting of immatures at their natal colony, including a pronounced peak followed by an almost equally marked drop (Fig. 1), has, to our knowledge, not previously been reported. One possible interpretation of the pattern is that it mirrors the behavior exhibited by immature birds. In survival analyses based on capture–mark–recapture methodology, the resighting rate (p) is often viewed as a nuisance parameter that indicates noise attributable to, for example, the effort of field workers. However, it contains biologically important information, because not all individuals alive are necessarily present. Birds not seen include not only dead birds (mortality) and those that have escaped the researchers (noise) but also, for instance, intermittent breeders (Jenouvrier et al. 2003, 2005). The pronounced pattern from Figure 1 indicates that the variation in resighting rates of immatures is biologically

TABLE 3. Comparison of local survival rates to maturity in five species of Alcidae. Parameters given are the estimated annual adult survival rate (Φ), annual survival rate of immatures (ϕ, averaged over the period from fledging until the age of first reproduction), number of chicks ringed (*n*), number of cohorts studied (*c*), and estimated age at first breeding (*a*).

Location	Φ	ϕ	*n*	*c*	*a*	Method	Time of ringing	Reference
Atlantic Puffin								
Hornøya, Norway	0.943	0.933	251	2	≤7	Capture–mark–resight modeling	Fledging	Present study
Gulf of Maine, USA and Canada	0.950	0.850	2,050	19	5	(Multistate) capture–mark–resight modeling	Chick stage	Breton et al. 2005, 2006
Isle of May, Great Britain	0.926	0.889	1,082	6	5	Capture–mark–resight modeling	Chick stage	Harris and Wanless 1991
Skomer, Great Britain	0.945	0.685	235	3	5	Resighting, no use of individual color rings	Chick stage	Ashcroft 1979
***Alca torda* (Razorbill)**								
Græsholmen, Denmark	0.953	0.814	68	1	4	Resighting	Chick stage	Lyngs (1994)
***Uria aalge* (Common Murre)**								
Isle of May, Great Britain	0.695	0.820	2,757	17	5	Multistate capture–mark–resight modeling	Chick stage	Crespin et al. (2006)
U. lomvia (*Thick-billed Murre*)								
Coats Island, Canada	0.873	0.807	13,960	7	5	Resighting, corrected for extrapolated emigration and non-sighting	Chick stage	Gaston et al. (1994)
***Cepphus grylle* (Black Guillemot)**								
Nordre Rønner, Denmark	0.862	0.649	1,476	31	2	Capture–mark–recovery modeling	Chick stage?	Frederiksen (1999)

informative, especially given that it was essentially parallel in the two cohorts of immatures and that adult resighting rates were fairly constant during the same period (see Fig. 1B).

Few recruits (<10%) were observed during the first two years after fledging. It is likely that these birds spend most of their time at sea (Harris 1983, Kress and Nettleship 1988). In their third year of life, however, 87% of the fledglings still alive were observed at Hornøya. This is a significantly higher proportion than even for adult birds (80%). It seems that virtually all recruits visit their natal colony at that age. It may be that resighting is higher for immatures than for adults because the former do not occupy breeding burrows, invest less time in foraging than breeders feeding their young, and, thus, spend more time ashore and above ground (Harris 1983).

Interestingly, there is a pronounced drop in resighting to ~60% during the immatures' fifth and sixth years of age. Crespin et al. (2006) also found a drop in local survival of potential Common Murre (*Uria aalge*) recruits after the age of four years, which they attributed to permanent emigration. By contrast, in our case, the drop was merely temporal: by their seventh year of age, resighting rates of recruits from both cohorts recovered to adult levels. There are several, not mutually exclusive, explanations for this pattern.

First, a certain proportion of recruits-to-be may not have visited Hornøya during these two years; instead, they may have been prospecting at other colonies or have spent those years offshore. The former explanation concurs with findings in Cory's Shearwater, where immature birds "tempora[ri]ly leave the studied colonies to potentially prospect actively other breeding habitats" (Jenouvrier et al. 2008:626). The latter explanation is unlikely, however, given the importance of finding high-quality breeding sites (Coulson 1968, Boulinier et al. 1996). Second, the birds may have been at Hornøya but were digging a burrow. For this activity, they would have to spend more time below ground than breeders. Third, the birds may have been at Hornøya and started breeding, but later than established breeders. They would, then, still have been incubating when most other birds had already started feeding chicks. Most ring observations were done during this latter part of the breeding period. A later arrival and breeding start is a well-documented feature of inexperienced breeders, both in the puffin (Ashcroft 1979, Harris 1983) and in other species of seabirds (Birkhead and Hudson 1977, Burger et al. 1996). A related explanation is that the feeding efficiency of inexperienced breeders is lower, so that the newly recruited birds may have spent more time offshore. Finally, the first breeding attempt may have failed and the birds may have left Hornøya thereafter. Hatching success of first-time breeders is often lower than that of experienced birds (Peter et al. 1991, Burger et al. 1996). After breeding failure, birds often desert their breeding site.

High survival of immatures.—With regard to the high survival estimates for immatures presented here, we cannot be entirely sure how representative these are for the colony on Hornøya because we have data for only two cohorts of fledglings. However, virtually all previous studies of auks (Alcidae; Table 3) and many other seabirds (Ainley et al. 1990, Massey et al. 1992, Weimerskirch et al. 1997, Waugh et al. 1999) have reported markedly lower survival rates for juveniles and immatures than for adults. One possible exception is the Common Murre study previously mentioned (Crespin et al. 2006). However, the authors noted that the adult survival rate reported is most certainly a severe underestimate, which may be caused by unrealistic assumptions in the multistate model used. The estimate of survival for adult murres from the same location derived using standard models is much higher (95%; Harris et al. 2000) than that for immatures (82%). The present study documents that lower survival of younger age-classes is not a general rule in seabird ecology. Given good environmental conditions, survival of immature puffins can reach the levels seen in established breeders. This underlines the importance of multiple studies at a range of colonies. Because of variability across colonies, findings from a single colony ought not to be generalized for the entire species.

Still, our findings do not rule out a somewhat lower survival than adult levels during the first three years. Models with an increasing linear trend in survival also received moderate support. These models also suggest that survival of five- to six-year-old birds was somewhat higher than that of (other) adults. There may be two, non-exclusive, explanations for this observation. The sample of adult birds (whose ages were unknown) may contain senescent individuals. On the other hand, the sample of young birds may contain individuals that have not yet started breeding. This would exempt them from survival costs of reproduction (Wernham and Bryant 1998).

A possible reason for lower estimated survival of immatures in earlier studies may be that these studies have underestimated the extent of permanent emigration or the inability of mature birds to establish themselves at the colony of their choice. As Danchin et al. (1991) pointed out, recruitment consists of several different processes. The first process is the survival of potential recruits to the age of first reproduction. Given that a bird has survived, it must choose a breeding colony, which may or may not be the natal one. Finally, given that a bird has survived and chosen a breeding colony, it has to become a breeder, which entails finding a sexual partner and competing for breeding sites with established breeders and other recruits. Normally, it is nearly impossible to distinguish between the effects of these processes, unless all other colonies in the vicinity are surveyed (Breton et al. 2006). Because of the very high estimates of local survival to maturity in the present study, however, we are confident that the fledglings ringed scored high on all three processes. Remembering that survival rates (ϕ) are estimates of local survival, permanent emigration is indistinguishable from mortality. This means that, unless the true survival rate for immatures was even higher than the estimated rate, hardly any fledglings from Hornøya could have dispersed to other colonies. Both this inference and the high survival rate in itself indicate that Hornøya seems to be an attractive colony for potential recruits. This is also compatible with the fact that the puffin population at Hornøya increased during the study period, whereas several other Norwegian breeding colonies have shown a weak decline in populations during the same interval (Lorentsen 2006). Obviously, Hornøya has attracted virtually all local fledglings that survived until breeding age to breed at their natal colony. In addition, the colony may have experienced immigration of recruits from other colonies, though all we can tell from our data is that there was hardly any emigration of fledglings. There is some evidence that puffins (Breton et al. 2006) and other species (Reed et al. 1999, Dittmann et al. 2005) recruit selectively to attractive colonies.

The last reason for our unusually high estimates of survival rates for immatures may be methodological. We included only fledglings in our analyses (i.e., birds known to have been alive when they left their breeding burrow). All previous studies apparently have marked chicks at an earlier stage (see Table 3), although in many cases, the exact age of the chicks at ringing was not stated. This allows for the interpretation that some earlier estimates of survival rates of immatures may not have distinguished properly between mortality before and after fledging.

Whatever the reason for the discrepancy between our findings and earlier ones, it may have great importance for the understanding of population dynamics. Models of population dynamics (e.g., Caswell 2001) require reliable estimates of breeding success, dispersal, and survival of immatures, but confounding these parameters may violate several of the models' assumptions. Especially if one identifies environmental correlates of population change, it is crucial to distinguish between mortality during different life stages, because the environmental factors involved can be very different. Survival to maturity in seabirds, and perhaps in other long-lived species, may sometimes be higher and less variable than previously assumed.

ACKNOWLEDGMENTS

This study was part of the project "Demography and Adult Mortality in Seabirds" organized by T. Anker-Nilssen, K. E. Erikstad, and R. T. Barrett and funded by the Norwegian Directorate for Nature Management. Further financial support came from the Norwegian Research Council and Norwegian Institute for Nature Research. We thank numerous field workers for contributing to the resighting database. T. Anker-Nilssen and anonymous referees commented on the manuscript.

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Associate Editor: J. F. Piatt