Reproductive consequences of natal dispersal in a highly philopatric seabird

Ulrich K. Steiner[a] and Anthony J. Gaston[b]
[a]Zoologisches Institut, Universität Zürich, Winterthurerstr. 190, 8057 Zürich, Switzerland,
and [b]Canadian Wildlife Service, National Wildlife Research Centre, Carleton University, Ottawa,
Ontario, K1A 0H3, Canada

Natal and breeding dispersal have a major impact on gene flow and population structure. We examined the consequences of natal dispersal on the reproductive success (proportion of pairs rearing chicks) of colonial-breeding Thick-billed murres (*Uria lomvia*). Reproductive success increased with distance dispersed for the first and second breeding attempt. The increase in breeding success leveled off at natal dispersal distances above 7 m. Our results were consistent with the idea that the relationship between dispersal and reproductive success is caused by site availability and mate choice as birds willing to disperse farther had a greater choice of potential sites and mates. This hypothesis was supported by the fact that birds dispersing farther were more likely to pair with an experienced breeder, which increases the likelihood of breeding success for young breeders. Explanations for increasing breeding success with increased dispersal based on inbreeding effects were unlikely because most breeding failures were caused by egg loss rather than infertility or nestling death. However, we could not explain why >50% of birds return within 3 m of the natal site, despite having an up to 50% lower reproductive success than birds dispersing 7 m or more. *Key words:* breeding success, natal dispersal, natal philopatry, optimal dispersal distance, reproductive success, *Uria lomvia*. *[Behav Ecol 16:634–639 (2005)]*

Natal dispersal is one of the driving forces behind gene flow and has a major impact on population structure and metapopulation dynamics (Clobert et al., 2001; Greenwood, 1980; Hanski, 1999). Organisms that disperse actively are faced with choices about how far they should disperse to optimize their prospects of survival and reproduction (Greenwood, 1980; Shields, 1982). In stable environments, where patterns of resource abundance are predictable, most species tend to remain close to their natal area (philopatry), while under variable conditions distant dispersal may be more common (Fagan et al., 2001). On balance, selection on dispersal seems to favor philopatry (Van Valen, 1971), although the mechanisms underlying selection for philopatry are poorly understood.

A wide variety of factors affecting natal dispersal have been identified. These include habitat quality, resource availability, and ectoparasites (Boulinier et al., 2001; Dobson and Jones, 1985; Hamilton, 1967; Lambin, 1994; Van Vuren, 1996). In addition, mate choice and site selection may have an impact on dispersal rates (Danchin et al., 1998; Kokko et al., 2004; Spinks et al., 2000). Given the great diversity of dispersal mechanisms available to animals and plants, it is not surprising that dispersal strategies vary widely among species with different life histories and breeding systems (Paradis et al., 1998).

In species where there is a severe threat of inbreeding depression or strong local competition for resources, we would expect an increase in fitness with dispersal distance. For other species, local adaptation or local knowledge might be important, perhaps leading to a decrease in fitness with increasing dispersal distance. In most cases, both the positive and negative fitness consequences of dispersal are likely to vary with dispersal distance, leading to the existence of an optimum dispersal distance, which is also suggested by optimality models of dispersal (Shields, 1982).

For colonial seabirds, studies of natal dispersal are numerous, and two levels of natal philopatry have been recognized: philopatry to the natal colony and within the colony philopatry to the natal breeding site. Many species show both of these tendencies (Frederiksen and Petersen, 1999; Gaston and Jones, 1998; Harris et al., 1996; Osorio-Beristain and Drummond, 1993; Pyle, 2001; Schjorring, 2001; Spear et al., 1998).

Here, we concentrate on potential factors selecting for within-colony dispersal, using long-term data on a highly colonial species, the Thick-billed murre (*Uria lomvia*). We analyze reproductive success in relation to natal dispersal distances to assess whether there is an optimal natal dispersal distance and what mechanisms influence this dispersal pattern.

Thick-billed murres exhibit high natal philopatry (50% breed within 2.6 m of their site of origin; Steiner, 2000; Gaston, unpublished) and high breeding philopatry (>90% return to their breeding site of the previous year; Gaston et al., 1994). The advantage in our study species compared to other species (Aebisher, 1995; Coulson and Nève de Mévergnies, 1992) is that dispersal away from the natal colony occurs very rarely (one report after banding >30,000 nestlings). At Coats Island where this study took place, very few banded birds (<0.06%) were sighted in the 1.5-km distant East subcolony (Steiner, 2000): good evidence that practically all chicks recruit to the same subcolony. This allowed us to focus on dispersal within the subcolony.

We assessed differences in dispersal strategies by examining the relationship between natal dispersal distances and breeding success. The hypotheses we tested were based on (1) outbreeding and local adaptation (Greenwood, 1980), where we would expect a decrease in breeding success with increasing natal dispersal; (2) inbreeding depression (Shields, 1982, 1987), where we would expect an increase in breeding success with increasing natal dispersal; or (3) mate choice, resource availability, and site selection, where we also would expect an increase in breeding success with increasing natal dispersal distance (Dobson and Jones, 1985; Hamilton, 1967; Kokko et al., 2004 Lambin, 1994). A combination of hypothesis (1) and
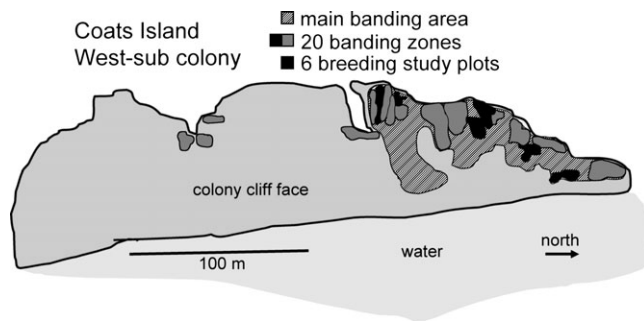
Figure 1
Thick-billed murre colony on Coats Island. All suitable ledges within the light gray area are occupied by breeding Thick-billed murres. Natal dispersal distances were calculated only for birds settling in one of the six breeding study plots (black areas) and banded in one of the 20 banding zones (dark gray and black areas).

either (2) or (3) would produce a peak in breeding success at an intermediate dispersal distance.

We also considered the effect of mate quality on dispersal. Our dispersal data relate mainly to birds in their first few years of breeding. At this stage, their breeding success is highly dependent on the age and experience of their mate: those mated to older, more experienced birds generally have higher reproductive success than average for their age (de Forest and Gaston, 1996; Gaston et al., 1994; Hipfner and Gaston, 2002; Gaston, unpublished). Hence, we examined how mate experience modified the relationship between dispersal distance and reproductive success.

METHODS

We collected data on Thick-billed murres banded as nestlings in a colony of approximately 33,000 breeding pairs on Coats Island, Nunavut, Canada (62° 30′ N, 83° 00′ W). Specific breeding sites at six monitoring study plots were observed (see Figure 1), and the breeding success of known-age birds was recorded annually over a 9-year period. Individual natal dispersal distance was estimated and, if possible, the experience of the mate determined.

The Thick-billed murre colony on Coats Island is divided in two subcolonies, separated by approximately 1.5 km of unoccupied cliff. The West subcolony comprises about 18,000 breeding pairs on a 70-m-high and 400-m-long cliff side. Approximately, 100 adults and 2000 chicks were banded annually within the West subcolony from 1984 onwards. All birds received a specially designed triangular metal band on the right leg. Those banded as adults received a light-green band above the metal band, while chicks received a year-code color band above the metal band. The numbers on the metal bands allowed us to identify individuals from distances up to 40 m.

Dispersal within the West subcolony

Within the West subcolony, we measured natal dispersal distances (distance from banding site to site of first breeding attempt) for birds banded as chicks at one of the 20 banding zones and found breeding up to the year 2000 on one of our six breeding study plots (see Figure 1). Only nestlings born and banded in one of the 20 banding zones and settling on one of the breeding study plots were included in the study. We calculated the natal dispersal distance based on the natal ledge or banding zones of origin and the exact position of the breeding site. Ledges where chicks were banded (natal site) and the breeding ledge (settlement site) were identified on eight

large format photos, and the distance between natal and settlement sites was measured by comparison with the nearest scale object (plywood blind of known dimensions) within the same image. Each image covered about 800 m^2. The number of pairs per breeding ledge varied between 1 and 33 (average 9.95 ± 0.78 SE, $n = 85$).

Breeding success and experience

Throughout the breeding seasons of 1991–1999, we monitored between 655 and 785 individual breeding sites (monitoring sites) per year distributed over six breeding study plots (see Figure 1) within the West subcolony and noted the breeding success of each pair (de Forest and Gaston, 1996; Gaston et al., 1994). To determine breeding success, each breeding site was checked daily between laying of the single egg and departure of the chick. Pairs with chicks surviving to an age of 15 days, which is the earliest departure age for a chick, were considered to have bred successfully (Gaston and Hipfner, 2000). Lost or unhatched eggs and the disappearance of chicks prior to 15 days of age were considered breeding failures. As site fidelity is very high for Thick-billed murres, we were able to monitor the breeding attempts of most individuals from their first breeding year onwards and thus could monitor their breeding success as they gained experience.

Only birds between 3 and 7 years of age and recorded for the first time as members of an egg-laying pair were considered to be first-time breeders because more than 95% of the birds do have their first breeding attempt between 3 and 7 years of age (Gaston and Hipfner, 2000; Gaston et al., 1994). We categorized breeders according to the number of breeding attempts they had made, aggregating data across cohorts. We sexed birds by position and vocalization during copulation: birds were only considered female if they produced the distinctive female call emitted during copulation (Lefevre et al., 2001).

For first-time breeders, we assessed the experience of their mates. Mates selected by first-time breeders were divided into two categories: (1) inexperienced birds, banded as chicks, known to be between 3 and 7 years of age and with fewer than three breeding attempts and (2) experienced birds, banded as breeding adults or as chicks and with more than three recorded breeding attempts since banding. The minimum age of "experienced" birds was 7 years (de Forest and Gaston, 1996).

Statistical analysis

Before we did the final analysis on dispersal and breeding success and the test for experience of mates chosen by first-time breeders at various dispersal distances, we tested for sex and age effects on breeding success and dispersal distances. In the final analysis, we categorized breeders by breeding attempts, rather than by age classes, because experience has a stronger effect on breeding success than age (Gaston, unpublished).

First, we tested for a sex difference in dispersal using a Mann-Whitney U test. To test for age effects of dispersal in first-time breeders we used a Kruskal-Wallis test, and to test for age or sex effects on breeding success, we used a χ^2 test for data from 1994 to 1998, during which time 85% of our data were obtained. There was no significant variation in breeding success during the years 1994–1998 ($\chi^2_4 = 8.274$, $p = .082$). However, there was a tendency for differences in breeding success between years, therefore, before pooling breeding success data for different years, we ran a logistic regression that included year, attempt, and the interaction between the two (proc genmod in SAS, Type III SS). None of these analyses indicated any problem with pooling the data across years. Hence, pooling should not affect the results of further analyses on breeding attempt (where different age classes of different cohorts were pooled). As
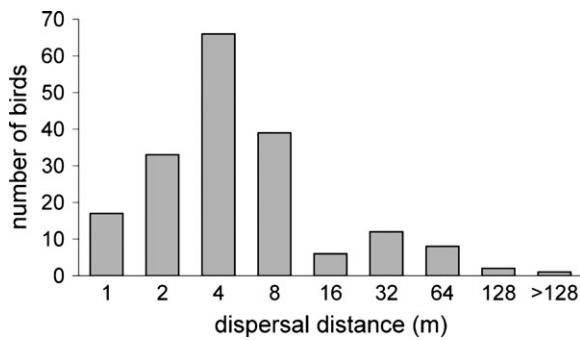
Figure 2
Observed distribution of natal dispersal distances of first-time breeders ($n = 138$).

expected for monogamously mated birds, there was no difference in breeding success between the sexes ($\chi^2 = 0.96$, $p = .33$, $n = 271$). Hence, we pooled the sexes for further analysis on breeding success.

For all the following analyses we used logistic regressions. For the influence of natal dispersal distance on breeding success, we combined all distances above 10 m for analysis: results were the same whether birds dispersing more than 10 m were excluded or combined for analysis. We combined distances above 10 m to avoid having the logistic regression overweighted by a few far-dispersing individuals. To describe the relationship between dispersal distance and breeding success, we included all birds dispersing at all distances and pooled all information across years. We applied model selection on two candidate models, using Akaike's information criterion for small sample sizes (AICc, Burnham and Anderson, 2002) on a logistic regression. The first model allowed a normal satiation effect (linear term for dispersal), and the second one allowed an increase and decrease in breeding success (linear and a linear and quadratic term for dispersal). In comparing mate experience with dispersal distance, we did not combine it with breeding success in one model because we had breeding success information for only 20 of the 30 birds for which we had information on mate experience.

RESULTS

The natal dispersal distance was estimated for 183 birds (58 females, 42 males, and 83 of unknown sex). Of these, the outcome of their first breeding attempt was known for 138 individuals (49 females, 35 males, and 54 of unknown sex). Approximately 60% of birds banded as chicks settled within 4 m of their natal ledge. The median distance was 2.6 ± 1.19 m (SE). Less than 10% settled more than 16 m away (Figure 2). Dispersal distances did not differ between the sexes (Mann-Witney $U = 1392.5$, $p = .166$, $n = 100$). For first-time breeders, dispersal distance did not vary significantly in relation to the age at their first breeding attempt (Kruskal-Wallis $H_4 = 4.566$, $p = .335$, $n = 183$). Hence, birds undertaking their first breeding attempt at a younger age did not disperse more or less than birds that first bred when older. The lack of a sex difference in dispersal was probably not due to small sample size because the same result was found for a bigger data set of 8798 resightings of 1309 individuals (mainly prebreeders) made within the same subcolony for which a median dispersal distance of 4.17 m was estimated (Steiner, 2000).

Reproductive success

The breeding success of birds during their first two breeding attempts increased significantly with distance from the natal
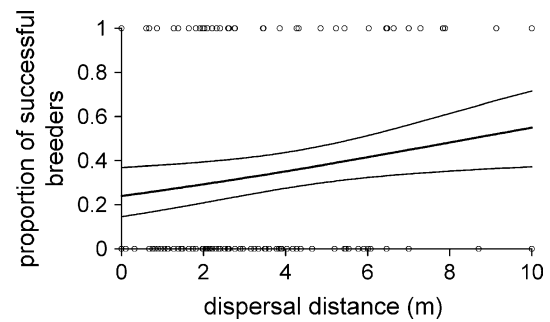

Figure 3
Logistic regression for breeding success and dispersal distance in the first breeding attempt. The thin lines are the 95% confidence interval lines. The circles show the distribution of the data points for the first attempt ($n = 138$). Statistics of logistic regression for dependence of breeding success on natal dispersal distance separated for breeding attempts, all distances greater than 10 m were categorized as 10 m (first breeding attempt: estimate = 0.135, SE = 0.058, $\chi^2 = 5.588$, $p = .018$, $n = 138$; second breeding attempt: estimate = 0.169, SE = 0.082, $\chi^2 = 4.497$, $p = .034$, $n = 62$; third breeding attempt: estimate = 0.142, SE = 0.128, $\chi^2 = 1.316$, $p = .251$, $n = 34$; >third breeding attempt: estimate = 0.140, SE = 0.108, $\chi^2 = 1.772$, $p = .183$, $n = 37$).

site (Figure 3). In later years, there was a similar, but non-significant, trend. When all the information on dispersal and breeding success was pooled across breeding attempts, the proportion of successful breeders increased from 0.28 ± 0.07 SE in birds dispersing less than 1 m ($n = 43$) to 0.55 ± 0.11 SE in birds dispersing 7–9 m ($n = 20$). Beyond 9 m, the average breeding success at 9–20 m was 0.55 ± 0.15 SE ($n = 11$), at 20–40 m 0.44 ± 0.09 SE ($n = 27$), and at >40 m 0.46 ± 0.14 SE ($n = 13$). Hence, the highest breeding success was achieved by birds settling 7–20 m from their natal site. There is some support for a peak in breeding success by the model selection procedure, where the model with the linear and quadratic term for distance (AICc = 411.524, $K = 4$, $n = 292$) is 3.8 times (evidence ratio) better supported than the other candidate model with only the linear term (AICc = 414.194, $K = 3$, $n = 292$).

The experience of mates that were chosen by inexperienced birds in their first breeding attempt increased with dispersal distance (logistic regression $p = .035$, $n = 30$). Only 11% ($n = 18$) of birds settling within 4 m of their natal site mated with an experienced partner in their first breeding attempt, compared with 57% ($n = 7$) of birds that settled more than 16 m from their natal site (Figure 4).
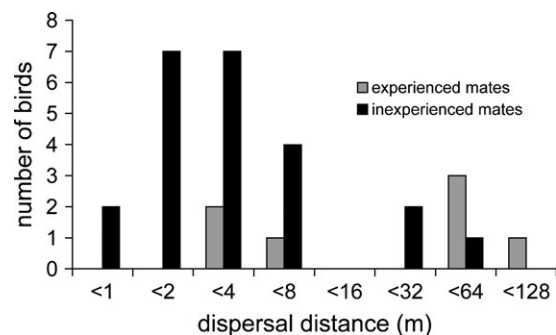

Figure 4
Comparison of the distribution of natal dispersal distances between inexperienced birds mating with experienced or inexperienced birds.

DISCUSSION

Proximate cause of dispersal–reproductive success relationship

Our results demonstrated an increase in breeding success with dispersal distance up to at least 7 m from the natal site: the area within which most birds settled. This pattern of breeding success in relation to dispersal distance is consistent with all hypotheses based on strong local resource competition (Hamilton, 1967; Lambin, 1994; Negro et al., 1997). The fact that those birds dispersing farthest had the greatest chance of mating with an experienced breeder supplies a potential mechanism for the high breeding success of dispersers. Given the strong influence of a mate's age/experience on breeding success and chick growth (de Forest and Gaston, 1996; Hipfner and Gaston, 2002), the increase in mate quality with dispersal distance appears to be the most parsimonious explanation for the trend in reproductive success with dispersal distance. If that is the case, there may be no effect of distance per se.

One explanation for this result would be that birds exhibiting strong natal philopatry are faced with reduced options to obtain a scarce resource (a site-holding mate or a vacant site). Hence, the availability of resources increases with distance from the site of origin (Waser, 1985). In seabirds, this assumption seems reasonable because not all pairs at all sites are successful in raising a chick every year and not all of the chicks of one cohort survive to recruitment age. A juvenile that does not disperse at all must await the death of its same-sex parent, whereas one that disperses has a higher chance of locating a vacant site. There may be a trade-off between the costs of finding these experienced mates (e.g., fights on ledges while searching, or the risk of losing a breeding season in failing to find a mate) and the benefits of having such a mate. However, we were unable to detect any effect of age on dispersal distance among birds breeding for the first time, suggesting that delayed breeding is not linked to any particular dispersal strategy. Information about other potential factors like better body conditions or larger size of dispersers is not available. Apparently, the birds that disperse farthest obtain the most experienced mates, something reported for other bird species (Forero et al., 2002; Grant and Grant, 1989).

The breeding success and predation rates of Thick-billed murres vary with site characteristics and numbers of neighbors (Birkhead et al., 1985; Gaston and Elliot, 1996; Gilchrist and Gaston, 1997). These differences apply on a fine scale within ledges and do not show any directional pattern on a larger scale (i.e., between different study plots). As the effects of site quality and mate experience are likely to be intercorrelated (e.g., Potts et al., 1980), we cannot distinguish between site quality and mate quality. In some cases the negative effect of a site might override an individual's breeding experience (Danchin et al., 1998), but equally a good quality site could compensate for the lack of experience of an individual. Breeding patch selection models and "public information" theories (Boulinier and Danchin, 1997; Danchin et al., 1998) also suggest links between site quality and mate quality. Although the observed pattern of increasing breeding success with increasing natal dispersal is consistent with a hypothesis based on inbreeding avoidance, it seems unlikely that inbreeding effects could explain our results. Molecular genetic information shows that inbreeding depression is unlikely to occur within our study colony because the average relatedness (Queller and Goodnight, 1989) between breeding partners within ledges is 0.024, and no significant correlation between relatedness and hatching or fledging success was detected (Ibarguchi, 1998; Steiner and Ibarguchi, unpublished). If inbreeding depression was expressed mainly through infertility of eggs, or problems with egg or chick development, we should have been able to detect differences in some of these traits at different dispersal distances, but we found no evidence (data not shown). Breeding failure in Thick-billed murres seems to be mainly related to behavior and hence experience because most of the unsuccessful breeding murres (85%) lose their eggs during incubation changeovers or fights, while most chick losses occurred from predation (Gaston and Elliot, 1996; Kober and Gaston, 2003). Hence, these losses are unlikely to be linked to inbreeding.

Any hypotheses based on avoidance of outbreeding or on local adaptation effects (Ehrlich and Raven, 1969; Johnson and Gaines, 1990; Slatkin, 1987) can be rejected because breeding success increased with natal dispersal distance. Outbreeding effects might be more relevant on a larger scale as shown by the best-supported model allowing a decline at distances above 20 m. However, our results suggest that dispersal outside the subcolony is rare. Consequently, we think that explanations based on the relatedness between partners are not supported.

Mismatch between optimum and observed dispersal distance

There appears to be a mismatch between the dispersal distance at which birds have the greatest breeding success (7–20 m) and the most common dispersal distance (median 2.6 m). Although, our observed dispersal distances are not a random sample and therefore may be somewhat biased, it seems inconceivable that true median dispersal could be as high as 10 m. If it was, the majority of birds would breed outside their natal banding zone, whereas earlier observations found that numbers reared and recruited within breeding plots (maximum radius <10 m) were sufficient to account for most recruitment (Gaston et al., 1994). Moreover, none of our observations, including many casual sightings of birds on all parts of the colony (more than 50,000 band readings in the colony), supported this possibility.

There are a few possible explanations for the mismatch:
1. The Coats Island colony expanded in most years included in our study. Consequently, the recruitment of potential breeders was higher than the availability of unmated experienced birds, which forces recruits to disperse further to find an unmated experienced mate. A more philopatric dispersal strategy might be more beneficial in a stable or decreasing population.
2. Thick-billed murres continue to increase their breeding success up to at least 10 years of age (Gaston and Hipfner, 2000). It is possible that the results we obtained for birds in their early years of breeding are not representative of lifetime reproductive success (Forero et al., 2002): greater dispersal may be initially advantageous but may become more costly after the first few breeding attempts. However, this seems unlikely because there is no reason to expect that advantages obtained by choosing an experienced mate or high-quality site would decay with time. Birds rarely move their site after becoming established, divorces are rare, and senescence in respect to breeding success is not known (up to ages >20 year, Gaston and Hipfner, 2000; Hipfner and Gaston, unpublished). This suggests that the decision on the initial breeding site and mate is very important.
3. There is currently no heritable variation in dispersal, so the trait is unable to respond to selection. We have no way to test this idea with our data.

Evolution of philopatry in the Thick-billed murre

Many studies have attempted to explain the evolutionary basis of philopatry (Forero et al., 2002; Greenwood, 1980; Johnson

and Gaines, 1990; Perrin and Mazalov, 2000; Spear et al., 1998). The variety of factors affecting natal dispersal constitutes a special case for most species, which applies also to Thick-billed murres. Most of the explanations proposed seem unlikely to apply to dispersal within subcolonies of Thick-billed murres and therefore can be excluded because, as stated earlier, dispersal outside the subcolony is negligible. At the scale of the approximately 10,000 m^2 of the West subcolony, differences in reproductive success with dispersal distance based on variation in mortality or predation caused by the risk of dispersal are unlikely (Bensch et al., 1998; Ims and Andreassen, 2000; Wheelwright and Mauck, 1998).

We assume that density avoidance (Spear et al., 1998) would not be important in determining dispersal among murres, because murres actively aggregate at very high densities for nesting as an anti-predator strategy (Birkhead, 1977; Gilchrist et al., 1998) and offspring from high density areas show no increased dispersal (Steiner, unpublished). The possibility that dispersal reduces parasite loads or is used to avoid spatially heterogeneous levels of parasites (Brown and Bomberger Brown, 1992; Boulinier et al., 2001) also seems unlikely to apply to murres within this subcolony because there is no evidence of any ectoparasite infestation despite the handling of thousands of adults and nestlings.

Likewise, the idea that dispersal functions to avoid poor conditions, either in terms of food resources (Altwegg et al., 2000) or in terms of habitat destruction and deterioration (Ganter and Cooke, 1998), is unlikely to apply on a within-subcolony scale. Thick-billed murres forage 30–120 km away from their colony (Bradstreet and Brown, 1985; Woo, 2002). The trifling differences in distance to foraging areas created by movements of <200 m seems very unlikely to create variation in access to food resources. Also, for Thick-billed murres breeding on bare rock, the nesting habitat is unaffected by the breeding activity of the birds. Peat deposit analysis shows that the colony at Coats Island has existed for more than 2000 years at the same location (Gaston and Donaldson, 1995).

We can also exclude theories that are based on advantages arising from local knowledge of patchy food resources, location of conspecifics, predator refugia, or predator movements and habits (Pärt, 1995; Bensch et al., 1998). Such local knowledge theories provide good explanations for why an individual should return to the same colony year after year, but local knowledge is unlikely to have an effect on natal dispersal within the colony. Thick-billed murre chicks leave the colony at an age of about 15–25 days, swim straight out to sea with their male parent, and initiate migration to distant wintering areas immediately (Gaston and Hipfner, 2000). It seems unlikely that they could gain any useful local knowledge within the colony during this very brief transit.

Conclusions

Given the positive correlation between dispersal distance and breeding success that we found, the cause of the extremely precise philopatry observed for Thick-billed murres remains unknown. However, our results rule out several hypotheses and suggest that the relationship between breeding success and natal dispersal distance is best explained by the tendency for birds dispersing further to acquire more experienced mates.

REFERENCES

Aebisher NJ, 1995. Philopatry and colony fidelity of Shags *Phalacrocorax aristotelis* on the east coast of Britain. Ibis 137:11–18.

Altwegg R, Ringsby TH, Saether B-E, 2000. Phenotypic correlates and consequences of dispersal in a metapopulation of House Sparrows *Passer domesticus*. J Anim Ecol 69:762–770.

Bensch S, Hasselquist D, Nielsen B, Hansson B, 1998. Higher fitness for philopatric than for immigrant males in a semi-isolated population of Great reed warblers. Evolution 52(3):877–883.

Birkhead TR, 1977. The effect of habitat and density on breeding success in the Common Guillemot *Uria aalge*. J Anim Ecol 46: 751–764.

Birkhead TR, Greene E, Biggins JD, Nettleship DN, 1985. Breeding site characteristics and breeding success in Thick-billed Murres. Can J Zool 63:1880–1884.

Boulinier T, Danchin E, 1997. The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. Evol Ecol 11:505–517.

Boulinier T, McCoy KD, Sorci G, 2001. Dispersal and parasitism. In: Dispersal (Clobert J, Danchin E, Dhondt AA, Nichols JD, eds). New York: Oxford University Press; 169–179.

Bradstreet MSW, Brown RGB, 1985. Feeding ecology. In: The Atlantic Alcidae (Nettleship DN, Birkhead TR, eds). London: Academic Press; 264–313.

Brown CR, Bomberger Brown M, 1992. Ectoparasitism as a cause of natal dispersal in cliff swallows. Ecology 73(5):1718–1723.

Burnham KP, Andersen DR, 2002. Model selection and multi model inference: a practical information-theoretic approach. New York: Springer.

Clobert J, Danchin E, Dhondt AA, Nichols JD (eds), 2001. Dispersal. New York: Oxford University Press.

Coulson JC, Nève de Mévergnies G, 1992. Where do young kittiwakes *Rissa trictyla* breed, philopatry or dispersal? Ardea 80(1):187–197.

Danchin E, Boulinier T, Massot M, 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79(7):2415–2428.

de Forest LN, Gaston AJ, 1996. The effect of age on timing of breeding and reproductive success in the Thick-billed murre. Ecology 77:1501–1511.

Dobson FS, Jones WT, 1985. Multiple causes of dispersal. Am Nat 126(6):855–858.

Ehrlich PR, Raven PH, 1969. Differentiation of population. Science 165:1228–1232.

Fagan WF, Meir E, Predergast J, Floarin A, Karieva P, 2001. Characterizing population vulnerability for 758 species. Ecol Lett 4:132–138.

Forero MG, Donázar JA, Hiraldo F, 2002. Causes and fitness consequences of natal dispersal in a population of Black kites. Ecology 83(3):858–872.

Frederiksen M, Petersen A, 1999. Philopatry and dispersal within a Black guillemot colony. Waterbirds 22(2):274–281.

Ganter B, Cooke F, 1998. Colonial nesters in a deteriorating habitat: site fidelity and colony dynamics of Lesser Snow Geese. Auk 115: 642–652.

Gaston AJ, de Forest LN, Donaldson G, Noble DG, 1994. Population parameters of Thick-billed Murres at Coats Island, Northwest Territories, Canada. Condor 96:935–948.

Gaston AJ, Donaldson G, 1995. Peat deposits and Thick-billed Murre colonies in Hudson Straight and northern Hudson Bay: clues to post-glacial colonization of the area by seabirds. Arctic 48:354–358.

Gaston AJ, Elliot RD, 1996. Predation by Ravens *Corvus corax* on Brunnick's Guillemot *Uria lomvia* eggs and chicks and its possible impact on breeding site selection. Ibis 138:742–748.

Gaston AJ, Hipfner JM, 2000. Thick-billed Murre (*Uria lomvia*). In: The birds of North America 497 (Poole A, Gill F, eds). Philadelphia: The Birds of North America Inc.; 1–32.

Gaston AJ, Jones IL, 1998. The auks. Oxford: Oxford University Press.

Gilchrist G, Gaston AJ, 1997. Factors affecting the success of departure by Thick-billed Murre chicks. Condor 99:345–352.

Gilchrist HG, Gaston AJ, Smith JNM, 1998. Wind and prey nest sites as foraging constraints on an avian predator, the Glaucous Gull. Ecology 79:2403–2414.

Grant BR, Grant PR, 1989. Evolutionary dynamics of natural population. Chicago: University of Chicago Press.

Greenwood PJ, 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162.

Hamilton WD, 1967. Extraordinary sex ratio. Science 156(3774): 477–488.

Hanski I, 1999. Metapopulation ecology. New York: Oxford University Press.

Harris MP, Halley DJ, Wanless S, 1996. Philopatry in the Common Guillemot Uria aalge. Bird Study 43:134–137.

Hipfner JM, Gaston AJ, 2002. Growth of nestling Thick-billed Murres in relation to parental experience and hatching date: a natural experiment. Auk 119:827–832.

Ibarguchi G, 1998. A study of kin groups and genetic structure in a philopatric seabird, the Thick-billed Murre (Uria lomvia) (MSc thesis). Kingston: Queen's University.

Ims RA, Andreassen HP, 2000. Spatial synchronization of vole population dynamics by predatory birds. Nature 408:194–196.

Johnson ML, Gaines MS, 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annu Rev Ecol Syst 21:449–480.

Kober K, Gaston AJ, 2003. Social interactions among breeding Brunnich's guillemots Uria lomvia suggest constraints in relation to offspring vulnerability. Ibis 145:413–418.

Kokko H, Harris MP, Wanless S, 2004. Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the Common guillemot Uria aalge. J Anim Ecol 73: 367–376.

Lambin X, 1994. Natal philopatry, competition for resources, and inbreeding avoidance in Townsend's voles (Microtus townsendii). Ecology 75(1):224–235.

Lefevre K, Gaston AJ, Montgomerie R, 2001. Repertoire, structure, and individual distinctiveness of Thick-billed Murre calls. Condor 103(1):134–142.

Negro JJ, Hiraldo F, Donazar JA, 1997. Causes of natal dispersal in the Lesser kestrel: inbreeding avoidance or resource competition? J Anim Ecol 66:640–648.

Osorio-Beristain M, Drummond H, 1993. Natal dispersal and deferred breeding in the Blue-footed Booby. Auk 110(2):234–239.

Paradis E, Baillie SR, Sutherland WJ, Gregory RD, 1998. Patterns of natal dispersal and breeding dispersal in birds. J Anim Ecol 67:518–536.

Pärt T, 1995. The importance of local familiarity and search costs for age- and sex-biased philopatry in the Collared flycatcher. Anim Behav 49:1029–1038.

Perrin N, Mazalov V, 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. Am Nat 155(1):116–127.

Potts GR, Coulson JC, Deans IR, 1980. Population dynamics and breeding success of the Shag, Phalacrocorax aristotelis, on the Farne Islands, Northumberland. J Anim Ecol 49:465–484.

Pyle P, 2001. Age at first breeding and natal dispersal in a declining population of Cassin's Auklets. Auk 118(4):996–1007.

Queller DC, Goodnight KF, 1989. Estimating relatedness using genetic markers. Evolution 43(2):258–275.

Schjorring S, 2001. Ecologically determined natal philopatry within a colony of great cormorants. Behav Ecol 12(3):287–294.

Shields WM, 1982. Philopatry, inbreeding, and the evolution of sex. Albany: State University of New York Press.

Shields WM, 1987. Dispersal and mating systems: investigating their causal connections. In: Mammalian dispersal patterns: the effects of social structure on population genetics (Chepko-Sade BD, Halpin ZT, eds). Chicago: University of Chicago Press; 3–24.

Slatkin M, 1987. Gene flow and the geographic structure of natural populations. Science 236(4803):787–792.

Spear LB, Pyle P, Nur N, 1998. Natal dispersal in the Western gull: proximal factors and fitness consequences. J Anim Ecol 67:165–179.

Spinks AC, Jarvis JUM, Bennett NC, 2000. Comparative patterns of philopatry and dispersal in two common mole-rat populations: implications for the evolution of mole-rat sociality. J Anim Ecol 69: 224–234.

Steiner UK, 2000. Populationsökologie von Dickschnabellummen (Uria lomvia) vor der ersten Brut (Diploma thesis). Göttingen: University of Göttingen.

Van Valen L, 1971. Group selection and the evolution of dispersal. Evolution 25(4):591–598.

Van Vuren D, 1996. Ectoparasites, fitness, and social behaviour of Yellow-bellied Marmots. Ethology 102:686–694.

Waser PM, 1985. Does competition drive dispersal? Ecology 66(4): 1170–1175.

Wheelwright NT, Mauck RA, 1998. Philopatry, natal dispersal, and inbreeding avoidance in an island population of Savannah sparrows. Ecology 79(3):755–767.

Woo KJ, 2002. Foraging ecology of the Thick-billed Murre: patterns of prey location and selection (MSc thesis). Ottawa: University of Ottawa.