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Natal and Breeding Dispersal of Razorbills (*Alca torda*) in Eastern North America

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Abstract.—Until recently, our understanding of the role of movement in animal populations was limited due to a prevalence of studies on single local populations. Here we report on local and regional movement patterns of Razorbill (*Alca torda*), the least numerous Atlantic alcid, through the use of multi-site capture-mark-recapture/resight for five breeding locations spanning their entire North American breeding range. Razorbill philopatry and breeding site fidelity rates for the Gannet Islands, Labrador were high with 83% of young birds (N = 340) and 97% of adults (N = 149) returning to the same colony to breed. The distance moved between the natal colony and the colony where an individual later bred was significantly greater for birds banded as chicks, both between colonies on the same island and within islands in the Gannet Islands cluster. Regional movements of 40 banded individuals were recorded during 2003-2006, including seven birds that were confirmed breeding at a location different from their natal colony. Emigration distances among colonies in North America ranged from 57 to 1,737 km, providing an unexpectedly high rate of movement of birds between breeding colonies that has not been previously reported for any auk species. One bird, banded as a chick on Digges Island, Nunavut in 1982 was recaptured 24 years later as a breeder on the Gannet Islands (1,737 km away). A chick banded on Handa Island, Scotland in 1971 was seen four times in 2004 at the Gannet Islands (3,210 km away). Despite exhibiting low productivity and survivorship, Razorbill populations at some Atlantic Canada breeding sites have been increasing. We conclude that the dispersal and recruitment of individuals into new colonies that are characteristic of other seabird species may also partly explain patterns of population dynamics at North American Razorbill colonies. *Received 27 February 2007, accepted 09 October 2007.*

Key words.—*Alca torda*, dispersal, movement, philopatry, Razorbill.

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Wildlife population dynamics are the result of four key components, namely birth, death, emigration and immigration (Sutherland *et al.* 2002). For most seabirds, especially the family Alcidae, birth and death rates have been well studied, but less is known about immigration and emigration (Greenwood and Harvey 1982; van Noordwijk 1993; Gaston and Jones 1998; Joe and Pollock 2002; Brooke 2004). This lack of knowledge on seabird dispersal is often a result of logistical limitations posed by the large distances over which birds can disperse (Lindberg *et al.* 1998; Cam *et al.* 2004), and difficulty of identifying marked individuals in large colonies. Dispersal has the potential to contribute significantly to spatial and temporal variation in population size (Breton *et al.* 2006). In particular, whether individuals of long-lived colonial seabird species habitually breed at their natal colony or disperse to other colonies is a crucial decision that has far-reaching implications for the monitoring and conservation of populations.

A number of seabird studies have recorded population growth far greater than can be explained by the species' biology (Leslie 1966; Hilden and Pahtamaa 1992; Montevecchi and Myers 1996; Oro and Pradel 2000). For example, expansion of Atlantic Puffin (*Fratercula arctica*) and Northern Fulmar (*Fulmarus glacialis*) colonies can be explained only by high immigration rates from larger, neighboring colonies (Harris 1983; Stenhouse and Montevecchi 1999; Burg *et al.* 2003). Genetic techniques have also provided support for high rates of dispersal in seabirds. Birt-Friesen *et al.* (1992) found that despite evidence of philopatry from resighting studies, there is little genetic differentiation between North Atlantic colonies of Thick-billed Murres (*Uria lomvia*) suggesting that

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extensive dispersal has likely occurred in the recent past. Nevertheless, there is still relatively little direct evidence (i.e., from individually marked birds) to provide quantitative assessments of seabird dispersal.

Dispersal of birds can occur both by established breeders changing breeding sites (breeding dispersal) or by birds nesting away from their natal breeding area (natal dispersal, Greenwood and Harvey 1982). The rate of breeding dispersal is low for most alcids ranging from 22% in the Ancient Murrelet (*Synthliboramphus antiquus*; Gaston 1992) to only 4% in the Common Murre (*Uria aalge*; Birkhead 1977). Breeding dispersal is often associated with a number of proximate factors including the presence of predators (Alonso *et al.* 1997; Bried and Jouventin 1999; Cam *et al.* 2004), environmental events such as flooding (Veit and Prince 1997; Schjørring 2001), and failed breeding attempts (Gaston 1992; Cam *et al.* 2004). Dispersal also occurs naturally in a population, independent of disturbance events. Irrespective of the cause, dispersal forms an essential component of metapopulation and source-sink dynamics, aiding in recolonization and maintaining gene flow (Paradis *et al.* 1998; Oro and Ruxton 2001; Breton *et al.* 2006).

The Razorbill (*Alca torda*) is the least numerous alcid breeding in Atlantic Canada with an estimated total breeding population of less than 38,000 breeding pairs (Chapdelaine *et al.* 2001). Most colonies are located from north-central Labrador to the Gulf of Maine and west into the Gulf of St. Lawrence (Hipfner and Chapdelaine 2002). Most colonies are small ranging from a few hundred to a thousand breeding pairs (Chapdelaine *et al.* 2001), and like many seabirds, the movement of individuals among colonies has been poorly studied. Here we present the results of a long-term study examining the dispersal behavior of the Razorbill in Atlantic Canada in relation to population change. In summary, the objectives of our study were to quantify Razorbill dispersal rates from two sites near the northern and southern limits of the species' range in Canada, and to evaluate the implications of dispersal rates for population monitoring methodology and Razorbill conservation.

METHODS

Study Area

The primary field study sites for this project were the Gannet Islands, Labrador, Canada (53°56'N, 56°30'W) and Machias Seal Island, New Brunswick, Canada (MSI; 44°3'N, 67°06'W). The Gannet Islands cluster includes six islands (GC1-GC6) ranging in size from four to 125 ha. The Gannet Islands are located 50 km southeast of Groswater Bay and are home to the largest Razorbill breeding colony in Atlantic Canada (Fig. 1) with an estimated 9,800 breeding pairs (Chapdelaine *et al.* 2001). MSI is a 9.5 ha island located in the Bay of Fundy and is home to approximately 550 Razorbill pairs (Fig. 1; Grecian *et al.* 2003). Additional field work was conducted on the Herring Islands, Labrador, Canada (54°20'N, 57°7'W), Petit Manan Island (PMI), Seal Island (SI), and Matinicus Rock (MR), Maine, United States (approximately 44°23'N, 67°49'W).

This study also had access to data on Razorbill chicks and adults banded in Quebec from 1986-2006 by Canadian Wildlife Service (CWS) personnel as part of a long-term monitoring program. Banding effort was concentrated primarily on île Sainte-Marie and île aux Perroquets located along the north shore of the Gulf of St. Lawrence (Fig. 1; 50°3'N, 59°6'W, approximately 7,300 breeding pairs, Chapdelaine *et al.* 2001).

Banding and Resighting

Razorbills were banded with size five CWS triangular stainless steel leg bands. Collectively more than 12,000 Razorbills have been banded (most as chicks) in eastern Canada from 1986-2006 (Table 1). Razorbill resighting effort was conducted regularly on the Gannet Islands and MSI from 2003 to 2006. In July 2005, we visited the Herring Islands, located 70 km north-west of the Gannet Islands in order to look for Razorbills which were banded on the Gannet Islands and are now breeding on the Herring Islands. Resighting data for Razorbills on PMI, SI, and MR were provided by U.S. Fish and Wildlife Service and National Audubon Society personnel. Razorbills resighted at a location other than where they were

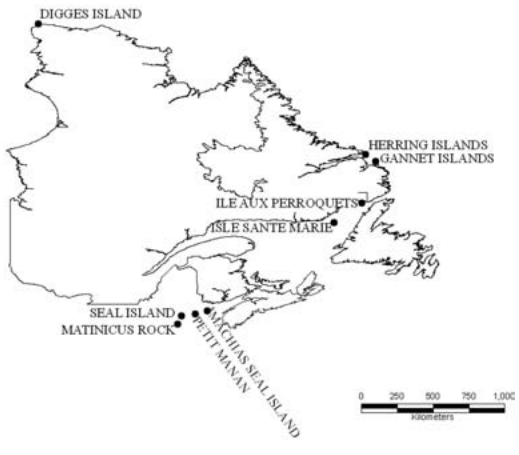


Figure 1. Map of eastern Canada showing some of the locations where Razorbills have been banded and resighted.

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Table 1. Summary of re-sightings of Razorbills at sites in Eastern Canada where >1,000 birds had been banded.

	No. of birds banded		No. of birds resighted at the Gannet Islands and Machias Seal Island	
Location and year of banding	Chicks	Adults	Banded as chicks	Banded as adults
Gannet Islands 1996-2006	5,575	350	330	160
Machias Seal Island 1995-2006	722	327	176	161
île Sainte-Marie 1986-2006	2,990	877	2	0
île aux Perroquets 1986-2006	1,144	279	1	1

banded were entered into a database. For all birds an attempt was made to confirm breeding status through observations of copulation, incubation of an egg or chick, chick-provisioning event, or presence of a brood patch. An individual bird was not considered to be confirmed or entered into the database until it had been resighted at least twice from 2003-2006, to account for the possibility of band reading error (Lavers unpublished data). This would likely reduce the chance of error to less than 0.001% (Lavers unpublished data), but unavoidably cause the omission of the individuals that were correctly resighted only once. For this reason our estimates of dispersal were likely minimum estimates.

Philopatry and Breeding Dispersal

Monitoring of individual breeding adults and their respective breeding sites has proven challenging in Razorbills because most birds nest in inaccessible crevices and under boulders (Rowe and Jones 2000; Hipfner and Chapdelaine 2002). To determine the nesting location of individuals, researchers often need to enter the colony and capture each bird on its nest. Razorbills on the Gannet Islands are highly sensitive to disturbance and will often abandon their nest if disturbed by people (Hipfner and Bryant 1999). In order to minimize disturbance, all observations were conducted from blinds or from cliff ledges using a spotting scope. As a result, for most marked individuals it was possible to determine only if a breeding adult had returned to the same colony (not breeding site) each year. A breeding colony is a group of occupied nest sites or crevices separated by at least 100 m of unoccupied habitat from other nest sites. Therefore a bird was considered to have changed its colony if its nest site was at least 100 m from its natal site (Fig. 1). All birds that moved between islands in the Gannet Island archipelago were considered to have changed colonies.

Multi-state capture-mark-recapture (CMR) models could not be used to calculate dispersal rates between the Gannet Islands, MSI, and Quebec and within islands in the Gannet Islands cluster due to uneven resighting effort across islands and years and the low number of birds involved in long-distance dispersal events. Philopatry and colony fidelity rates were determined for the Gannet Islands based on more than 3,300 resightings of individually marked birds during 1996-2006. A position fix for each sighting was recorded using GPS and the distance that individual birds dispersed between banding as a chick and return as an adult, and for adults between breeding seasons was calculated. To calculate dispersal rates between colonies and islands within the Gannet Islands cluster and to account for mortality of birds, it was determined whether birds were: (a) resighted at the same colony where banded (N_p = number philopatric), (b) resighted at a different colony site on the same island where banded (N_c = number that changed colony), or (c) resighted on a different island within the Gannet Islands cluster ((N_i = number that changed island). Dispersal rates between islands were calculated using the following formula: $N_i/(N_p+N_c+N_i)$.

RESULTS

Long-distance Dispersal Events

Forty Razorbills (37 banded as chicks and three banded as adults) that were banded in one colony were later resighted at a different colony during 1971-2006 (Table 2). Ten birds dispersed to the Gannet Islands from across eastern Canada including one from MSI (1,298 km away) and three from Quebec (474 km away). One bird (band number 785-41398) banded as a chick on Digges Island (62°34'N, 77°42'W), Nunavut in 1982, was later resighted and recaptured on the Gannet Islands in 2003-2006 (1,737 km away). Another bird (band number M-16909), banded as a chick on Handa Island, Scotland (58°23'N, 5°11'W) in 1971 was seen four times on the Gannet Islands in 2004, more than 3,200 kilometers away. Fifteen of the birds that were resighted were three years of age or younger, so likely were not breeding (Lloyd and Perrins 1997). However, breeding status was confirmed for seven birds including the bird banded in Nunavut and two from Quebec.

Philopatry and Breeding Dispersal

Of 314 birds banded as a chick on the Gannet Islands, 260 (83%) were observed breeding on their natal island (Table 3). Of these, 214 (82%) returned to within 100 m of their natal colony. Fidelity was higher for

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Table 2. Summary of the inter-island long-distance movements of Razorbills recorded from 1971 to 2006.

Banding Location	Resighting Location	Number of individuals		Distance (km)
		Banded as Chicks	Banded as Adults	
Gannet Islands	Herring Islands	5	0	57
	Machias Seal Island	2	1	1,298
Herring Islands	Gannet Islands	4	0	57
Machias Seal Island	Gannet Islands	1	1	1,298
	Petit Manan	10	0	136
	Seal Island	3	0	195
	Matinicus Rock	7	0	161
Digges Island	Gannet Islands	1	0	1,737
Quebec	Gannet Islands	3	1	474
Handa Island	Gannet Islands	1	0	3,210

birds banded as adults (N = 149) with 97% of birds returning to the same breeding colony. Mean distance moved (in meters) between breeding sites on the same island was 241 ± 29 SE (N = 43) for birds banded as chicks and 317 ± 128 SE (N = 4) for adults. Mean distance moved between different islands (within the Gannet Islands cluster) for birds banded as chicks and adults was 541 ± 34 SE (N = 41) and 783 ± 198 SE (N = 4), respectively. Dispersal rates for each island (GC1-GC5) in the cluster varied greatly with GC3 and GC5 exhibiting the highest emigration rates (80-100%; Table 3).

DISCUSSION

Emigration of immature birds can greatly influence estimates of local survival to breeding age (Harris 1983; Cilimburg *et al.* 2002; Marshall *et al.* 2004). Therefore it is necessary to quantify emigration and immigration rates before detailed life tables for the species are constructed. The main difficulty with this is that observers tend to concentrate their search efforts at the colonies where birds were banded. Ideally, neighboring colonies should be visited regularly or at least until no new sightings or recoveries are recorded. Furthermore, seabird breeding colonies are sometimes regarded as independent entities in population surveys, neglecting the possibility that declines at one colony could reflect dispersal to alternate sites. In order to clarify the rate and role of dispersal in Razorbill population dynamics, we collated and interpreted resighting records from five locations that extend over almost the entire North American breeding range of the species.

Numerous records of long-distance movements in Razorbill exist, ranging from 250 to 4,130 kilometers (Lloyd 1974; Mead 1974; Bakken *et al.* 2003; Lyngs 2003). However, all of these records involve birds that were shot or found dead during the winter (i.e., the result of seasonal migration). Therefore, to our knowledge, our study provides the first records of long-distance dispersal of Razorbills to a new breeding colony

Table 3. Movements of Razorbills between islands within the Gannet Islands, Labrador cluster.

Island	Number banded		Number resighted		Number breeding at different colony		Number breeding on different island		Dispersal rate	
	Chicks	Adults	Chicks	Adults	Chicks	Adults	Chicks	Adults	Chicks	Adults
GC1	1,423	1	43	0	3	0	16	0	0.37	N/A
GC2	1,474	233	143	120	33	4	0	3	0.00	0.03
GC3	1,084	31	20	0	1	0	20	0	1.00	N/A
GC4	1,299	80	104	29	9	0	14	1	0.13	0.03
GC5	190	1	4	0	0	0	4	0	1.00	N/A

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as well as the first trans-Atlantic dispersal event for this species.

Prior to 2004, no Razorbills were known to breed on PMI or SI (L. Welch and S. Hall, pers. comm.). The recent colonization of these islands by Razorbills appears to be at least partially the result of dispersal of individuals from nearby MSI. In 2006 alone, 15 MSI-banded Razorbills were resighted on PMI, SI, and MR (one bird, age three, has been confirmed as a breeder on PMI).

Census data for Razorbills breeding on the Gannet Islands over the past 28 years suggest that the local population is increasing (Robertson and Elliot 2002). However, recent survival and productivity parameter estimates do not support this trend (i.e., estimates are too low to explain a stable or increasing population without immigration; Lavers 2007; Lavers and Jones 2007). The role of dispersal in maintaining populations is widely accepted and may thus explain the observed local population increases on the Gannet Islands. Eleven banded individuals from across eastern Canada and one from Scotland were observed on the Gannet Islands over the course of this study. These individuals likely represent only a small proportion of the birds recruiting to the Gannet Islands because the appearance of new, un-banded individuals can not be detected. This pattern has also been reported for Razorbills on Graesholmen, Denmark where birds from foreign colonies may account for up to 50% of annual population increase (Hipfner and Chapdelaine 2002). At the Gannet Islands during 1996-2006, researchers inadvertently afforded protection to the Razorbill breeding colonies there by deterring human predation (hunting, egging and associated disturbance) and removing Arctic Foxes (*Alopex lagopus*) that regularly invade, thus creating conditions that may be attractive to immigrants. While the local population increase at the Gannet Islands may be taken as possible 'good news' for a species considered to be depleted by centuries of hunting and egging and possibly by recent fisheries bycatch and oil pollution, the reported increase would have low overall population significance if it was due mainly to immigration from other sites.

Philopatry rates of Razorbills banded as chicks on the Gannet Islands were high with 87% of individuals returning to breed on their natal island and 66% returning to their natal colony. These findings are comparable to those for closely related species such as the Common Murre and Atlantic Puffin (Harris *et al.* 1996; Breton *et al.* 2006), but were significantly lower than reported for Razorbills on Skokholm, Wales (philopatry = 99.5%, Lloyd 1974).

Overall, philopatry and therefore dispersal rates within the Gannet Islands cluster varied between islands due to variation in the type and frequency of disturbance events and uneven resighting effort. Individuals banded on islands GC3 and GC5 exhibited the lowest rates of philopatry with 80% and 100% of individuals dispersing to breed on another island, respectively. Although GC5 suffers from small sample size (due in part to low resighting effort), the behavior of these few birds is likely representative of the island population as a whole. In seabirds, high levels of disturbance and breeding failures have been shown to cause divorce of established pairs and encourage dispersal to new and potentially more productive sites (Greenwood and Harvey 1982; Choudhury 1995). Compared to other islands in the cluster, GC5 is the most frequently invaded by Arctic Foxes, which in the past resulted in the complete abandonment of all colonies on the island (Robertson and Elliot 2002; Lavers unpublished data). Similar issues exist on GC1 and GC3 with both islands suffering from gull predation (Lavers pers. obs). In addition, the main Razorbill colony on GC3, located on a low-lying beach, is affected by occasional flooding during high seas resulting in chick mortality. Emigration from MSI to other (until recently unoccupied) islands in the Gulf of Maine can be explained by high population density at the tiny MSI (population rapidly expanding), providing emigrants to nearby small islands with abundant available breeding sites.

Current survival estimates for Razorbills on the Gannet Islands and MSI have been quantified with the inclusion of resighting records for birds which dispersed to other colonies (Lavers *et al.*, in press). These esti-

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mates are lower than other estimates for this species and do not predict a stable population without immigration. For seabird population managers, our results indicate the need for complete surveys of all colonies in the region, to ascertain whether the overall population is stable, increasing, or decreasing and the relative roles of different anthropogenic factors in Razorbill population dynamics.

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