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## COLONIAL NESTERS IN A DETERIORATING HABITAT: SITE FIDELITY AND COLONY DYNAMICS OF LESSER SNOW GEESE

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**ABSTRACT.**—Birds that exhibit a high degree of natal and breeding philopatry and normally breed in stable environments may suffer costs of philopatry if their habitat deteriorates. Female Lesser Snow Geese (*Chen caerulescens caerulescens*) are highly site faithful; however, recent increases in numbers of breeding birds have resulted in widespread habitat destruction in some colonies. Using capture-recapture modeling techniques on multiple resightings of marked individuals, we examined whether breeding-site fidelity of adult Snow Geese has changed over time in a colony that has grown rapidly and in which habitat quality has declined severely during the past two decades. In addition, we examined the age structure of breeding birds to investigate natal-site fidelity to formerly central areas of the colony. Only slight changes in adult breeding-site fidelity were detected over 10-year periods, despite the deterioration of nesting and brood-rearing habitats in and near the investigated areas. However, increasing mean ages of breeding birds in formerly central areas of the colony indicated a lack of recruitment into those areas; young birds must have preferred to settle at the colony periphery even when vacant spaces in the center were available. Together with a small amount of movement by adult birds, the settlement pattern of young birds has led to a long-term shift in the colony location as a whole. Received 12 June 1997, accepted 5 December 1997.

FIDELITY to breeding, staging, and wintering areas is a widespread phenomenon in birds. If philopatry results in familiarity with an area, it may lead to improved food finding and predator avoidance (Gauthreaux 1982, Anderson et al. 1992). Philopatry can increase levels of inbreeding and may be favored where individuals are adapted to local ecological conditions (Greenwood 1987). The degree of site fidelity exhibited by birds should be correlated with the stability of the habitat they are using such that a high degree of site fidelity is expected in stable habitats, and a lower degree of site fidelity is expected in unstable habitats (McNicholl 1975).

Patterns of natal and breeding-site fidelity in colonial nesters can influence spatial structure and age composition of colonies. Vacancies in the colony are occupied by young recruits if natal and breeding-site fidelity are high, resulting in a constant nest density over time. With a new cohort of breeders being added and old birds disappearing each year, the age structure of the

colony will reach a stable equilibrium after an initial establishment phase (Coulson and White 1956).

Lesser Snow Geese (*Chen caerulescens caerulescens*) breed colonially in subarctic and arctic regions of the Western Hemisphere. Colonies are located in areas that have suitable nesting habitat and access to extensive brood-rearing areas of coastal salt marsh or wet tundra. The Lesser Snow Goose colony at La Pérouse Bay (LPB), Manitoba (58°04'N, 94°04'W), has been intensively studied since 1968 (Cooke et al. 1995). Snow Geese in LPB show a high degree of breeding-site fidelity; Cooke and Abraham (1980) found that 73% of all birds nested within 500 m of their previous nest site, and 43% within 100 m. Natal philopatry of females is also high, with young females tending to settle near the area where they were raised (Abraham 1980).

The nature of the interaction between Lesser Snow Geese and their habitat depends on local population density, which has increased dramatically during recent decades on the west coast of Hudson Bay (Kerbes et al. 1990, Cooke et al. 1995). Up to a certain density, grazing by geese triggers a positive feedback mechanism that enhances plant productivity (Jefferies 1988a, b). With increasing goose density, how-

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ever, this relationship breaks down and is replaced by habitat destruction through overgrazing and grubbing, resulting in bare, unvegetated substrate (Kerbes et al. 1990, Iacobelli and Jefferies 1991, Srivastava and Jefferies 1996). A dramatic decline of the vegetated area in LPB has been documented for nesting areas (Ganter et al. 1996) and brood-rearing areas (Cooch et al. 1993, Williams et al. 1993). In the latter areas, the biomass of the remaining salt marsh sward has declined as well.

This loss of suitable habitat through goose feeding activities in turn may negatively influence various reproductive parameters of the goose population. Clutch size in LPB has undergone a long-term decline (Cooch et al. 1989), which in part may be attributable to decreased feeding opportunities for females on the breeding grounds before and during egg laying (Ganter and Cooke 1996). Likewise, growth rates (Cooch et al. 1991) and survival of goslings (Williams et al. 1993) also have declined.

During 1976 to 1978 in LPB (the study period of Abraham 1980), the colony was in the stage of positive-feedback interaction between geese and their food plants, and the habitat appeared to be stable. Current conditions of severely deteriorated nesting and brood-rearing habitat warrant reexamination of site fidelity with a view to potential changes over time. If breeding adults stay despite the deteriorating environment, they may suffer costs of philopatry (Cooch et al. 1993, Rockwell et al. 1993, Williams et al. 1993). Alternatively, breeding birds may show an increased tendency to move to other areas. Similarly, natal-site fidelity may have changed over time, with fewer young birds settling in deteriorated areas of the colony. According to Francis and Cooke (1993), there is no evidence that female natal philopatry at the LPB colony has changed over time. However, recruitment rates into specific sections of the colony may have changed. Lower levels of breeding or natal-site fidelity to the former centers of density will in the long term cause a spatial shift of the entire colony.

In this paper, we document spatial changes in the LPB Snow Goose colony as a whole, and then use data from marked individuals to examine whether long-term habitat changes have been accompanied by decreased breeding and/or natal-site fidelity.

A variety of terms has been used to refer to

issues of individuals returning to certain areas, and there is no general agreement about which terms are best. We use "philopatry" (natal and breeding) to refer to the return to a larger area (i.e. the whole colony) and "site fidelity" (natal and breeding) to refer to the return to a more specific location within the colony.

#### STUDY AREA AND METHODS

*Study population and general field methods.*—The Snow Goose colony of LPB was first established in the early 1950s and has grown from approximately 2,000 pairs in 1968 to 22,500 pairs in 1990 (Cooke et al. 1995). Data on nest history have been collected since 1968, and we use data from the years 1973 to 1992 in this paper.

During the annual molting period, large numbers of adults and juveniles were caught each year and individually marked with alphanumeric colored leg bands. If birds were banded as juveniles, their exact age could be determined later from the color and position of their leg band. Each year until 1990, areas containing approximately 200 to 250 nests ("hatching areas") were established in the densest parts of the colony. Each nest in these areas was visited daily during the hatching period, and individually marked attending parents were identified where possible. Although often both parents were marked, the following analyses were restricted to data from females only, because females determine the pair's nesting location (Cooke et al. 1975), and sightings of both partners were highly correlated. The approximate perimeter of the colony was recorded from ground assessment of the entire colony until 1980 and, in later years, from occasional aerial surveys and long walks to more distant parts of the colony.

*Breeding-site fidelity of adults.*—We used capture-mark-recapture techniques that produce maximum-likelihood estimates of parameters from capture histories of individuals (Lebreton et al. 1992). From multiple resightings of marked individuals, it is possible to estimate on an annual basis the "apparent survival" rate ( $\phi$ ; Lebreton et al. 1992) of groups of nesting birds. Apparent survival is the complement of the annual disappearance rate (mortality and permanent emigration). Because "true" mortality rates are known from independent analyses of band-recovery data for Lesser Snow Geese (Francis et al. 1992), we could infer rates of permanent emigration in these birds by assessing the difference between apparent and true survival.

We divided the colony into 10 regions for the purpose of our analysis, a modification of the regions used by Hik (1986; Fig. 1). Borders between regions were drawn so that the regions were approximately equal in area; in part, they represented clear natural boundaries. Because the location of hatching areas

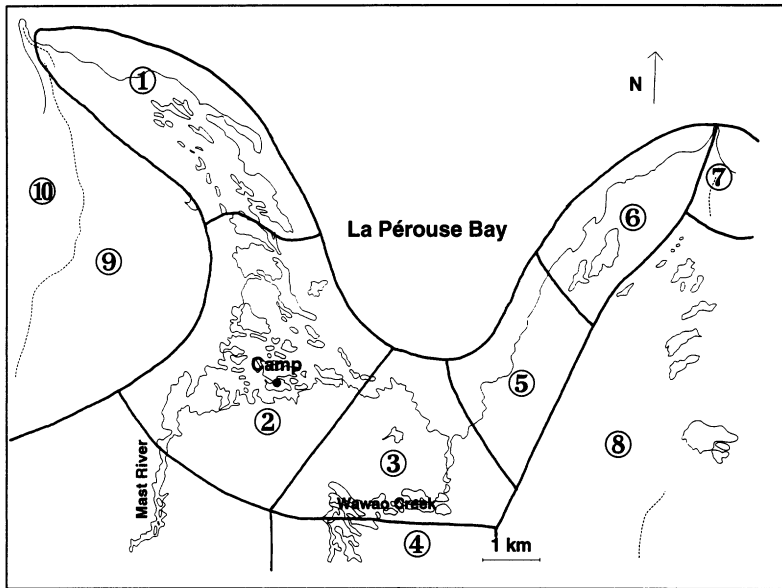


FIG. 1. Snow Goose nesting regions at La Pérouse Bay. Dotted lines are beach ridges.

varied from year to year, borders of hatching areas and regions did not always coincide. In spite of this slight imprecision, each hatching area in the years 1973 to 1992 was assigned to one of the regions.

All sightings of banded nesting females (regardless of whether they had first been banded as adults or as goslings) during the hatching period were subjected to a "capture-recapture" analysis. Although data collection in this case did not involve physical capture of the birds, the same analytical methods as for capture-recapture data can be applied (see Lebreton et al. 1992).

The total data set of resightings of nesting females at hatching was divided into regions, and resighting-history arrays (Burnham et al. 1987) of individual birds were constructed for each region separately. Apparent survival ( $\phi$ ) and resighting probabilities ( $p$ ) were then estimated for each region using programs RELEASE (Burnham et al. 1987) and SURGE (Pradel and Lebreton 1991). In these programs,  $\phi$  and  $p$  are estimated from the data simultaneously. Given that an individual bird nests in a certain region of the colony, apparent survival is the probability of that bird returning to the region in subsequent years, i.e. neither dying nor permanently emigrating to other regions or other colonies. The resighting probability is the probability that a marked individual is seen in the region in a particular year, given that it is alive. Resighting probabilities fluctuate with variation in observer number and effort, observer skill, weather conditions, and other external factors. Temporary emigration of birds from the area during the study period will manifest itself as a temporary decrease in  $p$ , whereas permanent emi-

gration is confounded with death and thus affects  $\phi$ . The emphasis in the interpretation of models will be on patterns in  $\phi$ , because we are mainly interested in possible long-term changes in permanent emigration.

Initially, we tested the goodness-of-fit of each data set to the basic model of full time-dependence in  $\phi$  and  $p$  (Cormack-Jolly-Seber [CJS] model, notation  $\phi, p_i$ ) using program RELEASE. The CJS model assumes homogeneity of  $\phi$  and  $p$  across individuals; if these assumptions are violated, either the data set or the basic model must be modified to achieve a starting model that fits the data. One component of the overall goodness-of-fit test in RELEASE (Test 3.SR) tests for a difference between survival of newly marked (in our case, newly resighted) and previously marked (previously resighted) animals (Pradel et al. 1997). The overall goodness-of-fit test showed that the CJS model did not fit any of the data sets well, and results of Test 3.SR indicated that this was primarily due to a difference in apparent survival after the first resighting versus subsequent resightings (see Results). Therefore, we used a two-encounter-class model with different apparent survival rates for the first ( $\phi^1$ ) and subsequent ( $\phi^2$ ) encounters. Notation for this model is  $\phi^1, \phi^2, p_i$ , and the goodness-of-fit of this model can be tested by eliminating Test 3.SR from the overall goodness-of-fit test in RELEASE (Pradel et al. 1997).

A number of reduced models, assuming linear trends (subscript "lin") or constancy (no subscript) in  $\phi$  and/or  $p$  across time, was then fitted using SURGE, which calculates the deviance of each model to the data and the maximum-likelihood estimates of

$\phi$  and  $p$ . Following Lebreton et al. (1992), selection of the "best" model was based on Akaike's Information Criterion (AIC; Akaike 1973), which is calculated from each model's deviance and number of estimable parameters. Minimization of AIC leads to the model that adequately describes the data using the fewest parameters, and thus achieves the best compromise between model fit and parsimony.

*Natal-site fidelity: Recruitment into central regions of the colony.*—Recruitment rates into the population are difficult to estimate directly from resighting data (Cooke and Francis 1993), but information about patterns of recruitment can be gained from the age structure of population segments. The most basic scenario of population development is that every disappearing breeding bird is replaced by a young immigrant. In this case, the population size is stable, and the mean age in the population is at equilibrium, the level of which depends on the yearly disappearance rate of older birds. A lack of young recruits will cause a departure from the stable equilibrium toward increasingly older birds, with a concurrent decrease in population size.

Most Lesser Snow Geese start breeding at two or three years of age (Cooke and Rockwell 1988), and the average life span of adult birds increased from 4.0 to 7.8 years between 1970 and 1987 (Francis et al. 1992). From 1969 to 1990, between 222 and 1,807 female goslings were banded at LPB each year, with the largest effort, >1,200 birds per year, from 1979 to 1988; these birds constituted the known-age sample in this analysis. Because Snow Geese are long-lived, the mean age of the total known-age banded sample continually increased over time, because a new banded cohort was added each year. Mean age of this sample during our study period (as estimated from annual survival rates in Francis et al. 1992) increased from 3 years in 1974 to 6.2 years in 1988, and was 5.7 years in 1990. When assessing changes in age structure of breeding females in regions 2 to 5 of the colony, the age bias in the banded sample must be accounted for; therefore, we used the deviance between regional and overall mean ages of banded females for this purpose.

RESULTS

*Long-term shift of the colony center.*—In the first half of the 1970s, the LPB colony was concentrated in the area of the Mast River delta and Wawao Creek (regions 2 and 3; Fig. 1). In later years, the colony expanded to the west, northeast, and southeast, and numbers in the formerly central areas declined until regions 2 and 3 were almost completely devoid of nesting birds. By the late 1980s, the centers of the colony had moved to regions 4 and 5. From 1991

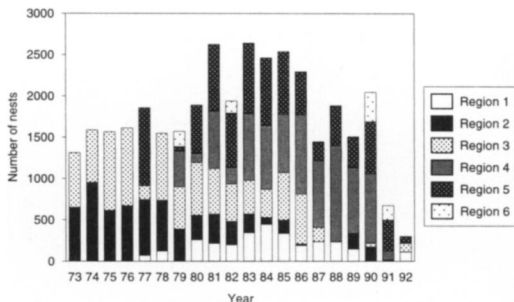


FIG. 2. Distribution of Snow Goose nests monitored during hatching by nesting region, 1973 to 1992 (see Fig. 1).

onward, the densest parts of the colony had moved too far away from the LPB base camp to allow the establishment of regular hatching areas, and the quantity of data collected during hatching declined steeply compared with the years 1973 to 1990 (Fig. 2).

The spatial distribution of nests checked daily during hatching from 1973 to 1992 changed over time (Fig. 2). Although the nests monitored during hatching did not cover the entire colony each year, the location of the hatching areas reflected the areas of highest nesting density, and a shift in the distribution of hatching areas followed a shift in the distribution of the birds. Beginning in about 1990, however, new nesting concentrations formed in regions 6 to 10 (Fig. 1), and these were not included in standard data collection owing to logistical problems. In the last three years of the study, nests monitored during hatching therefore were no longer representative of the entire colony. The approximate perimeter of the colony changed dramatically from 1975 to 1990 (Fig. 3). Although nesting densities in each region are not shown here, the general expansion of the colony and the abandonment of formerly central areas in later years are apparent.

*Breeding-site fidelity of adults.*—Taking the spatial and temporal distribution of resighting data into account, we did not construct resighting-history arrays spanning the full 20 years in each region, but chose the 10-year interval with the highest cumulative number of individually identified females for each region (Table 1). Regions 1 and 6 to 10 were not included in the analyses of individual site fidelity because the data were too sparse. For the four remaining data sets (regions 2 to 5), goodness-of-fit tests

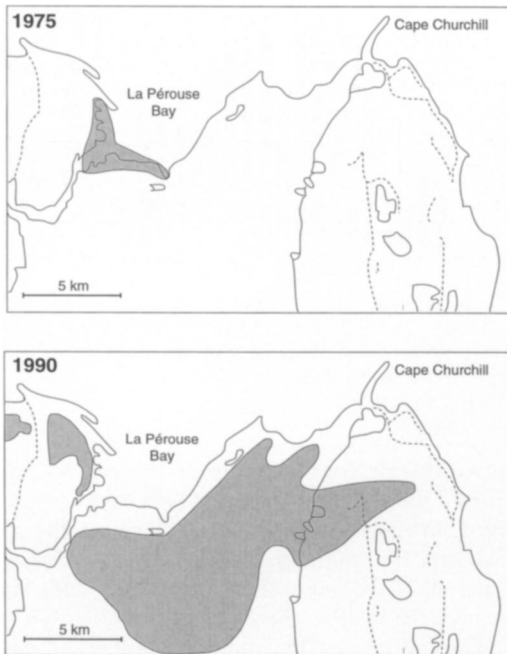


FIG. 3. Approximate perimeter of the La Pérouse Bay Snow Goose colony, 1975 and 1990. Shaded areas were occupied by various densities of nesting geese; dotted lines are beach ridges. Data for 1990 from aerial survey by R. H. Kerbes, Canadian Wildlife Service.

and modeling of apparent survival ( $\phi$ ) and recapture probabilities ( $p$ ) were carried out separately.

The general CJS model (time-dependence in  $\phi$  and  $p$ ) did not fit any of the data sets for regions 2 to 5 (overall goodness-of-fit test in RELEASE, all  $P$ s  $< 0.005$  for regions 2 to 5). Heterogeneity was revealed primarily in Test 3.SR, indicating different apparent survival rates for birds seen the first time versus birds seen before. Several possible reasons could explain such a difference, including trap effects, age effects, and the presence of transients (see Loery et al. 1997). In our case, the presence of transients in the sample is the most likely explanation, transients being birds that breed in a region once without having a particular attachment to the region. The two-encounter-class model fit the data sets from regions 2 to 4 (goodness-of-fit test after Pradel et al. 1997;  $P = 0.498, 0.265,$  and  $0.378$  for regions 2 to 4, respectively). Data in region 5 contained further heterogeneity ( $P < 0.001$ ); therefore, all further

TABLE 1. Number of bands read on Snow Geese in regions 2 to 5 each year (females only; both known-age and unknown-age birds included). The 10-year intervals with the highest cumulative number of bands read are in bold.

Year	Bands read in region			
	2	3	4	5
1973	95	86	—	—
1974	<b>109</b>	65	—	—
1975	<b>126</b>	<b>232</b>	—	—
1976	<b>212</b>	<b>241</b>	—	—
1977	<b>277</b>	71	—	200
1978	<b>171</b>	<b>252</b>	—	—
1979	<b>115</b>	<b>165</b>	94	16
1980	<b>135</b>	<b>205</b>	17	119
1981	<b>90</b>	<b>156</b>	<b>69</b>	<b>126</b>
1982	<b>94</b>	<b>172</b>	<b>39</b>	<b>166</b>
1983	<b>100</b>	<b>192</b>	<b>128</b>	<b>114</b>
1984	59	<b>156</b>	<b>182</b>	<b>266</b>
1985	90	190	<b>155</b>	<b>139</b>
1986	15	179	<b>151</b>	<b>95</b>
1987	—	40	<b>160</b>	<b>69</b>
1988	—	—	<b>241</b>	<b>149</b>
1989	20	—	<b>140</b>	<b>91</b>
1990	52	18	<b>104</b>	<b>120</b>
1991	22	28	4	119
1992	2	24	6	40

analyses were restricted to regions 2 to 4. Among the models tested, that with constant  $\phi^1$ ,  $\phi^2$ , and  $p$  had the lowest AIC and thus described the data adequately while using the minimum number of parameters; this was true for all three regions (Table 2). Thus, there was no indication for annual variation or a linear trend (positive or negative) in apparent survival rate of birds breeding in regions 2 to 4. Maximum-likelihood estimates in the "best" models ranged from 0.52 to 0.59 for  $\phi^1$ , from 0.74 to 0.80 for  $\phi^2$ , and from 0.28 to 0.39 for  $p$  (Table 3). The proportion of transients ( $\tau$ , calculated as  $1 - [\phi^1/\phi^2]$ ; Pradel et al. 1997) ranged from 0.22 to 0.30 and was constant over time in each region (Table 3)

*Recruitment into central regions of the colony.*—For analyses of patterns in age structure, as for analyses of breeding-site fidelity, we used the 10-year interval with the highest cumulative number of resighting records for each region (Table 1). The mean age of known-age females, corrected for the increase in mean age of the total banded sample, increased significantly over time in each of regions 2 to 5 (Fig. 4). Thus, the age distribution in these regions was not at equilibrium over the investigated 10-year pe-

TABLE 2. Results of capture-recapture models in regions 2 to 4, including deviance (DEV), number of estimable parameters (np), and Akaike's Information Criterion (AIC). Only a selection of models is shown; all possible combinations of time dependence, linearity, and constancy in  $\phi^1$  and  $\phi^2$  were run. The apparent survival models are centered in bold; the selected models with the lowest AIC (in bold italics) incorporate constant apparent survival for both encounter classes and constant recapture rates.

	Recapture model					
	Region 2		Region 3		Region 4	
	$p_t$	$p$	$p_t$	$p$	$p_t$	$p$
	$\phi^1_t, \phi^2_t$					
DEV	286.78	288.78	335.23	339.66	254.38	257.66
np	25	18	25	18	25	18
AIC	336.78	324.55	385.23	375.66	304.38	293.66
	$\phi^1_{in}, \phi^2_{in}$					
DEV	287.55	290.77	339.59	348.08	257.25	261.94
np	13	5	13	5	13	5
AIC	313.55	300.77	365.59	358.08	283.25	271.94
	$\phi^1, \phi^2$					
DEV	288.35	<b>292.37</b>	339.77	<b>348.46</b>	257.49	<b>262.33</b>
np	11	<b>3</b>	11	<b>3</b>	11	<b>3</b>
AIC	310.35	<b>298.37</b>	361.77	<b>354.46</b>	279.49	<b>268.33</b>

riods. At the end of the periods, birds in region 2 to 5 were on average between 2 and 3.5 years older than at the beginning. This increase in age was probably caused by a shortage of young birds (i.e. 2- and 3-year-old first-time breeders) recruiting into the regions to replace any disappearing older birds. If no young birds recruited into these areas, the mean age of birds nesting there would increase by one year each year; the somewhat slower increase shown by our data indicates that some young birds did still settle in these areas. This is confirmed by sightings of small numbers of marked 2- and 3-year-old breeders in the regions at the end of the investigated periods, although variation in observer effort precluded quantification of their proportion among all breeding birds.

DISCUSSION

*Breeding-site fidelity of adults.*—The observed habitat deterioration at LPB and the resulting

costs of philopatry (see Cooch et al. 1993, Rockwell et al. 1993, and Williams et al. 1993) lead to the prediction that the high degree of breeding-site fidelity observed by Cooke and Abraham (1980) may not be maintained in this colony. Rates of permanent emigration of residents from degraded areas of the colony may increase over time, as may the proportion of transients (i.e. one-time breeders). When examining the apparent survival ( $\phi$ ) of birds in different regions of LPB, we did not detect time dependence or a linear trend in this parameter for either of the two encounter classes, i.e. neither apparent survival of residents nor the proportion of transients changed over time. However,  $\phi$  is a function of both mortality and permanent emigration, and annual mortality of adult geese from LPB, as estimated from hunting recoveries, has declined from 22% in 1970 to 12% in 1987 (Francis et al. 1992). Constant  $\phi$  at the same time as increasing true survival suggests that emigration rates must have in-

TABLE 3. Parameter estimates for apparent survival rates after first ( $\phi^1$ ) and subsequent ( $\phi^2$ ) resightings, resighting probabilities ( $p$ ), and proportion of transients ( $\tau$ ) in regions 2 to 4 under model  $\phi^1\phi^2p$ ; 95% confidence intervals are in parentheses.

Region	Years	$n^a$	$\phi^1$	$\phi^2$	$p$	$\tau$
2	1974 to 1983	1,090	0.52 (0.47 to 0.58)	0.75 (0.72 to 0.78)	0.39 (0.36 to 0.43)	0.30
3	1975 to 1984	1,622	0.57 (0.51 to 0.64)	0.74 (0.70 to 0.77)	0.31 (0.28 to 0.34)	0.22
4	1981 to 1990	1,013	0.59 (0.52 to 0.67)	0.80 (0.76 to 0.84)	0.28 (0.25 to 0.32)	0.26

<sup>a</sup> Number of individual resighting histories.

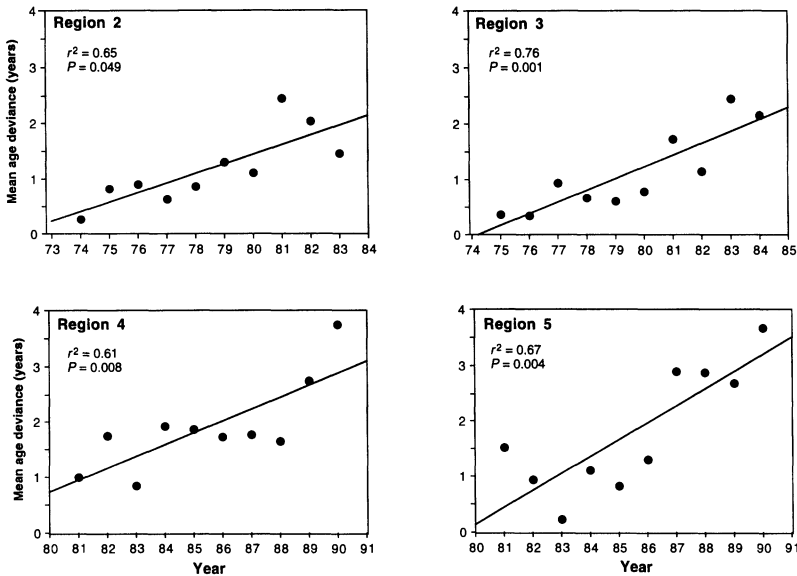


FIG. 4. Deviance between regional and overall mean age of known-age banded female Snow Geese in regions 2 to 5. The regional mean age increased faster than the overall mean age, indicating a lack of young recruits in these regions.

creased slightly over time (see Francis and Cooke 1993), and this increase can be estimated. For instance, in the time interval investigated for region 2 (1974 to 1983), true survival ( $s$ ) of all LPB females increased approximately from 0.803 to 0.855 (after Francis et al. 1992), whereas apparent survival was constant at 0.75. Consequently, permanent emigration rates ( $1 - \phi/s$ ) increased from about 7% to about 12% in this 10-year period; similar increases are estimated for regions 3 and 4. Moreover, a steeper drop in breeding-site fidelity may have occurred in each region after the analyzed time intervals; this is impossible to examine owing to the inherent difficulty that a decrease in nesting density in an area, whether from death or emigration of adults, eventually results in cessation of data collection in that area, and so capture-recapture analysis in each region cannot extend into the periods of almost complete abandonment of the region. Because we examined site fidelity only at the level of colony subregions, slightly increased emigration from the investigated central regions of LPB does not necessarily imply decreased philopatry to the larger area; birds may have relocated to other more recently settled regions of the same colony.

In spite of slightly increased local emigration

rates, it is still surprising that such a high level of site fidelity is maintained by individuals at least until shortly before areas are abandoned by most birds. Most geese that are residents in a region remain residents, even if the quality of nesting habitat (Ganter et al. 1996) and nearby brood-rearing habitat (Cooch et al. 1993) deteriorates such that the birds suffer from reduced fitness.

*Natal-site fidelity: Recruitment into central regions of the colony.*—The changes in age structure in regions 2 to 5 indicate that the rate at which young birds came into these regions was lower than that at which old birds disappeared from them. A possible explanation for this phenomenon, which does not involve any changes in natal-site fidelity, is that the number of young birds produced in LPB is no longer sufficient to fill the gaps left by disappearing old birds: first-year survival of birds raised in LPB has declined over time (Francis et al. 1992). However, the number of breeding pairs in the colony has continued to grow throughout the course of the study, and although data on the absolute number of young recruits each year are lacking, it is safe to assume that enough young birds would have existed to fill the gaps left by disappearing adults in the central areas. Age at first breeding has not changed system-



atically over time in LPB (E.G. Cooch pers. comm.); thus, increasing age at recruitment cannot explain the increase in mean age in the central regions, and the avoidance of these areas by young recruits in spite of available space remains the most likely explanation for our results. This deficit of recruits is, at first glance, at odds with the finding of Francis and Cooke (1993) that natal philopatry of females reared in LPB has not changed over time. However, Francis and Cooke examined philopatry to LPB as a whole, not site fidelity to specific regions. Female Snow Geese that return to breed tend to nest close to where they were raised, rather than to the area of their natal nest (Cooke and Abraham 1980). Similarly, female Canada Geese are philopatric to brood-rearing areas (Lessells 1985). Because habitat deterioration in the central salt marshes at LPB has resulted in an increasing shift of brood-rearing areas toward coastal areas to the east and south (Cooch et al. 1993), new recruits should tend to settle near those areas. Although recruits may still be philopatric to the natal colony as a whole, the area where young birds nest has gradually shifted as a consequence of the shift in the brood-rearing areas; as a result, natal-site fidelity of birds hatched in formerly central regions has declined.

*Long-term habitat change and colony dynamics.*—Even in a steadily declining habitat, Lesser Snow Geese maintain a high degree of breeding-site fidelity. However, young birds tend to settle in more peripheral areas rather than in vacated sites within the traditional areas of the colony. Among seabirds, recruitment of young birds into peripheral areas of a colony (Kharitonov and Siegel-Causey 1988) has been attributed to lack of space and the presence of older (i.e. dominant) birds in the center of the colony. If this is the case, recruits should move from peripheral to more central (and preferred) nesting sites as they become available (Kharitonov and Siegel-Causey 1988). In contrast, Cooke et al. (1983) reported that young Snow Geese in LPB tended not to relocate after they had settled in peripheral areas of the colony; they assumed, however, that new recruits would occupy spaces in central areas as they became available. Directional natal dispersal into little-used areas of a colony was also reported for Black Brant (*Branta bernicla nigricans*; Lindberg and Sedinger 1997). In this case, va-

cancies in a formerly dense area remained unoccupied, and the colony as a whole moved during the 7-year study period. Our study documents the same phenomenon for Snow Geese at LPB; however, although Lindberg and Sedinger (1997) did not report deterioration of nesting habitat and expected the regions with declining nest densities to be occupied by new recruits in future years, we do not expect the abandoned areas in the center of LPB to be recolonized in the foreseeable future.

Although competition with older breeders may have kept young recruits from settling in the central areas of the colony in earlier years, habitat deterioration now acts as a second factor that leads to the same result. Directional natal dispersal, which initially was a mechanism of colony expansion (Lindberg and Sedinger 1997), now also results in long-term colony movement. A small fraction of adult breeders moving from central to other regions accelerates this movement. Thus, central nesting locations in bird colonies are not always superior to and preferred over peripheral ones (see also Brunton 1997). Far from being at a stable equilibrium, the LPB Snow Goose colony is spatially and temporally dynamic.

The phenomenon of "moving" goose colonies may be part of a natural, long-term cycle of habitat destruction by geese breeding at high densities, gradual abandonment of areas by the geese, and subsequent recovery of the habitat. Alternatively, the observed phenomenon may be the result of anthropogenic disturbance of an equilibrium between population levels of geese and their food resources: the global increase of Snow Goose populations has been attributed to the occurrence of new food sources as a result of agricultural changes within the wintering range (Cooch and Cooke 1991, Ankney 1996). In this case, increased pressure on arctic breeding habitats may in the long term lead to an overall reduction in fecundity for the species as a whole, as has been documented for LPB geese (Cooch et al. 1989, 1991). If this reduction in fecundity is large enough, it will result in declining population levels. This may again lead to a long-term cycle of goose-habitat interaction, although on much broader spatial and temporal scales. Vegetation in salt marshes that have been stripped to bare sediment by grubbing geese will take a long time to regen-

erate, most likely on the order of decades (Srivastava and Jefferies 1996).

The question remains: Why do individual birds retain strong fidelity to their nest sites even after both nesting and brood-rearing habitats have become unfavorable? It may be that once a bird is established in a region as a resident, site fidelity has always been a better strategy (over evolutionary time) than relocation in reaction to unfavorable conditions, because the risks associated with relocation are too great. On the other hand, Greater Snow Geese (*C. c. atlantica*) in the High Arctic of eastern Canada generally exhibit much lower site fidelity than Lesser Snow Geese at LPB, with whole colonies moving over distances of several km between years depending on snow melt patterns and predation pressure (Lepage et al. 1996). Thus, even closely related populations of the same species may exhibit different degrees of breeding-site fidelity. The net superiority of the philopatric strategy may have persisted during the time period we investigated at LPB. However, if the anthropogenic changes mentioned above have really altered Lesser Snow Goose populations beyond the level that can be supported by traditional breeding habitats, this may have severely changed the cost-benefit relationship of site fidelity in LPB, and increased flexibility would now be favored. In every population, individuals will exhibit different degrees of site fidelity and flexibility (e.g. Cooke and Abraham 1980, Ganter 1994), and although selection traditionally may have favored site-faithful individuals, that selection regime may now have changed. Hence, we may still see long-term changes in site fidelity occurring over a time span greater than that of our study.

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