

ECOLOGICAL SIGNIFICANCE OF BROOD-SITE FIDELITY IN BLACK BRANT: SPATIAL, ANNUAL, AND AGE-RELATED VARIATION

MARK S. LINDBERG¹ AND JAMES S. SEDINGER

*Institute of Arctic Biology and Department of Biology and Wildlife, University of Alaska,
Fairbanks, Alaska 99775, USA*

ABSTRACT.—We examined use of brood-rearing sites by female Black Brant (*Branta bernicla nigricans*) that nested at Tutakoke River, Alaska, 1987 to 1993. Adult females exhibited fidelity to brood-rearing sites; however, we observed site-specific and annual variation in movements among sites. Site fidelity of adults was not related to their hatching date, and hatching dates of females did not vary among brood-rearing sites, suggesting that site selection was unaffected by competition. Movement among sites was affected by distance between sites, but this relationship varied annually and among sites. Variation in forage characteristics may affect movements among sites. Natal-site fidelity was equal to fidelity probability of adults, indicating social inheritance of sites and perhaps facilitation through nepotism. We observed heterogeneity in survival probabilities of goslings and adults among sites. For goslings, heterogeneity in survival was probably related to variation in growth. We observed no relationship between hatching date and use of brood-rearing sites. Previously documented seasonal declines in growth of goslings are more likely affected by declines in forage quality and abundance than by site-specific variation in forage characteristics because use of brood-rearing sites was not related to hatching dates. Received 23 April 1997, accepted 11 November 1997.

ENVIRONMENTAL CONDITIONS that precocial young experience before fledging may affect their growth, survival, and future fecundity (Sedinger et al. 1995). The relationship between environment and fitness is particularly evident in northern latitudes where growing seasons are short. Fitness of geese nesting in arctic and subarctic regions is affected by seasonal (Sedinger and Raveling 1986) and spatial variation (Cooch et al. 1993) in forage quality and abundance. Goslings hatching late grow slower (Cooch et al. 1991, Sedinger and Flint 1991, Lindholm et al. 1994) and have lower survival and fecundity than goslings hatching early (Sedinger et al. 1995). Growth of young Lesser Snow Geese (*Chen c. caerulescens*) and Barnacle Geese (*Branta leucopsis*) varies among brood-rearing sites (Larsson and Forslund 1991, Cooch et al. 1993). Spatial variation in habitat quality may lead to heterogeneity in survival and subsequent reproductive performance (Cooch et al. 1993, Rockwell et al. 1993). In addition, fidelity to natal sites may cause genetic-environmental covariance and inflated estimates of heritability

for growth metrics (Larsson and Forslund 1992). Although the distribution of goslings among brood-rearing sites affects the fitness of these birds, the use of brood-rearing habitats and factors affecting the distribution of birds during brood rearing are poorly described.

The distribution of birds among habitats may be influenced by fitness costs and benefits associated with those habitats (Nichols et al. 1983). Birds should occupy the highest quality habitats, but by using these habitats, they may decrease habitat quality. As habitat quality declines, birds should select unoccupied habitats of similar quality as the habitat currently occupied (Fretwell 1972). If all birds occupy habitats of similar suitability, then their distribution may be described as ideal free (Fretwell and Lucas 1970). In an ideal free distribution, all individuals would have similar fitness. The pattern of habitat selection in geese may be particularly complex because geese may initially improve the quality of the habitat through fecal nitrogen deposition, which increases above-ground primary productivity (Hik and Jefferies 1990). Furthermore, movements among habitats may be opposed by competition with conspecifics. Alternatively, advantages of site familiarity may favor fidelity. Ecological advantages of site fidelity and resulting site familiar-

¹ Present address: Institute for Wetland and Waterfowl Research, Ducks Unlimited, Inc., One Waterfowl Way, Memphis, Tennessee 38120, USA. E-mail: mlindberg@ducks.org

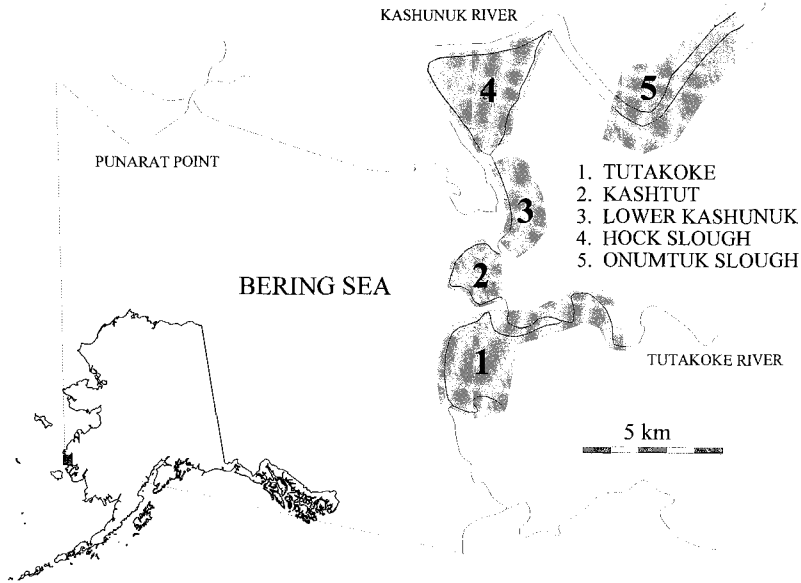


FIG. 1. Location and names of sites used to examine variation in movement probabilities among brood-rearing sites for female Brant at Tutakoke River, Alaska, 1987 to 1993. The majority of Brant nests are in site 2 and the western portion of the site 1. Area of detail is indicated by the small rectangle on the map of Alaska.

ity may include improved feeding efficiency and higher survival (Lack 1954, Anderson et al. 1992). However, in areas with spatial variation in habitat quality, fidelity to brood-rearing sites may be maladaptive (Levin et al. 1984, Cooch et al. 1993).

In this study, we examined the distribution of Black Brant (*Branta bernicla nigricans*; hereafter "Brant") among brood-rearing sites and tested the hypothesis that Brant are distributed in an ideal free manner by examining variation in survival probability among brood-rearing sites. If Brant exhibit an ideal free distribution during brood rearing, we predict that survival probability will not vary among sites. We also examined two factors that may result in deviations from an ideal free distribution: competition and site fidelity. We tested the effects of competition on site use by comparing hatching dates of individuals using each site. If individuals that hatch late are excluded from sites through competition with individuals that hatch early (and presumably occupy optimal habitats), then hatching dates will vary among sites. Moreover, a nonrandom distribution of hatching dates among sites may indicate that seasonal declines in growth of goslings result from a covariance between hatching date and brood-rearing site, rather than a decline in for-

age quantity and quality, because individuals that hatch late use lower quality sites than individuals that hatch early. Finally, we quantified fidelity of Brant to brood-rearing sites. We examined the effects of age, distance between sites, and hatching date on site fidelity and tested for site-specific and annual variation in fidelity probability.

STUDY AREA AND METHODS

The study area (which included brood-rearing sites at the Tutakoke River colony) comprised portions of the Tutakoke and Kashunuk river corridors on the Yukon-Kuskokwim River Delta, Alaska (Fig. 1). Following hatching, Brant families from the Tutakoke River colony (61°N, 165°W) feed in salt marshes in the vicinity of these tidally inundated rivers (Sedinger et al. 1995). Salt marsh communities are dominated by *Carex subspathacea* and *Puccinellia phryganodes* (Kincheloe and Stehn 1991). We divided the study area into five sites to examine movements among sites and variation in hatching dates at these sites (Fig. 1). Site boundaries were largely defined by geographic features. The size of each site was approximately the area covered by each banding drive used to capture geese (see below).

Capture and marking.—During late July and early August, 1987 to 1993, we captured adults and pre-fledging goslings by driving them into nets. We conducted drive-trapping 22 to 34 days after the peak of

hatching, which corresponded to the period when goslings and molting adults were flightless. On average, trapping was conducted over a five-day period (range three to seven days). Flightless Brant were driven into nets using boats and personnel on foot. We determined sex and age of Brant by cloacal examination and feather characteristics. We marked Brant with leg bands and tarsal tags that were engraved with an individual code (Sedinger et al. 1995). We also recorded tarsal-tag codes of Brant that had been banded in previous years. Capture location was mapped on aerial photos. All captured Brant were released simultaneously after each drive.

Modeling movement among brood-rearing sites.—We estimated annual movements of female Brant among brood-rearing sites (capture locations) using multi-state models and program MSSURVIV (Brownie et al. 1993, Hines 1994). We restricted our analysis to females because Brant form long-term pair bonds such that estimates of movement probabilities for adult pairs are not independent (Schmutz et al. 1995). Movements of males banded as goslings likely are independent of female goslings, but few males return to the Tutakoke colony (Lindberg 1996). Therefore, data for males marked as goslings were insufficient to obtain estimates of movement from an individual's natal site to the site it used as an adult.

Data used for multistate models are similar to input for capture-recapture models of survival analysis, except that capture histories reflect both encounters and location or state at capture. Thus, capture history AA0B describes an individual captured at site A in periods 1 and 2, not captured in period 3, and captured at site B in period 4. We obtained maximum-likelihood estimates of the following parameters using MSSURVIV: (1) p_i^s , the probability of capture in year i for a bird in site s at i ($i = 1988, 1989, \dots, 1993$); (2) S_i^r , the probability that a bird in site r in year i survives and is in any sampled site in year $i + 1$ ($i = 1987, 1988, \dots, 1992$); and (3) Ψ_i^s , the probability of a bird being in site s in year $i + 1$ for a bird that was in site r in year i and survived to year $i + 1$ ($i = 1987, 1988, \dots, 1992$).

We assumed that survival was dependent on the site occupied in year i and not the site occupied in year $i + 1$ (Brownie et al. 1993). This assumption is reasonable because birds occupied sites in year $i + 1$ at the end of the survival interval. Brant do not breed until they are at least two years old; therefore, estimates of survival for birds banded as goslings (S_{i0}^r) equaled survival from banding until two years of age (Nichols et al. 1990). Similarly, estimates of movement probabilities for goslings (Ψ_{i0}^s) reflect movement from the brood-rearing site to the site occupied at two years of age. We use natal-site fidelity to describe the return of individuals banded as goslings to the site where they were raised.

We used a step-down modeling approach (Lebreton et al. 1992) to reduce sources of variation in cap-

ture and survival probabilities and then tested hypotheses about annual, site-specific, and age-related variation in movement probabilities. We used Akaike Information Criteria (AIC; Akaike 1973) and likelihood-ratio tests (LRT) to compare competing models.

We modeled movements among all five brood-rearing sites (Fig. 1) for individuals captured as adults from 1987 to 1993. We tested whether movements among sites and fidelity to a site were equally probable by comparing models with variable movement probabilities and a model with all movement parameters fixed at 0.2 (i.e. 1.00/5). We tested whether movements were constant among years, sites, or both years and sites. We used the structure of the stepping-stone model of gene flow to examine the relationship between movement probability and distance between sites (Nichols and Kendall 1995). That is, we considered movements between adjacent brood-rearing sites, and between sites separated by one site, and so forth, up to movements separated by three sites, to be equal. For example, movement from site 3 to site 2 equals that from site 3 to site 4, and movement from site 3 to site 1 equals that from site 3 to site 5. This structure is a general form of the stepping-stone model because we did not constrain short-distance movements (e.g. site 3 to 2) greater than longer-distance movements (e.g. site 3 to 1). Use of stepping-stone models does not imply measures of gene flow among brood-rearing sites. Rather, it is a structure for modeling the relationship between distance and movement probability.

To address hypotheses regarding natal-site fidelity, we reduced the number of sites from five to two because subsequent captures of individuals initially banded as goslings were too few to obtain meaningful estimates of movement among all five sites. This analysis also provided estimates of movements for adults at a larger scale than the five-site analysis and a test of age-specific differences in site fidelity. We reduced the number of sites by combining captures from sites 1 and 2 (Tutakoke River area) and from sites 3, 4, and 5 (Kashunuk River area; Fig. 1). We eliminated all captures of one-year-old birds ($n = 48$) for estimates of natal-site fidelity because we have not observed Brant breeding until they are two years old. We tested for annual variation in capture probabilities, but we assumed that capture probabilities of two-year-old Brant were equal to capture probabilities of Brant > two years old because our data were too sparse to consider age and annual variation in capture probabilities. This assumption may produce overestimates of detection probability for two-year-old Brant because younger Brant have a lower breeding probability than older Brant (Sedinger et al. unpubl. data), and nonbreeding Brant (i.e. molting birds) are not available for capture during banding. Biased estimates of detection probability also may bias estimates of survival probability. Therefore, we

TABLE 1. Akaike information criteria (AIC), and number of parameters in models used to examine annual (*i*) and spatial (*rs*) variation in capture (*p*) and survival (*S*) probabilities of adult female Brant at five brood-rearing sites at Tutakoke River, Alaska, 1987 to 1993. In all models, movement probabilities among sites are year- and site-specific.

Model	Description	AIC	No. of parameters
$p_i^i S_i^i$	General model (no constraints)	1241.3	170
$p^i S_i^i$	<i>p</i> constant over years	1596.0	150
$p_i S_i^i$	<i>p</i> constant over sites	1342.2	150
$p S_i^i$	<i>p</i> constant over years and sites	1354.9	146
$p_i^i S^i$	<i>S</i> constant over years	1218.1	151
$p_i^i S_i$	<i>S</i> constant over sites	1232.5	151
$p_i^i S$	<i>S</i> constant over years and sites	1233.1	147

use estimates of survival probability only for relative comparisons. Survival probabilities of adults and individuals banded as goslings were not comparable because they spanned a different time period, one and two years, respectively. We examined annual and site-specific variation in natal-site fidelity. We could not structure movements in the two-site analysis using the stepping-stone models because all movements were the same distance (one site). We tested if natal-site fidelity was equal to fidelity probability of adults.

We examined the effects of hatching date on site fidelity of adult females by comparing hatching dates in year *i* + 1 of females that were faithful to brood-rearing sites between year *i* and year *i* + 1 with hatching dates of females that moved to a new brood-rearing site between year *i* and year *i* + 1. We determined hatching dates by visiting nests on alternate days during the hatching period (Sedinger et al. 1995). A relationship between hatching date and probability of site fidelity may indicate that age or competition affect fidelity because younger Brant generally nest later (Flint and Sedinger 1992), and Brant that hatch early occupy brood-rearing sites before Brant that hatch late. In this ANOVA model,

hatching date was the dependent variable, and year, state (faithful or disperser), and state × year interaction were included as fixed factors.

Covariance between hatching date and brood-rearing sites.—We examined the relationship between hatching date and brood-rearing location of adult females breeding at Tutakoke River from 1987 to 1993 to test the effects of competition on use of brood-rearing sites. We used ANOVA to test the hypothesis that hatching dates of females did not vary among brood-rearing locations (with hatching date as the dependent variable). Brood-rearing site (Fig. 1), year, and year × site interaction were included as fixed factors.

RESULTS

Movement among brood-rearing sites for adults.—We made 2,588 captures of 407 adult female Brant from 1987 to 1993. Model structures were similar for adult females in the analyses that included two and five sites. Capture probabilities of adults were both year- and site-specific (Tables 1 and 2). We observed spatial variation in survival, but survival probability was constant

TABLE 2. Akaike information criteria (AIC), and number of parameters in models used to examine annual (*i*) and spatial (*rs*) variation in capture (*p*) and survival (*S*) probabilities of female Brant at two brood-rearing sites at Tutakoke River, Alaska, 1987 to 1993. Survival probability for the two-year period from banding as goslings to two years of age (S_g) and annual survival of adult Brant (more than two years old; S_a) were modeled separately. In all models, movement probabilities among sites are year- and site-specific.

Model	Description	AIC	No. of parameters
$p_i^i S_{ia}^i S_{ig}^i$	General model (no constraints)	810.8	54
$p_i S_{ia}^i S_{ig}^i$	<i>p</i> constant over sites	820.0	49
$p_i^i S_{ia} S_{ig}^i$	<i>p</i> constant over years	816.8	46
$p_i^i S_{ia} S_{ig}$	<i>p</i> constant over years and sites	825.6	45
$p_i^i S_{ia} S_{ig}^i$	Adult <i>S</i> constant over sites	808.0	49
$p_i^i S_{ia} S_{ig}$	Adult <i>S</i> constant over years	805.5	46
$p_i^i S_{ia} S_{ig}$	Adult <i>S</i> constant over years and sites	807.9	45
$p_i^i S_{ia} S_{ig}$	Adult <i>S</i> constant over years, juvenile <i>S</i> constant over sites	813.8	42
$p_i^i S_{ia} S_{ig}$	Adult <i>S</i> constant over years, juvenile <i>S</i> constant over years	823.1	38
$p_i^i S_{ia} S_{ig}$	Adult <i>S</i> constant over years, juvenile <i>S</i> constant over years and sites	831.6	37

TABLE 3. Akaike information criteria (AIC), and number of parameters in models used to examine annual (i) and spatial (rs) variation in movement probabilities (Ψ) of adult female Brant at five brood-rearing sites at Tutakoke River, Alaska, 1987 to 1993. Models with movement probabilities structured following stepping-stone models are designated at Ψ_d . In all models, capture probability is year- and site-specific (p_i^s), and survival probability is site-specific (S_i^r).

Model	Description	AIC	No. of parameters
Ψ_{eq}	Ψ equally probable	1960.3	54
Ψ_i^{rs}	No constraints	1218.1	151
Ψ_i^s	Ψ constant over sites	1329.8	41
Ψ_i^{rs}	Ψ constant over years	1582.4	40
Ψ	Ψ constant over sites and years	1331.3	36
Ψ_{id}^{rs}	Ψ dependent on distance between sites	1203.2	127
Ψ_{id}^s	Ψ dependent on distance between sites and constant over sites	1247.5	61
Ψ_d^{rs}	Ψ dependent on distance between sites and constant over years	1529.8	51
Ψ_d	Ψ dependent on distance between sites and constant over sites and years	1256.3	40

among years within sites (Tables 1 and 2). Movement probabilities (Ψ^{rs} , $r \neq s$) and fidelity probability (Ψ^{rs} , $r = s$) were not equally probable. In both the two- and five-site analyses, the model with equally probable movements and fidelity probabilities (i.e. all $\Psi^{rs} = 0.2$ for $r \neq s$ and $r = s$) had the highest AIC value and was rejected ($P < 0.001$) in the LRT with the most general model (Tables 3 and 4). In the analysis with five sites, AIC values were lowest for the model that constrained movement as a function of distance between brood-rearing sites (i.e. stepping-stone model structure), and this relationship varied among years and sites (Table 3, model Ψ_{id}^{rs}). Based on LRT, model Ψ_{id}^{rs} was favored over the model (Ψ_i^{rs}) with no constraints ($X^2 = 33.0$, $df = 24$, $P = 0.10$). LRTs between model Ψ_{id}^{rs} and all reduced parameter forms of the stepping-stone models (e.g. no year or state specificity) rejected ($P < 0.001$) the simpler models.

We were more limited in our ability to model variation in movement in the analysis with only

two sites because we could not consider models with movement estimated as a function of distance between sites (i.e. both movements were of equal distance). Nonetheless, AIC values indicated that adult movement probabilities were both site- and year-specific (Table 4). Therefore, despite differences in scale, model structures for the two- and five-site analyses were similar.

We report parameter estimates from the models with the lowest AIC values (i.e. most parsimonious). A model with year- and site-specific capture probabilities, site-specific survival probability, and year- and site-specific movement probabilities that were related to distance between sites ($p_i^s S_i^r \Psi_{id}^{rs}$) was used for five-site analysis (Table 3). The model structure for the two-site analysis was the same as the five-site analysis, except survival probability differed between juveniles and adults, and movement probability could not be related to distance between sites ($p_i^s S_a^r S_i^s \Psi_i^{rs}$; Table 4). Goodness-of-fit tests indicated that both of these models adequately explained the data (P

TABLE 4. Akaike information criteria (AIC), and number of parameters in models used to examine annual (i) and spatial (rs) variation in movement probabilities (Ψ) of female Brant at two brood-rearing sites at Tutakoke River, Alaska, 1987 to 1993. Except for model Ψ_i^{rs} , movement probabilities for adult (Ψ_a) and goslings (Ψ_g) are modeled separately. In all models, capture probability is year- and site-specific (p_i^s), and survival probability is site-specific for adults (S_i^r) and year- and site-specific for juveniles (S_i^s).

Model	Description	AIC	No. of parameters
$\Psi_{eqa} \Psi_{ig}^{rs}$	Adult Ψ equally probable	1121.6	34
$\Psi_{ia}^{rs} \Psi_{ig}^{rs}$	No constraints	805.5	46
$\Psi_a^{rs} \Psi_{ig}^{rs}$	Adult Ψ constant over years	845.5	36
$\Psi_{ia}^{rs} \Psi_{ig}^{eqg}$	Natal Ψ equally probable	823.0	36
$\Psi_{ia}^{rs} \Psi_{ig}^{rs}$	Natal Ψ constant over years	811.9	38
Ψ_i^{rs}	Natal and adult Ψ equal within years and sites	799.7	36

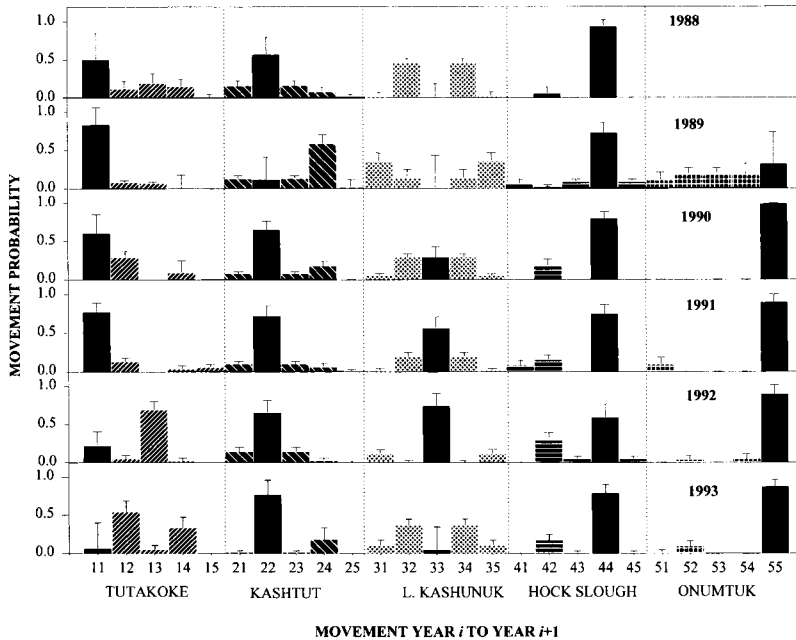


FIG. 2. Movement probabilities between year i and year $i + 1$ for adult female Brant among five brood-rearing sites at Tutakoke River, Alaska, 1987 to 1993. Rows are years of the study with year $i + 1$ shown at the far right. Numbers at the bottom of columns indicate movements between sites (e.g. 13, movement from Tutakoke [site 1] to Lower Kashunuk [site 3]). Fidelity to sites (e.g. 22) is represented by solid bars; error bars are 1 SE.

> 0.94). Capture probability estimates ranged from 0.01 (SE = 0.001) to 1.00 (SE = 0.001) in the five-site analysis and from 0.08 (SE = 0.023) to 0.30 (SE = 0.028) in the two-site analysis. Adult survival probability was 0.70 (SE = 0.033) for site 1, 0.88 (SE = 0.031) for site 2, 0.72 (SE = 0.037) for site 3, 0.76 (SE = 0.049) for site 4, and 0.76 (SE = 0.077) for site 5 in the five-site analysis. In the two-site analysis, adult survival probability was approximately the average of survival for the sites that were combined. Survival probability was 0.83 (SE = 0.020) for the Tutakoke River area (sites 1 and 2) and 0.74 (SE = 0.030) for the Kashunuk River area (sites 3 to 5).

Although movement was best modeled as function of distance between sites in the five-site analysis, movement probabilities did not always follow the pattern expected for the stepping-stone model (i.e. Ψ declines with dispersal distance; Fig. 2). Negative relationships between movement probability and dispersal distance were observed in only 4 of the 29 possible combinations of site- and year-specific movements (site 2, 1991 and 1992; site 3, 1991; site 5,

1989; Fig. 2). Fidelity probability (i.e. Ψ^{rs} where $r = s$) was higher than all movement probabilities (i.e. Ψ^{rs} where $r \neq s$) in 76% (22/29) of the cases. Fidelity probabilities were higher than all dispersal probabilities for sites 4 and 5 in all years; however, this pattern was observed in only two of the six years at site 3. Fidelity probability ranged from 0.01 (SE = 0.090) to 0.99 (SE = 0.001). In the two-site analysis, fidelity probability was higher than all dispersal probabilities in 90% (9/10) of the cases (Fig. 3). Fidelity probability ranged from 0.49 (SE = 0.123) to 1.00 (SE = 0.001) in the two-site analysis.

We captured 187 adult females during banding in year $i + 1$ that also were captured in year i . We found no evidence that state (faithful or disperser) was related to hatching date. Hatching date varied among years ($F = 51.9$, $df = 6$ and 179, $P < 0.001$), but not between states ($F = 0.7$, $df = 1$ and 179, $P = 0.405$); the state \times year interaction also was not significant ($F = 1.15$, $df = 6$ and 173, $P = 0.335$).

Movement among natal sites.—We recorded the natal sites of 2,937 female goslings between

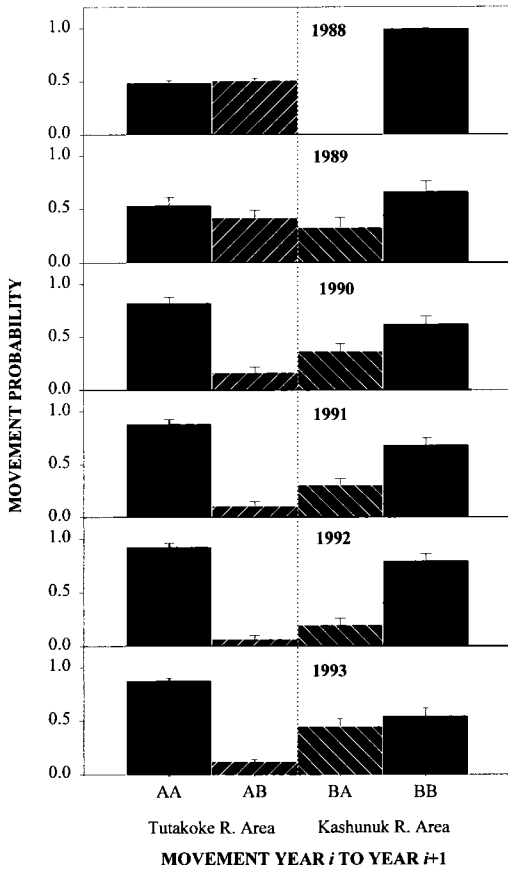


FIG. 3. Movement probabilities between year *i* and year *i* + 1 for female Brant among two brood-rearing sites at Tutakoke River, Alaska, 1987 to 1993. Movement probabilities were equal for adults and goslings and therefore are shown by the same bars, except for 1988, which represents only movements of adults. Movements of goslings are movements from the natal site to the site occupied when two years old (e.g. 1990 movements are probabilities for goslings banded in 1988), whereas movements of adults are between consecutive years. Rows are years of the study with year *i* + 1 shown at the right side of the row. Columns are sites with site names and letters shown at the bottom of each column. The Tutakoke River area (A) includes sites 1 and 2, and the Kashunuk River area (B) includes sites 3 to 5 (Fig. 1). Letters at the bottom of the columns are movements between sites (e.g. AB is movement from the Tutakoke area to the Kashunuk area). Fidelity to sites (e.g. AA) is represented by solid bars.

TABLE 5. Survival probability (\hat{S}) of Brant for the two-year interval following banding at Tutakoke River, Alaska, 1987 to 1991. The Tutakoke River area includes brood-rearing sites 1 and 2, and the Kashunuk River area includes sites 3 to 5 (see Fig. 1).

Band- ing year	Tutakoke River area		Kashunuk River area	
	\hat{S}	SE	\hat{S}	SE
1987	0.391	0.052	0.129	0.048
1988	0.274	0.046	0.126	0.047
1989	0.385	0.045	0.303	0.060
1990	0.218	0.028	0.178	0.039
1991 ^a	0.049	0.011	0.016	0.008

^a Survival estimates for the 1991 cohort are the product of survival from 1991 to 1993 and capture probability in 1993.

1987 and 1991. We observed site- and year-specific variation in juvenile survival (i.e. survival from banding to two years old; Table 2). In the two-site analysis, the model with the lowest AIC value (model Ψ_i^s) constrained movements of adults and movements of individuals banded as goslings equal, but movement probability varied by both year and site (Table 4). In addition, the LRT between model Ψ_i^s and the model with age-specific movement probability ($\Psi_{ig}^s \Psi_{ia}^s$) failed to reject model Ψ_i^s ($X^2 = 14.1$, $df = 10$, $P = 0.167$). As noted in the two-site analysis for adults, we report parameter estimates from model $p_i^s S_a^s \Psi_i^s$. Juvenile survival probability for the two-year period following banding ranged from 0.126 (SE = 0.052) to 0.39 (SE = 0.047; Table 5). Movement probabilities were described in the section on two-site analysis above (Fig. 3).

Covariance between hatching date and brood-rearing site.—Between 1987 and 1993, we recaptured 518 adult females with known hatching dates. We observed no covariance between hatching date and brood-rearing site. Hatching dates varied among years ($F = 188.2$, $df = 6$ and 507, $P < 0.001$) but not among sites ($F = 1.25$, $df = 4$ and 507, $P = 0.289$), and the interaction between years and sites was not significant ($F = 1.23$, $df = 17$ and 490, $P = 0.233$).

DISCUSSION

Variation in brood-site fidelity.—Philopatry of female waterfowl to breeding areas and nesting sites has been well documented (Anderson et al. 1992). Female Brant are philopatric to breeding colonies (Lindberg 1996) and to nest sites

within colonies (Lindberg et al. 1995). Our results indicate that Brant exhibit fidelity to brood-rearing areas, but we observed significant variation in fidelity probability. Brant displayed high probabilities of fidelity to some sites (e.g. site 4, >0.73), but fidelity probabilities to other sites varied considerably (e.g. site 1, range 0.06 to 0.84). Although parameter estimates changed when we examined brood-site fidelity at a larger scale (i.e. two sites), this analysis also revealed significant variation in fidelity to brood-rearing sites.

Sources of the observed variation in site fidelity were not apparent. Fidelity probability was not age-specific. Effects of dispersal distance varied among sites and among years in magnitude and direction. We observed no difference in hatching dates between Brant that exhibited fidelity to brood-rearing sites and those that moved to new sites, and no variation in hatching dates among sites, suggesting that neither competition nor age were important in determining site fidelity.

Ecological advantages of fidelity to brood-rearing sites may include improved feeding efficiency, reduced aggression with conspecifics, and knowledge of predators. In areas with deteriorating habitat conditions, however, fidelity may be maladaptive (Levin et al. 1984). Growth, survival, and reproduction of Lesser Snow Geese was lower for individuals that were philopatric to traditional brood-rearing areas than for individuals that dispersed or established philopatry to a non-traditional brood-rearing area near Cape Churchill, Manitoba (Cooch et al. 1993, Rockwell et al. 1993). These authors attributed the fitness differences to variation between sites in forage quality and abundance. We lack measures of habitat quality for our sites, but we suggest that differences in forage quality and abundance may affect distribution patterns of Brant. However, comparing fitness of individuals philopatric to sites with poor forage conditions with individuals that dispersed to higher-quality sites is not a critical test of cost or benefits of philopatry. Additional studies that compare philopatric and dispersing individuals that occupy the same habitats (or habitats with similar forage characteristics) are needed to fully understand the possible costs or benefits of philopatry.

Although survival probability is only one component of fitness, the site-specific variation

in survival that we observed suggests that the distribution of Brant was not ideal free. Departures from the ideal free distribution were not caused by territorial behavior. Site fidelity and ecological advantages of this behavior may contribute to the observed deviation from the ideal free distribution (Nichols et al. 1983). Many factors (e.g. harvest, weather) may affect spatial variation in survival for the annual (adults) or two-year (juveniles) period for which survival was estimated. The site occupied in year $i + 1$ probably had little effect on survival because this site was occupied at the end of the survival interval. If segregation observed on brood-rearing areas was maintained over the survival interval, then variation in survival may reflect site-specific mortality during migration and winter. Because Brant from the Tutakoke colony use common migration corridors and wintering areas (Ward et al. 1997), factors affecting postfledging survival likely are homogeneous from different brood-rearing sites. Early growth affects survival and future fecundity of Brant goslings (Sedinger et al. 1995). Thus, spatial variation in growth of goslings may explain variation in survival probability among brood-rearing sites. The effect of brood-rearing habitat on subsequent condition of adult Brant is poorly described. Nonetheless, female geese are at their annual minimum body mass at the end of incubation (Raveling 1979), and brood rearing may be a critical period for subsequent survival of these individuals. We cannot, however, separate spatial variation in survival from a variation caused by site-specific emigration. Our sampling of brood-rearing areas did not include all sites used by Brant. If emigration from the brood-rearing sites we sampled was related to distance to sites not sampled (Barrowclough 1978), then we would expect lower survival probabilities, as a result of emigration, for Brant using areas near the edge of our sampling distribution. This pattern was not obvious in our estimates of survival. Therefore, we suggest that our estimates reflect true differences in survival among sites, rather than variation in emigration probability.

Our results are similar to previous studies of brood-site fidelity in geese. Studies at La Perouse Bay, Manitoba, suggest that Lesser Snow Geese are philopatric to brood-rearing sites (Cooke and Abraham 1980, Healy et al. 1980).

Cooch et al. (1993) observed that Lesser Snow Geese may disperse when habitat conditions deteriorate. Comparison of parameter estimates between our study and those for Lesser Snow Geese are tenuous because of differences in scale and estimation techniques. Estimates for Lesser Snow Geese represent the product of several parameters (e.g. detection and fidelity probability) and are based on an assumption of no annual or site-specific variation in capture and survival probability, which we observed for Brant. We suggest that researchers consider this variation in future studies.

Fidelity to natal sites.—We observed no age-specific difference in movement patterns. Comparison of our results with other studies is difficult because of differences in analysis techniques and spatial scale. Natal-site fidelity occurs in Lesser Snow Geese (Healy et al. 1980, Cooke and Abraham 1980), but as with brood-site fidelity, the pattern is variable. Larsson and Forslund (1991) determined natal-site fidelity of Barnacle Geese based on the percentage of observations occurring in one of two brood-rearing areas. As adults, about 88% of the Barnacle Goose families were observed at the natal site 75% of the time (Larsson and Forslund 1991). Larsson and Forslund concluded that social inheritance of brood-rearing areas, when spatial variation of habitat quality exists, may lead to genetic-environment covariance.

Patterns of fidelity to natal brood-rearing sites differed from those we observed for nest-site fidelity in Brant, where first-time breeders had a higher probability of dispersal from natal sites than did adults (Lindberg and Sedingler 1997). Natal-site fidelity to brood-rearing areas may indicate social inheritance of these sites (Larsson and Forslund 1992). Brant may be more likely to recognize brood-rearing areas because they spend more time at these foraging sites than at nest sites (Brant generally brood at the nest for <48 h) and because they fledge from brood-rearing areas. In addition, natal-site fidelity may be facilitated through nepotism (Anderson and Titman 1992), although little is known about social interactions during brood rearing (Mulder et al. 1995)

Movement within years.—Our sampling was limited to the period of brood rearing from 22 to 34 days following the peak of hatching. Therefore, our measure of brood-site fidelity represents a "snapshot" of the areas occupied

during the brood-rearing period. Brant goslings may exploit different areas pre- and post-capture, but analysis of radio-tagged females suggests that movements are limited following initial dispersal from the breeding area (P. Flint unpubl. data). Studies of Lesser Snow Geese and Barnacle Geese indicate that within-season movements among brood-rearing sites are uncommon (Healy et al. 1980, Larsson and Forslund 1992). Hughes et al. (1994), however, observed significant variation in the home-range size of 20 radio-tagged Greater Snow Geese (*Chen caerulescens atlantica*). They classified families as sedentary, shifters, and wanderers based on home-range size and patterns of habitat use. Clearly, additional detailed studies of movement patterns of geese during the entire brood-rearing period are needed.

Covariance between hatching date and brood-rearing sites.—Hatching dates of adult female Brant did not vary significantly among brood-rearing sites. Cooch et al. (1993) noted that hatching date and brood-rearing site tended to covary in Lesser Snow Geese at La Pérouse Bay, but we know of no other study that directly tested this relationship. Our results are consistent with previous studies of Brant that suggest that seasonal declines in growth of goslings are caused by a decline in factors affecting growth (e.g. habitat quality; Sedingler and Flint 1991). Our study does not, however, preclude the explanation of covariance between parent quality and hatching date as a mechanism for observed seasonal declines in growth (Price et al. 1988, Sedingler et al. 1997). Parent quality did not affect growth of Lesser Snow Geese (Cooch et al. 1991).

Our modeling techniques provide a useful approach to quantify movements of animals among habitats. We suggest that studies combining quantitative measures of site fidelity and habitat quality are needed to clearly identify the environmental factors that affect movement patterns of precocial young and their parents, and the costs or benefits associated with fidelity. Modeling movement patterns based on the theoretical framework of ideal free distributions, where animals select habitats based on realized suitability and fitness gains (Fretwell and Lucas 1970), should provide a means to critically test factors that affect use of brood-rearing habitats (Nichols 1996).

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