The Condor 99:25–38

ECOLOGICAL CONSEQUENCES OF NEST SITE FIDELITY IN BLACK BRANT[1]

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Abstract. Empirical tests of ecological advantages of site fidelity in birds are few because consequences of dispersal are rarely measured. We examined the relationship between dispersal distance between consecutive nesting attempts and age, nest success, reproductive performance, and spring environment for female Black Brant (*Branta bernicla nigricans*) nesting colonially at the Tutakoke River, Alaska, 1987–1993. We found little evidence of fidelity to natal sites. Young brant moved towards a peripheral area of the colony. Successfully breeding brant dispersed shorter distances than those failing to nest successfully. Brant that initiated nests early dispersed farther than brant that initiated nests late. Neither nest success nor initiation date in year $t + 1$ were related to dispersal distance (year t to year $t + 1$), but clutch size declined with dispersal distance. Although generally not significant, annual variation (interaction) in the relationship between dispersal distance and measures of reproductive performance (i.e., initiation date and clutch size) suggest that this relationship may be influenced by spring weather conditions. Evidence for the advantages of site fidelity in brant was equivocal. Dispersal distance explained little variation associated with reproductive performance. Variation in individual bird quality, environmental conditions, and demographic status may be more important determinants of breeding performance in brant than potential benefits of site fidelity.

Key words: Alaska, Black Brant, Branta bernicla nigricans, *dispersal, fidelity, natal fidelity.*

INTRODUCTION

Ecological advantages of site familiarity have been proposed as a mechanism explaining the evolution of philopatry (Lack 1954, Hinde 1956). Although fidelity to specific nest sites or nesting territories has been documented for a variety of avian species (Greenwood 1980, Anderson et al. 1992), studies of ecological advantages of site fidelity are few because consequences of movement are rarely measured (Greenwood 1987, but see Hepp and Kennamer 1992). Instead, research has focused on correlations between reproductive success and probability of return to a breeding area or fidelity to a nest site (Greenwood and Harvey 1982). If reproductive success is site specific (Blancher and Robertson 1985) and consistent among years, then birds that return to previously successful sites should be favored by natural selection (Gavin and Bollinger 1988). However, a direct assessment of factors important in the evolution of site fidelity would entail a comparison of reproductive performance for site faithful and dispersing individuals.

For female waterfowl, potential advantages of nest site fidelity resulting from site familiarity may include improved nest success, increased survival, improved feeding efficiency, and higher brood rearing success following hatch (Anderson et al. 1992). Although a number of waterfowl studies (e.g., Doty and Lee 1974, Majewski and Beszterda 1990, Hepp and Kennamer 1992) have demonstrated a correlation between nest success and probability of site fidelity, direct evidence for advantages of fidelity is generally lacking (Anderson et al. 1992). In one of the most extensive studies of site fidelity in waterfowl, Dow and Fredga (1983) observed earlier nesting, larger clutch sizes, and increased nest success for female Common Goldeneyes (*Bucephala clangula*) that exhibited fidelity to specific nest boxes. Gauthier (1990) reported similar findings for female Buffleheads (*Bucephala albeola*). Other studies detected no advantage of site fidelity (Hepp et al. 1989) or poorer reproductive performance (Hik 1986) by site-faithful females. More rig-

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[1] Received 3 June 1996. Accepted 30 October 1996.

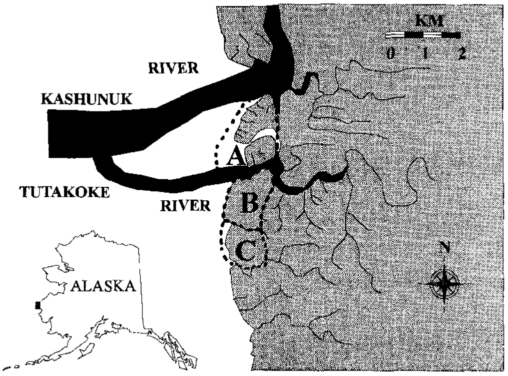

FIGURE 1. Location of the Tutakoke River Black Brant colony on the Yukon-Kuskokwim River Delta, Alaska. Tidal sloughs are shown with thin black lines and strata boundaries are shown with dashed lines.

orous tests of potential advantages of site fidelity in waterfowl are therefore needed (Anderson et al. 1992). Furthermore, studies of nest-site fidelity in waterfowl are generally limited to cavity nesting species (Dow and Fredga 1983, Gauthier 1990, Hepp and Kennamer 1992) or species with well-defined nest structures (Doty and Lee 1974, Majewski and Beszterda 1990). Therefore, most studies have regarded fidelity as a discrete variable (i.e., faithful or not faithful to a specific nest site). Magnitude of dispersal effects, however, may increase as dispersal distance increases and familiarity with a new nesting location declines.

Our goals were to investigate ecological advantages of nest site fidelity in Black Brant, *Branta bernicla nigricans* (hereafter brant) breeding at the Tutakoke River, Alaska. In contrast to most previous studies, we tested potential advantages of site fidelity by examining the relationship between dispersal distance and breeding parameters. We therefore had a direct assessment of the relationship between breeding performance and declining site familiarity. As in previous studies, we also examined factors affecting probability of fidelity. Specifically, we studied the relationship between demographic (age), reproductive (egg loss, nest initiation dates, and clutch size), and environmental (spring phenology) parameters and future fidelity to nest sites. We used capture-recapture analysis to estimate probability of fidelity to natal sites.

STUDY AREA

Brant are small geese (1.0–1.5 kg) that nest in coastal areas of Alaska, eastern Russia, and western Arctic Canada (Sedinger et al. 1993). Our study area was the Tutakoke River colony (61°15′N, 165°37′W) on the Yukon-Kuskokwim River Delta of western Alaska (Fig. 1). Since 1986, the number of brant nesting at Tutakoke has increased from approximately 1,100 pairs (Sedinger et al. 1993) to 6,000 pairs in 1992 (Anthony et al. 1995). The colony currently occupies approximately 6 km of coast bounded by the Kashunuk River to the north and diminishing densities of nesting brant to the south. Brant nest predominantly within 1 km of coastal mudflats and the colony is intersected by numerous tidal sloughs. The portion of the colony north of the Tutakoke River is characterized by islands of vegetation (largely *Carex ramenskii* and *Elymus arenarius*) surrounded by tidal mudflats, whereas south of the Tutakoke, meadows of predominantly *C. ramenskii* are interspersed with numerous ponds and lakes. Habitat characteristics of this region are described in detail by Kincheloe and Stehn (1991).

For estimates of age-related fidelity and dispersal we divided the colony into geographic strata. In earlier analyses (Lindberg et al. 1995) we defined four strata bounded by tidal sloughs and rivers. We maintained these definitions of strata for age-related estimates of fidelity. We did not mark (web tag) goslings in the southernmost portion of the Tutakoke colony (stratum D) and we therefore restricted our analysis to three strata (A, B, and C; Fig. 1). Stratum C was expanded slightly to include the southern limit of our web tagging.

METHODS

BANDING AND NEST SEARCHING

Since 1986, we captured brant at the Tutakoke colony during the adult regimal molt (July) and marked both goslings and adults with individually coded 2.5 cm high tarsal tags (Sedinger et al. 1995). We observed marked female brant during subsequent summers (May–July) and mapped their nest locations with ARC/INFO (Lindberg et al. 1995). We located nests of marked brant by flushing females from nests and reading their tags with binoculars or 15–60× spotting scopes. During egg laying and incubation (mid-May to mid-June) we located nests by searching 50 m radius plots (n = 34 to 49). Plots were located in a stratified random design throughout the breeding colony. We searched each plot every fourth day until egg laying was complete. Nests of marked females not on plots were located opportunistically while traveling between plots. During hatch (mid- to late-June), when females are more tenacious to nest sites, we intensified our search effort by attempting to visit all nests in the colony at least every other day.

AGE RELATED MOVEMENT PROBABILITY

We used multistate modeling (Brownie et al. 1993) and program MSSURVIV (Hines 1994) to obtain estimates of fidelity (Ψ_i^{rr}), dispersal (Ψ_i^{rs}; hereafter collectively referred to as movement probability [Ψ]), survival (S_i^r), and detection (p_i^s) probabilities. Multistate modeling can be used to estimate demographic parameters for populations stratified by location or other state variables (Brownie et al. 1993, Nichols and Kendall 1995). This approach was previously used to estimate site fidelity and philopatry of birds to wintering (Hestbeck et al. 1991) and breeding sites (Lindberg et al. 1995, Spendelow et al. 1995). Program MSSURVIV is a modified version of program SURVIV (White 1983), which produces maximum likelihood estimates of parameters based on capture histories of individuals. Capture histories in MSSURVIV, however, include not only time of capture for marked individuals, but also the state or stratum of capture (Brownie et al. 1993). For example, the capture history for a marked brant observed nesting in stratum C at age i, not seen at age $i + 1$, and observed nesting in stratum A at age $i + 2$, is C0A. Fidelity probability was defined as the probability of being in stratum r at age $i + 1$ for brant that were in stratum r at age i and survived and returned to the Tutakoke colony at age $i + 1$. Dispersal probability was defined as the probability of being in stratum s at age $i + 1$ for brant that were in stratum r at age i and survived and returned to the Tutakoke colony at age $i + 1$. Survival probability was defined as the probability of being alive and returning to the Tutakoke colony at age $i + 1$ for brant alive and in stratum r at age i, and detection probability was defined as the probability of detection at age i for a bird in stratum s. Although we included age- and stratum-specificity in these parameter estimates, we were unable to consider year-specificity because we could not obtain meaningful estimates of all parameters with our sample sizes (Table 1). If age, strata, and year effects were all considered simultaneously, 171 movement probabilities would be possible. By limiting our estimates to age- and strata-specificity, we reduced the maximum number of movement probabilities to 45 (Table 1). Although elimination of year-specificity reduced parameter space, this assumption also affected our estimates of survival. Our estimates of survival probability were lower than true survival because of permanent emigration and right censoring of year cohorts. For example, estimates of survival between ages 4 and 5 reflect mortality, permanent emigration, and censoring of the 1989, 1990, and 1991 cohorts (Table 1).

TABLE 1. Sampling protocol used to estimate age specific movement probabilities of Black Brant nesting at the Tutakoke River colony, Alaska, 1987–1993. For each cohort, 0 indicates that the cohort was not used to estimate a parameter, whereas cells filled with a parameter show what parameter was estimated.

Cohort	Age 0–2	 2–3	 3–4	 4–5	 5–6
1986	0	Ψ_2	Ψ_3	Ψ_4	Ψ_5
1987	Ψ_1	Ψ_2	Ψ_3	Ψ_4	Ψ_5
1988	Ψ_1	Ψ_2	Ψ_3	Ψ_4	0
1989	Ψ_1	Ψ_2	Ψ_3	0	0
1990	Ψ_1	Ψ_2	0	0	0
1991	Ψ_1	0	0	0	0

We used a step-down approach to obtain parameter estimates and test specific hypotheses (Lebreton et al. 1992). With this approach we first attempted to reduce the number of parameters in our models by constraining detection and survival probability equal over ages (p^s, S^r), strata (p_i, S_i), or both (p, S), while movement probabilities remained both age- and stratum-specific. This approach reduced variance in estimates of the movement probabilities and increased power for hypothesis tests about fidelity and dispersal (Lebreton et al. 1992). We considered 16 models that constrained detection and survival probabilities over ages and strata and selected the most parsimonious model that fit our data, based on the Akaike information criteria (AIC, Akaike 1973), likelihood ratio tests (LRT) between nested models, and χ^2 goodness-of-fit tests (Brownie et al. 1993). After selecting this model, we maintained model constraints on detection and survival probabilities and considered models that constrained movement probabilities and tested hypotheses regarding age and strata effects on movements.

Our sample of brant for estimates of natal movement was limited to brant web tagged in the nest as goslings (known natal site) that were subsequently captured during banding and marked with tarsal tags. These birds were tarsal tagged as goslings or during the next summer because we have not observed brant nesting at Tutakoke until 2 years of age. Therefore, our estimates of natal movement were from natal nest sites to nest sites at age 2. We obtained a tagged sample of brant ages 2 to 5 from the above sample, by recapturing previously web tagged goslings >1 year old, or by tarsal tagging brant that were identified as 1-year-old birds based on plumage characteristics (Jones 1964). Our sample of known-age brant included birds banded between 1986 and 1991 that were subsequently observed nesting at Tutakoke between 1987 and 1993.

NEST SUCCESS AND MOVEMENT PATTERNS

Between 1988 and 1993 we digitized and calculated distances between nest sites of marked female brant nesting at Tutakoke River using ARC/INFO (Lindberg et al. 1995). We only estimated distances between sites for females observed nesting in consecutive years. Because some females were observed nesting in more than two consecutive years we randomly selected one pair of observations for these females to avoid pseudoreplication in subsequent analysis.

We examined the relationship between nest fate in year *t* and dispersal distance between year *t* and year *t* + 1 by comparing the distribution of dispersal distances for brant whose nests suffered no detectable reduction in clutch size (SUC) and brant whose nests suffered partial or complete loss of eggs (UNSUC). We determined fate of nests by labeling eggs with permanent markers when nests were initially discovered and recording loss of eggs during subsequent visits (Flint and Sedinger 1992). Potential causes of egg loss included predation, nest abandonment, flooding, and dead or addled eggs. Because brant classified as SUC included some nests where we failed to detect an event that reduced clutch size, our test of differences in dispersal distances between SUC and UNSUC brant was conservative. We tested for among-year variation in dispersal distances within SUC and UNSUC groups with Kruskal-Wallis tests (PROC NPAR1WAY, SAS Institute 1990). We tested the hypothesis that median dispersal distance for SUC brant was different from median dispersal distance of UNSUC brant with randomization tests (Manly 1991).

To examine the relationship between dispersal distance and nest fate, we compared nest fate in year *t* + 1 and dispersal distance between year *t* and year *t* + 1. Nest fate was defined as above (i.e., SUC and UNSUC). We used Kruskal-Wallis tests to examine among-year differences in dispersal distances and randomization tests for differences in median dispersal distances (year *t* to year *t* + 1) for SUC and UNSUC brant in year *t* + 1. We could not specifically test for age effects or an interaction between age and nest success in either of the analyses described above because few brant in our sample were of known age. We minimized the effects of age by limiting our samples to females >2 years old in year *t*.

REPRODUCTIVE PERFORMANCE AND DISPERSAL PATTERNS

Previous studies of site fidelity have used a variety of measures of reproduction to examine the relationship between reproductive performance and site fidelity. Clutch size is a common measure of reproductive performance in birds, so we examined the relationship between dispersal distance and clutch size. We also examined the relationship between initiation date and dispersal distance, because in brant, both clutch size (Flint and Sedinger 1992) and subsequent growth and development of goslings (Sedinger and Flint 1991) are correlated with initiation date. If poor reproductive performance results in greater dispersal distance (year *t* to year *t* + 1), then we would expect brant with later initiation dates and smaller clutches in year *t* to disperse farther. Conversely, if greater dispersal distance reduces site familiarity, and therefore reproductive performance, then brant dispersing farther (year *t* to year *t* + 1) should have later initiation dates and smaller clutches in year *t* + 1.

Initiation date was defined as the day the first egg was laid, and for nests found during laying was calculated by assuming 1 egg was laid each day, or by backdating from hatch date for nests found after laying. Clutch size was defined as the maximum number of eggs observed in a nest. Our sample of clutches included nests found during laying and incubation. We eliminated nests with >6 eggs because these clutches may result from parasitic laying (Flint and Sedinger 1992). To avoid pseudoreplication, we again randomly selected one pair of observations for females that were observed more than once. We reduced effects of age by limiting our sample to females >2 years of age in year *t*. We removed the effects of nest fate on dispersal distance by excluding from our sample females that were UNSUC nesters in year *t*.

We used ANCOVA (PROC GLM, SAS Institute 1990) to test for a relationship between reproductive performance and dispersal distance. Dispersal distance between year t and year $t + 1$ was the dependent variable, year t and clutch size in year t were fixed factors, and initiation date in year t was the covariate in the analysis that examined effects of reproductive performance on dispersal distance. In the ANCOVAs comparing dispersal distance and resulting reproductive performance, year $t + 1$ was the fixed factor, dispersal distance between year t and year $t + 1$ was the covariate, and either initiation date in year $t + 1$ or clutch size in year $t + 1$ was the dependent variable. Initiation date in year $t + 1$ was included as a covariate in the latter model.

Relationship between reproductive performance and dispersal distance was complicated by variation in spring weather. Timing of spring snowmelt affects initiation dates and clutch size (Lindberg et al., unpubl. data) and also may be correlated with dispersal distance (Abraham 1980). Date that the study area was 100% snow free ranged from 17 May to 2 June between 1988 and 1993. We classified 1989 and 1992, which were 100% snow free between 28 May and 2 June, as late years. All remaining years (1988, 1990, 1991, and 1993) were considered early because 100% snowmelt occurred between 17 May and 21 May in these years. We investigated effects of spring snowmelt on the relationship between dispersal distance and reproductive performance of brant by including interaction terms in the ANCOVA models described above. Specifically, we tested if the relationship between initiation date and dispersal distance (initiation date × year interaction), clutch size and dispersal distance (clutch size × year), and dispersal distance and reproductive performance (dispersal distance × year) varied by year.

REPEATABILITY

Repeatability among individuals provides a maximum estimate of heritability by estimating the amount of variance in a character resulting from among-, rather than within-, individual variation (Falconer 1989). We obtained estimates of among-individual repeatability (Lessels and Boag 1987) of dispersal distance for adult female brant nesting at Tutakoke using individuals for which we had measured distances between consecutive nest attempts on at least two occasions between 1988 and 1993. We estimated standard error of repeatability following Becker (1984).

RESULTS

AGE RELATED MOVEMENT PROBABILITY

From 1987–1993 we recorded nesting strata of 551 marked females of known age, totaling 782 observations. We determined natal nesting strata of 371 of these females. Dispersal distance averaged 1,316 m ($n = 11$, SE = 320 m) between natal nest sites and the nest site first detected when these birds were 2 or 3 years old. This sample was small because not all nest sites were mapped even though nesting strata were recorded.

Of the 16 MSSURVIV models that constrained capture and survival probability over ages and strata, the model with the lowest AIC value (277) was a model with age-specific capture and survival probabilities ($p_iS_i\Psi_i^{rs}$). Therefore, we adopted these model constraints and tested for age and stratum effects on movement probability.

With MSSURVIV only $n - 1$ of the movement parameters per strata are estimated directly (Brownie et al. 1993). Therefore, one movement probability per strata is estimated by subtraction. For our analysis, movements to stratum A (i.e., Ψ_i^{AA} Ψ_i^{BA}, and Ψ_i^{CA}) were obtained by subtraction. We tested if all movement probabilities were equally probable by constraining all directly estimated movement probabilities to 0.33 (model $p_iS_i\Psi_{0.33}$). Based on AIC values and the LRT between this model (model $p_iS_i\Psi_{0.33}$) and the more general model with age and stratum specific movement prob-

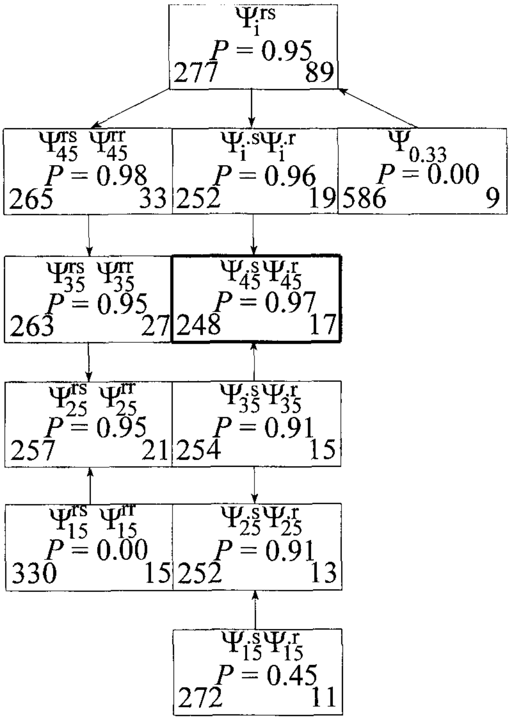

FIGURE 2. Diagram of hierarchy used to select model for estimates of age-related movement probabilities of Black Brant. Model names are shown at top of box, P-values for χ^2 goodness-of-fit tests in the center of the box, AIC values in the lower left corner, and number of parameters in the model in the lower right corner. Arrows between boxes point to model selected based on likelihood ratio tests between nested models. Bolded box highlights model selected based on AIC and LRT.

abilities ($p_iS_i\Psi_i^{rs}$), we rejected ($\chi^2_{30} = 369.5$, $P < 0.001$) the hypothesis of equally probable movement among strata (Fig. 2). We therefore constrained fidelity (Ψ_i^{rr}) and dispersal (Ψ_i^{rs}) probabilities separately for subsequent tests.

We considered two groups of models (Fig. 2); for the first group, we removed strata variation in fidelity and dispersal probabilities, and then progressively removed age effects within both these parameters by equating 4- and 5-year-olds equal (model $\Psi_{45}^{\cdot s}\Psi_{45}^{\cdot r}$); then 3-, 4- , and 5-year-olds equal (model $\Psi_{35}^{\cdot s}\Psi_{35}^{\cdot r}$), until all age classes were equal (model $\Psi_{15}^{\cdot s}\Psi_{15}^{\cdot r}$). For the second group of models we maintained strata specificity in fidelity and dispersal probabilities and again progressively removed age effects (models $\Psi_{45}^{rs}\Psi_{45}^{rr}$ through $\Psi_{15}^{rs}\Psi_{15}^{rr}$).

Based on AIC and LRT, models that maintained strata-specific movement probabilities were selected over the more general model ($p_iS_i\Psi_i^{rs}$); however, these models generally had AIC values higher than the group of models that removed strata specificity (Fig. 2). Model $\Psi_{45}^{\cdot s}\Psi_{45}^{\cdot r}$ had the lowest AIC value (248) in the group without strata specificity and also was selected over other models in this group based on LRT. We therefore concluded that neither fidelity nor dispersal probabilities were strata-specific and that both parameters were equal for 4- and 5-year-old brant.

Finally, we tested if all natal movements were equally probable by comparing model $\Psi_{45}^{\cdot s}\Psi_{45}^{\cdot r}$ to a model ($\Psi_{45}^{\cdot s}N\Psi_{45}^{\cdot r}N$) with identical constraints except that all natal movement probabilities were constrained equal to 0.33. The AIC for model $\Psi_{45}^{\cdot s}N\Psi_{45}^{\cdot r}N$ was 255 and the LRT between models rejected ($\chi^2_2 = 10.9$, $P = 0.004$) the hypothesis of equally probable natal movements. We therefore used model $\Psi_{45}^{\cdot s}\Psi_{45}^{\cdot r}$ to obtain parameter estimates.

When we examined parameter estimates under model $\Psi_{45}^{\cdot s}\Psi_{45}^{\cdot r}$, we noticed fidelity probability to stratum A was higher than fidelity probabilities for strata B and C, and both dispersal from stratum B to A and stratum C to A were higher than all remaining dispersal probabilities. We were concerned that these differences were an artifact of our model design because all fidelity and dispersal probabilities were never directly compared (i.e., some were obtained by subtraction). Therefore, we maintained model $\Psi_{45}^{\cdot s}\Psi_{45}^{\cdot r}$ constraints, but designed the model (i.e., we changed the flag to 0, Hines 1994) so all fidelity probabilities were obtained by subtraction and all dispersal probabilities were directly estimated (model $\Psi_{45}^{\cdot s}0\Psi_{45}^{\cdot r}0$). The AIC for model $\Psi_{45}^{\cdot s}0\Psi_{45}^{\cdot r}0$ was 254 and we again rejected the hypothesis that all dispersal probabilities were equal. We therefore concluded that fidelity to stratum A was higher than to strata B or C, and dispersal from strata B and C to stratum A was higher than all other dispersal probabilities.

Under model $\Psi_{45}^{\cdot s}\Psi_{45}^{\cdot r}$, fidelity probability increased with age for all strata and was equal to 1.00 ($\widehat{SE} < 0.13$) for 4- and 5-year-old brant (Fig. 3). Dispersal probabilities were directional (i.e., towards stratum A) before stabilizing at age 4. Fidelity probability to natal strata ranged from 0.72 ($\widehat{SE} = 0.10$) for stratum A to 0.35 ($\widehat{SE} = 0.12$) for strata B and C. Detection probability in-

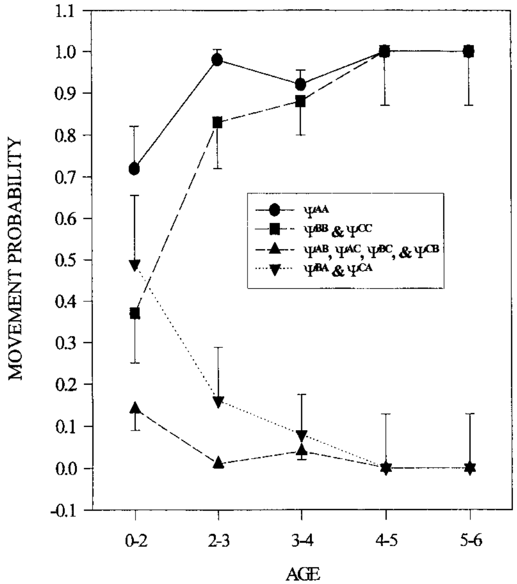

FIGURE 3. Estimates of age-related fidelity (Ψ^{rr}) and dispersal (Ψ^{rs}) probabilities among strata (A, B, and C) for Black Brant breeding at Tutakoke River, Alaska, 1987–1993. Error bars represent 1 standard error.

creased from 0.27 ($\widehat{SE}$ = 0.07) for 2-year-olds to 0.64 ($\widehat{SE}$ = 0.09) for 5-year-old brant. Survival probability from 0 to 2-years-old was 0.14 ($\widehat{SE}$ = 0.02) and survival increased to 0.77 ($\widehat{SE}$ = 0.07) for 2-year-old brant. Survival probability declined (e.g., $\hat{S}_i = 0.63$, $\widehat{SE}$ = 0.09, for ages 4 to 5) with age as cohorts were progressively removed from the sampling design (Table 1).

NESTING SUCCESS AND MOVEMENT PATTERNS

As previously reported (Lindberg et al. 1995), distribution of dispersal distances was highly skewed (Figs. 4 and 5). Ranks of dispersal distances (year t to year $t + 1$) differed among years for brant that were SUC ($\chi^2_4 = 9.35$, $P = 0.05$), but not for brant that were UNSUC ($\chi^2_3 = 0.33$, $P = 0.95$) in year t. We therefore pooled data across years for subsequent analysis. Brant that were UNSUC in year t dispersed farther ($P = 0.03$, $n = 5{,}000$ replicates) between year t and year $t + 1$ than brant that were SUC in year t (Fig. 4). Median dispersal distance (year t to year $t + 1$) was 110 m (n = 268) and 171 m (n = 74) for SUC and UNSUC brant, respectively.

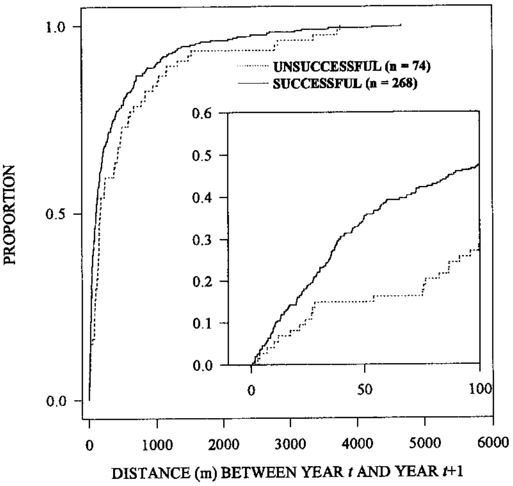

FIGURE 4. Distribution of dispersal distances (year t to year $t + 1$) between consecutive nesting attempts for successful and unsuccessful Black Brant (in year t) at the Tutakoke River, Alaska, 1988–1993. Successful nests were those with no detectable loss of eggs and unsuccessful nests had at least 1 egg that did not hatch. Insert shows distribution of dispersal distances for 0 to 100 m.

We failed to observe annual variation in ranks of dispersal distances between year t and year $t + 1$ for brant that were SUC ($\chi^2_4 = 9.21$, $P = 0.06$) or UNSUC ($\chi^2_4 = 5.59$, $P = 0.23$) in year $t + 1$. Data were therefore pooled across years. Nest fate (year $t + 1$) was not related to

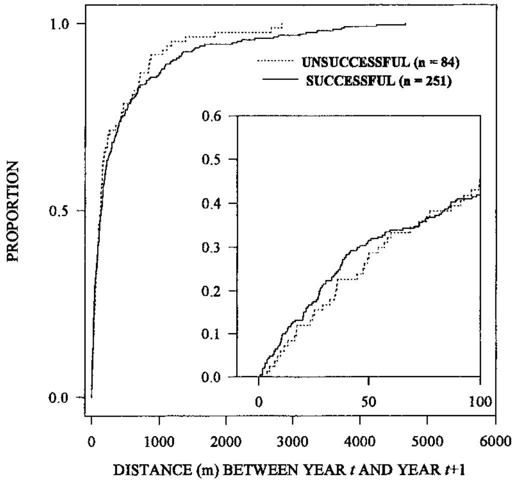

FIGURE 5. Distribution of dispersal distances (year t to year $t + 1$) between consecutive nesting attempts for successful and unsuccessful (year $t + 1$) Black Brant at the Tutakoke River, Alaska, 1988–1993. Successful nests were those with no detectable loss of eggs and unsuccessful nests had at least 1 egg that did not hatch. Insert shows distribution of dispersal distances for 0 to 100 m.

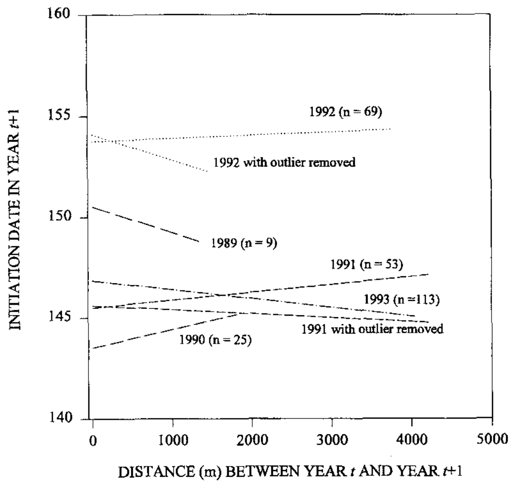

FIGURE 6. Relationship between dispersal distance (year t to year $t + 1$) and nest initiation date for Black Brant nesting at Tutakoke River, Alaska, 1989–1993.

dispersal distance (year t to year $t + 1$) because we failed to detect a difference ($P = 0.65$, $n = 5{,}000$ replicates) between median dispersal distance (year t to year $t + 1$) for SUC (139 m, $n = 251$) and UNSUC (130 m, $n = 84$) brant (Fig. 5).

REPRODUCTIVE PERFORMANCE AND MOVEMENT PATTERNS

Effects of reproductive performance on dispersal distance. Examination of residual and normal scores plots from analysis of effects of initiation date and clutch size in year t on dispersal distance between year t and year $t + 1$ revealed that dispersal distances were skewed and that error variance was not constant (heteroscedasticity). We therefore performed a natural log transformation on dispersal distances, which stabilized error variance and improved normality, and then conducted analyses on transformed distances.

We found no variation ($F_{4,189} = 1.03$, $P = 0.40$) in ln(dispersal distance) among years. Neither clutch size ($F_{4,189} = 0.13$, $P = 0.97$) nor initiation date ($F_{4,189} = 0.44$, $P = 0.51$) in year t was significantly related to ln(dispersal distance) between year t and year $t + 1$, and these relationships did not vary among years (year × initiation date interaction, $F_{4,189} = 0.98$, $P = 0.42$; year × clutch size interaction, $F_{11,189} = 1.67$, $P = 0.08$). After the interaction terms were removed from the model, year ($F_{4,204} = 0.56$, $P = 0.69$) and clutch size effects ($F_{4,204} = 0.29$, $P = 0.88$) remained nonsignificant, but we observed a significant ($F_{1,204} = 4.94$, $P = 0.03$) negative relationship between initiation date in year t and ln(dispersal distance) between year t and year $t + 1$.

Effects of dispersal distance on reproductive performance. Although initiation dates varied among years ($F_{4,259} = 98.9$, $P < 0.001$), we found no relationship ($F_{1,259} = 0.02$, $P = 0.88$) between dispersal distance (year t to year $t + 1$) and initiation date in year $t + 1$, and no significant ($F_{4,259} = 1.29$, $P = 0.27$) interaction in the full ANCOVA model (Fig. 6). These results were largely unchanged after the interaction term was removed (year effect $F_{4,263} = 133.5$, $P < 0.001$; distance effect $F_{1,263} = 0.03$, $P = 0.87$). However, analysis of influential points using Cook's distance measure revealed one observation in both 1991 and 1992 that exceeded the 50th percentile of the corresponding F distribution (Neter et al. 1985). These observations are not surprising considering the highly leptokurtic distribution of dispersal distances. Therefore, we performed the ANCOVA after removing these points. Again we found significant ($F_{4,257} = 93.18$, $P < 0.001$) variation in initiation dates among years. Both distance ($F_{1,257} = 1.26$, $P = 0.26$) and interaction ($F_{4,257} = 0.94$, $P = 0.44$) effects remained nonsignificant (Fig. 6).

Clutch size in year $t + 1$ varied significantly ($F_{4,241} = 2.88$, $P = 0.02$) among years, and clutch size declined with dispersal distance (year t to year $t + 1$; $F_{1,241} = 3.96$, $P = 0.05$) and initiation date (year $t + 1$; $F_{1,241} = 13.6$, $P < 0.001$; Table 2). We found no significant ($F_{4,241} = 1.26$, $P = 0.29$) interaction between dispersal distance and year. The interaction between initiation date and year was significant ($F_{4,241} = 2.87$, $P = 0.02$).

Effects of spring breakup patterns. Although only one interaction term was significant in models describing the relationship between reproductive performance and dispersal distance, we observed two trends in reproductive performance related to spring phenology. The negative relationship between dispersal distance and initiation date (year $t + 1$) was strongest in late years (1989 and 1992, Fig. 6). That is, brant nesting relatively early in late years generally had dispersed farther from nests in the preced-

TABLE 2. Regression parameters for the relationship between clutch size in year $t + 1$, initiation date in year $t + 1$, and dispersal distance between year t and year $t + 1$.

Year	β_{ID}[a]	SE(β_{ID})	β_{DD}[b]	SE(β_{DD})	n
1989	−0.3548	0.4134	−0.00122	0.0009	9
1990	−0.1996	0.0936	0.00003	0.0004	25
1991	−0.0864	0.0302	−0.00003	0.0001	51
1992	−0.1693	0.0537	−0.00023	0.0002	64
1993	−0.2429	0.0331	0.00001	0.0001	107

[a] Estimated slope of relationship between clutch size and initiation date.

[b] Estimated slope of relationship between clutch size and dispersal distance.

ing year. Conversely, declines in clutch size (year $t + 1$) with increasing dispersal distance were more prevalent in late years (Table 2).

REPEATABILITY

Between 1988 and 1993 we measured distance between consecutive nest attempts on more than one occasion for 104 females totaling 242 measured distances. Estimated repeatability of dispersal distance was 0.47 (SE = 0.07) (Table 3). Repeatability was significantly ($P < 0.05$) different from 0.

DISCUSSION

AGE-RELATED MOVEMENT PROBABILITY

Dispersal from natal sites was strongly directional for brant females that returned to the Tutakoke River colony. Goslings hatched in all three strata were more likely to nest in stratum A as 2-year-olds than any other strata. Based on the social behavior of brant we anticipated a low probability of fidelity to natal nest sites. Precocial young are brooded at the nest for a maximum of 48 hr before departure to brood rearing areas (Afton and Paulis 1992). During brood rearing, mixing of goslings from different families is common (Flint et al. 1995) and goslings may therefore associate with nonbiological parents before fledging. Unlike many goose species which maintain family integrity until return to the breeding grounds the following summer (Owen 1980), family disintegration has been observed in brant as early as fall staging (Jones and Jones 1966). Brant goslings therefore have little opportunity for site recognition. Finally, competition for nest sites, which results from colonial nesting (Welsh 1988) and earlier nesting by older birds (Finney and Cooke 1978, Flint and Sedinger 1992), may force younger birds to initially nest in peripheral areas of the colony (Kharitonov and Siegel-Causey 1988).

Although a number of studies have estimated return rates of female waterfowl to natal breeding areas (Rohwer and Anderson 1988, Anderson et al. 1992), few studies have investigated settlement pattern of females relative to natal nest sites. Based on 17 individuals that returned to their study area, Dow and Fredga (1983) suggested that female Common Goldeneyes nested in proximity to natal nest boxes. Coleman and Minton (1979) observed that female Mute Swans (*Cygnus olor*) generally breed within 5 km of their natal nest site, and Lessels (1985) suggested that female Canada Geese (*Branta canadensis*) breed in areas where they were banded as goslings. Hepp et al. (1989) reported that female Wood Ducks (*Aix sponsa*) generally dispersed short distances from natal wetlands. Although most non-waterfowl species exhibit male-biased philopatry to breeding areas, those females that do return tend to nest in proximity to natal sites (Greenwood 1980, Greenwood and Harvey 1982).

Some colonial nesting seabirds (Kharitonov and Siegel-Causey 1988) attempt to establish territories in the center of the colony in later breeding attempts. In contrast, we observed an increase nest-site fidelity with age indicating that brant tend to breed in the same area following initial nesting. Lesser Snow Geese (*Chen caerulescens caerulescens*) nesting at La Perouse Bay, Manitoba exhibited a similar pattern of site fidelity (Cooke et al. 1983). Cooke

TABLE 3. ANOVA table values used to estimate repeatability of dispersal distances for adult female Black Brant nesting at Tutakoke River, Alaska from 1988 to 1993.

Source	df	SS	MS	F	Pr > F
Among Individuals	103	80829800	784755	3.06	0.0001
Within Individuals	138	35436469	256786		
Total	241	116266269			

et al. (1983) further demonstrated that Lesser Snow Geese exhibit a cohort settlement pattern in which geese of similar age nest in proximity to one another. The strong directional movements we observed over 5 years suggest the potential for cohort affiliations in brant. We observed little evidence that these cohorts associated with natal areas.

In 1992 and 1993, nest densities in stratum A exceeded densities in all other strata. Natal movement therefore altered the nesting distribution of brant at Tutakoke as stratum A was nearly vacant in 1985. We expect natal dispersal patterns for future recruits will change if nest densities and competition for available nest sites continues to increase in stratum A. Our results indicate that natal dispersal is a mechanism for colony expansion in brant. During the 1960's the Tutakoke colony ranged approximately 5 km further north along the banks of the Kashunuk River (Shepard 1964, Sedinger et al. 1993). We suspect that these areas may be reoccupied if current levels of recruitment are maintained and suitable nesting habitat exists. Alternatively, nest densities in stratum C of the Tutakoke colony have continually declined since the current study was initiated and future recruits may reoccupy these areas as densities decline as a result of mortality in older birds.

Dispersal from natal sites has been proposed as a mechanism for inbreeding avoidance (Greenwood 1987). Even if female brant nested in close proximity to natal sites, inbreeding would still be unlikely. Black brant, like most waterfowl species, exhibit a pattern of male-biased dispersal from breeding areas (Anderson et al. 1992), and pair formation generally occurs on wintering grounds (Rohwer and Anderson 1988, McKinney 1992).

DOES NEST FATE OR REPRODUCTIVE PERFORMANCE AFFECT SITE FIDELITY?

We observed an increase in dispersal distance (year *t* to year *t* + 1) for female brant that experienced a reduction in clutch size (i.e., that were UNSUC) in year *t*. As described in other studies of waterfowl (Doty and Lee 1974, Dow and Fredga 1983, Gauthier 1990, Lokemoen et al. 1990, Majewski and Beszterda 1990, Hepp and Kennamer 1992) and non-waterfowl species (Greenwood et al. 1979, Harvey et al. 1979, Burger 1982, Newton and Marquiss 1982, Drilling and Thompson 1988, Gavin and Bollinger 1988), nest fate was an important determinant of future site fidelity.

Dow and Fredga (1983) suggested that increased dispersal distance by unsuccessful nesters is an adaptive strategy to avoid repeated nest depredation by predators with established territories. Burger (1982) demonstrated that Black Skimmers (*Rynchops niger*) were more likely to abandon colonies destroyed by predators than colonies destroyed by flooding. Similarly, Gavin and Bollinger (1988) suggested that nest failure resulting from predation was the most important factor for predicting probability of fidelity for Bobolinks (*Dolichonyx oryzivorus*). During our study, Arctic foxes (*Alopex lagopus*), the major nest predator of brant on our study area, were removed and fox predation was minimal compared to years immediately preceding our study (Anthony et al. 1991). Of the 74 nests classified as UNSUC, 76% ($n = 56$) were identified based exclusively on the presence of dead or addled eggs in the nests. Only 13 nests (18%) showed evidence of predation by Arctic foxes, Glaucous Gulls (*Larus hyperboreus*), or flooding, and 5 nests experienced total loss of the clutch. Predation therefore is not the only form of nest failure related to movement patterns of brant. Small sample sizes, however, precluded testing whether dispersal distances would be greater for nests destroyed by predators compared to losses from other factors.

Brant that initiated nests earlier had greater dispersal distances, but we found no relationship between clutch size and dispersal distance. This result was not expected because brant that nest early lay larger clutches (Flint and Sedinger 1992) and produce larger goslings that grow faster (Sedinger and Flint 1991) than brant that initiate nesting later. In addition, other studies (Harvey et al. 1979, Blancher and Robertson 1985, Drilling and Thompson 1988, Gavin and Bollinger 1988) indicate that higher reproductive performance at a nest site results in lower dispersal probability. Why then, would brant disperse from nest sites that apparently afford early initiation dates? This pattern might be explained by lower nest success for brant nesting early, as was observed for Barnacle Geese (*Branta leucopsis*; Prop and de Vries 1993), but we restricted our sample for analysis of the relationship between initiation date and dispersal distance to nests with no detectable loss of eggs.

We also would expect a decline in dispersal distance with later initiation date if younger brant nested earlier. Two-year-old brant nest later than older brant (Flint and Sedinger 1992) and we reduced age-related variation in our analysis by restricting our sample to females >2 years old in year *t*.

Earlier analysis (Lindberg et al. 1995) indicated that brant moving >200 m from a previous nest site had a lower probability of remaining at the new nest site than those individuals that remained within 200 m of their previous nest site. We suspect that brant may disperse from nest sites to achieve early initiation dates, particularly in late years (see below). Hence, greater dispersal distance by brant nesting earlier may reflect movement from new nest sites or return to previous nest sites.

IS SITE FIDELITY ADVANTAGEOUS?

We found no evidence that dispersal distance influenced probability of egg loss (Fig. 5). Our findings are in contrast to those of Dow and Fredga (1983) who reported lower nest success for female Goldeneyes that moved to new nest boxes. Hik (1986), however, reported lower hatching success and higher rates of gosling abandonment for Lesser Snow Geese faithful to nesting areas. Similarly, Hepp and Kennamer (1992) found no difference in nest success for Wood Ducks nesting in the same box and those moving to new nest boxes. Unlike cavity nesting species (Dow and Fredga 1983, Gauthier 1990) for which nest success may be related to characteristics of the nest location (Blancher and Robertson 1985, Savard 1985), habitat characteristics of nest sites for brant show little variation among locations. Brant nesting in higher densities may delay or retard predation by Arctic foxes through predator swamping (Raveling 1989), but, except for nests sites on islands (Sedinger, pers. observ.), predation rates do not appear to vary across habitat types (Stickney 1989). Between 1988 and 1993 only 21% (n = 5,300) of nests at Tutakoke were located on islands and a proportion of these island sites were located in ponds with shallow water (<50 cm) or in ephemeral ponds. Nest success at Tutakoke was 2% in 1984 and 7% in 1985 indicating that few nests sites were protected from fox predation (Anthony et al. 1991). Therefore, we do not believe nest success would be higher for brant faithful to nest sites in years with higher rates of predation by Arctic foxes.

We found no evidence that nest initiation date was positively related to dispersal distance of brant. In fact, in late years, brant that disperse tend to nest earlier (Fig. 6). Several studies have observed earlier nesting by waterfowl that return to nest sites than for individuals that disperse to new sites (Dow and Fredga 1983, MacInnes and Dunn 1988, Gauthier 1990, Hepp and Kennamer 1992). Newton and Marquiss (1982) suggested that Sparrowhawks (*Accipter niscus*) may experience a tradeoff between fidelity and local food supplies. Similarly, we believe a tradeoff between site fidelity and timing of nest initiation may explain the relationship we observed. We suggest that dispersal from nest sites is a strategy to nest earlier than would otherwise be possible in late years.

Timing of nest initiation is important for subsequent reproductive performance of brant (Sedinger and Flint 1991) and other species breeding at high latitudes (e.g., Cooch et al. 1991). Nesting chronology, particularly for Arctic nesting geese, is closely regulated by spring breakup phenology (Raveling 1978). Nest initiation dates at Tutakoke River vary among years relative to spring snowmelt conditions, and earliest nesting brant use highest elevation nest sites (Lindberg et al., unpubl. data). If nest sites are not available when brant arrive on breeding grounds, geese may delay breeding until sites become available (Raveling 1978), lay their eggs in the nests of other geese (dump-nesting, e.g., MacInnes and Dunn 1988), abandon breeding for that year, or disperse to available nest sites (Abraham 1980). We found little evidence of long delays between arrival and nest initiation (Raveling 1978) or dump nesting (Lindberg et al., unpubl. data) by brant in late springs. Estimates of breeding propensity are approximately 1.00 for brant >5 years old (Sedinger et al., unpubl. data). Even if some individuals abandon nesting in late years, our current analysis indicates that some brant breeding in late years disperse to available nest sites within the Tutakoke colony. Selective pressures for early nesting associated with increased growth and development of goslings may be greater in late years (Cooch et al. 1991). We suggest that brant do not delay breeding to maintain fidelity in these years. Rather, brant nesting early in late springs (year $t + 1$) generally dispersed farther between year *t* and year $t + 1$ than brant nesting later (Fig. 6). Brant dispersing 1,000 m in late springs advanced their initiation date by approximately 1.3 days. Reduced availability of nests sites caused by meltwater flooding (Lindberg et al., unpubl. data) and heightened competition for fewer nest sites (Barry 1962) are likely causes of these dispersal patterns. We lack data on variation in timing of availability of all nests, but even in late years traditional nest sites of some individuals were available immediately upon arrival. Some brant moving <100 m in late years nested as early as those brant moving $>1{,}000$ m, probably because they acquired higher elevation nests.

Clutch size in brant declined with dispersal distance, particularly in late years (Table 2). Dow and Fredga (1983) and Gauthier (1990) demonstrated that birds returning to nest boxes had larger clutches than individuals moving to new nest boxes. This increase in clutch size may reflect a relationship between nest initiation date and clutch size (Klomp 1970) because birds faithful to nest boxes nested earlier in both studies (Dow and Fredga 1983, Gauthier 1990). Furthermore, Dow and Fredga (1983) failed to observe a relationship between dispersal distance and clutch size. Fidelity to nest sites may reduce time spent searching for new nest sites and increase familiarity with local resources (Lack 1954, Hinde 1956), thereby reducing expenditure of nutrient reserves devoted to egg production (Raveling 1978, Alisaukas and Ankney 1992).

Alternatively, lower clutch size may not result from dispersal, but may instead reflect variation in quality of individual brant. We could not determine if brant would have laid larger clutches if they had maintained fidelity to previous nest sites. If competition for available nest sites is heightened in late years (Barry 1962), we suspect that lower quality individuals, which also may lay smaller clutches, may be more likely to disperse.

We could not experimentally distinguish effects of dispersal per se from those resulting from individual quality. We found little evidence, however, to suggest fidelity to nest sites was advantageous. Similarly, Hepp and Kennamer (1992) found little advantage to site fidelity in Wood Ducks. Despite several theoretical explanations for ecological advantages of site fidelity (Lack 1954, Greenwood and Harvey 1982, Anderson et al. 1992), little empirical evidence is available to test these hypotheses. During nesting, brant frequently fly to coastal areas to feed rather than feeding in the immediate vicinity of nest sites (Welsh 1988). Therefore, familiarity with local food resources may not be enhanced by fidelity to specific nest sites. Benefits of site fidelity may be realized at other geographic scales (i.e., philopatry to colonies) or during periods of the breeding cycle (e.g., brood rearing) when familiarity with available food resources is more important (but see Cooch et al. 1993).

Dispersal distance may be an additional factor affecting reproductive strategies of individuals (Drent and Daan 1980), as brant that dispersed nested early, but laid smaller clutches than those individuals faithful to nest sites. Our estimate of repeatability indicates that dispersal strategies may have some genetic basis; however, these estimates may be biased by return of females to traditional nest sites following dispersal as well as other sources noted by van Noordwijk (1987). We suggest that environmental effects, age, and nest fate are more important parameters affecting movement patterns of brant.

ACKNOWLEDGMENTS

This research was supported by the Alaska Fish and Wildlife Research Center and Migratory Bird Management, Region 7, U.S. Fish and Wildlife Service. We thank D. V. Derksen, E. A. Rexstad, K. E. Schwaegerle, and G. F. Shields for their comments on earlier drafts of the manuscript. Many technicians provided valuable field assistance; N. D. Chelgren, P. L. Flint, B. T. Person, and M. W. Eichholz provided important assistance in more than one year.

LITERATURE CITED

ABRAHAM, K. F. 1980. Breeding site selection of Lesser Snow Geese. Ph.D. diss., Queen's University, Kingston, Ontario.

AFTON, A. D., AND S. T. PAULIS. 1992. Incubation and brood care, p. 62–108. *In* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, [eds.], Ecology and management of breeding waterfowl. Univ. Minnesota Press, Minneapolis.

AKAIKE, H. 1973. Information theory as an extension of the maximum likelihood principle, p. 267–281. *In* B. N. Petran and F. Cáski [eds.], International symposium on information theory, 2nd ed. Akadémiai Kiadi, Budapest, Hungary.

ALISAUKAS, R. T., AND C. D. ANKNEY. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl, p. 30–61. *In* B. D. J. Batt,

A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, [eds.], Ecology and management of breeding waterfowl. Univ. Minnesota Press, Minneapolis.

ANDERSON, M. G., J. M. RHYMER, AND F. C. ROHWER. 1992. Philopatry, dispersal, and the genetic structure of waterfowl populations, p. 396–422. *In* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, [eds.], Ecology and management of breeding waterfowl. Univ. Minnesota Press, Minneapolis.

ANTHONY, R. M., W. H. ANDERSON, J. S. SEDINGER, AND L. L. MCDONALD. 1995. Estimating populations of nesting brant using aerial videography. Wildl. Soc. Bull. 23:80–87.

ANTHONY, R. M., P. L. FLINT, AND J. S. SEDINGER. 1991. Arctic fox removal improves nest success of Black Brant. Wildl. Soc. Bull. 19:176–184.

BARRY, T. W. 1962. Effects of late seasons on Atlantic Brant reproduction. J. Wildl. Manage. 26:19–26.

BECKER, W. A. 1984. Manual of quantitative genetics. Academic Enterprises, Pullman, WA.

BLANCHER, P. J., AND R. J. ROBERTSON. 1985. Site consistency in Kingbird breeding performance: implications for site fidelity. J. Anim. Ecol. 54:1017–1027.

BROWNIE, C., J. E. HINES, J. D. NICHOLS, K. H. POLLOCK, AND J. B. HESTBECK, JR. 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. Biometrics 49:1173–1187.

BURGER, J. 1982. The role of reproductive success in colony-site selection and abandonment in Black Skimmers (*Rynchops niger*). Auk 99:109–115.

COOCH, E. G., D. B. LANK, A. DZUBIN, R. F. ROCKWELL, AND F. COOKE. 1991. Body size variation in Lesser Snow Geese: environmental plasticity in gosling growth rates. Ecology 72:503–512.

COOCH, E. G., R. L. JEFFERIES, R. F. ROCKWELL, AND F. COOKE. 1993. Environmental change and the cost of philopatry: an example in the Lesser Snow Goose. Oecologia 93:128–138.

COLEMAN, A. E., AND C. D. T. MINTON. 1979. Pairing and breeding of Mute Swans in relation to natal area. Wildfowl 30:27–30.

COOKE, F., C. S. FINDLAY, R. F. ROCKWELL, AND K. F. ABRAHAM. 1983. Life history studies of the Lesser Snow Goose (*Anser caerulescens caerulescens*) II. Colony structure. Behav. Ecol. Sociobiol. 12:153–159.

DRENT, R. H., AND S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252.

DOTY, H. A., AND F. B. LEE. 1974. Homing to nest baskets by wild female Mallards. J. Wildl. Manage. 38:714–719.

DOW, H., AND S. FREDGA. 1983. Breeding and natal dispersal of the Goldeneye, *Bucephala clangula*. J. Anim. Ecol. 52:681–695.

DRILLING, N. E., AND C. F. THOMPSON. 1988. Natal and breeding dispersal in House Wrens (*Troglodytes aedon*). Auk 105:480–491.

FALCONER, D. S. 1989. Introduction to quantitative genetics. John Wiley and Sons, New York.

FINNEY, G., AND F. COOKE. 1978. Reproductive habits in the Snow Goose: the influence of female age. Condor 80:147–158.

FLINT, P. L., AND J. S. SEDINGER. 1992. Reproductive implications of egg-size variation in the Black Brant. Auk 109:893–903.

FLINT, P. L., J. S. SEDINGER, AND K. H. POLLOCK. 1995. Survival of juvenile Black Brant during brood rearing. J. Wildl. Manage 59:455–463.

GAUTHIER, G. 1990. Philopatry, nest-site fidelity, and reproductive performance in Buffleheads. Auk 107:126–132.

GAVIN, T. A., AND E. K. BOLLINGER. 1988. Reproductive correlates of breeding-site fidelity in Bobolinks (*Dolichonyx oryzivorus*). Ecology 69:96–103.

GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28:1140–1162.

GREENWOOD, P. J. 1987. Inbreeding, philopatry and optimal outbreeding in birds, p. 207–222. *In* F. Cooke and P. A. Buckley [eds.], Avian genetics: a population and ecological approach. Oxford Univ. Press, Oxford.

GREENWOOD, P. J., AND P. H. HARVEY. 1982. The natal and breeding dispersal of birds. Annu. Rev. Ecol. Syst. 13:1–21.

GREENWOOD, P. J., P. H. HARVEY, AND C. M. PERRINS. 1979. The role of dispersal in the Great Tit (*Parus major*): the causes, consequences and heritability of natal dispersal. J. Anim. Ecol. 48:123–142.

HARVEY, P. H., P. J. GREENWOOD, AND C. M. PERRINS. 1979. Breeding area fidelity of Great Tits (*Parus major*). J. Anim. Ecol. 48:305–313.

HEPP, G. R., R. A. KENNAMER, AND W. F. HARVEY, IV. 1989. Recruitment and natal philopatry of Wood Ducks. Ecology 70:897–903.

HEPP, G. R., AND R. A. KENNAMER. 1992. Characteristics and consequences of nest-site fidelity in Wood Ducks. Auk 109:812–818.

HESTBECK, J. B., J. D. NICHOLS, AND R. A. MALECKI. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada Geese. Ecology 72:523–533.

HIK, D. S. 1986. Local philopatry and dispersal in the Lesser Snow Goose: the role of reproductive success. B.Sc. thesis, Queen's University, Kingston, Ontario.

HINDE, R. A. 1956. The biological significance of territories in birds. Ibis 98:340–369.

HINES, J. E. 1994. MSSURVIV user's manual. Natl. Biol. Survey, Patuxent Environmental Sci. Center, Laurel, MD.

JONES, R. D. 1964. Age group counts of Black Brant in Izembek Bay, Alaska. Wildfowl Trust Annu. Rep. 15:147–148.

JONES, R. D., AND D. M. JONES. 1966. The process of family disintegration in Black Brant. Wildfowl Trust Annu. Rep. 17:75–78.

Kharitonov, S. P., and D. Siegel-Causey. 1988. Colony formation in seabirds. Current Ornithol. 5:223–272.

Kincheloe, K. L., and R. A. Stehn. 1991. Vegetation patterns and environmental gradients in coastal meadows on the Yukon-Kuskokwim Delta, Alaska. Can. J. Bot. 68:1616–1627.

Klomp, H. 1970. The determination of clutch-size in birds. Ardea 58:1–124.

Lack, D. 1954. The natural regulation of animal numbers. Oxford Univ. Press, London.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing hypotheses using marked animals: a unified approach with case studies. Ecol. Monogr. 62:67–118.

Lessells, C. M. 1985. Natal and breeding dispersal of Canada Geese *Branta canadensis*. Ibis 127:31–41.

Lessells, C. M., and P. T. Boag. 1987. Unrepeatable repeatabilities: a common mistake. Auk 104:116–121.

Lindberg, M. S., J. S. Sedinger, and E. A. Rexstad. 1995. Estimating nest site fidelity of adult female Black Brant with multistate modeling and geographic information systems. J. Appl. Stats. 22:725–735.

Lokemoen, J. T., H. F. Duebbert, and D. E. Sharp. 1990. Homing and reproductive habits of Mallards, Gadwall, and Blue-winged Teal. Wildl. Monogr. 106.

MacInnes, C. D., and E. H. Dunn. 1988. Components of clutch size variation in arctic-nesting Canada Geese. Condor 90:83–89.

Majewski, P., and P. Beszterda. 1990. Influence of nesting success on female homing in the Mallard. J. Wild. Manage. 54:459–462.

Manly, B. F. J. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, London.

McKinney, F. 1992. Courtship, pair formation, and signal systems, p. 214–250. *In* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, [eds.], Ecology and management of breeding waterfowl. Univ. Minnesota Press, Minneapolis.

Neter, J., W. Wasserman, and M. H. Kutner. 1985. Applied linear statistical models, 2nd ed. Irwin, Homewood, IL.

Newton, I., and M. Marquiss. 1982. Fidelity to breeding area and mate in Sparrowhawks *Accipiter nisus*. J. Anim. Ecol. 51:327–341.

Nichols, J. D., and W. L. Kendall. 1995. The use of multi-state capture-recapture models to address questions in evolutionary ecology. J. Appl. Stats. 22:835–846.

Owen, M. 1980. Wild geese of the world. B. T. Batsford, London.

Prop, J., and J. de Vries. 1993. Impact of snow and food conditions on the reproductive performance of Barnacle Geese *Branta leucopsis*. Ornis Scand. 24:110–121.

Raveling, D. G. 1978. The timing of egg laying by northern geese. Auk 95:294–303.

Raveling, D. G. 1989. Nest-predation rates in relation to colony size of Black Brant. J. Wild. Manage. 53:87–90.

Rohwer, F. C., and M. G. Anderson. 1988. Female-biased philopatry, monogamy and the timing of pair formation in waterfowl. Current Ornithol. 5:187–221.

SAS Institute, Inc. 1990. SAS/STAT user's guide, version 6, 4th ed., vol. 2. SAS Institute, Cary, NC.

Savard, J-P, L. 1985. Evidence of long-term pair bonds in Barrow's Goldeneye (*Bucephala islandica*). Auk 102:389–391.

Sedinger, J. S., and P. L. Flint. 1991. Growth rate is negatively correlated with hatch date in Black Brant. Ecology 72:496–502.

Sedinger, J. S., P. L. Flint, and M. S. Lindberg. 1995. Environmental influence on growth, survival, and fecundity in Black Brant (*Branta bernicla*). Ecology 76:2404–2414.

Sedinger, J. S., C. J. Lensink, D. H. Ward, R. M. Anthony, M. L. Wege, and G. V. Byrd. 1993. Current status and recent dynamics of the Black Brant breeding population. Wildfowl 44:49–59.

Shepard, P. E. K. 1964. Nesting ecology of the Black Brant in Alaska. Unpubl. Report, Alaska Dept. Fish and Game, Juneau, AK.

Spendelow, J. A., J. D. Nichols, I. C. T. Nisbet, H. Hays, G. D. Cormons, J. Burger, C. Safina, J. E. Hines, and M. Gochfeld. 1995. Estimating annual survival and movement rates of adults within a metapopulation of Roseate Terns. Ecology 76:2415–2428.

Stickney, A. A. 1989. The foraging behavior, habitat use, and diet of Arctic foxes (*Alopex lagopus*) in a goose nesting area near Kokechik Bay, Alaska. M.Sc. thesis. Univ. Alaska, Fairbanks.

van Noordwijk, A. J. 1987. Quantitative ecological genetics of Great Tits, p. 363–380. *In* F. Cooke and P. A. Buckley [eds.], Avian genetics: a population and ecological approach. Oxford Univ. Press, Oxford.

Welsh, D. 1988. The relationship of nesting density to behavior and reproductive success of Black Brant. M.Sc. thesis, Univ. Idaho, Moscow, ID.

White, G. C. 1983. Numerical estimation of survival rates from band-recovery data and biotelemetry data. J. Wildl. Manage. 47:716–728.