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DEMOGRAPHIC CHARACTERISTICS OF MOLTING BLACK BRANT NEAR TESHEKPUK LAKE, ALASKA

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Abstract.—Molting Brant (*Branta bernicla*) in the Teshekpuk Lake Special Area (TLSA) on the Arctic Coastal Plain of Alaska were studied from 1987 to 1992 using capture-mark-recapture techniques to determine origin, age and sex composition, return rates and site fidelity. Brant originated from 10 nesting colonies in Canada and Alaska. The captured birds were 76% adults and 57% males. Ninety-one percent of known-age recaptures were <6-yr-old. Fewer 1-yr-olds and more 2-yr-olds were present than expected. Sixty-one percent of adult females were failed breeders. Brant were not segregated by nesting colony on lakes in the TLSA, but those returning exhibited high site fidelity (Ψ = 0.945) to the lake of initial capture. Recapture rates for Brant banded in the Teshekpuk area were greater (τ = 0.156) than for Brant banded at nesting colonies. Highest recapture rates (τ = 0.059) of Brant banded at nesting colonies were from those located closest to the molting area.

CARACTERÍSTICAS DEMOGRÁFICAS DE INDIVIDUOS DE *BRANTA BERNICLA* DURANTE EL PERÍODO DE MUDA CERCA DEL LAGO TESHEKPUK, ALASKA

Sinopsis.—De 1987 a 1992 se estudiaron individuos de *Branta bernicla* en el Lago Teshekpuk de Alaska, durante el período de muda de las aves. Se utilizó el método de marca y recaptura para determinar el origen, edad, composición sexual, tasa de retorno y fidelidad a la localidad de estos gansos. Las aves se originaron de 10 colonias de anidamiento en Canadá y Alaska. De las aves capturadas el 76% resultaron ser adultos y el 57% machos. El 91% de las aves de edad conocida fue menor a 6 años. Se encontró un número menor de individuos de un año y un número mayor de individuos de dos años, a lo esperado. El 61% de las hembras capturadas fracasó en reproducirse. Los gansos no estuvieron agregados por colonias reproductivas en los lagos de Teshekpuk. Sin embargo, aquellos que regresaron exhibieron una alta fidelidad (Ψ = 0.945) al lago en donde fueron capturados. La tasa más alta de recaptura (τ = 0.059) de aves anilladas en colonias de anidamiento fue de aquellos individuos localizados cerca de los lugares de muda.

Few waterfowl studies have focused on molt migration, although this behavior has been attributed to seven of 13 tribes in the Anatidae (Hohman et al. 1992, Salomonsen 1968). Brant (*Branta bernicla*) are coastal marine geese that nest in colonies in Alaska, Canada and Siberia (Derksen and Ward 1993). Some Brant, which do not attempt to nest or that fail at nesting, migrate to remote, high arctic areas before molting (King 1970, Uspenski 1965). The largest known concentration of molting Brant is in the Teshekpuk Lake area on Alaska's Arctic Coastal Plain that annually supports ≤22% of the Pacific Brant (*B. b. nigricans*) population during the summer molt period (R. J. King, unpubl. data). King and Hodges (1979) reported band recoveries from this population and suggested that all non-breeding Brant from nesting areas north of the Bering Strait in Alaska, Canada and Siberia molted in the Teshekpuk Lake area. An international marking program at nesting colonies in Canada and

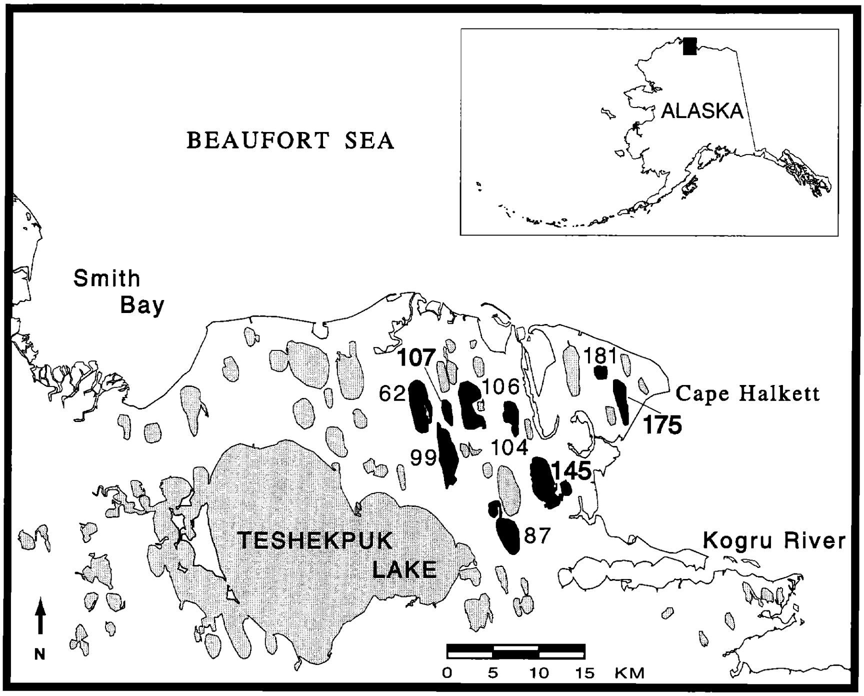

FIGURE 1. Teshekpuk Lake Special Area, Alaska and location of lakes where banding occurred.

Alaska (Sedinger et al. 1993) and at molting areas on Wrangel Island, Russia (Ward et al. 1993) and near Teshekpuk Lake (Derksen et al. 1992) resulted in banding of 30,000 individuals between 1985 and 1992. This large sample of banded Brant presented a unique opportunity to study further the dynamics of molting Brant in the Teshekpuk Lake area. We evaluated: (1) the origin, age, sex and breeding status of molting birds, (2) the distribution and recapture rate of birds previously marked at breeding colonies, and (3) the rate of return and fidelity to specific lakes of birds that molted in the Teshekpuk Lake area multiple years.

STUDY AREA

The Teshekpuk Lake Special Area (TLSA; U.S. Department of the Interior 1977; Fig. 1; 70°45′N, 153°00′W) is characterized by continuous permafrost, tundra vegetation, ice-wedge polygons and poorly drained soils (Spetzman 1959). Thaw lakes ($\leq$25 km^2) lie along a NNW-SSE axis (Livingstone 1954, Sellmann et al. 1975) and, with numerous smaller lakes, dominate the landscape. Many of these lake basins are drained or partly drained (Weller and Derksen 1979) resulting in shallow margins vegetated by grasses and sedges comprising important foods for molting geese (Derksen et al. 1982). Molting geese occur mainly in the area north and east of Teshekpuk Lake from the Kogru River to Smith Bay (Fig. 1). Lakes that traditionally are used extensively by Brant are concentrated primarily within a 1500 km^2 area in the northeastern corner of the TLSA (Derksen et al. 1979; Fig. 1).

METHODS

Brant were captured on nine lakes in the Teshekpuk Lake area from 10–27 Jul. 1987–1992 (Table 1; Fig. 1). We used inflatable boats to drive flightless birds slowly to trap sites established on dry, low-relief shorelines.

We sexed and aged all birds and original captures were fitted with U.S. Fish and Wildlife Service stainless-steel bands. We determined sex by cloacal characteristics of the clitoris or penis (Hanson 1967, Hochbaum 1942) and age by plumage and cloacal characteristics. Brant retain white-tipped middle wing coverts that are characteristic of juveniles until molt at 1 yr of age. These birds in their second-year of life (SY) can be distinguished from older birds (Bent 1925:243). Absence of white-tipped coverts in conjunction with a pigmented clitoris (females) or a sheathed penis (males) indicate Brant at least 2-yr-old or in, at least, their third summer, (i.e., after-second-year [ASY] birds). Brant that could not be aged because of conflicting evidence were classified as after-hatching-year ([AHY] i.e., birds at least 1-yr-old or in, at least, their second summer). Ages recorded for recaptured birds were based on age at original capture. Females with brood patches were classified as failed breeders; females without brood patches were considered non-breeders.

Gauthreaux (1982) defined site fidelity as returning to an area previously inhabited after a period of absence. We distinguished between rate of return to the general area and frequency of fidelity to a specific site (i.e., lake) within that area. Return rates of molters, based on recaptures of birds previously marked or captured in the molting area, were compared to recapture rates of birds previously marked at breeding colonies or another molting site.

Statistical analyses.—All data were used to document the origin, age, sex, breeding status and recapture rate of birds. Analysis of the distribution of birds from nesting colonies in the TLSA and site fidelity of molters returning to the TLSA required a complete data set; as capture operations were not conducted on all lakes each year, we used data from three lakes for three consecutive years for these two analyses (lakes 107, 145 and 175 for 1990, 1991 and 1992; Table 1; Fig. 1).

We calculated percent yearlings in the total summer population using age ratios and total population estimates obtained at staging and wintering areas the previous year (Bartonek 1992) and applying survival estimates of 50% for juveniles and 85% for older birds (D. H. Ward, unpubl. data). These same survival estimates were used in determining numbers of banded Brant available for capture that we used in our analyses of age structure and recapture rates.

Distribution of Brant from nesting colonies.—Log-linear modeling techniques (Dixon et al. 1990, Freeman 1987) were used to assess differential

TABLE 1. Number of Brant captured and banded in the Teshekpuk Lake Special Area, 1987–1992.

	No. Brant													
	1987		1988		1989		1990		1991		1992		Total	
Lake	Captured	Banded	Captured	Banded	Captured	Banded	Captured	Banded	Captured	Banded	Captured	Banded	Captured[a]	Banded
62	299	247	296	222	109	94	—	—	—	—	—	—	704	563
63	—	—	—	—	25	23	—	—	—	—	—	—	25	23
99	—	—	—	—	350	330	—	—	—	—	—	—	350	330
104	—	—	—	—	—	—	—	—	503	326	—	—	503	326
106	—	—	—	—	855	704	—	—	—	—	—	—	855	704
107	—	—	646	517	272	201	654	319	908	316	789	500	3269	1853
145	240	235	417	381	37	33	218	201	881	425	1618	500	3411	1775
175	—	—	—	—	—	—	340	320	632	340	403	325	1375	985
181	—	—	—	—	—	—	—	—	1086	351	—	—	1086	351
Total	539	483	1359	1120	1648	1385	1212	840	4010	1758	2810	1325	11,578	6910

[a] Total number captured includes 415 individuals captured more than once in the same year.

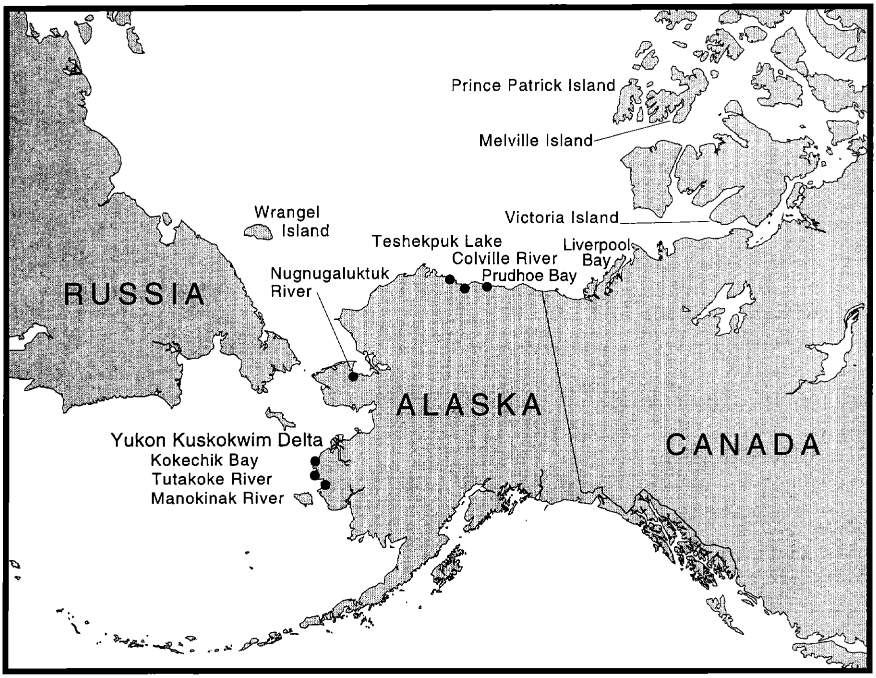

FIGURE 2. Locations where Brant had been banded that were recaptured in the Teshekpuk Lake Special Area, Alaska.

use of lakes in the TLSA by Brant from the Tutakoke and Colville River nesting colonies (Fig. 2). Sample sizes from other nesting colonies were not sufficient to permit analysis. Categorical variables included in the models were number of recaptures of Brant previously banded at these two nesting colonies, lake where recaptured, year of recapture, and year interval between banding and recapture. The independent structure of log-linear models allowed exploratory analysis of all interactions among these four variables. Comparison of number of recaptures with each of the other three variables permitted analysis of differential use of lakes, variation among years in the number of Brant migrating from a nesting colony to the TLSA to molt, and the trend in recapture rates as banded birds from nesting colonies aged, respectively. Model selection was based on the partial-association method using hierarchical procedures (Dixon et al. 1990, Freeman 1987).

Recapture rates.—Recapture rates of Brant were calculated using the equation

$$\tau = \frac{n_{ij}}{b_{ij}\dfrac{e_j}{N_j}},$$

where: n_{ij} = number of birds recaptured in year j from banding year i; b_{ij} = number of birds banded in year i that survived to year j; e_j = total number of birds captured in year j; and N_j = total number of birds available for capture in year j (Finney and Cooke 1978). Number of Brant available for capture was determined by aerial census of birds molting on the lake before banding. Recapture rates were calculated for constant-year intervals between capture and recapture to minimize confounding effects caused by differences in yearly survival and nesting success. Recapture rates discussed here include both recapture of birds banded elsewhere (recapture rate) and recapture of birds banded in the TLSA (return rate).

Site fidelity.—Site fidelity was measured as the probability that Brant returning to the TLSA would molt on the same or a different lake compared with the previous year. As the three lakes differed in size and degree of aircraft accessiblity, we did not assume that the probability of capturing birds was identical, an assumption that could have simplified estimating the relative probabilites of moving or returning. We used capture-recapture models described by Brownie et al. (1993), Hestbeck et al. (1991), and Nichols et al. (1993) to estimate relevant parameters because these models did not require restrictive assumptions such as equal sampling (capture) probabilities.

Three parameters were estimated in our analyses: (1) survival and return, S_i^r; (2) movement, Ψ_i^{rs}; and (3) capture, P_i^r, probabilities. Five models were constructed incorporating various constraints on these three parameters.

The most general model (denoted model A) included three groups of parameters: S_i^r = the probability that a bird on lake r in year i survives until year $i + 1$ and returns to one of the three lakes in the study area; Ψ_i^{rs} = the probability that a bird on lake r in year i is on lake s in year $i + 1$ given that the bird is alive in $i + 1$; and P_i^r = the probability that a bird on lake r in year i is caught in year i. Note that the complement of the survival probability $(1 - S_i^r)$ includes both death or failure to return to one of the three studied lakes (permanent emigration from the study system).

To investigate sources of variation in the probabilities of these parameters (i.e., survival, movement, and capture), we constructed models incorporating various constraints. In model E, the probability of returning in year $i + 1$ to the lake used in year i was set equal for all three lakes, $\Psi_i^{11} = \Psi_i^{22} = \Psi_i^{33}$. All other movement, survival, and capture probabilities were both time- and lake-specific as in model A. Model F imposed the additional constraint that the probability of moving to each of the other two lakes was the same for all three lakes. So, under model F constraints, $\Psi_i^{11} = \Psi_i^{22} = \Psi_i^{33}$, and $\Psi_i^{12} = \Psi_i^{13} = \Psi_i^{21} = \Psi_i^{23} = \Psi_i^{31} = \Psi_i^{32}$. The likelihood ratio test of model E compared to model A thus tests the hypothesis that birds exhibit equal degrees of fidelity to the three lakes; and the comparison of model F to model E tests the hypothesis that movement between lakes was equal.

We next imposed constraints on survival probabilities, while permitting variation among all probabilities of moving and returning that had been constrained in models E and F (i.e., the Ψ_i^{rs} were modeled as under model A). Model G thus incorporated the hypothesis of equal survival probabilities among the three lakes, $S_i^1 = S_i^2 = S_i^3$.

In the final model we imposed all three previous constraints. Model H represented the hypothesis of equal probabilities of surviving ($S_i^1 = S_i^2 = S_i^3$), of returning to the same lake ($\Psi_i^{11} = \Psi_i^{22} = \Psi_i^{33}$), and of moving to different lakes ($\Psi_i^{12} = \Psi_i^{13} = \Psi_i^{21} = \Psi_i^{23} = \Psi_i^{31} = \Psi_i^{32}$).

We used program MSSURVIV (Brownie et al. 1993, Nichols et al. 1993) to compute parameter estimates under these different models and to compute the likelihood ratio tests between competing models (see Lebreton et al. 1992). These tests treat the less general model (more assumptions, fewer parameters) as the null hypothesis and the more general model (fewer constraints) as the alternative hypothesis. Rejection of the null hypothesis indicates that the additional parameters of the alternative hypothesis model are needed to describe the data adequately. Goodness-of-fit statistics were computed to assess the fit of each model to the capture-recapture data. Finally, we used Akaike's Information Criterion (AIC) to determine the most parsimonious model that fit the data (Burnham and Anderson 1992, Lebreton et al. 1992). The AIC is an objective method of model selection based upon optimization of the selected criteria. The parsimony results from the simultaneous improved fit of the model and associated penalties as parameters are added to the model. Models with lower AIC values represent more appropriate choices.

RESULTS

We captured and examined 11,578 Brant in molting flocks in the TLSA between 1987 and 1992 (Table 1), but banded only 6910 because of limited time and concern for welfare of the captives. A total of 961 previously banded birds was captured 1042 times. Sixty-seven percent (642) of these recaptured individuals were originally banded in the Teshekpuk Lake area and 33% (319) had been banded at nesting colonies or the molting area on Wrangel Island (Fig. 2).

Origin of molting Brant.—Brant molting in the TLSA originated from nesting colonies throughout their range in the Pacific Flyway (Fig. 2), including those of Gray-bellied Brant (Boyd and Maltby 1979) from Melville Island in the western Canadian high arctic (Table 2). Recaptures included birds from all areas where >100 Brant have been banded since 1960 (Table 2). Percentages of birds banded at each nesting colony that were recaptured in the TLSA varied from 0.2 (Melville Island, Northwest Territories, Canada) to 10.4% (Teshekpuk Lake area nesting colony).

Age, sex and breeding status.—Of the Brant captured and banded between 1987 and 1992 in the TLSA, SY birds averaged 24% and never exceeded 40% of the total birds captured in any year (Table 3). Age ratios of Brant differed among years ($\chi^2 = 329$, df = 5, $P < 0.01$) and among lakes within a given year during four of the 6 yr.

TABLE 2. Frequency distribution of recaptures of Brant from nesting colonies and a molting site in the Teshekpuk Lake Special Area, 1987–1992.

Banding location	n[b]	No. recaptures by TLSA Lake[a] 62	99	104	106	107	145	175	181	Total	Percent recaps[c]
Nesting colony											
Canada											
Melville Island	839	1	0	0	0	0	0	0	1	2	0.2
Victoria Island	331	0	0	1	0	0	1	0	0	2	0.6
Liverpool Bay	588	4	2	0	0	6	7	1	1	21	3.6
Alaska											
North Slope											
Prudhoe Bay	328	—[d]	—	—	—	0	7	2	—	9	2.8
Colville	1429	—	—	0	—	9	27	13	2	51	7.8
Teshekpuk	77	—	—	0	—	0	8	0	0	8	10.4
Seward Peninsula											
Nugnugaluktuk	0	0	0	0	1	1	4	0	0	7	—
Yukon-Kuskokwim											
Kokechik	1515	0	0	2	1	6	4	6	6	25	1.6
Tutakoke	12,445	11	8	14	10	57	60	29	17	206	1.6
Manokinak	0	0	0	0	0	1	1	0	1	3	—
Molting area											
Russia											
Wrangel Island	1061	—	—	0	—	3	4	0	6	13	1.2
Total recaptures		16	10	17	12	83	123	51	34	338	
Total captured		659	349	503	751	3117	3335	1363	1086	11,163	

[a] See Figure 1.
[b] Number banded at that site 1986–1991.
[c] Percent of total birds marked at banding location during 1987–1991 that were recaptured at Teshekpuk. A dash indicates that birds recaptured were banded before 1987.
[d] A dash indicates no recaptures were possible; i.e., no Brant banded at the site subsequent to capture at nesting or molting areas.

TABLE 3. Age, sex and breeding status of Brant captured in the Teshekpuk Lake Special Area, 1987–1992.

	Age composition			Sex composition		Age/sex composition				Breeding status	
						SY		ASY			
Year	n[a]	% SY	No. AHY	n[a]	% female	n[a]	% female	n[a]	% female	n[b]	% failed breeders
1987	245	11.0	248	493	44.2	27	44.4	218	46.8	102	68.6
1988	1204	38.2	2	1206	45.8	460	49.1	743	43.6	318	61.3
1989	1474	22.5	8	1482	45.0	331	50.4	1143	43.4	496	71.2
1990	935	31.9	2	936	41.6	298	48.7	637	38.2	229	61.1
1991	2078	13.0	21	2098	39.8	271	43.2	1807	39.5	709	54.3
1992	1733	24.4	4	1734	44.5	422	48.6	1311	43.2	566	58.5
Total 1987–1992	7669	23.6	285	7949	43.2	1809	48.2	5859	41.7	2420	60.9

[a] Numbers include banded birds and unique recaptures. Differences in sample sizes are the result of exclusion of birds aged as AHY or of unknown sex when determining percentages of age and sex, respectively.

[b] Numbers include ASY females only. Second-year females were not included because only 2.0% (n = 868) had brood patches.

Yearling Brant were present at Teshekpuk at percentages slightly above those for the entire Pacific Flyway population (r^2 = 0.75, df = 5, P = 0.05). This result indicated that only a fraction of all yearlings migrated to molt in the TLSA.

Percentages of known-age recaptures (n = 317) were 21, 37, 20, 9 and 4%, respectively, for Brant aged 1–5 yr. The remaining 9% included birds aged 6–23 yr. The oldest Brant captured in the Teshekpuk Lake area was a 23-yr-old male banded as a SY bird in a molting flock at the Manokinak River (Fig. 2) on the Yukon-Kuskokwim Delta (YKD) in 1969, recaptured there in 1972, and again in the TLSA in 1991. We assume the age-structure of known-age recaptures to be the same as that for all banded Brant in the TLSA because percentage of yearlings did not differ between these two groups (χ^2 = 0.7, df = 1, $P > 0.50$). The age distribution of known-age recaptures differed from the expected (χ^2 = 23.7, df = 5, $P < 0.01$). SY birds were under-represented (21.4 vs. 32.6%) and 2-yr-olds, over-represented (37.2 vs. 32.7%) in comparison to their relative abundance among banded Brant. Number of Brant aged 3–6 yr varied little from expected (19.6 vs. 18.9%, 9.2 vs. 10.5%, 4.1 vs. 5.3% and 1.3 vs. 0.6%, respectively).

Females averaged 43% of the captured Brant (Table 3), although sex ratios differed among lakes (χ^2 = 70.5, df = 7, $P < 0.01$) and among years (χ^2 = 17.6, df = 5, $P < 0.01$). When data from 1991 were excluded, sex ratios did not vary among the remaining 5 yr (χ^2 = 4.2, df = 4, P = 0.38). Percent females on individual lakes ranged from 33–53%. Lake 107 consistently had the smallest ($\bar{x}$ = 37.6 ± 0.7 SD, n = 2272) and lake 145, the largest ($\bar{x}$ = 48.6 ± 3.3 SD, n = 2010) percentage of females. The proportion of ASY females was lower (41.7%) than that of yearlings (48.2%; Table 3). Relatively fewer females (43.2 vs. 45.9%, χ^2 = 6.8, df = 1, $P < 0.01$) molted at Teshekpuk during our study than in the 1970s (King and Hodges 1979).

Of 2420 ASY females, 60.9% had brood patches that indicated nest failure rather than non-breeding (Table 3). Differences in this ratio among years were significant (χ^2 = 38.9, df = 5, $P < 0.01$). Only 2.0% of 868 SY females captured during the 6 yr of banding had brood patches.

Distribution of Brant from nesting colonies.—Segregation by nesting colony did not occur on the sampled lakes (Table 2). Number of Brant captured differed among lakes in the TLSA for birds from the Colville River Delta colony (P = 0.045; Table 4), but were similar among lakes for birds from the Tutakoke River colony (P = 0.72). All recaptures of Brant banded at the Teshekpuk colony came from one lake in the TLSA (Table 2).

Approximately equal numbers of Brant from Tutakoke were present in the TLSA from 1990 to 1992 (P = 0.72); but more birds from the Colville were recaptured in 1992 compared to 1991 ($P < 0.01$; Table 4). Mortality is assumed to account for the decrease in numbers of Tutakoke Brant recaptured at Teshekpuk as number of years since banding increased ($P < 0.01$; Table 4).

TABLE 4. Frequency distribution of recaptures of Brant from the Tutakoke River and Colville River Delta colonies in the Teshekpuk Lake Special Area, 1990–1992.

Interval (yr) between banding and recapture	No. recaptures by year and lake								
	1990			1991			1992		
	107	145	175	107	145	175	107	145	175
Tutakoke River colony[a]									
1	6	1	2	5	2	3	1	10	5
2	3	0	1	8	9	6	2	4	1
3	3	1	0	3	1	1	3	9	5
4	1	1	0	2	3	1	1	3	0
Colville River Delta colony[b]									
1				2	2	5	5	15	7
n^c	654	206	329	908	836	632	789	1618	402

[a] Log linear model: $l_{ijkl} = m + L_i + R_j + Y_k + I_l + LY_{ij} + RI_{jl}$ where m is the overall mean; L_i characterizes the lake effect; R_j, the recapture effect; Y_k, the year effect; and I_l, the interval effect. Likelihood ratio chi-square for lack of fit: $\chi^2_{56} = 33.35$, $P = 0.99$.

[b] Log linear model: $l_{ijk} = m + L_i + R_j + Y_k + LR_{ij} + LY_{ik} + RY_{jk}$ where m is the overall mean; L_i characterizes the lake effect; R_j, the recapture effect; Y_k, the year effect. Likelihood ratio chi-square for lack of fit: $\chi^2_2 = 0.21$, $P = 0.90$.

[c] n = total number of birds captured.

Recapture rates.—Brant that previously molted at Teshekpuk were recaptured at higher rates in the TLSA compared to Brant originally banded at nesting colonies or the molting site on Wrangel Island (Table 5). Direct recapture rates (recaptures in the first summer after banding) of Teshekpuk banded Brant measured 0.156 during the 6 yr of our study. Rates declined slightly as the interval between banding and recapture increased.

Highest recapture rates for nesting Brant were from colonies located closest to the molting area (Teshekpuk, Colville River and Prudhoe Bay; Fig. 2). As a result of the disparity in size of nesting colonies, however, the greatest number of foreign recaptures in the TLSA originated from the YKD (Table 2). Brant from Victoria Island and Gray-bellied Brant from the western Canadian high arctic (Melville Island; Fig. 2) had the lowest direct recapture rates ($\tau = 0.000$ and 0.004, respectively). The trend in recapture rates as the interval between banding and recapture increased was not consistent among colonies; but little variation in recapture rates ($\bar{x} = 0.020 \pm 0.003$ SD, $n = 6$) existed for Tutakoke Brant recaptured 1–6 yr after banding.

Return intervals.—We captured 657 Brant in the TLSA more than once. Number of years each bird was captured ranged from 2–5. As expected, most (600) were captured twice; 51 were captured 3 times, 5 were captured 4 times and 1 was captured 5 times.

The interval between captures ranged to 21 yr, but 57% were captured in successive years; 19% were recaptured after a 1-yr interval, and 11%, after a 2-yr interval.

TABLE 5. Recapture rates by banding location of Brant in the Teshekpuk Lake Special Area, 1987–1992.

Status	Years between capture and recapture											
	1			2			3			4		
Location	No. yr[a]	Σn_{ij}[b]	τ[c]	No. yr	Σn_{ij}	τ	No. yr	Σn_{ij}	τ	No. yr	Σn_{ij}	τ
Non-breeding												
Teshekpuk Lake	5	372	0.156	4	141	0.100	3	87	0.090	2	39	0.067
Wrangel Island	3	11	0.023	2	1	0.003	1	0	0.000	—	—	—
Breeding												
Tutakoke River	6	74	0.019	5	63	0.022	4	31	0.017	3	16	0.016
Kokechik River	3	17	0.026	2	2	0.014	1	2	0.086	1	0	0.000
Teshekpuk Lake	1	2	0.057	1	6	0.182	—	—	—	—	—	—
Colville River	2	38	0.059	1	13	0.042	—	—	—	—	—	—
Prudhoe Bay	1	8	0.048	—	—	—	—	—	—	—	—	—
Liverpool Bay	3	8	0.032	2	1	0.010	1	0	0.000	—	—	—
Victoria Island	4	0	0.000	4	1	0.010	3	1	0.018	2	0	0.000
Melville Island	1	1	0.004	1	0	0.000	1	0	0.000	1	1	0.004

[a] Number of years of data on which sample is based.
[b] The summation of n_{ij} over the years on which the sample is based.
[c] $\tau = \Sigma \{n_{ij}/[b_{ij}(e_j/N_j)]\}$, where n_{ij} = number of birds banded in year i and recaptured in year j, b_{ij} = number of birds banded in year i that survived to year j, e_j = number of birds captured in year j, and N_j = number of birds available for capture in year j. Values are summed over the sample years.

TABLE 6. Capture-recapture data summarized in m_{ij}^{rs}-array format for Brant on the studied lakes in the Teshekpuk Lake Special Area during 1990–1992.

Year of release	No. released[a]	No. recaptured by year and lake: 1991, 107	1991, 145	1991, 175	1992, 107	1992, 145	1992, 175
1990	$R_{90}^{107} = 402$	59	0	0	14	2	0
	$R_{90}^{145} = 207$	2	9	0	0	15	1
	$R_{90}^{175} = 329$	3	1	33	0	3	6
1991	$R_{91}^{107} = 473$				63	3	5
	$R_{91}^{145} = 473$				1	43	2
	$R_{91}^{175} = 397$				0	5	32

[a] Notation follows Brownie et al. (1993). m_{ij}^{rs} = number of animals released and banded in year i at location r that were recaptured in year j at location s. R_i^r = number of animals released in year i at location r.

Site fidelity.—Recapture data from lakes 107, 145 and 175 during 1990–1992 (Table 6) were used in the MSSURVIV program to draw inferences about site fidelity using the probability estimates of three parameters: survival/return, movement and capture. For the model we selected as the most reasonable fit of the data (Model E, Table 7), the only assumption

TABLE 7. Summary of models tested using the MSSURVIV program to estimate movement probabilities based on recapture data from lakes 107, 145 and 175 in the Teshekpuk Lake Special Area, 1990–1992.

Model	Constraints	χ^2	df	P	AIC value
Individual models					
A		5.8	6	0.45	121.62
E[a]	$\psi_i^{11} = \psi_i^{22} = \psi_i^{33}$	13.4	11	0.27	119.23
F[b]	$\psi_i^{11} = \psi_i^{22} = \psi_i^{33}$ $\psi_i^{12} = \psi_i^{13} = \psi_i^{21} = \psi_i^{23} = \psi_i^{31} = \psi_i^{32}$	9.2	13	0.76	127.06
G[c]	$S_i^1 = S_i^2 = S_i^3$	19.6	10	0.03	127.42
H	$\psi_i^{11} = \psi_i^{22} = \psi_i^{33}$ $\psi_i^{12} = \psi_i^{13} = \psi_i^{21} = \psi_i^{23} = \psi_i^{31} = \psi_i^{32}$ $S_i^1 = S_i^2 = S_i^3$	28.8	17	0.04	122.60
Tests between models					
E vs. A	Return to the same lake	7.6	5	0.18	
G vs. A	Survival probabilities	13.8	4	<0.01	
F vs. E	Movement probabilities	11.8	2	0.02	
H vs. E	Survival and movement probabilities	15.4	6	0.02	

[a] Probability of a Brant returning to the same lake in succeeding years is equal for all three lakes. ψ_i^{rs} = the probability that a bird alive in lake r in year i is in lake s in year $i + 1$ given that the bird is alive in $i + 1$.

[b] Probability of a Brant moving to each of the other two lakes is equal for all three lakes.

[c] Probability of a Brant surviving and returning to the TLSA is equal for all three lakes. $\hat{S}_i^r$ = the probability that a bird alive in lake r in year i survives and returns to lake r in year $i + 1$.

TABLE 8. Estimates of survival rate (S^r_{90}) and capture probability (p^r_{91}) for the three lakes (r) under model E.

Lake (r)	$\hat{S}^r_{90}$	$\widehat{SE}\ (\hat{S}^r_{90})$	$\hat{p}^r_{91}$	$\widehat{SE}\ (\hat{p}^r_{91})$
107	0.41	0.070	0.385	0.071
145	0.74	0.183	0.062	0.024
175	0.46	0.118	0.233	0.069

made was that the probability of returning to the same lake in successive years was equal for the three lakes; no assumptions about equal probabilities of survival and return, movement between lakes and capture were imposed. The non-significant likelihood test between models A and E was the basis for making this assumption ($\chi_5{}^2 = 7.6$, $P = 0.18$; Table 7) and was supported by the AIC values. Evidence that survival/return probabilities and movement probabilities differed among lakes was shown when comparing models (Table 7); different capture probabilities were expected because of differences in relative numbers of Brant captured on each lake. Estimates then were calculated under our selected model for the three parameters of interest. Results showed that: (1) Brant that molted on lake 145 survived and returned to molt in the TLSA at almost twice the rate as Brant that molted on either lake 107 or 175 (Table 8); and (2) Brant exhibited high site fidelity to the lake on which they had molted before (94.5%, Table 9). Movement between lakes 107 and 145 was estimated to be higher than movement between lake 175 and either of these lakes; and (3) Brant that molted on lake 107 and 175 were 6.2 and 3.8 times more likely to be captured than Brant that molted on lake 145 (Table 8).

For comparison, we calculated rates for fidelity using all the data and without taking into account capture and survival/return probabilities. For all lakes, 59% of the Brant were recaptured on the same lake and 79% within 1.5 km of the original lake. For lakes 107, 145 and 175, 81% were captured on the same lake and 87% within 1.5 km of the original lake. Fidelity to the area remained constant over a 4-yr period (80%), but fidelity to a specific lake decreased (40%).

TABLE 9. Estimates of movement probabilities (ψ_i^{rs})[a] among the three lakes under model E.

Lake used in 1990 (r)	Lake used in 1991 (s): 107		145		175	
	$\hat{\psi}^{r1}_{90}$	$\widehat{SE}\ (\hat{\psi}^{r1}_{90})$	$\hat{\psi}^{r2}_{90}$	$\widehat{SE}\ (\hat{\psi}^{r2}_{90})$	$\hat{\psi}^{r3}_{90}$	$\widehat{SE}\ (\hat{\psi}^{r3}_{90})$
107	0.945	0.026	0.055	0.055	0.000	0.080
145	0.055	0.026	0.945	0.026	0.000	0.000
175	0.027	0.019	0.028	0.032	0.945	0.026

[a] ψ_i^{rs} = the probability that a bird alive in lake r in year i is in lake s in year $i + 1$ given that the bird is alive in $i + 1$.

DISCUSSION

Origin of molting Brant.—The TLSA attracts molt-migrants from all Pacific Flyway colonies in Alaska and Canada where Brant have been marked. Although no Brant were banded in Russian colonies before or during the years of our study, it seems probable that individuals from some or even all of these relatively small nesting populations (Derksen and Ward 1993) migrate across the Arctic Ocean to the TLSA. Marked Brant from breeding areas on the Yukon-Kuskokwim Delta in Alaska and the Anderson River near Liverpool Bay, Canada crossed the Bering, Beaufort and Chukchi seas to Wrangel Island where they were recaptured during molt (Ward et al. 1993). Interestingly, molting birds marked at Wrangel Island have been recaptured at Teshekpuk Lake (this study), and Ward et al. (1993) on Wrangel Island recaptured Brant that had been banded during the molt at the TLSA. It seems that flock composition at the TLSA is regulated by the experience and association of individual migrants with conspecifics and by the proximity of breeding colonies to the molting area.

Age, sex and breeding status.—Salomonsen (1968) concluded that within Anserini molt migration is restricted to non-breeders that are mostly young, immature birds. More recent studies of molt migration in waterfowl were summarized by Hohman et al. (1992) who stated that molt migration in Anserini involves mostly subadults, but may include non-breeding adults, failed breeders and successful breeders. Our study showed that these generalizations do not accurately describe the TLSA population of molting Brant, where there were more ASY than SY birds, more males than females and more failed breeding than non-breeding females. The Wrangel Island population of molting Brant was composed of mostly (74–83%) ASY birds, 45% males of all ages, and in 2 of 3 yr more non-breeding females than failed breeding females (Ward et al. 1993). Variations in age, sex and breeding status between years and among molting areas are probably influenced by variables at colonies (Barry 1967, Eisenhauer 1977, Mickelson 1975, Sedinger et al. 1993) that affect nest initiation and rearing success.

Distribution of Brant from nesting colonies.—Gray-bellied Brant from Canadian high arctic colonies (Boyd et al. 1988) segregate from darker plumaged, low arctic nesting birds during staging in fall (Reed et al. 1989b) and in some winter habitats (Reed et al. 1989a). We recaptured only two birds from the Canadian high arctic (Melville Island) and trapped or observed <10 other Brant with lighter belly color that could have been the gray-bellied form. These individuals were mixed with the dominant black-bellied morph on several lakes in the TLSA. A general pattern of spatial segregation of breeding stocks from other colonies outside of the Canadian high arctic did not exist within the lakes we sampled.

Recapture rates.—The propensity to molt in the TLSA, measured by recapture rates among nesting colonies, was evidently influenced by distance between nesting colonies and the TLSA. The greater the distance between breeding and molting area the lower the recapture rate. We assume that the inverse relationship we found results from the greater energetic cost of long-distant migration; survival probabilities being inversely related to migration distances (Nichols et al. 1983). Indeed, the occurrence of large molting flocks of Brant at the more distant colonies (western high arctic Canadian islands, Boyd and Maltby 1979; YKD, C. Lensink, unpubl. data) from the TLSA would seem to support this assumption. Further research comparing survival rates of Brant that molt in nesting areas with those that undertake molt migrations to the TLSA or Wrangel Island may help to elucidate survival value of these behaviors.

Site fidelity.—We believe actual rate of site fidelity of Brant molting in the TLSA lies between the two rates we calculated. Results of the MSSURVIV analysis, however, should be considered a maximum rate, because our sample was limited to three lakes from among more than 50 used by Brant in the TLSA (Derksen et al. 1979). Likewise, the analysis employing all capture data is a minimal rate, because we sampled different lakes in each of the 6 yr and capture and survival probabilities were not considered in this analysis. Each measure represents a high degree of homing to specific lakes or lake complexes, a behavior that may have evolved if survival is enhanced (Bowman and Longcore 1989) because of few predators, low human disturbance and abundant food and cover (Bowman and Brown 1992, Sterling and Dzubin 1967). These criteria are met in the TLSA where few predators of Brant exist (Derksen et al. 1979), anthropogenic disturbances are limited (Jensen 1990), extensive grass-sedge foraging sites are abundant (Markon and Derksen 1994) that provide nutrient-rich foods (Derksen et al. 1982), and escape cover (open water, ice floes, and islands) is extensive (Weller et al. 1994).

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