MIGRATION PATTERNS OF BLACK BRANT IN BOUNDARY BAY, BRITISH COLUMBIA

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Abstract: Management strategies to address population declines and changing patterns of winter distribution of black brant (*Branta bernicla nigricans*) require a better understanding of timing of migration and mixing of migrant and wintering birds along the Pacific Coast of North America. We studied migration patterns of brant in Boundary Bay, British Columbia, using population censuses and sightings of individually marked birds during 1994–95 and 1995–96. There was no detectable turnover of individuals through the area in fall, and brant that first arrived in Boundary Bay in November and early December stayed until at least the first week of March. The first spring transients appeared in mid-February 1995 and 1 week later in 1996. The first spring departures coincided with the opening of brant hunting in Boundary Bay in both years, suggesting that early migrants stayed for a shorter period of time in 1996. Spring brant hunting could have adverse effects on reproductive success if migrants depart early from staging areas and opportunities to compensate for decreased nutrient intake farther north are limited. The methods we used could be applied by managers in other areas to establish local hunting regulations appropriate for both wintering and spring staging populations.

Black brant (hereafter, brant) winter along the West Coast of North America and, in small numbers, in Japan (Bellrose 1980). The winter range in North America extends from Alaska to Baja California and the mainland coast of Mexico (Bellrose 1980, Reed et al. 1998). A small proportion of the population winters in Boundary Bay, British Columbia (Campbell et al. 1990).

Winter survey counts have shown that the Pacific Flyway population of brant has declined markedly since 1961 (Derksen and Ward 1993). A similar decline was observed in the number and size of nesting colonies of brant on the Yukon–Kuskokwim Delta, Alaska, in the 1970s and early 1980s (Sedinger et al. 1993). Also, substantial fluctuations have been reported in the number of brant wintering in particular areas of the Pacific Coast. Numbers of brant wintering

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in California have decreased by >50% since the late 1950s, whereas those in Mexico increased substantially (Bellrose 1980).

The Strait of Georgia, which includes Boundary Bay, British Columbia, is an important stopover site for Pacific Flyway brant during spring migration (Campbell et al. 1990). Brant were considered "abundant winter residents" in the vicinity of Boundary Bay and near Vancouver Island at the turn of the 20th century (J. Fannin. 1891. Checklist of British Columbia birds, unpublished. British Columbia Provincial Museum, Victoria, British Columbia, Canada), but Christmas Bird Count data (Campbell et al. 1990, Reed 1997) indicated the number of brant wintering in Boundary Bay declined between 1936 and 1950, and had all but disappeared by 1965. Thereafter, numbers remained low until an increase was noted in 1988 (Reed 1997).

Whether the reduction of brant wintering in Boundary Bay represents a decrease in population size or a change of fall migration and wintering behavior is unclear. In California, increased human activity, especially hunting and

pleasure boating, were believed responsible for the shift in distribution to Mexico (Denson 1964). In British Columbia, hunting during winter was potentially responsible for the observed decline (e.g., Leach 1979).

Prior to 1977–78, hunting seasons in Boundary Bay typically took place over a 3-month period during winter and early spring. Starting in 1977–78, management efforts to protect the wintering population in Boundary Bay involved reducing bag limits and restricting hunting to 1–10 March (W. T. Munro, British Columbia Ministry of Environment, unpublished data) to concentrate the harvest on spring migrants. A decade after introduction of these hunting regulations, the population began to recover (Reed 1997). However, it would be premature to infer from these changes that historical declines reflected anthropogenic factors, and it is important to gain a better understanding of migration patterns of brant to facilitate management of local wintering units throughout the Pacific Flyway. In this paper, we analyze censuses and mark–resight data from individually marked brant to determine migration patterns and to assess the status (resident vs. transients) of brant seen during winter and spring in Boundary Bay.

STUDY AREA

This study was conducted in the Boundary Bay and Roberts Bank area of southwestern British Columbia. Boundary Bay is large and shallow, and 55% of its extensive intertidal area (5,162 ha) is covered by eelgrass (*Zostera marina* and *Z. japonica*; Ward et al. 1992). Within Boundary Bay, an area known locally as Beach Grove contains a freshwater outlet and a spit of gravel and sand. Brant use this spit during winter and spring to rest on land, preen, and ingest grit. The leg band sightings and most of the brant counts analyzed in this paper were collected at Beach Grove. The Roberts Bank area is also important for brant, with >50% (516 ha) of its surface covered by eelgrass (Ward et al. 1992). Use of Roberts Bank varied during winter, and there were no spits where we could read leg bands of brant resting on land; therefore, only brant censuses were conducted in this area. Brant usually were present in the study area from approximately 1 November until the first week of May.

METHODS
Data Collection

Brant have been banded with individually coded plastic leg bands at 5 major breeding or molting locations in Alaska, Russia, and the Northwest Territories since 1986 (Sedinger et al. 1993, Ward et al. 1993, Bollinger and Derksen 1996). During our study, approximately 8% of the brant seen in Boundary Bay had bands. Marked birds have been recorded in winter and spring in Boundary Bay since 1992–93, but we restricted our analyses to large datasets from 1994–95 and 1995–96. We conducted observations from shore with spotting scopes on most days brant were present in Boundary Bay (early Nov–early May). Brant use of the study area varied daily and occurred mostly in the morning. Field effort was thus concentrated in the morning and was constant within seasons and between years (band sighting effort: 91% of possible days in 1994–95, 88% in 1995–96). We also collected information on age, pair, and family status of marked birds, and age ratios of marked and unmarked birds, and we estimated the maximum number of brant present at Beach Grove, Boundary Bay, and Roberts Bank during each visit.

Data Analysis

We used mark–resight analyses to assess the probability of entry and departure of brant into the sampling area. Although these methods generally confound true mortality with permanent emigration, winter mortality of brant is generally low (Ward et al. 1997), and we attributed changes in apparent survival (hereafter, survival) to emigration.

For both years, we could not gather enough data to estimate daily survival rates with satisfactory precision, and we had to pool data into consecutive 7-day periods. Alternate period lengths were tested (2, 5, 7, and 10 days); however, 7 days was the shortest interval for which sufficient data were available, and results were similar to those obtained via longer intervals. Although pooling observations in this way often is necessary to achieve satisfactory precision when data are sparse, doing so violates the assumption that sightings are instantaneous relative to the interval between sightings; that is, individuals seen at the beginning of 1 7-day interval are likely to have a different probability
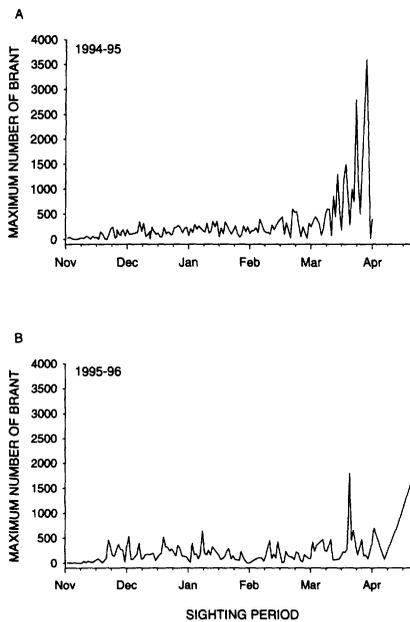
Fig. 1.   Maximum daily number of brant present in Boundary Bay and Roberts Bank, British Columbia during (A) 1994–95, and (B) 1995–96.

of remaining in the area than individuals seen at the end of the same 7-day interval.

Interpretation is further complicated because birds probably do not enter the population at the same time. The fact that birds do not enter the population at the same time will be a problem especially in spring because migration spans a long period and is not synchronous in the population. Individuals arriving later in the study area may not have the same probability of staying in the area as birds that have been present for a longer time.

Brant were present for a maximum of 180 days (26 potential sighting periods). We modeled fall and winter (hereafter, winter) separately from spring data to reflect the influx of transients in spring (see Fig. 1) and to allow for return of fall migrants during spring. Otherwise, individuals seen only in fall and in spring would be considered as having been present in the study area during winter, thus increasing estimates of survival rates, decreasing estimates of sighting rates during winter, and contributing to heterogeneity in sighting rates. Winter included 10 sighting periods from 22 November to 7 February, whereas spring spanned 14 periods from 17 January to 25 April. The first 4 weeks of November and the last week of April were dropped from the mark–resight analyses be-

cause we lacked observations in 1 or both years. We allowed overlap between winter and spring (17 Jan–7 Feb) to provide a stable period prior to onset of migration, which increased precision of parameter estimates at the start of spring migration.

Model Notation.—Model notation followed Lebreton et al. (1992). The factorial structure of a model was represented by subscripting survival (Φ) and sighting rate (p). Relations among factors were indicated via standard linear models notation (McCullagh and Nelder 1989). The general time-specific Cormack-Jolly-Seber model (hereafter, CJS), where survival and sighting probabilities are time-specific, is denoted as (Φ_t, p_t). For models in which survival following the first observation of an individual was allowed to differ from subsequent survival, the notation Φ_{a2} was used, where the subscript "a" reflected structural equivalence with "age" models (sensu Lebreton et al. 1992), and the subscript "2" indicated 2 classes with different survival probabilities (first encounter and subsequent encounters). Sighting probabilities followed the same notation. When general models were identical between years, we tested differences in survival and sighting rates by comparing years as 2 distinct groups in the models. When general models differed, we compared survival rates via program CONTRAST.

Model Selection.—Model selection procedures followed Lebreton et al. (1992). First, we tested fit of the full time-dependent CJS model (Φ_t, p_t) on data from each year separately with goodness-of-fit (GOF) tests provided by program RELEASE (Burnham et al. 1987). Program RELEASE uses 2 tests (TEST2, TEST3) to assess deviations from assumptions of the CJS model. Random variation in observed frequencies relative to expected values may reflect extra binomial variation in the data, whereas systematic deviations may reflect an important biological factor. We paid particular attention to TEST3.SR, which compares, for each sighting occasion, the fates (seen again vs. not seen again) of animals entering the experiment (newly sighted) on a given occasion with those seen previously. Rejection of TEST3.SR suggests a difference in survival among individuals, depending on whether they were seen for the first time on or before sighting occasion (I). A systematic trend in TEST3.SR may reflect true age effects, "handling" effects (Brownie and Robson 1983), transients in the population (Pradel et al.

1997), or sighting heterogeneity (Loery et al. 1987, Prevot-Julliard et al. 1998). In such cases, age-dependent models (i.e., Φ_{a2}, p_t) are more appropriate. We assessed GOF of these models using the sum of chi-square statistics from the 3 remaining GOF tests in RELEASE (TEST3.Sm, TEST2.Cm, TEST2.Ct; Lebreton et al. 1992).

Once a suitable general model was identified via GOF tests, we tested the significance of factors in the model and their interactions by sequential model fitting with program SURGE (Lebreton et al. 1992). To compare nested models, we computed likelihood-ratio tests (LRTs) with the relative deviance for each model provided in the SURGE output. The difference in deviance between nested models is distributed asymptotically as chi-square, with degrees of freedom equal to the difference in number of estimable parameters. The Akaike Information Criterion (AIC) was used to compare unnested models. To decrease our Type II error rate, we used an alpha level of 0.15 for identification of the general model and all subsequent testing, as suggested in Lebreton et al. (1992).

We used model selection tools in program CAPTURE (Otis et al. 1978) to test for heterogeneity in sighting rates. Although models in CAPTURE assume closed populations, it is the only software currently available that allows testing for heterogeneity in sighting rates.

RESULTS

Counts

1994–95 Season.—The first brant were recorded 1 November 1994; thereafter, numbers slowly increased until early December (Fig. 1A). Daily variation in counts occurred throughout the year; however, no major influx was noted from December to early February (maximum = 363 brant; Fig. 1A). An increase to 450 birds on 14 February probably indicated the beginning of spring migration, which peaked during the last half of March (Fig. 1A).

1995–96 Season.—The first brant were recorded 11 November 1995, 10 days later than the previous year (Fig. 1B). Few brant were seen until 21 November, when arrival was apparently complete with >450 brant in the study area. The maximum number of brant observed during winter (634) was higher than the year before, and there was no indication of an early spring migration.

Immigration

To estimate the proportion of immigrants in the population, we divided the number of marked birds seen in the study area for the first time by the total number of marked individuals seen during the same time period (Fig. 2). The pattern was similar both years: (1) a period with a high proportion of marked birds observed for the first time, indicating arrival of brant from fall staging areas; (2) a period with a low proportion of newly sighted marked birds during early December–early March, indicating limited immigration; and (3) a period with a high proportion of new birds associated with arrival of spring migrants. Arrival of spring transients in Boundary Bay occurred a week later in 1996 than in 1995, when the proportion of new birds did not increase until the period 28 February–6 March 1996.

Emigration

Winter: Identification of the General Model.—The basic CJS model adequately fit the data from 1994–95 and was used as a general model for the first winter (TEST2 + TEST3 with sufficient data: $\chi^2_{11} = 9.06$, $P = 0.62$). Although overall results from program RELEASE indicated the CJS model was adequate for winter 1995–96 (TEST2 + TEST3 with sufficient data: $\chi^2_{11} = 14.43$, $P = 0.21$), TEST 3.SR was rejected ($\chi^2_5 = 12.40$, $P = 0.03$). An alternate model including 2 encounter classes fitted the data satisfactorily ($\Phi_{a2 \cdot t}$, p_t: $\chi^2_6 = 2.02$, $P = 0.92$) and was used as a general model for the second winter.

Winter 1994–95.—Survival rates varied linearly with time in winter 1994–95 (Model 2 vs. 1: $\chi^2_7 = 4.57$, $P = 0.71$; Table 1). Further, the slope of the linear model was not significant, so the weekly survival rate was constant during winter (Model 3 vs. 2: $\chi^2_1 = 0.11$, $P = 0.74$). Because there was temporal variation in sighting rates (Model 4 vs. 3: $\chi^2_9 = 35.15$, $P < 0.01$), the model could not be reduced further. Therefore, a model with a constant survival rate and time-specific sighting rates (Model Φ, p_t) explained the data in the most parsimonious way. The estimated survival rate between weekly intervals was 0.965 ± 0.023 ($\bar{x} \pm$ SE not significantly different from 1.00; Fig. 3A), indicating there was little emigration from Boundary Bay between 22 November 1994 and 7 February
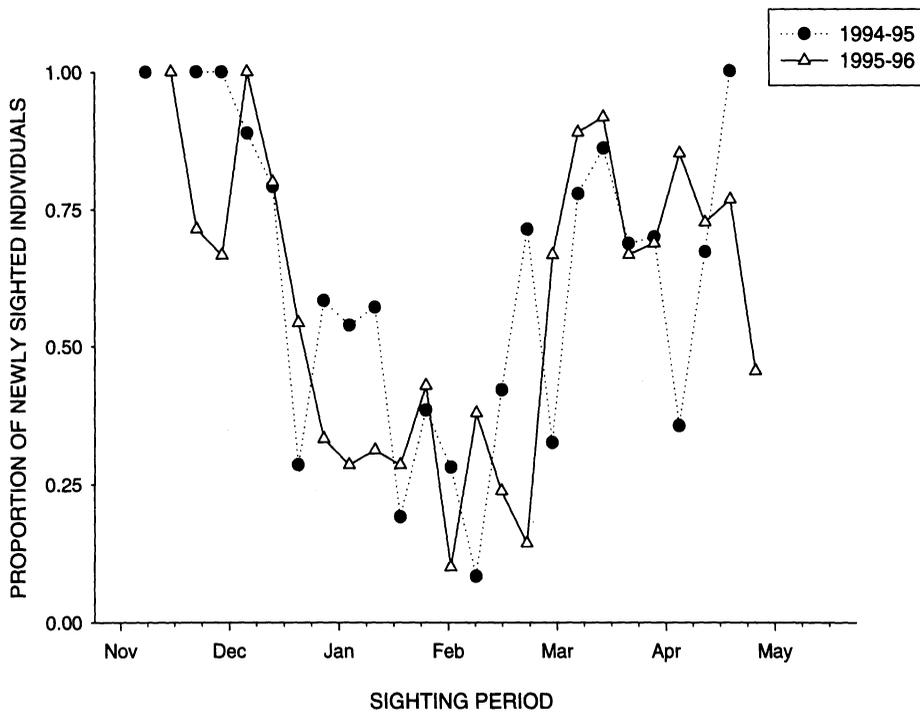
Fig. 2.   Proportion of newly sighted brant for 7-day intervals during 1994–95 and 1995–96 in Boundary Bay, British Columbia. The proportion represents the number of brant individually marked with leg bands that were sighted for the first time divided by the total number of individually marked brant observed during that 7-day interval. This proportion is indicative of the amount of immigration occurring in the study area.

1995. Mean sighting rate was 0.20 ± 0.09 (range = 0.00 ± 0.00 to 0.33 ± 0.08).

Winter 1995–96.—Temporal variation in survival rates of the 2 encounter classes was additive rather than independent (Model 2 vs. 1: χ^2_7 = 8.08, P = 0.43; Table 2). However, we could not constrain survival rates to be linear over time (Model 3 vs. 2: χ^2_6 = 4.03, P = 0.01), or constant (Model 4 vs. 2: χ^2_9 = 17.20, P = 0.05). A model in which the survival estimate of the first encounter class was constant over time and the second estimate of encounter class varied

with time (Model $\Phi_{a1, a2*t}$, p_t) did not provide a better fit when AIC was used for comparison (Model 6: AIC = 445.28 vs. Model 2: AIC = 440.20). A model in which the survival estimates of the first encounter class varied over time and the survival estimates of the second encounter class were constant (Model $\Phi_{a1*t, a2}$, p_t) had a slightly higher AIC than the additive survival model (441.10 vs. 440.20). However, the difference in AIC between models was <1, and we concluded they fit equally well.

Sighting rates could not be constrained in any

Table 1.   Model selection for mark–resighting data on individually marked black brant in Boundary Bay, British Columbia, winter 1995. Sightings are pooled over 7-day periods from 22 November to 6 February. Np = number of parameters, DEV = model deviance, AIC = Akaike's Information Criterion.

No. and model[a]	Np	DEV	AIC[b]	Likelihood-ratio test[c]
(1) ϕ_t, p_t	19	395.47	433.47	
(2) ϕ_{lin}, p_t	12	400.04	424.04	(2) vs. (1): χ^2_7 = 4.57, P = 0.71
(3) ϕ, p_t	11	400.15	422.15	(3) vs. (2): χ^2_1 = 0.11, P = 0.74
(4) ϕ, p	2	435.30	439.30	(4) vs. (3): χ^2_9 = 35.15, P < 0.01

[a] Subscripts indicate factors allowed to vary. For Example, in Model 2, ϕ varies linearly over time, and resighting rates (p) vary for each sighting period without constraints.
[b] Smallest AIC values indicate the most appropriate model and were used to compare unnested models such as Model 2 and Model 3.
[c] Likelihood-ratio tests compare a general model with its reduced form (nested models).
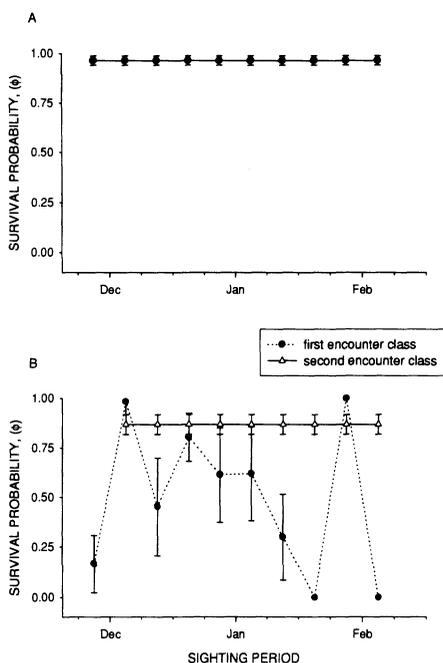
Fig. 3. Apparent survival estimates for the (A) 1994–95 winter period (22 Nov 1994–7 Feb 1995) in Boundary Bay, British Columbia (derived from Model [Φ, p_t]), and (B) 1995–96 winter period (derived from Model [$\Phi_{a1\cdot t, a2}$, p_t]). The first encounter class refers to survival probabilities following the first sighting of an individual in the study area, and the second encounter class refers to survival probabilities for individuals seen in >1 7-day period.

way. Model $\Phi_{a1\cdot t, a2}$, p_t was consistent with the model selected for winter 1994–95, where resident wintering birds (i.e., the second encounter class in the winter 1995–96 model) had a constant survival rate from 22 November 1995 to 7 February 1996, so we chose it for further analysis. Mean (± SE) survival of winter residents (second encounter class) was 0.868 ± 0.050 (Fig. 3B) during winter 1995–96 and was not different ($P > 0.05$) from the estimate (0.965 ±

0.023) for winter 1994–95. Mean sighting rate was 0.37 ± 0.13 (range = 0.06 ± 0.01 to 1.00 ± 0.00).

Using program CAPTURE (Otis et al. 1978), we determined that heterogeneity in sighting rates was not important in winter 1994–95 (best models: M_{tb} [1.00] and M_b [0.85]), but heterogeneity in sighting rates was in winter 1995–96 (best models: M_{tbh} [1.00] and M_{th} [0.88]). Although 3 of these models indicated presence of trap response, we did not think this result had a biological meaning, because we did not capture the birds, and the sighting method should not have influenced behavior.

Spring: Identification of the General Model.—Goodness-of-fit tests from program RELEASE indicated assumptions of the CJS model were not met for the spring 1995 data (TEST2 + TEST3 with sufficient data: $\chi^2_{16} = 27.22$, $P = 0.04$). Most of the variation could be explained by TEST3.SR ($\chi^2_5 = 15.31$, $P = 0.01$); all cells contributing to this test deviated in the same direction, indicating that birds entering the population at a given time period were less likely to be seen again than those sighted previously. Adding an encounter effect on survival resulted in a better fit (Model $\Phi_{a2\cdot t}$, p_t: $\chi^2_{11} = 11.91$, $P = 0.37$) and an acceptable general model.

We did not have sufficient data to calculate TEST3.Sm or TEST2.Cm for spring 1996. However, TEST3.SR was rejected ($\chi^2_4 = 9.18$, $P = 0.06$), and all cells deviated in the same direction as the 1995 data. Because TEST2.Ct was not significant ($\chi^2_3 = 0.95$, $P = 0.81$), we used a model with 2 encounter classes [$\Phi_{a2\cdot t}$, p_t] as a general model. Because the general model was the same for both years, we could directly compare years as 2 distinct groups.

Table 2. Model selection for mark–resighting data on individually marked black brant in Boundary Bay, British Columbia, winter 1996. Sightings are pooled over 7-day periods from 22 November to 6 February. Np = number of parameters, DEV = model deviance, AIC = Akaike's Information Criterion.

No. and model[a]	Np	DEV	AIC[b]	Likelihood-ratio test[c]
(1) $\phi_{a2\cdot t}$, p_t	28	392.12	448.12	
(2) ϕ_{a2+t}, p_t	20	400.20	440.20	(2) vs. (1): $\chi^2_8 = 8.08$, $P = 0.43$
(3) $\phi_{a2lin+t}$, p_t	14	416.74	444.74	(3) vs. (2): $\chi^2_6 = 16.54$, $P = 0.01$
(4) ϕ_{a2}, p_t	12	417.40	441.40	(4) vs. (2): $\chi^2_8 = 17.20$, $P = 0.03$
(5) $\phi_{a1\cdot t, a2}$, p_t	21	399.10	441.10	
(6) $\phi_{a1, a2\cdot t}$, p_t	21	403.28	445.28	
(7) ϕ_{a2+t}, p	12	431.80	455.80	(7) vs. (2): $\chi^2_8 = 31.60$, $P < 0.001$

[a] Subscripts indicate factors allowed to vary. All models have a 2 encounter-class structure in ϕ. See RESULTS for description of the models.
[b] Smallest AIC values indicate the most appropriate model and were used to compare unnested models such as Model 4 and Model 7.
[c] Likelihood-ratio tests compare a general model with its reduced form (nested models).

Table 3. Model selection for mark–resighting data on individually marked black brant in Boundary Bay, British Columbia, springs 1995 and 1996. Sightings are pooled over 7-day periods from 17 January to 25 April. Np = number of parameters, DEV = model deviance, AIC = Akaike's Information Criterion.

No. and model[a]	Np	DEV	AIC[b]	Likelihood-ratio test[c]
(1) $\phi_{a2 \cdot t \cdot yr}, p_{t \cdot yr}$	74	1,651.88	1.799.88	
(2) $\phi_{a2 \cdot t}, p_{t \cdot yr}$	51	1,675.88	1,777.88	(2) vs. (1): $\chi^2_{23} = 24.00, P = 0.40$
(3) $\phi_{a2 \cdot t \cdot yr}, p_t$	62	1,681.76	1,805.76	(3) vs. (1): $\chi^2_{12} = 29.88, P < 0.01$
(4) $\phi_{a2 \cdot t}, p_t$	37	1,751.57	1,825.37	(4) vs. (2): $\chi^2_{14} = 75.69, P < 0.001$
(5) $\phi_{3cons, 10a2 \cdot t}, p_{t \cdot yr}$	47	1,680.67	1,774.67	
(6) $\phi_{5cons, 8a2 \cdot t}, p_{t \cdot yr}$	43	1,682.58	1,768.58	
(7) $\phi_{5cons, 8a2 + t}, p_{t \cdot yr}$	35	1,686.24	1,756.24	(6) vs. (5): $\chi^2_{14} = 10.13, P = 0.75$

[a] Subscripts indicate factors allowed to vary. Models 5–7 have a constant ϕ for the first 3, 5, and 7 sighting periods, respectively, whereas the remaining ϕ have a 2 encounter-class structure for the remainder of the spring period. See RESULTS for a detailed description of models.
[b] Smallest AIC values indicate the most appropriate model and were used to compare unnested models.
[c] Likelihood-ratio tests compare a general model with its reduced form (nested models).

Further Modeling.—There was no annual variation in survival (Model 2 vs. 1: $\chi^2_{23} = 24.00, P = 0.40$), but there was variation in sighting rates (Model 3 vs. 1: $\chi^2_{12} = 29.88, P < 0.01$; Model 4 vs. 2: $\chi^2_{14} = 75.69, P < 0.001$; Table 3). Thus, we could pool data between
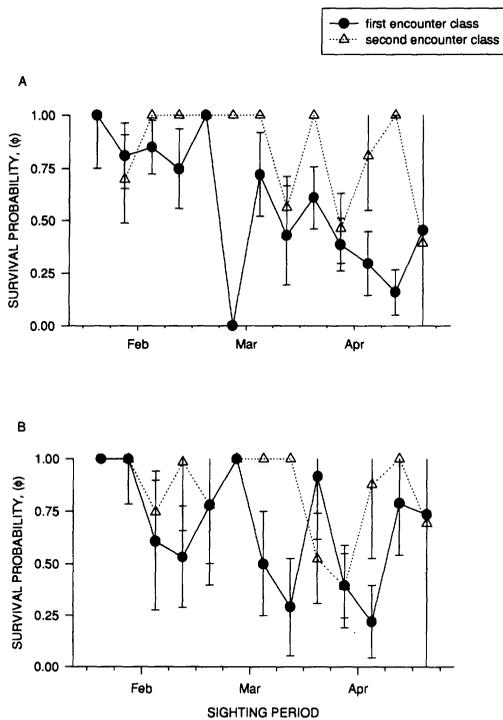

Fig. 4. Apparent survival estimates for (A) spring 1995 and (B) spring 1996 (17 Jan–25 Apr) in Boundary Bay, British Columbia. Estimates are derived from the general Model [$\Phi_{a2 \cdot t \cdot yr}$, $p_{t \cdot yr}$]. The first encounter class refers to survival probabilities following the first sighting of an individual in the study area, and the second encounter class refers to survival probabilities for individuals seen in >1 7-day period. The spring period overlapped with the winter period to increase precision of parameter estimates at the beginning of spring.

years to model survival but not sighting rates. The first 3 sighting periods in spring (17 Jan–7 Feb) were the same as the last 3 periods of winter. Because models derived from the winter data indicated survival for these 3 periods was constant, we fitted a model where the first 3 survival estimates were constant and the remaining 10 were time dependent with 2 encounter classes. This model ($\Phi_{3cons, 10a2 \cdot t}$, $p_{t \cdot yr}$) fit better than model ($\Phi_{a2 \cdot t}$, $p_{t \cdot yr}$) when compared with AIC.

We knew that birds were entering the population between the second and the third week of February because of increases in population size (Fig. 1) and in the proportion of newly sighted banded individuals (Fig. 2); however, because sighting rates were low, we did not know exactly when birds departed. Results from the general model [$\Phi_{a2 \cdot t \cdot yr}$, $p_{t \cdot yr}$] indicated departures started at the end of February or early March (Fig. 4). However, further comparisons were required to test specific hypotheses concerning spring departure because large standard errors affected survival estimates and prevented us from drawing strong conclusions.

Several combinations of intervals were tested. A model in which the first 5 survival rates (17 Jan–28 Feb) were held constant and the remaining 8 (1 Mar–25 Apr) were encounter- and time-dependent (Model $\Phi_{5cons, 8a2 \cdot t}$, $p_{t \cdot yr}$) had the lowest AIC (Table 3), suggesting birds did not start to emigrate from the study area before the first week of March. Pooling the 1995 and 1996 data resulted in lower survival estimates between 17 January and 28 February than estimated by the winter models, because heterogeneity in sighting rates from winter 1996 was not accounted for. When we constrained the
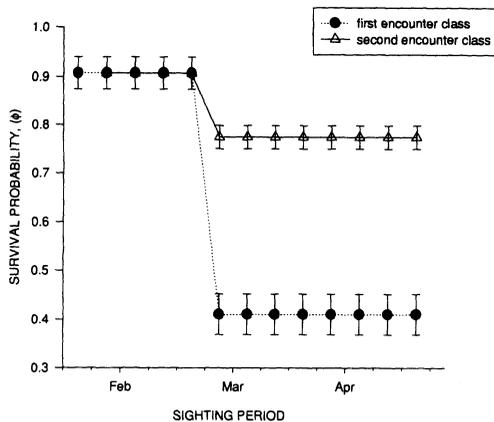
Fig. 5. Apparent survival estimates for spring 1995 and 1996 (17 Jan–25 Apr) in Boundary Bay, British Columbia. The first encounter class refers to survival probabilities following the first sighting of an individual in the study area, and the second encounter class refers to survival probabilities for individuals seen in >1 7-day period. Estimates were derived from Model [$\Phi_{5cons, 8a2+b}$ p_{t*yr}]. The spring period overlapped with the winter period to increase precision of parameter estimates at the beginning of spring.

last 8 survival estimates to be constant over time but different between encounter classes (Model 7 vs. 6: $\chi^2_{14} = 10.13$, $P = 0.75$), this model fit the data better than the model where survival of both encounter classes was constant (Model Φ_{a2}, p_{t*yr}). This model provided further evidence that brant did not start emigrating from the study area until the first week of March (Fig. 5). The model also suggested the rate of emigration from Boundary Bay was constant during spring migration (Fig. 5), at least until 25 April. The mean (± SE) sighting rate was 0.22 ± 0.06 (range = 0.00 ± 0.00 to 0.51 ± 0.09) during spring 1995, and 0.21 ± 0.09 (range = 0.04 ± 0.01 to 0.47 ± 0.29) during spring 1996.

DISCUSSION

Survival estimates for winter 1994–95 and 1995–96 (Fig. 3) were high and constant during 22 November to 7 February, indicating there was no important turnover of brant in Boundary Bay in the fall. Census data also indicated there was no major passage of transients through Boundary Bay prior to 22 November. Thus, Boundary Bay is not a staging area for brant wintering on the West Coast of the United States or Mexico. These results are consistent with Dau (1992), who suggested brant migrated directly from their autumn staging area in Iz-

embek Lagoon, Alaska, to wintering grounds in Baja California.

We estimated weekly survival rates during winter 1994–95 as 0.965 ± 0.023 (Fig. 3A). True survival of brant during winter has been estimated at 1.00 ± 0.0 (Ward et al. 1997); thus, any departure from a survival rate of 1.00 is likely a result of emigration. Although our results indicate there was a resident group of brant wintering in Boundary Bay, there was some emigration (approx 3%/week) during winter 1994–95. A similar pattern was observed in winter 1995–96, when there were 2 encounter classes in the model (Fig. 3B). The constant survival rate for the second encounter class (0.868 ± 0.050 and not significantly different from the estimate for winter 1994–95) suggested emigration was more prevalent during winter 1995–96. The weather during that winter was harsh, and Boundary Bay was frozen for several days in January, which likely decreased food availability and increased emigration. Similarly, Pradel et al. (1997) reported small numbers of green-winged teal (*Anas crecca*) emigrated from wintering areas despite favorable weather, whereas exceptional departures occurred during cold spells.

Including encounter classes in the model for winter 1995–96 was necessitated by violation of the assumption of equal sighting probability of individuals under the CJS model. Heterogeneity in sighting rates was indicated by poor fit of the general CJS model and by model selection with program CAPTURE (Otis et al. 1978). Heterogeneity can affect model selection and negatively bias survival estimates in CJS models. Estimates of survival in the general models are biased, whereas only survival estimates from the first age or encounter class are affected in age- or encounter-structured models (Loery et al. 1987, Prevot-Julliard et al. 1998). Heterogeneity may have influenced parameter estimates for winter 1994–95, but it was not detected during model selection. Heterogeneity is common in mark–recapture experiments, but relatively few studies have assessed its effect on model selection and parameter estimation. Future research should concentrate on these problems and on ways to remove the bias in survival estimates.

Fluctuations in daily counts (Fig. 1), band observations, and radiotracking data suggest temporary emigration between Boundary Bay and nearby areas (i.e., Birch Bay, Lummi Bay, and Padilla Bay in northern Washington, and Sidney

Island and Vancouver Island in British Columbia; Reed 1997). Thus, differences in heterogeneity of sighting probabilities among individuals between winter 1994–95 and 1995–96 were likely caused by different movement rates between Boundary Bay and adjacent sites.

Differences in movement rates may have been due to higher recruitment in winter 1995–96 (21.0% juv) than in winter 1994–95 (5.3%). Family bonds in brant usually are maintained throughout winter and into spring (Reed 1993). Thus, because family groups of geese are dominant over pairs without goslings and single birds (Lamprecht 1986, Black and Owen 1989), increased competition could occur during winters of years in which production of young is high, which, in turn, could lead to increased dispersal of subordinate individuals and heterogeneity in sighting rates. Lambeck (1990) also noted that family groups of brent geese (*B. b. bernicla*) were more exploratory than individuals without goslings, suggesting increased rates of movement during high production years.

Arrival of resident brant on the wintering grounds in fall 1995–96 was later than in 1994–95, coincident with a 1-week delay of spring migration in 1996. We do not know if this delay represents normal variation in migration phenology or indicates 1996 was truly a late year and brant were not physiologically ready to migrate at the same time in 1996 as they were in 1995. In Boundary Bay, 12.4% (*n* = 484 observations) of all marked individuals sighted during 1994–95 were subsequently seen in other locations of coastal British Columbia during spring migration (R. I. Goudie, unpublished data). After accounting for sighting probabilities (0.70 ± 0.08 in Boundary Bay and 0.70 ± 0.05 in Qualicum, British Columbia, during spring 1995; Reed et al. 1998), the probability of observing interchange between these sites was 0.49. The high number of birds stopping at different sites in the same general area in spring provides evidence for a "stepping-stone" migration and may reflect the need for brant to avoid depleting reserves and deposit fat during spring migration so that they arrive on the breeding grounds with sufficient energy reserves to produce and lay a clutch of eggs (Ankney and MacInnes 1978, Ankney 1984, Ebbinge and Spaans 1995). Advantages of accumulating sufficient body reserves prior to spring migration might constrain the amount of time brant spend on the wintering grounds. However, we cannot dis-

regard other factors, such as weather patterns and food availability, in explaining the difference between years. A comparative study of body condition of early migrants in early, normal, and late years would provide a better understanding of factors controlling spring migration phenology.

Although arrival of migrants was delayed by 1 week in spring 1996, our model suggested that timing of departure from Boundary Bay did not differ between years (Fig. 5). The first major movement of brant migrating from Boundary Bay occurred between the last week of February and the first week of March in both years, coincident with the opening of the brant hunting season. Although we could not distinguish effects on emigration resulting from hunting disturbance, mortality, and voluntary emigration, spring hunting may have influenced timing of migration. Therefore, the first migrants to arrive in Boundary Bay in 1996 stayed for a shorter period in Boundary Bay than the first migrants in 1995.

Chronology of spring migration differs between ages among brant, and paired breeders generally are the first migrants (Palmer 1976). If hunting pressure influences migration patterns of brant, the spring hunt in Boundary Bay could adversely affect nutrient acquisition for early migrants in years when migration is delayed, especially if opportunities to acquire nutrients elsewhere are limited. Thus, the most productive segment of the population could have reduced breeding success. Spring hunting also can adversely affect breeding success if 1 member of a pair is killed and the other member does not have enough time to acquire another mate before the breeding season.

Two categories of spring migrants were represented in the models: those that staged in Boundary Bay for a short period of time (first encounter class), and those that staged for an extended period of time (second encounter class). When probabilities of survival are constant over a period, such as is in our study, we can estimate mean residence time as $1/-\ln(\Phi)$ (Brownie et al. 1985). Some spring migrants remained in the study area for an estimated 1.1 period (8 days; first encounter class), whereas others stayed for 3.9 periods (27 days; second encounter class). Thus, some brant seemed to be using Boundary Bay as their primary staging site, whereas others only stopped briefly. We do not know if these different patterns of use of

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Boundary Bay reflect different migration strategies or if brant that had a short residence time staged in other areas for extended periods.

The method we used to analyze migration patterns will allow researchers to detect migratory events in a given area by estimating emigration rates more precisely than with conventional census techniques. This technique would provide a useful tool for managers when concerns pertaining to individual stocks or populations arise. The technique would also be useful for research planning if 1 component (e.g., residents vs. transients) of a population or 2 distinct sympatric populations, each with different movement or survival patterns, are targeted for study.

MANAGEMENT IMPLICATIONS

Management of local populations must account for factors that may influence other local populations or larger metapopulations. Our study indicates the first detectable emigration from Boundary Bay occurred concurrently with the opening of the brant hunting season (1–10 Mar) during spring 1995 and 1996. Individuals from different wintering subpopulations were likely affected by spring hunting in Boundary Bay because spring migrants were present in the area during the legal hunting season in both years.

On a local scale, existing harvest regulations seem to fulfill the mandate of protecting the resident population wintering in Boundary Bay because mostly spring migrants are harvested, and the number of birds killed is small ($\bar{x} = 223$ for 1995 and 1996; Reed 1997). Although the strategy of delaying the hunting season did not result in an immediate population increase, the wintering population is now recovering (Reed 1997). Arrival of spring migrants should be closely monitored if spring hunting is used as a management tool for this or other wintering brant populations.

Brant wintering and staging in Boundary Bay during spring include birds from most major breeding and molting areas (Reed et al. 1998). Hence, local management could have implications for the entire Pacific Flyway brant population. The migration patterns of brant we documented could be representative of the Pacific Coast of North America. Until further studies describe the migration patterns of brant in other localities of the Pacific Coast of North America, the results presented in this study should help managers establish harvest regulations appropriate for both wintering and spring staging stocks of brant.

ACKNOWLEDGMENTS

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