

Estimating Numbers of Black Brant Using Sequential Spring-Staging Sites

KATHERINE R. HAGMEIER,^{1,2} *Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada*

BARRY D. SMITH, *Science & Technology Branch, Environment Canada, 5421 Robertson Road, Delta, BC V4K 3N2, Canada*

W. SEAN BOYD, *Science & Technology Branch, Environment Canada, 5421 Robertson Road, Delta, BC V4K 3N2, Canada*

ABSTRACT Estimating total number of birds using a particular staging site during migration is challenging because counts alone do not account for turnover in the local population. Robust statistical methods are needed to more fully assess the conservation value of such sites. We used the multi-strata model in Program MARK to estimate time-dependent transition probabilities between sequential staging sites to estimate lengths of stay for spring-staging Pacific black brant (*Branta bernicla nigricans*) on the Fraser River delta and Parksville-Qualicum areas in the Strait of Georgia, British Columbia, Canada. Using resightings of marked individuals in combination with ground counts, we estimated the total number of brant, with associated uncertainties, staging at these sites during the spring migrations of 1999 and 2000. We estimated between 28,927 and 33,181 individual brant transited the Fraser River delta and Parksville-Qualicum sites in 1999 and between 21,621 and 25,405 individuals in 2000. These totals correspond to approximately 18–26% of the entire Pacific Flyway brant population, suggesting the need for continued conservation and management efforts at these sites. Given the importance of staging sites to migratory populations, we believe this method could be applied to other species and locations. (JOURNAL OF WILDLIFE MANAGEMENT 72(6):1342–1351; 2008)

DOI: 10.2193/2007-145

KEY WORDS abundance, brant, *Branta bernicla nigricans*, British Columbia, capture–mark–recapture, leg-bands, multi-strata, Program MARK, spring staging, volume estimates.

Spring-staging is a critical phase in the annual cycle of Arctic-nesting geese. Condition of spring staging habitats and behavior of birds during this time can have important consequences for individual fitness and, subsequently, population dynamics. Nutrient reserves accumulated at staging sites are used by both males and females to fuel northward migration and by females to develop and incubate eggs (Ankney and MacInnes 1978, Raveling 1979, Ebbinge 1988, Black et al. 1991).

Arctic-nesting geese exhibit fidelity to spring-staging sites (Greenwood 1980). This dependence upon traditional staging sites means that changes to, or loss of, these sites may negatively affect nutrient acquisition rates and hence overall fitness at the population level. Conservation efforts require an understanding of the relative importance of known staging sites, which is equivalent to the total number of birds (i.e., vol) using the site (Thompson 1993, Frederiksen et al. 2001). For populations transiting staging sites (i.e., migrating birds) estimating volume requires that residence times be estimated in addition to abundance (Frederiksen et al. 2001).

Previous volume estimates for Arctic geese have been generated through statistical (e.g., Routledge et al. 1999) and modeling approaches (e.g., Frederiksen et al. 2001). The statistical approach uses estimates of mean residency (or length of stay [LOS]) and counts. Because LOS varies among individuals and over time (van Eerden et al. 1991), use of a mean value for an entire staging period may bias volume estimates and underestimate uncertainty in the

calculation of volume (Frederiksen et al. 2001). Frederiksen et al. (2001) used estimates of bird abundance in combination with survival probabilities for birds at a staging site to improve volume estimation. In the latter application, survival probability refers to the probability of a bird remaining at a site for a specified time interval, a metric directly related to LOS.

We used capture–mark–recapture data in conjunction with counts for specified time periods to yield estimates of volume and associated uncertainty to estimate total number of Pacific black brant (*Branta bernicla nigricans*; hereafter, brant) staging on the Fraser River delta (FRD) and at Parksville-Qualicum (PQ) in the Strait of Georgia, British Columbia, Canada. Together, these sites account for >75% of all brant staging in the Strait (K. R. Hagmeier, EBB Environmental Consulting Inc., unpublished data; E. L. Nygren, Nygren Consulting, unpublished reports). Brant from wintering areas to the south start arriving in the Strait by late February and reach a peak by late March or early April. Reed et al. (1998c) documented levels of interannual fidelity of 81% and 87%, respectively, to these sites. Although brant have been counted over many years, the actual total numbers of individuals staging at these 2 sites have never been estimated. Consequently, the relative importance of these sites to the Pacific Flyway Brant Population (PFBP) is difficult to ascertain. Our objective was to develop a method that allowed us to estimate the volumes of brant, with associated uncertainties, transiting two important staging sites on the Strait of Georgia, British Columbia. In addition, we would be able to estimate the extent of interchange, if any, between the sites to help assess the importance of the sites to the PFBP.

¹ E-mail: hagmeier@ebbconsulting.ca

² Present address: EBB Environmental Consulting Inc., P.O. Box 18180, 1215c 56th Street, Delta, BC V4L 2M4, Canada



Figure 1. North America, highlighting the Strait of Georgia, British Columbia, Canada, and showing the 2 most important staging sites there for brant during spring migration (from mid-Feb to May): the Fraser River delta site (collectively Roberts Bank, Point Roberts, and Boundary Bay) near the city of Vancouver on the mainland coast, and the Parksville-Qualicum site (collectively Qualicum Bay and Parksville) on the east coast of Vancouver Island, where we observed birds in 1999–2000. Wintering (Baja California, Mexico) and breeding (Izembek Lagoon and the Yukon-Kuskokwim Delta, AK) areas are also shown.

STUDY AREA

The FRD is located near the city of Vancouver on the mainland coast of British Columbia (approx. 49°N), and PQ is on the east coast of Vancouver Island (Fig. 1). Specific study sites on the FRD included Boundary Bay and Roberts Bank (BC) and Point Roberts (WA; Fig. 1). The PQ study site consisted of a 17-km stretch of beach between Parksville and Qualicum, designated as a provincial Wildlife Management Area.

The FRD is the largest estuary in British Columbia and one of the most important ecosystems for migrant and wintering waterfowl in Canada (Important Bird Areas Canada 2004). At low tide, expansive mudflats and eelgrass beds (*Zostera marina* and *Z. japonica*) were exposed. The PQ site was characterized by beaches and eelgrass. Each spring along the PQ coastline, Pacific herring (*Clupea pallasii*) broadcast roe on eelgrass and adjacent beaches, providing a pulse of nutrients for migrating waterbirds, including brant.

Upland areas adjacent to both the FRD and PQ sites were experiencing high human population growth rates (British Columbia Ministry of Labor and Citizens' Services 2006).

As a result, these sites were under increasing threat from urban and industrial development and pressure from recreation and tourism (Transboundary Georgia Basin-Puget Sound Environmental Indicators Working Group 2002).

METHODS

Data Collection

Beginning in 1985, brant have been marked on their northern breeding and molting grounds with individually coded, plastic leg bands (Lindberg et al. 1998). These bands are readable with a 60× spotting scope at a distance of up to 300 m (Sedinger et al. 1995). Roughly 8–10% of the brant observed in British Columbia carry these bands (Reed 1997; K. R. Hagmeier, unpublished data). Most of the marked birds we observed were tagged on the Yukon-Kuskokwim Delta, Prudhoe Bay, and Teshepuk Lake (AK), on Banks Island in Arctic Canada and on Wrangel Island (Russia).

We recorded leg-bands daily at the FRD and PQ sites from mid-February until mid-May in 1999 and 2000. Each survey involved driving a specific coastal route to access all beaches and embayments used by staging brant. Generally, surveys were conducted by 1–2 observers each day, and travel direction was alternated on consecutive days. We estimated abundance daily at PQ but only 2–3 times per week on the FRD.

Multi-Strata Model of Brant Residency

Program MARK's multi-strata model (White and Burnham 1999) is an extension of the generalized Cormack-Jolly-Seber model, which facilitates estimation of transition probabilities between strata (Hestbeck et al. 1991, Brownie et al. 1993). In our study, strata refer to geographic locations along a northward migration route transited by migrating brant. The conceptual design of our model required that, in addition to the FRD and PQ sites, we needed 2 additional reference sites to model northern migration through the Strait of Georgia. We defined the first site as, collectively, all sites south of the Strait of Georgia, where migration begins. We defined the fourth site as, collectively, all sites north of the Strait of Georgia, where migration ends, such that the 4 strata were A = south (migration starts), B = FRD (staging site), C = PQ (staging site), and D = north (migration ends).

A complete encounter history records the stratum where the bird is seen in a particular time interval, in our case a weekly interval, e.g., AAAB0BB0BBBDDDD, where 0 represents no sighting, and where we tacitly assume that brant were in stratum A before arrival at stratum B or C, then arrived in stratum D once having departed stratum B or C. Note that although strata B and C are geographically close, movement from B to C or C to B was extremely rare. For each year, we divided our capture-mark-recapture (CMR) data into 7-day periods, which is a compromise between a loss of resolution in the raw data and a manageable amount of data and associated parameters for analysis. As illustrated in the above-mentioned example encounter history, 15 weekly periods covered the time from

mid-February until the end of May, with those weekly periods corresponding across years and strata.

Before analysis, we divided the leg-band data into 2 groups and modeled them separately for each year. Group 1 contained band data for birds observed only once within a year (hereafter single-sight data), and group 2 contained data for birds observed multiple times (hereafter multi-sight data). Notwithstanding that we may have missed some single-sight birds during searches, these groups represented 2 qualitatively distinct staging patterns consistent with previous observations of brant staging in the Strait of Georgia (Routledge et al. 1999). Single-sight brant did not seem to use staging sites to accumulate body reserves but moved quickly through the area. Conversely, multi-sight birds staged for varying lengths of time, accumulating reserves for flight to and breeding on the Arctic nesting grounds. Using the multi-strata Recaptures Only option in MARK, we used 3 separate analyses for each year to estimate transition probabilities for the following movement segments: 1) single-sight A to B or C, 2) multi-sight A to B or C, and 3) multi-sight B or C to B, C, or D. (Note that single-sight B or C to D is equivalent to single-sight A to B or C, positively offset by 1 week, and that the multi-sight models accommodated the rare, but observed, transition between strata B and C.)

Model notation followed Cooch and White (2007) where p_i^r = probability that a marked bird in stratum r at time i is sighted at time i .

Ψ_i^{rs} = transition probability that a marked bird in stratum r at time i is in stratum s at time $i + 1$.

We defined apparent survival between strata as $\Phi_i^{rs} = S_i^r \Psi_i^{rs}$ where we assumed probability of individual survival S_i^r to be 1 because mortality during the low-risk staging tenures is considered insignificant (Hestbeck et al. 1991, Reed et al. 1998c), thus $\Phi_i^{rs} = \Psi_i^{rs}$.

Standard assumptions for CMR analysis included 1) every marked bird had the same probability (p) of being observed, 2) all observations were considered equally likely within the time interval i , 3) individuals and individual fates were independent, 4) marking of individuals was random, and 5) there were no behavioral effects from marking (Seber 1982, Pollock et al. 1990, Hestbeck et al. 1991). Assumptions specific to our MARK analyses included 1) leg-band data sets contained insignificant observation errors, 2) mortality between weekly time periods was negligible (i.e., $S_i^r = 1$), 3) probability of sighting on stratum A = 1, because we considered an individual to be in stratum A until it was observed in either B or C, 4) probability of sighting on stratum D = 1, because we considered an individual to have arrived in stratum D when it was no longer observed in either B or C, 5) once in stratum B or C, individuals could not return to A (i.e., spring migration was consistently north), and 6) once in stratum D, individuals could not return to B or C (i.e., spring migration was consistently north).

We used MARK's Multi-strata Recaptures Only option to evaluate competing model structures to describe the pattern

of the transition probabilities among strata over time. We determined that we had sufficient data to entertain model structures that presumed that transitions probabilities varied either independently by week, or as logit-linear or logit-quadratic functions of week or cohort. A cohort refers to all brant arriving on a stratum in a particular week. We chose the best models based on the Quasi Akaike's Information Criterion adjusted for small sample size (QAIC_c), to take into account the extra-binomial dispersion of error variance resulting from the nonindependent behavior of individual birds (Anderson et al. 1994, Burnham and Anderson 2002). Because MARK does not offer a parametric bootstrap goodness-of-fit (GOF) test for multi-strata models, we estimated \hat{c} conservatively using the mean of 1,000 deviance values obtained by generating randomized encounter history frequencies from the expected encounter history frequencies for comparison with the deviance obtained from the observed encounter history frequencies (see Pollock et al. 1990 on GOF testing).

Length of Stay

The expected LOS for an individual brant in the multi-sight category was estimated for each weekly cohort of brant. First, for each of FRD and PQ we sequentially calculated the unconditional probability of a brant leaving stratum B or C in week i (pD_i), having first been seen on that stratum in week w ($1 < w < k - 1$) where

$$pD_i = (1 - pR_i) \left(1 - \sum_{j=w}^{i-1} pD_j \right)$$

for $i <$ the last week (k) of staging at the stratum

$$pD_i = \left(1 - \sum_{j=1}^{i-1} pD_j \right) \quad \text{for } i = k,$$

where pR_i is MARK's estimate of the conditional probability of remaining at the stratum in week i having been present there in week $i - 1$, and j is an index for week. We then calculated expected LOS (T_w) for each arrival week, w , as

$$T_w = \sum_{i=w}^k pD_i.$$

We corrected a posteriori the values for LOS we calculated above for the assumption that birds arrived on stratum B or C the first week they were observed, using the multi-sight resighting probabilities (p_i^r) estimated generated by MARK. We did not apply these adjustments to the single-sight data, because we defined birds in the single-sight category as those that arrived and departed within the week in which they were observed.

We calculated the revised estimate for the week of arrival (\hat{A}) using

$$\hat{A} = \sum_{i=1}^w iP'_{A,i}$$

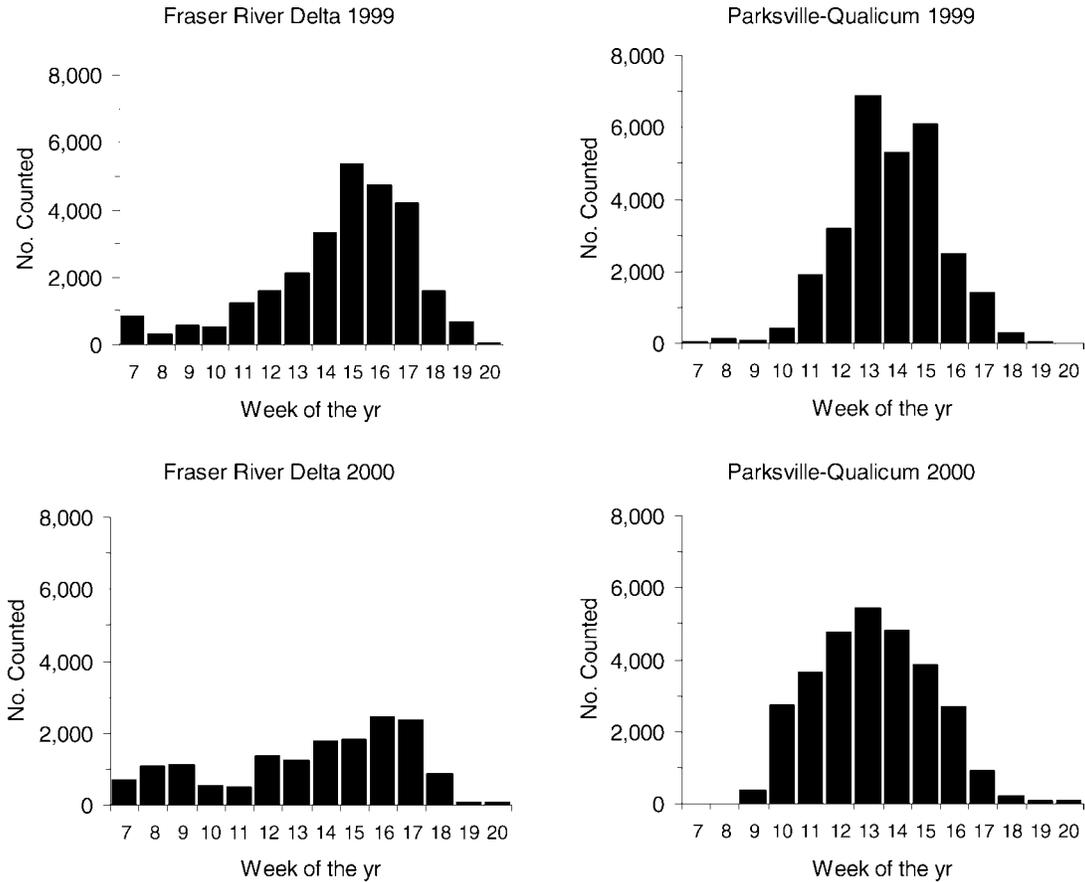


Figure 2. Weekly surveys of Pacific Flyway Brant on the Fraser River Delta and Parksville-Qualicum, British Columbia, Canada, spring-staging sites in 1999 and 2000. We took weekly counts to be the maximum number of brant counted on any day of that week.

where w is the first week a marked bird was seen, i is week, and $P'_{A,i}$ is the probability that the marked bird arrived in week i or later if it had not been seen before w . We calculated $P'_{A,i}$ as

$$P'_{A,i} = P_{A,i} \prod_{j=i}^w (1 - p_j^r)$$

where

$$P_{A,i} = \left(\frac{1}{N - \sum_{j=1}^{i-1} 1} \right),$$

i.e., the probability that the marked bird arrived in week i , given it had not arrived before i and p_i^r is the probability of a marked bird having been seen in week $i = 2, \dots, N$, given that it was present. We estimated the standard error of \hat{A} as follows:

$$\hat{S}_A = \sqrt{\sum_{i=1}^w i^2 P'_{A,i} - \hat{A}^2}.$$

Volume Estimates

We calculated volume estimates for each stratum by summing the independently estimated numbers of single-sight and multi-sight brant that arrived each week. First, for each week we estimated the abundance from the count data

and the proportion of birds that were classified as single-sight or multi-sight from the band observation data, which led directly to an estimate of the volume of single-sight brant

$$\hat{V}_{SS} = \sum_{i=1}^k (n_i)(pSS_i)$$

where \hat{V}_{SS} is the volume estimate for single-sight brant, n_i is the estimate of weekly abundance, and pSS_i is the proportion of single-sight brant in the week. Second, for each week we derived an estimate of the number of multi-sight brant from $M_i = (n_i)(pMS_i)$, where M_i is the number of multi-sight brant, n_i is the estimate of weekly abundance taken as the maximum daily count for that week, and pMS_i is the proportion of multi-sight brant in the week.

We estimated total volume of multi-sight brant using M_i and pR_i

$$\hat{V}_{MS} = M_{1,1} + \sum_{i=2}^k \left\{ M_{1,1} - \sum_{j=1}^{i-1} (M_{i-1,j} pR_{i-1,j}) \right\}$$

such that the estimate of the volume of brant arriving over all weeks is

$$\hat{V}_T = \hat{V}_{SS} + \hat{V}_{MS}.$$

Error in the volume estimates arises from 2 independent

Table 1. Model rankings, based on Quasi Akaike's Information Criterion adjusted for small sample size ($\Delta QAIC_c$), characterizing the pattern of weekly transition (departure) probabilities for single-sight and multi-sight data for brant migrating from their southern winter breeding sites (stratum A) through the Fraser River Delta (stratum B) and Parksville-Qualicum (stratum C) in the Strait of Georgia, British Columbia, Canada, 1999–2000, to their northern breeding sites (stratum D). The effective sample size (ESS) is given for each analysis.

Model	Model characteristics				
	K^a	$\Delta QAIC_c^b$	$\Delta Deviance^b$	$\hat{\epsilon}^c$	1 SE
Single-sight					
1999 and 2000 from A to (B or C); ESS = 17,724					
Week ^d (Q ^e), yr 1999 and 2000 separate	12	0	0		
Week (Q), yr 1999 and 2000 combined	6	2.29	49.19		
Week (I ^f), yr 1999 and 2000 separate	28	13.14	-65.15	3.44	0.76
Week (L ^g), yr 1999 and 2000 separate	10	26.32	104.31		
Week (L), yr 1999 and 2000 combined	4	41.67	198.41		
Multi-sight					
1999 from A to (B or C); ESS = 10,346					
Week (Q)	8	0	0		
Week (I)	28	9.18	-69.06	2.23	0.72
Week (L)	6	134.78	309.48		
2000 from A to (B or C); ESS = 9,492					
Week (Q)	8	0	0		
Week (I)	28	2.68	-185.50	4.95	1.30
Week (L)	6	27.47	155.83		
1999 from (B or C) to (B, C or D); ESS = 5,587					
Week (L), cohort ^h (Q)	31	0	0		
Week (L), cohort (L)	29	2.37	41.57		
Week (Q), cohort (Q)	33	3.05	-6.45	6.48	0.92
Week (Q), cohort (L)	31	5.60	36.28		
Week (L), cohort (I)	27	10.77	122.20		
Week (I), cohort (L)	27	94.55	665.09		
Week (I), cohort (I)	25	105.6	762.84		
2000 from (B or C) to (B, C, or D); ESS = 5,713					
Week (L), cohort (L)	29	0	0		
Week (L), cohort (Q)	31	1.54	-15.49		
Week (Q), cohort (L)	31	2.24	-11.18		
Week (Q), cohort (Q)	33	5.45	-16.36	6.20	0.68
Week (L), cohort (I)	27	9.13	81.65		
Week (I), cohort (L)	27	67.77	445.25		
Week (I), cohort (I)	25	97.56	654.98		

^a K is the no. of estimated parameters.

^b Expressed relative to a value of zero for the best approximating model (Burnham and Anderson 2002).

^c The estimate of $\hat{\epsilon}$ was obtained from the most highly parameterized (K) reasonable model.

^d Refers to any week that a cohort may depart a site.

^e Weeks or cohorts modeled using a logit-quadratic function.

^f Transition probabilities estimated independently for each week.

^g Weeks or cohorts modeled using a logit-linear function.

^h Refers to all brant arriving in a particular week.

sources: 1) random counting error in abundance estimates and 2) statistical error in MARK's estimates of transition probabilities between strata. Concerning random counting error, there was no explicit measure of error for abundance estimates, because they were derived from the maximum daily counts for a particular week. To incorporate measurement error into our estimates, we simulated different degrees of counting error by imposing 3 percentages of random counting error encompassing a reasonable range of error (a 5%, 10%, and 20% CV). Second, we generated uncertainty in estimates of transition probabilities assuming a normal error distribution for MARK's logit-transformed Beta estimates for those probabilities. We then performed 1,000 randomizations of the Cholesky decomposed (square root) deviations of the $\hat{\epsilon}$ -adjusted covariance matrix of those Beta estimates to generate randomized volume estimates. Finally, we added uncertainty in the volume estimates

arising from uncertainty in the transition probability estimates to the statistically independent measurement error associated with counts to calculate total uncertainty for the volume estimates.

RESULTS

The peak of migration occurred at similar times each year, and in both years it occurred about 2 weeks later on the FRD than at PQ (Fig. 2). In 1999 and 2000, we observed 316 and 382 discrete bands on the FRD and 1,094 and 900 at PQ, respectively. Single-sight bands made up approximately 40% of PQ and 70% of FRD observations.

Using $QAIC_c$ as a model selection criterion, a model that treated each year 1999 and 2000 as a separate group, and constrained the logit of transition probabilities to conform to a quadratic function of week, was the best approximating model (Burnham and Anderson 2002) for describing the

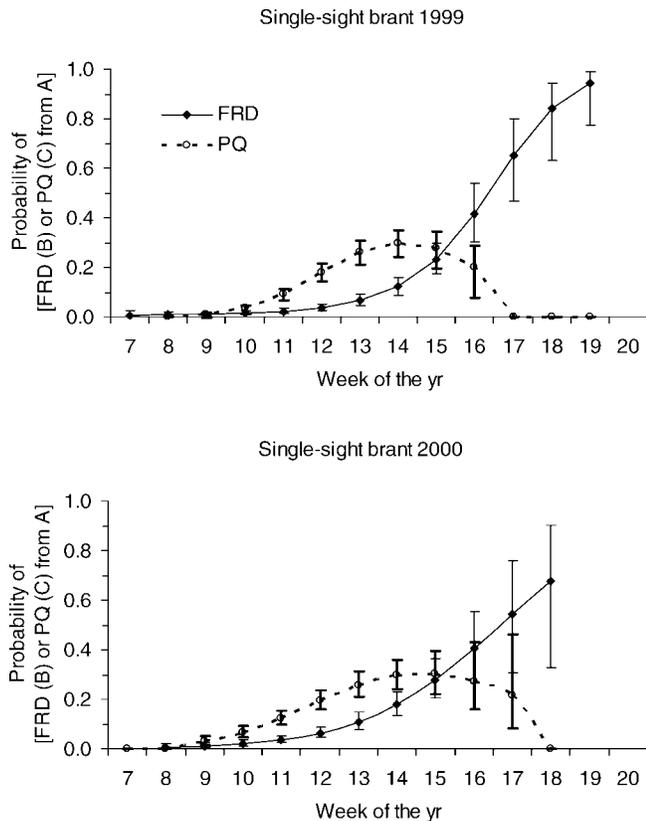


Figure 3. Weekly arrival probabilities for single-sight brant leaving their southern wintering sites (stratum A) for the Fraser River Delta (FRD; stratum B) or Parksville-Qualicum (PQ; stratum C) in 1999 and 2000. We calculated probabilities ($\pm 95\%$ CI) using MARK, and they should be interpreted as the probability of a brant arriving on stratum B or C on week $i + 1$, if it was on stratum A in week i .

transition of single-sight brant from their southern winter location (A) to either the FRD (B) or PQ (C). The same model also best described the multi-sight brant (Table 1). The best approximating models for multi-sight brant departing FRD (B) or PQ (C) for the northern breeding sites (D) modeled the transition probabilities as logit-linear functions of time (week) and cohort (arrival week) in 1999, and as a logit-linear function of time (week) and a logit-quadratic function of cohort (arrival week) in 2000 (Table 1). High values for \hat{c} (approx. 2–6) indicate considerable overdispersion in resighting data.

We used single-sight models to estimate transition probabilities from stratum A to either stratum B or C for individuals observed only once. These models predicted that early in migration, probability of moving from stratum A (southern wintering sites) to B (FRD) was low, but as time progressed the transition probability increased (Fig. 3). Probability of moving from A to C (PQ) was initially low but increased with time, with brant being more likely to arrive at PQ than FRD during the peak time of arrival of brant to the Strait of Georgia. Subsequent migration from stratum B (FRD) or C (PQ) to D (northern breeding sites) is shifted positively by 1 week (Fig. 3).

The first part of the migration was the transition from stratum A (southern wintering sites) to either B (FRD) or C

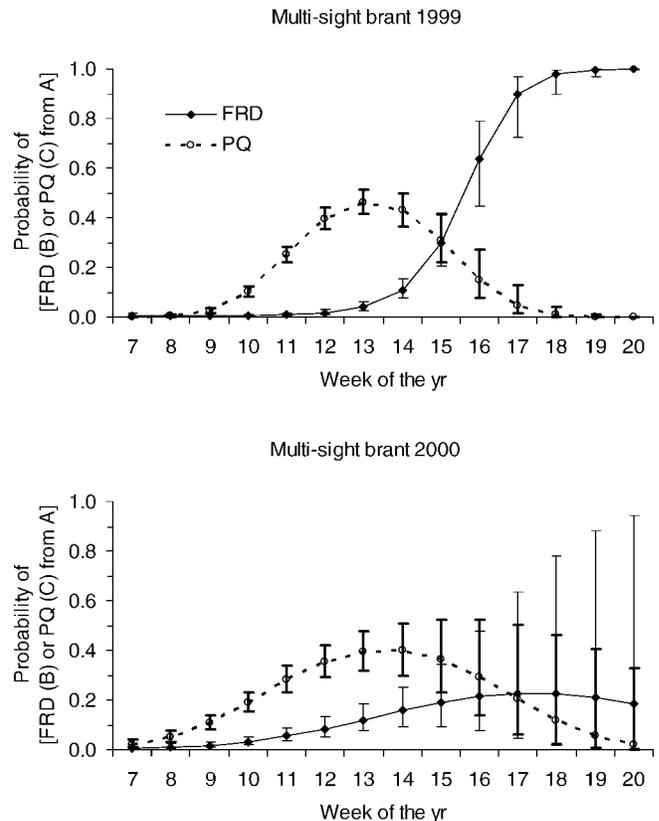


Figure 4. Weekly arrival probabilities for multi-sight brant leaving their southern wintering sites (stratum A) for the Fraser River Delta (FRD; stratum B) or Parksville-Qualicum (PQ; stratum C) in 1999 and 2000. We calculated probabilities ($\pm 95\%$ CI) using MARK, and they should be interpreted as the probability of a brant arriving on stratum B or C on week $i + 1$, if it was on stratum A in week i .

(PQ). Similar to single-sight brant, in 1999 there was a higher probability of migrating from stratum A to C than to B early in migration (Fig. 4). Later in migration, we expected brant to migrate to stratum B. In 2000, the early week probability of migrating from stratum A to C was higher than to stratum B. Later in the season, this trend seemed to reverse, but there is considerable uncertainty in the transition probability estimates and it is conceivable the true pattern is not unlike that for multi-sight brant in 1999 or single-sight brant in 1999 and 2000 (Fig. 3).

The second part of the migration was the transition from stratum B or C to B, C, or D after an LOS of a week or more at B or C. In general, the probability of a brant migrating to D in a particular week increased as the migration season progressed (Fig. 5). Expressed in terms of the more familiar and interpretable metric of LOS, a brant that arrived to either B or C in the first week of migration tended to have a longer residence time than a brant that arrived later (Fig. 6). Transition probabilities for PQ brant in 1999 differed from the general pattern (Fig. 5), with later arrivals seeming to have disproportionately shorter residence times than earlier arrivals compared with other years and the FRD. However, as mentioned above, there is considerable uncertainty in the transition probability estimates, and it is conceivable the true pattern is not unlike that for year 2000

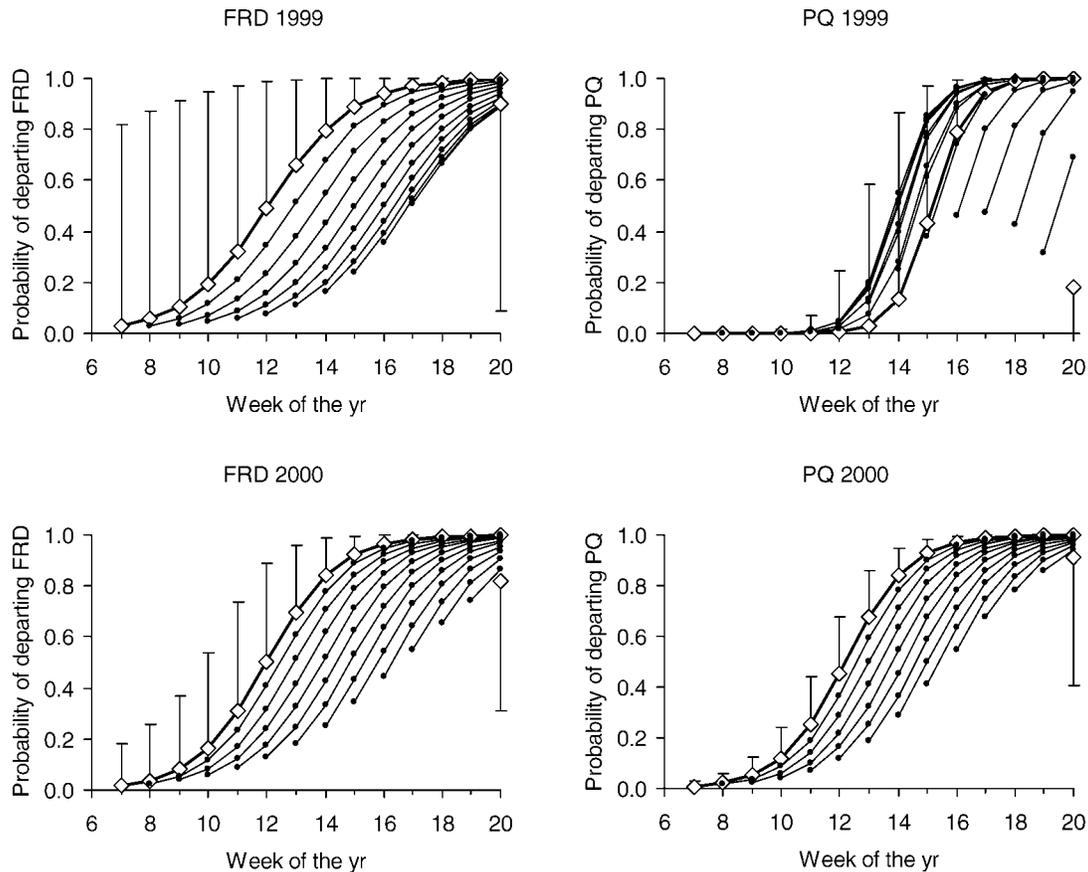


Figure 5. Weekly departure probabilities (p_{D_i} , as defined in Methods) for multi-sight brant leaving either the Fraser River Delta (FRD; stratum B) or Parksville-Qualicum (PQ; stratum C) staging sites for their northern breeding sites in 1999 and 2000. We calculated probabilities using MARK, and they should be interpreted as the probability of a brant leaving for stratum D on week $i + 1$, if it was on stratum B or C in week i . Each curve represents the transition probabilities associated with a particular week of arrival on stratum B or C. With the exception of PQ in 2000, typically later arriving brant have a lower probability of departing stratum B or C for a particular week of arrival on stratum B or C. Likewise, typically brant arriving later to stratum B or C have a higher probability of leaving those strata sooner. For presentation clarity, a 95% confidence limit for the transition probabilities is shown only for the earliest (upper CI) and latest (lower CI) week of arrival, but note that these are the least confidently estimated probabilities. Week 7 is approximately 17 February; week 20, approximately 18 May.

and the FRD. We observed very limited interchange between the strata (approx. 0.5% in 1999 and 3% in 2000).

We estimated similar volumes for 1999 and 2000 on stratum C (PQ), but volumes decreased between years on stratum B (FRD; Fig. 7). The PQ site hosted about 1,200 more brant than did the FRD site over both years, with approximately 15,000 brant hosted in PQ in both years. The FRD hosted about 9,000 brant in 1999 and 14,000 in 2000. Given the above-mentioned limited interchange between strata B and C, we consider the volumes for FRD and PQ to be additive to achieve a cumulative estimate for these 2 staging sites. We estimated (± 1 SE at 0%, 5%, 10%, and 20% measurement error, respectively) that 31,054 ($\pm 1,288$, 1,355, 1,538, and 2,127) brant transited FRD and PQ in 1999 and that 23,513 ($\pm 1,386$, 1,414, 1,532, and 1,892) brant transited FRD and PQ in 2000. The midwinter indices for the PFBP were 119,993 and 127,129 for 1999 and 2000, respectively (point estimates, no SEs available; U.S. Fish and Wildlife Service 2004; Table 2). Hence, our volume estimates represent about 26% (1999) and 18% (2000) of the PFBP.

DISCUSSION

We estimated that the FRD and PQ together supported between 18 and 26% of the PFBP in the years 1999 and 2000. These numbers likely underestimate true volumes, because ground counts tend to be negatively biased, and it is seldom possible to detect all animals during a survey (Lancia et al. 1994, Boyd 2000), which may be particularly true of the FRD. Here, brant concentrated in fewer locations compared with PQ, but there were fewer vantage points for observers to count brant and read leg-bands, which also may have partially accounted for the difference in the proportion of single-sight bands between the FRD and PQ. Although band-reading effort was similar at both sites, FRD had substantially more single-sight observations. We speculate that a higher proportion of multi-sight birds were actually observed only once on the FRD compared with PQ because of fewer vantage points for viewing bands.

Routledge et al. (1999) estimated the volume of spring-staging brant using the PQ study site in 1990. Similar to our study, the volume estimate was based on daily counts and records of marked birds. Using a maximum likelihood

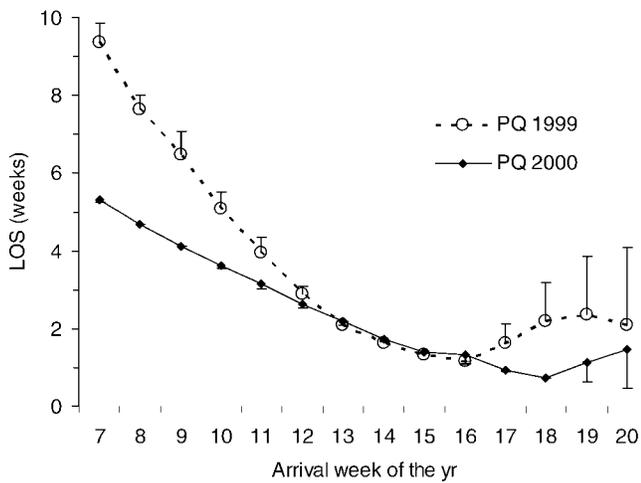
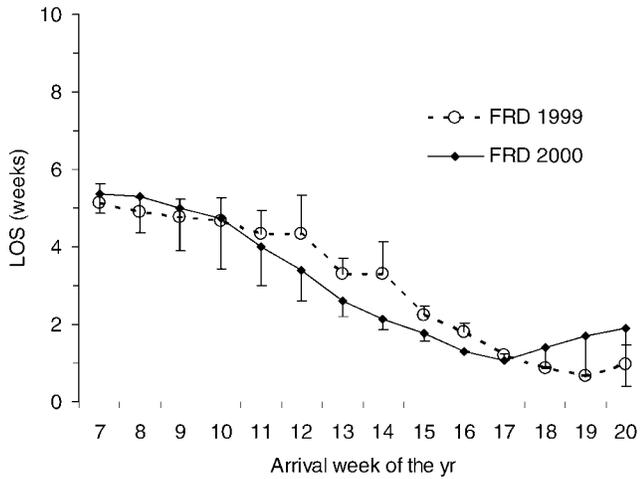


Figure 6. Expected length of stay (LOS [weeks]; T_w as defined in Methods) for brant as a function of the week of their arrival on either the Fraser River Delta (FRD; stratum B) or Parksville-Qualicum (PQ; stratum C) in 1999 and 2000, corrected, as described in the text, for the possibility that brant were present in the weeks before they were seen. T-bars descend from the corrected weekly LOS estimate to the uncorrected LOS estimate, which typically differs only slightly from the corrected estimate due to generally high weekly resighting probabilities.

approach, Routledge et al. (1999) estimated the population size by exploiting the ratio of the estimated total number of days that birds stayed in the site to estimated mean LOS. Using a mean LOS of about 6 days, Routledge et al. (1999) estimated the volume of brant to be 12,100 (95% CL, 8,600–16,000), or roughly one-half to one-third of our volume estimates for 1999 and 2000. This difference in volume estimates could be real. However, as stated in the introduction, we argue that because LOS varies among individuals and over time (van Eerden et al. 1991), use of mean statistics can lead to biased estimates, and more importantly, it can disguise features of migration behavior related to LOS. Additionally, our approach incorporates uncertainty in a more robust manner because we include 1) uncertainty in transition probability estimates, 2) uncertainty in counts, and 3) uncertainty related to over-

Table 2. Mean and mode of volume estimates as a percentage (%) of the Pacific Flyway Brant Population (PFBP) for each year and staging site in the Strait of Georgia, British Columbia, Canada. The estimated population size of the PFBP was 119,993 (1999) and 127,129 (2000; U.S. Fish and Wildlife Service 2004).

Variable	Staging site			
	Stratum B 1999 (FRD) ^a	Stratum B 2000 (FRD)	Stratum C 1999 (PQ) ^b	Stratum C 2000 (PQ)
Mean volume	17,071	9,078	13,983	14,435
Proportion of mean vol	14.2	7.1	11.7	11.4
Mode vol	17,071	8,100	13,983	14,435
Proportion of mode vol	14.2	6.4	11.7	11.4

^a FRD = Fraser River delta.

^b PQ = Parksville-Qualicum.

dispersion, a result of brant tending to migrate in pairs and as family groups. We anticipated high values for \hat{c} because geese make group decisions to migrate as pairs or families (Hestbeck et al. 1991), and they are influenced by weather and other migration timing considerations (Prevett and MacInnes 1980, Hestbeck et al. 1991, Reed 1993, Anderson et al. 1994). We should also note that marking of individuals is not random because families are often captured and marked together. As such, the true effective sample size is smaller than the actual number of marked birds and results in an underestimation of true variance (Schmutz et al. 1995) unless, as we have done, a correction for overdispersion is applied. Finally, our method requires a less onerous field effort than the Routledge et al. (1999) method because observers do not need to record the number of birds checked for bands.

Brant have staged on the FRD and PQ sites since before formal record-keeping began (Fannin 1891). High resighting rates for PQ and FRD (Reed et al. 1998a, b; K. R. Hagmeier, unpublished data) and the lack of interchange between local sites support the finding of other researchers that brant are highly site faithful (see Reed et al. 1998a). Site fidelity results in familiarity with local food resources and predation risks (Bengtsson 1978) and, as such, it allows individuals to build critical body reserves more efficiently than if different sites are used each year. This behavior is learned by offspring that typically spend their first year in family groups (Prevett and MacInnes 1980, Reed 1993, Warren et al. 1993, Ebbing and Spaans 1995).

Despite the advantages of tradition noted above, brant have shown the capacity to make large-scale distributional shifts (Sedinger et al. 1994) and will respond to changes in land use by colonizing new sites (Ganter 1994). Although the timing of migration was similar in 1999 and 2000, the number of brant staging on the FRD was markedly lower in 2000 compared with 1999, which was not likely a result of observer bias because counts were consistently lower for all researchers and volunteers, all of whom were experienced at counting brant. The decline seemed to be local and was not reflected in overall PFBP estimates (U.S. Fish and Wildlife

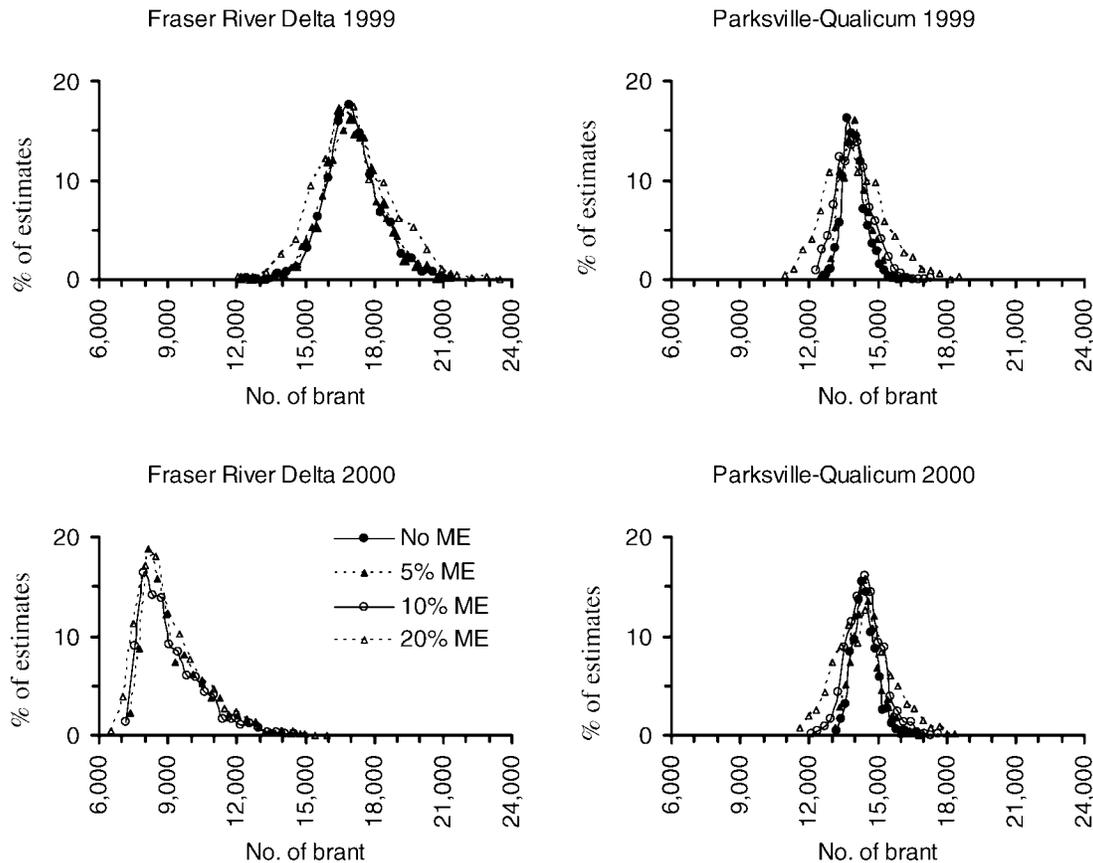


Figure 7. Estimates, and their uncertainty, of the volume of brant transiting the Fraser River Delta (stratum B) and Parksville-Qualicum (stratum C) in 1999 and 2000. Volume uncertainty includes the uncertainty associated with the transition probability parameter estimates from MARK as well as 4 levels of random measurement error (ME; 0%, 5%, 10%, and 20%) for the weekly field counts of brant.

Service 2004). Volumes were similar at PQ across years, so we do not suspect that missing birds (i.e., birds accounting for the difference in 1999 and 2000 vol estimates) staged there, and this interpretation is supported by the lack of interchange between sites. Alternatively, we cannot rule out the possibility that these missing birds chose an alternate migration route or staging sites. Several smaller staging sites exist within the Strait (e.g., at Denman Island, the Seal Islets, and the Trent River Estuary on Vancouver Island). During the peak of migration, >1,000 brant are present at each of these sites (Hagmeier 2002). A cursory analysis of leg-band observations suggests that individuals using these small sites do not use PQ or the FRD. To further refine volume estimates for the entire Strait of Georgia, the extent of interchange between primary and minor staging sites should be examined.

Staging brant must balance their need for food (i.e., rate of nutrient accumulation) and risk of predation (perceived or real). It is unknown at what point the energy required to respond to risk (usually a flight response) results in the food intake rate declining below a critical threshold and a staging site becoming unprofitable. To more fully understand the migration ecology of brant in the Strait of Georgia, volume estimates need to be interpreted in the context of individual body condition, timing of migration, and external factors such as disturbance and predation risk. Also, by estimating

brant volumes over a longer time period we may discover patterns not detectable with the 2-year data set (e.g., changes in vol, LOS, and departure times) and explain some of the variation encountered in relation to time-dependent population demographics and environmental factors.

MANAGEMENT IMPLICATIONS

Our results reinforce the relative importance of the FRD and PQ sites to spring-staging brant at the flyway scale. These sites are subject to increasing urbanization pressures in a region of rapid human population growth and increased disturbance to wildlife. Conservation efforts by local governments should include restricting public access to important brant staging sites during spring migration and influencing land use planning at these sites. More generally, our modeling approach can also be applied to other marked, transient populations to rank the importance of migration stopover habitats and help determine the strategic allocation of conservation resources.

ACKNOWLEDGMENTS

We gratefully acknowledge the Arctic Goose Joint Venture for funding our research. In addition, we thank the volunteers, students, and researchers (particularly J. Sedinger and his group) who have marked brant and collected leg-

band observation data. For our field sites, we thank R. Swanston, J. Hammonds, J. Dove, T. Martin, and B. Andres. We also thank D. Esler and 2 anonymous reviewers for providing valuable comments on the manuscript.

LITERATURE CITED

- Anderson, D. R., K. P. Burnham, and G. C. White. 1994. AIC model selection in overdispersed capture-recapture data. *Ecology* 75:1780–1793.
- Ankney, C. D., and C. D. MacInnes. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. *Auk* 95:459–471.
- Bengtsson, B. O. 1978. Avoiding inbreeding: at what cost? *Journal of Theoretical Biology* 73:439–444.
- Black, J. M., C. Deerenberg, and M. Owens. 1991. Foraging behaviour and site selection of barnacle geese *Branta leucopsis* in a traditional and newly colonized spring staging habitat. *Ardea* 79:349–358.
- Boyd, W. S. 2000. A comparison of photo counts versus visual estimates for determining the size of snow goose flocks. *Journal of Field Ornithology* 71:686–690.
- British Columbia Ministry of Labor and Citizens' Services. 2006. BC stats: sub-provincial population projections. <<http://www.bcstats.gov.bc.ca/data/pop/popproj.asp#admin>>. Accessed 15 Dec 2006.
- Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. *Biometrics* 49:1173–1187.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York, USA.
- Cooch, E., and G. C. White. 2007. Program MARK: analysis of data from marked individuals, a gentle introduction. Fifth edition. <<http://www.phidot.org/software/mark/docs/book>>. Accessed 20 Mar 2007.
- Ebbinge, B. S. 1988. A multifactorial explanation for variation in breeding performance of Brent geese *Branta bernicla*. *Ibis* 131:196–204.
- Ebbinge, B. S., and B. Spaans. 1995. The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in dark-bellied Brent geese, *Branta b. bernicla* in the high Arctic. *Journal of Avian Biology* 26:105–113.
- Fannin, J. 1891. Checklist of British Columbia birds. Royal British Columbia Provincial Museum, Victoria, British Columbia, Canada.
- Frederiksen, M., A. D. Fox, J. Madsen, and K. Colhoun. 2001. Estimating the total number of birds using a staging site. *Journal of Wildlife Management* 65:282–289.
- Ganter, B. 1994. Site tenacity and mobility of staging barnacle geese. *Ardea* 82:231–240.
- Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behavior* 28:1140–1162.
- Hagmeier, K. 2002. Winter and spring migration ecology of black brant (*Branta bernicla nigricans*) in the Strait of Georgia, British Columbia. Thesis, Simon Fraser University, Burnaby, British Columbia, Canada.
- 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.
- Important Bird Areas Canada. 2004. IBA BC017. <<http://www.bsc-eoc.org/iba/site.jsp?siteID=BC017>>. Accessed 14 Dec 2006.
- Lancia, R. A., J. D. Nichols, and K. H. Pollock. 1994. Estimating the number of animals in wildlife populations. Pages 215–253 in T. A. Bookhout, editor. Research and management techniques for wildlife and habitats. Fifth edition. The Wildlife Society, Bethesda, Maryland, USA.
- Lindberg, M. S., J. S. Sedinger, D. V. Derksen, and R. F. Rockwell. 1998. Natal and breeding philopatry in a black brant *Branta bernicla nigricans* metapopulation. *Ecology* 79:1893–1904.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107.
- Prevet, J. P., and C. D. MacInnes. 1980. Family and other social groups in snow geese. *Wildlife Monographs* 71.
- Raveling, D. G. 1979. The annual cycle of body composition of Canada geese with special reference to the control of reproduction. *Auk* 96:234–252.
- Reed, A. 1993. Duration of family bonds in Brent geese *Branta bernicla* on the Pacific Coast of North America. *Wildfowl* 44:33–38.
- Reed, A., D. H. Ward, D. V. Derksen, and F. S. Sedinger. 1998a. Brant, *Branta bernicla*. Account 3337 in A. Poole and F. Gill, editors. The birds of North America, life histories of the 21st century. Cornell Laboratory of Ornithology and the Academy of Natural Sciences, Ithaca, New York, USA.
- Reed, E. T. 1997. Migration patterns and philopatry of the black brant (*Branta bernicla nigricans*) in the Strait of Georgia, British Columbia. Technical Report Series No. 294. Canadian Wildlife Service, Pacific and Yukon Region, Vancouver, British Columbia, Canada.
- Reed, E. T., E. G. Cooch, F. Cooke, and R. I. Goudie. 1998b. Migration patterns of black brant in Boundary Bay, British Columbia. *Journal of Wildlife Management* 62:1521–1531.
- Reed, E. T., E. G. Cooch, R. I. Goudie, and F. Cooke. 1998c. Site fidelity of black brant wintering and spring staging in the Strait of Georgia, British Columbia. *Condor* 100:426–437.
- Routledge, R. D., G. E. J. Smith, L. Sun, N. Dawe, E. Nygren, and J. S. Sedinger. 1999. Estimating the size of a transient population. *Biometrics* 55:224–230.
- Schmutz, J. A., D. H. Ward, J. S. Sedinger, and E. A. Rexstad. 1995. Survival estimation and the effects of dependency among animals. *Journal of Applied Statistics* 22:673–681.
- Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. The Blackburn Press, Caldwell, New Jersey, USA.
- Sedinger, J. S., P. L. Flint, and M. S. Lindberg. 1995. Environmental influence on life-history traits: growth, survival, and fecundity in Black Brant (*Branta bernicla*). *Ecology* 76:2404–2414.
- Sedinger, J. S., D. H. Ward, R. M. Anthony, D. V. Derksen, C. J. Lensink, K. S. Bollinger, and N. K. Dawe. 1994. Management of Pacific brant: population structure and conservation issues. Pages 50–62 in Transactions of the 59th North American Wildlife and Natural Resources Conference, 18–23 March 1994, Anchorage, Alaska, USA.
- Thompson, J. J. 1993. Modeling the local abundance of shorebirds staging on migration. *Theoretical Population Biology* 44:299–315.
- Transboundary Georgia Basin-Puget Sound Environmental Indicators Working Group. 2002. Georgia Basin-Puget Sound Environmental Indicators Report. Georgia Basin Ecosystem Initiative Publication. <<http://www.env.gov.bc.ca/spd/gbsei/document/gbpsci.pdf>>. Accessed 15 Dec 2006.
- U.S. Fish and Wildlife Service. 2004. Waterfowl population status, 2004. U.S. Department of the Interior, Washington, D.C., USA. <http://library.fws.gov/Bird_Publications/waterfowl_population04.pdf>. Accessed 15 Dec 2006.
- van Eerden, M. R., M. Zijlstra, and M. J. J. E. Loonen. 1991. Individual patterns of staging during autumn migration in relation to body condition in greylag geese, *Anser anser* in The Netherlands. *Ardea* 79:261–264.
- Warren, S. M., A. D. Fox, A. Walsh, and P. O'Sullivan. 1993. Extended parent-offspring relationships in Greenland white-fronted geese (*Anser albifrons flavirostris*). *Auk* 110:145–148.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46(Supplement):S120–S139.

Associate Editor: Collier.