

AGE-SPECIFIC STOPOVER ECOLOGY OF BLACK BRANT AT HUMBOLDT BAY, CALIFORNIA

DEREK E. LEE,^{1,3,6} JEFFREY M. BLACK,¹ JEFFREY E. MOORE,^{1,4} AND JIM S. SEDINGER^{2,5}

ABSTRACT.—We analyzed capture-mark-recapture (CMR) data from 1,061 Black Brant (*Branta bernicla nigricans*) using Humboldt Bay, California, during northward migration (Jan–May), 2000–2001. We estimated immigration and emigration rates, and calculated stopover duration (length of stay), volume (total number of birds using the Bay), and chronology (time frame of the migration at this site). Migration of Brant through Humboldt Bay began in late December and ended in mid-May with peak numbers occurring in mid-March (i.e., 13% of the entire flyway population). Median age of newly arrived birds was highest in the first half of February. Immigration probability was nearly constant, but emigration probability increased through time, indicating a seasonally progressive migratory state. Mean (\pm SE) stopover duration from all birds for January–April at Humboldt Bay was 26 ± 2 days. Stopover duration was inversely related to bird age due to age-specific emigration probabilities; older birds arrived sooner and stayed for less time than younger birds. Estimates of stopover duration from concurrent radiotelemetry of 12 birds were consistent with CMR model selection-derived estimates. Humboldt Bay was visited by approximately 28% of the Pacific Flyway Black Brant population in 2000 and 58% in 2001. Estimates derived from this technique offer statutory authorities improved information upon which to base management action along migratory pathways. Received 5 December 2005. Accepted 24 July 2006.

Annual movements of migratory birds cover vast distances. Understanding behavior at stopover sites—where migrants accumulate or replenish energy stores en route (Alisauskas and Ankney 1992, Prop et al. 2003)—is crucial to understanding reproductive success, life history, and population dynamics (Owen and Black 1991, Ebbinge and Spaans 1995, Yong et al. 1998). Stopover behavior is primarily shaped by time, energy, and predation forces (Alerstam and Lindstrom 1990), and affects migration strategy (Alerstam and Hedstrom 1998). Stopover behavior also has conservation implications because these sites function as geographic bottlenecks where large portions of the population congregate (Myers 1983), sometimes differentially by age

(Yong et al. 1998, Restani 2000). Under the Ramsar Convention (Ramsar Convention Bureau 1988), any staging area that hosts >1% of one or more waterbird populations is considered of international importance and should be safeguarded. Thompson's (1993) theoretical model to describe shorebird migration provides an excellent framework for examining migratory behavior of all birds from the perspective of the stopover site. The key parameters in Thompson's (1993) model are immigration and emigration probabilities, which can be accurately estimated with capture-mark-recapture (CMR) models (Schaub et al. 2001). Stopover duration (called residence time in Routledge et al. 1999) can be calculated from immigration and emigration rates (Pradel et al. 1997b, Schaub et al. 2001). Stopover duration, the total time an animal spends in a defined area between migratory bouts, is an important component of optimum migration models (Weber and Houston 1997). By combining emigration probabilities with periodic census data, volume or superpopulation (the total number of birds that passed through the area during migration) can be computed (Frederiksen et al. 2001, Schaub et al. 2001).

We used CMR data from Black Brant (*Branta bernicla nigricans*) migrating through

¹ Waterfowl Ecology Research Group, Department of Wildlife, Humboldt State University, Arcata, CA 95521, USA.

² Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99775, USA.

³ Current address: PRBO Conservation Science, Marine Ecology Division, 3820 Cypress Dr. #11, Petaluma, CA 94954, USA.

⁴ Current address: Purdue University, Forestry and Natural Resources, 195 Marsteller St., West Lafayette, IN 47907, USA.

⁵ Current address: University of Nevada, Reno, Natural Resources and Environmental Science, 1000 Valley Rd./MS 186, Reno, NV 89512, USA.

⁶ Corresponding author; e-mail: dlee@prbo.org

Humboldt Bay, California, during winter and spring (Jan–May, 2000–2001), and program MARK (White and Burnham 1999) to model and estimate periodic immigration, emigration, and recapture probabilities. We used MARK's ability to include individual covariates to examine how bird age affected immigration and emigration probabilities. We computed stopover duration, volume, and proportion of transients (birds observed only once), and described overall migration chronology and age-specific chronology. We validated our estimates of stopover duration computed from CMR data with simultaneously collected radiotelemetry data.

HYPOTHESES

Age-specific Stopover and Chronology.—Gauthreaux (1978) reported that dominance is the primary underlying force behind intraspecific behavioral variation. Geese increase their migratory experience, dominance, and reproductive investment as they age (Rockwell et al. 1983, Black and Owen 1989, Stearns 1992). Peak reproduction for geese is from ages 6 to 14 years (Black and Owen 1995; Sedinger et al. 1998, 2001), and reproductive success contributes to increased dominance (Black and Owen 1989). Reproductive success in geese has also been found to depend upon individuals arriving at the farthest north stopover area early, and maximizing time spent there (Madsen 2001). Palmer (1976) suggested differential chronology of spring migrants by age with paired breeders generally among the first migrants. Humboldt Bay is a Brant stopover area in the southern to middle portion of their range. We expected older (more experienced and dominant) birds would make most efficient use of resources available by arriving earlier than young birds, and have shorter stopover duration before moving to staging sites closer to breeding areas.

Volume.—Humboldt Bay is believed to be the most important spring staging area for Brant in California (Pacific Flyway Subcommittee on Pacific Brant 1992), and one of the most important in the entire flyway (Humboldt Bay National Wildlife Refuge, U.S. Fish and Wildlife Service, unpubl. data). We expected our estimates of volume to confirm that

Humboldt Bay was used by a large proportion of the population.

Seasonal Progression and Transience.—Previous studies of stopover ecology have detected a seasonally progressive trend in emigration probability (Pradel et al. 1997b) and an excess of animals that are not observed again after their first observation (Pradel et al. 1997a, 1997b; Reed et al. 1998a). We incorporated these possibilities and tailored the analyses to include tests of transience and temporal trends in emigration probability.

Techniques.—We computed two CMR modeling-derived estimates of stopover duration (Reed et al. 1998a, Schaub et al. 2001) and used radiotelemetry-derived estimates to validate each method.

METHODS

Capture-Recapture Data Collection

We conducted this study on Humboldt Bay National Wildlife Refuge (HBNWR), on the coast of northern California (40° 48' N, 124° 07' W). Humboldt Bay is a 62.4-km² estuary (Barnhart et al. 1992) with 1,044 ha of eelgrass (*Zostera marina*) in discrete beds interlaced with a dendritic network of channels (Moore et al. 2004). Black Brant feed almost exclusively on eelgrass during the non-breeding season (Derksen and Ward 1993). South Humboldt Bay (South Bay) contains 70% of the eelgrass beds in Humboldt Bay, and supports 78–94% of Humboldt Bay Brant use each year (Humboldt Bay National Wildlife Refuge, U.S. Fish and Wildlife Service, unpubl. data). Humboldt Bay is the only large estuary containing substantial eelgrass beds (>300 ha) for 350 km to the south and 600 km to the north along the coast (Moore et al. 2004), making it an insular study area with little potential for regional foraging movements. South Spit, the sandy peninsula separating South Bay from the Pacific Ocean, has one large, and many small intertidal sand bars along its eastern shoreline that are used by Black Brant as the tide ebbs to rest, preen, and ingest grit.

Annually, samples of all ages of individual Black Brant are marked with uniquely coded tarsal bands at major breeding and molting locations in western and northern Alaska, Russia, and the Northwest Territories (Sedinger et

al. 1993, Ward et al. 1993, Bollinger and Derksen 1996). In fall, most Black Brant migrate south to overwinter on coastal lagoons of Baja California, Mexico (Reed et al. 1998b). During all daylight ebbing tides from 1 January to 1 May in 2000 and 2001, we used 60–120 \times spotting scopes to read tarsal bands of Brant on Humboldt Bay sand bars. Successful reading of a band constituted an encounter for each individual, and the entire record of encounters constituted the individual's encounter history. In terms of capture-recapture data, the first observation of a marked bird is considered its capture, and subsequent observations are recaptures. Observed birds were classified by gender, and real (banded as a gosling or yearling) or minimum (banded after second year) age from information in banding records (Sedinger et al. 1993).

In July 1999, 45 Brant were fitted with radio transmitters on the Yukon-Kuskokwim Delta, Alaska (D. H. Ward, pers. comm.). Transmitters consisted of a crystal and battery encased in epoxy with a 20-cm whip antenna, and were surgically implanted. Thirty-four of these radio-marked birds were relocated alive with operational transmitters in Baja California, Mexico in winter 1999–2000 (D. H. Ward, pers. obs.), prior to northward migration. During 2000, we monitored all 34 radio frequencies daily from two elevated (50–75 m) locations (Bell Hill and Table Bluff) overlooking South Bay to collect presence-absence data for each radio-marked bird. Receivers at Bell Hill and Table Bluff identified transmitters at distances spanning the farthest extent of South Bay from the receiver sites (5 km and 8 km, respectively). Thus, radio-marked birds present on the Bay should have been detectable at all times.

Capture Recapture Analysis

We used encounter histories to model and estimate recapture, emigration (the complement of residence) and immigration (the complement of seniority) probabilities using program MARK 1.8 (White and Burnham 1999) following methods described by Schaub et al. (2001). The three parameters we modeled and estimated were (1) recapture (p_i), the probability that a previously observed bird is observed at time i , given that it is present in the

study area at time i ; (2) residence (ϕ_i), the probability that a bird in the study area at time i remains in the study area until time $i + 1$; and (3) seniority (γ_i), the probability that a bird present at time i , was present in the study area at time $i - 1$.

Recapture.—The superiority of CMR modeling methods of analyzing bird band data lies in the estimation of recapture probability (p). Residence and seniority estimates are otherwise biased low because they do not account for the proportion of banded birds that are alive and present, but not seen. We were able to more accurately estimate arrival and departure probabilities by modeling recapture probability for residence and seniority.

Emigration.—During spring, emigration from the study area is much greater than natural mortality. The parameter ϕ_i , properly defined as apparent survival, is the product of true survival and residence probability, defined as the probability of remaining in the study area between times i and $i + 1$. True survival of Brant was previously estimated for winter (1 Jan–1 Mar) as 1.00 and early spring (1 Mar–15 Apr) as 0.988 (Ward et al. 1997). We assumed zero mortality during the entire study period (1 Jan–1 May), making apparent survival equal to residence probability. Thus, in our case, ϕ_i can be subtracted directly from 1 to calculate emigration probability, the probability of an individual leaving the study area between times i and $i + 1$.

Immigration.—Pradel (1996) developed a CMR model parameterization that produces estimates of γ_i , called the seniority probability, defined as the probability of an animal having been in the population previous to the first capture. During spring, the occurrence of all new Brant in the study area is due to immigration (birth rate = zero). Thus, the probability of immigration into the study area between times i and $i + 1$ is $1 - \gamma_i$.

Pooling.—Due to weather-restricted visibility, Brant leg bands were not observable on some days. These gaps in the daily capture histories made daily estimates of immigration and emigration probabilities impossible. Thus, for model selection we used the common technique of pooling the data (Pradel et al. 1997b, Reed et al. 1998a). Pooling violates model assumptions of independent observations and instantaneous sampling periods, and can lead

to biased parameter estimates (Hargrove and Borland 1994), but was necessary in this study to permit modeling (Schaub et al. 2001). Different pooling intervals were tried for each year's data. The intervals ultimately chosen were the shortest periods that met two criteria: (1) global models successfully converged, and (2) global models passed goodness of fit criteria (data deviance ranked $<90/100$ simulated deviances). Data were pooled into 7- and 5-day periods for 2000 and 2001, respectively. The number of observation periods with no data was one in 2000 and three in 2001; no gaps were consecutive. Gaps were accounted for by changing the time interval between observations from one to two in program MARK. The pooling interval differed by year, precluding direct between-year comparisons, but minimized biases within years from excessive pooling. Tests of true age effects used a subset of the data that was pooled into 14-day periods based on convergence and goodness of fit criteria. Only year 2001 data were used for true age model selection because known age data were too sparse in 2000 to permit modeling. There were no data gaps in the true age data.

True Age.—We tested a subset of known-age birds for differences in immigration and emigration due to true age (years since hatching). These models were designed with bird age as a standardized, continuous, individual covariate of the parameter of interest. The covariate was considered to have a significant effect on the parameter if the model including the age covariate had a lower QAIC_c value than the model without it. The sign of the beta coefficient for age in ϕ and γ indicates the relationship between emigration and immigration to age. In each observation period with sample size >5 of newly arrived known-age birds, median age and proportion of birds >5 years old were calculated to investigate age differences in migration chronology.

Model Subscripts.—We used notation similar to that suggested by Lebreton et al. (1992) to designate the models. We designated a fully time-dependent parameter with a “*t*” subscript, and a constant parameter with a “*c*” subscript for residence (ϕ), seniority (γ), and recapture (p) probabilities. Parameters were also modeled as linear and quadratic trends through time, denoted with subscripts “*T*”

and “*T*”, respectively. When true bird age was included as an individual covariate of a parameter we used the subscript “*age*.” The subscript “*e*#” was used to control for extreme parameter heterogeneity between the initial observation and subsequent observations. The “*e*” subscript denoted encounter class structure, and the # denoted how many encounter classes were present. Encounter class structure was included in residence, but is not possible to model in the seniority probability.

Transience.—The RELEASE goodness-of-fit procedure in program MARK showed that residence probability of newly observed and previously observed individuals differed, indicating a large portion of the newly observed individuals was present for only one observation period. Transients (individuals with a zero probability of residence after their initial observation) are a likely explanation of this disparity in our data (Pradel et al. 1997a). Presence of large numbers of transients required encounter class structure ($\phi_{e\#}$) to be added to residence models to account for this extreme form of heterogeneity. In these model structures, the first # encounter classes are a mixture of residents and transients, with subsequent encounter classes made up solely of residents. Thus, the notation “*e*2” would denote two encounter classes—the first a mixture of transients and residents, the second composed entirely of residents.

Model Selection.—Model selection was based on Akaike's information criterion corrected for small sample size (AIC_c; Akaike 1974, Burnham and Anderson 1998). All models used the logit link function. We assessed goodness-of-fit (GOF) for the most general model in each set by the bootstrapping method included in program MARK. We calculated the deviances from 100 simulations of data that are not over-dispersed. We accepted a general model if its deviance ranked <90 of the 100 rank-ordered deviances simulated. The ratio of the data's deviance to the mean deviance from the bootstrapping simulations was computed as the variance inflation factor (\hat{c}) for each data set. The bootstrapping method cannot be directly applied to immigration models, so the variance inflation factor from the emigration model for a given data set was applied to both model selection procedures.

Individual covariates cannot be included in bootstrapping simulations. When \hat{c} was applied to a data set, AIC_c values became quasi-likelihood AIC_c ($QAIC_c$) values. Parameter standard errors were multiplied by the square root of \hat{c} to adjust for lack of fit. Once the fit of the general model was assessed, reduced models were fitted to the data. The most parsimonious models were selected from among the pool using $QAIC_c$. The model with the lowest $QAIC_c$ value was considered the best or most parsimonious model. Akaike weights (Burnham and Anderson 1998) were computed to denote relative strength of evidence supporting each model.

The general emigration model was first reduced by finding the optimum number of encounter classes for ϕ with time dependence in each class. Once the best time-dependent reduced encounter class model was found for ϕ (two encounter classes), we ranked all combinations of c , t , T , and T^2 in each encounter class of ϕ (including additive models; i.e., $e2 + T$) and all combinations of c , t , T , and T^2 in p for a total model set of 67 emigration models. For immigration, we ranked all combinations of c , t , T , and T^2 in γ and p for a total of 16 immigration models.

For true age, we first found the optimum number of encounter classes in ϕ (2), and then simplified the general model by reducing p , then ϕ or γ to keep the number of total models tested reasonable in light of the reduced data set (Lebreton et al. 1992). We reduced p by ranking all combinations of age , c , t , and T in p including additive and multiplicative relationships of age with temporal terms (e.g., $age + T$ and $age \times T$) while holding ϕ or γ in its most general form. Then, we held p in its most parsimonious form while reducing ϕ or γ by ranking all combinations of age , c , t , and T including additive and multiplicative relationships of age with temporal terms for a total of 24 emigration and 16 immigration models.

Several models often appear equally plausible in the final set, with $\Delta QAIC_c$ values near zero and $QAIC_c$ weights comparable to the best model. Model averaging was used to create parameter estimates to account for apparent model selection uncertainty (Burnham and Anderson 1998). Model averaging uses AIC_c weights to calculate the weighted average of

each real parameter across all models with AIC_c weights greater than zero.

Stopover Duration

Methods for computing stopover duration are dependant upon the true distribution of stopover durations in the population (Efford 2005). We used model-averaged parameter estimates of ϕ_i and γ_i in Schaub et al.'s (2001) equation to calculate stopover duration (D_i). D_i is defined as the mean stopover duration in days for birds present in time i and assumes most birds spend approximately the same time at the stopover site. We made a second estimate for stopover duration using only ϕ_i (Reed et al. 1998a), that assumed a Poisson distribution in stopover durations. Confidence intervals of stopover duration were calculated using a non-parametric bootstrap procedure (Schaub et al. 2001).

$$D_i = \sum_{k=i}^n \left(\prod_{j=i}^{k-1} \phi_j \right) \left(-\frac{1 - \phi_k}{\ln \phi_k} \right) + \left(\prod_{j=i}^n \phi_j \right) \frac{-1}{\ln \phi_{n+1}} \\ + \sum_{k=n-i+1}^n \left(\prod_{j=i}^{k-1} \gamma_j \right) \left(-\frac{1 - \gamma_k}{\ln \gamma_k} \right) \\ + \left(\prod_{j=n-i+1}^n \gamma_j \right) \frac{-1}{\ln \gamma_{n+1}}$$

Mean stopover duration for radio-marked Brant was calculated directly from detection data because fate of all radio-marked animals was assumed known with certainty ($p = 1$). Mean stopover duration of radio-marked Brant was compared with mean stopover duration of banded Brant computed from the two CMR-derived estimates by GLM using a Poisson distribution and log link function (clustered by date of arrival). Radio-marked birds were present at the study site for only a portion of the 2000 band observation period, and the test compared stopover duration estimates only for the time interval when radio-marked birds were present.

Volume

The number of Brant present on South Humboldt Bay was measured by census every week in 2000, and every fortnight in 2001. Censuses were conducted hourly using 60× spotting scopes from Bell Hill, Table Bluff, and South Spit during the 4 hrs before and after daylight low tides; mean counts were

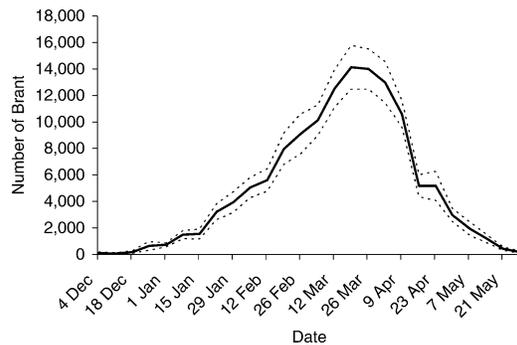


FIG. 1. Ten-year mean (1990–99) number of Black Brant present on Humboldt Bay, California, by date, during northward migration. Dotted lines are mean \pm 1 SE.

then computed. The mean count data were combined with emigration rates to calculate volume and the total number of birds using the site during each migratory season using the Frederiksen et al. (2001) estimator. For estimates of emigration for time intervals between censuses, the number of Brant present on South Bay was interpolated by fitting a line between the two censuses that bracketed the missing time. Volume estimates for South Bay were divided by 0.83 (mean proportion of Humboldt Bay Brant use occurring on South Bay from 1992 to 2000) to estimate volume for all of Humboldt Bay.

RESULTS

We had 452 observations of 320 uniquely banded individuals between January and April 2000, and 1,466 observations of 741 individuals between January and April 2001. Numbers of Brant on Humboldt Bay ($\geq 1,000$) sufficient to obtain adequate sample sizes of band readings appeared at the end of December, and ended in mid May, with peak numbers ($\sim 17,000$) in mid-March. This pattern of migration chronology was typical for Humboldt Bay Brant use over the past decade (Fig. 1).

Model Selection 2000.—The initial model considered in estimating emigration ($1 - \phi_i$) for all Brant using Humboldt Bay in winter and spring 2000 was that with fully interactive time- and transient encounter class-dependent residence and time-dependent recapture probabilities $\{\phi_{e12t}, p_t\}$. Bootstrapping indicated this model was an adequate general model to begin selection (deviance rank = 84/100). Although GOF was acceptable, a variance inflation factor of $\hat{c} = 1.286$ was used as a measure of conservatism. The best residence model selected by QAIC_c was $\{\phi_T, p_T\}$ (Table 1). Residence and recapture in this model followed a linear trend through time. QAIC_c weights showed several competing models with appreciable strength of evidence (Table 1) that contributed information (such as transient en-

TABLE 1. Model selection results (top 95% model set by weight) for Black Brant during January–May 2000 at Humboldt Bay, California with variance inflation factor $\hat{c} = 1.286$, ϕ = residence probability, γ = seniority probability, and p = recapture probability. Model with zero Δ QAIC_c is considered the most parsimonious. QAIC_c weight is the relative strength of evidence supporting a given model.

Model	QAIC _c	Δ QAIC _c	QAIC _c weight	Parameters	QDeviance
Emigration					
$\{\phi_T, p_T\}$ ^a	606.72	0.00	0.26	4	158.77
$\{\phi_{e2+T}, p_c\}$	607.82	1.10	0.15	4	159.87
$\{\phi_{e2+T}, p_T\}$	607.91	1.19	0.14	5	157.91
$\{\phi_c, p_T\}$	608.95	2.23	0.09	3	163.05
$\{\phi_T, p_i\}$	609.06	2.34	0.08	13	142.22
$\{\phi_{e2+T}, p_T\}$	609.13	2.41	0.08	6	157.06
$\{\phi_T, p_c\}$	609.34	2.62	0.07	3	163.44
$\{\phi_c, p_i\}$	609.68	2.97	0.06	12	144.99
$\{\phi_{e2}, p_T\}$	610.95	4.24	0.03	4	163.01
Immigration					
$\{\gamma_c, p_T\}$	617.64	0.00	0.47	3	171.74
$\{\gamma_c, p_i\}$	619.22	1.58	0.21	11	156.71
$\{\gamma_T, p_T\}$	619.27	1.63	0.21	4	171.33
$\{\gamma_T, p_i\}$	621.33	3.69	0.07	12	156.70

^a Subscripts: t = time dependence (each week differs), c = constant through time, T = logit-linear trend through time, and $e2$ = two encounter classes.

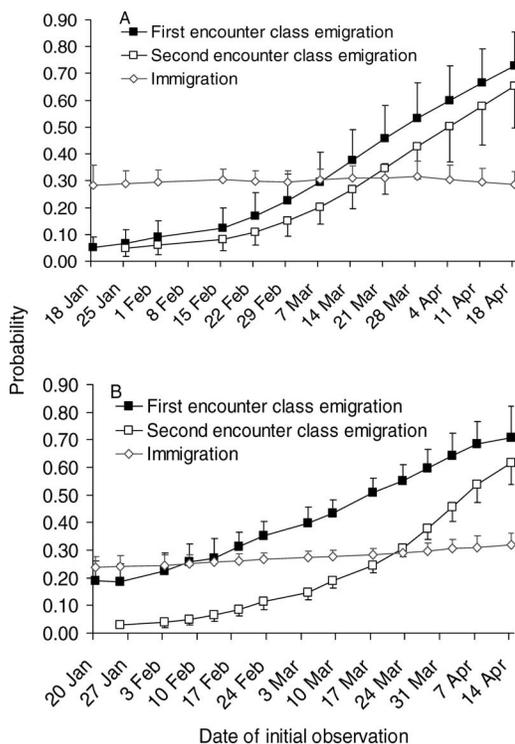


FIG. 2. Model average estimates (± 1 SE) of immigration (\diamond) and emigration probabilities for first encounter class (\blacksquare) and second encounter class (\square) Black Brant during northward migration 2000 (A) and 2001 (B) in Humboldt Bay, California. First encounter class is a mixture of transients and residents; the second encounter class is entirely residents.

counter class structure) during model averaging. The model-averaged estimates (Fig. 2A) of emigration probabilities through time for birds observed in the first (mixture of transients and residents) and second (residents) encounter classes were similar in 2000.

The best immigration model for 2000 was $\{\gamma_c, p_T\}$, where seniority was constant and recapture probability followed a linear trend through time (Table 1). QAIC_c weight was high for the best model. The only other model with appreciable weight had seniority following a linear trend through time, but this trend was not significantly different from constant (Fig. 2A).

Model Selection 2001.—The full model considered in 2001 $\{\phi_{e12}, p_i\}$ was an adequate general model to begin selection (deviance rank = 69/100). A variance inflation factor ($\hat{c} = 1.062$) was applied to emigration and immigration model selection. The most parsimonious emigration model was $\{\phi_{e2,T}, p_i\}$ (Table 2). Residence had two encounter classes in this model that followed a linear trend through time. Recapture also varied through time. QAIC_c weight was high for this model, and no others contributed much information to the model-averaged parameters (Fig. 2B).

The most parsimonious immigration model in 2001 was $\{\gamma_c, p_i\}$ (Table 2). Seniority was constant and recapture varied through time in this model. The next best immigration model had seniority following a positive linear trend through time (Fig. 2B).

Model Selection True Age.—We analyzed a subset of 171 birds observed 235 times in

TABLE 2. Model selection results (top 95% model set by weight) for Black Brant during January–May 2001 at Humboldt Bay, California, with $\hat{c} = 1.062$ variance inflation factor, ϕ = residence probability, γ = seniority probability, and p = recapture probability. Model with zero Δ QAIC_c is considered the most parsimonious. QAIC_c weight is the relative strength of evidence supporting a given model.

Model	QAIC _c	Δ QAIC _c	QAIC _c weight	Parameters	QDeviance
Emigration					
$\{\phi_{e2,T}, p_i\}^a$	1159.18	0.00	0.85	18	305.34
$\{\phi_T^2, p_i\}$	1163.87	4.68	0.08	16	314.15
$\{\phi_{e1,e2T}, p_i\}$	1165.67	6.49	0.03	31	284.68
Immigration					
$\{\gamma_c, p_i\}$	1191.80	0.00	0.52	16	342.10
$\{\gamma_T, p_i\}$	1192.01	0.21	0.47	17	340.26
$\{\gamma_T, p_i\}$	1202.38	10.58	0.01	28	327.77

^a Subscripts: t = time dependence (each week differs), c = constant through time, T = logit-linear trend through time, T^2 = quadratic trend through time, $e2$ = two encounter classes, $e1$ = transients and residents, and $e2$ = residents only.

TABLE 3. Model selection results for effects of true age as an individual covariate for Black Brant during January–May 2001 at Humboldt Bay, California, with $\hat{c} = 1.16$ variance inflation factor, ϕ = residence probability, γ = seniority probability, and p = recapture probability. Model with zero ΔQAIC_c is considered the most parsimonious. QAIC_c weight is the relative strength of evidence supporting a given model. Top 70% model set by weight for ϕ , and top 100% model set by weight for γ are shown.

Model	QAIC_c	ΔQAIC_c	QAIC_c weight	Parameters	QDeviance
Emigration					
$\{\phi_{e2^{*T+age}}, p_c\}^a$	298.41	0.00	0.20	6	286.01
$\{\phi_{e2+T+age}, p_c\}$	298.92	0.51	0.15	5	288.64
$\{\phi_{e2^{*T+age}}, p_c\}$	300.27	1.86	0.08	7	285.73
$\{\phi_{i+age}, p_c\}$	300.65	2.24	0.06	7	286.11
$\{\phi_{e2^{*T}}, p_c\}$	300.79	2.38	0.06	5	290.50
$\{\phi_{e2+T}, p_c\}$	300.81	2.41	0.06	4	292.62
$\{\phi_{T+age}, p_c\}$	300.88	2.47	0.06	4	292.69
$\{\phi_{e2+i+age}, p_c\}$	302.44	4.04	0.03	8	285.75
$\{\phi_T, p_c\}$	302.53	4.12	0.03	3	296.42
Immigration					
$\{\gamma_T, p_c\}$	319.62	0.00	0.46	6	307.2
$\{\gamma_{i^{*age}}, p_c\}$	320.26	0.64	0.34	11	297.1
$\{\gamma_{i+age}, p_c\}$	321.43	1.82	0.19	7	306.9
$\{\gamma_c, p_c\}$	326.24	6.63	0.02	2	322.2

^a Subscripts: t = time dependence, c = constant through time, T = linear trend through time, and age = age individual covariate included.

2001 whose true ages were known for tests of true age effects on ϕ and γ . The general model tested for GOF was $\{\phi_{e6t}, p_i\}$. This general model was sufficient (deviance rank = 76/100), but a variance inflation factor of $\hat{c} = 1.16$ was applied. Model selection for ϕ indicated a transient effect, requiring two encounter classes. We detected a significant effect of true age on ϕ_i , but only weak evidence of a true age effect was detected for γ_i (Table 3). The relationship between age and ϕ was

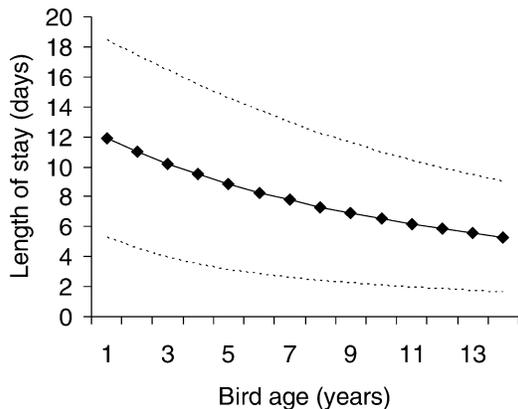


FIG. 3. Mean stopover duration in days as a function of true age for Black Brant at Humboldt Bay, California. Dashed lines indicate ± 1 SE.

negative ($\beta = -0.456 \pm 0.231$, 95% confidence interval -0.908 to -0.004), indicating emigration probability was positively related with age. Thus, stopover duration was shorter for older birds than younger birds (Fig. 3). Temporal trends in emigration probability followed a pattern similar to that in the full data set (Fig. 2B). Chronology also differed by age, with older birds arriving at Humboldt Bay earlier than younger birds. In both 2000 and 2001, the median age of birds was highest in the first half of February (Fig. 4).

Techniques.—We detected 12 radio-marked Brant during January–May 2000. The first detection was on 20 February and the last radio-marked bird in the study area departed on 14 April. The GLM indicated that mean stopover duration measured by radiotelemetry (8 ± 3 days, range = 1–29 days, $n = 12$) was not significantly different from the CMR-derived estimate computed from residence probability alone (mean = 12 ± 2 days, $z = 1.11$, $P = 0.268$, $n = 320$). However, stopover duration measured by radiotelemetry was significantly different from the CMR-derived estimate computed from residence and immigration probabilities (mean = 21 ± 2 days, $z = 2.83$, $P = 0.005$, $n = 320$). This indicates the CMR-derived estimate computed from residence probability alone is preferred in this system.

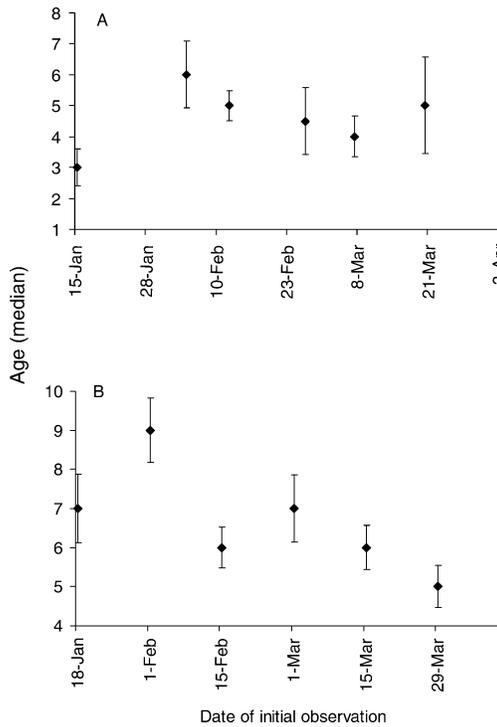


FIG. 4. Median true age (± 1 SE) of newly observed Black Brant on Humboldt Bay by date during northward migration 2000 (A) and 2001 (B).

Stopover Duration.—Based on our comparison of techniques, we used the CMR-derived estimate computed from residence probability alone to compute stopover duration. Stopover durations were similar between years (Fig. 5), especially for birds in the second encounter class (residents). Residents that arrived ~ 25 January had stopover durations of ~ 36 days and stopover durations of both encounter classes decreased steadily throughout the season in both years (Fig. 5). Mean (\pm SE) stopover duration for all resident birds from 25 January to 11 April was 17 ± 2 days and for transient birds was 10 ± 1 days.

Volume.—The estimated total number of Brant using Humboldt Bay was 37,600 birds in 2000 and 77,800 birds in 2001. The total Pacific Flyway Brant population in 2000 was estimated at 135,000 birds, and we estimate that 28% and 58% of the population used Humboldt Bay in 2000 and 2001, respectively. Thirty-five percent of the population of radio-marked Brant ($n = 34$) used Humboldt Bay.

DISCUSSION

We found age-dependent variation in chronology and stopover duration. Our research indicated the older, more productive (Black and Owen 1995; Sedinger et al. 1998, 2001), and more dominant (Black et al. 1992) segment of the population made use of Humboldt Bay primarily early in the migratory season, and stayed for a shorter period than younger birds. Reproductive success in geese is dependent upon individuals getting to the farthest north stopover area early and maximizing time at that location (Palmer 1976, Madsen 2001). Thus, older birds were maximizing resource efficiency by spending less time at Humboldt Bay, a stopover site in the middle of the northward migration route, to arrive earlier at northern sites where reproductive success is determined (Madsen 2001).

Younger birds may take longer to gain condition for the next migratory flight due to lower foraging efficiency (Wunderle 1991), competitive exclusion by older, more dominant birds (Raveling 1970, Gauthreaux 1978, Black et al. 1992), or by encountering food resources depleted by earlier arriving older birds (Prop and Loonen 1989, Rowcliffe et al. 2004). Alternatively, a longer stopover could be a strategy to minimize energy reserve flux and increase survival of younger birds that are not likely to breed successfully in their early attempts. Life history theory predicts the trade-off between somatic and reproductive investment would favor somatic investment in young ages of a “survivor” species (*sensu* Sæther et al. 1996) such as Brant to retain residual reproductive value (Stearns 1992).

Mean emigration probability in both years steadily increased with each time step from January to April, indicating a seasonally progressive migratory state. Thus, stopover durations were much shorter for birds arriving late in the migration versus those that arrived earlier (when true age is controlled), similar to other studies (Pradel et al. 1997b, Reed et al. 1998a, Prop et al. 2003). Humboldt Bay’s “wintering” resident Brant population in January and early February was not entirely stable, with turnover from 3% to 8% per week until 15 February. This constant turnover in winter is evidence for steady, low-intensity movement of the Brant population, even dur-

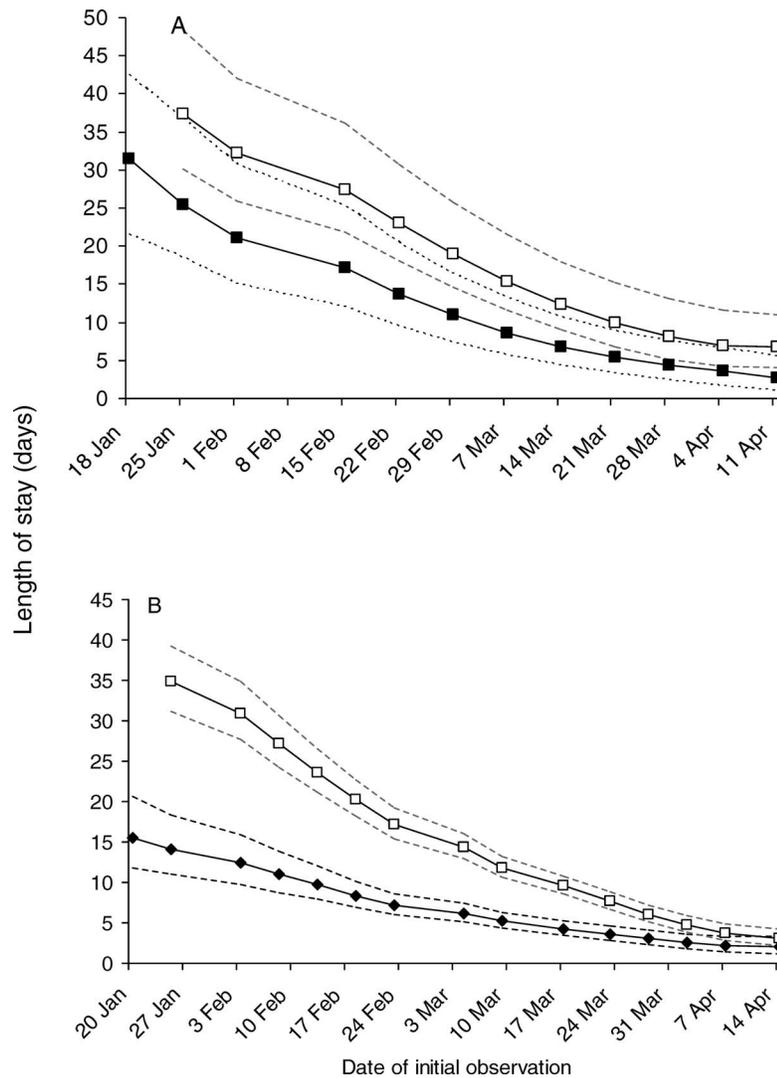


FIG. 5. Mean stopover duration in days (± 1 SE) for first encounter class (■) and second encounter class (□) Black Brant at Humboldt Bay, California on a given date. Stopover duration for year 2000 (A), and 2001 (B). First encounter class is composed of a mixture of transients and residents; second encounter class is composed entirely of residents. Stopover durations were computed using model-averaged immigration and emigration parameters.

ing so-called winter residency. These findings agree with those of Reed et al. (1998a) who detected turnover rates of $\sim 3\%$ per week at Boundary Bay, British Columbia.

There was also variation in stopover duration due to individual heterogeneity. We detected a large proportion of transients in the population. Transients were birds with a zero residence probability after the initial encounter (*sensu* Pradel et al. 1997a). Transients were

also detected in other studies of this population (Reed et al. 1998a, Routledge et al. 1999). Resident and transient status are problematic as there are no universally agreed upon definitions. Thompson (1993) defined a resident as a bird present in its final wintering area. However, considering migrations as a continuous and dynamic process involving multiple sites along the migratory route make defining a final wintering site problematic. We

suggest a probabilistic framework for categorizing stopover sites by immigration and emigration probabilities, stopover durations, and volume. All birds are ultimately transient visitors to sites along migratory routes. Immigration and emigration probabilities and stopover duration provide universal metrics of that transience. Model selection procedures provide a framework for examining sources of variation in those metrics.

The distribution of minimum stopover durations (days between first and last observation) in our raw data approximated an inverse power curve. This is similar to the distribution reported by Routledge et al. (1999) for Brant staging at Parksville-Qualicum Beach, Vancouver Island, British Columbia. Our *a priori* model set did not include this inverse power curve distribution, but used encounter class structure (ϕ_{e2}) to control for the extreme heterogeneity between birds observed once, and those observed more than once. This structure allowed emigration estimates to differ for the encounter class composed of many transients versus the subsequent encounter class composed of residents. Transient models are useful tools to account for heterogeneity between groups of individuals. Transient models remove the substantial negative bias that transient animals can introduce to mean emigration estimates without sacrificing any data. Migrations are characterized by movements of large numbers of animals. Those that pause only briefly at a given stopover site should be included when considering use and impact of stopover habitats. More data and shorter time between observation periods might resolve the apparent curvilinear distribution of stopover durations, or the distribution may ultimately be most parsimoniously modeled by the encounter class structure used.

Routledge et al. (1999), incorporating the full distribution of stopover durations, estimated mean stopover duration for Brant in spring at Parksville-Qualicum Beach, British Columbia to be 5.92 days. This is significantly lower than our mean estimate from all birds for January to April at Humboldt Bay of 13 ± 2 days. However, Routledge et al.'s (1999) estimates came from a site much farther north, and used different methods. Reed et al.'s (1998a) estimates of mean stopover duration for spring at Boundary Bay, British Columbia,

using methods similar to ours, were 8 days for transients and 27 days for residents. The differences between Reed et al.'s (1998a) and Routledge et al.'s (1999) results could be due to site-specific reasons. A comparison of methods at the same site would illuminate this disparity.

Our comparison of stopover duration estimators using radio-marked birds as a validation tool supported use of emigration alone to compute stopover duration (Reed et al. 1998a, Efford 2005), as opposed to using both immigration and emigration (Schaub et al. 2001). Efford (2005) and the response by Pradel et al. (2005) indicate the Schaub et al. (2001) method performs well (is unbiased) when most birds spend the same amount of time at the stopover site, as is the case with many passerines (Bairlein 1986). However, in cases where stopover durations follow a Poisson distribution, the Schaub et al. (2001) method overestimates stopover duration by nearly double and the Reed et al. (1998a) method is preferred. Routledge et al. (1999) assumed that residence time distribution was an extended, negative binomial. Efford (2005) proposed another method that may be a good candidate for computing stopover duration. Another aspect of stopover duration deserving more attention is how the amount of time a bird has already spent at the stopover site affects its emigration probability (Pradel et al. 2005).

Conservation/management activity along flyways is usually based on peak counts achieved, and sites with the highest "internationally important" numbers receive priority in action plan prescriptions (e.g., Stroud 1992, Hunter and Black 1996, Black 1998). We could assume that at least 13% of the population made use of the site based on the average peak counts of Brant at Humboldt Bay (~17,000). Moore et al. (2004) ranked Humboldt Bay as the fourth most important site in the Pacific Flyway for Brant using this method. We calculated that 28% and 58% of the population used the Bay in the years 2000 and 2001, respectively using the more precise CMR estimates. Calculating the total volume of species that pass through migratory staging sites provides managers with more information with which to prioritize management action. In the last 100 years, California has lost

more than 70% of its intertidal wetlands to anthropogenic alterations (Speth 1979). Eelgrass meadows of the Pacific Flyway on which Black Brant depend are particularly under threat from human activity (Ganter 2000, Moore et al. 2004, Ward et al. 2005). Migrants are often viewed as highly mobile, but the ability of individuals to find alternative sites when habitat is lost may not be assured (Dolman and Sutherland 1995, Ganter et al. 1997). Predicting the outcome of potential habitat change is a challenging procedure that relies on sound empirical data (Goss-Custard and Sutherland 1997, Pettifor et al. 2000). The large disparity between estimates of volume for the two years of this study indicate the need for repeated sampling efforts to increase precision and elucidate sources of annual variation.

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