

Black Brant Harvest, Density Dependence, and Survival: A Record of Population Dynamics

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ABSTRACT We analyzed 53 years of banding and band recovery data along with estimates of harvest and population size to assess the role of harvest and density dependence in survival patterns and population dynamics of black brant (*Branta bernicla nigricans*) over the period 1950–2003. The black brant population has declined steadily since complete annual surveys began in 1960, so the role of harvest in the dynamics of this population is of considerable interest. We used Brownie models implemented in Program MARK to analyze banding data. In some models, we incorporated estimated sport harvest to test hypotheses about the role of harvest in survival. We also examined the hypothesis of density-dependent regulation of mortality by incorporating estimates of population size as a covariate into models of survival. For a shorter period (1985–2003), we also assessed hypotheses about the role of subsistence harvest and predation as sources of mortality. The best supported model of variation in survival and band recovery allowed survival rates to vary among 2 age classes (juv, second-yr plus ad brant) and the 2 sexes. We constrained survival probabilities to be constant within decades but allowed them to vary among decades. We also constrained band recovery rates to be constant within decades and to vary in parallel among age and sex classes. We were limited to decade-specific estimates of survival and band recovery rates because some years before 1984 lacked any banding, and banding in some other years was sparse. A competitive model constrained survival estimates to be the same for males and females. No model containing harvest or population size was competitive with models lacking these covariates (relative quasi-Akaike's Information Criterion adjusted for small sample size [$\Delta QAIC_c$] > 13). In the best supported model, band recovery rates declined from 0.038 ± 0.0028 (F) and 0.040 ± 0.0031 (M) to 0.007 ± 0.0007 (F) and 0.007 ± 0.0007 (M) between the 1950s and 2000s, a clear indication that harvest rates declined over this period. Survival rates increased from 0.70 ± 0.02 and 0.71 ± 0.02 for adult males and females, respectively, in the 1950s to 0.88 ± 0.009 and 0.88 ± 0.01 for males and females, respectively, in the 1990s. Survival rates in the 1990s were among the highest estimated for brant and did not increase in the 2000s with additional reductions in sport harvest. For the shorter data set from 1985 to 2003, models containing covariates for either sport or subsistence harvest were less competitive than models lacking these terms ($\Delta QAIC_c > 3$). For the best model containing subsistence harvest, the estimate of β linking subsistence harvest to survival, although imprecisely estimated, was near zero ($\beta = -0.04 \pm 0.30$), consistent with the hypothesis that subsistence harvest had little impact on survival during this period. We conclude that while harvest likely influenced survival and population dynamics in earlier decades, it is most likely that continued population decline at least since 1990 is a result of low recruitment. (JOURNAL OF WILDLIFE MANAGEMENT 71(2):496–506; 2007)

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Dynamics of populations are governed by the balance among survival, recruitment, emigration, and immigration. When there is concern about dynamics of an entire population, immigration and emigration are not important because individuals cannot enter or leave the global population except by birth or death. In relatively large-bodied species with high survival rates, rate of population increase (λ) is most sensitive to variation in adult mortality (Rockwell et al. 1997, Schmutz et al. 1997, Cooch et al. 2001, Coulson et al. 2004). Selection, however, constrains variation in life-history traits to which fitness is most sensitive. As a result, survival probability may be constrained, although components of recruitment of offspring into the breeding population remain highly variable (Charlesworth 1994, Coughenour and Singer 1996, Monson et al. 2000, Cooch et al. 2001). Two studies of waterfowl have shown that λ was influenced most strongly by recruitment. In mallards

(*Anas platyrhynchos*), variation in nest success explained 43% of the variation in λ (Hoekman et al. 2002), whereas in lesser snow geese (*Anser caerulescens caerulescens*) variation in survival of young from hatch to 1 year of age was about 6 times as important as variation in adult survival in explaining variation in λ (Cooch et al. 2001). In the study by Cooch et al. (2001), density-dependent declines in food quantity reduced growth of goslings before fledging (Cooch et al. 1991), which caused lower survival over the first fall and winter (Francis et al. 1992).

The role of harvest in population dynamics of North American waterfowl remains controversial (Smith and Reynolds 1992, Sedinger and Rexstad 1994), largely because harvest rates are typically confounded with density-dependent processes in the management of these populations. That is, harvest regulations tend to be more conservative, resulting in low harvest rates when populations are low, and the opposite is true when populations are high. This confounding between population size and harvest mortality tends to

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favor models of additive harvest mortality when examining the relationship between harvest and survival because survival rates decline at high harvest rates (Sedinger and Rexstad 1994), which are associated with high population sizes. Conn and Kendall (2004) demonstrated this phenomenon occurred in the North American adaptive waterfowl management program (Johnson et al. 1997); simulations of population dynamics and model selection favored models of additive harvest mortality even when populations were regulated entirely by density-dependent processes. Despite the potential bias favoring additive harvest models, most early studies of the relationship between harvest and survival in duck populations failed to detect evidence for additive harvest mortality (Anderson and Burnham 1976, Nichols and Hines 1983, Burnham and Anderson 1984, Trost 1987, but see Conroy and Krementz 1990).

Harvest by humans is generally believed to be additive to other forms of mortality for adult geese (Rexstad 1992, Sheaffer et al. 2004). Annual survival probabilities in unharvested or lightly harvested European populations of geese suggest that maximum annual survival probabilities in geese are approximately 0.83–0.94 (Ebbinge et al. 1991, Clausen et al. 2001). In harvested North American goose populations, direct band recovery rates range from 1% to 9% (Francis and Cooke 1992, Menu et al. 2002, Sheaffer et al. 2004). Although reporting rates for leg bands of harvested geese are unknown, if they are similar to those for ducks (approx. 38% of bands obtained by hunters are reported to the Bird Banding Laboratory; Nichols et al. 1995), harvest rates range from 2% to 24% of specific age and sex classes across populations of geese. These harvest rates are associated with annual survival probabilities of adult geese in harvested populations, ranging from 0.54 to 0.87 in North America and, generally, higher harvest rates are associated with lower adult survival probabilities (Francis and Cooke 1992, Menu et al. 2002, Sheaffer et al. 2004). It is of interest, however, whether low harvest rates (<5%) remain additive to other sources of mortality in geese.

Black brant (hereafter, brant) wintering along the Pacific coast of North America have declined steadily since 1960 (Reed et al. 1998; B. Conant and R. J. King, United States Fish and Wildlife Service [USFWS], unpublished report). Harvest of this population was substantial in the 1950s and 1960s and was approximately 15% of the population during some years in the 1950s (USFWS, unpublished data). Harvest by subsistence hunters in Alaska, USA, and Canada can also be substantial (Klein 1966; C. Wentworth and S. G. Seim, USFWS, unpublished report) and appears to follow a functional response (Sedinger 1996). Despite a declining population, Sedinger et al. (1998, 2004) showed substantial density-dependent regulation of recruitment in brant during the early to mid-1990s, resulting from a complex feedback between grazing by geese and maintenance of grazing lawns essential for adequate growth of goslings (Person et al. 2003). Carrying capacity declined in the 1980s because of plant responses to reduced grazing pressure, creating density-dependent declines in recruitment

even at population levels well below historic levels (Person et al. 2003). High nest success between 1986 and 1995 increased grazing intensity on lawns, resulting in greater extent of grazing lawns and reduced density dependence during the late 1990s (Person et al. 2003).

We used a 53-year data set of banding and sport hunter recovery of brant to examine the long-term pattern in both harvest and survival of brant. Our goal was to assess the relationship between harvest and annual survival and the role of harvest in the long-term decline in brant. We also examined the effect on survival of population size itself to assess the hypothesis that density-dependent mechanisms influenced adult survival. We directly examined the relationship between harvest by subsistence hunters in Alaska and survival for a shorter period, approximately 15 years. We recognize that our study cannot simultaneously control the multiple components of the recruitment and survival processes that could regulate population dynamics. Thus, inference cannot be as strong as it might be if we could independently control specific demographic components experimentally. Nevertheless, substantial variation in harvest and survival rates in brant and their population size creates a unique opportunity to assess the relationship between harvest and survival and to examine hypotheses about population regulation.

METHODS

Field Methods

We captured brant by herding them into corral traps during the adult remigial molt when adults were flightless and before goslings could fly (Sedinger et al. 1997) during July 1950–2002. We determined sex by cloacal examination (Owen 1980). We separated second-year (SY; individuals approx. 13 months old) from adult brant by the presence of juvenile wing-coverts on SY individuals (Bellrose 1980). We applied a steel USFWS (now United States Geological Survey) band to each individual. We applied plastic neck collars to 1,523, 158, and 128 individuals in the 1960s, 1970s, and 1980s (before 1985), respectively. After 1984, individuals also received a uniquely coded engraved plastic tarsal band (Sedinger et al. 1997). Substantial banding of brant has been conducted in Arctic Canada and on Alaska's North Slope, but we restricted analysis to brant banded on Alaska's Yukon-Kuskokwim (Y-K) Delta because 1) effort there was relatively continuous back to 1950, 2) brant on the Y-K Delta represent >70% of the breeding population (Sedinger et al. 1993), and 3) substantial numbers of molt migrants were present in arctic samples in some years (Barry 1967, Sedinger et al. 1994, Reed et al. 1998), making it difficult to assign these individuals to specific breeding populations. Capture and handling of brant was approved by the Institutional Animal Care and Use committees of both the University of Alaska Fairbanks and the University of Nevada, Reno (most recent protocol no. A03/04-37).

Population and Harvest Estimates

We estimated the number of brant in the population each January by flying over bays and estuaries of the west coast of

Baja California, Mexico (Bahia San Quintin in the north to Bahia Magdalena in the south) and the mainland coast of the Sea of Cortez (from the mouth of the Colorado River to Tuxpan; B. Conant and R. J. King, unpublished report). About 75% of the population wintered in Mexico each year (Sedinger et al. 1994). We surveyed bays and estuaries in each of the coastal states (CA to WA) in the United States using similar procedures during the same January period (Pacific Flyway Council, unpublished report). A few hundred brant wintered in British Columbia, Canada, but because surveys there were not conducted using the same procedures as in the United States and the numbers were small, we did not include these brant in our midwinter population data. Similarly, brant wintering in Alaska have only been counted since 1986, and we did not include these brant in our midwinter numbers.

Staff of the USFWS estimated harvest by sport hunters in the United States using harvest survey programs of the USFWS (Martin and Carney 1977, Blohm 1989, Pendleton 1992). These surveys had 2 parts. First, staff sent a mail questionnaire to a stratified random sample of hunters who purchased a federal waterfowl stamp and asked them to report their harvest of ducks and geese. They used this first sample to estimate the total harvest of waterfowl in the United States. Second, they asked a random subsample of the questionnaire sample to provide a wing from each duck and brant shot and a tail-fan from each goose. They used the second sample to partition the total harvest among species, ages, and the 2 sexes. Because there were few brant hunters, a small sample of brant hunters was often selected to provide wings, which caused estimates of brant harvest to be highly variable. Nevertheless, these harvest surveys provided the only consistently collected estimates of brant harvest over the duration of our study. We acquired harvest data for the years 1962–2001 from the United States harvest surveys.

The Pacific states have also estimated brant harvest, but methodology for these surveys has not been constant through time (Pacific Flyway Council, unpublished report). We, nevertheless, used estimates from state surveys to adjust one clearly anomalous estimate (1998) from the federal survey. For this year, we calculated the ratio of the 1998 harvest to the average harvest for 1997 and 1999 based on state estimates. We then applied this ratio to the average United States harvest estimates for 1997 and 1999 to estimate harvest in 1998 for assessing hypotheses about the relationship between survival and harvest (see below).

We based estimates of waterfowl harvest by subsistence hunters on Alaska's Y-K Delta on stratified random sampling of hunters in the area (C. Wentworth and S. G. Seim, unpublished report). The goal was to sample 25% of the households in the region participating in subsistence harvest. This survey randomly selected 23 villages from 5 regions of the Y-K Delta, then randomly selected a total of 541–998 households from within the selected villages. Villages were able to opt out of the survey, resulting in between 19–24 villages annually participating in the survey between 1985 and 2000. We also surveyed households (100–

200 households annually) from the city of Bethel (approx. 1,400 Native residents in 1990) each year, resulting in between 748–1,098 households in the sample annually. We asked each selected household to report the harvest of all species of waterfowl on forms depicting these species pictorially. A local resident surveyor visited each selected household to explain the survey and again to collect survey forms at the end of each of 5 survey periods: 1) spring (9 Apr–20 May), 2) early summer (21 May–24 Jun), 3) midsummer (25 Jun–29 Jul), 4) late summer (30 Jul–31 Jul), and 5) fall (1 Sep–15 Oct). We estimated total harvest from the total contributions of each village in each stratum. We analyzed trends in population and harvest data using the General Linear Models procedure of SAS version 9.1 (SAS Institute, Cary, NC).

We estimated nest success at the Tutakoke River brant colony on the Y-K Delta (Sedinger et al. 1993) as the proportion of nests visited on 100-m-diameter plots that hatched ≥ 1 egg. We visited 45 plots each year, beginning when about 10% of brant had initiated egg laying. We visited plots every fourth day until laying was complete, again just before the first nests were scheduled to hatch, and again after the fates of all nests had been determined.

Survival Models

We analyzed band recovery rates and annual survival probabilities using Brownie models (Brownie et al. 1985) implemented in Program MARK (White and Burnham 1999). The most general model allowed for annual variation (1950–2002) in both recovery and survival rates, variation among 3 age classes, and differences between males and females. This model contained 642 parameters and, likely because of the combination of model complexity and missing or sparse bandings in some years, failed to converge. Thus, the most general models presented below either constrained variation to be additive across age and sex classes (i.e., we constrained annual variation in survival and recovery rates to be parallel across age and sex classes) or we constrained survival and recovery rates to be constant within decades. We first compared models in which we allowed SY individuals to differ from adults (3 age classes) with models in which we assumed SY individuals shared parameter estimates with adults (2 age classes). We also considered models in which survival probability was described by a trend. We used the logit to link all response variables to explanatory variables in models of survival and recovery rates. We did not view estimates of band recovery rates as nuisance parameters so we evaluated models including various combinations of band recovery rate and survival rate, rather than first constraining models of band recovery rate then assessing models of survival.

We assessed hypotheses about the relationship between population size and survival by including the January survey count of brant as a covariate in analyses of band recoveries. Because the midwinter survey was not standardized until 1960, we only applied this covariate to survival estimates beginning in 1960 and estimated survival rates for the period 1951–1959 separately from those potentially influenced by

Table 1. Numbers of individual black brant banded on the Yukon-Kuskokwim Delta, Alaska, USA, and recovered along the Pacific coast of North America in each decade from the 1950s through the 2000s.

Decade	Juv				SY ^a				Ad			
	F		M		F		M		F		M	
	Banded	Recovered	Banded	Recovered	Banded	Recovered	Banded	Recovered	Banded	Recovered	Banded	Recovered
1950s	888	77	772	67	0	0	0	0	838	80	731	84
1960s	867	49	833	45	1,917	220	1,221	163	4,169	530	3,584	513
1970s	72	3	76	4	1,201	87	740	51	251	24	263	35
1980s	2,095	87	2,110	125	116	8	51	2	1,869	146	1,761	137
1990s	7,780	241	7,330	246	333	13	149	10	4,487	286	4,962	313
2000s	939	7	1,022	10	36	1	11	0	1,063	22	1,249	28
Total	12,641	464	12,143	497	3,603	329	2,172	226	12,677	1,088	12,550	1,110

^a Second-yr brant, approx. 13 months old when banded.

population size. We constrained survival to be constant for 1950–1959 in models containing the covariate population size. We expected that if there were negative density-dependent effects of population size on survival, we would observe a negative relationship between January counts and annual survival. We used Akaike weights (Burnham and Anderson 2002) and the sign and 95% confidence intervals for estimates of regression coefficients (β) relating January counts to survival in the logit to assess this hypothesis.

We examined the effects of sport harvest similarly to our approach for population size. We incorporated estimates of sport harvest as a covariate into models of survival. Harvest data were only available from 1965 to 2001 and it was necessary to estimate survival rates from 1951 to 1964 separately from those for which we could explore the effects of harvest.

To depict the relationship between band recovery rate (a correlate of sport harvest) and annual survival, we present decadal estimates of survival plotted against band recovery rate. Estimates of annual survival and band recovery rate typically have a negative sampling covariance when estimated from the same data (Anderson and Burnham 1976, Brownie et al. 1985). To assess the importance of this sampling covariance, we estimated the mean sampling covariance between decadal estimates of annual survival and recovery rate for each age and sex class. We used estimates of sampling covariance reported by Program MARK for the best model of the data, which constrained estimates to be constant within decades. We estimated total covariance between annual survival and recovery estimates using linear regression of the point estimates of decadal survival and recovery rates. We then calculated the proportion of total covariance between annual survival and recovery rate that was accounted for by sampling covariance.

We also directly examined hypotheses about the relationship between harvest by humans or predation and survival using a subset of the banding and recovery data restricted to years 1985–2003 for which estimates of sport harvest, Alaskan subsistence harvest, and predation pressure were available. Estimates of subsistence harvest were from the subsistence harvest survey conducted by Region 7, USFWS (C. Wentworth and S. G. Seim, unpublished report). We

restricted harvest estimates to those for the Y-K Delta because this was the only region of Alaska with annual estimates before 1995. We recognize that subsistence harvest occurred in other areas of Alaska and Canada, but insufficient data existed for these other areas to include them in our analyses. Because >70% of brant nested on the Y-K Delta, even males that typically dispersed from their natal area (Lindberg et al. 1998) were primarily subjected to subsistence harvest on the Y-K Delta in years when they bred. Thus, variation in subsistence harvest should have produced variation in survival in models we considered if survival was influenced by subsistence harvest.

We used apparent nest success at the Tutakoke River colony as an index of predator pressure in models of mortality factors for the shorter data set. Our rationale was as follows. Most annual variation in nest success was associated with variation in predation on brant eggs by arctic foxes (Anthony et al. 1991). Arctic foxes (*Alopex lagopus*) also killed adult brant (J. S. Sedinger, University of Nevada, Reno, personal observation). Thus, nest success provided an index of arctic fox activity in the Tutakoke River colony and we hypothesized that if fox predation had an important influence on survival, models of survival containing a term for nest success would perform better than models not containing nest success, and survival would be negatively correlated with nest success. We standardized all covariates and trends by subtracting the mean and dividing by the standard deviation before analysis. We assessed hypotheses about factors influencing survival or band recovery rates using relative quasi-Akaike's Information Criterion adjusted for small sample size (ΔQAIC_c) scores and Akaike weights (Burnham and Anderson 2002). As for the full data set, we further assessed the importance of covariates using estimates ($\pm 95\%$ CI) of β s linking covariates to the dependent variable of interest in the logit transformation. We obtained \hat{c} , the overdispersion parameter, using the median \hat{c} procedure implemented in Program MARK (White and Burnham 1999), applied to our most general model of decadal variation in survival and recovery rates. Because models containing midwinter survey data or sport harvest performed substantially poorer than time-only models (see below), we adjusted confidence intervals for β s for these

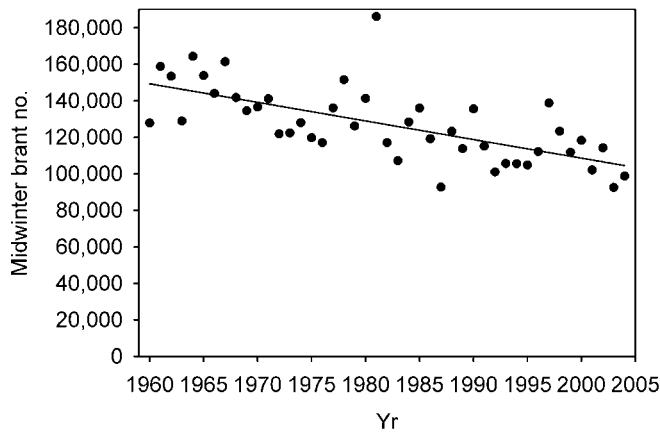


Figure 1. Numbers of black brant counted during January aerial surveys in the Pacific states (except Alaska), USA, and Mexico, from the 1960s through the 2000s.

variables using \hat{c} for the best model containing these variables. This procedure produced confidence intervals slightly broader than those estimated using \hat{c} from the most general model.

RESULTS

We banded 57,786 brant during July on the Y-K Delta between 1950 and 2003, resulting in 3,714 recoveries (Table 1). We estimated $\hat{c} = 1.11$, which we used to adjust AIC_c , producing $QAIC_c$ quasi-likelihood values. The brant midwinter survey declined 28% between the 1960s and the 2000s (Fig. 1). Sport harvest in the United States also declined over this same period (Fig. 2). In contrast, subsistence harvest on the Y-K Delta increased >4-fold between the early 1980s and 2000 (Fig. 3).

In our analysis of the full data set, the best supported model, based on $QAIC_c$ scores (Table 2), allowed for 2 age classes (goslings, and SY plus ad brant) and both survival and recovery rates varied among decades. The best performing model also allowed for additive effects of age and sex on

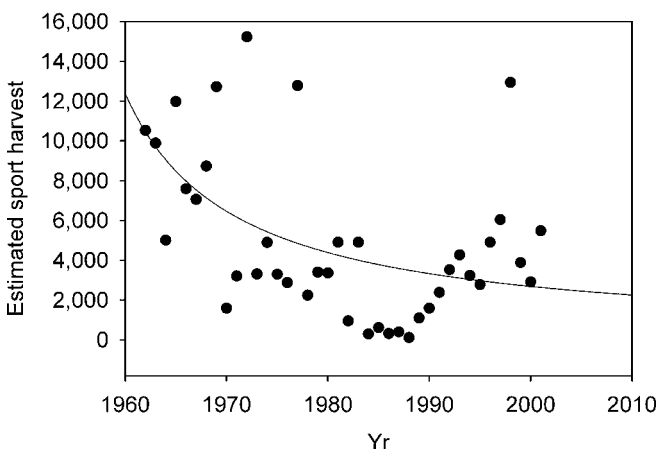


Figure 2. Estimated harvest of black brant by sport hunters along the Pacific coast of North America, 1963–2001. The United States Fish and Wildlife Service estimated harvest annually from a randomly selected sample of hunters.

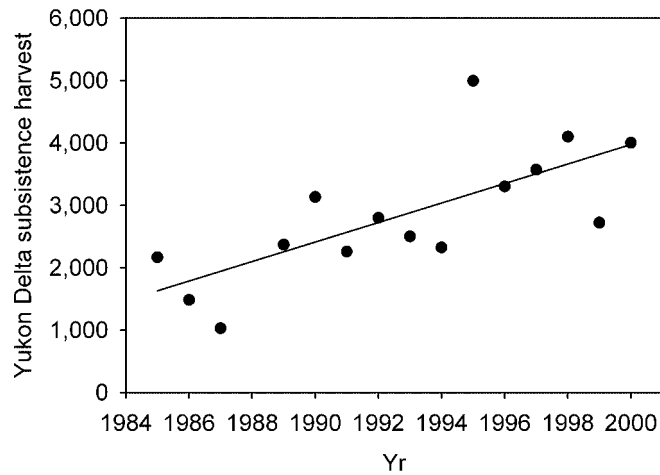


Figure 3. Estimated harvest of black brant by subsistence hunters on the Yukon-Kuskokwim Delta, Alaska, USA, 1985–2000. We based estimates on self-reported harvest from randomly selected households within a stratified random sample of villages on the Yukon-Kuskokwim Delta.

survival, indicating that survival of the age–sex classes varied in parallel among decades. The only other model receiving support constrained survival to be equal for males and females but retained decadal variation in survival and recovery rates. Lack of support for other models indicated that other hypothesized patterns in survival or recovery rates were substantially less likely than those included in the 2 best performing models. Specifically, we found no support for models with 3 age classes. The third best model, which included terms for midwinter population size and sport harvest, had <0.01 probability that it was the best model of survival. Interestingly, the 95% confidence interval for the β linking midwinter population size to survival did not include zero ($\beta = -0.25 \pm 0.11$ [$\pm 95\%$ CI]), whereas the 95% confidence interval for the β for sport harvest did include zero ($\beta = 0.11 \pm 0.19$). Confidence intervals of β s in models containing either midwinter population size or sport harvest by themselves excluded zero for both variables (midwinter population size $\beta = -0.19 \pm 0.08$; sport harvest $\beta = -0.77 \pm 0.15$). Weak support for models containing harvest or midwinter population size (Table 2) suggested substantial temporal variation in survival unexplained by these covariates. Caution is thus warranted when interpreting confidence intervals for parameter estimates from these models, and inference about the relationships between survival and harvest or population size should be considered preliminary.

Covariation between harvest and population size through time makes it difficult to clearly separate the effects of the 2 variables, although superior performance of midwinter population size in a model containing both variables suggests the possibility that population size was more closely associated with survival than was harvest. All of the best models of band recovery rate contained 2 age classes, and variation among decades was additive across age and sex classes. Models including a fixed time trend in survival were

Table 2. Models of survival and recovery rates based on Brownie models of band recoveries for black brant banded and recovered between 1950 and 2003. Relative quasi-Akaike's Information Criterion adjusted for small sample size (ΔQAIC_c) weights provide the probability that a given model is the best model of survival and recovery among models considered.

Model ^a	QAIC _c	ΔQAIC_c	QAIC _c wt	Estimable parameters	QDeviance
S(s+2a+decade), f(s+2a+decade)	38,750.59	0.00	0.53	16	2,181.48
S(2a+decade), f(s+2a+decade)	38,750.82	0.24	0.47	15	2,183.71
S(s+2a+midwinter+harvest), f(s+2a+decade)	38,763.70	13.11	0.00	14	2,198.59
S(s+2a+midwinter+harvest+mid×har), f(s+2a+decade)	38,769.80	19.22	0.00	16	2,200.69
S(s+2a+T), f(s+2a+decade)	38,775.36	24.77	0.00	12	2,214.25
S(s+2a+harvest), f(s+2a+decade)	38,778.39	27.80	0.00	13	2,215.28
S(s+2a+midwinter), f(s+2a+decade)	38,781.21	30.63	0.00	13	2,218.11
S(s+2a+T+T ²), f(s+2a+T)	38,833.34	82.76	0.00	9	2,278.24
S(s+2a+T), f(s+2a+T)	38,927.27	176.68	0.00	8	2,374.17
S(s×2a+decade), f(s+2a+decade)	38,973.96	223.37	0.00	17	2,402.85
S(s×2a+decade), f(s×2a+decade)	39,051.01	300.42	0.00	17	2,479.90
S(s×2a+T+T ²), f(s×2a+T+T ²)	39,079.62	329.04	0.00	13	2,516.52
S(s×3a+t), f(s×3a)	39,107.88	357.30	0.00	64	2,442.63
S(s+2a), f(s+2a)	39,180.69	430.10	0.00	6	2,631.59
S(s×3a), f(s×3a)	39,186.61	436.03	0.00	12	2,625.51
S(s+3a), f(s+3a)	39,199.40	448.81	0.00	8	2,646.30
S(s+2a), f(s+2a)	39,243.84	493.25	0.00	6	2,694.74
S(s), f(s)	39,715.05	964.46	0.00	4	3,169.95
S(.), f(.)	39,718.21	967.62	0.00	2	3,177.11

^a Model notation generally follows Lebreton et al. (1992). Sex and age are indicated by “s” and “a,” respectively. “2a” indicates 2 age classes were included in a model, while “3a” indicates 3 age classes (juv, second yr [SY], and ad). We combined SYs and ad in 2-age-class models. “Harvest” and “midwinter” variables indicated that we included sport harvest and population size (midwinter index), or their interaction (mid×har) in a model as covariates. “Decade” indicates that we constrained survival or recovery rate estimates constant within decades, whereas “T” and “T²” indicate linear and quadratic trends, respectively.

also not well supported, indicating that changes in survival probability have not been constant across time.

Band recovery rates estimated from the best model declined in each decade from the 1950s through the 2000s (Fig. 4). Band reporting rates for brant were unknown but if they were similar to those for mallards (38%; Nichols et al. 1995), recovery rates (Fig. 4) translated into harvest rates that ranged from 10% for adult males in the 1950s to <3% for adult females in the 2000s. Recovery rates were consistently higher (7% of estimates) for males than for females, and recovery rates were consistently higher for SY and adult brant (3% of estimates) than for goslings. Consistent with the hypothesis that harvest by humans influenced survival in brant, survival probabilities increased in each decade from the 1950s through the 1990s for each age and sex class (Fig. 4). Mean annual survival probabilities from the best supported model for adult male and female brant in the 1990s were 0.88 ± 0.009 and 0.88 ± 0.01 , respectively. The additional decline in band recovery rates from the 1990s to the 2000s, however, was not associated with an increase in survival from the 1990s to the 2000s. Because we began using metal bands with a toll-free telephone number in 1997, band reporting rates were undoubtedly higher in the 1990s and 2000s than in earlier decades, resulting in an even greater decline in harvest in the 1990s and 2000s than indicated by band recovery rates (Figs. 4, 5). When we plotted decade-level estimates of annual survival probability against estimated recovery rates (Fig. 5), there was no relationship between recovery and survival rates at low harvest rates. Although the negative correlation between recovery rate and survival rates across decades was

clear, at least until the 2000s, models in which we directly assessed the annual relationship between harvest and survival performed poorly. Sampling covariance accounted for only 2.3% (first-yr M) to 3% (ad M) of the covariance between annual survival and recovery rates, indicating that sampling covariance had little influence on the negative covariance between these parameters (Fig. 5). The absence of a strong annual relationship between harvest and survival, however, suggests a complex relationship between these 2 variables.

In the best supported model, adult males consistently had the highest annual survival (all 6 decades) followed by adult females, and adult male survival averaged 1.4% higher than that for adult females. Survival of goslings averaged 44% that of adults. Male goslings survived at higher rates than female goslings in every decade ($\bar{x} = 4.8\%$ higher). Small differences in annual survival between the sexes are consistent with relatively strong support for a model in which survival did not differ between the sexes.

In our analysis of the shorter data set for which we could directly assess the roles of subsistence harvest, sport harvest, and predation, no models containing terms for either harvest or predation received strong support (Table 3); models containing a term for subsistence harvest received 15% of model weight. We interpret these results to indicate that variation in sport and subsistence harvest between 1985 and 2003 did not strongly influence either survival or band recovery rates for brant during this period. We considered only 2-age-class models in these analyses because 3-age-class models did not perform well on the full data set. The best performing model in the shorter data set contained an

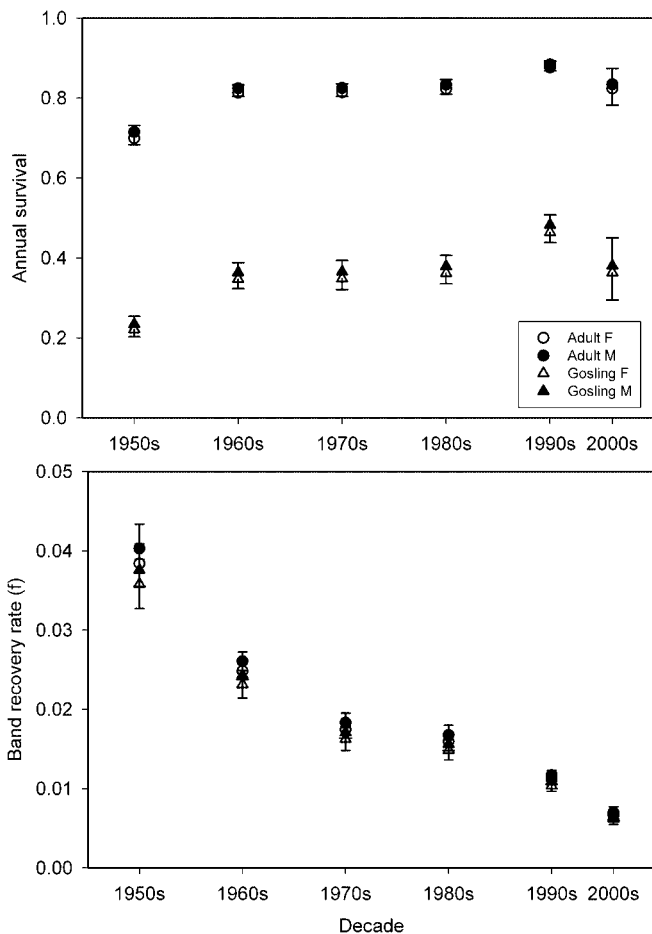


Figure 4. Decade-specific estimates of survival and band recovery rates for adult and juvenile black brant from the 1950s through the 2000s. We based estimates on the best model, which constrained survival estimates to be constant within decades but allowed survival estimates to vary in parallel among age and sex classes (Table 1). We also constrained band recovery rates to be constant within decades and to vary in parallel among age and sex classes.

additive term for both age and sex and a linear trend in survival. Two very competitive models also included both linear and quadratic trends in survival. The β linking subsistence harvest to annual survival in the best model including this variable was -0.04 ± 0.30 . All of the best performing models of recovery rate allowed recovery rates to vary annually and among age classes. Some competitive models also contained a difference between males and females. Model-averaged survival estimates (Fig. 6) increased slightly until the mid-1990s, then declined.

DISCUSSION

Our analyses show clearly that survival in brant increased as band recovery rates (harvest) declined between 1950 and about 2000. This result is consistent with the observation that harvest mortality is largely additive to other forms of mortality in other populations of geese (Rexstad 1992, Sheaffer et al. 2004). Harvest in the early 1950s annually exceeded 20,000 brant (USFWS, unpublished data). These harvest levels are approximately consistent with our estimate of a band recovery rate near 0.04 and a harvest rate of 0.12

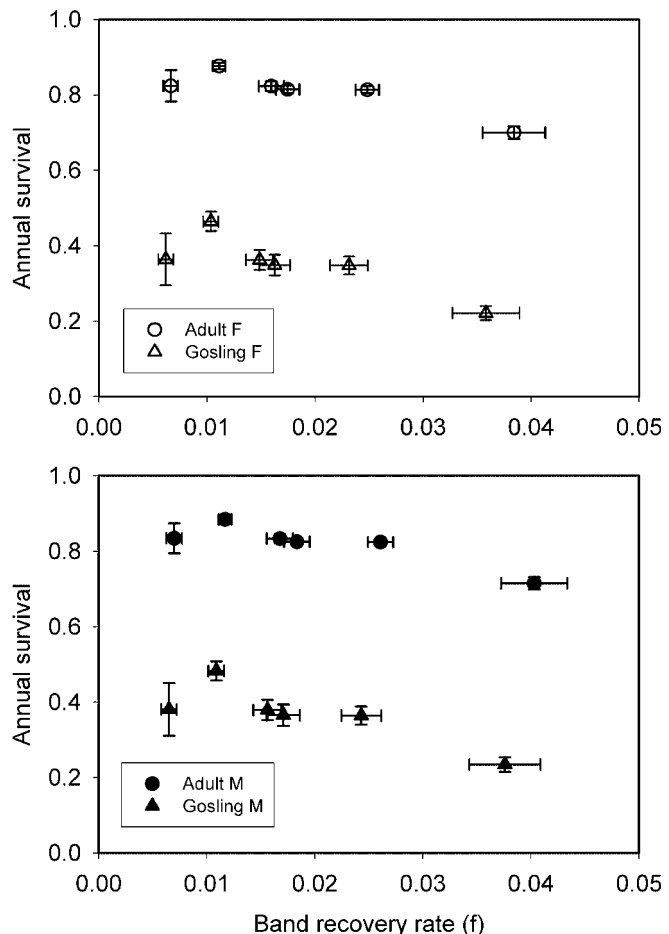


Figure 5. The relationship between decade-specific survival and band recovery rates based on the best performing model of variation in these 2 sets of parameters (Table 1). Sampling covariance between estimates of band recovery and survival rates resulting from estimation of both sets of parameters from the same data represented between 2.3% (juv M) and 3% (ad M) of total covariance between parameter estimates. Consequently, the negative covariance apparent in this figure was not strongly influenced by sampling covariance.

because the population at the time contained approximately 160,000 individuals (Pacific Flyway Council, unpublished report).

Annual survival rates for adult females were approximately 0.7 during the 1950s, a low value for geese. The brant population declined from the 1950s to the present, and low adult survival rates in the 1950s likely contributed to population decline during that period. Higher adult survival probabilities since the 1950s suggest that harvest may have had less influence on population dynamics since the 1950s, although brant are less fecund than most other geese (Reed et al. 1998) and likely require higher annual survival rates to maintain stable populations than is true for some other geese.

Increases in annual survival in each decade from the 1950s to the 1990s while recovery rates declined (Figs. 4, 5) are consistent with the hypothesis that harvest by humans influenced survival probability of brant. Poor performance of models explicitly linking harvest to survival, however, suggests that either 1) other factors also influence survival,

Table 3. Performance of models of survival and recovery rate for black brant from 1985 to 2003. We show a representative sample of models considered for which relative quasi-Akaike's Information Criterion adjusted for small sample size ($\Delta QAIC_c$) > 10.

Model ^a	QAIC _c	$\Delta QAIC_c$	$\Delta QAIC_c$ wt	Estimable parameters ^b	QDeviance
S(2a+T), f(2a+t)	12,257.96	0.00	0.37	22	12,213.91
S(2a+T+T ²), f(2a×s+t)	12,258.76	0.80	0.25	25	12,208.70
S(2a+T+T ²), f(2a+t)	12,258.87	0.91	0.23	23	12,212.81
S(2a+suh), f(2a×s+t)	12,261.02	3.06	0.08	24	12,212.96
S(2a+suh) ² , f(2a+t)	12,261.19	3.23	0.07	22	12,217.14
S(2a×s+t), f(2a+s+t)	12,273.19	15.22	0.00	37	12,199.05
S(2a×s+T), f(2a+t)	12,280.33	22.37	0.00	23	12,234.28
S(2a×s+T), f(2a×s+t)	12,280.70	22.74	0.00	25	12,230.64
S(2a+s+t), f(2a+s+t)	12,281.32	23.35	0.00	36	12,209.18
S(2a×s+suh), f(2a×s+t)	12,281.65	23.69	0.00	25	12,231.59
S(2a+s+t), f(2a+s+t)	12,287.34	29.37	0.00	39	12,209.18
S(t), f(t)	12,295.71	37.75	0.00	35	12,225.59
S(2a×s+ns), f(2a×s+t)	12,298.03	40.07	0.00	24	12,249.97
S(2a+s+suh), f(2a×s+t)	12,299.43	41.47	0.00	23	12,249.37
S(2a+s+T+sph), f(2a×s+t)	12,299.64	41.67	0.00	25	12,249.57
S(2a+s+T+suh), f(2a×s+t)	12,301.94	43.98	0.00	26	12,249.87

^a We incorporated subsistence harvest (suh), sport harvest (sph), and nest success (ns) in a subset of models considered. Other independent variables we considered were age (indicated by "a"), sex (s), and time (t). "T" indicates we constrained temporal variation to be a linear trend and "T²" indicates a quadratic time trend. Notation generally follows Lebreton et al. (1992); a "×" between 2 variables indicates an interaction between their effects on survival or recovery rates, and a "+" indicates effects are additive.

^b Models containing subsistence harvest required one more parameter than those containing sport harvest because no subsistence harvest estimates existed for 2001–2003, requiring separate estimates of survival for these yr.

or 2) substantial noise existed in our harvest estimates. Estimates of United States harvest for populations harvested by a relatively small number of hunters are imprecise because of the small number of hunters returning parts for these populations (Blohm 1989). Thus, it is certainly possible that such imprecision obscured a relationship between survival and estimated harvest in the analysis of the long-term data.

Survival probabilities between 1990 and 1999 averaged 0.88 both for males and females. These survival probabilities are among the highest recorded for North American geese and are comparable to those of unharvested European populations (Ebbinge et al. 1991, Clausen et al. 2001). Similarity of Pacific brant survival rates to those of unharvested populations suggests that brant during the

1990s experienced survival rates near the maximum possible for free-ranging geese. More importantly, survival rates in the 1990s exceeded those of other brant (Kirby et al. 1986, Ebbinge 1992, Clausen et al. 1998) and goose populations (Francis and Cooke 1992, Madsen et al. 1999, Menu et al. 2002, Frederiksen et al. 2004, Sheaffer et al. 2004) that were increasing. Therefore, high survival rates in brant during the 1990s indicate that declines in the brant population after (and possibly before) 1990 likely resulted from low recruitment rates rather than from low survival rates and the primary limiting factor for this population shifted from adult survival to recruitment between the 1950s and the 1990s.

Of general importance, survival probabilities did not respond to the continued decline in harvest rates between the 1990s and the 2000s (Fig. 5), and across the decades there appears to be diminishing response of survival to successive declines in harvest. We recognize that subsistence harvest was increasing in Alaska during the last 2 decades of this study, which could have influenced the observed relationship between sport harvest rates and survival. Ward et al. (1997) found that late spring (early 1990s), when brant are subjected to most subsistence harvest, was the period of lowest survival throughout the year. Direct assessment of the relationship between subsistence harvest and survival in our study, however, failed to detect a strong relationship between these 2 variables and it is possible that at low overall harvest levels even subsistence harvest is compensated during other times of year. It is thus a reasonable hypothesis that harvest in geese becomes compensatory to other forms of mortality at very low harvest rates. Understanding of compensation for human harvest is important not only for small or declining populations but also for management of

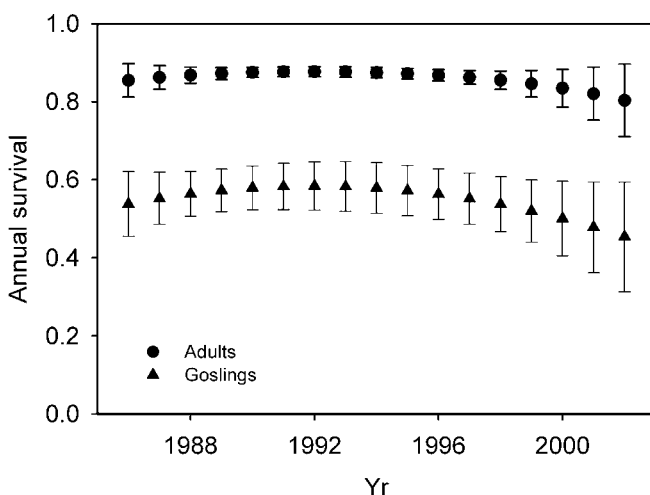


Figure 6. Annual variation in survival of adult and juvenile black brant, 1986–2002. We based estimates on model-averaged estimates (Table 2) for data from this period.

large populations, such as lesser snow geese in the mid-continent of North America. Managers are attempting to use harvest to reduce population size of lesser snow geese and reduce damage to arctic nesting areas associated with foraging by these geese (Jefferies et al. 2004). The large size of this lesser snow goose population ($>10^7$ individuals) has meant that annual survival is high and harvest rates are low (Cooke et al. 2000) because hunters have not been capable of harvesting a larger proportion of these geese. Thus, understanding the relationship between harvest and survival in geese when harvest rates are low has important conservation implications across a range of population sizes.

Declining density-dependent effects on survival represent an alternative hypothesis for higher survival rates in brant between 1950 and 2000. Adult survival can decline at higher density, as observed in other populations of long-lived species (Mduma et al. 1999, Festa-Bianchet et al. 2003). It is noteworthy that in the model containing both midwinter population size and sport harvest only the 95% confidence interval for the population size β did not include zero, although we caution that confidence intervals for these parameter estimates may be unreliable.

Assessment of the relative roles of harvest and population size is weakened by the similar long-term trends in the 2 variables. This problem has generally confounded assessment of the role of harvest in North American waterfowl populations (e.g., Sedinger and Rexstad 1994). We cannot rule out the possibility that poor precision in estimates of population size or harvest resulted in the failure of these variables to explain substantial annual variation in survival. Poor performance of models containing either population size or harvest is, however, consistent with the hypothesis that other factors had important influences on survival of adult brant.

Density-dependent effects, shown to be important in survival of geese during their first year (Francis et al. 1992; Sedinger et al. 1995, 1998), are associated with slower growth on breeding areas and lower survival after leaving the breeding grounds. A substantial proportion of first-year mortality occurs before individuals reach the wintering area (Owen and Black 1989, Francis et al. 1992, Ward et al. 2004). Most harvest of brant occurs from mid-November through February. Thus, young brant for which we estimated survival had already survived the period when density-dependent mortality is thought to be greatest before the beginning of the period over which we estimated band recovery rates and survival. Francis et al. (1992) interpreted lower direct recovery rates for juvenile snow geese as an indication of higher mortality before they reached areas where they could be harvested. In our study, recovery rates of juveniles declined as population size declined, opposite the expected effect if density-dependent effects were the primary driver of long-term patterns in direct recovery rates of juveniles. Furthermore, in contrast to the case for lesser snow geese, recovery rates of juveniles did not decline more than those of adults.

Adult pink-footed geese (*Anser brachyrhynchus*) had lower

summer and annual survival rates when population size was larger (Madsen et al. 2002), although survival during the hunting season did not vary, consistent with a hypothesis of density-dependent adult survival. For North American populations of snow geese, harvest rates are confounded with population size (Francis et al. 1992, Menu et al. 2002). For lesser snow geese, survival rates were higher at larger population size and lower harvest (band recovery rates; Francis et al. 1992). In greater snow geese (*Anser caerulescens atlanticus*), point estimates of annual survival were lower at higher population size (although differences were not significant) but the difference in survival was associated with higher harvest rates when the population was larger (Menu et al. 2002). Taken together, our study and others provide some evidence for density dependence in adult mortality, but confounding between harvest rates and population size makes it difficult to draw firm conclusions about the general relationship between population size and survival.

Direct analyses of the relationship between harvest and survival since 1985 indicate that neither sport or subsistence harvest had a measurable effect on survival during this period. These results are consistent with 1) the lack of an increase in survival between the 1990s and 2000s despite additional reduction in sport harvest between decades and 2) survival rates near those observed in unharvested populations of geese. These results are also consistent with the hypothesis that at the low harvest and high survival rates for brant in the 1990s, sport harvest was primarily compensatory (Anderson and Burnham 1976) to other causes of mortality. Most importantly, for managers these results indicate that further reductions in sport harvest may have little influence on survival rates and, consequently, on population dynamics. Continued decline of the brant population through the 1990s, therefore, likely resulted from recruitment rates that were too low.

We note that declines in annual survival since the mid-1990s are counter to the long-term trend. We cannot presently rule out the hypothesis that high rates of subsistence harvest in the late 1990s and early 2000s might have contributed to declining survival rates. Estimated subsistence harvest increased steadily from the mid-1980s through the end of the study, however (Fig. 3), although survival rates only began to decline during the late 1990s (Fig. 6). Predation on nests by arctic foxes was substantially higher after the mid-1990s (J. S. Sedinger, unpublished data) and might have been associated with reduced survival of adults, but this does not seem to be a viable hypothesis for juveniles that are not yet breeding. Furthermore, our index of predation risk (nest success) was unrelated to annual survival between 1984 and 2003 (Table 3).

The 1997–1998 El Niño substantially impacted eelgrasses (*Zostera marina*) in important brant wintering areas (Ward et al. 2005) and it is possible that these and other changes in winter habitat influenced annual survival since 1997–1998. We detected substantial effects on breeding probability of increased sea surface temperatures during El Niño events, consistent with the hypothesis that winter food affects

reproductive performance later in the same year (Sedinger et al. 2006). We did not detect a negative trend in breeding probability over this period, however, which we might expect if winter habitat conditions had deteriorated. Additional studies are needed to address hypotheses about patterns in survival over the past 20 years. Overall, our analyses suggest that sometime during the past decades principal regulation of brant shifted from human harvest to reproduction. Continued decline of brant experiencing the high survival probabilities of the 1990s is of substantial conservation concern.

Our study shows that annual survival of brant increased in each decade from the 1950s through the 1990s, associated with declining harvest rates. Population size also declined during this period and, combined with other studies, suggests the possibility of density-dependent mortality in geese. It is currently impossible to fully discriminate between effects of harvest and reduced population size in increased survival for most populations of geese. Annual survival did not respond to continued decline in harvest rates from the 1990s to the 2000s, indicating that at the low harvest rates of the 1990s, harvest had become compensatory. Most importantly for conservation of brant, adult survival in the 1990s was near the maximum possible and continued decline of the brant population in the 1990s must have resulted from recruitment rates that were too low to sustain population growth.

MANAGEMENT IMPLICATIONS

Our analyses are consistent with the hypothesis that harvest of brant was largely additive to other sources of mortality before the 1990s, although there was some support for density-dependent effects on annual survival. High survival rates in the 1990s and lack of a response of survival to continued decline in harvest between the 1990s and 2000s, however, suggest that at current very low sport harvest levels, harvest may no longer be an additive mortality factor. Of greatest importance, continuing population declines coincident with among the highest survival probabilities observed for any brant population, indicate that in recent years recruitment has been too low to maintain a stable or increasing population. Continued decline of the brant population in the 1990s and 2000s in spite of high annual survival indicates the immediate need for management action to increase recruitment.

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