Research Article

Declining Survival of Black Brant From Subarctic and Arctic Breeding Areas

ALAN G. LEACH,[1] *Department of Natural Resources and Environmental Science, University of Nevada, Reno, 1664 North Virginia Street, Reno, NV 89557, USA*

DAVID H. WARD, *U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, USA*

JAMES S. SEDINGER, *Department of Natural Resources and Environmental Science, University of Nevada, Reno, 1664 North Virginia Street, Reno, NV 89557, USA*

MARK S. LINDBERG, *Institute of Arctic Biology and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775, USA*

W. SEAN BOYD, *Science and Technology Branch, Environment and Climate Change Canada, Pacific Wildlife Research Centre, RR1-5421 Robertson Road, Delta, BC V4K 3N2, Canada*

JERRY W. HUPP, *U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, AK 99508, USA*

ROBERT J. RITCHIE, *ABR, Environmental Research & Services, P. O. Box 80410, Fairbanks, AK 99708, USA*

ABSTRACT Since the mid 1990s, the number of black brant (*Branta bernicla nigricans*; brant) nests on the Yukon-Kuskokwim Delta (YKD), Alaska, USA, the historically predominant breeding area of brant, has declined steadily. This has caused researchers and managers to question if arctic breeding populations can compensate for the reduction in brant nests on the YKD. An important component of the assessment of brant population dynamics is having current estimates of first-year and adult survival. We banded brant at 4 locations in Arctic Alaska and western Canada, and at 1 location in the subarctic, the Tutakoke River (TR) colony on the YKD, 1990–2015. We used joint live and dead mark-recapture models to estimate first-year and adult ($\geq$1 yr old) survival of brant. We also used band recovery rates from a Brownie model to assess temporal trends in band recovery rates of adult brant. First-year survival of brant hatched at TR declined from approximately 0.60 to <0.20 and, although first-year survival generally was higher for goslings marked in the Arctic, their survival declined from approximately 0.70 in the early 1990s to $\leq$0.45 in the 2010s. Annual survival of adult females decreased from an average of 0.881 (95% CI = 0.877–0.885) to 0.822 (95% CI = 0.815–0.829) at TR and from 0.851 (95% CI = 0.843–0.860) to 0.821 (95% CI = 0.805–0.836) in the Arctic, from 1990 to 2014. Band recovery rates of adults generally were <1.25% until the last several years of study, when they reached $\leq$3.5%. Although the current harvest rates may be partially additive to natural mortality, we do not believe that harvest is the main influence on the declines in survival. The general decline in survival rates of brant breeding across a large geographic area may be influenced by a reduction in the quality of migration and wintering ground habitats. We suggest an analysis of seasonal survival of brant to test the hypothesis that declining habitat quality on wintering or spring migration areas is reducing survival. Our results suggest that the number of breeding pairs at TR will continue to decline and also brings into question the ability of arctic breeding populations to grow at a rate necessary to offset the declines on the YKD. Researchers should continue to closely monitor survival and harvest rates of brant, and assess methods currently used to monitor their abundance. © 2017 The Wildlife Society.

KEY WORDS band recovery rates, *Branta bernicla nigricans*, Brownie models, joint live and dead mark-recapture, population dynamics, Seber reporting rate.

The breeding range of black brant (*Branta bernicla nigricans*; brant) extends from northeastern Russia east to the North Slope of Alaska and the western Canadian Arctic, and south to the Yukon-Kuskokwim Delta (YKD) of southwestern Alaska (Sedinger et al. 1993, Ward et al. 2005, Lewis et al. 2013). The YKD was the primary brant production area as

recently as the early 1990s, supporting >75% of the overall breeding population (Sedinger et al. 1993). Since the mid 1990s, the number of brant nests at the 4 major brant breeding colonies and low-density breeding congregations of the YKD have declined by approximately 34% (Stehn et al. 2011, Wilson 2014). Available data indicate that the numbers of breeding brant may be increasing on some breeding areas of the North Slope of Alaska; however, to date, the number of brant nests documented in the Arctic (Ritchie et al. 2015) does not appear adequate to offset losses on the YKD. Management decisions for brant populations

are currently based on estimates derived from the mid-winter survey, which after a long-term decline, have increased substantially since approximately 2005 (Olson 2015). Negative trends in nest counts on the YKD and current suggestions that the numbers of brant nests at monitored sites in the Arctic are inadequate to offset these declines seem to conflict with increasing mid-winter counts and have created uncertainty about the abundance of black brant.

In addition to accurate abundance estimates, having current demographic information on populations is important for understanding population trajectory (Koons et al. 2007). Data on vital rates from brant populations breeding in the Arctic are relatively limited and survival has not been estimated since the 1990s (Sedinger et al. 2002, Ward et al. 2004, Hines and Brook 2008). Likewise, demographic rates of brant breeding on the YKD have not been assessed since 2007 (Sedinger and Nicolai 2011). Although progress has been made in demographic estimation and modeling in recent years, unbiased, precise estimation of population vital rates often are difficult to obtain for animals with long distance migratory behaviors and wide ranging breeding concentrations (Griffith et al. 2016). Several past assessments of long-term annual survival of brant have used band recovery only models (Brownie parameterization; Sedinger et al. 2007, Hines and Brook 2008, Sedinger and Nicolai 2011). However, band recovery rates of brant were low in the 1990s and early 2000s (<1.5%; Sedinger et al. 2007, Hines and Brook 2008, Sedinger and Nicolai 2011), often leading to imprecise estimates and an inability to estimate annual variation in survival (Sedinger and Nicolai 2011). Because brant are gregarious and congregate in only a few coastal lagoons during the non-breeding season (Pacific Flyway Council 2002; Ward et al. 2005, 2009), researchers have been able to collect large numbers of live encounters of color-marked brant throughout the annual cycle (Ward et al. 2004, Sedinger et al. 2011). This provides the opportunity to compile live encounter data collected at breeding, wintering, and migration areas with band recovery data from hunters to improve the precision of survival estimates by using joint live and dead mark-recapture models (Barker 1997).

Despite the relatively poor precision of survival estimates from Brownie band recovery models in the case of brant, these models provide estimates of band recovery rate (Brownie et al. 1985). If band reporting rates (i.e., the proportion of banded birds harvested by hunters that are reported) can also be estimated (Zimmerman et al. 2009), then band recovery rates provide an estimate of harvest rate (Sedinger et al. 2007). In contrast, joint live and dead mark-recapture models implemented in Program MARK use the Seber parameterization of band reporting rates (i.e., proportion of banded individuals that died and were subsequently reported during an interval [r]; Seber 1970). Although, Brownie band recovery rates can be calculated from Seber's r ($f_t = r_t [1 - S_t]$ where f_t = Brownie band recovery rate and S_t = survival), confounding near the end of our study period for joint live-dead models made Brownie parameterization more informative for our questions about harvest.

We had 2 objectives: estimate true survival of goslings and adult brant marked at 1 colony on the YKD and 4 breeding areas from the Arctic, 1990–2015, and assess temporal variation of band recovery rates and proportion of annual mortality attributable to harvest. We expected that first-year survival of brant from the YKD would be low compared to the 1990s (Sedinger and Nicolai 2011). We reasoned that if survival rates of brant in the Arctic remained high during our study, this may indicate that long-term declines in survival of goslings hatched on the YKD could be influenced solely by local factors (e.g., forage quantity during brood-rearing [Sedinger et al. 2001a]). Alternatively, declines in survival rates of brant across a large portion of their range may indicate common factors could be affecting demographics of the black brant population at large, such as degradation of migration habitat.

STUDY AREA

We marked brant at the subarctic Tutakoke River colony (TR) on the YKD (Fig. 1), a colony that once represented 20% of the entire black brant breeding population (Sedinger et al. 1993). The TR colony consists of nesting meadows primarily composed of Ramensk's sedge (*Carex ramenskii*) and grazing lawns primarily composed of Hoppner's sedge (*C. subspathacea*) generally located <1 km from, but occasionally inundated by, high tides from the Bering Sea (Lindberg et al. 1997, Lindberg and Sedinger 1998). We have continuously marked and collected reencounter data on color-marked brant breeding at TR since 1986 (Sedinger et al. 2008, Sedinger and Nicolai 2011).

Our sample of marked brant from Arctic areas came from 4 of the largest known nesting areas, including the Colville River Delta and numerous small colonies throughout the Kuparuk oil field to the Sagavanirtok River area (Stickney and Ritchie 1996) on the North Slope of Alaska, and the Tuktoyaktuk Peninsula-Liverpool Bay region of the mainland and on Banks

Figure 1. Locations of bandings and summer encounters (circles), and non-breeding season resighting locations (triangles) of black brant, 1990–2015.

Island and Victoria Island, Northwest Territories, Canada (Fig. 1; Sedinger et al. 1993, Cotter and Hines 2001, Pacific Flyway Council 2002, Hines and Brook 2008).

In Arctic Alaska and western Canada, brant generally nest in small aggregations (tens of nests) within 2 km of the coast on islands of river deltas, lakes, or small ponds, but some nests may occur up to 27 km inland (Ritchie et al. 2000, Cotter and Hines 2001). The nesting islands are typically low lying and those close to the coast (e.g., outer deltas) may be tidally influenced. Habitat of nesting sites is dominated by ≥1 of the following communities: grass (*Gramineae*), sedge (*Carex* spp.), dwarf birch (*Betula nana*), and dwarf willow (*Salix* spp.; Armstrong 1996, Hines and Brook 2008).

The wintering range of brant extends coastally from southwest Alaska to northwest Mexico where they use embayments containing their preferred food, eelgrass (*Zostera marina*; Ward et al. 2005, 2009). During our study, most (∼70%) of the brant population wintered in Mexico primarily within 3 lagoons of the central Pacific coast of Baja California (∼60%) and to a lesser extent (10%) along the Gulf of California coasts of Sonora and Sinaloa (E. J. Mallek, U.S. Fish and Wildlife Service, unpublished data; https://www.fws.gov/alaska/mbsp/mbm/waterfowl/reports.htm, accessed 26 Jul 2016). The remainder of the wintering population outside of Mexico (30%) was distributed among Alaska (15%), Washington and British Columbia (5%), and California (10%; Olson 2015). Generally, brant from the YKD winter in Mexico and more southerly winter locations, whereas a somewhat larger proportion of birds from the Arctic may winter in Alaska and more northerly locations (Ward et al. 2009). In recent years, a large portion of the brant population has undergone a northward shift in wintering distribution, resulting in a large number of brant wintering in Izembek Lagoon, Alaska (Ward et al. 2009).

We recorded live resights at 3 wintering lagoons along the central Pacific coast of Baja California. We made observations at Bahia San Quintin during winters 1991–1993, 1997–2006, and 2011–2013 and at Lagunas Ojo de Liebre and San Ignacio, during winters 1999–2001 (Ward et al. 1997, Lindberg et al. 2007, Sedinger et al. 2011). From spring 1991–2015, we recorded resights of brant at wintering and migration areas in southeastern Vancouver Island and Boundary Bay, British Columbia, Canada (Reed et al., 1998*a,b*; Smith et al. 2012). We also periodically collected live resights of brant during migration and wintering at Izembek Lagoon, Alaska (Ward et al. 2004, 2009); Humboldt (Lee et al. 2007) and Morro (Lindberg et al. 2007) bays, California; and Puget Sound, Washington, USA (Fig. 1).

METHODS

Field Methods
We captured brant by herding them into pens during the adult remigial molt between 14 July and 11 August, 1986–2015; we also captured 34 brant at their nest in June and early July (Sedinger et al. 1997, Hupp et al. 2017). Following capture, we marked brant with a unique metal band issued by the Bird Banding Lab, United States Geological Survey, and a uniquely

engraved plastic tarsal band, and recorded bands from recaptures. We sexed brant using cloacal examination and aged them as goslings (local), second-year, or after second-year using plumage characteristics (Bellrose 1980, Owen 1980). For analysis, we combined second-year and after second-year brant into 1 adult group to reduce model complexity and acknowledge previous results indicating survival is similar between these age classes (Sedinger et al. 2007, Sedinger and Nicolai 2011). We marked most brant with corrosion-resistant bands (i.e., Monel or stainless steel); however, 620 and 8 brant marked in Canada (1995–2000) and TR (1986), respectively, were released with aluminum bands. We believe inclusion of these aluminum bands, which are more likely to be lost, resulted in no bias in survival estimates because they were a small proportion of our sample and most encounters were collected through live resights of the color bands (Table S1, available online in Supporting Information).

Because arctic banding drives can include molting flocks of failed breeders that may nest outside the Arctic (Bollinger and Derksen 1996), we limited our sample of adults to those captured in a brood drive (≥1 gosling captured) to reduce the number of failed and non-breeding birds from elsewhere. Banding efforts on the North Slope of Alaska occurred from 1990–2000 and 2011–2015, and banding efforts in western Canada occurred from 1990 to 1999 (Table S1).

Prior to banding each summer, we recorded live resights of color-marked brant on breeding areas using 20–50× spotting scopes (Sedinger et al. 2008). We included all summer encounters in our analysis (not just breeding encounters) to improve the precision of our survival estimates. We obtained band recovery information of brant harvested (i.e., how obtained code = 01) from August 1990 to May 2016 from the United States Geological Survey Bird Banding Laboratory in Patuxent, Maryland, USA. Our recovery window for each year was 1 August–31 July. We included only brant that were color-marked in our analysis. All handling of animals was approved by Institutional Animal Care and Use committees at the United States Geological Survey-Alaska Science Center, University of Alaska Fairbanks and the University of Nevada, Reno (most recent protocol number 00056).

Joint Live-Dead Recovery Models
We used the joint live and dead encounters model (Barker 1997) in Program MARK (White and Burnham 1999) with the primary goal of estimating survival and Seber reporting rates (i.e., the probability of reported mortality; Alisauskas et al. 2012) of gosling and adult brant (Barker 1997). We sorted individuals into 2 groups: those marked at subarctic and those marked in arctic locations (Lindberg et al. 1998). We included 2 age classes in our analysis: gosling and adult brant, and allowed goslings to graduate to adults after their second summer. Though most individual capture histories began with initial banding during summer, we included 2,953 brant marked at TR before 1990 whose capture histories began with their first live summer reencounter during or after 1990.

The joint live-dead mark recapture model estimates a large number of parameters including true survival probability from time t to $t + 1$ (S_t), probability of encounter at a breeding area

given alive at t (p_t), probability a mortality between t and $t+1$ is reported (r_t), probability of being resighted given alive between t and $t+1$ (R_t), probability that an individual was resighted before death between t and $t+1$ (R'_t), probability of being available for encounter during summer given encounter in year $t-1$ (F_t), and probability of being available for encounter during summer given not being encountered in year $t-1$ (F'_t). We fixed $F'=0.0$ so that F approximated $1 -$ permanent emigration, although we do not report these estimates because we included summer encounters of individuals away from their colony of initial marking and long-term encounter data was not available for individual sites in the Arctic.

The number of parameters estimated by the Barker model; the fact that we had 2 age classes, 2 sexes, and 2 banding locations; our large sample (55,912 individuals); and long-term encounter effort (26 years) made running all possible models computationally prohibitive (Townsend et al. 2016). Fortunately, there was a wealth of previous demographic analyses that we could reference to create informed *a priori* models of area- and sex-specific variation in permanent emigration (Lindberg et al. 1998, Sedinger et al. 2008), summer detection rates (Sedinger et al. 2001*b*), and survival (Ward et al. 1997, 2004; Sedinger et al. 2002, 2007; Hines and Brook 2008; Sedinger and Nicolai 2011).

We approached modeling as a 2 step process: first, using our most general structure for S, which included a full interaction among breeding areas, age classes, and year, we found the optimal structure (i.e., converged and produced the lowest corrected Akaike's Information Criterion [AIC$_c$] score) for p, r, R, R', and F; and second, we kept that optimal structure and built a small set of models to explore variation in survival (Table 1). Because brant do not start breeding until 2 years of age, we built models testing for differences in p between second-year and after-second-year brant (Sedinger et al. 2001*b*). For models that included full annual variation in survival, we had to constrain the last 2 years to be the same; likewise, we constrained the last 3 probabilities of reported mortality (r), to achieve model convergence. We marked few goslings (<40) at TR in 2001 and 2003 because of poor production caused by egg predation by arctic foxes (*Vulpes lagopus*), which resulted in poor precision of estimates for these cohorts; thus, we constrained first-year survival of the 2001–2002 and 2003–2004 TR cohorts to be the same. We used AIC$_c$ corrected for overdispersion ($\hat{c}=1.11$; $\hat{c}$ was obtained by Sedinger et al. [2007] through the median $\hat{c}$ approach) to evaluate support among models with different structures on age class, breeding area, and annual variation (including trends) on survival (Burnham and Anderson 2002). We built all models using the program R (R Core Team 2014) package RMark (Laake 2013) and we used the high performance computing system at the University of Nevada, Reno, to run all models. We did not release brant from arctic breeding areas from summer 2001–2010; thus, we fixed all parameters for these cohorts to 0.0.

Brownie Models

We used Brownie dead recovery models implemented with RMark (Laake 2013) to estimate band recovery rates. We

Table 1. Model selection results for joint live-dead (Barker 1997) mark-recapture models used to explain variation in first-year and adult survival (S) of black brant released from arctic breeding areas (north slope of Alaska and western Canadian Arctic) and the Tutakoke River colony, southwestern Alaska, USA, 1990–2015. We report the number of model parameters (K), Akaike's Information Criterion corrected for sample size and overdispersion (QAIC$_c$; $\hat{c}=1.11$) of model i compared with the best model (ΔQAIC$_c$), the weight of each model in the candidate set (Akaike weight; w_i), and Quasi Deviance (QDev) of each model.

Survival structure	K	ΔQAIC$_c$	w_i	QDev
S(area × age × yr + sex)	209	0.00	1.00	127,054.1
S(area × age + yr + sex)	141	540.00	0.00	127,730.5
S(area × age × trend + sex)	121	762.39	0.00	127,993.0
S(area × age + trend + sex)	118	1,133.86	0.00	128,370.5
S(area × age + sex)	117	1,701.22	0.00	128,939.8
S(area + age + sex)	116	1,918.67	0.00	129,159.3
S(.)	113	5,627.48	0.00	132,874.1

Variables: age = represents 2 age classes (gosling and adult); area = arctic breeding areas and Tutakoke River colony, yr = full annual variation, trend = fitted annual trend. All models included the same structure for summer encounter probability (p), probability of reported mortality (r), resighting probability during winter or spring (R), and breeding area fidelity (F). Probability of mortality after being resighted alive during winter or spring (R') and probability of being available for encounter during summer given not being available for encounter the previous year (F') were fixed to 0.0.

limited this analysis to only individuals released as adults because previous analyses reported little variation in recovery rates between age classes (Sedinger et al. 2007, Sedinger and Nicolai 2011). We fixed S and band recovery rate (f) to 0.0 for the 2001–2010 cohorts of our arctic group because we did not release individuals from this area during this period. We compared models with variation between breeding areas in survival and band recoveries and included models with full annual variation and annual trends in our candidate set (Table 2). If there was support for >1 model (i.e., ΔQAIC$_c$ <2.0) we model averaged estimates over the full model set.

RESULTS

Joint Live-Dead Recovery Models

Our analysis included 22,509 brant released as goslings and 18,772 brant released as adults from TR and 7,508 goslings and 7,123 adult brant from the Arctic. In step 1 of the modeling process, our best model included a summer encounter rate (p) structure with additive effects of age class and banding area, and an interaction between banding area and full annual variation (Table S2, available online in Supporting Information); an interaction between age class and banding area, plus the additive effect of year on probability of reported mortality (r); additive effects of banding area and year on R; and an interaction between banding area, age class, and sex on F. Models that included age, banding area, or annual variation on R' failed to converge or did not improve model support; therefore, we fixed this parameter to 0.0 (Nicolai et al. 2014).

In the second step of our modeling process, the model structure of S with a full interaction between banding area, age class, and year, plus an additive effect of sex on survival was the only model with support ($w_i = 1.00$; Table 1). Males generally had lower survival ($\hat{\beta}_{S(\text{males})} = -0.13$; 95% CI = -0.16 to

Table 2. Model selection results for Brownie dead recovery models used to explain variation in true survival (S) and band recovery rates (f) of adult black brant released from arctic breeding areas (north slope of Alaska and western Canadian Arctic) and the Tutakoke River colony, southwestern Alaska, USA, from 1990–2015. We report the number of model parameters (K), Akaike's Information Criterion corrected for sample size and overdispersion ($QAIC_c$; $\hat{c} = 1.11$) of model i compared with the best model ($\Delta QAIC_c$), the Akaike weight (w_i), and Quasi Deviance (QDev) of each model.

Model structure	K	$\Delta QAIC_c$	w_i	QDev
$S(\text{trend})\,f(\text{area} + \text{yr})$	29	0.00	0.80	1,077.1
$S(.)\,f(\text{area} + \text{yr})$	28	3.68	0.13	1,082.8
$S(\text{area})\,f(\text{area} + \text{yr})$	29	5.09	0.06	1,082.2
$S(\text{area})\,f(\text{yr})$	28	7.87	0.02	1,086.9
$S(\text{trend})\,f(\text{yr})$	28	15.68	0.00	1,094.8
$S(.)\,f(\text{yr})$	27	16.25	0.00	1,097.3
$S(\text{trend})\,f(\text{area} \times \text{yr})$	54	23.00	0.00	1,049.9
$S(.)\,f(\text{area} \times \text{yr})$	53	26.68	0.00	1,055.6
$S(\text{area})\,f(\text{area} \times \text{yr})$	54	26.92	0.00	1,053.8
$S(\text{trend})\,f(.)$	3	228.40	0.00	1,357.5
$S(\text{area})\,f(.)$	3	263.86	0.00	1,393.0
$S(.)\,f(.)$	2	279.73	0.00	1,410.9

Variables: area = arctic breeding areas and Tutakoke River colony, yr = full annual variation, trend = fitted annual trend.

Figure 2. Estimates of gosling (first-year) and adult survival (±95% CI; only estimates for females shown) of black brant banded at the Tutakoke River colony in southwestern Alaska, USA, and arctic breeding areas, 1990–2014. Estimates are from a joint live and dead (Barker 1997) mark-recapture model, which included an interaction between age class, banding area, and year on survival.

−0.10) than females; however, because year was modeled additively to sex (i.e., annual patterns were similar) we only report estimates for female survival. Estimates of first-year survival of female goslings from TR were high (∼0.60) in the early 1990s and have since declined substantially, with 4 of the 5 gosling cohorts released at the end of our study (2009–2013) having first-year survival rates <0.20 (Fig. 2; Table S3, available online in Supporting Information). Female goslings marked at arctic breeding colonies generally had higher first-year survival than those marked at TR; however, their survival declined in the late 1990s, and by the end of the study was ≤0.45, down from approximately 0.70 in the early 1990s (Fig. 2).

Parameter estimates from our model with an annual trend on survival indicated that survival of adult females declined from 0.881 (95% CI = 0.877–0.885) to 0.822 (95% CI = 0.815–0.829) at TR ($\hat{\beta} = -0.021$; 95% CI = −0.024 to −0.017) and from 0.851 (95% CI = 0.843–0.860) to 0.821 (95% CI = 0.805–0.836) in the Arctic ($\hat{\beta} = -0.010$; 95% CI = −0.016 to −0.003) from 1990 to 2014. Estimates from our model with full annual variation indicated that much of the decline in adult survival occurred since 2008 (Fig. 2). For female goslings, parameter estimates from our model with an annual trend indicated that first-year survival declined from 0.624 (95% CI = 0.610–0.638) to 0.188 (95% CI = 0.171–0.205) at TR ($\hat{\beta} = -0.086$; 95% CI = −0.092 to −0.079) and from 0.717 (95% CI = 0.691–0.742) to 0.404 (95% CI = 0.344–0.467) in the Arctic ($\hat{\beta} = -0.057$; 95% CI = −0.072 to −0.043) from 1990 to 2014.

Probability of reported mortality was greater for adults than goslings and generally increased during our study period (Fig. 3). Live resighting rates during the non-breeding season were lower for brant marked at TR ($\hat{\beta} = -0.099$; 95% CI = −0.136 to −0.062) than for those from the Arctic, and generally declined during the study period (Fig. 4).
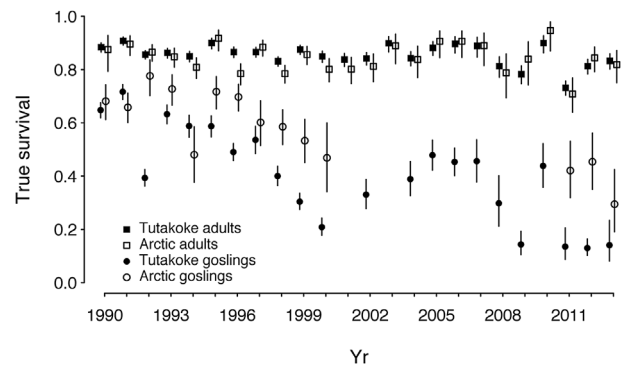
Brownie Models

This analysis included 15,819 after-second-year brant banded at TR and 7,123 after-second-year brant banded at Arctic breeding areas, 1990–2015. Our best supported model included an annual trend on survival and the additive effects of banding area and full annual variation on recovery rates (Table 2). Parameter estimates from our best performing model indicated adult survival declined during our study period ($\hat{\beta} = -0.023$; 95% CI = −0.042 to −0.004), similar to results from our joint live and dead model.

Brant banded at TR had band recovery rates that were higher ($\hat{\beta}_{f\,(\text{TR})} = 0.247$; 95% CI = 0.130–0.365) than those banded in the Arctic (Fig. 5). Except for several years in the late 1990s, band recovery rates of brant were generally <0.0125; however, since 2009 band recovery rates have generally been >0.0125 (Fig. 5). Fall-spring 2014–2015 had the highest recovery rates of the study, varying from 0.035 (95% CI = 0.029–0.043) for adults banded at TR to 0.028 (95% CI = 0.023–0.034) for adults banded in the Arctic (Fig. 5).
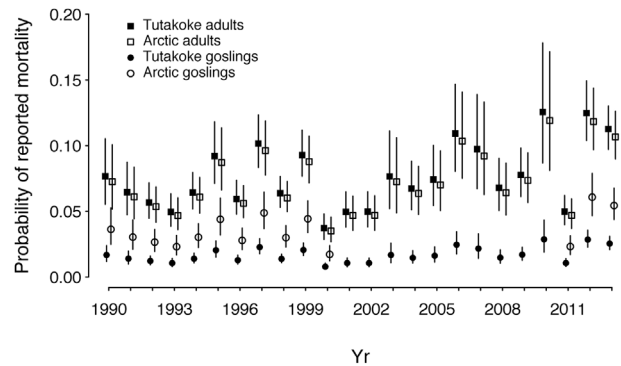

Figure 3. Estimates of the probability of reported mortality (±95% CI) of gosling and adult black brant from the Tutakoke River colony and arctic breeding areas from 1990–2014. Estimates are from a joint live and dead (Barker 1997) mark-recapture model, which included an interaction between age class and banding area and an additive effect of time on probability of reported mortality.
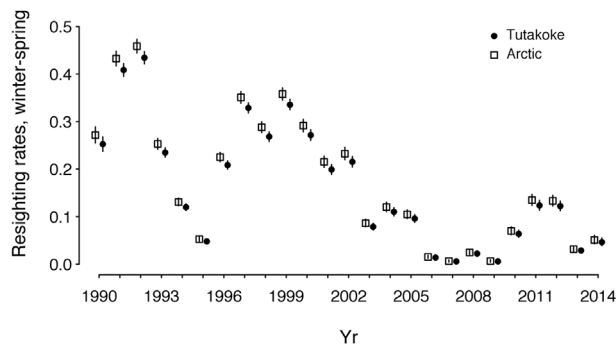
Figure 4. Estimates of live resighting rates during the non-breeding season (±95% CI) for black brant from the Tutakoke River colony and arctic breeding areas from 1990–2015. Estimates are from a joint live and dead (Barker 1997) mark-recapture model, which included the additive effects of banding area, and year on resighting rates.

DISCUSSION

First-year and adult survival of brant banded across their breeding range generally declined between 1990 and 2014. For birds banded at TR, the decline in first-year survival we report is consistent with previous work (Sedinger and Nicolai 2011). However, the decline in adult female survival (from 0.88 to 0.82), estimated from our joint live-dead recovery model with an annual trend, is previously unreported. Even small declines in adult survival are concerning, because growth rates of goose populations are most sensitive to changes in this vital rate (Cooch et al. 2001). Our trends in adult survival differed from Sedinger and Nicolai (2011), who reported weak support for a positive trend in adult survival at TR from 1986 to 2007; however, we do not believe our results are contradictory because much of the decline in adult survival we report appears to have occurred since 2008 (Fig. 2). Because of the previously high survival of breeders at TR, researchers have pointed solely to low recruitment rates as the primary influence on declining colony size (Sedinger et al. 2007, 2016; Sedinger and Nicolai 2011). The current rates of first-year survival suggest that recruitment will remain below replacement levels at TR and because of the

decline in adult survival, recruitment will likely lag further behind replacement levels than previously reported (Sedinger et al. 2016). Given the declines in first-year and adult survival, the number of breeding pairs at TR will likely continue to decline.

Our finding of declining first-year and adult survival of brant banded in the Arctic was previously unreported in the literature. Our results indicated that average survival of adult female brant banded in the Arctic declined from 0.85 to 0.82 from 1990 to 2014. Our average estimate of survival for adult females from the Arctic in the 1990s (0.85) is lower than previous estimates from this period (0.88–0.94; Sedinger et al. 2002, Hines and Brook 2008). This difference in survival could result from the fact we combined adults marked throughout the Arctic into 1 group, including previously unanalyzed data from brant marked on the North Slope of Alaska in the mid to late 1990s, and excluded many failed or non-breeding adults. Our average estimates of first-year survival of female brant banded in the Arctic from 1990 to 1996 (i.e., prior to the decline after 1997) were 0.68, which is similar to the estimates of Hines and Brook (2008) who reported first-year survival of 0.69 from brant marked in the western Arctic of Canada from 1991 to 1999. Additionally, our results support the conclusion of Ward et al. (2004) that first-year survival of brant goslings from the Arctic is generally greater than those from the YKD (Fig. 2). This higher survival is likely related to the superior growth rates of goslings in the Arctic compared to the YKD (Sedinger et al. 2001a; Hupp et al. 2017). The declining first-year and adult survival for brant banded in the Arctic raises questions about whether populations nesting in the Arctic can offset losses in the nesting population on the YKD. However, estimates of additional vital rates (e.g., nest success, breeding probability, recruitment) from arctic populations are needed to more fully assess the health of these populations. Along with these vital rates, an accurate estimate of the number of breeding pairs in the Arctic would aid our understanding of the productivity potential and contribution of these northern populations to the overall brant population.

The recent increase in band recovery rates of brant was an unexpected result because previous studies indicated that harvest rates of brant were at historically low levels in the 1990s (Sedinger et al. 2007, Hines and Brook 2008, Sedinger and Nicolai 2011). When adjusted for the band reporting rate of harvested North American geese (0.73; Zimmerman et al. 2009) and averaged across banding regions, the average harvest rate of brant increased from 0.9% for the 2000–2002 hunting seasons to 3.3% for the 2013–2015 hunting seasons. The probabilities of reported mortality (Fig. 3) indicated that the proportion of adult mortality accounted for by harvest doubled from 6.1% for the 2000–2002 hunting seasons to 12.8% for the 2011–2013 hunting seasons. The current harvest rates of brant are still lower than the maximal recorded harvest rate of approximately 10% for adults during the 1950s–1960s (Sedinger et al. 2007, Hines and Brook 2008), but could be high enough to be at least partially additive to natural mortality (Sedinger et al. 2007). We acknowledge that our analysis of band recovery rates did not
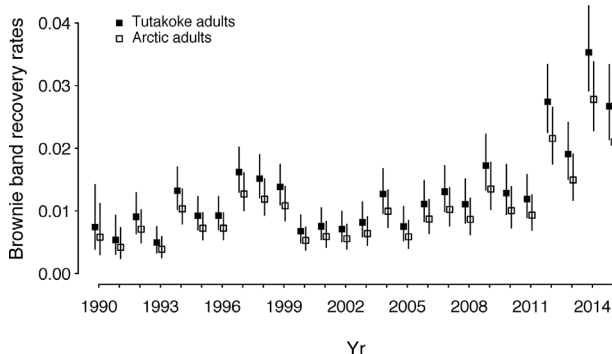

Figure 5. Estimates of band recovery rates (±95% CI) for adult black brant from the Tutakoke River colony and arctic breeding areas, 1990–2016. Estimates are from a Brownie model, which included an annual trend on survival and an additive effect of banding area and year on band recovery rates.

account for whether bands had toll-free numbers inscribed or were address only (mostly applied prior to 1996). Regardless, the increases in band recovery rates we report occurred more than a decade after toll-free bands became commonplace; thus, the increases in band recoveries we observed were likely influenced primarily by increased harvest rates, not increased reporting rates. It is unclear if these higher harvest rates resulted from an increase in the total brant harvest, or relatively stable harvest and a declining population. Annual estimates of brant harvest based upon the Migratory Bird Harvest Information Program (HIP) are highly variable (Olson 2015). Therefore, accurate estimates of brant harvest (including subsistence harvest) are needed to fully under-stand the role of harvest on brant population dynamics.

We interpret the low probability of reported mortality of goslings (Fig. 3), especially those marked at TR, as an indication that non-harvest mortality is greater for goslings than adults, similar to lesser snow geese (*Chen caerulescens caerulescens*; Francis et al. 1992). The lower probability of reported mortality of goslings is likely related to their higher mortality than adults prior to arriving at fall staging or wintering areas (Ward et al. 2004), and because of this a smaller proportion of goslings are available to hunters for harvest. Given the magnitude and long-term nature of the decline in first-year survival, the recent increase in harvest rate may, at most, explain only a small proportion of the decline in first-year survival.

The range-wide reduction in first-year and adult survival we reported in this study suggests common factors (i.e., degradation of the quality of wintering and migration habitat) may be affecting demographics of brant. For example, Bahia San Quintin, Mexico, a previously high-quality habitat for brant, based on the breeding probability of birds wintering there (Sedinger et al. 2011), experienced long-term declines in eelgrass abundance (Ward et al. 2003). Additionally, stopover times of brant at Vancouver Island, British Columbia, have declined, which could indicate reduced profitability of this site resulting from reduced forage or increased disturbance from humans and bald eagles (*Haliaeetus leucocephalus*; Smith et al. 2012). Black brant are one of the few nearctic goose species that rarely forage in agricultural fields, and are especially vulnerable to degradation of wintering and migration embayments (Cottam et al. 1944, Ward et al. 2005). Finally, the effects of the recent increase in the number of brant wintering in Izembek Lagoon on brant demographics and the amount of eelgrass available to brant during spring migration, remains unknown.

Complementing our work here, analyses conducted on the long-term trends in age ratios of brant staging at Izembek Lagoon, Alaska, where the entire black brant population stages in fall, reported a decline in the proportion of juveniles in recent years (D. H. Ward, U.S. Geological Survey, unpublished data). Declining age ratios, combined with our finding of a decline in survival rates of brant, suggest that the overall brant population could be declining. In contrast, the mid-winter surveys, which are flown from Mexico to Alaska and are used to make decisions about the management of brant populations, showed a decline in brant numbers prior

to 2005 but have been stable or increasing since (Olson 2015). It is imperative that the discrepancy between trends in demographic estimates and survey data be reconciled.

MANAGEMENT IMPLICATIONS

Because of the positive trend in counts of brant estimated from mid-winter inventories (Olson 2015), brant have not recently been a species of management concern. However, the widespread declines in survival we report here, combined with declines in the number of brant nests on the YKD (Stehn et al. 2011), and recent declines in fall age ratios (D. H. Ward, U.S. Geological Survey, unpublished data) suggest that brant may not be as abundant as the winter population assessment indicates. We suggest an independent, retrospective analysis of brant population trends, for instance with Lincoln's estimator (Alisauskas et al. 2011, 2014) or mark-resight estimators (Sanders and Trost 2013).

Continued banding of brant on the YKD, in northern Alaska, and at least periodic banding in the western Canadian Arctic is important to long-term brant population monitoring. Continued generation of precise survival estimates for brant (and potentially mark-resight estimates of population size) will require ongoing efforts to collect live resights during the non-breeding period (Kendall et al. 2013, Penaloza et al. 2014); therefore, we encourage surveys to obtain resightings of color-marked brant at wintering and migration locations, such as Izembek Lagoon, Alaska; Parksville-Qualicum and Boundary Bay, British Columbia; Humboldt Bay, California; and Bahia San Quintin, Mexico. Researchers should also consider assessing long-term trends in eelgrass abundance on key wintering and migration areas and estimate seasonal survival of brant since the early 1990s to test the hypothesis that a decline in the quantity and quality of wintering or migration habitat may be contributing to the decline in brant survival.

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