

TEMPORAL AND GEOGRAPHIC VARIATION IN SURVIVAL OF JUVENILE BLACK BRANT

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Abstract. First-year survival has important implications for the structure and growth of populations. We examined variation in seasonal survival of first-year Pacific Black Brant (*Branta bernicla nigricans*) marked late in summer in Alaska at two brood-rearing areas on the Yukon-Kuskokwim Delta (Tutakoke and Kokechik) and one area on the Arctic Coastal Plain to provide insight into the magnitude and timing of mortality during fall migration. First-year survival was lower in early fall (15 July–1 October), when birds fledged from brood-rearing areas and migrated to their primary fall staging area at Izembek Lagoon, Alaska, than during late fall and early winter (1 October–15 February), when birds made a long-distance transoceanic flight (>5000 km) to wintering areas in Baja California, Mexico. When compared to other years, monthly survival during early fall was 20–24% lower in 1992, the year of latest hatch dates and slowest growth of goslings. There was strong evidence to indicate that survival varied geographically within the early fall period. Monthly survival estimates during early fall were lowest for birds from Tutakoke, highest for birds from the Arctic Coastal Plain, and intermediate at Kokechik. Our findings revealed that most juvenile mortality occurred during the first 2 months following banding, and variation in juvenile survival during this period was likely influenced significantly by environmental parameters and habitat conditions on the breeding grounds. Monthly survival estimates during the subsequent 4 months were similar across geographic areas, and long-distance migration was likely the most important contributor to juvenile mortality during this period.

Key words: Alaska, Black Brant, *Branta bernicla nigricans*, fall migration, juveniles, survival.

Variación Temporal y Geográfica en la Supervivencia de Juveniles de *Branta bernicla nigricans*

Resumen. La supervivencia durante el primer año de vida tiene implicancias importantes para la estructura y el crecimiento de las poblaciones. Examinamos la variación en la supervivencia estacional en individuos añales de *Branta bernicla nigricans* marcados al final del verano en Alaska en dos áreas de cría del Delta Yukon-Kuskokwim (Tutakoke y Kokechik) y un área en la planicie costera ártica para brindar información sobre la magnitud y el esquema temporal de mortalidad durante la migración de otoño. La supervivencia durante el primer año fue menor a principios del otoño (15 July–1 October), cuando las aves abandonaron las áreas de cría y migraron hacia el área principal de permanencia otoñal en Izembek Lagoon, Alaska, que durante fines de otoño y comienzos del invierno (1 October–15 February), cuando las aves realizaron un vuelo transoceánico de larga distancia (>5000 km) hacia las áreas de invernada en Baja California, México. Comparando con otros años, la supervivencia mensual durante principios del otoño fue un 20–24% menor en 1992, el año con fechas más tardías de eclosión y con crecimiento más lento de los polluelos. Hubo fuerte evidencia para indicar que la supervivencia varió geográficamente a principios del otoño. Las estimaciones mensuales de supervivencia durante principios del otoño fueron menores para las aves de Tutakoke, mayores para las aves de la planicie costera ártica, e

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intermedias para Kokechik. Nuestros resultados revelaron que la mayoría de la mortalidad juvenil ocurrió durante los dos primeros meses luego del anillado, y la variación en la supervivencia de los juveniles durante este período fue probablemente influenciada de forma significativa por parámetros ambientales y condiciones del hábitat en las áreas de cría. Las estimaciones mensuales de supervivencia durante los cuatro meses siguientes fueron similares para las distintas áreas geográficas, y la migración de larga distancia fue probablemente la causa más importante de mortalidad juvenil durante este período.

INTRODUCTION

Survival in the first year of life is an important source of variation in lifetime reproductive success of long-lived species (Charlesworth 1994). Although variations in adult survival can exert greater effects on population dynamics (Schmutz et al. 1997) and be more relevant to anthropogenic factors such as harvest management, first-year survival is inherently more variable. Thus, over evolutionary time it likely adds a comparable net effect on the population dynamics of the species and the evolution of its life history (Pfister 1998). The influence of variation in first-year survival is further highlighted when considered in a metapopulation context, because juveniles typically disperse at much higher rates than breeding adults (Lindberg et al. 1998). Therefore, understanding when and where mortality of first-year birds occurs is important to managers and scientists.

In general, juvenile birds marked just before fledging experience lower and more variable survival in their first year of life than adults (Clutton-Brock 1988, Newton 1989); thereafter survival improves and approximates that of adults. This pattern is consistent across long-lived species such as the Common Buzzard (*Buteo buteo*; Kenward et al. 2000), Goshawk (*Accipiter gentilis*; Kenward et al. 1999), and Barnacle Goose (*Branta leucopsis*; van der Jeugd and Larsson 1998). It is somewhat less apparent in shorter-lived species, for example the Grasshopper Sparrow (*Ammodramus savannarum floridanus*; Perkins and Vickery 2001), and Willow Tit (*Parus montanus*; Orell and Belda 2002). Relatively little is known about the timing of most juvenile mortality within the first year of life and life-cycle events associated with this mortality. For arctic-nesting geese, most mortality of nearly fledged juveniles occurs during the 4–6 months following banding (Owen and Black 1989, Francis et al. 1992, Sedinger et al. 1997). This interval spans three important stages in their life cycle: fledging from brood-rearing areas, fall migration, and arrival at wintering areas.

The ecological processes that may affect year-to-year variability in juvenile survival are likely to be very different among these life-cycle stages, and determining the timing and location when juveniles are at greatest risk is important to understanding what factors may be driving survival patterns.

The majority of this 4–6 month interval includes a long-distance migration (>3000 km) between breeding and wintering areas (Bellrose 1980). Geese often augment their body condition during this energetically costly flight by stopping at staging areas during fall migration. Variations in survival may reflect differences in distances traveled and habitat conditions encountered at brood-rearing and staging areas. Estimates of survival between fledging and pre- and postmigration staging areas in fall have not been assessed nor have studies adequately addressed variation in juvenile survival across geographic areas.

We examined first-year survival of Pacific Black Brant (*Branta bernicla nigricans*) from different nesting populations to gain insight into the timing of mortality by partitioning survival into two discrete fall periods. Partitioning was possible because Brant complete their southward migration in two phases. Brant migrate from breeding areas in late August and stop for about 2.5 months at Izembek Lagoon at the end of the Alaska Peninsula (Reed et al. 1989; Fig. 1). From there, most Brant make a >5000-km transoceanic flight in November to primary wintering areas in Baja California, Mexico, where they remain for the winter (Dau 1992, Reed et al. 1998). These migrations are energetically costly (Ward and Stehn 1989, Dau 1992). We predicted that a substantial proportion of the mortality would occur during initial fall migration when body mass of juveniles is lowest (Ward and Stehn 1989). We also predicted that juveniles that travel farthest to Izembek Lagoon would experience the lowest survival. Our objectives were to use marking and resighting data from two colonies on the Yukon-Kuskokwim Delta,

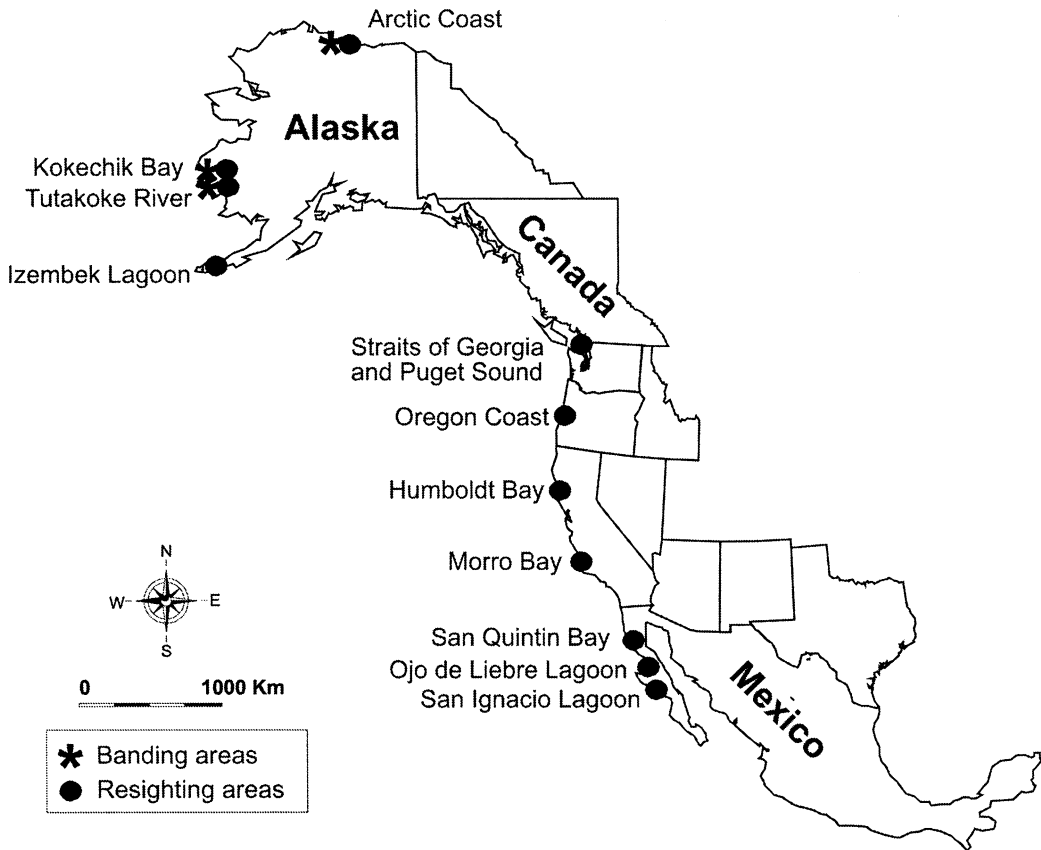


FIGURE 1. Locations of banding and resighting areas for Black Brant, 1990–1997.

Alaska, and one colony on the Arctic Coastal Plain of Alaska to test for seasonal (pre- vs. postmigration staging at Izembek Lagoon) differences in survival and determine whether seasonal survival varied among years (cohort) and across geographic areas. We therefore provide novel insight into the timing and variability of mortality of juvenile geese (defined here as the period from just before fledging to midwinter of their first year).

METHODS

In July and August, we captured 7442 Brant goslings at three brood-rearing areas in Alaska: along the Tutakoke River (Tutakoke) in 1990–1993, near Kokechik Bay (Kokechik) in 1991 and 1993, and between the Colville and Sagavanirktok Rivers (Arctic Coast) in 1991 and 1993 (Fig. 1). The Tutakoke and Kokechik areas are located on the Yukon-Kuskokwim Delta, where >70% of the Pacific Flyway population

of Brant breeds (Sedinger et al. 1993). These areas represent two of the four largest Brant breeding colonies in the world (Reed et al. 1998) and contain annually about 7000 (Kokechik) and 3000 nests (Tutakoke; R. Anthony, unpubl. data). The Arctic Coast area supports 500–1500 breeding pairs, and the highest nest concentrations are found on the Colville River Delta (400–1000 nests) and the Sagavanirktok River Delta (50–300 nests; Stickney and Richie 1996, Sedinger and Stickney 2000).

We captured Brant about 1 month after the peak of hatching at each location. Goslings were sexed by cloacal examination (Hochbaum 1942). We banded each individual with a United States Fish and Wildlife Service stainless steel tarsus band on the left leg and a 2.5-cm-wide plastic tarsus band marked with a unique combination of three alphanumeric characters on the right leg. We considered plastic leg band loss to be negligible because leg band loss for releases of

3361 female goslings and 5672 adults over a similar time span resulted in only four lost color bands in 1396 recaptures (Sedinger et al. 1997). To reduce stress and mortality due to banding, we placed marked geese in holding pens until they all could be released together with parents.

We observed marked birds from early September through October 1990–1993 at Izembek Lagoon and from early November to late March 1990–1993 at three sites in Baja California (San Quintín Bay, Ojo de Liebre Lagoon, and San Ignacio Lagoon; Fig. 1). Izembek Lagoon and adjacent bays support virtually the entire Brant population in fall, and the three sites in Baja California host >50% of this same population each winter (Reed et al. 1998; B. Conant and J. Voelzer, unpubl. data). In addition, we obtained resighting and recapture records gathered during other field studies conducted in 1991–1997. These data were collected at breeding areas in Alaska and at winter and spring staging areas in Baja California, California, Oregon, Washington, and British Columbia, Canada (Fig. 1).

ESTIMATION OF SURVIVAL RATES

Sampling effort differed among the three breeding areas: Tutakoke was sampled in four years (1990–1993) and Kokechik and Arctic Coast in two years (1991 and 1993). Thus, to provide the most powerful examination of annual variation in seasonal survival, we restricted analysis for that objective to the Tutakoke data set (1764 unique resightings of 5832 bandings). Analyses of geographic variation in seasonal survival were limited to two cohorts (1991 and 1993) for which banding and resighting occurred at all three sites (Tutakoke: 939 unique resightings of 3096 bandings; Kokechik: 193 unique resightings of 622 bandings; Arctic Coast: 264 unique resightings of 972 bandings).

For each bird in an analysis, we summarized its encounter history by denoting a 0 (not seen) or a 1 (seen at least once) for each encounter occasion: banding (July), resighting at Izembek Lagoon (September–October), resighting in Baja California (January–March), and resighting during any future season in any year up through 1997. Thus, birds from the 1990–1992 cohorts had four-occasion encounter histories. Because no sampling occurred in Baja California during January–March 1994, the 1993 cohort had only a three-occasion encounter history. We used Cormack-Jolly-Seber models (Lebreton et al.

1992) and program MARK (White and Burnham 1999) to estimate resighting and survival probabilities from these encounter histories. We calculated monthly rates of survival within seasonal periods based on the approximate midpoints of the banding and resighting periods: early fall (banding to Izembek Lagoon: 15 July–1 October), 2.33 months; late fall (Izembek Lagoon to Baja California: 1 October–15 February), 4.5 months; and the remainder of the study (Baja California to last resighting period), 5.16 months. Although our resighting periods extended over several months and violated the mark-recapture assumption of an instantaneous sample, the distributions of resightings within a season at Izembek Lagoon and in Baja California were similar annually and likely did not bias survival estimates (Smith and Anderson 1987, Hargrove and Borland 1994). Analysis of the four-occasion encounter histories allows estimation of three survival parameters (early fall, late fall, and remainder of study), but this last parameter is actually a confounded product of survival and resighting in the last period. Thus, we only interpret variation in the early fall and late fall survival rates. Further, we did not constrain the confounded remainder-of-study parameters among cohorts due to differences among cohorts in the numbers of years of data contributing to the final encounter occasion.

Bands from dead Brant were reported to the Bird Banding Laboratory, Laurel, MD ($n = 233$ from >7000 goslings banded during this study). However, we chose to use just live-resighting data and Cormack-Jolly-Seber models rather than a Burnham model (1993) that combines both live-resighting and dead-recovery data. Our rationale for this approach was twofold. First, unlike the first two resighting periods in each encounter history, our final resighting period was geographically expansive. Therefore, data from this resighting period functioned analogous to dead-recovery data by detecting many individuals that had never previously been seen, and importantly, the number of such detections was more than four times what was possible from dead-recovery data. Second, use of the Burnham model would have required estimation of more total parameters, without having much additional data, and thus may have limited our ability to detect patterns revealed by the Cormack-Jolly-Seber analysis.

Our general strategy for defining models and testing hypotheses about survival was to begin with a fully parameterized model that contained variation due to season, area, sex, and year for both survival and resighting probabilities. We then reduced parameter space by constraining resighting probabilities (Lebreton et al. 1992), which allowed for a more powerful examination of variation in survival. Using the most parsimonious resighting model, we built a series of survival models with progressively greater numbers of constraints. A large number of models could be constructed from all the possible combinations of area, year (cohort), sex, and season-specific survival. However, we used our biological knowledge to develop a limited set of *a priori* models that represented logical hypotheses for how survival may vary among these factors (Burnham and Anderson 1998). For instance, life-history theory predicts that annual variation in survival rates is most prevalent in the youngest age classes (Charlesworth 1994). Therefore, we developed models that first constrained survival among years and sexes within the late fall period so that we would maximize power to detect variations in the early fall period. Also, in our consideration of annual variations, we considered a model where survival of the 1992 cohort differed from other years because that cohort had a smaller average body size than all other cohorts (Sedinger et al. 1998). In our geographic analysis, we also considered a model where survival of Brant from the two Yukon-Kuskokwim Delta colonies was similar to each other but different from Brant on the Arctic Coast. This followed from Sedinger et al.'s (2001) finding that grazing pressure and biomass of preferred plants was similar among colonies on the Yukon-Kuskokwim Delta and substantially different from that on the Arctic Coast. In building models with progressively fewer survival parameters, we first reduced variation due to sex, then variation due to year, then variation due to area (for the geographic analysis), and then finally variation between seasons.

We selected among *a priori* models within an analysis using Akaike's Information Criterion adjusted for small sample size (AIC_c), where the model with the lowest AIC_c value represented the most parsimonious fit to the data (Burnham and Anderson 1992, 1998, Burnham et al. 1995). We assessed goodness-of-fit of the most-parameterized model in each analysis using Test 2 +

Test 3 results from program Release (White 2002). These tests revealed that the general model fit the data for the analysis of annual variation in seasonal survival using the four years of data from Tutakoke ($\chi^2_{12} = 10.6$, $P = 0.56$) and for the analysis of geographic variation among three sites ($\chi^2_{12} = 9.8$, $P = 0.64$). We also used the parametric bootstrap procedure in program MARK and confirmed goodness of fit in that the mean deviance from 500 bootstrap samples was greater than the observed deviance from the actual data (White 2002). Because no lack of fit was detected in either analysis, we treated \hat{c} to equal 1.0 for both analyses and therefore did not have to adjust AIC_c values or parameter estimates (White and Burnham 1999).

Often, several models have similar AIC_c values, and thus some ambiguity about which model best represents the data (Burnham and Anderson 1998). To quantitatively incorporate this uncertainty into model selection, we calculated weights for each AIC_c as per Buckland et al. (1997). These weights reflect what proportion of n times a given model would be selected if n similar resampled data sets were analyzed with the same set of candidate models. These weights were then used to calculate parameter estimates with unconditional standard errors (i.e., SEs were not dependent on selection of a single model, Burnham and Anderson 1998). In discussing differences in survival (ϕ), we refer to proportional (ϕ_a/ϕ_b) rather than absolute ($\phi_a - \phi_b$) differences.

RESULTS

ANNUAL VARIATION IN SEASONAL SURVIVAL

The most parsimonious model for estimates of seasonal survival of nearly fledged Brant was one in which survival varied among years in early fall, was similar among years in the late fall, and was substantially lower in early fall than in late fall (Model 1, Table 1). We show the parameter index matrix for this model in Table 2. In all years, monthly survival was 5–27% lower in early fall than in late fall. Monthly survival during early fall was 20–24% lower in 1992 than in any other year (Table 3). The extremely poor fits of models with similar survival in early and late fall (Model 10) or no annual variation in early fall survival (Model 11, Table 1) are indicative of the magnitude of differences among years and seasons in survival estimates (Table 3).

TABLE 1. Summary of models estimating monthly survival rates during early and late fall for juvenile Black Brant banded at the Tutakoke River, Alaska, 1990–1993. Estimates were based on resightings during fall at Izembek Lagoon, Alaska, and during winter in Baja California, Mexico, 1990–1993, and during any future season in any year through 1997. Models were ranked using AIC_c ; ΔAIC_c is the difference between a given model and the model with the lowest AIC_c score. AIC_c weights sum to 1 and indicate the relative likelihood of a given model being the most appropriate, given the data and the model set.

Model	Hypothesis represented by model		k^a	ΔAIC_c^b	AIC_c weight
	Survival in early fall	Survival in late fall			
1	varies by year	constant	18	0.0	0.39
2	varies by year and sex	constant	19	0.4	0.32
3	varies by year such that 1990 = 1991 = 1993 \neq 1992	constant	16	1.2	0.21
4	varies by year, sex, and year \times sex	constant	22	5.0	0.03
5	varies by year, sex, and year \times sex	varies by year	24	6.6	0.02
6	varies by year, sex, and year \times sex	varies by year such that 1990 = 1991 \neq 1992	23	6.7	0.01
7	varies by year, sex, and year \times sex	varies by sex	23	6.7	0.01
8	varies by year, sex, and year \times sex	varies by year and sex	25	8.6	0.01
9	varies by year, sex, and year \times sex	varies by year, sex, and year \times sex	27	9.4	0.00
10	varies by year	early fall survival = late fall survival	17	47.8	0.00
11	constant	constant	15	97.4	0.00

^a Number of parameters. Count includes the resighting parameters for early and late fall and the confounded parameter from the last resighting period in each cohort.

^b The lowest AIC_c score was 13 599.5; \hat{c} was treated as 1.0.

GEOGRAPHIC VARIATION IN SEASONAL SURVIVAL

Evidence was strong that survival varied geographically within early fall in 1991 and 1993 as indicated by the model with the lowest AIC_c score and highest AIC_c weight (Model 1, Table 4). No evidence supported geographic variation in survival during late fall in 1991 (Models 10–12, Table 4). No estimates for late fall 1993 were possible due to the lack of resightings in Mexico during winter 1993–1994. Monthly survival estimates during early fall were lowest for birds from Tutakoke, highest for birds from Arctic Coast, and intermediate at Kokechik (Table 5). The sum of AIC_c weights including a year effect on early fall survival suggests that there was an area \times year interaction in early fall survival (Table 4). Juvenile Brant from the Arctic Coast had a larger between-year difference in early fall survival than for Brant from either of the two other colonies (Table 5).

RESIGHTING RATES

In the analysis of annual variability in seasonal survival using the Tutakoke data, resighting rates ranged from 0.07 to 0.24 among years. The lowest rates occurred in 1990 when we had the

fewest personnel in the field. Among subsequent years, resighting rates varied annually at Izembek Lagoon but not in Baja California. For the analysis of geographic variation using the 1991 and 1993 cohorts, resighting rates did not differ between Izembek and Baja California, perhaps due to fewer years of data resulting in less variability than in the analysis of Tutakoke-only data. Resighting rates were similar for Brant originating from the two colonies from the Yukon-Kuskokwim Delta (0.24) and higher than for Brant from the Arctic Coast (0.19), likely due to the spatial differences among breeding populations in their use of these staging and wintering habitats (Reed et al. 1989, Ward et al. 1997).

DISCUSSION

ANNUAL VARIATION IN SEASONAL SURVIVAL

Survival rates were consistently lower during the first 2 months following late-summer banding than during the subsequent 2 months, and this trend was conspicuous across years and three nesting locations. This result indicates that most juvenile mortality occurs prior to arrival at their primary staging area and likely occurs at

TABLE 2. The Parameter Index Matrix (PIM) from program MARK (White and Burnham 1999) for the most parsimonious model fit to data from Tutakoke River, 1990–1993. The PIM shows the entire parameter structure for models in Table 1, including both survival and resighting parameters, and a total of 18 unique parameters estimated for this particular model. Note that parameters 3, 4, 6, 7, 9, 10, 12, and 13 represent confounded parameters in that they are a product of the final survival and resighting parameters. The structure for these confounded parameters and the remainder of resighting parameters was identical for all models in Table 1. Therefore, the various *a priori* models examined in this analysis differed only by which parameters in the first two columns of this PIM were uniquely estimated.

Year Sex	Survival			Resighting		
	Early fall	Late fall	Remainder of study	Early fall	Late fall	Remainder of study
1990						
Females	1	2	3	14	15	3
		2	3		15	3
		3	3		3	
Males	1	2	4	14	15	4
		2	4		15	4
		4	4		4	
1991						
Females	5	2	6	16	17	6
		2	6		17	6
		6	6		6	
Males	5	2	7	16	17	7
		2	7		17	7
		7	7		7	
1992						
Females	8	2	9	16	18	9
		2	9		18	9
		9	9		9	
Males	8	2	10	16	18	10
		2	10		18	10
		10	10		10	
1993						
Females	11	12	—	16	12	—
		12	—		12	—
		—	—		—	
Males	11	13	—	16	13	—
		13	—		13	—
		—	—		—	

brood-rearing or initial stopover areas. Similar to juveniles, adult female Brant from Tutakoke experienced lower survival between mid-July and mid-September than between mid-September and early January and, for them, subsistence hunting was likely the most important mortality factor (Ward et al. 1997). A portion of juvenile mortality can also be attributed to subsistence and sport hunting. However, even if we double the 1990–1993 fall harvest estimates from the Yukon-Kuskokwim Delta and Alaska Peninsula (Wentworth and Wong 2001) and account for the proportion of juveniles taken in the harvest, we can only attribute 10–40% of the mortality of Yukon-Kuskokwim Delta fledglings to hunting

in any year of the study (Ward and Sedinger, unpubl. data). This suggests that most ($\geq 60\%$) juvenile mortality in early fall is related to non-hunting sources.

Lower survival during early fall migration could also be influenced by mortality associated with capture and handling (Williams et al. 1993, Menu et al. 2001), but Sedinger et al. (1997), using similar data from Tutakoke over the same years, did not find a relationship between size of banding drives and survival during the next year. Thus, we do not believe that the banding process significantly altered survival estimates.

Annual variation in juvenile seasonal survival has been linked to environmental conditions and

TABLE 3. Annual variation in monthly survival rates of juvenile Black Brant banded at the Tutakoke River, Alaska, 1990–1993. Parameter estimates (\pm SE) are weighted averages from all considered models in Table 1, and unconditional standard errors were calculated as per Buckland et al. (1997).

Year Seasonal period ^a	Survival	
	Female	Male
1990		
Early fall	0.906 \pm 0.020	0.899 \pm 0.022
Late fall	0.954 \pm 0.009	0.954 \pm 0.009
1991		
Early fall	0.863 \pm 0.014	0.893 \pm 0.011
Late fall	0.953 \pm 0.008	0.953 \pm 0.008
1992		
Early fall	0.691 \pm 0.019	0.681 \pm 0.022
Late fall	0.953 \pm 0.009	0.952 \pm 0.009
1993		
Early fall	0.866 \pm 0.024	0.856 \pm 0.028

^a Early fall (banding to Izembek Lagoon) = 15 Jul–1 Oct; late fall (Izembek Lagoon to Baja California) = 1 Oct–15 Feb.

food quality on breeding grounds (Cooch et al. 1991, Sedinger et al. 1995). Lowest estimates of survival during early fall occurred in 1992 at Tutakoke, the year of slowest growth of goslings (Sedinger et al. 1998) and latest hatch dates (Bowman et al. 2002) on the Yukon-Kuskokwim Delta. In 1992 nesting was late for geese and poor hatching and fledging success occurred throughout the Arctic (Ganter and Boyd 2000). Gosling growth rates vary in response to environmental conditions (Cooch et al. 1991, Sedinger and Flint 1991), and size and mass of goslings late in their first summer strongly affects subsequent survival (Owen and Black 1989, Cooch et al. 1991, Schmutz 1993, Sedinger et al. 1995, van der Jeugd and Larsson 1998). Therefore, the low survival rate we detected during the initial fall migration for juvenile Brant was likely influenced significantly by size and mass of goslings at banding, as has been found in Emperor Geese (*Chen canagica*; Schmutz 1993).

Between 1991 and 1993, mean seasonal survival rate of juvenile female birds from Tutakoke was higher in late fall (0.81 ± 0.02) than in early fall (0.61 ± 0.02) but was still substantially (18%) lower than that of adult female Brant (0.99 ± 0.04) during the same period

(Ward et al. 1997). This result is consistent with the contention that survival of juvenile geese continually improves throughout their first year, and does not approximate that of adults until the latter half of the first year or second year (Francis et al. 1992, Sedinger et al. 1997, van der Jeugd and Larsson 1998). Similar to the pattern in early fall, most juvenile mortality in late fall was likely associated with natural sources because hunting accounted for a minor proportion of the adult mortality during this season (Ward et al. 1997) and proportionately fewer juveniles are shot than adults (Sedinger et al. 1993; DHW, unpubl. data). Much of the mortality during late fall was likely associated with long-distance migration from Izembek Lagoon to Baja California. This migration is energetically costly (Dau 1992) because about half of the >5000-km flight involves crossing the Gulf of Alaska with no refueling opportunities. The survival cost for juveniles during long-distance migration may be different from adult geese, where no significant survival cost has been detected during long-distance migration (>3000 km; Ward et al. 1997, Gauthier et al. 2001).

The similar late-fall survival rates for birds from Tutakoke and Arctic Coast support the hypothesis that juveniles that survived to Izembek Lagoon may be capable of recouping any deficits in mass and attaining adequate conditioning for migration to Baja California. Brant food resources (i.e., seagrasses) are abundant at Izembek Lagoon and adjacent embayments that Brant frequent during fall (Ward and Stehn 1989, Ward et al. 1996) and individuals, regardless of their condition, should be able to easily access food. An alternative hypothesis for similar late-fall survival rates between populations is that smaller, weaker individuals from the Tutakoke population died before reaching Izembek Lagoon and surviving birds were of similar mass and condition as the Arctic Coast population. In absence of a strong size effect on survival, behavioral factors such as recognition of predators and danger, social status in the flock, and experience in finding food may play an increasing role in survival during late fall.

The product of our early and late fall estimates of juvenile survival were similar to those reported in an earlier survival analysis of first-year female Brant over a single period that spanned both our early and late fall seasons (i.e., from pre fledging at Tutakoke to wintering

TABLE 4. Summary of models estimating monthly survival rates during two seasons, early fall and late fall, for juvenile Black Brant banded at three locations: Tutakoke River, Kokechik Bay, and Arctic Coast, Alaska, 1991 and 1993. Estimates were based on resightings during fall at Izembek Lagoon, Alaska, and during winter in Baja California, Mexico, 1990–1993, and during any future season in any year through 1997. Models were ranked using Akaike’s Information Criterion; ΔAIC_c is the difference between a given model and the model with the lowest AIC_c score. AIC_c weights sum to 1 and indicate the relative likelihood of a given model being the most appropriate, given the data and the model set.

Model	Hypothesis represented by model		k^a	ΔAIC_c^b	AIC_c weight
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2	varies by year and area	constant	19	0.8	0.21
3	varies by year, area, and year \times area such that Tutakoke = Kokechik \neq Arctic Coast	constant	19	0.8	0.21
4	varies by year, area, and year \times area	constant	21	1.8	0.14
5	varies by year, sex, area, and year \times area	constant	22	3.6	0.05
6	varies by year, sex, area, and all interactions	constant	27	4.7	0.03
7	varies by year, sex, area, and all interactions	varies by area such that Tutakoke = Kokechik \neq Arctic Coast	28	6.3	0.01
8	varies by year, sex, area, and all interactions	varies by area	29	6.9	0.01
9	constant	constant	16	8.6	0.00
10	varies by year, sex, area, and all interactions	varies by area and sex	30	8.9	0.00
11	varies by year	constant	17	10.3	0.00
12	varies by year, sex, area, and all interactions	varies by area, sex, and area \times sex	32	10.8	0.00

^a Number of parameters. Count includes the resighting parameters for early and late fall and the confounded parameter from the last resighting period in each cohort.

^b The lowest AIC_c score was 11 387.9; \hat{c} was treated as 1.0.

TABLE 5. Geographic variation in monthly survival rates of juvenile Black Brant banded at the Tutakoke River, Kokechik Bay, and Arctic Coast, Alaska. Parameter estimates are weighted averages from all considered models in Table 4, and unconditional standard errors are calculated as per Buckland et al. (1997).

Site Sex	Monthly survival		
	1991		1993
	Early fall ^a	Late fall ^a	Early fall ^a
Tutakoke			
Females	0.875 \pm 0.014	0.955 \pm 0.008	0.857 \pm 0.019
Males	0.877 \pm 0.014	0.955 \pm 0.008	0.852 \pm 0.021
Kokechik			
Females	0.903 \pm 0.024	0.956 \pm 0.008	0.873 \pm 0.039
Males	0.896 \pm 0.023	0.956 \pm 0.008	0.872 \pm 0.039
Arctic Coast			
Females	0.943 \pm 0.028	0.955 \pm 0.008	0.982 \pm 0.029
Males	0.937 \pm 0.029	0.955 \pm 0.008	0.984 \pm 0.024

^a Early fall period (banding to Izembek Lagoon) = 15 Jul–1 Oct; late fall (Izembek Lagoon to Baja California) = 1 Oct–15 Feb.

grounds in Mexico, Sedinger et al. 1997). In that study and with a subsample of our present dataset, Sedinger et al. (1997) estimated first-year female survival rates to be 0.58 in 1990 and 0.50 in 1991 compared to our estimates of 0.64 in 1990 and 0.57 in 1991. Our slightly higher estimates were not unexpected because we used a longer term data set with more sampling locations (i.e., four additional years of resightings and five extra locations in the Pacific Flyway), which provided increased opportunities to resight individuals that had temporarily or permanently emigrated out of the sampling areas used by Sedinger et al. (1997).

GEOGRAPHIC VARIATION IN SURVIVAL

We found evidence of geographic variation in first-year survival during the initial fall migration. Unexpectedly, we found that Arctic Coast juveniles survived at a higher rate than birds from Tutakoke and Kokechik despite a longer migration (three times longer) and exposure to a potentially greater subsistence harvest (Wolfe and Paige, unpubl. data). We also detected differences in survival in early fall between first-year birds from Kokechik and Tutakoke, even though these brood-rearing areas are located close together (<60 km apart) and birds likely travel a similar distance to reach Izembek Lagoon. We suspect the geographic variation in survival detected in our study is of environmental origin. Specifically, we contend that variation in juvenile survival is linked to growth rates of goslings at brood-rearing areas. It has been established that Arctic Coast goslings grow faster and are 30% larger than Tutakoke goslings (Sedinger et al. 2001), and growth rates of Brant goslings are directly related to their subsequent survival (Sedinger et al. 1995). This contention that survival in early fall is linked to environmental and habitat conditions on the breeding grounds is consistent with data collected on other species of geese (Barnacle Geese, Owen and Black 1989, van der Jeugd and Larsson 1998; Emperor Geese, Schmutz 1993; Greater White-fronted Geese [*Anser albifrons frontalis*], Schmutz and Ely 1999). Our study is an important piece of corroborating evidence for these other studies in that here we document survival rates in early fall versus later periods and thus identify when the survival cost of small body size likely is most strongly exacted.

Juvenile survival is also likely dependent on environmental and habitat conditions at stopover sites during the initial fall migration. Abundant and highly productive staging areas are especially important for juvenile Brant from northern colonies that must meet the energetic demands of long-distance flight to reach Izembek Lagoon (2500–5000 km) and continued growth. Based on surveys, recoveries, and resightings of banded birds, Arctic Coast Brant likely stop at several coastal areas during their early fall migration to Izembek Lagoon (Reed et al. 1998). The most important of these areas (i.e., the ones most frequented by the largest number of Brant and for the longest time) are Kasegaluk Lagoon (Johnson 1993), lagoons along the northwest Seward Peninsula, western Yukon-Kuskokwim Delta, and Nanvak Bay (Reed et al. 1998; DHW, unpubl. data). These highly productive sites are nearly evenly spaced (about 250–350 km apart) between the Arctic Coastal Plain of Alaska and Izembek Lagoon and likely provide important refueling opportunities for Brant.

The higher survival of Arctic Coast juveniles relative to Yukon-Kuskokwim Delta juveniles may also be an important life-history characteristic for maintaining Arctic Brant populations. In general, Arctic-nesting Brant have lower breeding propensity and nesting success than Brant nesting in the sub-Arctic on the Yukon-Kuskokwim Delta (Barry 1962, 1967; JSS, unpubl. data). Life-history theory suggests that lower reproductive investment should be compensated by higher adult survival (Charlesworth 1994). However, Sedinger et al. (2002) found that adult survival was only marginally higher for Arctic Coast than Yukon-Kuskokwim Delta Brant. They suggested that reduced reproductive productivity of Arctic Brant must be balanced during other life-history stages, perhaps through increased first-year survival, to sustain current Arctic population levels. Results of our study are consistent with this hypothesis. It is also conceivable that lifetime reproductive success is the same for the two areas, but is achieved by different means (low reproductive investment, but higher juvenile survival and recruitment in the Arctic vs. high reproductive investment, but lower juvenile survival and recruitment in the Yukon-Kuskokwim Delta). We recommend further research into the evolutionary consequences of breeding in the Arctic by comparing lifetime

reproductive success of Arctic and Yukon-Kuskokwim Delta breeders.

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