



## SURVIVAL AND BREEDING ADVANTAGES OF LARGER BLACK BRANT (*BRANTA BERNICLA NIGRICANS*) GOSLINGS: WITHIN- AND AMONG-COHORT VARIATION

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**ABSTRACT.**—We examined the relationship between mass late in the first summer and survival and return to the natal breeding colony for 12 cohorts (1986–1997) of female Black Brant (*Branta bernicla nigricans*). We used Cormack-Jolly-Seber methods and the program MARK to analyze capture–recapture data. Models included two kinds of residuals from regressions of mass on days after peak of hatch when goslings were measured; one based on the entire sample (12 cohorts) and the other based only on individuals in the same cohort. Some models contained date of peak of hatch (a group covariate related to lateness of nesting in that year) and mean cohort residual mass. Finally, models allowed survival to vary among cohorts. The best model of encounter probability included an effect of residual mass on encounter probability and allowed encounter probability to vary among age classes and across years. All competitive models contained an effect of one of the estimates of residual mass; relatively larger goslings survived their first year at higher rates. Goslings in cohorts from later years in the analysis tended to have lower first-year survival, after controlling for residual mass, which reflected the generally smaller mean masses for these cohorts but was potentially also a result of population-density effects additional to those on growth. Variation among cohorts in mean mass accounted for 56% of variation among cohorts in first-year survival. Encounter probabilities, which were correlated with breeding probability, increased with relative mass, which suggests that larger goslings not only survived at higher rates but also bred at higher rates. Although our findings support the well-established linkage between gosling mass and fitness, they suggest that additional environmental factors also influence first-year survival. Received 15 January 2006, accepted 8 November 2006.

**Key words:** Black Brant, *Branta bernicla nigricans*, density, growth, life history, recruitment, survival.

### Supervivencia y Ventajas Reproductivas de los Pichones de Mayor Tamaño de *Branta bernicla nigricans*: Variación entre y dentro de las Cohortes

**RESUMEN.**—Examinamos la relación del peso al final del primer verano con la supervivencia y el regreso a la colonia natal de cría para 12 cohortes (1986–1997) de hembras de *Branta bernicla nigricans*. Usamos los métodos de Cormack-Jolly-Seber y el programa MARK para analizar los datos de captura–recaptura. Los modelos incluyeron dos tipos de residuos obtenidos a partir de las regresiones

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entre el peso y los días luego del punto máximo de eclosión, cuando se midieron los pichones; uno basado en la muestra entera (12 cohortes) y otro basado sólo en los individuos de la misma cohorte. Algunos modelos incluyeron la fecha del punto máximo de eclosión (una covariable de grupo relacionada al atraso en la nidificación en ese año) y el peso residual promedio de la cohorte. Finalmente, los modelos permitieron que la supervivencia variara entre las cohortes. El mejor modelo de la probabilidad de encuentro incluyó un efecto del peso residual sobre la probabilidad de encuentro y permitió que la probabilidad de encuentro varíe entre las clases de edad y entre los años. Todos los modelos competitivos contuvieron un efecto de uno de los estimadores del peso residual; los pichones relativamente más grandes sobrevivieron su primer año a una tasa más alta. Los pichones de las cohortes de los últimos años del análisis tendieron a presentar una supervivencia más baja en el primer año, luego de controlar por el peso residual. Esto reflejó un peso promedio generalmente menor para estas cohortes, pero fue potencialmente también el resultado de los efectos de la densidad de la población además de los efectos del crecimiento. La variación entre las cohortes en el promedio del peso significó el 56% de la variación entre las cohortes en el primer año de supervivencia. Las probabilidades de encuentro, las que se correlacionaron con la probabilidad de cría, incrementaron con el peso relativo, lo que sugiere que los pichones más grandes no sólo sobrevivieron a tasas más altas sino que también nidificaron a tasas más altas. Aunque nuestros hallazgos apoyan el nexo entre el peso de los pichones y la adecuación biológica, ellos sugieren que los factores ambientales adicionales también influyen en la supervivencia del primer año.

EARLY GROWTH IS highly correlated with lifetime fitness in long-lived vertebrates. Ungulates that grow faster survive their first year at higher rates (Clutton-Brock et al. 1987, Milner et al. 2000), achieve larger adult size (Skogland 1983), and have greater reproductive success (Clutton-Brock 1988, Gaillard et al. 1992, Cameron et al. 1993, Sæther and Heim 1993). Similar patterns for survival (Owen and Black 1989, Schmutz 1993, van der Jeugd and Larsson 1998, Cooch 2002, Reed et al. 2003), adult size (Cooch et al. 1991a, b; Larsson and Forslund 1991; Sedinger et al. 1995; Loonen et al. 1997), and reproductive success (Sedinger et al. 1995, Choudhury et al. 1996) have been observed in geese, which are large-bodied herbivorous birds. Greater first-year survival in larger goslings is believed to result from their increased ability to store energy in preparation for long fall migrations (Owen and Black 1989).

Growing goslings are nearly entirely herbivorous (Sedinger 1992), which limits their rate of nutrient intake in natural environments (Sedinger and Raveling 1988, Sedinger 1997). Growth in geese, therefore, is governed by nutrient availability in foraging habitats during the growth period in the first summer

of life (Larsson and Forslund 1991, Cooch et al. 1993, Manseau and Gauthier 1993, Sedinger et al. 2001a), and variation in gosling growth rate reflects variation in both availability (Person et al. 1998, 2003) and quality of foods (Sedinger et al. 2001a). Consequently, growth of goslings is largely governed by environmental influences (Larsson et al. 1998, Leafloor et al. 1998, Herzog 2002) and nongenetic parental attributes (Herzog 2002), which likely include social status (Loonen et al. 1999). We are not arguing that genes play no role in determining growth rate. Differences in body size among species of geese offer clear evidence of genetic influences on growth. Studies of natural variation in food abundance and growth suggest, however, that nutritional constraints prevent goslings from achieving genetically possible growth rates under most circumstances in nature (e.g., Black et al. 1997, Leafloor et al. 1998, Sedinger et al. 2001a). For the Black Brant (*Branta bernicla nigricans*; hereafter "brant") population in the present study, Herzog (2002) could account for ~70% of variation in gosling growth with nongenetic factors. The importance of nongenetic factors is consistent with the general lack of response to selection on

body size in geese (Cooch et al. 1991b, Sedinger et al. 1995), though antagonistic pleiotropy has not been ruled out as an explanation.

Hatch date in relation to those of other nests in the same year influences growth (Cooch et al. 1991a, Sedinger and Flint 1991, Sedinger et al. 1997), because early-hatching goslings gain access to the most nutritious foods first (Sedinger and Raveling 1986; Lepage et al. 1998, 1999) and graminoid foods undergo a decline in nutrient concentration beginning about the time goslings hatch (Sedinger and Raveling 1986). Population density also influences growth, because there is less *per capita* food available at higher densities (Cooke et al. 1995, Sedinger et al. 2001a) and growth is slowed (Cooch et al. 1991b, Black et al. 1997, Loonen et al. 1997). Thus, relative hatch date and population density have both been identified as factors influencing fitness in populations of geese.

Growth of goslings also varies both spatially (Larsson and Forslund 1991, Cooch et al. 1993, Sedinger et al. 2001a, Herzog 2002) and among years (Cooch et al. 1991b, Person et al. 2003). In brant, spatial and among-year variation are substantially greater than that associated with hatch date; both annual variation and variation among brood-rearing areas accounted for >10× as much of the variation in gosling size as relative hatch date (Herzog 2002). Growth and other factors associated with breeding areas strongly influence first-year survival, and much of this influence is manifested during the first fall migration (Owen and Black 1989, Francis et al. 1992, van der Jeugd and Larsson 1998). Substantial variation may exist in first-year survival in addition to variation associated with growth (Ward et al. 1997, 2004). Mechanisms underlying such variation remain largely unknown, though weather during migration influences duration of migration (Dau et al. 1992) and could influence mortality of young of the year. An additional plausible hypothesis is that food availability on fall staging areas, by its effect on nutrient storage, may influence survival during the first fall migration.

We used a 14-year study of brant weighed and uniquely marked as goslings to assess the relationship between size in their first summer and subsequent survival and reproduction using Cormack-Jolly-Seber (CJS) capture-recapture models (Lebreton et al. 1992, White and Burnham 1999). We considered models of

first-year survival containing two estimates of residual mass (in relation to all individuals in the study or in relation to other individuals in the same cohort) and cohort mean mass. These models allowed us to assess effects of both within- and among-cohort variation in mass on first-year survival. They also allowed us to differentiate between effects of variation in mass among cohorts and all other factors that may have varied among cohorts. We also considered mean hatch-date effects on first-year survival to evaluate the effect of early and late seasons on survival (Cooch 2002).

## METHODS

*Study area.*—The present study was conducted at the Tutakoke River brant colony (61°N, 165°W) on the Bering Sea coast of the Yukon-Kuskokwim (Y-K) Delta, Alaska. Tutakoke River was one of four major colonies on the Y-K Delta (Sedinger et al. 1993). Brant nesting on the Y-K Delta represented >70% of the entire breeding population, and Tutakoke River represented ~20% of the breeding population (Sedinger et al. 1993). During the study, numbers of breeding pairs at Tutakoke River increased from ~1,100 pairs in 1985 (Sedinger et al. 1993) to >7,000 pairs in 2000 (R. M. Anthony unpubl. data). Density-dependent effects on food abundance reduced growth rates of goslings and first-year survival between 1986 and 1992, after which changes in vegetation induced by grazing by geese increased gosling growth rates (Person et al. 2003). Goslings were reared on areas that extended from the colony itself to ≤30 km away (Lindberg and Sedinger 1998). Adult brant were generally faithful to individual brood-rearing areas (Lindberg and Sedinger 1998), but some changed the areas to which they took their goslings in some years. Growth of goslings varied substantially and consistently among brood-rearing areas (Herzog 2002), as did the mean age of parents using these areas (Herzog 2002).

*Field methods.*—Goslings were captured by herding them into corral traps during the adult remigial molt, when they were between 25 and 40 days old (Sedinger et al. 1997). Growth is essentially linear over this range of ages (Sedinger et al. 2001a). Goslings released from 1986 through 1998 were included in this analysis. Following capture, we weighed individuals (±5 g) and placed a metal federal band on one leg

and a plastic band with a unique engraved code on the other. We detected surviving individuals during three periods within summers following the initial capture and release. During nesting, we searched about fifty, 100-m-diameter circular plots every four days throughout egg laying, typically ~2.5 weeks. Following completion of egg laying and through the hatch period, we checked individuals at nests throughout the colony for the presence of bands. We detected 50% of nesting two-year-old goslings and >60% of nesting three-year-old goslings that were present during nesting (Sedinger et al. 2001b). One-year-old females did not nest but were present in flocks of nonbreeders during the incubation period, and we recorded them during that period (Lindberg et al. 1998). We also recorded individuals during brood rearing from blinds mounted atop observation towers, using 120× spotting scopes. Finally, previously banded individuals were recorded following recapture during brood drives in late summer. We used observations and recaptures for the years 1987–1999 in analyses. Using robust design (Kendall and Nichols 1995), we estimated that we detected 61–77% of two-year-old females and 72–82% of three-year-old and older females that were present on the colony each year between 1987 and 1993 (Sedinger et al. 2001b). We detected an average of 41% of one-year-old females present on the breeding colony during this period.

*Analytical methods and evaluation of hypotheses.*—We used Cormack-Jolly-Seber (CJS) methods (Lebreton et al. 1992) to analyze capture histories of goslings released between 1986 and 1998. Because first-year survival of the 1998 cohort was confounded with encounter probability in 1999, the last year of observations, we report estimates of first-year survival only through 1997. We restricted our analysis to female brant because most males dispersed to other breeding colonies and were not detected breeding at Tutakoke River (Lindberg et al. 1998). Analyses were conducted using MARK (White and Burnham 1999), and we used Akaike's Information Criterion (AIC) adjusted for overdispersion (QAIC) to evaluate models (Burnham and Anderson 2002). We considered multiple hypotheses to explain variation in first-year and subsequent survival and encounter probability. Akaike weights ( $w_i$ ) were used to assess the cumulative evidence in

support of a particular hypothesis (Burnham and Anderson 2002). We adjusted AIC values for potential overdispersion in the data, and other sources of lack of model fit, by estimating  $\hat{c}$  as the ratio of the deviance for a model containing variation in survival and encounter probability and the mean deviance for this model applied to bootstrapped data (Schmutz and Ely 1999).

We considered four covariates in models of first-year survival and encounter probability. Preliminary consideration of covariate effects on survival beyond the first year indicated that they were not important, and we did not consider them further. All covariates were standardized to mean zero and standard deviation one. We included relative mass of goslings in their first summer, which was estimated from the regression of mass for all goslings in the data set against days, following peak of hatch in the year they were first captured. We refer to this estimate as "residual mass." We also considered mass residuals related only to other individuals in the same cohort. We refer to this estimate as "cohort residual mass." We considered cohort residual mass primarily in models that also contained a covariate for mean cohort residual mass (hereafter "cohort mean mass"), a group covariate describing mean mass of individuals in a given cohort in relation to other cohorts. Explicit consideration of cohort residual mass and cohort mean mass allowed us to partition overall residual mass variation into within- and among-cohort variation in mass. These estimates of residual mass allowed us to include in the analysis goslings that were not of precisely known age (in days). We also included date of peak of hatch as a covariate in these models to account for variation in the timing of peak of hatch among years.

Our rationale for hypotheses was as follows. Models containing residual mass, in relation to all individuals in the sample, evaluated the importance of individual mass itself. Models containing both cohort mean mass and cohort residual mass allowed us to partition the effects of within- and among-cohort variation in mass. Models containing date of peak of hatch assessed the importance of annual variation in phenology (i.e., years in which breeding was late vs. years in which breeding was early). We estimated the proportion of the variance in first-year survival among cohorts associated

with variation in mass as follows. We regressed annual first-year survival estimates from a time-only model against those from a cohort-mean-mass-only model and calculated  $r^2$ , the proportion of the variance associated with the regression. Because we modeled variation in first-year survival solely as a function of cohort mean mass, this approach provided an assessment of the role of mass in variation in first-year survival among cohorts.

Our principal interest was in models containing the effects of mass on survival, but we also explored a set of models for encounter probability, including the effects of covariates on encounter probability. In standard capture-recapture analysis, encounter probability represents the product of two probabilities: that of being present on the breeding colony (synonymous with "breeding" in our case) for individuals that are alive and in the sample population, and that of being detected conditional on being present (Kendall and Nichols 1995). We interpreted performance of models containing effects of covariates on encounter probabilities as preliminary evidence regarding the effects of these covariates on probability of being present, synonymous with "breeding" in this study (Sedinger et al. 2001b). Finally, we considered a model with only cohort- and age-related variation in survival and recapture probability to assess the overall importance of covariates in explaining first-year survival. Parameter estimates represent weighted averages across candidate models.

We first evaluated a suite of models for encounter probability in which we allowed the latter to vary with age, time, and residual mass. For the assessment of models for encounter probability, we used a relatively general model for survival that allowed first-year survival to vary with cohort and two covariates: relative mass and date of peak of hatch. We used the best-performing model for encounter probabilities to assess hypotheses about first-year survival.

We did not include observations away from the breeding colony, so our estimates represent apparent survival, because we could not distinguish between mortality and dispersal. Because many female dispersers do not breed at other locations (Lindberg et al. 1998), dispersal had the same practical effect on fitness as mortality for many dispersers.

## RESULTS

We captured, weighed, marked, and released 2,584 female goslings between 1986 and 1998. The ratio of the deviance of a model allowing for variation between two age classes (first year and older) in survival and variation among four age classes (first three years and four years and older) in encounter probability and the mean deviance of this model fit to bootstrapped data was 1.10. We used this ratio as an estimate of  $c$  to adjust for potential overdispersion in the data.

Encounter probabilities were best modeled as varying across years and among age classes, with an effect of residual gosling mass on detection probability at each age. We used this structure for encounter probability in our assessment of models of survival. Encounter probability of all age classes increased as residual mass increased (Fig. 1). Encounter probabilities averaged across candidate models ranged from  $0.07 \pm 0.04$  (1997) to  $0.27 \pm 0.07$  (1987) for one-year-old females, and from  $0.23 \pm 0.03$  (1997) to  $0.54 \pm 0.10$  (1990) for females four years and older (Table 1).

All competing models of first-year survival contained effects of residual mass, either within or among cohorts (Table 2). Models of first-year survival containing the combination of cohort mean mass and cohort residual mass were somewhat competitive with the best-performing model, which contained only residual mass and a cohort effect. Performance of these models suggested that cohort mean mass accounted for a substantial proportion of the variation in first-year survival. Models containing date of peak of hatch received only modest support (14% of total model weight) (Table 2), which indicates that variation in seasonal phenology had only moderate influence on first-year survival beyond that associated with variation in growth. A model of first-year survival lacking covariates and containing age-specific survival through age two and older and age-specific encounter probability through age four and older performed poorly in relation to models containing some measure of mass (Table 2). Regression of first-year survival estimates from a model containing only cohort variation in first-year survival (no covariates) against first-year survival estimates from a model containing only cohort mean mass estimated that cohort mean mass accounted for 56% of the variance in first-year survival estimates.



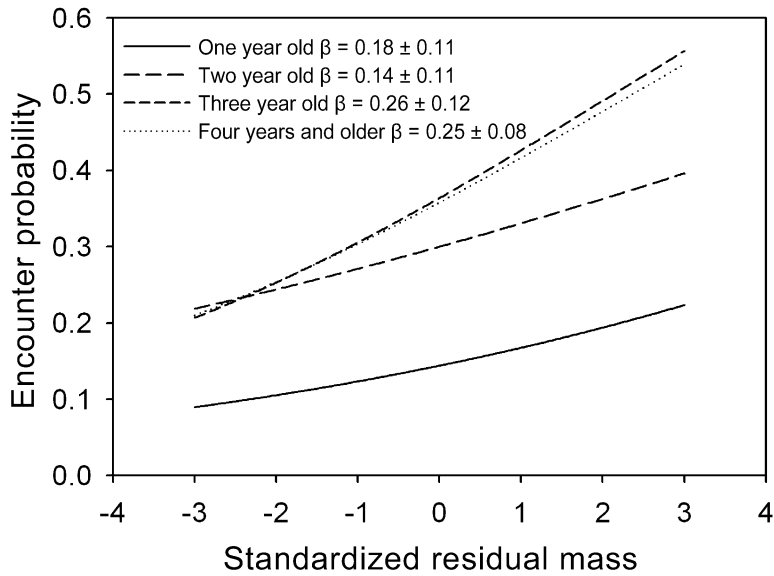


FIG. 1. Relationship between encounter probability and residual mass based on the  $S1(t + r)$  model in Table 2. Betas presented are for the relationship between residual mass and encounter probability.

TABLE 1. Annual encounter probabilities of goslings (one to four years and older) at the Tutakoke River brant colony. Estimates were based on weighted averages across candidate models from Table 2 and were adjusted for gosling mass.

Year	Encounter probability (mean $\pm$ SE)			
	One-year-old <sup>a</sup>	Two-year-old	Three-year-old	Four years and older
1987	0.27 $\pm$ 0.07			
1988	0.14 $\pm$ 0.03	0.42 $\pm$ 0.09		
1989	0.18 $\pm$ 0.04	0.40 $\pm$ 0.06	0.53 $\pm$ 0.10	
1990	0.26 $\pm$ 0.05	0.41 $\pm$ 0.06	0.36 $\pm$ 0.06	0.54 $\pm$ 0.10
1991	0.19 $\pm$ 0.04	0.33 $\pm$ 0.06	0.41 $\pm$ 0.06	0.41 $\pm$ 0.06
1992	0.20 $\pm$ 0.05	0.38 $\pm$ 0.06	0.41 $\pm$ 0.07	0.44 $\pm$ 0.05
1993	0.16 $\pm$ 0.08	0.27 $\pm$ 0.06	0.27 $\pm$ 0.05	0.31 $\pm$ 0.04
1994	0.09 $\pm$ 0.03	0.23 $\pm$ 0.11	0.38 $\pm$ 0.07	0.34 $\pm$ 0.04
1995	0.17 $\pm$ 0.06	0.27 $\pm$ 0.06	0.52 $\pm$ 0.16	0.38 $\pm$ 0.04
1996	0.21 $\pm$ 0.06	0.29 $\pm$ 0.09	0.28 $\pm$ 0.07	0.53 $\pm$ 0.04
1997	0.07 $\pm$ 0.04	0.17 $\pm$ 0.05	0.37 $\pm$ 0.10	0.23 $\pm$ 0.03
1998	0.19 $\pm$ 0.23	0.18 $\pm$ 0.08	0.23 $\pm$ 0.07	0.32 $\pm$ 0.04
1999	0.19 $\pm$ 0.23	0.23 $\pm$ 0.29	0.20 $\pm$ 0.09	0.34 $\pm$ 0.04

<sup>a</sup> Encounter probabilities for one-year-old females in 1998 and 1999 were constrained to be equal.

Survival after the first year varied among age classes but was constant across cohorts in this and all other competitive models; survival of one-year-old females =  $0.80 \pm 0.069$ , survival of two-year-old females =  $0.86 \pm 0.069$ , and survival of females three years and older =  $0.83 \pm 0.069$ . Under the model containing only residual mass and cohort, first-year survival increased

substantially as residual mass increased (Fig. 2). The largest goslings when measured in the early cohorts survived at essentially adult rates. There was a tendency for first-year survival, averaged across models, to decline through time (Figs. 2 and 3); the five cohorts with the lowest first-year survival all occurred in the 1990s, whereas four of the six cohorts with

TABLE 2. QAIC<sub>c</sub> values, model weights (*w<sub>i</sub>*), numbers of parameters (*K*), and deviance for models of first-year and subsequent survival in Black Brant from the Yukon-Kuskokwim Delta, Alaska.

Model <sup>a</sup>	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	<i>w<sub>i</sub></i>	<i>K</i>	QDeviance
S1( <i>t</i> + <i>r</i> ), P( <i>a</i> * [ <i>t</i> + <i>r</i> ])	7575.84	0.00	0.46	67	7439.49
S1( <i>rm</i> + <i>cohmean</i> ), P( <i>a</i> * [ <i>t</i> + <i>r</i> ])	7577.45	1.61	0.21	56	7463.80
S1( <i>t</i> + <i>rm</i> ), P( <i>a</i> * [ <i>t</i> + <i>r</i> ])	7578.54	2.70	0.12	67	7442.19
S1( <i>rm</i> + <i>h</i> + <i>cohmean</i> ), P( <i>a</i> * [ <i>t</i> + <i>r</i> ])	7578.55	2.71	0.12	57	7462.84
S1( <i>t</i> * <i>r</i> ), P( <i>a</i> * [ <i>t</i> + <i>r</i> ])	7580.79	4.95	0.04	75	7427.83
S1( <i>r</i> ), P( <i>a</i> * [ <i>t</i> + <i>r</i> ])	7580.88	5.04	0.04	55	7469.29
S1( <i>r</i> + <i>h</i> ), P( <i>a</i> * [ <i>t</i> + <i>r</i> ])	7582.69	6.85	0.02	56	7469.04
S1( <i>t</i> ), P( <i>a</i> * [ <i>t</i> + <i>r</i> ])	7589.59	13.75	0.00	66	7455.30
S1( <i>rm</i> + <i>h</i> ), P( <i>a</i> * [ <i>t</i> + <i>r</i> ])	7590.23	14.39	0.00	56	7476.58
S1( <i>cohmean</i> ), P( <i>a</i> * [ <i>t</i> + <i>r</i> ])	7592.09	16.25	0.00	55	7480.50
S1( <i>rm</i> ), P( <i>a</i> * [ <i>t</i> + <i>r</i> ])	7593.36	17.52	0.00	55	7481.77
S1( <i>h</i> + <i>cohmean</i> ), P( <i>a</i> * [ <i>t</i> + <i>r</i> ])	7593.57	17.73	0.00	56	7479.92
S1( <i>h</i> ), P( <i>a</i> * [ <i>t</i> + <i>r</i> ])	7602.69	26.85	0.00	55	7491.10

<sup>a</sup>Model notation generally follows that of Lebreton et al. (1992). Additive effects among variables are indicated by a plus sign, whereas allowance for fully interactive effects is indicated by an asterisk. For example, *t* + *r* models have a single beta (β) for the relationship between residual mass and first-year survival and a separate beta for each cohort, producing parallel relationships between residual mass and logit-transformed survival among cohorts. S1 = first-year survival. We modeled survival after the first year as age-specific and constant across years. Variables and covariates were as follows: *t* = cohort, *r* = residual mass in the first summer (based on the regression for the entire sample of mass on days since peak of hatch in the year when measured), *rm* = residual mass in the first summer in relation to other members of the same cohort (cohort residual mass), *cohmean* = mean residual mass for the cohort (cohort mean mass), *h* = date of the peak of hatch in the hatching year (a measurement of earliness or lateness of the nesting season), and *a* = age in years.

<sup>b</sup>QAIC<sub>c</sub> values were calculated using  $\hat{c} = 1.10$ .

the highest first-year survival rates occurred in the 1980s. An effect of delayed spring thaw, generally cold summer temperatures, and early fall freeze-up associated with Mt. Pinetubo’s eruption in 1991 was apparent in the first-year survival of the 1992 cohort, which was the second lowest in the study (Fig. 3). It is noteworthy that after controlling for residual mass, goslings from the 1992 cohort survived at less than half the rate of those in the 1986 cohort.

DISCUSSION

*First-year survival, growth rate, and fitness.*—Larger goslings, after controlling for measurement date in relation to hatching phenology, had substantially higher probabilities of surviving their first year. This finding is generally consistent with other studies showing that gosling size in late summer is an important determinant of first-year survival (Francis et al. 1992, Schmutz 1993, van der Jeugd and Larsson 1998, Cooch 2002). Support for models containing residual mass suggests that size in relation to other individuals in a given cohort influenced first-year survival in addition to effects of mean

size of individuals in a cohort. Similarly, strong performance of models containing cohort mean mass indicates that, overall, summer growth in the first year is a major determinant of first-year survival in brant.

Numerous factors influence gosling growth, including the date on which they hatch (Cooch et al. 1991a, Sedinger and Flint 1991), local population density (Black et al. 1997, Sedinger et al. 1998), the area where they are reared (Larsson and Forslund 1992, Aubin et al. 1993), the size of the brood they are in (Cooch et al. 1991a, Loonen et al. 1999), the age of their parents (Herzog 2002), and other, generally unmeasured, attributes of their parents (Herzog 2002). All these factors, except possibly population density, are associated with social status or other measures of “quality” of the parents. Relative nesting date (within years), and consequently hatch date, is affected by parental age: older individuals tend to nest earlier than younger ones (Hamann and Cooke 1987, Flint and Sedinger 1992, Forslund and Larsson 1992). Larger individuals also nest earlier (Sedinger et al. 1995), and males of earlier-nesting pairs are more likely to engage in extrapair copulations (Mineau and Cooke 1979,

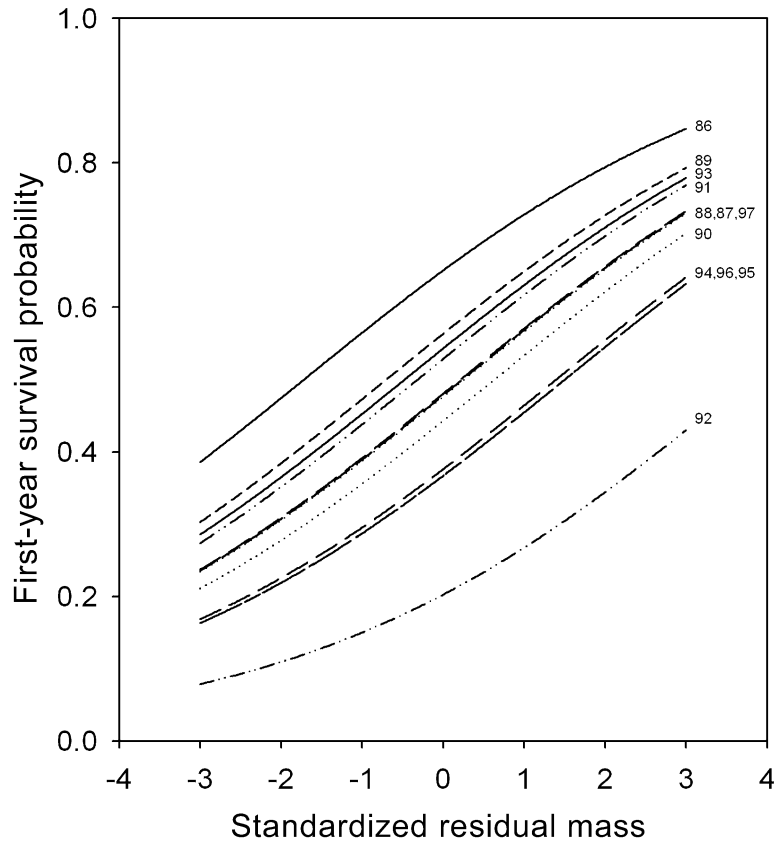


FIG. 2. Relationships between residual mass in the first summer and first-year survival for goslings from cohorts produced on the Tutakoke River colony from 1986 through 1997 on the basis of the  $S1(t + r)$  model from Table 2. Beta ( $\beta = 0.36 \pm 0.093$ ) relating residual mass to first-year survival was the same for all cohorts under the best model, whereas there was an additional cohort effect on survival. Survival estimates for the 1997 cohort may be biased low, because not all members of this cohort had recruited into the breeding population by the end of the study.

Svete 1999), an indication of higher social status. Parental age is associated with the area on which they rear their broods in brant (Herzog 2002) and other geese (Larsson and Forslund 1992). In Barnacle Geese (*B. leucopsis*), sizes of offspring and parents are correlated, which is associated with sharing the same rearing area (Larsson and Forslund 1992). Brood size is associated with parental age (Forslund and Larsson 1992, Rockwell et al. 1993) and dominance status (Lamprecht 1986), though the relationship to dominance status is complex, as indicated by the fact that dominance status of parents can be enhanced by artificially increasing the size of their broods (van der Jeugd and Larsson 1998). In sum, numerous factors, all correlated with

each other, influence growth, and our results indicate that these factors, through their influence on growth, are important determinants of fitness.

Substantial variation exists in lifetime reproductive success of long-lived vertebrates with a few individuals producing many offspring, whereas most individuals produce few or none (Clutton-Brock 1988). The strong influence of early environment on characters associated with fitness (Skogland 1983, Kojola 1993, Sedinger et al. 1995, Coulson et al. 1997, Cam et al. 2003), combined with use of similar environments by parents and their offspring (Larsson and Forslund 1992), suggest that fitness of offspring covaries with that of their parents. Generally,



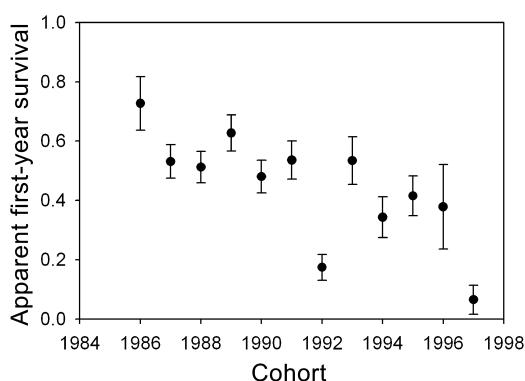


FIG. 3. Variation in first-year survival among cohorts. Survival estimates from model  $S1(t)$  to assess patterns in the absence of modeled covariate effects. The estimate of first-year survival for the 1997 cohort is likely negatively biased, because some individuals had not yet entered the breeding population to be recorded by 1999 (Sedinger et al. 2001b), the last year of observations for the present study.

these relationships between parental and offspring fitness have the potential to generate substantial variation among lineages in lifetime reproductive success.

**Cohort effects on survival.**—We detected substantial variation in first-year survival among cohorts, even after controlling for gosling mass (Figs. 1 and 2). About 56% of the variance in survival among cohorts was explained by variation in gosling mass and, consequently, growth conditions on the breeding area. We found only modest support for an effect of absolute timing of nesting on first-year survival; goslings from cohorts produced in years when overall nesting was later were only slightly less likely to survive their first year. This effect of late nesting, however, appeared to be particularly pronounced in 1992, when the eruption of Mt. Pinetubo cooled global climate and delayed snowmelt throughout the circumpolar Arctic (Ganter and Boyd 2000).

There was a generally declining trend in first-year survival throughout our study. Declines in survival were not entirely a result of declining gosling size across cohorts, because gosling size actually increased after 1992, associated with grazing conditions around the Tutakoke River colony (Person et al. 2003). Furthermore, it is evident from Figure 2 that goslings in later

cohorts experienced lower first-year survival even after controlling for mass. We hypothesize that additional density-related effects occur after hatching that influence the ability of individuals to survive their first fall migration. Such effects likely occur before families arrive at Izembek Lagoon (Ward et al. 2004), a major premigration staging area on the Alaska Peninsula (Reed et al. 1989), or at Izembek Lagoon itself.

**Breeding and gosling size.**—Probability of detecting an individual on the breeding area provides an index of breeding probability, so long as the effort devoted to locating marked individuals is constant (Clobert et al. 1994). In our case, it is also necessary to assume that encounter probability conditioned on presence on the colony did not vary as a function of size in an individual's first summer. Robust design methods have been developed to estimate both the probability of presence on the breeding area (probability of breeding if presence is synonymous with breeding) and the probability of encounter, conditioned on presence (Kendall and Nichols 1995). Because our goal here was primarily to assess the factors influencing survival, we did not apply robust design methods to our data. Nevertheless, exploration of models of encounter probability clearly showed that residual gosling mass was positively associated with encounter probability of the same individuals for all age classes of brant. Clearly, annual variation in encounter probabilities (Table 1) suggests some variation among years in our ability to encounter breeding brant, but estimates of encounter probabilities are influenced by breeding probability as well as search effort. Most importantly, we do not believe that variation in encounter probability associated with mass (Fig. 1) can be explained by variation in our ability to encounter individuals that were present on the colony. Therefore, we interpret our results to suggest that for brant goslings that survive their first year, those that are larger enjoy a higher probability of breeding throughout their lifetime. Confirmation of this result will require a robust design analysis (Kendall et al. 1997) of breeding probability that explicitly estimates both probability of presence on the breeding area and probability of encounter conditioned on presence. We are planning such an analysis for the future. Our result is unlikely to be caused by temporarily breeding at other brant colonies, because direct examination of individuals at

other brant colonies cannot account for those that dispersed from the Tutakoke colony (Lindberg et al. 1998). Overall, our results are consistent with the hypothesis that individuals vary in their probability of breeding and that growth influences this variation.

#### ACKNOWLEDGMENTS

This research was supported by the Alaska Fish and Wildlife Research Center, National Biological Service (now Biological Resources Discipline, U.S. Geological Survey); Migratory Bird Management, Region 7, U.S. Fish and Wildlife Service; University of Alaska Foundation through the Angus Gavin Migratory Bird Research Fund; Ducks Unlimited; and the National Science Foundation (OPP 9214970, DEB 9815383, OPP 9985931). Logistic support was provided by Yukon Delta National Wildlife Refuge. M. Anderson, M. Anteau, J. Beagley, K. Bollinger, J. Chakuchin, M. Chambers, R. Crain, W. Don, B. Dugger, D. Eichholz, M. Eichholz, W. Eldridge, S. Farley, T. Fenske, P. L. Flint P. Freshman, J. Hall, J. Hill, D. Hoffman, D. Johnson, T. Jones, S. Keane, I. Kharitonov, S. Kharitonov, J. Kiesau, P. Kugzruk, L. Lake, J. Lawler, M. Lindberg, L. Lipinski, J. Mason, G. M. Moydel, A. Nash, T. Obritchkewitz, W. O'Connell, T. Olson, T. F. Paragi, J. Pearce, A. Perez-Arteaga, B. Person, D. Person, R. F. Rockwell, T. Rogers, J. Schamber, A. Seidl, M. Shellicans, S. Sindelar, C. Slats, C. Solek, P. Svete, T. W. Trapp, S. van Laer, D. Wheeler, R. Wheeler, J. White, D. Welsh, B. Wenzel, and D. Youkie all assisted with field work. M. P. Herzog, E. G. Cooch, and M. S. Lindberg commented on an earlier version of the manuscript. Research supported in part by Nevada Agricultural Experiment Station, publication #52077053.

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Associate Editor: G. R. Hepp