Notes

Life-History Implications of Large-Scale Spatial Variation in Adult Survival of Black Brant (*Branta bernicla nigricans*)

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Abstract.—We used capture–recapture methods to estimate adult survival rates for adult female Black Brant (*Branta bernicla nigricans*; hereafter ''brant'') from three colonies in Alaska, two on the Yukon-Kuskokwim Delta, and one on Alaska's Arctic coast. Costs of migration and reproductive effort varied among those colonies, enabling us to examine variation in survival in relation to variation in these other variables. We used the Barker model in program MARK to estimate true annual survival for brant from the three colonies. Models allowing for spatial variation in survival were among the most parsimonious models but were indistinguishable from a model with no spatial variation. Point estimates of annual survival were slightly higher for brant from the Arctic (0.90 ± 0.036) than for brant from either Tutakoke River (0.85 ± 0.004) or Kokechik Bay (0.86 ± 0.011). Thus, our survival estimates do not support a hypothesis that the cost of longer migrations or harvest experienced by brant from the Arctic reduced their annual survival relative to brant from the Yukon-Kuskokwim Delta. Spatial variation in survival provides weak support for life-history theory because brant from the region with lower reproductive investment had slightly higher survival.

Resumen.—Usamos métodos de captura–recaptura para estimar la tasa de supervivencia de hembras adultas de *Branta bernicla nigricans* en tres colonias en Alaska, dos en el delta de Yukon-Kuskokwim, y una en la costa ártica de Alaska. Los costos de migración y esfuerzo reproductivo variaron entre estas colonias, permitiéndonos examinar estas variables en relación a variaciones en la supervivencia. Usamos el modelo Barker del programa MARK para estimar la supervivencia anual verdadera de individuos de *B. b. nigricans* de tres colonias. Los modelos que consideran variación espacial en la supervivencia estuvieron entre los más parsimoniosos, pero fueron indistinguibles de un modelo que no considera variación espacial. Las estimaciones puntuales de supervivencia anual fueron un poco mayores para *B. b. nigricans* del Ártico (0.90 ± 0.036) que para individuos provenientes del Río Tutakoke (0.85 ± 0.004) o de Bahía Kokechik (0.86 ± 0.011). De este modo, nuestras estimaciones de supervivencia no apoyan la hipótesis que los costos de migraciones más largas o de cosecha experimentados por *B. b. nigricans* en el Ártico reducen su supervivencia anual en relación a individuos del delta de Yukon-Kuskokwim. La variación espacial en la supervivencia sustenta sólo parcialmente las teorías sobre historias de vida, ya que los individuos de *B. b. nigricans* de la región con menor inversión reproductiva presentaron una supervivencia un poco mayor.

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Variation in adult survival rates is hypothesized to be an important selective force on other life-history traits (Charlesworth 1994) because adult survival is an important determinant of lifetime reproductive success in long-lived species (Clutton-Brock 1988). Furthermore, adult survival may be traded off against reproductive investment (Charlesworth 1994). Population dynamics of long-lived species in the absence of density-dependent factors are most

sensive to changes in adult survival (Caswell 1989, Schmutz et al. 1997), and understanding variation in survival is, therefore, of interest to both scientists and managers.

Although estimates of annual survival have become common for waterfowl and some other birds (Lebreton et al. 1992, Nichols 1992), few studies have examined spatial variation in survival because of logistic constraints on simultaneously marking and recapturing individuals from multiple regions (for exceptions see Blondel et al. 1992, Francis et al. 1992, Smith and Reynolds 1992). We used six years of marking and capture of Black Brant (*Branta bernicla nigricans*; hereafter ''brant'') from two colonies on the Yukon-Kuskokwim Delta, Alaska, and one colony on Alaska's Arctic coast to test for spatial variation in adult survival of brant breeding in those three locations, and to evaluate patterns of survival variation in the context of variation among those three colonies in other life-history traits, including migration distance and reproductive effort.

Methods.—We captured and observed brant at the Tutakoke River (61°N, 165°W; ~6,000 pairs) and the Kokechik Bay colonies (62°N, 166°W; ~7,000 pairs; Anthony et al. 1995) on the Yukon-Kuskokwim Delta. Brant were captured and observed in brood-rearing areas near Oliktok Point (70°N, 149°W; Sedinger and Stickney 2000) on Alaska's Arctic coast. Brant using those brood-rearing areas nest predominantly in the Colville River Delta but small aggregations of brant also nested up to 15 km inland from the coast (Stickney and Ritchie 1996); we refer to those as coming from the Arctic coast. We released 3,410, 642, and 210 unique adult female brant from Tutakoke River, Kokechik Bay, and the Arctic coast, respectively.

Estimates of survival were based on observation or capture of individually marked brant during the breeding season, and winter and spring migration. We also used recoveries of brant shot by hunters. We observed brant during nesting (all three colonies) or brood rearing (Tutakoke River and Arctic coast) (Sedinger et al. 1995, 1998) and we captured brant during the adult remigial molt about a month after the peak of hatch at each location. During banding, each individual received a metal federal band and a uniquely engraved three-character plastic leg band (2.5 cm wide). For our analyses, we recorded individuals as present if they were either observed in nesting or brood-rearing areas or captured in brood flocks.

Capture and observation effort varied among colonies. At Tutakoke River, we established 50 randomly located, 50 m radius plots throughout the colony. Those plots were searched every four days throughout egg laying, beginning after ~10% of nests were initiated. We also searched the entire colony daily throughout the hatching period when females were most attentive to their nests. During searches, we flushed females from their nests and read the codes

on their bands. We also read bands on adults associated with broods, following hatch, from up to seven 3–7 m high observation towers located in brood-rearing areas used by brant from the Tutakoke River colony. We captured and observed brant at Tutakoke River each year from 1990 through 1996.

We did not maintain a permanent camp at Kokechik Bay, so observations of marked brant were more limited than at Tutakoke River. One investigator visited Kokechik Bay in 1990, 1991, and 1993 and spent three days during late incubation flushing females and recording band codes. In 1994, 1995, and 1996, two investigators spent a week reading bands at Kokechik Bay. A single investigator spent two days at Colville River reading bands in each of 1992, 1993, 1995, and 1996. Bands also were read on a single brood-rearing area (Oliktok Point) used by brant from the Colville River throughout brood rearing in 1995 and 1996.

Brant were captured at all three areas during the adult remigial molt by driving them into corral traps. Brant were captured at Tutakoke River in every year and on brood-rearing areas for the Arctic coast in 1991–1996. Brant were captured at Kokechik Bay during 1990, 1991, and 1993–1995. Our sampling effort varied substantially among areas, but the estimation methods we used incorporate such variation, primarily into estimates of detection probability (Pollock et al. 1990). Thus, our estimates of survival should not have been biased (Pollock et al. 1990, Brownie et al. 1993). We restricted analyses to adult females released in 1990–1994 and observed in 1991–1999.

Brant were observed away from breeding colonies during fall staging at Izembek Lagoon on the Alaska Peninsula (1990–1993; $n = 2,511$ observations) and at three bays in Baja California, Mexico ($n = 4,411$ observations; Ward et al. 1997). Brant were observed in Mexico during 1990–1993 and 1996–1999. We also included a small number of observations from Humboldt Bay, California ($n = 96$ observations in 1997–1999), and Washington State ($n = 31$ observations in 1998). Brant away from breeding areas were observed during daily high tides when they roosted on sandbars.

We used program MARK (White and Burnham 1999) for model selection and parameter estimation. We used Barker's (1997) model in program MARK, which incorporates observations outside the breeding season, recaptures (including observations) during the breeding season, and dead recoveries. Use of Barker's (1997) model allowed separation of mortality from permanent emigration because permanent emigrants from breeding colonies were subject to observation and harvest away from breeding colonies. We use the term ''capture'' to indicate individuals that were only observed as well as those that were captured. The model had the following parameters:

TABLE 1. AIC scores and number of parameters for a selection of MARK models of survival and movement among colonies for brant from Tutakoke River, Kokechik Bay (both on the Yukon-Kuskokwim Delta) and the Arctic coast.

Model[a]	AIC_c	ΔAIC_c	AIC_c weight	Number of parameters
$S^b_{tut}P_{c*t}r_tR_tR'_tF_cF'_c$	57380.5	0.0	0.253	45
$S.P_{c*t}r_tR_tR'_tF_cF'_c$	57380.6	0.1	0.233	44
$S^b_{arc}P_{c*t}r_tR_tR'_tF_cF'_c$	57381.0	0.5	0.200	45
$S^b_{kok}P_{c*t}r_tR_tR'_tF_cF'_c$	57381.2	0.7	0.180	45
$S.P_{c*t}r_tR_tR'_tF_cF'_c$	57381.7	1.2	0.136	46
$S.P_{c*t}r_tR_tR'_tF.F'.$	57400.9	20.4	<0.0001	42
$S_{c*t}P_{c*t}r_tR_tR'_tF.F'_c$	57419.8	39.3	<0.0001	59
$S.P_{c*t}r_tR_tR'_tF.F'_c$	57534.2	153.7	<0.0001	47
$S_{c+t}P_{c*t}r_tR_tR'_tF_cF'_c$	57536.6	156.1	<0.0001	49
$S.P_{c*t}r.R..F_cF'_c$	63634.6	6254.1	<0.0001	28
$S.P_{c*t}r.R.R'.F.F'.$	63651.0	6270.5	<0.0001	24

[a] Model notation follows Lebreton et al. (1992). S, P, r, R, and F represent survival, detection probability, band recovery rate, nonbreeding resighting rate, and colony fidelity, respectively. R was the probability an individual that survived from i to $i + 1$ was observed away from the breeding colony, whereas R' was the probability that an individual that died in the interval i to $i + 1$ was observed away from the breeding colony before it died. F was the probability that an individual present at its breeding colony at time i was again present at time $i + 1$, whereas F' was the probability that an individual absent from its breeding colony at time i was present at time $i + 1$. Subscripts, c and t, represent colony of origin and time, variables over which parameters were allowed to vary. A single subscript indicates parameter varied only with respect to that variable and was constant with respect to the other variable. $c * t$ indicates that the parameter was allowed to vary independently with respect to both colony and year. $c + t$ indicates that the parameter was allowed to vary additively with respect to colony and year, for example, survival varied among colonies in parallel across years.

[b] Subscript ''tut'', ''kok'', and ''arc'' each represent models in which survival at the identified colony (Tutakoke River, Kokechik Bay, and Arctic coast, respectively) was allowed to differ from all other areas combined.

S_i = probability an individual alive at time i was alive at time $i + 1$;

p_i = probability an individual at risk of capture on occasion i was captured;

r_i = probability a marked individual in the interval i to $i + 1$ was found dead and its band reported;

R_i = probability that a marked individual alive at $i + 1$ was resighted alive between i and $i + 1$;

R'_i = probability that a marked individual that died in the interval i to $i + 1$ was resighted alive before it died;

F_i = probability that an individual at risk of capture at time i was again at risk of capture at time $i + 1$;

F'_i = probability that an individual not at risk of capture at time i was at risk of capture at time $i + 1$.

Under this model, survival estimates represented true (as opposed to apparent) survival because permanent emigration and mortality were not confounded. Parameters F_i were not strictly comparable to fidelity parameters in Lindberg et al. (2001) because individuals could re-enter the breeding population at their colony of origin with probability F_i. Therefore, we chose not to present estimates of F. Data were too sparse to fully generalize models for R_i, R'_i, F_i and F'_i. We selected the best models for those parameters (time or colony specific) before analyzing different models of survival.

When individuals were observed to have changed breeding location, we terminated the capture history because the Barker model cannot estimate movement among breeding units. Lindberg et al. (1998) estimated movement among breeding units as <5% annually, consistent with a separate analysis we conducted on the present data using multistate modeling (Brownie et al. 1993).

There is currently no good procedure for assessing model fit for the Barker model within program MARK because the bootstrap method available in MARK produces biased estimates of $\hat{c}$, the overdispersion parameter. Nevertheless, we calculated $\hat{c}$ and examined the effect of adjusting for overdispersion on model selection.

Results.—Models with the lowest Aikake information criterion (AIC) scores had detection probabilities on colonies that were year- and colony-specific, band recovery rates that were year-specific, nonbreeding season resighting rates that were year-specific, and fidelity rates that were colony specific (Table 1). A model in which annual survival was constant among colonies was indistinguishable from models in which survival at one colony differed from that at all others. Model weights for the set of models with constant or spatially varying detection probabilities, time-varying resighting rates, and fidelity rates that were colony specific summed to 0.998 (Table 1), providing no support for alternative models for the nonsurvival parameters. Models in which em-

TABLE 2. Survival and detection probabilities on three breeding colonies of brant estimated from the Barker model in program MARK. Model structure was $S_c P_{ct} r_t R_t R'_t F_c F'_c$.

Parame- ter-year	Survival and detection probabilities (±SE) on colonies		
	Tutakoke	Kokechik	Arctic
Survival			
	0.85 ± 0.004	0.87 ± 0.004	0.90 ± 0.04
Detection			
1991	0.59 ± 0.018	0.05 ± 0.04	0.0
1992	0.73 ± 0.016	0.0	0.12 ± 0.06
1993	0.61 ± 0.016	0.32 ± 0.28	0.67 ± 0.10
1994	0.50 ± 0.014	0.25 ± 0.19	0.25 ± 0.03
1995	0.69 ± 0.017	0.39 ± 0.29	1.0 ± 0.0008
1996	0.63 ± 0.020	0.08 ± 0.06	0.97 ± 0.08

igration was modeled as only permanent ($F' = 0$) or nonexistent ($F = F' = 0$) performed more poorly than models we present.

The bootstrapped estimate of $\hat{c}$ was 1.34, suggesting moderate lack of fit of the data to the most general model. Because the bootstrap produces somewhat biased estimates of $\hat{c}$ (G. C. White unpubl. data), model selection is somewhat conservative when AIC scores are adjusted for lack of fit. Adjusting for that moderate lack of fit, a model with spatially and temporally constant survival had the lowest QAIC and was 2.4 QAIC points better the next best model. This model had a model weight of 0.52. Models with spatial but not temporal variation in survival had total weights of 0.48, providing some support for spatial variation in survival.

Detection probabilities (±SE) for both Kokechik Bay and the Arctic were lower and more poorly estimated (range 0.05 ± 0.04 to 1.0 ± 0.0008) than for Tutakoke River (range 0.50 ± 0.01 to 0.73 ± 0.02), reflecting less intensive and more variable sampling at colonies other than Tutakoke River (Table 2). In contrast to our expectation, relative to cost of migration, annual survival (±SE) was slightly higher for Arctic brant (0.90 ± 0.04) than for brant from the two Yukon-Kuskokwim Delta colonies (0.85 ± 0.004 and 0.87 ± 0.004) using a model allowing spatial but not temporal variation in survival. Band recovery rates (±SE) varied from 0.046 ± 0.008 to 0.094 ± 0.012.

Discussion.—We found only moderately weak evidence for a difference in survival between brant nesting on the Yukon-Kuskokwim Delta and those nesting in the Arctic. The point estimate for brant from the Arctic was slightly higher than those for brant on the Yukon-Kuskokwim Delta. Brant nesting in the Arctic migrate longer distances between wintering and staging areas and breeding areas than brant nesting on the Yukon-Kuskokwim Delta. Brant nesting in the Arctic are also potentially subjected to ad-

ditional subsistence harvest relative to those nesting on the Yukon-Kuskokwim Delta (Sedinger 1996, R. J. Wolfe and A. W. Paige unpubl. data). Moreover, brant breeding in the Arctic experience a shorter reproductive season than do brant nesting on the Yukon-Kuskokwim Delta (Sedinger and Raveling 1986). Nevertheless, there was no evidence that the combination of longer migration and greater exposure to harvest resulted in greater mortality rates for brant nesting in the Arctic relative to those on the Yukon-Kuskokwim Delta.

Survival estimates from this study are comparable to those of Sedinger et al. (1997) and Ward et al. (1997) for brant from the Yukon-Kuskokwim Delta, which is not surprising as both studies had data in common. Survival estimates for the Yukon-Kuskokwim Delta are somewhat higher than those of Kirby et al. (1986) who estimated an annual survival rate of 0.78 for Atlantic Brant (*Branta bernicla hrota*). The estimate for Arctic coast brant was substantially higher than that of Barry (1982; 0.70). Barry could not account for permanent emigration, which could have negatively biased his survival estimate. Similarity between Barry's (1982) estimate and an estimate (0.69 ± 0.03) we produced from models that did not include winter encounters is consistent with the hypothesis that Barry's inability to account for permanent emigration may have biased his estimate.

Life-history variation.—Clutch sizes do not differ substantially between Arctic and Yukon-Kuskokwim Delta breeders (Barry 1967, Flint and Sedinger 1992, Sedinger and Stickney 2000), except when delayed spring thaw causes reduced clutch sizes in the Arctic (Barry 1962, 1967). Reproduction is more variable in Arctic breeding areas than on the Yukon-Kuskokwim Delta (Barry 1967, Sedinger and Stickney 2000), associated with delayed availability of nest sites in some years (Barry 1962, 1967) and predation in some locations (Barry 1967). More variable reproduction in the Arctic, combined with similar fecundities, results in lower average recruitment for Arctic breeding brant than for brant from the Yukon-Kuskokwim Delta (Sedinger and Stickney 2000).

Life-history theory predicts that reduced adult survival favors earlier and increased investment in reproduction (Charlesworth 1994). In brant, reproductive investment was lower in the Arctic than on the Yukon-Kuskokwim Delta (Barry 1962, 1967; J. S. Sedinger unpubl. data), whereas adult survival was only slightly higher in the Arctic. Thus, our findings are only marginally consistent with theory that predicts that adult survival rate and reproductive investment should each evolve to compensate for reduced levels of the other. Thus, we interpret patterns in brant as consistent with the hypothesis that current large-scale variation in their life-history traits is primarily of environmental origin. It is possible that reduced reproductive investment by Arctic brant compensates for greater migration costs enabling

Arctic brant to survive at similar rates to those on the Yukon-Kuskokwim Delta.

The brant breeding populations at Tutakoke River and Kokechik Bay were relatively stable during this study (Anthony et al. 1995, J. S. Sedinger unpubl. data). Thus, our data suggest that lower reproductive productivity for Arctic brant must be offset during other life-history stages to sustain Arctic populations. Goslings in the Arctic grow more rapidly than those on the Yukon-Kuskokwim Delta, associated with greater food abundance in the Arctic (Sedinger et al. 2001). Recruitment is related to gosling growth in geese (Owen and Black 1989, Sedinger et al. 1995). Thus, reduced reproduction in the Arctic may be balanced by increased first-year survival, associated with lower densities of broods on foraging areas, relative to the Yukon-Kuskokwim Delta.

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