

sit time of *Manacus vitellinus* and *Pipra mentalis*. *Oecologia* 80:381–389.

WRANGHAM, R. W., N. L. CONKLIN, G. ETOT, J. OBUA, K. D. HUNT, M. D. HAUSER, AND A. P. CLARK. 1993. The value of figs to chimpanzees. *International Journal of Primatology* 14:243–256.

YOUNG, V. R. 1986. Nutritional balance studies: Indicators of human requirements or of adaptive mechanisms? *Journal of Nutrition* 116:700–703.

Received 29 December 1999, accepted 30 April 2001.

Associate Editor: C. Bosque

The Auk 118(4):1088–1095, 2001

Large-Scale Variation in Growth of Black Brant Goslings Related to Food Availability

JAMES S. SEDINGER,^{1,6} MARK P. HERZOG,¹ BRIAN T. PERSON,¹ MORGAN T. KIRK,^{1,4} TIM OBRITCKEWITCH,^{1,5} PHILIP P. MARTIN,² AND ALICE A. STICKNEY³

¹*Institute of Arctic Biology and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, Alaska 99775, USA;*

²*Northern Alaska Ecological Services, U.S. Fish and Wildlife Service, 101 12th Avenue, Fairbanks, Alaska 99701, USA; and*

³*ABR Inc., P.O. Box 80410, Fairbanks, Alaska 99709, USA*

ABSTRACT.—We examined variation in growth of Black Brant (*Branta bernicla nigricans*) goslings among two colonies on the Yukon-Kuskokwim Delta in southwestern Alaska and the Colville River Delta on Alaska's Arctic coast. We simultaneously measured abundance and quality of a key food plant, *Carex subspathacea*, and grazing pressure on that plant at the three colonies. Our goal was to measure variation in gosling growth in relation to variation in grazing pressure and food abundance because growth of goslings is directly linked to first-year survival, and consequently is the principal mechanism for density-dependent population regulation. Goslings grew substantially faster on the arctic coast and were nearly 30% larger than those on the Yukon-Kuskokwim Delta at four to five weeks old. Faster growth on the arctic coast was associated with 2× greater standing crop of *C. subspathacea* during brood rearing than on the Yukon-Kuskokwim Delta. Dispersal rates are high enough (Lindberg et al. 1998) to rule out local adaptation and genetic variation as explanations for observed variation in growth. Our results are consistent with lower survival of goslings from the Yukon-Kuskokwim Delta during their first fall migration and stronger density-dependent reg-

ulation on the Yukon-Kuskokwim Delta than on the Arctic coast.

The growth period of long-lived animals is a period when selection acts strongly (Rose 1991), likely because adults have evolved to maintain their survival in variable environments (Charlesworth 1994). Furthermore, growing young require diets of higher quality than those adequate for adult maintenance, because higher dietary concentrations of digestible energy and protein are required for tissue production (O'Connor 1984, Seding 1992, 1997). Consequently, growth rates vary considerably in response to environmental conditions (Cooch et al. 1991, Larson and Forslund 1991, Seding and Flint 1991).

Growing geese appear to be especially susceptible to nutrient limitation during growth, probably because they are small bodied herbivores and many plant foods contain inadequate concentrations of nutrients, especially protein, to support maximum rates of growth (Seding 1992, 1997). Goslings, therefore, are highly selective foragers (Seding and Raveling 1984), and preferred foods that will support rapid growth frequently may be depleted (Cargill and Jefferies 1984, Seding and Raveling 1986, Person et al. 1998). As a result, several studies have reported spatial (Aubin et al. 1993, Cooch et al. 1993, Leafloor et al. 1998) or temporal (Cooch et al. 1991, Seding and Flint 1991, Seding et al. 1998) variation in growth of goslings.

Growth is especially important in geese because size of goslings at the end of their first summer strongly influences their probability of surviving

⁴ Present address: 3291 East Acacia, Fresno, California 93726, USA.

⁵ Present address: Northern Alaska Ecological Services, U.S. Fish and Wildlife Service, 101 12th Avenue, Fairbanks, Alaska 99701, USA.

⁶ E-mail: fjjss@uaf.edu

their first year (Owen and Black 1989, Sedinger et al. 1995, van der Jeugd and Larsson 1998), adult body size (Cooch et al. 1991, Sedinger et al. 1995, Leafloor et al. 1998) and fecundity (Sedinger et al. 1995). Environmentally induced variation in adult body size has been observed in other populations of birds (James 1983). Relationship between growth and individual fitness indicates that variation in growth is likely an important mechanism of population regulation in response to changing density (Larsson et al. 1998, Sedinger et al. 1998).

Because of the importance of growth to both individual fitness and population dynamics, we studied growth of Black Brant (*Branta bernicla nigricans*) (hereafter "brant") breeding in three widely separated colonies: Tutakoke River and Kokechik Bay on the Yukon-Kuskokwim Delta, Alaska, and the Colville River Delta on Alaska's Arctic coast. We analyze variation in growth rates of goslings among those colonies and relate variation in growth to food quality and abundance and grazing intensity at the three colonies.

Methods.—We marked and recaptured brant on the Tutakoke River (61°N, 165°W) (1994–1996) and Kokechik Bay (62°N, 166°W) (1994–1995) colonies (Sedinger et al. 1993) and associated brood-rearing areas on the Yukon-Kuskokwim Delta. The colonies were within 1 km of the Bering Sea coast or the coast of Kokechik Bay. Vegetation in the colonies was dominated by graminoids, primarily *Carex ramenskii* meadows or a mixed sward dominated by *Elymus arvensis*, *C. ramenskii*, and forbs (Kincheloe and Stehn 1991). Brant from those colonies took their broods up to 40 km from the colony (Flint 1993). Broods fed primarily in two communities: (1) monospecific saltmarsh swards of either *C. subspathacea* or *Puccinellia phryganodes*, where they maintained grazing lawns (Jefferies 1989, Person et al. 1998), or (2) levee communities, which supported mixed stands of graminoids and forbs. Levees supported high densities of *Triglochin palustris* (arrowgrass), which was an important food for growing geese (Sedinger and Raveling 1984, Mulder et al. 1996). We report data from goslings recaptured on brood-rearing areas used by brant from the Tutakoke River colony. All of those areas were along the Tutakoke or Kashunuk Rivers. We captured brant goslings at a single brood-rearing area used by brant from the Kokechik Bay colony.

The Colville River colony (70°N, 149°W) occurred primarily on large islands in the Colville River Delta (Sedinger and Stickney 2000). Broods from that colony and smaller breeding aggregations inland from the coast (Sedinger and Stickney 2000) moved onto saltmarshes within the oilfields in the vicinity of Prudhoe Bay (Sedinger et al. 1998), which were dominated by *C. subspathacea* grazing lawns. We captured brant at eight brood-rearing areas used by brant from the Colville River colony. We refer to those brant as Colville River brant throughout.

To measure growth rates of goslings in each area, we visited nests when eggs were hatching and attached uniquely numbered fish-fingerling tags to the webs of goslings (Alliston 1975, Sedinger and Flint 1991). Goslings varied in their stage of hatching when web-tagged from pipped eggs to dry goslings. Because goslings require ~24 h to complete hatching and may remain in the nest for a day following hatch, our estimates of gosling age had a precision of about two days. We captured goslings at between 25 and 39 days old by driving broods and flightless (molted) brant into corral traps (Sedinger et al. 1997). The fledging period for brant is ~42 days (Bellrose 1980). We weighed each web-tagged gosling (± 5 g), and measured their diagonal tarsus and culmen (both ± 0.1 mm) (Dzubin and Cooch 1992).

Multiple observers measured standing crop and apparent offtake of vegetation by geese in swards of *C. subspathacea* in brood-rearing areas used by all three colonies in 1995 using methods described by Person et al. (1998). Briefly, those methods involved erecting three-sided enclosures (2 × 2 m) before hatching began. Each enclosure included a diagonal fence running from one corner of the open side to the opposite rear corner. That fence, thus, divided the enclosure into two triangular sections, one open to geese and the other enclosed. By switching the diagonal to the opposite front and rear corners, we created four grazing treatments: (1) always protected; (2) always grazed; (3) protected during the first interval and grazed during the second; and (4) grazed during the first interval and protected during the second. Those treatments enabled us to estimate various aspects of vegetation performance and effect of grazing geese on the vegetation. In this paper we report (1) standing crop of continuously grazed vegetation, (2) nitrogen concentration of grazed vegetation, and (3) offtake of plant biomass by geese.

We established 10 replicate enclosures at each of four distinct brood-rearing areas used by brant from the Tutakoke River colony (Person et al. 1998). We also established 10 replicate enclosures at each of two brood-rearing areas associated with each of the Kokechik Bay and Colville River colonies (Person et al. 1998, Sedinger et al. 1998). Enclosures were set up on 7 June at the Tutakoke river colony, 10 June at the Kokechik Bay colony, and 20 June at the Colville River colony. Peak of hatch was 16 June at the Tutakoke River in 1995 and 30 June in the Colville River Delta. We did not measure peak of hatch at Kokechik Bay, which typically occurs one to two days after that at Tutakoke River (J. S. Sedinger pers. obs.). Therefore, plots were set up about 9 to 10 days before peak of hatch.

Our sampling protocol varied slightly among colonies. Specifically, we removed one turve from each treatment at Tutakoke River and Kokechik Bay and three turves from each treatment at Colville river on each sampling occasion. We sampled plots at Colville

TABLE 1. Analysis of variation in growth of Black Brant goslings using the general linear models procedure of SAS. Mean Squares are based on Type III sums of squares. We examined variation among years, colonies, and sexes. We also included a term for gosling age (days) because goslings were growing over the capture period and not all goslings were captured at the same age. We used among-brood variation as an estimate of the error MS.

	df	Mass			Tarsus			Culmen		
		MS	F	P	MS	F	P	MS	F	P
Year	2	348710	66.9	<0.0001	4531	5.6	0.004	517	0.63	0.53
Colony	2	767395	147.2	<0.0001	22870	28.3	<0.0001	4522	5.5	0.0043
Sex	1	195871	37.6	<0.0001	59725	74.0	<0.0001	2584	3.2	0.076
Age	1	343974	66.0	<0.0001	7915	9.8	0.0019	5924	7.2	0.0075
Error	482	17039			1407			742		

River more intensively to gain a more precise estimate of grazing pressure because we anticipated lower grazing pressure there. We removed 10×10 cm turves from each plot when established during the brant incubation period. Turves were removed with a large knife and consisted of soil to a depth of ~ 2 cm and associated surface vegetation. At 21 days after establishment, immediately posthatch we removed 10×10 cm turves from both treatments, grazed and ungrazed, within each plot and switched the movable diagonal divider. We sampled the four treatments within each plot in the same way again following an additional 21 days, approximately mid-brood-rearing. Our samples, therefore, corresponded to the incubation period, immediately posthatch and mid-brood-rearing.

Turves were returned to camp where vegetation was clipped to the surface level, dead material was removed, and vegetation was washed in fresh H_2O . Samples were dried in the field at $60^\circ C$ and stored for shipment back to Fairbanks where samples were re-dried to constant mass (± 0.01 g). We estimated nitrogen concentration in plant samples using a LECO CNS 2000 autoanalyzer. We estimated apparent off-take by geese as difference between the final biomasses of vegetation that was ungrazed and grazed over the preceding interval.

We tested for variation in gosling metrics (mass, culmen, and tarsus) using the General Linear Models (PROC GLM) procedure of SAS (SAS Institute 1989). We used a model containing colony, year, sex, brood, age in days, and all two-way interactions to examine variation in size measures. The term for brood in our model accounted for potential dependence among brood mates in growth. We used among-brood variation to estimate error MS for hypothesis tests involving other variables. When interaction terms were not significant ($P > 0.05$) we removed them and reran the model. We used Type III sums of squares to test hypotheses from the final model and least significant differences for pairwise comparisons (Carmier and Swanson 1973).

Because our replicate enclosures were randomly placed within but not across brood-rearing areas, we

used a nested design (PROC GLM) to analyze vegetation data. Specifically, our model had colony and brood-rearing area nested within colony as factors in the model. Thus, brood-rearing areas were our replicates for examination of among-colony variation, which produced a conservative analysis because we sampled four, two, and two brood-rearing areas at Tutakoke River, Kokechik Bay, and Colville River, respectively. We calculated mean mass of vegetation for the three turves collected in each sample on the Colville River brood-rearing areas for statistical analyses so results were comparable to those from the Yukon-Kuskokwim Delta. We analyzed data for each sampling period (plot establishment, hatch, and mid brood-rearing) separately.

Results.—We captured 722, 34, and 98 web-tagged goslings on the Tutakoke River, Kokechik Bay, and Colville River colonies, respectively and those goslings represented 487 unique broods. Gosling mass varied significantly among colonies, years and sexes, and mass increased with age (Table 1), but no two-way interactions were significant. Goslings from the Colville River averaged from 211–286 g heavier than those from the Yukon-Kuskokwim Delta ($t > 9.7$; $P < 0.0001$, comparison of each Yukon-Kuskokwim Delta colony with Colville River)(Fig. 1). Similarly, tarsus length varied among colonies, years, and sexes, and increased significantly with age (Table 1). Tarsus length was significantly longer for goslings from the Colville River Delta than for those from the Yukon-Kuskokwim Delta ($t > 7.1$; $P < 0.0001$, comparison of each Yukon-Kuskokwim Delta colony with Colville River). Culmen length also varied significantly among colonies, but not years, with culmen lengths of goslings from the Colville River greater than those from either of the two Yukon-Kuskokwim Delta colonies (Table 1) ($t > 6.3$; $P < 0.0001$).

Standing crop of grazed *C. subspathacea* varied significantly among colonies during incubation, shortly after hatching and three weeks after hatch (Table 2). Standing crop was $> 2\times$ greater near the Colville River colony than at the two Yukon-Kuskokwim Delta colonies (Fig. 2). Nitrogen concentration was significantly lower on Colville River brood-rearing ar-

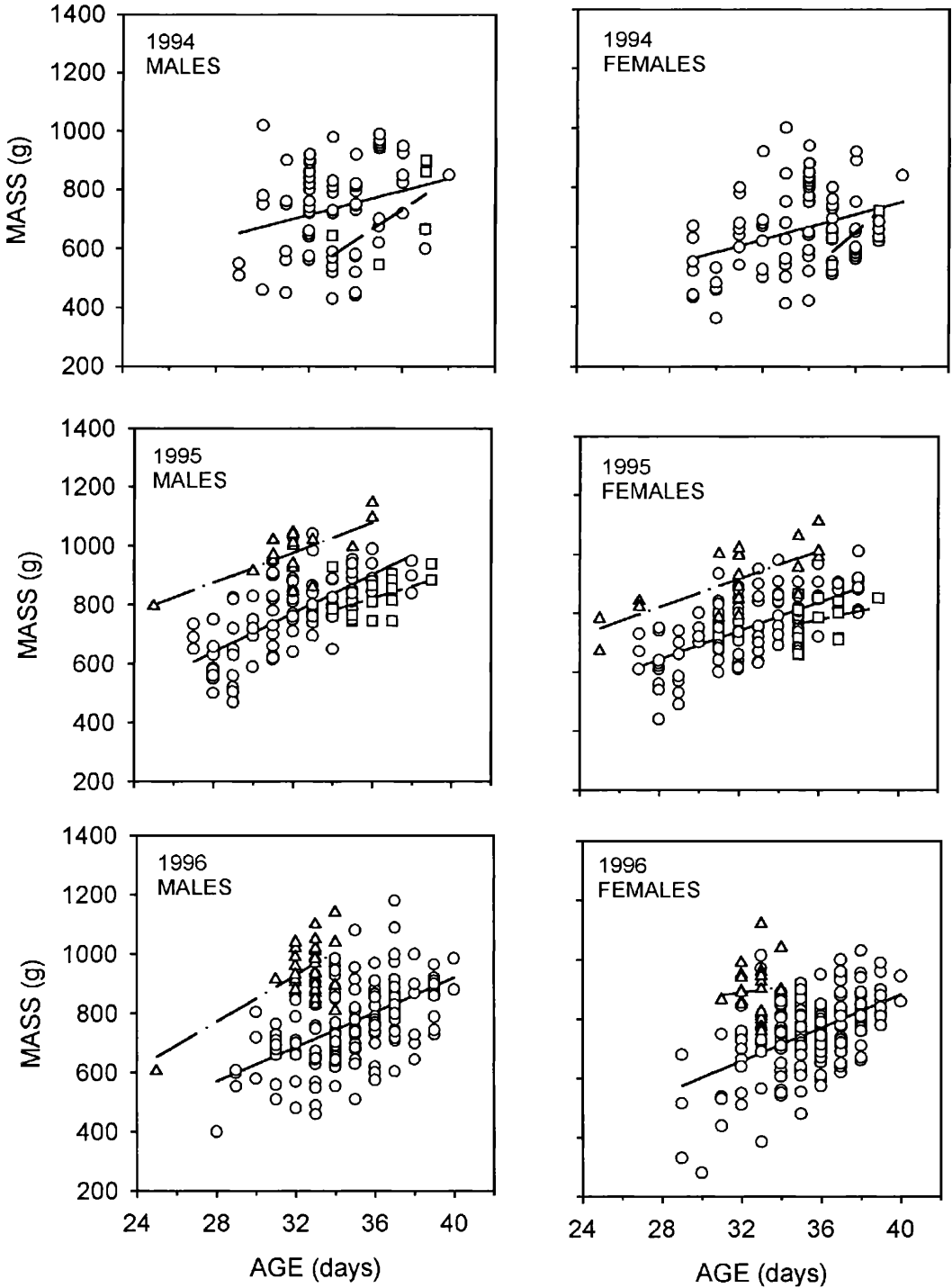


FIG. 1. Variation in size of known-age brant goslings among the Tutakoke River (circles), Kokechik Bay (squares) (both on the Yukon-Kuskokwim Delta), and Colville River (triangles) colonies in 1994, 1995, and 1996. Goslings from Tutakoke River were sampled in all three years, whereas those from Kokechik Bay were sampled in 1994 and 1995, and those from the Colville River were sampled in 1995 and 1996. Regression lines represent least-squares fits to the data for each colony-year combination.

TABLE 2. Results from general linear models analysis of variation in *Carex subspathacea* with respect to grazing and colony. Results are reported for the incubation, early post hatch, and mid-brood-rearing periods. Brood-rearing areas sampled at each colony were nested within colonies, therefore among-colony variations was tested using the colony and brood-rearing area mean squares.

Vegetation Parameter	Colony MS	Location MS	F	P ^a
Incubation ^b				
Biomass ^c	10321	712	14.5	0.0083
Nitrogen	18.7	0.84	22.3	0.0032
Post-hatch ^b				
Exclosed biomass ^c	6771	2715	2.49	0.18
Grazed biomass ^c	21277	1853	11.5	0.014
Offtake	5648	330	17.1	0.0058
Nitrogen	10.9	1.10	9.9	0.018
Mid brood-rearing ^b				
Exclosed biomass ^c	2717	5317	0.51	0.63
Grazed biomass ^c	18043	4861	3.71	0.103
Offtake ^d	2818	515	5.47	0.055
Offtake ^e	5113	2747	1.86	0.25
Nitrogen	12.1	2.53	4.77	0.069

^a All hypothesis tests had df = 2 and 6.

^b Vegetation characteristics and response to grazing were measured during incubation, immediately posthatch (21 days after incubation samples), and mid-brood-rearing (21 days after posthatch samples).

^c Biomass during incubation was measured when plots were established. Exclosed biomass had been protected from grazing since the establishment of plots during incubation, whereas grazed vegetation had been continuously grazed.

^d Offtake calculated as the difference between standing crop of *C. subspathacea* exclosed from early to mid-brood-rearing and *C. subspathacea* grazed continuously throughout.

^e Offtake calculated as the difference between *C. subspathacea* exclosed from incubation through mid-brood-rearing and *C. subspathacea* grazed from early to mid-brood-rearing.

eas than on brood-rearing areas on the Yukon-Kuskokwim Delta during incubation and early brood-rearing, and nearly so during mid brood-rearing (Table 2, Fig. 2). Offtake of above-ground biomass was significantly higher at both sites on the Yukon-Kuskokwim Delta than near the Colville River colony, despite reduced standing crop at the Yukon-Kuskokwim Delta sites (Table 2, Fig. 2).

Discussion.—Standing crop of *C. subspathacea* was 2–2.6× greater near the Colville colony as in brood-rearing areas used by brant on the Yukon-Kuskokwim Delta. That variation was principally a result of differences in grazing intensity among areas, as evidenced by convergence among areas in biomass protected from herbivory (Table 2). Importance of grazing as a cause of spatial variation in food abundance is further supported by substantially greater removal of vegetation by geese in areas with lowest standing crops.

Greater biomass of *C. subspathacea* in areas near the Colville colony was associated with lower concentrations of nitrogen than in *C. subspathacea* near colonies on the Yukon-Kuskokwim Delta. That finding is consistent with the generally negative correlation between standing crop and nitrogen concentration in Arctic graminoids (Sedinger and Raveling 1984, Gadallah and Jefferies 1995, Person et al. 1998). Total above-ground standing crop of nitrogen was substantially greater near the Colville colony than on the Yukon-Kuskokwim Delta because greater plant biomass more than compensated for reduced nitrogen

concentration on Colville River brood-rearing areas relative to those on the Yukon-Kuskokwim Delta. Brant, therefore, experienced greater availability of dietary protein near the Colville colony than near colonies on the Yukon-Kuskokwim Delta.

Similar tradeoffs between above-ground biomass and nitrogen concentration exist between preferred foods (e.g. *C. subspathacea*) and relatively unused plants on the Yukon-Kuskokwim Delta (Sedinger and Raveling 1984, 1986). Apparently, nitrogen concentrations in plant foods were adequate to enable increased plant biomass to support more rapid growth of brant near the Colville colony relative to the Yukon-Kuskokwim Delta.

Our results demonstrate large-scale spatial variation in growth of brant goslings, consistent with findings for other populations of geese (Aubin et al. 1993, Larsson and Forslund 1991). Large-scale variation in growth of brant is associated with variation in grazing intensity and, consequently, availability of food for goslings. Spatial variation in growth of Barnacle Goose goslings and Lesser Snow Goose goslings also has been related to variation in food abundance (Larsson and Forslund 1991, Cooch et al. 1993). Density dependent declines in gosling growth (Cooch et al. 1991, Sedinger et al. 1998) further support a direct linkage between food abundance and growth.

Variation in growth among populations is likely to produce variation in population dynamics because growth of goslings affects first-year survival (Owen

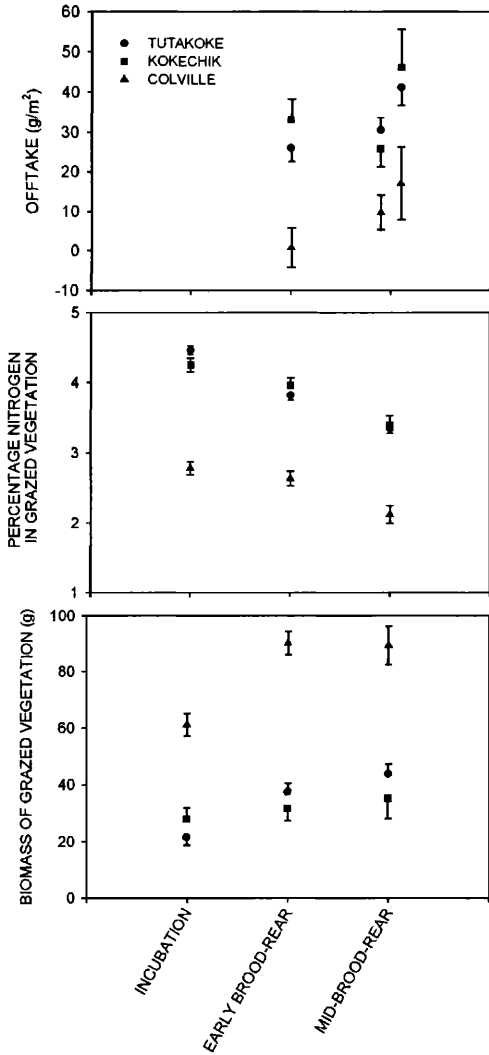


FIG. 2. Biomass, nitrogen concentration, and off-take by brant broods of grazed aboveground *C. subspathacea* (all \pm SE) on brood-rearing areas used by brant from the Tutakoke River, Kokechik Bay, and Colville River colonies during the late incubation, early brood-rearing and mid-brood-rearing periods.

and Black 1989, Sedinger et al. 1995, van der Jeugd and Larsson 1998). We have not directly examined variation in first-year survival in those populations but D. H. Ward (U.S. Geological Survey unpubl. data) has detected variation in survival during fall migration consistent with expectation, given observed variation in growth; goslings from the Colville colony survived that period at higher rates than those from the Yukon-Kuskokwim Delta. Modeling of those populations suggests that first-year survival has an

important effect on local population size (N. D. Chelgren unpubl. data)

It is unlikely that variation in growth we observed is primarily of genetic origin because gene flow between the Yukon-Kuskokwim Delta and the Colville colony is sufficient (Lindberg et al. 1998) to prevent local adaptation by brant in those two areas. Furthermore, ~80% of the variation in gosling growth on the Yukon-Kuskokwim Delta can be explained by gosling sex, age (days), brood density, brood-rearing area, and hatch date, suggesting little of that variation has an additive genetic basis (M. P. Herzog unpubl. data).

Variation in growth at large spatial scales suggests that brant do not respond numerically to food abundance at those scales. Female brant are strongly philopatric to their location of birth (Lindberg et al. 1998) as is true for other geese (Cooke et al. 1995). Lack of numerical response to large-scale variation in per capita food abundance suggests that expected increase in fitness from changing breeding location is insufficient to outweigh risks of dispersal. Individuals from the two Yukon-Kuskokwim Delta colonies potentially would have benefited from dispersing to the Colville River colony in terms of recruitment of their offspring. The Colville colony, however, is a substantial distance (>2,000 km) from the Yukon-Kuskokwim Delta colonies and nesting pairs in the Colville region represent <4% of nesting pairs in the brant population. Thus, it is difficult to envision how females from the Yukon-Kuskokwim Delta could compare habitat quality in their natal area with that on the arctic coast. Because some colonies do not appear to be limited by density dependent feedbacks, it is possible that the Pacific brant population is held below maximum potential size by its inability to distribute itself in an ideal-free manner.

Acknowledgements.—This research was supported by the Alaska Fish and Wildlife Research Center, National Biological Service (now Biological Resources Division, U.S. Geological Survey), Migratory Bird Management, Region 7, U.S. Fish and Wildlife Service; Northern Alaska Ecological Services, U.S. Fish and Wildlife Service; University of Alaska Foundation through the Angus Gavin Migratory Bird Research Fund; ARCO Alaska Inc.; BP Exploration Inc.; and the Office of Polar Programs, National Science Foundation (OPP 92 14970). Logistic support was provided by Yukon Delta National Wildlife Refuge. Permission to work at Kokechik Bay was provided by Sea Lion Corporation. D. Person, P. Freshman, S. Sindelar, M. Chambers, J. Schamber, W. O'Connell, S. Keane, B. Wenzel, J. Hill, S. van Laer, D. Johnson, R. Crain, D. Eichholz, M. Eichholz, R. Ritchie, J. Rose, D. Bohick, B. Boyle, L. Bright, D. Garibay, E. McIntosh, K. Marcouiller, C. Moiteret, B. Nelson, L. Quackenbush, E. Taylor, R. Taylor, P. Sousa, and T. Walker all assisted with field work.

LITERATURE CITED

- ALLISTON, W. G. 1975. Web-tagging ducklings in pipped eggs. *Journal of Wildlife Management* 45:625–628.
- AUBIN, A. E., A. DZUBIN, E. H. DUNN, AND C. D. MACINNES. 1993. Effects of summer feeding area on gosling growth in Snow Geese. *Ornis Scandinavica* 24:255–260.
- BELLROSE, F. C. 1980. Ducks, Geese and Swans of North America, 3rd ed. Stackpole Books, Harrisburg, Pennsylvania.
- CARGILL, S. M., AND R. L. JEFFERIES. 1984. The effects of grazing by Lesser Snow Geese on the vegetation of a sub-arctic salt marsh. *Journal of Applied Ecology* 21:669–686.
- CARMER, S. G., AND M. R. SWANSON. 1973. An evaluation of ten pairwise multiple comparisons procedures by Monte Carlo methods. *Journal of the American Statistical Association* 68:66–74.
- CHARLEWORTH, B. 1994. *Evolution in Age-structured Populations*, 2nd ed. Cambridge University Press, Cambridge, United Kingdom.
- COOCH, E. G., D. B. LANK, R. F. ROCKWELL, AND F. COOKE. 1991. Long-term decline in body size in a Snow Goose population: Evidence of environmental degradation. *Journal of Animal Ecology* 60:483–496.
- COOCH, E. G., R. L. JEFFERIES, R. F. ROCKWELL, AND F. COOKE. 1993. Environmental change and the cost of philopatry: An example in the Lesser Snow Goose. *Oecologia* 93:128–138.
- COOKE, F., R. F. ROCKWELL, AND D. B. LANK. 1995. *The Snow Geese of La Pérouse Bay*. Oxford University Press, Oxford.
- DZUBIN, A., AND E. G. COOCH. 1992. *Measurements of Geese: General Field Methods*. California Waterfowl Association, Sacramento, California.
- FLINT, P. L. 1993. Prefledging survival and reproductive strategies in Black Brant. Ph.D. dissertation, University of Alaska-Fairbanks, Fairbanks.
- GADALLAH, F. L., AND R. L. JEFFERIES. 1995. Comparison of the nutrient contents of the principal forage plants utilized by Lesser Snow Geese on summer breeding grounds. *Journal of Applied Ecology* 32:263–275.
- JAMES, F. C. 1983. Environmental component of morphological differentiation in birds. *Science* 221:184–186.
- JEFFERIES, R. L. 1989. Pattern and process in Arctic coastal vegetation in response to foraging by Lesser Snow Geese. Pages 281–300 in *Plant Form and Vegetation Structure. Adaptation, Plasticity and Relationship to Herbivory* (M. J. A. Werner, P. J. M. van der Art, H. J. Daring, and J. T. A. Verhoeven, Eds.). SPB Academic Publishing, The Hague, The Netherlands.
- KINCHELOE, K. L., AND R. A. STEHN. 1991. Vegetation patterns and environmental gradients in coastal meadows on the Yukon-Kuskokwim Delta, Alaska. *Canadian Journal of Botany* 69:1616–1627.
- LARSSON, K., H. P. VAN DER JEUGD, T. VAN DER VEEN, AND P. FORSLUND. 1998. Body size declines despite positive directional selection on heritable size traits in a Barnacle Goose population. *Evolution* 52:1169–1184.
- LARSSON, K., AND P. FORSLUND. 1991. Environmentally induced morphological variation in the Barnacle Goose. *Journal of Evolutionary Biology* 4:619–636.
- LEAFLOOR, J. C., D. ANKNEY, AND D. H. RUSCH. 1998. Environmental effects on the body size of Canada Geese. *Auk* 115:26–33.
- LINDBERG, M. S., J. S. SEDINGER, D. V. DERKSEN, AND R. F. ROCKWELL. 1998. Natal and breeding philopatry in a Black Brant, *Branta bernicla nigricans*, metapopulation. *Ecology* 79:1893–1904.
- MULDER, C. P. H., R. W. RUESS, AND J. S. SEDINGER. 1996. Effects of environmental manipulations on *Triglochin palustris*: Implications for the role of goose herbivory in controlling its distribution. *Journal of Ecology* 84:267–278.
- O'CONNOR, R. J. 1984. *The Growth and Development of Birds*. John Wiley and Sons, Chichester, United Kingdom.
- OWEN, M., AND J. M. BLACK. 1989. Factors affecting the survival of Barnacle Geese on migration from the breeding grounds. *Journal of Animal Ecology* 58:603–617.
- PERSON, B. T., C. A. BABCOCK, AND R. W. RUESS. 1998. Forage variation in brood-rearing areas used by Pacific Black Brant Geese on the Yukon-Kuskokwim Delta, Alaska. *Journal of Ecology* 86:243–259.
- ROSE, M. R. 1991. *Evolutionary Biology of Aging*. Oxford University Press, New York.
- SAS INSTITUTE. 1989. *SAS User's Guide*, version 6, 4th ed. SAS Institute Inc., Cary, North Carolina.
- SEDINGER, J. S. 1992. Ecology of prefledging waterfowl. Pages 109–127 in *Ecology and Management of Breeding Waterfowl* (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.) University of Minnesota Press, Minneapolis.
- SEDINGER, J. S. 1997. Adaptations to and consequences of an herbivorous diet in grouse and waterfowl. *Condor* 99:314–326.
- SEDINGER, J. S., AND P. L. FLINT. 1991. Growth rate is negatively correlated with hatch date in Black Brant. *Ecology* 72:496–502.
- SEDINGER, J. S., P. L. FLINT, AND M. S. LINDBERG. 1995. Environmental influence on life-history traits: Growth, survival, and fecundity in Black Brant (*Branta bernicla*). *Ecology* 76:2404–2414.
- SEDINGER, J. S., C. J. LENSINK, D. H. WARD, R. M. ANTHONY, M. L. WEGE, AND G. V. BYRD. 1993. Status

- and recent dynamics of the Black Brant breeding population. *Wildfowl* 44:49–59.
- SEDINGER, J. S., M. S. LINDBERG, M. W. EICHHOLZ, AND N. D. CHELGREN. 1997. Influence of hatch date versus maternal and genetic effects on growth of Black Brant goslings. *Auk* 114:129–132.
- SEDINGER, J. S., M. S. LINDBERG, B. T. PERSON, M. W. EICHHOLZ, M. P. HERZOG, AND P. L. FLINT. 1998. Density-dependent effects on growth, body size, and clutch size in Black Brant. *Auk* 115:613–620.
- SEDINGER, J. S., AND D. G. RAVELING. 1984. Dietary selectivity in relation to availability and quality of food for goslings of Cackling Geese. *Auk* 101:295–306.
- SEDINGER, J. S., AND D. G. RAVELING. 1986. Timing of nesting of Canada Geese in relation to the quality and availability of their food plants. *Journal of Animal Ecology* 55:1083–1102.
- SEDINGER, J. S., AND A. A. STICKNEY. 2000. Brant. Pages 221–232 in *The Natural History of an Arctic Oil Field* (J. C. Truett and S. R. Johnson, Eds.). Academic Press, London.
- VAN DER JEUGD, H., AND K. LARSSON. 1998. Pre-breeding survival of Barnacle Geese *Branta leucopsis* in relation to fledgling characteristics. *Journal of Animal Ecology* 67:953–96.

Received 24 January 2000, accepted 27 March 2001.

Associate Editor: C. Bosque

The Auk 118(4):1095–1101, 2001

Bounce and Double Trill Songs of Male and Female Western Screech-Owls: Characterization and Usefulness for Classification of Sex

BRIAN L. HERTING AND JAMES R. BELTHOFF¹

Department of Biology and Raptor Research Center, Boise State University, Boise, Idaho 83725, USA

ABSTRACT.—Both sexes of adult Western Screech-Owls (*Otus kennicottii*) sing in response to playback of conspecific song within their territories. Two primary songs are the bounce and double trill. Using sonographic analysis of tape-recorded vocalizations, our study quantified characteristics of bounce and double trill songs uttered by individuals within a population of Western Screech-Owls inhabiting riparian woodlands in southwestern Idaho. We asked if songs of males and females differed and, if so, how accurately could songs be classified by sex. On average, male bounce songs were ~30% lower in frequency than bounce songs of females, but song duration, note duration, number of notes per bout, and internote duration did not differ. Similarly, double trill songs of males were significantly lower in frequency than those of females, and double trill songs uttered by females had significantly greater internote distances in the leading portion. A discriminant model based on frequency at maximum amplitude of bounce songs correctly classified all males and females in our sample. Presence of sex-specific patterns of vocalizations in that species would allow owls to assess the sex of potential intruders and respond appropriately. Moreover, sonographic analy-

sis of Western Screech-Owl songs provides a means for noninvasive classification of sex.

Males of many species of birds utter songs in relation to territorial defense and attraction of mates, although female singing is now recognized as a regular feature of female behavior with distinct biological functions (Ritchison 1983, Arcese et al. 1988, Baptista et al. 1993), including territorial defense (Galeotti et al. 1997). Often, there are sex specific patterns of vocalizations, and assessing such differences in vocal behavior and characteristics of vocalizations between males and females has become a useful and noninvasive means for classification of sex (Carlson and Trost 1992, Farquhar 1993, Ballintijn and Ten Cate 1997).

Both sexes of the Western Screech-Owl (*Otus kennicottii*) utter songs in relation to conspecific intrusion of territories and in other situations (Marshall 1967), although the suite of vocalizations and contexts in which they are produced have not been well characterized (Johnsgard 1988). To help better understand vocal characteristics of that species, we elicited and tape-recorded songs from both male and female Western Screech-Owls from a population inhabiting riparian woodlands in southwestern Idaho. Our objectives were to (1) quantify characteristics of two primary song types, the bouncing ball (bounce) and double trill songs (Marshall 1967), and (2) compare vocal characteristics of adult males and

¹ Address correspondence to this author. E-mail: jbeltho@boisestate.edu