ENVIRONMENTAL EFFECTS ON BODY SIZE OF CANADA GEESE

JAMES O. LEAFLOOR,[1,4] C. DAVISON ANKNEY,[2] AND DONALD H. RUSCH[3]

[1]*Ministry of Natural Resources, P.O. Box 190, Moosonee, Ontario P0L 1Y0, Canada;*
[2]*Department of Zoology, University of Western Ontario, London, Ontario N6A 5B7, Canada; and*
[3]*Department of Wildlife Ecology, 226 Russell Laboratories, University of Wisconsin,*
Madison, Wisconsin 53706, USA

ABSTRACT.—Canada Geese (*Branta canadensis interior*) breeding on Akimiski Island, Northwest Territories, and those breeding on the Ontario mainland southwest of James Bay, share a common wintering range and are considered to be part of the same population, but differ significantly in size (e.g. skull length of mainland birds averages ca. 8% greater than that of Akimiski birds). We collected eggs in each area and raised the goslings in a common environment to determine environmental effects on differences in body-size traits observed in wild birds. We found no differences in asymptotic size or growth periods for skull, culmen, and tarsus length among birds from different origins ($P > 0.05$) but significant differences between sexes ($P < 0.05$). Estimated asymptotes for skull length of captives were intermediate to those of wild insular and mainland adults but closer to those of the larger mainland birds. Captive goslings from Akimiski Island had structural measurements that averaged 8 to 17% larger than those of wild goslings of the same age on the island. These results suggest a significant environmental effect on observed differences in body size between insular and mainland populations in southern James Bay. We suggest that lower per capita food availability explains the smaller size of Canada Geese on Akimiski Island. *Received 24 October 1996, accepted 29 May 1997.*

VARIATION IN BODY SIZE of birds can be influenced by genetics (Boag and van Noordwijk 1987) and by environmental factors (James 1983; Richner 1989; Cooch et al. 1991a, b; Larsson and Forslund 1991; Sedinger and Flint 1991; Rhymer 1992; Lindholm et al. 1994). Thus, differences in body size between populations of the same species do not necessarily indicate genetic differences (Boag and van Noordwijk 1987, Larsson and Forslund 1991). For example, body size of Canada Geese (*Branta canadensis*) generally decreases with increasing latitude (Aldrich 1946), presumably in response to shorter growing seasons in the north (Dunn and MacInnes 1987).

Skull lengths of Canada Geese from Akimiski Island are significantly smaller than those of conspecifics nesting on the mainland less than 200 km away, and they are smaller than expected based on the latitude at which the geese nest (Leafloor and Rusch 1997). Canada Geese that nest in these two areas share a common wintering range and are considered to be part of the Southern James Bay population

(Leafloor and Rusch 1997, Trost et al.1997). We equate differences in skull length with differences in overall body size because these variables are significantly correlated in *B. c. interior* (Moser and Rusch 1988), but we recognize that univariate measures usually are not the best indicators of body size (e.g. Willig et al. 1986, Alisauskas and Ankney 1987, Rising and Somers 1989, Freeman and Jackson 1990). Such differences in body size conceivably could result from local genetic differentiation in the absence of gene flow between the island and mainland populations (e.g. Mayr 1963, Shields and Wilson 1987, Van Wagner and Baker 1990), and/or from environmental factors differentially affecting gosling growth and subsequent adult size in each area (e.g. Ehrlich and Raven 1969; Cooch et al. 1991a, b; Larsson and Forslund 1991).

We measured growth of Canada Goose goslings hatched from eggs collected from Akimiski Island, Northwest Territories and near Kinoje Lake, Ontario (Fig. 1) and raised in a common environment to evaluate the effect of environment on differences in body size. We also compared measurements from a sample of known-aged goslings raised naturally on Akimiski Island with those that we raised in cap-

[4] Present address: Ministry of Natural Resources, P.O. Box 730, Cochrane, Ontario P0L 1C0, Canada. E-mail: leafloj2@epo.gov.on.ca
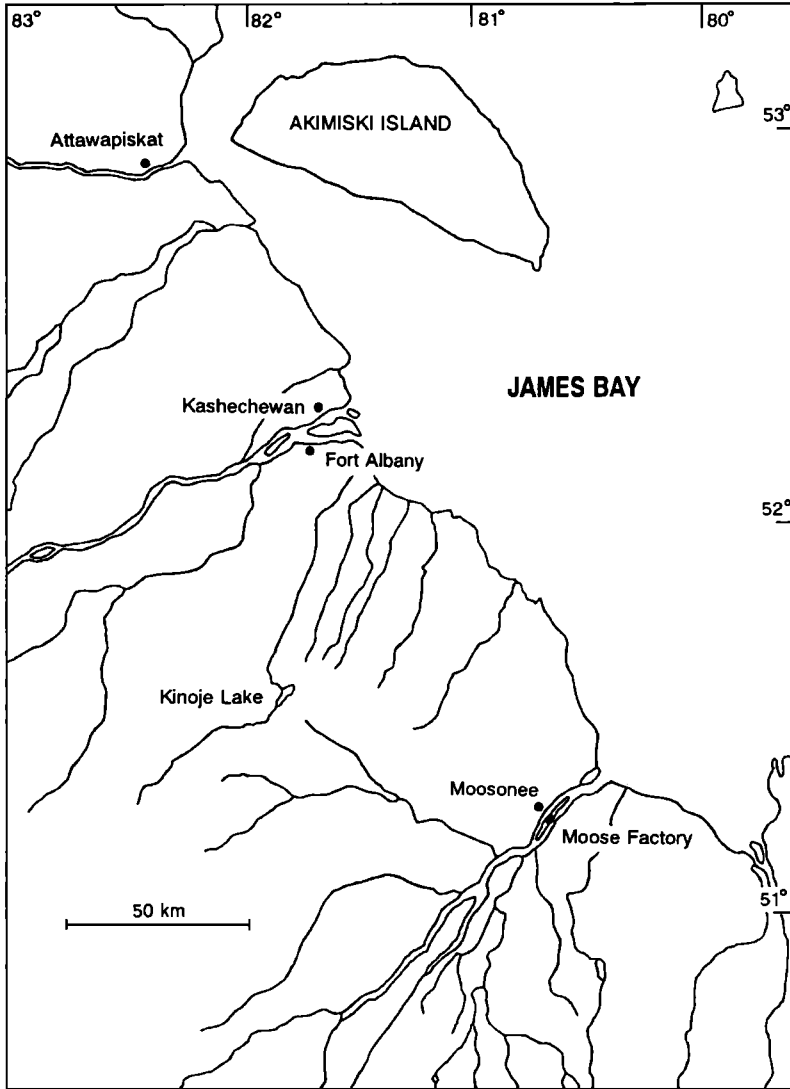
FIG. 1.   Egg collection sites near Kinoje Lake, Ontario and on Akimiski Island, Northwest Territories.

tivity. Hereafter, we use "island" to refer to Akimiski Island and "mainland" to refer to the area south of Attawapiskat, Ontario shown in Figure 1.

METHODS

We randomly collected one Canada Goose egg from 40 different nests on Akimiski Island (53°12'N, 81°30'W) and 40 eggs from 26 different nests (maximum two eggs per nest) near Kinoje Lake (51°30'N, 81°45'W) on 27 and 28 May 1993. We measured maximum length and width of all eggs with digital calipers (± 0.1 mm). Eggs were placed in portable in-

cubators and flown to Lake St. Clair National Wildlife Area, Ontario (42°30'N, 82°30'W) on 28 May, where they were kept in a larger incubator until goslings hatched between 2 and 14 June. We marked all goslings at hatching with individually numbered size 1 Monel web tags. When goslings were dry, we weighed them with a Pesola spring scale (± 1 g) and measured head length, culmen length, and tarsus length with digital calipers (± 0.1 mm; Dzubin and Cooch 1992). Thereafter, goslings were weighed and measured every three days until age 21, then every four days until 8 September, and finally every seven days until 13 October. We stopped measuring tarsus length when three consecutive measurements indi-

cated no further growth. Geese were killed to provide tissue for genetic analyses, and sex of each gosling was confirmed postmortem.

We kept goslings indoors under heat lamps for the first few days (until they learned to feed on commercial chow by themselves) and then moved them outdoors to portable wire cages (2 × 3 × 1 m). Goslings had unlimited access to commercial chow (Purina Duck Grower, 18% protein) and were allowed out of their cages to feed on a mowed lawn *ad libitum* during the day. Goslings also fed on grass that grew beneath their wire cages, and we moved the cages every few days to ensure a constant supply of growing grasses. As goslings approached fledging in mid-August, we transferred them to larger pens (ca. 7 × 3 × 2 m) that provided access to water from a creek but no access to vegetation. Thereafter, goslings were fed only Purina Duck Grower *ad libitum* until 13 October.

Visual inspection of individual growth curves suggested that an asymptotic curve would accurately represent growth trajectories of goslings. We used the nonlinear regression program in SYSTAT (Wilkinson 1989) to fit growth data to the following asymptotic regression equation:

$$X = a \cdot \{1 - \exp[b \ (age - c)]\}, \qquad (1)$$

where X is the structural measure of interest (e.g. skull, culmen, tarsus), *age* is the age of the gosling in days, and a, b, and c are parameters estimated by the model for asymptote, shape, and the x-intercept, respectively. We used starting values of $a = 120$, 50, and 90; $b = -0.03$, -0.03, and -0.05; and $c = -14$, -15, and -5 for skull, culmen, and tarsus curves, respectively. For each structure, we used estimates of b and c to calculate the time required to grow to 50% and 90% of asymptotic size for each gosling using the following general equation:

$$T_x = c + \ln(y) \ / \ -(b). \qquad (2)$$

The value (y) in the above equation can be changed to calculate the time to reach any percentage (x) of the asymptote by:

$$y = 1 \ / \ (100 - x)(0.01). \qquad (3)$$

For example, the time to reach 90% of the asymptote can be calculated as:

$$T_{90} = c + \ln(10) \ / \ -(b). \qquad (4)$$

Our sample of mainland geese contained 11 pairs of siblings that were not independent, and the overall sex ratio was heavily skewed toward males. To ensure that nonindependence did not affect our results, we made statistical comparisons in two ways. First, we conducted our analyses using all available data. Next, we repeated our analyses after randomly removing one member of three female-female sibling pairs, and seven females and one male from eight male-female sibling pairs. We removed mostly females to keep the sex ratio

as close to even as possible, while including only one gosling per nest in the analysis.

We compared maximum egg dimensions of island and mainland samples using t-tests. Structural size at hatching was compared using two-way analysis of covariance (ANCOVA) with sex and origin as main effects. We controlled for egg-size effects by using an index of egg volume (maximum length × [maximum breadth]²) as the covariate (PROC GLM, Type III SS; SAS Institute Inc. 1988). We compared univariate measures and derived an overall index of structural size from a principal components analysis of the correlation matrix of culmen length, skull length, tarsus length, and mass¹⁄₃ at hatching (i.e. PCI). Hatching date can affect growth rates in geese (Cooch et al. 1991a, Sedinger and Flint 1991, Lindholm et al. 1994), but we did not use hatching date as a covariate in our analyses because: (1) almost no overlap occurred in hatching dates of eggs from Akimiski Island and those from the mainland, and (2) hatching-date effects are thought to be related to variation in nutrient quality and availability of food plants (Sedinger and Flint 1991, Lindholm et al. 1994). The quality and availability of nutrients did not change during our study, and linear regressions of hatching date and structural asymptotes, and of hatching date and growth periods (i.e. T_{50} and T_{90}) were not significant for any combination of sex and origin (with Bonferroni adjustment of significance level for 36 regressions, $P > 0.0014$ in all cases). We examined effects of sex and origin on estimated asymptotes (a) and growth periods for each structural variable using two-way analysis of variance (ANOVA). Growth curves of body mass were not adequately described by the asymptotic regression model because geese continued to gain mass throughout the study. Therefore, we compared body mass of geese at hatching and at the time they were killed using two-way ANOVA with sex and origin as main effects.

We also obtained measurement data from a sample of goslings that were web-tagged at hatching on Akimiski Island, raised by their parents under natural conditions, and then recaptured in late July as part of another study (Leafloor et al. 1997). We calculated least-squares means of structural variables with age held constant at the mean for each sex using ANCOVA. We compared growth of captive goslings from Akimiski Island with that of wild goslings by plotting curves of predicted culmen length, skull length, and tarsus lengths from our nonlinear models and comparing them to least-squares means of wild goslings.

RESULTS

Unless stated otherwise, results of analyses did not change when we reduced the mainland sample size to one randomly selected individ-

TABLE 1. Body-size traits of newly hatched Canada Goose goslings collected on Akimiski Island, Northwest Territories and near Kinoje Lake, Ontario in 1993 (values are $\bar{x} \pm$ SE, uncorrected for egg volume). PCI is an overall index of structural size based on culmen length, skull length, tarsus length, and body mass$^{1/3}$.

Sex	n	Skull length (mm)	Culmen length (mm)	Tarsus length (mm)	PCI	Body mass (g)
			Akimiski Island			
Males	23	47.9 ± 0.2	16.3 ± 0.1	34.0 ± 0.3	−0.24 ± 0.2	106.8 ± 0.6
Females	11	47.3 ± 0.5	16.3 ± 0.2	34.1 ± 0.4	−0.49 ± 0.4	106.8 ± 2.4
			Kinoje Lake			
Males	13	48.5 ± 0.4	17.0 ± 0.3	33.8 ± 0.5	0.16 ± 0.2	102.7 ± 2.1
Females	22	48.5 ± 0.3	16.9 ± 0.2	34.2 ± 0.3	0.40 ± 0.3	106.4 ± 2.1
			Two-way ANCOVA factors[a]			
Egg volume		0.35	0.76	0.007	0.002	0.0001
Sex		0.002	0.08	0.02	0.0009	0.63
Origin		0.002	0.04	0.20	0.002	0.32

[a] *P*-values from two-way ANCOVA using all available data (see Methods). Egg volume × sex was significant for skull, tarsus, and PCI; egg volume × origin was significant for skull, culmen, and PCI; sex × origin and egg volume × sex × origin were not significant for any variable (Type III SS).

ual per nest. We found no difference in mean maximum length (84.9 vs. 85.6 mm) or width (57.6 vs. 57.3 mm) of eggs from Akimiski Island and Kinoje Lake, respectively (*t*-tests, *P* > 0.30 in both cases). Eleven of 80 eggs did not hatch (5 mainland, 6 Akimiski), and four goslings died before three weeks of age; three goslings that died after day 65 were included in our growth analyses. Mainland eggs hatched six days earlier, on average, than eggs from the island ($\bar{x}$ = 6 June vs. 12 June). Little overlap occurred in hatching dates; 32 of 35 mainland eggs hatched before the first egg from Akimiski Island hatched. Mass, tarsus length, and PCI (all at hatching) were significantly related to egg volume (Table 1). After accounting for egg-size variation, tarsus length, skull length, and PC1 differed between sexes at hatching, and culmen length approached significance (Table 1). Mainland goslings had larger culmens, longer skulls, and larger overall body size (i.e. PCI) at hatching after accounting for the effects of sex and egg volume; body mass of newly hatched goslings did not differ between areas or sexes after accounting for egg volume (Table 1).

The asymptotic regression model fit our growth data extremely well (r^2 = 0.99 to1.0 in all cases) and provided realistic estimates of asymptotic size. Predicted asymptotes for culmen length and skull length consistently were 2 to 2.5% larger than final measurements taken on 13 October (tarsus was not measured at this time, but growth probably was completed; see

below), suggesting that structural growth was not quite complete on that date. Asymptotic size and growth periods (T_{50} and T_{90}) did not differ between goslings from the two areas (*P* > 0.05) but did differ between sexes (two-way ANOVA, *P* < 0.05; Table 2). The time to grow to 90% of asymptotic size for skull, culmen, and tarsus did not differ between sexes when only one individual per nest was included in our mainland sample. Females were smaller than males in all structural characters and grew to 50% of asymptotic size about one day faster than did males. The structures that we measured required 1.4 to 4.2 days longer to reach 90% of asymptotic size in males than in females (Table 2). Tarsus reached 90% of asymptotic size when goslings were about one month old (average 31 to 33 days), but skull length and culmen length did not reach 90% of asymptotic size until goslings were nearly two months old (Table 2). Mean body mass on 13 October did not differ between areas (*F* = 0.31, *P* = 0.58) or between sexes (*F* = 3.11, *P* = 0.08). Mean body masses (SE in parentheses) on 13 October were: Akimiski Island males 3,965 g (125 g), females 3,687 g (208 g); Kinoje Lake males 3,993 g (77 g), females 3,811 g (101 g).

Captive goslings raised from eggs collected on Akimiski Island were larger than those raised naturally and captured on the island in late July (Fig. 2). The mean age of goslings captured on Akimiski Island was 42.5 days for males (*n* = 50) and 44.1 days for females (*n* = 43; we measured more males early and more

TABLE 2. Estimated asymptotes and growth statistics ($\bar{x} \pm$ SE) for body-size traits of captive Canada Geese raised from eggs collected on Akimiski Island, Northwest Territories and near Kinoje Lake, Ontario in 1993.[a]

| Character[b] | Akimiski Island | | Kinoje Lake | |
	Males ($n = 20$)	Females ($n = 10$)	Males ($n = 13$)	Females ($n = 22$)
Skull length (mm)	124.4 ± 1.0	119.1 ± 1.8	125.1 ± 1.2	119.2 ± 0.7
Culmen length (mm)	55.4 ± 0.8	52.3 ± 0.9	56.3 ± 0.9	53.7 ± 0.7
Tarsus length (mm)	99.4 ± 1.0	93.2 ± 1.3	97.9 ± 0.9	92.0 ± 0.7
T_{50} Skull (days)	7.4 ± 0.3	6.1 ± 0.4	7.1 ± 0.3	6.0 ± 0.1
T_{50} Culmen (days)	10.9 ± 0.3	9.5 ± 0.5	10.5 ± 0.3	9.7 ± 0.3
T_{50} Tarsus (days)	6.1 ± 0.2	5.1 ± 0.3	6.1 ± 0.3	5.2 ± 0.2
T_{90} Skull (days)	56.6 ± 1.2	53.0 ± 1.8	56.0 ± 1.1	53.5 ± 0.8
T_{90} Culmen (days)	58.1 ± 1.2	53.9 ± 2.2	57.9 ± 1.5	55.3 ± 1.6
T_{90} Tarsus (days)	33.0 ± 0.8	31.1 ± 1.1	33.0 ± 1.0	31.6 ± 0.6

[a] All variables differed ($P < 0.05$) between sexes, but none differed ($P > 0.05$) between areas (two-way ANOVA).
[b] T_{50} = no. days to grow to 50% of asymptote; T_{90} = no. days to grow to 90% of asymptote.

females later in July). Structural measurements ($\bar{x} \pm$ SE; age held constant at the mean for each sex) were: males, skull length 97.1 ± 0.35 mm, tarsus length 86.3 ± 0.43 mm, culmen length 40.1 ± 0.27 mm; females, skull length 93.6 ± 0.36 mm, tarsus length 80.8 ± 0.44 mm, culmen length 38.4 ± 0.27 mm. Among males at 42.5 days of age, mean skull length, tarsus length, and culmen length of captives exceeded those of wild birds by 8.2, 8.7, and 14.5%, respectively. Captive females at 44.1 days of age were, on average, 10.6, 10.4, and 17.4% larger than their wild counterparts in skull length, tarsus length, and culmen length, respectively (Fig. 2).

DISCUSSION

Structural size of Canada Geese from Akimiski Island and Kinoje Lake did not differ when goslings were raised in a common environment, even though mainland geese were structurally larger at hatching. Growth of goslings raised in the wild on Akimiski Island was slower than that of captives for all morphometric traits examined, and adult geese on the island were structurally smaller than the asymptotic sizes reached by captive goslings. On average, captive geese originating from Akimiski Island had asymptotic culmen measurements 5 to 8% larger, and tarsus measurements 11 to 14% larger, than those of wild-caught adults on the island (Moser and Rolley 1990, Merendino et al. 1994). We did not measure tarsus length and culmen length of wild mainland adults, but Leafloor and Rusch (1997:table 1) reported mean skull lengths of 120.8 mm and

112.0 mm for breeding females from the southern James Bay mainland and Akimiski Island, respectively. Asymptotic skull length of captive females from Akimiski Island (119.1 mm) exceeded that of wild adults by 6.3%, but skull length of captive mainland females (119.2 mm) was only 1.3% smaller than that of their wild counterparts. Thus, captive geese from Akimiski Island grew faster and larger than their wild counterparts, but mainland geese grew to about their "normal" size. This demonstrates that environmental factors can have a profound effect on growth and structural size and suggests that phenotypic differences between geese from these two geographic areas reflect environmental differences between the sites.

Environmental effects on gosling growth and adult size have been reported for several species of geese. In each case, reduced growth rates were attributed to limited quality and/or quantity of available forage plants (e.g. Sedinger and Raveling 1986; Cooch et al. 1991a, b; Sedinger and Flint 1991; Larsson and Forslund 1991, 1992; Aubin et al. 1993; Lindholm et al. 1994). We found no effect of hatching date on growth rates or final size of goslings when food was provided ad libitum, supporting the suggestion that effects of hatching date are mediated by seasonal changes in the quality or availability of forage (Sedinger and Raveling 1986, Sedinger and Flint 1991, Lindholm et al. 1994, Sedinger et al. 1997). Although other possibilities exist (e.g. lower ambient temperatures, feeding and/or antipredator tradeoffs, disturbance of feeding, etc.), we believe that reduced
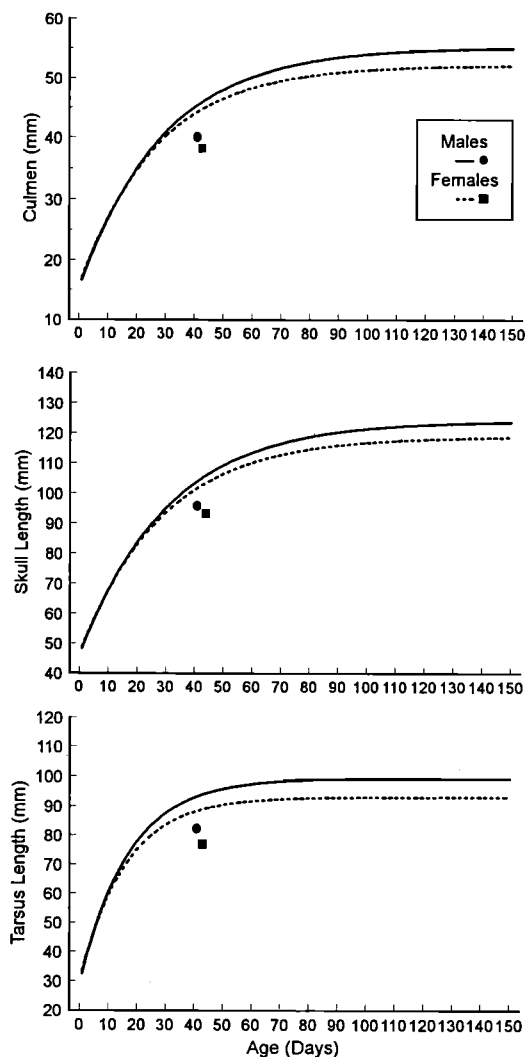
FIG. 2. Asymptotic growth curves for skull, culmen, and tarsus of captive Canada Goose goslings raised from eggs collected on Akimiski Island, Northwest Territories. Curves were derived using mean values of a, b, and c and equation 1 in text. Plotted values are least-squares means of structural measurements (age held constant), from wild-caught goslings on Akimiski Island.

body size of Canada Geese on Akimiski Island results from lower per capita food availability on the island compared with the mainland.

We have no direct measures of food availability, but overall nesting densities of Canada Geese on Akimiski Island averaged about seven times higher than those on the mainland during 1991 to 1995, and they may have been much higher before that (Leafloor et al. 1996). Canada Geese nest in very high densities in coastal areas of Akimiski Island in particular, and geese nesting in inland areas also bring their broods to the coast after hatching (Leafloor et al. 1997). Nesting densities along the north coast of Akimiski Island from 1993 to 1996 (after the island population had declined by ca. 65% from 1985 levels; Leafloor et al. 1996) averaged up to 300 times higher than those reported for the Kinoje Lake area (Raveling and Lumsden 1977, Leafloor et al. 1997). Coastal brood-rearing habitats also are used by large numbers of staging and nesting Lesser Snow Geese (*Chen c. caerulescens*), and by molting, nonbreeding Canada Geese. Recently, foraging activities of large numbers of geese have caused severe habitat degradation in brood-rearing areas along the north shore of Akimiski Island (R. L. Jefferies pers. comm.). Similar degradation led to a 4% decline in mean culmen length of adult female Lesser Snow Geese at La Perouse Bay during 1969 to 1986 (Cooch et al. 1991b). However, culmen length of adult Canada Geese shot by Cree hunters on Akimiski Island in late April 1977 (males: $\bar{x}$ = 53.5 ± SE of 0.26 mm, n = 88; females, $\bar{x}$ = 49.3 ± 0.37 mm, n = 58; H. G. Lumsden unpubl. data) did not differ (t-tests, P > 0.05) from those measured in July 1991 by Merendino et al. (1994). Thus, we have no evidence of a decline in adult body-size traits for Canada Geese over at least the past two decades on Akimiski Island, suggesting the existence of long-standing differences in per capita food availability between the island and mainland.

The relatively small structural size of Canada Geese that nest on Akimiski Island is contrary to the overall pattern of decreasing size with increasing latitude in Canada Geese (Leafloor and Rusch 1997). In fact, Canada Geese from Akimiski Island are the same size as those nesting at Cape Churchill, Manitoba, 600 km north of the island (Moser and Rolley 1990). MacInnes (1966) suggested that smaller Canada Geese should occur in the most extreme environments, and Dunn and MacInnes (1987) suggested that small body size might be a necessity for raising goslings in the short nesting seasons of the far north. Persistent ice cover on James Bay causes Akimiski Island to be colder than adjacent mainland areas (Martini and Glooschenko 1984), and nesting occurs later as

a result (i.e. the growing season is shortened). Canada Geese at Cape Churchill, nest about two weeks later than geese on Akimiski Island (Leafloor et al. 1997) and are similarly affected by persistent ice cover on Hudson Bay, but they grow to be the same size as Akimiski Island birds. Thus, despite a longer growing season, Canada Geese on Akimiski Island are the same size as geese nesting much farther north. We suggest that lower per capita food availability, and perhaps a more severe climate, contribute to reduced growth rates and smaller adult body size of Canada Geese on Akimiski Island compared with the surrounding mainland. Captive mainland geese, on the other hand, grew to be the same size as their wild counterparts, suggesting that growth is maximized when environmental conditions in the wild are favorable.

LITERATURE CITED

ALDRICH, J. W. 1946. Speciation in the white-cheeked geese. Wilson Bulletin 58:94–103.

ALISAUSKAS, R. T., AND C. D. ANKNEY. 1987. Age-related variation in the nutrient reserves of breeding American Coots (*Fulica americana*). Canadian Journal of Zoology 65:2417–2420.

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.

BOAG, P. T., AND A. J. VAN NOORDWIJK. 1987. Quantitative genetics. Pages 45–78 *in* Avian genetics: A population and ecological approach (F. Cooke

and P. A. Buckley, Eds.). Academic Press, London.

COOCH, E. G., D. B. LANK, A. DZUBIN, R. F. ROCKWELL, AND F. COOKE. 1991a. Body size variation in Lesser Snow Geese: Environmental plasticity in gosling growth rates. Ecology 72:503–512.

COOCH, E. G., D. B. LANK, R. F. ROCKWELL, AND F. COOKE. 1991b. Long-term decline in body size in a Snow Goose population: Evidence of environmental degradation? Journal of Animal Ecology 60:483–496.

DUNN, E.H., AND C.D. MacINNES. 1987. Geographic variation in clutch size and body size of Canada Geese. Journal of Field Ornithology 58:355–371.

DZUBIN, A., AND E. G. COOCH. 1992. Measurements of geese: General field methods. California Waterfowl Association, Sacramento, California.

EHRLICH, P. R., AND P. H. RAVEN. 1969. Differentiation of populations. Science 165:1228–1232.

FREEMAN, S., AND W. M. JACKSON. 1990. Univariate metrics are not adequate to measure avian body size. Auk 107:69–74.

JAMES, F.C. 1983. Environmental component of morphological differentiation in birds. Science 221:184–186.

LARSSON, K., AND P. FORSLUND. 1991. Environmentally induced morphological variation in the Barnacle Goose, *Branta leucopsis*. Journal of Evolutionary Biology 4:619–636.

LARSSON, K, AND P. FORSLUND. 1992. Genetic and social inheritance of body and egg size in the Barnacle Goose (*Branta leucopsis*). Evolution 46:235–244.

LEAFLOOR, J. O., K. F. ABRAHAM, D. H. RUSCH, R. K. ROSS, AND M. R. J. HILL. 1996. Status of the Southern James Bay Population of Canada Geese. Pages 103–108 *in* Proceedings of the 7th International Waterfowl Symposium (J. T. Ratti, Ed.). Ducks Unlimited, Memphis, Tennessee.

LEAFLOOR, J. O., M. R. J. HILL, D. H. RUSCH, K. F. ABRAHAM, AND R. K. ROSS. 1997. Nesting ecology and gosling survival of Canada Geese on Akimiski Island, Northwest Territories. Canadian Wildlife Service Occasional Paper in press.

LEAFLOOR, J. O., AND D. H. RUSCH. 1997. Clinal size variation in Canada Geese: Implications for the use of morphometric discrimination techniques. Journal of Wildlife Management 61:183–190.

LINDHOLM, A., G. GAUTHIER, AND A. DESROCHERS. 1994. Effects of hatch date and food supply on gosling growth in arctic-nesting Greater Snow Geese. Condor 96:898–908.

MacINNES, C. D. 1966. Population behavior of eastern arctic Canada Geese. Journal of Wildlife Management 30:536–553.

MARTINI, I. P., AND W. A. GLOOSCHENKO. 1984. Emergent coasts of Akimiski Island, James Bay, Northwestern Territories, Canada: Geology,

geomorphology, and vegetation. Sedimentary Geology 37:229–250.

MAYR, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, Massachusetts.

MERENDINO, M. T., C. D. ANKNEY, D. G. DENNIS, AND J. O. LEAFLOOR. 1994. Morphometric discrimination of Giant and Akimiski Island Canada Geese. Wildlife Society Bulletin 22:14–19.

MOSER, T. J., AND R. E. ROLLEY. 1990. Discrimination of Giant and Interior Canada Geese of the Mississippi Flyway. Wildlife Society Bulletin 18: 381–388.

MOSER, T. J., AND D. H. RUSCH. 1988. Indices of structural size and condition of Canada Geese. Journal of Wildlife Management 52:202–208.

RAVELING, D. G., AND H. G. LUMSDEN. 1977. Nesting ecology of Canada Geese in the Hudson Bay Lowlands of Ontario: Evolution and population regulation. Ontario Ministry of Natural Resources, Fish and Wildlife Research Report No. 98.

RHYMER, J. M. 1992. An experimental study of geographic variation in avian growth and development. Journal of Evolutionary Biology 5:289–306.

RICHNER, H. 1989. Habitat-specific growth and fitness in Carrion Crows (*Corvus corone corone*). Journal of Animal Ecology 58:427–440.

RISING, J. D., AND K. M. SOMERS. 1989. The measurement of overall body size in birds. Auk 106: 666–674.

SAS INSTITUTE, INC. 1988. SAS/STAT user's guide, release 6.03. SAS Institute, Inc., Cary, North Carolina.

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., M. S. LINDBERG, M. EICHOLZ, AND N. CHELGREN. 1997. Influence of hatch date versus maternal and genetic effects on growth of Black Brant goslings. Auk 114:129–132.

SEDINGER, J. S., AND D. G. RAVELING. 1986. Timing of nesting by Cackling Canada Geese in relation to the quality and availability of their food plants. Journal of Animal Ecology 55:1083–1102.

SHIELDS, G. F., AND A. C. WILSON. 1987. Subspecies of the Canada Goose (*Branta canadensis*) have distinct mitochondrial DNA's. Evolution 41:662–666.

TROST, R. E., K. F. ABRAHAM, J. C. DAVIES, K. E. BEDNARIK, AND H. G. LUMSDEN. 1997. The distribution of leg-band recoveries from Canada Geese banded in the southern James Bay region of Canada. In press *in* Proceedings of the 1991 International Canada Goose Symposium (D. H. Rusch, D. D. Humburg, M. D. Samuel, and B. D. Sullivan, Eds.).

VAN WAGNER, C. E., AND A. J. BAKER. 1990. Association between mitochondrial DNA and morphological evolution in Canada Geese. Journal of Molecular Evolution 31:373–382.

WILKINSON, L. 1989. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, Illinois.

WILLIG, M. R., R. D. OWEN, AND R. L. COLBERT. 1986. Assessment of morphometric variation in natural populations: The inadequacy of the univariate approach. Systematic Zoology 35:195–203.

Associate Editor: I. J. Ball