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SEASONAL VARIATION OF FEMUR AND TIBIOTARSUS CONSTITUENTS IN CANADA GEESE

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The time of reproduction and number of eggs produced by wild birds are usually narrowly limited which results in optimum productivity by a population, especially in the seasonally variable temperate and high latitudes. Canada Geese (*Branta canadensis*) are adapted to nesting as early as the spring thaw and are at their heaviest upon arrival at their breeding grounds (Hanson 1962). Energy stores necessary for egg production are accumulated during spring migration. During the course of an investigation of seasonal changes in body weight and lipid content in relation to reproductive success of Cackling Canada Geese (*B. c. minima*), femurs and tibiotarsi of some birds were obtained. The objective of this study is to document changes in medullary bone, marrow, and calcium in the long bones of a wild species which fluctuates widely in body weight and lipid stores, nests within a brief period, and depends upon endogenous reserves for egg production. Specifically, we wished to evaluate changes in these constituents in relation to their potential as factors limiting clutch size.

Studies of skeletal metabolism in birds, especially the availability of calcium for the eggshell, have focused upon the domestic chicken (see Taylor et al. 1971). Data for wild species are sparse (Simkiss 1967). Calcium deficiency during the egg-laying process in domestic fowl results in an increased dependency upon the skeleton for minerals (Taylor and Moore 1954, 1956, Urist 1959, Taylor et al. 1962). The most labile source of minerals in the skeleton appears to be medullary bone which can be reformed at the expense of cortical bone. Thus, shafts of cortical bones become thinner until no more mineral can be supplied, at which time eggshells become thinner.

Cackling Geese spend the winter (November–March) in the Central Valley of California and arrive on their breeding grounds on the delta of the Kuskokwim and Yukon rivers, Alaska, in mid-May (Nelson and Hansen 1959, Mickelson 1975). In 1974, the major arrival of Cackling Geese was on 13 May; 89% of all nests were begun between 21 May and 1 June; and the average clutch size was 4.8 (N = 66) (Raveling, unpubl. data). Eggs are laid at an average rate of one per day; incubation begins after the last egg of a clutch is laid and proceeds for 26 days (Mickelson 1975).

Fifteen adult female geese were collected for this study. Five of the birds were collected in December 1973 at the Sacramento National Wildlife Refuge near Willows, California (39°30′N, 122°10′W). The rest of the birds were collected during the breeding season (eight in May and two in June) of 1974 on the Clarence Rhode National Wildlife Range, Alaska (61°23′N, 165°27′W). Body weights were recorded at the time of collection. The right femur and tibiotarsus of each bird were removed and fleshed. Fresh weight of bones was recorded. Bones were then air-dried and frozen at –20°C until further laboratory analyses were conducted.

Individual bones were sawed into two approximately equal portions at their midpoints. Both distal and proximal halves of the femur and tibiotarsus were examined for medullary bone and marrow at 10× magnification under a dissecting microscope.

For chemical analysis of bones, the distal half of the femur and the proximal half of the tibiotarsus were used. These portions of the bones were oven-dried for 48 h at 65°C under 25 PSI (pounds per square inch) and oven-dry weights were recorded. Lipids were extracted from the bones with ethyl ether using a soxhlet refluxing apparatus for 24 h and oven-dry, fat-free bone weights were recorded. Lipid content was determined as the difference between pre- and post-extraction dry weights. The same bones were placed individually in separate crucibles and ashed at 600°C for 12 h and then cooled in a desiccator until constant weight was attained. The ash was dissolved by adding 10 ml of 12 N HCl to each crucible. Each solution was made up to a 250 ml total giving a final solution of 1.08 N HCl to which was added 1% lanthanum oxide in order to minimize interference with calcium determination by atomic absorption spectrophotometry (Perkin-Elmer Model 303).

Small sample sizes prohibit statistical analyses, but certain trends were pronounced. Samples from the breeding ground (May–June) were divided to examine bone content in relation to the dramatic changes in body weight associated with events during the reproductive cycle (Table 1). Four adult females were collected in May before they had laid eggs. Two light females exhibited body weights 15% above winter levels, no medullary bone in femurs or tibiotarsi, and largest ovarian follicle sizes of 8.2 and 9.2 mm. In contrast, the two heaviest females exhibited a 52% greater body weight than geese in winter, medullary bone development, and a 22.5 mm ovarian follicle in one bird and a partially calcified egg in the shell gland of the other bird. Average diameter of egg yolks was 39 mm (N = 19, T. Roudybush, pers. comm.). Cackling Geese have little food available, and do little feeding, when they arrive on the breeding grounds. Hence, we think that the two light females with relatively small ovarian follicles were not going to lay eggs that season. Data from these birds were therefore separated from those of the two heavy, pre-laying females (Table 1).

Only the bones of the two heaviest geese in the entire sample contained medullary bone. A 1910-g bird was estimated to be about six days away from oviposition based on known rates of follicle development (12–13 days, Grau 1976) in relation to mature follicle size. Her femur contained only a thin layer of medullary bone and none was present in the tibiotarsus. There was extensive medullary ossification in the femur and partial ossification in the tibiotarsus of a 1890-g female who had her first egg in the oviduct. The anastomosed trabeculae were hard and brittle and the cavities were filled with a dark red-grey marrow. It appears that medullary bone in geese is extensively deposited during the last half of rapid ova development (6–7 days) and is depleted after the clutch is laid.

The dry, fat-free weights of the femur and tibiotarsus of females that were going to lay eggs were 79 and 61% heavier, respectively, than the mean

TABLE 1. Body weights and characteristics of femurs and tibiotarsi of adult female Cackling Canada Geese.

		Time of year and stage of reproductive cycle					
Item measured	Bone	December (N = 5)	May—not going to lay eggs (N = 2)[a]	May—going to lay eggs (N = 2)[a]	May—first or second day of incubation (N = 4)[b]	June—after 13 days of incubation (N = 1)	June—after 26 days of incubation (N = 1)
Body weight (g)		1250[c]	1435	1900	1450	1200	1020
		1180–1370[d]	1350–1520	1890–1910	1280–1550		
Dry fat-free bone weight (g)	Femur	1.46	1.49	2.62	1.91	1.35	1.36
		1.41–1.51	1.36–1.62	2.22–3.01	1.70–2.14		
	Tibiotarsus	2.37	3.42	3.82	2.95	2.28	3.50
		2.34–2.41			2.31–3.35		
Percent of fat-dry bone	Femur	37	6	2	trace	36	19
		23–64	trace–12	trace–4	0–trace		
	Tibiotarsus	33	17	2	4	35	21
		26–40			3–7		
Ash weight (g)	Femur	0.78	0.75	1.52	1.05	0.57	0.66
		0.70–0.92	0.62–0.87	1.07–1.96	0.81–1.28		
	Tibiotarsus	1.29	1.76	2.48	1.61	1.32	1.01
		1.25–1.32			1.34–1.97		
Percent calcium of dry fat-free bone	Femur	31	30	32	29	28	31
		31–32	29–30	31–32	26–31		
	Tibiotarsus	28	25	30	28	29	27
		28–28			25–31		
Percent calcium of bone ash	Femur	60	50	58	52	66	63
		51–64	44–55	49–66	51–53		
	Tibiotarsus	52	49	46	51	50	50
		51–52			48–54		

[a] For body weight and femur; N = 1 for tibiotarsus.
[b] For body weight and tibiotarsus; N = 3 for femur.
[c] Mean.
[d] Range.

weight of the bones from females collected during winter (Table 1). These changes indicate the formation of medullary bone; however, these bones were also 31 and 24% heavier, respectively, in females collected at the onset of incubation (when medullary bone was absent) than those from birds collected during winter. The femur of the single female collected at the end of incubation was slightly (7%) lighter than the mean weight of the femur from birds collected during winter, but the tibiotarsus was heavier.

It appears that marrow fat may enter the metabolic pool which is important for yolk development. Fat was depleted from the femur and tibiotarsus prior to egg laying (Table 1), at a time when the geese were at their heaviest and contained abundant deposits of subcutaneous and abdominal lipid. Marrow fat was also markedly reduced in the two pre-laying females that did not exhibit medullary bone development. By mid-incubation (and probably much sooner), the marrow level had risen again to winter levels, although body weight had decreased 36%. Females incubate nearly continuously and are emaciated by the end of incubation. Lipid content of the femur and tibiotarsus of the goose collected at the end of incubation was markedly lower than the lipid content of those bones from birds collected during winter. This bird was very light and contained only 1.96% lipid in her entire carcass. This emaciated condition is typical of females at the time of hatching of their eggs (Raveling, unpubl. data). Thus, except for the period during egg formation when body weights are high, depleted bone marrow indicates starvation conditions as it does for mammals (cf. Cheatum 1949).

The individual with the highest ash component (Table 1) was, expectedly, that female which contained extensive medullary bone. Ash weights of femur and tibiotarsus were 35 and 25%, respectively, greater in geese at the onset of incubation as compared to geese collected during the winter nonreproductive period. By the end of incubation, however, ash weights of the femur and tibiotarsus were, respectively, 15 and 22% below winter levels.

Percent calcium of fat-extracted bone was very stable (Table 1), indicating no calcium deficiency throughout nesting. In incubating geese, lower femur ash contents contained a higher calcium component

(Table 1), thus resulting in a stable proportion of calcium in the bone. Depletion of cortical bone during egg laying was not evident. The geese in this study did not appear to suffer from a calcium deficiency. Medullary bone seemed to be sufficient to provide the calcium for the average clutch, because the femur and tibiotarsus bone and ash weights, and their calcium contents were greater at the end of egg laying than during the non-reproductive season. However, the contribution of minerals from other bones, especially ribs, sternum, vertebrae and pelvic girdle should be examined for a definitive conclusion (Taylor and Moore 1954).

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TONIC IMMOBILITY RESPONSES OF HERRING GULL CHICKS

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Following physical restraint, many birds exhibit a state of pronounced immobility (Armstrong 1947). Such tonic immobility (TI), which may be accompanied by eye closure, leg extension and muscle tremors, has often been referred to as "death feigning." Animals in this state are sensitive to external stimulation. Immobility of captured prey can inhibit the attack behavior of a predator and may allow for escape, if the predator is distracted (Sargeant and Eberhardt 1975, Gallup 1977). With very few exceptions (e.g. Sargeant and Eberhardt 1975) almost all studies of tonic immobility in birds have been conducted in the laboratory with domesticated species.

During June and July 1976, 54 Herring Gull chicks (*Larus argentatus*) and eight Great Black-backed Gull chicks (*L. marinus*) on Little Bell Island, Con-

TABLE 1. Tonic immobility reactivity of Herring Gull chicks in relation to weight.

Group	Weight range (g)	N	TI duration (s) ($\bar{x} \pm$ S.E. s)	No response (< 5 s)	Maximum response (600 s)
1	50–190	6	12.3 ± 9.6	5 (83%)	0
2	205–340	7	70.4 ± 37.7	2 (29%)	0
1+2	50–340	13	43.6 ± 21.7	7 (54%)	0
3	420–580	11	293.2 ± 69.3	1 (9%)	3 (27%)
4	600–675	8	392.3 ± 82.6	0	4 (50%)
3+4	420–675	19	387.5 ± 51.7	1 (5%)	7 (37%)
5	710–790	13	457.8 ± 63.8	0	9 (69%)
6	830–1175	9	317.7 ± 93.0	0	4 (44%)
5+6	710–1175	22	400.5 ± 54.3	0	13 (59%)
L. marinus	490–1200	8	410.0 ± 87.5	0	4 (50%)