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# GEOGRAPHIC VARIATION IN CLUTCH SIZE AND BODY SIZE OF CANADA GEESE

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Abstract.—Geographic variation in clutch size of Canada Geese (*Branta canadensis*) was analyzed with respect to female body weight, latitude, longitude, altitude, and weather. Weather variables were long-term means of monthly temperatures, precipitation, and actual evapo-transpiration of both breeding and wintering sites, combined into 8 principal components. Both body size and clutch size decreased with latitude. There was little evidence that clutch size varied independently of body weight, except that clutch size decreased slightly with increasing altitude. Weather variables accounted for as much variation in clutch and body size as did latitude, longitude, and altitude. Body size decreased with increasing latitude to a greater extent than clutch size, such that the weight of an entire clutch in proportion to female weight actually increased as body size decreased.

## VARIACIÓN GEOGRÁFICA EN EL TAMAÑO CORPORAL Y DE LA CAMADA DE *BRANTA CANADENSIS*

Sinopsis.—La variacioń geográfica en el tamaño de la camada de Ganso de Canada (*Branta canadensis*) fue analizada con respecto al peso de hembras, latitud, longitud, altitud y condiciones climatológicas. Las variables del último, consistieron de promedios mensuales de temperatura, precipitación, y evapotranspiración tanto en áreas de anidamiento como en lugares en donde las aves pasan el invierno, combinados en 8 componentes principales. El tamaño del cuerpo de las aves y de la camada disminuyó con la latitud. Fue poca la evidencia que indicara que el tamaño de la camada variara independientemente del peso, a excepción de que a mayor altitud hubo una ligera disminución en el tamaño de la camada. Las variables climatológicas dieron lugar a variación en tamaño del cuerpo y de la camada al igual que la latitud, longitud y la altitud. El tamaño del cuerpo disminuuyó en mayor grado que la camada a latitudes mayores, de tal forma que el peso de las camadas, en proporcion al peso de las hembras, fue en aumento, mientras que el tamaño de estas disminuía.

Geographic variation in clutch size is common in birds, with the most frequent trend being an increase in clutch size with latitude (Klomp 1970). This is often accompanied by a small increase in body size of northern nesters, in accordance with Bergmann's Rule. Geese do not fit the usual geographic trends in either clutch size or body size, as both decrease with increasing latitude (Owen 1980). The two traits may be intertwined (Raveling and Lumsden 1977). Alternatively, clutch size may vary independently of body size.

We present an analysis of clutch size of the Canada Goose (*Branta canadensis*) across North America and its relation to weather in the breeding and wintering areas and to body size. The Canada Goose offers an opportunity for detailed analysis, since its clutch size has been widely documented in the course of management studies. Our analysis includes data for 40,000 clutches and 315 site-years, from 59 breeding localities.

## METHODS

Sources of published clutch size data were obtained from Craven (1981) and Wildlife Review, and numerous individuals and agencies contributed unpublished information. Table 1 summarizes the data included in our analyses, and Figure 1 shows the locations of study sites. We limited our analysis to geese nesting within or close to areas thought to have been traditionally occupied by Canada Geese (based on Bent 1925, Hanson 1965, Johnsgard 1975, Palmer 1976), thereby excluding two studies from the gulf states. Data from sites close to each other (usually within the same degree block) were combined.

In most cases, clutch size was reported as the average clutch in all nests found being incubated (and therefore presumed complete). A few studies reported clutch size of only those nests that successfully hatched at least one egg, a figure shown by Krohn and Bizeau (1980) with a large sample to average 9.9% lower than the average for all complete clutches. We therefore corrected these figures upward prior to analysis (see Table 1). In about one third of the studies the method was not specified and these were assumed to be based on complete clutches. Exclusion of all studies not known to be based on complete clutches did not importantly alter the results.

Essentially all populations of large Canada Geese east of the Rocky Mountains were reintroduced from western stocks following extirpation by hunting (Palmer 1976). Some remain at least partially captive (Table 1), but most have long since been allowed to go wild. Exclusion of all eastern large Canada Goose breeding sites (numbers 42–59, Table 1) did not alter our results qualitatively.

Mean clutch size for a given locality is an approximation whose error cannot be measured completely, because it is based on samples that are likely to be biased in various ways (e.g., by age structure of the population, egg-dumping, partial predation of nest contents, and by timing of laying within the season; Cooper 1978). Therefore, mean clutch sizes based on a few years of data are not necessarily unbiased estimates of long-term regional means. However, clutch size in the first year of long studies ($\geq 5$ yrs, $n = 23$) deviated from the long-term mean by an average of only 0.25 eggs (with a maximum deviation of 0.86 eggs). Additional years of data reduced the discrepancy. As study locations with only 1–2 yrs of data were well scattered geographically (Table 1), and geographic variation was larger than within-site variation, we included all data sets on an equal basis. A few sites (6, 8 and 11, Table 1) had data for fewer than 20 clutches from a single year, but omission of these sites did not qualitatively alter the results.

Female body weights (Table 2) were obtained from the literature. Although weights can vary up to 50% over the year (Raveling 1979), those in Table 2 represent lean weights from females at the end of incubation or in molt.

Coordinates and altitude of breeding sites were determined from topographic maps. Wintering areas were determined from maps in Bellrose

TABLE 1. Summary of data included in geographical analysis of Canada Goose clutch size, arranged by race.

| Location[a] | Yrs. studied | Mean clutch[b] | No. of nests | Lat-long[c] | | Altitude[d] (m) | Source[e] |
|---|---|---|---|---|---|---|---|
| *minima* | | | | | | | |
| 1 Yukon River delta, Alaska | 19 | 4.71 | 3504 | 61 | 165 | 10 | Yukon Delta NWA unpubl., Spencer et al. 1951,[e] Mickleson 1975[e] |
| *leucopareia* | | | | | | | |
| 2 Buldir Island, Alaska | 4 | 5.56 | 188 | 52 | 176 | 10 | Byrd and Woolington 1983 |
| *hutchinsii* | | | | | | | |
| 3 Victoria and Jenny Lind Islands, Northwest Territories | 2 | 5.52 | 31 | 68 | 103 | 100 | Parmelee et al. 1967 |
| 4 McConnell River, Northwest Territories | 10 | 4.34 | 580 | 60 | 94 | 10 | MacInnes 1962,[e] MacInnes et al. 1974[e] |
| 5 Southampton Island, Northwest Territories | 1 | 3.90 | 39 | 64 | 85 | 10 | MacInnes unpubl. |
| 6 Baffin Island, Northwest Territories | 1 | 3.89 | 9 | 65 | 73 | 10 | Canadian Wildlife Service unpubl. |
| *occidentalis* | | | | | | | |
| 7 Copper River, Alaska | 9 | 5.22 | 1497 | 60 | 145 | 10 | Trainer 1959,[e] Bromley 1976,[e] Alaska Dept. Fish and Game unpubl. |
| 8 Admiralty Island, Alaska | 1 | 4.40 | 19 | 57 | 134 | 10 | Lebeda and Ratti 1979 |
| *interior* | | | | | | | |
| 9 North Indian Lake, Manitoba | 1 | 4.10 | 30 | 57 | 97 | 230 | Raveling 1977 |
| 10 Cape Churchill, Manitoba | 16 | 4.10 | 2355 | 58 | 94 | 10 | D. Rusch unpubl., Pakulak 1969,[e] Malecki 1976[e] |
| 11 Sutton River, Ontario | 1 | 5.50 | 9 | 55 | 84 | 45 | Hanson 1965 |
| 12 Kinoje Lake, Ontario | 3 | 4.57 | 272 | 51 | 82 | 67 | Raveling and Lumsden 1977 |
| *moffitti* | | | | | | | |
| 13 Westham Island, British Columbia | 3 | 6.32 | 122 | 49 | 123 | 10 | Dawe and Davies 1975,[e] Vermeer and Davies 1978 |

TABLE 1. Continued.

| Location[a] | Yrs. studied | Mean clutch[b] | No. of nests | Lat-long[c] | | Altitude[d] (m) | Source[e] |
|---|---|---|---|---|---|---|---|
| 14 Columbia and Okanagan Rivers, British Columbia | 5 | 5.16 | 406 | 49 | 119 | 360 | Munroe 1960[e] |
| 15 Grant County, Washington | 4 | 5.12 | 140 | 47 | 119 | 500 | Yocum et al. 1956, Knight 1978, Fletcher 1979 (in Ball et al. 1981) |
| 16 Hanford Reach, Washington | 29 | 5.64 | 3816 | 46 | 119 | 120 | Hanson and Eberhardt 1971,[e] Fitzner and Rickard 1983 |
| 17 Umatilla, Oregon and McNary, Washington | 3 | 5.80 | 363 | 45 | 119 | 80 | Blus et al. 1979, McCabe 1979 |
| 18 Malheur, Oregon | 1 | 4.40 | 78 | 43 | 119 | 1340 | Jarvis and Harris 1967 |
| 19 Tule Lake, California | 2 | 5.30 | 368 | 41 | 121 | 1220 | Miller and Collins 1953,[e] Rienecker and Anderson 1960[e] |
| 20 Honey Lake, California | 5 | 5.26 | 860 | 40 | 120 | 1200 | Dow 1943,[e] Naylor 1953,[e] Naylor and Hunt 1954,[e] Anderson 1965 |
| 21 McArthur, Idaho | 6 | 4.42* | 492 | 48 | 116 | 600 | Idaho Dept. Fish and Game unpubl. |
| 22 Clarkston, Washington | 18 | 5.85 | 785 | 46 | 117 | 300 | Buss and Wing 1966,[e] Gibson and Buss 1972,[e] Ball et al. 1981 |
| 23 Southwest Idaho | 13 | 5.15* | 9345 | 43 | 116 | 700 | Idaho Dept. Fish and Game unpubl., Salter 1956,[e] Krohn and Bizeau 1980 |
| 24 Flathead Valley, Montana | 7 | 5.37 | 1105 | 47 | 114 | 880 | Geis 1956,[e] Craighead and Stockstad 1961[e] |
| 25 Dowling Lake, Alberta | 10 | 5.02 | 920 | 51 | 112 | 915 | Alberta Fish and Wildlife Division unpubl. |
| 26 Lake Newall, Alberta | 1 | 5.80 | 41 | 50 | 111 | 760 | Vermeer 1970[e] |
| 27 Freezeout Lake, Montana | 2 | 5.37* | 68 | 47 | 112 | 1150 | Hook 1973[e] |
| 28 Madison River, Montana | 2 | 5.66 | 59 | 45 | 111 | 1470 | Childress 1971 |
| 29 Southeast Idaho | 16 | 4.61* | 5201 | 43 | 111 | 1850 | Idaho Dept. Fish and Game unpubl., Jenson and Nelson 1948, Reeves 1954, Salter 1956,[e] Steel et al. 1957,[e] Merrill and Bizeau 1972, Krohn and Bizeau 1980 |

TABLE 1. Continued.

| | Location[a] | Yrs. studied | Mean clutch[b] | No. of nests | Lat-long[c] | | Altitude[d] (m) | Source[e] |
|---|---|---|---|---|---|---|---|---|
| 30 | Ogden Bay and Bear River, Utah | 10 | 5.28 | 1020 | 41 | 112 | 1295 | Williams and Marshall 1937,[e] Jenson and Nelson 1948, Martin 1964, Dey 1966, Arneson 1970, Saul 1970,[e] Bone 1972[e] |
| 31 | Jackson Hole, Wyoming | 4 | 5.08 | 131 | 43 | 110 | 2000 | Craighead and Craighead 1949,[e] Dimmick 1968[e] |
| 32 | Yampa and Green Rivers, Colorado | 4 | 5.26 | 68 | 40 | 108 | 1675 | Grieb et al. 1961[e] |
| 33 | Waterhen Marsh, Saskatchewan | 2 | 5.63 | 222 | 52 | 105 | 460 | Brace 1972[e] |
| 34 | South Saskatchewan and Deer Rivers, Saskatchewan | 3 | 5.75 | 101 | 50 | 107 | 570 | Caldwell 1967[e] |
| 35 | Condie Refuge, Saskatchewan | 2 | 5.56 | 296 | 50 | 104 | 580 | Marshall 1979,[e] 1981,[e] L. Scott (in Marshall 1979) |
| 36 | Larimer County, Colorado | 3 | 4.72 | 688 | 40 | 105 | 1550 | Will 1969,[e] Szymczak 1975[e] |
| 37 | Denver, Colorado | 1 | 4.88 | 169 | 39 | 105 | 1600 | Szymczak 1967[e] |
| 38 | West central South Dakota | 2 | 5.20 | 82 | 44 | 102 | 750 | Lengkeek 1973 |
| 39 | Dog Lake and Reykjavik, Manitoba | 4 | 4.93 | 232 | 51 | 98 | 250 | Canadian Wildlife Service unpubl., Klopman 1958,[e] Johnson 1981 |
| 40 | Marshy Point, Manitoba | 3 | 5.63 | 477 | 50 | 98 | 67 | Cooper 1978 |
| 41 | Waubay, South Dakota | 2 | 5.20 | 248 | 45 | 97 | 530 | Hilley 1976 |
| 42 | Northwest Iowa[f] | 5 | 5.35 | 348 | 43 | 94 | 380 | Bishop and Howing 1972,[e] Nigus 1979 |
| 43 | Twin Cities, Minnesota | 3 | 5.60 | 281 | 45 | 93 | 240 | Sayler 1977 |
| 44 | Crex Meadows, Wisconsin[f] | 9 | 4.99 | 259 | 45 | 92 | 290 | Hunt and Jahn 1966,[e] Zicus 1981 |
| 45 | Trimble, Missouri[f] | 1 | 5.60 | 147 | 39 | 94 | 285 | Brakhage 1975 |
| 46 | Horicon Marsh, Wisconsin[f] | 6 | 5.03 | 111 | 43 | 88 | 260 | Hunt and Jahn 1966[e] |
| 47 | Seney, Michigan | 3 | 5.13 | 442 | 46 | 86 | 215 | Sherwood 1966b[e] |
| 48 | Cook County, Illinois[f] | 2 | 4.98 | 140 | 41 | 87 | 190 | Kossack 1950[e] |
| 49 | Southeast Michigan[f] | 10 | 5.62 | 770 | 42 | 84 | 250 | Wiegand et al. 1968,[e] Kaminski et al. 1979 |
| 50 | Mercer County, Ohio | 1 | 5.90 | 72 | 40 | 84 | 270 | Bednarik 1965[e] |
| 51 | Wyandot County, Ohio | 4 | 5.17 | 490 | 40 | 83 | 235 | Bednarik 1965,[e] Wang 1982 |
| 52 | Old Hickory, Tennessee | 1 | 5.36 | 64 | 36 | 86 | 135 | Poly 1979 |

TABLE 1. Continued.

| Location[a] | Yrs. studied | Mean clutch[b] | No. of nests | Lat-long[c] | | Alti-tude[d] (m) | Source[e] |
|---|---|---|---|---|---|---|---|
| 53 Norris Lake, Tennessee[f] | 7 | 5.50 | 267 | 36 | 83 | 300 | Hubbard 1976,[e] Yates and Whitehead 1978 |
| 54 Luther Marsh, Ontario | 5 | 5.59 | 123 | 43 | 80 | 490 | Joyner 1981 |
| 55 Toronto Island, Ontario | 4 | 5.47 | 429 | 43 | 79 | 75 | Ontario Ministry of Natural Resources unpubl. |
| 56 Mosquito Creek, Ohio[f] | 5 | 5.18 | 204 | 41 | 80 | 275 | Bednarik 1965[e] |
| 57 McClintic, West Virginia | 3 | 5.52 | 71 | 38 | 82 | 215 | Moser 1973, Waggy 1973[e] |
| 58 Lake St. Lawrence, Ontario | 5 | 5.73 | 349 | 45 | 75 | 55 | Ontario Ministry of Natural Resources unpubl. |
| 59 State of Rhode Island | 4 | 5.50 | 63 | 41 | 71 | 100 | Allin 1980 |

[a] Number codes correspond to sites on Figure 1.

[b] Unweighted mean of annual mean clutch sizes. Asterisk indicates that the original clutch size was based on successful clutches only. Figure given here has been corrected (see Methods).

[c] Latitude longitude at SE corner of degree block.

[d] Any altitudes less than 10 m listed as "10."

[e] Full citation appears in Craven (1981) and is omitted here from Literature Cited.

[f] Population captive or semi-captive.

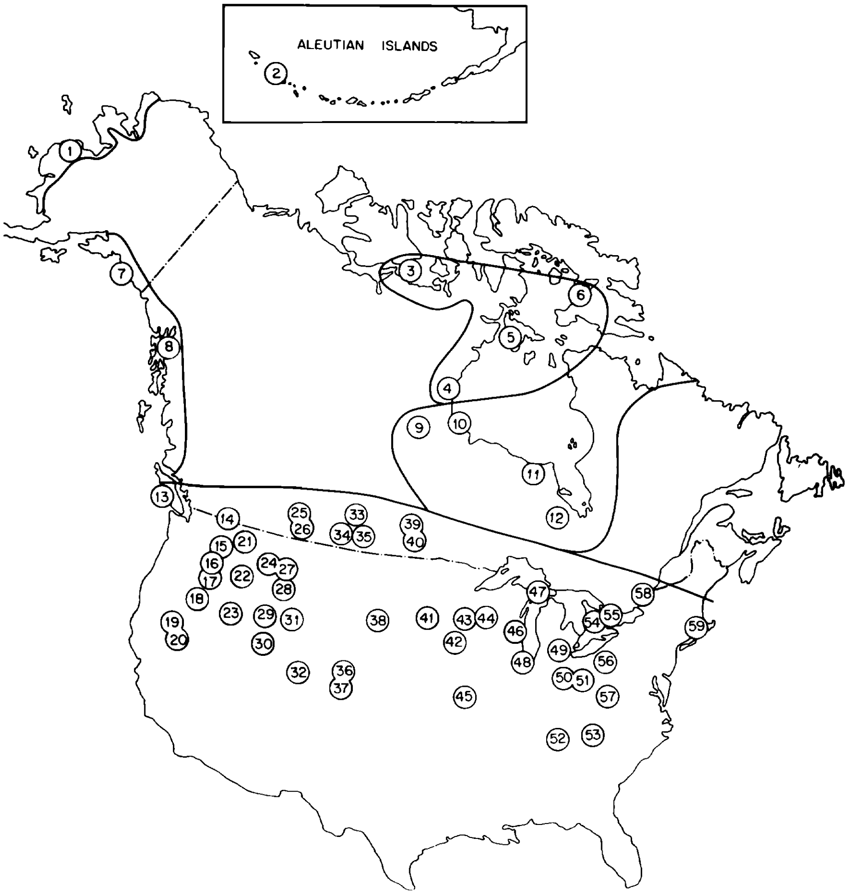

FIGURE 1. Origins of clutch size data analyzed in this paper. Outlines show approximate breeding ranges of races (based on Johnsgard 1975), and numbers refer to sites listed in Table 1.

(1976) and must be regarded as approximate, given our lack of knowledge about particular populations, and individual variability in choosing a wintering site. Weather variables for each breeding site and presumed wintering area included long-term monthly means of temperature, precipitation and actual evapo-transpiration (Canadian Climate Normals 1982; Climatological Data, National Summary, Annual 1965; Thornthwaite Associates 1964; Wernstedt 1972). Actual evapo-transpiration should be a better index of primary plant productivity in an area than precipitation or temperature, as it is a measure of moisture available for plant growth after evaporation and run-off have been taken into account (Ricklefs 1980). As grazers, geese are directly dependent on primary plant productivity. In most cases, at least one weather station was located within

TABLE 2. Weights and measurements of adult female geese of the races included in this paper.[a]

| Race | Weight (gm) | Culmen (mm) | Tarsus (mm) | Wing (mm) (across chord) |
|---|---|---|---|---|
| *minima* | 1200 | 28 | 66 | 364 |
| *leucopareia* | 1700 | 33 | 73 | 385 |
| *hutchinsii* | 1800 | 35 | 68 | 378 |
| *occidentalis*[b] | 2600 | 45 | 85 | 479 |
| *interior* | 3400 | 50 | 84 | 510 |
| *moffitti*[c] | 4000 | 55 | 93 | 520 |

[a] Lean weights, based on data in Bellrose (1976), Johnson et al. (1979), Owen (1980), Palmer (1976), Raveling (1979) and Raveling and Lumsden (1977).

[b] Includes *fulva* (Palmer 1976).

[c] Includes *maxima* (Palmer 1976).

the same quarter degree block as the breeding or wintering site. When several were nearby, the weather station was chosen whose altitude was closest to that of the breeding site. Because no weather data were available close to two breeding sites, weather for McConnell River, Northwest Territories was taken as the average values for Chesterfield Inlet, Northwest Territories (63°N, 90°W) and Churchill, Manitoba (58°N, 94°W); and data for Buldir Island, Alaska were the average of those from Adak (51°N, 176°W) and Dutch Harbor (54°N, 166°W), Alaska.

Principal components were calculated from the monthly values of temperature, precipitation and actual evapo-transpiration on both the breeding and wintering grounds (Nie et al. 1975; Varimax method of rotation). The weather variables represented by each principal component are shown in Table 3.

TABLE 3. Principal components calculated from weather variables.

| PC Name | Eigen-value | % of total variation | Cumulative % of variation | Identity[a] | |
|---|---|---|---|---|---|
| | | | | Breeding area | Wintering area |
| PC 1 | 19.68 | 27.3 | 27.3 | all year T's, Mar–May and Oct–Nov AE | |
| PC 2 | 17.42 | 24.2 | 51.5 | Jul–Aug AE | Apr–Oct P, Apr–Oct AE |
| PC 3 | 11.55 | 16.0 | 67.6 | | all year T's, Jan–Feb AE |
| PC 4 | 9.48 | 13.2 | 80.7 | all year P's but Jun | |
| PC 5 | 5.17 | 7.2 | 87.9 | | Jan–Mar and Nov P's, Mar and Nov AE |
| PC 6 | 2.12 | 2.9 | 90.8 | Dec–Feb AE | |
| PC 7 | 1.18 | 1.6 | 92.5 | Jun AE | |
| PC 8 | 0.85 | 1.2 | 93.7 | | Dec P and AE |

[a] All variables which loaded at 0.6 or greater. All loadings were positive. T = temperature, AE = actual evapo-transpiration, P = precipitation. The following did not load onto PC's 1–8: breeding area P in June, and AE in March, June, July and September; winter area P in October, and AE in February–March.

Variables were checked for normality before we chose methods of analysis, and residuals of regressions were examined to insure linearity of relationships. All variables under consideration in a regression were entered simultaneously, to avoid the inflation of degrees of freedom which can occur with a stepwise procedure.

## RESULTS

Clutch size in Canada Geese decreased with latitude (Fig. 2), although latitude accounted for only 16% of the variability in the data set (see $r^2$ of regression #1, Table 4). When added with latitude to the regression, longitude and altitude also were significantly correlated to clutch size (regression #2). Female body weight explained about the same amount of variation in clutch size as did latitude alone (regression #3, Table 4).

Clutch size and female weight will not have evolved in response to geographical coordinates per se; instead, responses are at least in part to environmental conditions at particular latitudes and longitudes. We examined the relationship of clutch size to weather, as this was the most readily available and easily interpretable index of biological conditions. Clutch size was correlated ($P < 0.05$) to 19 of the 72 basic weather variables (average monthly temperature, precipitation and actual evapotranspiration in the breeding and wintering areas), as summarized in Table 5. This was too many for a statistically valid multiple analysis aimed at determining which were most important and which may have had independent effects. Rather than make *a priori* judgements in choosing a sub-set of variables, we ran a principal component analysis on the entire set of weather data. This procedure selects those variables that are cor-

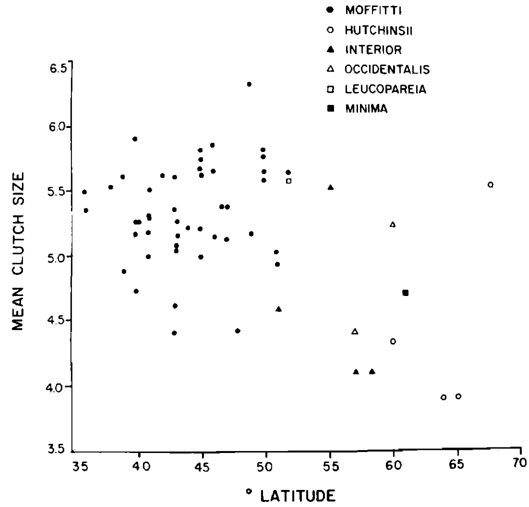

FIGURE 2. Mean clutch size of North American Canada Geese with respect to latitude.

TABLE 4. Results of multiple regression analyses, with various dependent variables.[a]

| | Regression equation | Probability | $r^2$ |
|---|---|---|---|
| Clutch size, all sites | | | |
| 1 | C = 6.60 − 0.03(LAT)<br>(0.00) (0.00) | 0.00 | 0.16 |
| 2 | C = 6.81 − 0.04(LAT) + 0.01(LONG) − 0.0004(ALT)<br>(0.00) (0.00) (0.04) (0.01) | 0.00 | 0.25 |
| 3 | C = 4.04 + 0.0003(WT)<br>(0.00) (0.00) | 0.00 | 0.18 |
| 4 | C = 5.19 + 0.24(PC1) − 0.05(PC2) − 0.09(PC3) + 0.04(PC4)<br>(0.00) (0.00) (0.42) (0.11) (0.50)<br>− 0.02(PC5) + 0.11(PC6) + 0.07(PC7) − 0.13(PC8)<br>(0.70) (0.07) (0.25) (0.03) | 0.00 | 0.28 |
| 5 | C = 4.15 − 0.02(LAT) + 0.01(LONG)<br>(0.00) (0.12) (0.01)<br>− 0.0004(ALT) + 0.0004(WT)<br>(0.00) (0.01) | 0.00 | 0.33 |
| Clutch size, large geese only | | | |
| 6 | C = 4.68 + 0.01(LAT)<br>(0.00) (0.30) | 0.30 | 0.00 |
| 7 | C = 5.10 + 0.003(LAT) + 0.003(LONG) − 0.0004(ALT)<br>(0.00) (0.48) (0.87) (0.00) | 0.01 | 0.18 |
| 8 | C = 5.37 − 0.05(PC1) + 0.08(PC2) − 0.05(PC3) + 0.05(PC4)<br>(0.00) (0.78) (0.40) (0.42) (0.80)<br>+ 0.07(PC5) + 0.11(PC6) + 0.02(PC7) + 0.01(PC8)<br>(0.34) (0.10) (0.81) (0.98) | 0.30 | 0.04 |
| Female weight | | | |
| 9 | WT = 7484 − 80(LAT)<br>(0.00) (0.00) | 0.00 | 0.63 |
| 10 | WT = 7582 − 70(LAT) − 6(LONG) + 0.2(ALT)<br>(0.00) (0.00) (0.04) (0.16) | 0.00 | 0.65 |
| 11 | WT = 3676 + 542(PC1) − 15(PC2) + 21(PC3) − 71(PC4)<br>(0.00) (0.00) (0.80) (0.72) (0.24)<br>− 158(PC5) + 3(PC6) + 119(PC7) − 184(PC8)<br>(0.01) (0.95) (0.05) (0.00) | 0.00 | 0.63 |

[a] Significance of repression coefficients given in parentheses under each variable. C = clutch size, LAT = latitude, LONG = longitude, ALT = altitude, WT = female weight, PC1 through PC8 = weather principal components (see Table 3 for identity).

related and loads them onto principal components that are mutually uncorrelated (Nie et al. 1975). These components can then be used as variables in other analyses. The admittedly more abstract principal components reduced the data set to a useable size without sacrificing any data or forcing any prejudgments, and also allowed us to determine which weather features varied independently (Table 3).

The principal components were correlated with latitude, longitude and altitude (Table 6), but not in a simple way. As the principal com-

TABLE 5. Average monthly weather variables on the breeding area correlated to clutch size in Canada Geese.[a]

| Variable | Correlation coefficient and probability[b] | Variable | Correlation coefficient and probability[b] |
|---|---|---|---|
| January T | 0.45*** | October T | 0.49*** |
| February T | 0.44*** | November T | 0.32* |
| March T | 0.45*** | December T | 0.46*** |
| April T | 0.31* | February AE | 0.30* |
| May T | 0.35** | April AE | 0.47*** |
| June T | 0.50*** | May AE | 0.44*** |
| July T | 0.45*** | June AE | 0.27* |
| August T | 0.45*** | October AE | 0.48*** |
| September T | 0.47*** | November AE | 0.36*** |
| | | December AE | 0.28* |

[a] Breeding area weather. No wintering area weather variables were significantly correlated with clutch size.

[b] Two-tailed Pearson or Spearman Rank correlations, depending on whether variables were normally distributed. Probability levels indicated as follows: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Abbreviations as in Table 4.

ponents are by definition uncorrelated to each other, the fact that latitude, longitude and altitude were correlated with several principal components suggested that weather variables did not all change in parallel over wide geographic areas.

Clutch size regressed on weather principal components alone explained slightly more variation than did latitude alone (regression #4, Table 4). Clutch size was higher where breeding area temperatures and spring and fall actual evapo-transpiration were high, and where December precipitation and actual evapo-transpiration in the wintering area were low (shown by the correlations of clutch size to principal compo-

TABLE 6. Correlation coefficients among independent variables.[a]

| | C | LAT | LONG | ALT | WT |
|---|---|---|---|---|---|
| LAT | −0.42*** | | | | |
| LONG | 0.04 | 0.24* | | | |
| ALT | 0.01 | −0.49*** | 0.26* | | |
| WT | 0.40** | −0.69*** | −0.04 | 0.64*** | |
| PC1 | 0.45*** | −0.91*** | −0.10 | 0.28* | 0.67*** |
| PC2 | −0.05 | −0.07 | −0.73*** | −0.44*** | −0.11 |
| PC3 | −0.22 | −0.02 | −0.29* | 0.12 | −0.16 |
| PC4 | 0.06 | −0.36** | −0.35** | −0.16 | 0.08 |
| PC5 | −0.04 | 0.24* | 0.28* | −0.44*** | −0.18 |
| PC6 | 0.04 | 0.16 | 0.09 | −0.11 | −0.22 |
| PC7 | 0.13 | −0.06 | −0.24* | −0.04 | 0.22 |
| PC8 | −0.07 | −0.23 | −0.08 | 0.15 | 0.16 |

[a] Probability levels and abbreviations as in Table 4.

nents 1 and 8; see Table 3). This result is consistent with the fact that larger-clutched geese nest farthest south, where principal component 1 had high values, and winter farthest north, where principal component 8 was low.

Female weight explained about as much variation in clutch size as did latitude alone (Table 4). When considered along with latitude, longitude and altitude, nearly twice as much variation was explained (regression #5). In this case, however, female weight (which was highly correlated to latitude) had a significant effect while latitude did not, suggesting that latitude and body size were not related independently to clutch size. This was confirmed by running the same set of regressions for large geese alone (regressions 6–8, Table 4), which showed that, of all variables examined, only altitude was significantly correlated with clutch size when body size was held constant.

Geographic coordinates and weather explained significant amounts of variation in female weight (Table 4), as well as in clutch size. Geese that bred in warm areas with high spring and fall actual evapo-transpiration were larger (principal components 1 and 7, Table 3), as were those that wintered in areas with low winter precipitation and low spring and fall actual evapo-transpiration (principal components 5 and 8). This corresponded, again, to the larger geese nesting farther south and wintering farther north than smaller forms. The regressions for female weight had higher $r^2$ values than those for clutch size, but this was an artifact of there being only 6 female weights (the average weight for a race being assigned to each case), as opposed to 59 clutch sizes.

## DISCUSSION

Our results showed that the geographic trend in average clutch size of Canada Geese was largely related to female weight, although altitude had a negative effect on clutch size independent of body size. Less than 30% of clutch size variation was explained by the variables examined here. In part, this was a result of extraneous variability in the data (see Methods), but other factors, not identified in this paper, probably have significant effects on the number of eggs laid in a given location.

The trend to small body size in arctic-nesting geese is opposite to that found in many other arctic animals (Bergmann's Rule). Our correlational analyses do not explain why geese are different. However, one factor must surely be the need of goslings to attain full size by the end of a very short growing season. Arctic-nesting geese grow rapidly for their size (Aubin et al. 1986), but are among the largest birds nesting in the north and must leave the nesting area within a few weeks of fledging to avoid freeze-up. The energetics of migration in relation to size probably have a further influence (many of the larger forms are non-migratory). Clutch size might have changed as a result of such selection pressures on body size, rather than being selected directly; a conclusion which bears on arguments that clutch size has evolved to match environmental food supply (Lack 1967).

Because arctic-nesting geese carry with them most of the reserves necessary to lay and incubate the clutch prior to the appearance of fresh plant growth on the breeding grounds (Raveling 1979, Ryder 1970), it seems logical that clutch size should decrease as migration distances increase. The trend should be compounded by the facts that females are smaller and proportionate egg weight is larger as one goes north (Owen 1980, Table 7). In fact, it is striking that clutch size in Canada Geese decreases as little in the arctic as it does. Despite an approximately 2-fold difference in linear measurements of the largest and smallest birds, and a 3–4-fold range in female weights (Table 2), the maximum difference in average clutch size between 2 North American sites was 2.4 eggs (6.32–3.89). This is only twice the average range of annual mean clutch sizes within a single site (1.1 eggs; based on 23 sites with 5+ years of data).

Because the decline in clutch size is small despite a large decrease in body weight, and at the same time proportionate egg weight increases, the weight of an entire clutch as a proportion of female weight increases slightly to the north as body size declines (Table 7; $x = 0.46 - 0.00006y$; $r = -0.83$, $n = 6$, $P < 0.05$). Thus, although the decrease in clutch size with latitude runs contrary to the trend in most other species, proportionate clutch weight, which can be considered one index of reproductive effort, does in fact increase. The unusually marked latitudinal decrease in body size appears sufficient in this case to counter any underlying tendency to increase clutch size in northern regions.

Although clutch size in Canada Geese and many other species is correlated with latitude, it is also correlated with anything else that varies latitudinally, such as many weather variables, productivity measures and daylength (see Tables 5 and 6). Although the principal component approach allowed us to consider a larger number of variables at one time, to look for independent relationships and to emphasize the complex nature of environments to which geese may be responding, we are still unable

TABLE 7. Egg and clutch weights in Canada Geese according to female weight. (All weights in grams.)

| Race | Egg weight[a] | Female weight[b] | Proportionate egg weight | Clutch size[c] | Clutch weight | Proportionate clutch weight |
|---|---|---|---|---|---|---|
| *minima* | 96 | 1200 | 0.08 | 4.7 | 451 | 0.38 |
| *leucopareia* | 127 | 1700 | 0.07 | 5.6 | 711 | 0.42 |
| *hutchinsii* | 116 | 1800 | 0.06 | 4.4 | 510 | 0.28 |
| *occidentalis* | 161 | 2600 | 0.06 | 4.8 | 773 | 0.30 |
| *interior* | 152 | 3400 | 0.04 | 4.6 | 695 | 0.20 |
| *moffitti* | 175 | 4000 | 0.04 | 5.3 | 933 | 0.23 |

[a] From Owen 1980 and, for *occidentalis,* Kortright 1942 (calculated from formula in Owen 1980).

[b] From Table 2.

[c] From Table 1.

to conclude that any particular condition(s) cause geographic variation in clutch size. This is because correlation does not demonstrate causation, and the true causative factors could be ones also correlated to latitude, but which we did not examine. Other recent studies showing correlations of clutch size with simple variables, even at much higher levels than in our study, are no closer to demonstrating causality than we are (Koenig 1984a, b, 1986; Moeller 1984; Ricklefs 1980). We need to find methods other than correlational analyses to determine why clutch size varies geographically (Hussell 1985).

In this paper we have examined the relationships among body size and long-term means of clutch size and weather, and have therefore been looking at biological adjustments that are probably mainly genetic. Both body size and clutch size are known to have heritable components in Canada Geese (Lessells 1982, MacInnes and Dunn unpubl. data). Weather on the wintering grounds in a given year has been shown to have an effect on clutch size the following summer in several waterfowl species (Davies and Cook 1983, Heitmayer and Frederickson 1981). This is most likely a phenotypic effect. We would expect to find a greater influence of weather on clutch size of Canada Geese if weather and clutch size were related on a year-by-year basis. Actual evapo-transpiration would be the most interesting variable to examine in its effects on annual clutch size, but its calculation is very complex and only long-term mean values are available for most sites.

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