COMPONENTS OF CLUTCH SIZE VARIATION IN ARCTIC-NESTING CANADA GEESE[1]

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Abstract. Clutch size and first egg date of neck-banded Canada Geese were studied at the McConnell River, Northwest Territories, Canada from 1965 to 1971. A maximum of 17% of clutch size variation within years was due to additive genetic variance, as estimated from repeatability of clutch size. Date of first egg showed no significant repeatability. Clutch size varied significantly among years (7% of total variation), and was usually smallest in late seasons and in years with a long delay between arrival on the breeding grounds and initiation of egg laying. Clutch size decreased by 0.18 eggs per day within a season, and this trend accounted for 19% of within-year variation in clutch size. Clutch size did not increase with age of the female. Mate change occurred annually in 30% of pairs, including 9% in which the previous mate was known to be still alive. Change of mate did not influence clutch size or first egg date, nor did change of nest site from the previous year. More than half of total clutch size variation remained unexplained. Weight of females arriving on the breeding grounds (not measured in this study) is probably the major influence on clutch size variation within and between seasons. Canada Geese appear to have a more flexible response to environmental conditions at or near the McConnell River than do Lesser Snow Geese nesting at the same site.

Key words: Canada Goose; Branta canadensis hutchinsii; *clutch size variation; timing of breeding; breeding biology; heritability.*

INTRODUCTION

Factors affecting clutch size of birds have been frequently studied (Klomp 1970 and many later papers), but few studies have examined whether clutch size variation is heritable (e.g., van Noordwijk et al. 1981, Findlay and Cooke 1983), or examined the relative importance of inheritance vs. specific nongenetic factors in contributing to clutch size variation. In this paper, we present data for the Canada Goose (*Branta canadensis hutchinsii*) nesting in the arctic. By studying individually marked geese, we estimated the relative proportions of additive genetic variance and other effects on variation in clutch size. The other factors studied were date of clutch initiation both within and among seasons, female age, and fidelity to nest site and mate. This approach helps to determine whether the major influences on clutch size have been identified, and the degree to which clutch size could be influenced by those factors amenable to management.

METHODS

Neck-banded Canada Geese were studied from 1965 to 1971 at the mouth of the McConnell River, Northwest Territories, Canada, on the western shore of Hudson Bay (60°50′N, 94°25′W). Other data were collected in 1959, 1960, and 1964. Postbreeding banding drives took place when goslings and molting adults were flightless, and birds were banded both with leg bands and with individually numbered neck bands (MacInnes et al. 1969). Yearlings normally did not nest and left the study area before the banding drives (MacInnes et al. 1974), so after-hatch-year birds banded in August were considered 2+ years of age. Neck bands reduced the probability of recapture of geese at the McConnell, but did not affect subsequent clutch size of birds which did return (MacInnes and Dunn, in press).

During each season, neck-band codes were recorded during nest and brood counts and, after the first year, during frequent observation from three elevated, self-contained permanent blinds built in the 62-km[2] main study area (MSA). Sightings of individuals and nest locations were designated by 1-km[2] quadrat (marked by a grid of poles).

On average, 80 pairs attempted to nest on the

MSA each year. Of those, an increasing percentage of pairs each year had one or both members individually identified, levelling off at about 50% in 1968. Essentially all marked birds spending at least 1 week on that area during each incubation period were likely to have been identified.

Nest searches were intensive and frequent, and fewer than 5% of nests on the MSA were likely to have been missed (MacInnes and Misra 1972). After 1967, extensive nest searches were conducted only after incubation began, since earlier experience indicated that increased predation resulted from disturbance by observers during laying (MacInnes et al. 1974). Most analyses included data only from the MSA, but occasionally it was appropriate to add data from subsidiary sites, where nest checks were usually done only once per year. Further details of the study site and methods used can be found in MacInnes et al. (1974).

Clutch size was taken as the number of eggs at incubated nests or at any nest first found after the last known laying date for the season. Date of hatch was determined by direct observation. Date of first egg was calculated from hatch date assuming that incubation lasted 25 days (MacInnes 1962), that egg-laying interval averaged 1.23 days (based on 93 laying intervals in 1964 to 1971), and that incubation began on the day that the last egg was laid.

Biases in our estimates of clutch size could result if there was a high frequency of partial predation during laying, or of intraspecific parasitic egg laying. MacInnes and Misra (1972) showed that partial predation was not common at the McConnell River prior to the first visit to a nest. As for egg parasitism, only four seven-egg or larger clutches were found on the MSA, out of 430 known to be complete, and evidence for three of these suggested parasitism (MacInnes et al. 1974). All four were omitted from our analyses. Parasitism could have occurred in smaller clutches (MacInnes and Misra 1972), but we have no way of assessing the seriousness of the problem or of correcting for it. The low frequency of clutches larger than six suggests that the magnitude of egg parasitism in smaller clutches was also low.

We standardized our clutch-size and first-egg-date data from different years by expressing the values for each female as deviations from population means for that year. This removed annual variation from the pooled data. We refer to these corrected values as "standardized" clutch size and first egg date.

Repeatabilities (r_i) of clutch size and first egg date were calculated for females with 2+ years of data. Repeatability is a measure of the constancy of a trait in an individual, and gives an upper estimate of additive genetic variance in the trait. It is estimated by r_i, the intraclass correlation coefficient (Sokal and Rohlf 1981, Lessells and Boag 1987). The SE of r_i is an approximate value, assuming normality of repeatability (Becker 1984).

RESULTS

Annual mean clutch size ranged from 3.84 to 4.76 eggs, with a mean of 4.34 ($n = 10$), while the annual midpoint of first egg dates ranged from 6 June to 17 June, averaging 11 June. We attempt here to elucidate the sources of variation within and among years.

REPEATABILITY

Our estimate for repeatability of clutch size ($r_i = 0.12$) indicated that a maximum of 12% of total clutch size variation resulted from differences among females. However, this value was not different from 0 ($P = 0.11$, Table 1). Repeatability of standardized clutch size, 0.17, was significant. Neither first egg date nor standardized first egg date showed significant repeatability (Table 1).

ANNUAL VARIATION

Differences among years accounted for 7% of total variation in clutch size (r_i, Table 2) and for 27% of total variation in dates of clutch initiation.

The midpoint of clutch initiation dates was highly correlated to the date at which 50% of the main study area became snow-free, such that laying began earlier relative to snowmelt when thaw took place late in a season (clutch date = 13.3 + 0.46 [date of 50% thaw], where May 25 = 1; $r^2 = 0.83$, $P < 0.001$, $n = 10$). Although clutch size appeared smaller in late breeding seasons, the relationship was not significant (MacInnes et al. 1974). By excluding one apparently anomalous year (1967), however, we could show a significant reduction in clutch size both with later breeding seasons and with increased delay between peak arrival of geese on the breeding grounds and first egg dates (Fig. 1). This relationship potentially accounts for a good deal of the between-year

TABLE 1. Repeatability (r_i) of reproductive characteristics in neck-banded McConnell River Canada Geese with data from 2 or more years.[a]

Character	F	df	P	r_i	SE
Clutch size	1.34	54, 88	0.11	0.115	0.007
Standardized clutch size	1.52	54, 88	0.04	0.166	0.006
First egg date	0.97	24, 41	0.52	−0.011	0.019
Standardized first egg date	1.55	24, 41	0.11	0.173	0.013

[a] Column headings beginning with F are: F-value from ANOVA of character within and among females, degrees of freedom, probability, intraclass correlation coefficient and standard error of r_i.

variation in clutch size, if the exclusion of 1967 can be justified (see Discussion).

WITHIN-SEASON VARIATION

Females that initiated clutches later in a given season laid smaller clutches (Fig. 2). This relationship was significant in 4 of the 7 years, as well as for all years combined, even though the range of first egg dates in a given year was narrow: 8 to 13 days, with 85% initiating (and 90% hatching) within 7-day periods. Within a season (as shown by standardized data), there was a decrease of 0.18 eggs for each day that clutch initiation was delayed, and this accounted for 19% of within-year clutch size variation (r^2 of the regression, Fig. 2). The slope for unstandardized data was lower (Fig. 2, top). Because the decrease of clutch size in late years was small (0.06 eggs/day, Fig. 1), combining data from all years obscured the within-season decline.

THE EFFECT OF FEMALE AGE

Although clutch size increased from ages 2 to 4 years (Table 3; clutch size = 3.66 + 0.20 (age); $r^2 = 0.01$, $P < 0.05$), most data for 3- and 4-year-olds were from 1970 and 1971, when average clutch size was higher (by about 0.8 eggs) than in earlier years. Standardized clutch size did not change with age (Table 3; $P > 0.05$), nor did first egg date or standardized first egg date. Our data

TABLE 2. Intraclass correlation of reproductive characteristics among years.[a]

Character	F	df	P	r_i	SE
Clutch size	2.51	6, 124	0.03	0.07	0.006
First egg date	69.18	6, 124	0.00	0.27	0.172

[a] Includes only 1 year of data (chosen at random) for each female, to avoid bias arising from repeated measurements in the same individual. Column headings as in Table 1, except that here, the F-value is from an ANOVA of the character within and among years.

were insufficient to determine whether clutch size changed with age in individual females.

THE EFFECT OF CHANGING MATE

Standardized clutch size and first egg date for pairs that had mates different from the previous year were not different from the values for unchanged pairs (Table 4). Of 82 females whose mate in two successive years was known, 30% had new mates in the second year. This figure included 9% (seven of 82) whose previous mate was known to be still alive, 6% whose original mate was known to have died, and 16% whose mate's fate was unknown. The proportion of pairs with new mates did not vary among years (χ^2, $P > 0.05$).

THE EFFECT OF CHANGING NEST SITE

Females showed a marked tendency to nest in the same general area (same or adjacent 1-km²) year after year, but only half the birds at the McConnell reused exactly the same site as in the
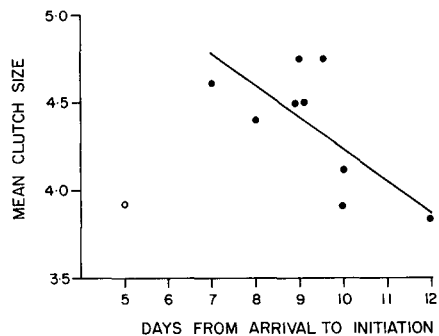

FIGURE 1. The relationship of mean clutch size to the number of days between date of peak arrival on the breeding grounds and mean date of clutch initiation. Regression line is for data without 1967 (open circle; see text). Clutch size = 6.94 − 0.17 (days between) − 0.06 (midpoint of clutch initiation dates); where May 25 = 1, $n = 9$, $r^2 = 0.74$, $P < 0.005$ for both coefficients and for the regression as a whole.
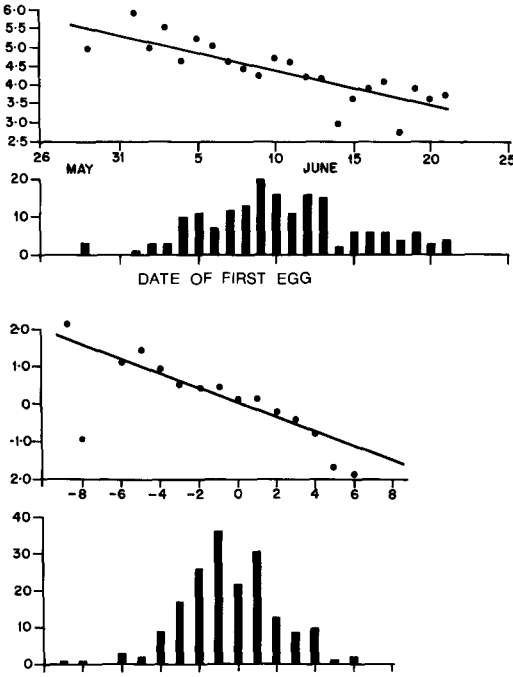
FIGURE 2. The relationship between date of clutch initiation and clutch size and the frequency distributions of laying dates. (For clarity, only the mean clutch size for each date is shown.) Top half of figure shows raw data, all years combined; bottom half shows standardized data. Regressions, calculated from all individual values, are as follows: clutch size = 6.051 − 0.092 (date of laying), $n = 176$, $r^2 = 0.171$, $P < 0.001$; standardized clutch size = 0.157 − 0.181 (date of laying) ($n = 176$, $r^2 = 0.187$, $P < 0.001$). In both regressions, May 25 = day 1.

previous year (R. N. Jones, pers. comm.). Females nesting in new 1-km² quadrats since the previous year had the same clutch size and date of first egg as those nesting for a second year in the same quadrat (Table 5), but those choosing a new quadrat had laid smaller clutches in the previous year. There was a nearly significant tendency to begin laying a day earlier in reused

TABLE 4. The effect of mate change since the previous year on clutch size and first egg date.[a]

	Standardized clutch size	Standardized first egg date
Same mate	0.12 ± 1.07 (53)	−0.20 ± 2.21 (40)
New mate	0.32 ± 1.13 (17)	−1.17 ± 1.76 (10)
P (t-test)	0.52	0.15

[a] Mean ± SD (n).

quadrats than when a new quadrat was occupied ($P = 0.07$).

DISCUSSION

We determined that 7% of clutch size variation was a result of between-year differences (Table 2). After removing this variability by standardizing data, we found that 17% of within-year variation resulted from differences among females (Table 1), 19% was related to date of clutch initiation within a season (Fig. 2), and none resulted from change of mate or nest location (Tables 5 and 6). Even if we make the assumption that these are completely independent, additive effects, only 36% of within-year variation in clutch size could be accounted for, and the addition of year effects still leaves less than half of all variation explained. We conclude that additional factors, not examined in this study, have large effects on clutch size variation. Arctic-nesting geese accumulate lipid and protein reserves prior to arrival on the breeding grounds which must see them through egg laying and incubation (Ankney and MacInnes 1978, Raveling 1978, McLandress and Raveling 1981). The unexplained 50+% of clutch size variation in McConnell Canada Geese probably depends largely on arrival weight of individual females rather than on factors operating at the breeding site.

Our figure for repeatability of standardized clutch size (0.17) is similar to that found by Lessells (1982) for giant Canada Geese nesting in

TABLE 3. Clutch size and first egg date in McConnell River Canada Geese according to age.[a]

Age (years)	Clutch size	Standardized clutch size	Standardized first egg date
2	3.82 ± 1.25 (11)	−0.45 ± 1.26 (11)	−0.66 ± 2.69 (7)
3	4.40 ± 0.83 (15)	0.00 ± 0.90 (15)	−0.08 ± 2.15 (11)
4	4.77 ± 0.60 (13)	0.20 ± 0.60 (13)	0.90 ± 0.61 (3)
5+	4.40 ± 1.23 (151)	0.17 ± 1.17 (151)	−0.19 ± 2.39 (76)

[a] Mean ± SD (n). Standardized values have year effects removed (see Methods).

TABLE 5.   The effect of changing nesting quadrat since the previous year on clutch size and first egg date.[a]

	Standardized clutch size in current year	Standardized clutch size in previous year	Standardized first egg date in current year
Same quadrat	0.33 ± 0.71 (29)	0.49 ± 0.88 (31)	−1.25 ± 1.83 (24)
New quadrat	0.19 ± 1.13 (39)	−0.19 ± 1.22 (34)	−0.11 ± 2.59 (32)
P (t-test)	0.57	0.01	0.07

[a] Mean ± SD (n).

England (0.16), and that for the Lesser Snow Goose (*Chen c. caerulescens*) nesting on Hudson Bay (0.26, Lessells and Boag 1987). Such low repeatability is expected in a trait closely associated with fitness, and indicates that most variation is environmentally induced, rather than passed on from parent to offspring.

The relationship between clutch size and timing of the breeding season was not simple. The midpoint of clutch initiation dates was highly correlated with the date when 50% of the breeding grounds became snow-free, with clutch initiation following thaw more closely in seasons with late thaw. In such years, clutch size was reduced. However, the date of peak goose arrival was not correlated to timing of thaw, so there was variation in the number of days between arrival and peak clutch initiation. Longer delay, i.e., earlier arrival with respect to snowmelt, was usually associated with lower clutch size (Fig. 1), suggesting that some of the energy which might otherwise have been allocated to eggs was used

for maintenance (MacInnes et ål. 1974, Raveling 1978). Our correlations among clutch size, lateness of the season, and interval between arrival and clutch initiation were only significant, however, if 1967 was omitted from the calculation. In that year, snowmelt was advanced by the time birds arrived, and laying began almost immediately. At Kinoje Lake, in interior Ontario (51°35′N, 81°45′W), the spring of 1967 was the latest of 17 years for which data were available (reported in Raveling 1978). Thaw was also late at Churchill, on southern Hudson Bay (58°5′N, 94°W), although normal at the McConnell River (MacInnes et al. 1974). McConnell geese perhaps found it difficult to maintain normal levels of reserves prior to and during migration, leading to a decrease in energy which could be allocated to eggs. Alternatively, a hold-up in migration after follicular development began could have caused follicular atresia (Raveling 1978). Davies and Cooke (1983) have demonstrated for Lesser Snow Geese that in some years unusual droughts

TABLE 6.   Comparison of breeding in Canada Geese and Snow Geese nesting at the McConnell River. Sample sizes in parentheses.

Characteristic	Canada Goose	Snow Goose
Mean date of peak arrival	June 1 (10)[a]	June 2 (10)[a]
Egg dimensions (mm)	78.5 × 53.4 (77)[a]	79.3 × 52.4 (229)[b]
Days of delay in clutch initiation after arrival on breeding ground	9 (10)[c]	4 (3)[d]
Measurements of female (mm):		
Tarsus	70.3 (40)[e]	79.9 (49)[f]
Culmen	38.5 (90)[e]	55.4 (49)[f]
Weight of females (g) in arriving flocks	2,297 (3)[a]	2,950 (78)[g]
Weight of adult females (g) in 2 weeks after peak hatch	1,900 (21)[a]	1,900 (35)[g]
Mean of annual mean clutch sizes and range (1966–1971)	4.27[h]	3.57[a]
	3.84–4.76	3.28–3.84

[a] C. D. MacInnes, unpubl. data.
[b] Eggs from Southampton Island (G. Cooch, pers. comm.). Egg weight for Snow Geese at the McConnell River is 124 g (*n* = 68, A. Aubin, pers. comm.), but is not available for Canada Geese.
[c] This paper.
[d] Harvey (1971), Ankney and MacInnes (1978), C. D. MacInnes, unpubl. data.
[e] MacInnes 1966.
[f] Data from McConnell River (A. Aubin, pers. comm.).
[g] Ankney and MacInnes 1978.
[h] MacInnes et al. 1974.

in the wintering and staging areas may be related to marked deviations in clutch size from its predicted relationship with timing of the season.

Our data (Fig. 1) show that the interval between arrival at the McConnell and date of clutch initiation normally has a strong negative effect on clutch size, three times more than does lateness of the season per se. Although a similar relationship has been noted by others (Cooch 1961, Barry 1962), the hypothesis that follicular atresia is involved has not yet been rigorously tested. Barry (1962) studied atresia in only 1 year, so could not relate it to annual variation in the interval between arrival and clutch initiation. Hamann et al. (1986) determined that follicular atresia in Snow Geese at La Perouse Bay (58°24'N, 94°24'W) did not increase either in a late nesting season ($n = 2$) or later within a season. Those results would be expected if clutch size variation is a function of energy reserves accumulated prior to the phase of rapid yolk development, or RYD (MacInnes et al. 1974, Ankney and MacInnes 1978). However, atresia has been hypothesized to occur if the start of laying is delayed beyond completion of RYD, and Hamann et al. (1986) were unable to test this.

We could not detect an influence of female age on clutch size, contrary to the situation in Snow Geese (Rockwell et al. 1983) and giant Canada Geese (Brakhage 1965, Cooper 1978. See, however, Lessells [1982], who found no effect of female age in giant Canada Geese when male age was held constant). Our unstandardized data showed an increase in clutch size with age, but were biased in that clutch size data for older known-age females came from years with unusually high population means. Standardization of our clutch size data corrected this problem. We cannot determine from the data in Brakhage (1965) and Cooper (1978) whether those studies might have been similarly biased.

It has been suggested that small Canada Geese start RYD at the time of departure from the last spring staging area while Snow Geese begin at the start, or even before arrival on final staging areas (Raveling 1978). Canada Geese should therefore have a more flexible response to conditions at or near the breeding grounds, while Snow Geese might hedge their bets against unpredictable conditions at the nesting area (Raveling 1978). Evidence from the McConnell River is compatible with these hypotheses.

Early arriving female Canada Geese collected in 1972 showed little ovarian development, but 40% of Snow Goose females shot from arriving flocks had an egg already in the oviduct (C. D. Ankney, pers. comm.). In 1968, a year when spring thaw occurred at an average date in southern Hudson Bay but was unusually retarded at the McConnell, Canada Geese delayed 12 days between arrival and laying. Snow Geese, arriving at similar dates, initiated laying right away. Over 90% of the ground was snow covered, and one isolated snow-free ridge became littered with eggs, with aggregations of up to 50. Snow Geese had clearly initiated RYD before they were far enough north to detect lateness of local thaw, while Canada Geese had not.

Although Canada Geese are slightly smaller than Snow Geese in measurements and perhaps in arrival weight (n is small, Table 6), their clutches were larger. This suggests a significant intake of energy on the breeding grounds (as suggested for Brant, *Branta bernicla*, Ankney 1984; and for Cackling Goose, *B. c. minima*, Raveling 1979a, 1979b).

Snow Geese at La Perouse Bay did not lay eggs until 11 days after arrival ($n = 8$ years, Cooke et al. 1982), providing contrary evidence for the suggestion that RYD in this species began at or before arrival on the final staging area. However, arrival and nesting at this relatively new, southern colony were about 2 weeks ahead of those at the McConnell, less than 200 km to the north. La Perouse Bay may historically have been a staging area, at which RYD began upon arrival, prior to being adopted as a breeding ground. The ability of Snow Geese nesting there to assess breeding ground conditions more precisely than can other populations may be reflected in the higher clutch size (by 0.8 eggs) than that at the McConnell River (Table 6, Cooke et al. 1982).

ACKNOWLEDGMENTS

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