EFFECTS OF EXPERIENCE AND BODY WEIGHT ON INCUBATION BEHAVIOR OF CANADA GEESE

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ABSTRACT.—During 1979 and 1980, we studied the incubation behavior and body-weight dynamics of captive Canada Geese (*Branta canadensis moffitti*) with known breeding histories. Females were attentive to their nests for 97.5% of the incubation period and lost 27% of their initial body weight. Heavier females were more attentive to their nests and lost more weight during incubation than did lighter females. Variation in body weight among females was greatest at the onset of incubation and least at hatch, which suggests that females invested maximum reserves in incubation. Recess frequency and duration increased throughout incubation, resulting in more foraging time for the female. Once a lower critical weight of about 3,200 g was reached, the amount of recess time taken increased dramatically, probably because lipid reserves were depleted. Females nesting for the first time began incubation at a lighter body weight and were less attentive than experienced females. All inexperienced females were either 4 or 5 yr old, but their egg production (4 eggs) was that of 2- or 3-yr-old wild females. This indicated that experience rather than age was the important variable affecting acquisition of reserves. Inattentiveness to a nest by a female prolongs the duration of incubation and exposes the nest to a greater risk of predation. The inability of inexperienced females to gain enough reserves to provide for both maximum clutch size and attentiveness during incubation may be a major explanation for the lower hatching success of geese nesting for the first time. *Received 2 August 1982, accepted 21 February 1983.*

AVIAN incubation has drawn the attention of ecologists for many years. From the perspective of energetics, many different incubation strategies are possible. The participation of one or both parents in incubation, the sources of energy needed to fuel incubation (e.g. endogenous, environmental), and the timing and length of incubation recesses are some of the many variables that can be optimally combined to form an energetically efficient incubation strategy. Evolutionarily, however, these variables must be combined in a way that maximizes the reproductive performance of individuals over their lifetimes. To understand the adaptive significance of an incubation pattern, one must understand the impact of the pattern on the parent(s) as well as on the hatching success of eggs. Numerous studies of waterfowl have shown how incubation behavior is influenced by environmental conditions (Low 1945, Breckenridge 1956, Caldwell and Cornwell 1975, Miller 1976, Cooper 1978, Afton 1980). The function of variability in incubation behavior within and among species has generally been attributed to maximizing the hatching success of eggs. Little is known, however, about how parental body condition affects incubation patterns. The lower attentiveness of renesting ducks suggests that the amount of endogenous reserves affects incubation behavior (Afton 1980). In geese, only the female incubates, and she depends mainly on endogenous reserves for the energetic demands of egg laying and incubation (Ankney and MacInnes 1978; Raveling 1979a, b). Consequently, incubation attentiveness in geese should be closely related to the body condition of the female. In this paper we examine the relationship of incubation behavior of Canada Geese (*Branta canadensis*) to body weight and compare the performances of birds nesting for the first time with those of experienced nesters.

METHODS

This study was conducted during the spring seasons of 1979 and 1980 at the Wildlife and Fisheries Biology experimental area located on the Davis campus of University of California (38°32′N). The goose flight pen measured 91 × 88 × 8 m high and enclosed two 45 × 15 m ponds, each containing three nesting islands. Sixteen nest sites, fabricated from tires and straw, were placed on the islands and dry land area. The pen was surrounded by fallow fields, and human access was controlled.

Canada Geese (*B. c. moffitti*) obtained from eggs collected from a wild population at Lake Almanor, Plumas County, California (40°17′N) in 1971 and their offspring were studied. We marked geese individually with a neck collar (Sherwood 1966) and leg band. Prior breeding histories of all geese were known. We defined inexperienced females as those that had not previously nested.

Approximately 80 other geese (*B. c. minima, B. c. fulva, B. bernicla, Chen rossii, C. caerulescens, C. canagica, Anser albifrons*) also were kept in the flight pen during the study. These birds did not nest. All geese were wing clipped to facilitate their capture. Rice, cracked corn, and commercial pigeon pellets (20% protein) were fed *ad libitum* before and during the study at two sites positioned outside territories of nesting pairs. Grasses and invertebrates were also available food items.

We weighed incubating females weekly, beginning on the first day of incubation and ending on the day their eggs hatched, and recorded nest-initiation dates (date of first oviposition) and clutch size for all females. The normal incubation period is 4 weeks in large subspecies of Canada Geese (Collias and Jahn 1959, Brakhage 1965, Hanson and Eberhardt 1971), and incubation longer than that was considered extended incubation in this study.

Nest attentiveness during incubation was measured with weight-activated nest platforms (Breckenridge 1956) and recorded on 12-v Rustrak strip chart recorders. Platforms were installed under the nests during egg laying, and chart records were checked daily to insure that they were operating correctly. Only when the recorders indicated a platform malfunction or on weighing days were the females flushed from the nest. Incubation period was defined as the number of days between the date that the last egg was laid and the date when all eggs had hatched. Recesses that we caused were excluded from all analyses except those in which we tested for the effect of recess time on the duration of incubation.

The effect of capturing and weighing females on their incubation behavior was tested by comparing within each week the total recess time taken on the day of weighing with the total daily recess times taken on the 2 days before and after that day. We compared data only from the 2 days following the first day of weighing and the 2 days preceding the last day of weighing, because these weighing days were the first and last days of incubation.

Activities of females during recesses were observed from blinds located on the perimeter of the pen. The amount of time each female spent feeding was determined by point sampling every 15 s (instantaneous sampling, Altman 1974) for the duration of the recess.

Differences in recess times and body weights were tested with t-tests. Changes in recess activities through time and differences between age groups were compared with Chi-square tests. We used Spearman's rank correlation (Siegel 1956) to relate body-weight losses to initial incubation body weights and to correlate total recess time with the duration of incubation. Linear regression procedures were those of Remington and Schork (1970).

Results

Incubation patterns.—Within each week of incubation, the total daily recess times taken by experienced and inexperienced females on weighing days were not significantly different from their daily recess times taken during the two days before or after that day (all $P < 0.05$). Consequently, data from weighing days (except for the time females were away from the nest during weighing; see methods) were included in all analyses.

Females ($n = 13$) spent an average of 97.5% of the 4 weeks of incubation on their nests. Attentiveness ranged from 95.3 to 98.6%, which represented almost a three-fold difference in the total amount of recess time taken among individuals. Modal recess length ($n = 1{,}010$) was 15 min, with recesses shorter than this occurring approximately twice as often as longer recesses. The proportion of recesses of varying length was as follows: 1–10 min, 39.9%; 11–20 min, 44.6%; 21–30 min, 10.1%; 31–50 min, 5.4%.

The initiation of incubation recesses during the day showed a bimodal pattern, with peaks at 0700–0800 PST (7.5%) and 1700–1800 (14.9%) ($n = 1{,}010$). Twenty-four percent of the recesses were initiated between 0600 and 1000, whereas 50.4% of the recesses were initiated between 1600 and 1900. Only 4.8% of the recesses were initiated during night time. Sunrise varied from 0630 PST on 12 March to 0505 on 11 May, and sunset ranged from 1814 to 1911, respectively. The average (± SE) recess length in the afternoon (15 ± 0.4 min, $n = 641$) was significantly longer than the average length of morning recesses (12 ± 0.5 min, $n = 359$, $t = 7.73$, $P < 0.001$).

Females became less attentive as incubation proceeded, because recesses increased in duration and frequency (Fig. 1). Total weekly recess time increased steadily through the first 3 weeks of incubation for both experienced and inexperienced females (Table 1). Recess times did not vary significantly with experience during the first 3 weeks, although the average weekly recess times were always longest for

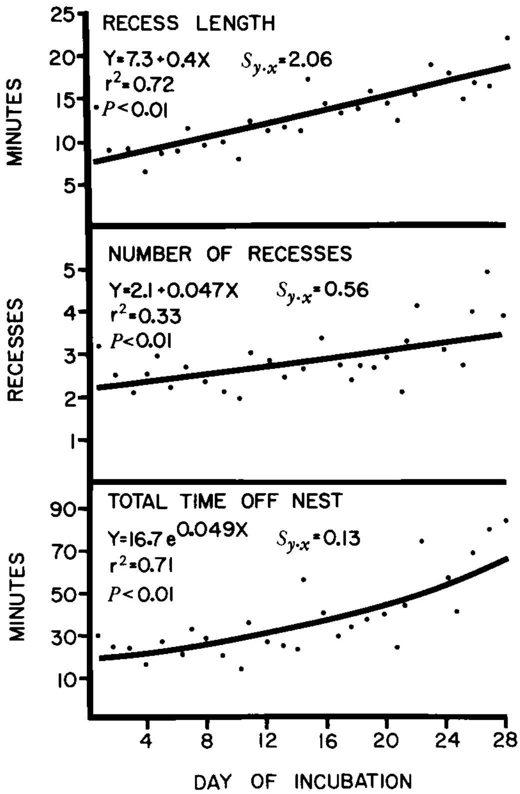

Fig. 1. Changes in incubation behavior (per day/female) of female Canada Geese related to the day of incubation (n = 13 females). Regressions and all statistics were calculated from individual data points for each female. For clarity of illustration, points plotted on each graph represent mean values.

inexperienced females. In the 4th week of incubation for inexperienced females and in the 5th week of extended incubation for two experienced females with infertile eggs, the total recess time increased approximately 3 and 2 times, respectively, over what it had been in the previous week. Inexperienced females spent approximately three times more time off the nest than did experienced females during the 4th week of incubation. The total amount of weekly recess time taken by experienced females was most similar to the amount of recess time taken by inexperienced females 1 week earlier in the incubation period.

Weight dynamics.—Females lost weight during all 4 weeks of the incubation period, but progressively less weight was lost each week as incubation continued (Table 2). The total

TABLE 1. Total weekly recess time (min ± SE) taken by female Canada Geese.

Week of incubation	Experienced females (n = 9)		Inexperienced females (n = 4)	Total (n = 13)
1	145 ± 20	ns[a]	175 ± 15	154 ± 19
2	170 ± 45	ns	219 ± 9	185 ± 12
3	237 ± 19	ns	299 ± 31	256 ± 18
4	285 ± 32	*	926 ± 144	482 ± 97
5[b]	643			

[a] ns = nonsignificant difference between experienced and inexperienced females; * = $P < 0.01$; t-test.
[b] Week 5 represents extended incubation of two females with infertile eggs.

amount of body weight lost during incubation varied with experience. Experienced females lost 1,243 g (28%), and inexperienced females lost 997 g (24%) ($t = 3.71$, $P < 0.01$). During the week of extended incubation, one experienced female lost 80 g in body weight, while the other gained 230 g over her weight the previous week.

Inexperienced females began incubation at a significantly lower body weight than did experienced females, but weights were not significantly different during the last week of incubation (Table 2). Chronologically, body weights of inexperienced females were most similar to body weights of experienced females 1 week later in the incubation period.

When we ranked all females according to body weight at the beginning of incubation, we found that heavier females lost more weight during the normal incubation period ($r_s = +0.89$, $P < 0.01$). These females also lost a greater proportion of their initial incubation weight than did lighter females ($r_s = +0.79$, $P < 0.01$). Variation in body weight among females at the end of incubation (CV = 3.8%) was less than at the beginning (CV = 5.3%).

Nest attentiveness of a female was related to her body weight at the beginning of incubation (Fig. 2). Heavier females left their nests for less total time than did lighter females ($r_s = -0.91$, $P < 0.01$). Total weekly recess time was related to the weight of the female at the beginning of each week (Fig. 3). Recess time gradually increased with decreasing body weight until a lower critical weight of around 3,200–3,300 g was reached. At that point, recess time increased dramatically. Experienced females began incubation at a high enough body

TABLE 2. Body-weight (g ± SE) changes of female Canada Geese during incubation.

Day of incubation	Experienced females (n = 9) Weight	Experienced females (n = 9) Change from previous week (%)		Inexperienced females (n = 4) Weight	Inexperienced females (n = 4) Change from previous week (%)
1	4,409 ± 56		**[a]	4,070 ± 77	
8	4,024 ± 48	−385 (−9)	**	3,742 ± 72	−328 (−8)
15	3,693 ± 58	−331 (−8)	*	3,465 ± 69	−277 (−7)
22	3,424 ± 50	−269 (−7)	ns	3,235 ± 67	−230 (−7)
29	3,166 ± 33	−258 (−8)	ns	3,073 ± 78	−162 (−5)
36	3,165[b]	+75[b]			

[a] ns = nonsignificant difference in body weights of experienced and inexperienced females; * = $P < 0.05$; ** = $P < 0.01$; t-test.
[b] Represents a weight gain from previous week for two females with infertile eggs.

weight that after 4 weeks of incubation their weight did not fall far below 3,200 g (Table 2). Inexperienced females, however, reached 3,200 g after 3 weeks of incubation.

Females that took more weekly recess time lost less weight during that week than did females that were more attentive (Fig. 4). As incubation proceeded, more recess time was taken for any given weekly weight loss, especially by inexperienced females during the 4th week of incubation.

Activity budgets.—The percentage of time spent feeding during recesses increased for both experienced ($\chi^2 = 20.80$, 3 df, $P < 0.01$) and inexperienced ($\chi^2 = 8.25$, 3 df, $P < 0.001$) females as incubation proceeded (Table 3). Inexperienced females fed for a higher proportion of their recess time during the 1st, 4th, and combined total weeks of incubation than did experienced females. Proportionately more time was devoted to feeding during long recesses (Fig. 5). During short recesses (<5 min), females generally spent their time in readjusting or adding nest material. Proportionately more time was spent feeding during afternoon recesses (42.9%) than during morning recesses (33.4%, $\chi^2 = 8.46$, 1 df, $P < 0.005$). This, however, may be because recesses during which those data were collected were longer in the afternoon (19 ± 1.6 min) than in the morning (11 + 1.2 min; $t = 3.5$, 59 df, $P < 0.001$).

Attentiveness and duration of incubation.—Total time spent off the nest during incubation was directly related to the duration of incubation (Table 4). Females that were the most attentive had the shortest incubation period ($r_s = -0.67$, $P < 0.05$). The variation in the duration of incubation among females (2 days), however, was more than the differences in the total amount of recess time taken among females (28 h). Clutch size tended to be inversely correlated with incubation length ($r_s = -0.50$, $0.1 > P > 0.05$) (Table 4).

Clutch size and body weight.—Females with clutches of 4 eggs began incubation at a lighter body weight ($\bar{x}$ = 4,070 g ± 76, n = 4; t = 3.41, $P < 0.01$, 11 df) than the average weight of females with 5- ($\bar{x}$ = 4,387 g ± 69, n = 3), 6- ($\bar{x}$ = 4,358 ± 64, n = 5), and 7-egg (4,730, n = 1) clutches. There was no difference in weight among females with clutches of 5 or 6 eggs (t = 0.29, $P > 0.5$, 6 df). All 4-egg clutches were laid by inexperienced females, and no inexperienced female laid more than 4 eggs.

DISCUSSION

The incubation pattern of a species is one aspect of the reproductive strategy that should maximize lifetime reproductive success. Canada Geese are long-lived and iteroparous, and only the female incubates. Her incubation behavior, consequently, should be a compromise between maximizing the hatching success of eggs and minimizing the risk of starvation or debilitation associated with incubation. A female's success in hatching her clutch is reduced by the failure of eggs to develop properly and by predation. Consequently, a female should behave in a fashion that minimizes these losses.

Thermal considerations.—Nest microclimate is an important factor in determining embryonic development. Optimal embryonic development occurs within narrow temperature limits, and death can result from extreme egg cooling

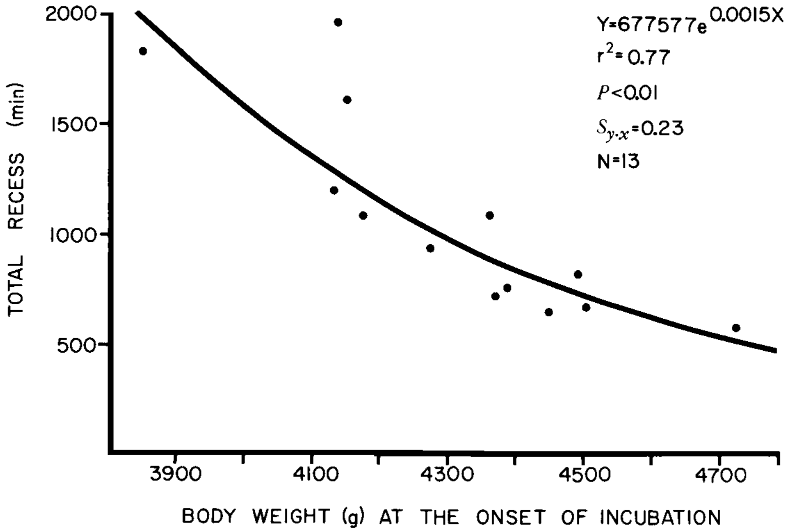

Fig. 2. Total recess time taken during incubation in relation to beginning incubation body weight of female Canada Geese.

(Lundy 1969). Because Canada Geese generally nest at latitudes that have ambient temperatures well below that necessary for egg development, body heat must be transferred to the eggs to promote growth. The longer incubation periods for females that were less attentive (Table 4) suggest that eggs require a given amount of heat to complete embryonic development. Although differences in the duration of incubation among females were more than the differences in the total amount of recess time taken by females, the amount of time females spent on the nest during egg laying was unknown and could have influenced the length of incubation. Clutch size tended to be inversely correlated with incubation length (Table 4) and

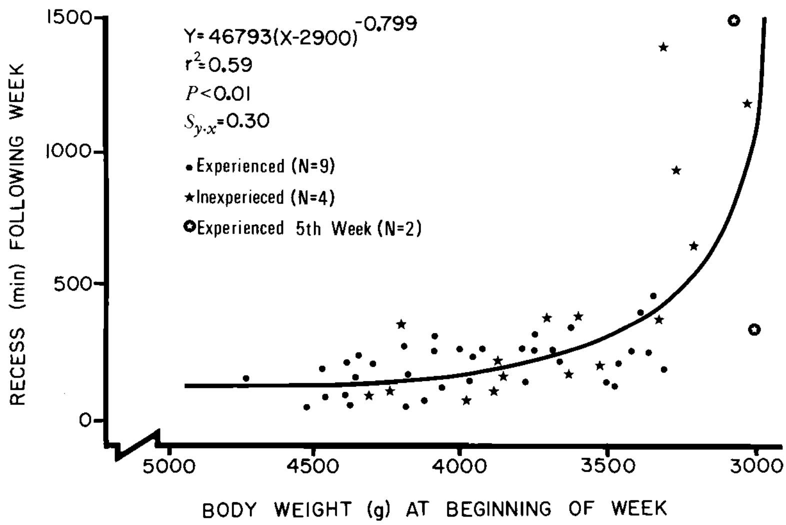

Fig. 3. Weekly recess time in relation to body weight of female Canada Geese at the beginning of each week of incubation.

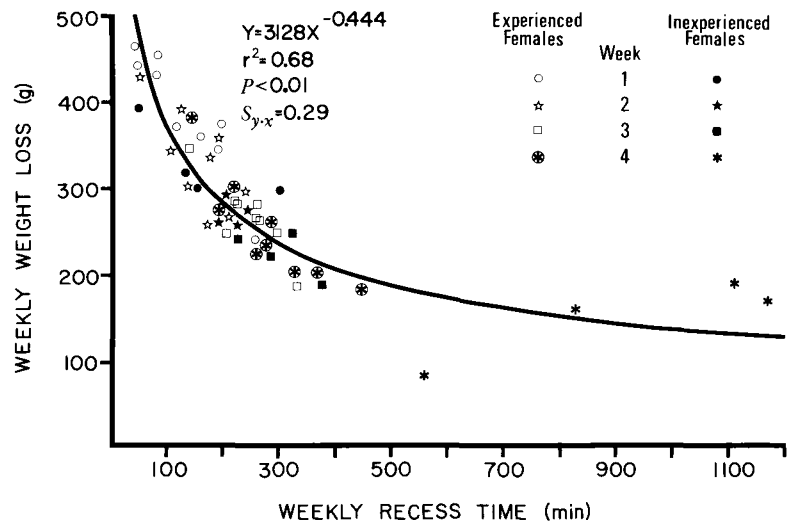

Fig. 4. Relationship between the amount of weekly recess time and the amount of weight lost during that week by incubating female Canada Geese.

may offer indirect evidence that females with larger clutches spent more time on the nest before clutch completion than did females with smaller clutches. Cooper (1978) found that female Canada Geese did not begin incubation abruptly but spent progressively more time on the nest with each egg laid. Cargill and Cooke (1981) concluded that some embryonic development takes place during egg laying in Lesser Snow Geese. Females with large clutches may therefore spend proportionately more time on the nest during egg laying and consequently have a shortened incubation period.

Differential heating and cooling rates of eggs may also contribute to the disproportionately long incubation periods of inattentive females.

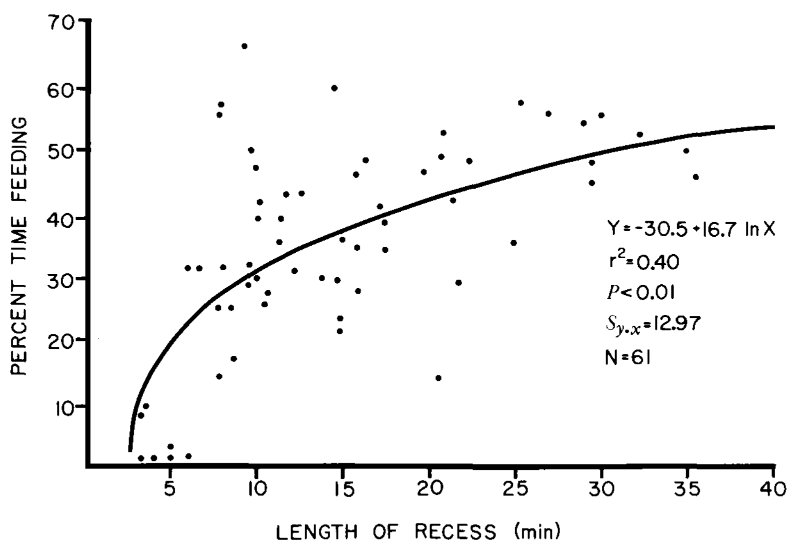

Fig. 5. Relationship between recess length and percentage of time spent feeding by incubating female Canada Geese.

TABLE 3. Foraging activity of female Canada Geese during incubation recesses.

Period of incubation	Experienced females ($n = 9$) n[a]	Experienced females ($n = 9$) Percentage of time feeding		Inexperienced females ($n = 4$) n[a]	Inexperienced females ($n = 4$) Percentage of time feeding	Total ($n = 13$) n[a]	Total ($n = 13$) Percentage of time feeding
Week 1	558	29	*[b]	280	41	838	33
Week 2	721	38	ns	283	40	1,004	39
Week 3	496	38	ns	188	45	684	40
Week 4	503	42	**	620	49	1,123	46
Week 5[c]	458	64				458	64
Total[d]	2,278	37	**	1,371	45	3,649	40

[a] Number of observations based on 15-s intervals (see Methods).
[b] Comparisons between experienced and inexperienced females; * = $P < 0.05$; ** = $P < 0.01$; ns = non significant; χ^2 test.
[c] Week 5 represents extended incubation of two females with infertile eggs.
[d] Total does not include week 5.

Drent (1973) showed that Herring Gull (*Larus argentatus*) eggs cooled more quickly than they could be reheated and suggested a thermal advantage may be gained by taking less total recess time or by taking fewer recesses of longer duration.

Timing, frequency, and length of incubation recesses taken by Canada Geese suggest that female behavior is adapted to facilitate egg development. Recesses were taken more often in the afternoon than in the morning and were rarely taken at night. Because ambient temperatures are generally highest in the afternoon, this behavior would minimize cooling of eggs. Females were also less attentive during the later stages of incubation, which coincided with increasing daily mean temperature and embryo thermogenesis.

Embryonic heat production may influence the timing of recesses within the incubation period. As incubation proceeds, an embryo generates increasing amounts of metabolic heat. The heat produced near the end of incubation represents a significant proportion of heat required for egg development (Drent 1970). Egg cooling during incubation recesses would consequently be less in the final stages of incubation and would allow a female to leave the nest for longer periods of time without incurring as great a penalty in egg development. Ricklefs (1974), however, did not believe that embryonic heat production generally had been a major factor in the evolution of incubation patterns, because its effects are significant only near the end of incubation. In geese, incubation occurs essentially under a fasting regime, and the female's body weight is the lowest of the annual cycle at the end of incubation. The decreased attentiveness observed at the conclusion of incubation is permissible because of embryonic heat production and suggests that maximum energy was put into the eggs and the early incubation effort.

Predator considerations.—The reproductive success of a female is also affected by predation, and patterns of incubation behavior that minimize these losses are adaptive. The importance of attentiveness to reproductive success has been demonstrated by a greater rate of loss of clutches of female geese that are least attentive (Harvey 1971, Inglis 1977, Raveling and Lumsden 1977). Female geese were lightest in body weight at the end of incubation (Table 2) and probably could not maintain a high degree of attentiveness past the normal incubation period without risking debilitation or starvation (Harvey 1971, Ankney and MacInnes 1978, Raveling 1979a). This indicates that females maximize their attentiveness and thereby reduce the risk of predation on their eggs. In ad-

TABLE 4. Duration of incubation related to attentiveness and clutch size of female Canada Geese.

Duration of incubation (days)	Total recess (h ± SE) taken during incubation (range)[a]	Clutch size
28 ($n = 2$)	15.2 (13.5–16.9)	5.5 (5–6)
29 ($n = 7$)	23.7 ± 3.8 (12.9–43.8)	5.3 (4–7)
30 ($n = 2$)	43.5 (40.2–46.9)	4.0 (4)

[a] For comparison these values include total recess time only through the 28th day.

dition to acting on the total recess time taken by incubating females, selection probably also operates on the frequency and length of recesses to minimize the risk of predation.

Physiological considerations.—Although environmental conditions and the requirements of developing eggs influence the incubation behavior of waterfowl (Low 1945, Breckenridge 1956, Caldwell and Cornwell 1975, Miller 1976, Cooper 1978, Afton 1980), they do not explain all the observed variation in attentiveness among individuals in this study, as females nesting at the same time and location showed widely different incubation patterns. As incubation is an energetically demanding period for geese, behavioral patterns should also be a reflection of the energy requirements of the female.

Increases in recess length and frequency were related to the day of incubation (Fig. 1) and coincided with decreasing body weights of females. Longer recesses provided more time to feed (Fig. 5) and were taken more frequently at the end of incubation (Fig. 1), when females were approaching their lowest body weight. A behavioral mechanism dependent on body weight, or a constituent of body weight, was probably operating. Sherry et al. (1980) demonstrated that any perturbation in the normal rate of weight loss during incubation in Red Junglefowl (*Gallus gallus spadiceus*) was countered with changes in the incubation and feeding behavior of the female, which brought body weights back to normal. The amount of weekly recess time taken by female Canada Geese was related to their body weight at the beginning of the week, which indicates a similar mechanism for the control of their behavior.

Although the mechanism for the control of behavior during most of the incubation period is probably based on a function of body weight, the abrupt change in behavior of inexperienced females in the 4th week and experienced females during extended incubation (Table 1) may be associated with the depletion of an essential nutrient reserve. The great increase in recess time and in the percentage of time spent feeding (Table 3) and the lack of a proportional decrease in weight loss in the 4th week of incubation for inexperienced females (Fig. 3) suggest that the depletion of lipids and the catabolism of body protein may have triggered the change in behavior. The use of protein increases at the end of incubation, after fat stores have been reduced (Ankney and MacInnes 1978). Protein contains only about one-half the energy per unit weight as does fat (4.2 vs. 9.5 kcal/g, cf. Ricklefs 1974). The catabolism of protein in late incubation would consequently result in a greater weight loss for a given amount of recess time and would explain the lack of response in body weight with increasing recess times.

Females that were heavier at the beginning of incubation were more attentive than lighter females (Fig. 2). This indicates that the differences in beginning incubation weights were partly related to differences in body reserves, even though some variation in the structural size of females probably existed. If the reduction of body protein to some critical level controls the cessation of egg laying (Jones and Ward 1976, Raveling 1979a), then nonstructural differences in beginning incubation weights were probably due to differences in lipid reserves. Any variable affecting the amount of fat available for incubation would consequently influence the attentiveness of a female. Shortened hyperphagic periods (McLandress and Raveling 1981) or delayed egg laying in spring (Raveling 1979a, b) would both decrease the amount of fat available for incubation and affect the attentiveness of the female.

Age and experience considerations.—In geese, older females lay larger clutches than do younger females (Brakhage 1965, Cooper 1978, Finney and Cooke 1978), which indicates that age influences the amount of reserves acquired for the reproductive effort. Our results suggest that experience is more important than age in affecting the acquisition of reserves. Females with no prior breeding experience laid fewer eggs and began incubation at a lighter body weight (Table 2) than did experienced females. The inexperienced females, however, were 4 and 5 yr old, but their egg production was that of 2- or 3-yr-old wild females nesting for the first time. Crowded conditions in captivity commonly result in delayed onset of reproduction of geese (Wood 1964, 1965).

Several mechanisms exist that may explain the differential incubation weights associated with experience. Unpaired adult geese are lighter during winter than are paired geese (McLandress and Raveling 1981). If inexperienced females were not paired during the previous winter, then they would begin hyperphagia in spring at a lower body weight than experienced females. Even if the rate of weight gain were equal for all females, inexperienced females would not be as heavy at the end of a given length of hyperphagia. We did not know the status of inexperienced females during the winter of this study.

Inexperienced geese may also be physiologically limited in their ability to acquire body reserves. Hormonal changes associated with reproduction are related to experience and generally occur later in inexperienced Canada Geese (Akesson and Raveling 1981). If hormonal changes associated with hyperphagia also are related to experience, then the timing and magnitude of spring weight gains in inexperienced females would also be affected.

Inattentiveness by a female prolongs incubation (Table 4) and exposes the nest to predation, which consequently could decrease the reproductive success of an individual. The energetic inability of inexperienced female geese to maintain a high degree of attentiveness throughout the incubation period may be the major explanation for their lower hatching success (Brakhage 1965, Cooper 1978).

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