

# PARENTAL BEHAVIOR OF CACKLING CANADA GEESE DURING BROOD REARING: DIVISION OF LABOR WITHIN PAIRS<sup>1</sup>

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**Abstract.** Behavior of pairs of Cackling Canada Geese (*Branta canadensis minima*) was studied on the Yukon-Kuskokwim Delta, Alaska, during the brood-rearing period in 1978 and 1979. Foraging time consisted of cycles of alert postures followed by periods of grazing, when individuals searched for, or consumed, food. Females had shorter alert periods ( $\bar{x}$  = 5.58 sec) than males ( $\bar{x}$  = 8.04 sec) during all four possible time periods (two time periods in each of 2 years), although differences were significant in only one of these periods. Females also had significantly longer grazing periods than males ( $\bar{x}$  = 10.67 sec vs. 8.42 sec) during three of the four time periods. Females spent an average of 74% and 58% of foraging periods actually grazing prior to and during the molt, respectively, whereas males spent only 52% and 58% of foraging time grazing during these two time periods. Less vigilance by females relative to males resulted in females spending a greater percentage of their total time budget grazing, although the difference was significant only before the molt in 1979. The proportion of foraging periods in which adults were alert was positively related to the number of goslings in their broods for both sexes, but when pairs associated with no goslings were removed from the analyses, the relationship was no longer significant for females. These data support the hypothesis that long-term monogamy in geese is beneficial in part because males are able to assume greater responsibility for vigilance after hatching, allowing females to replace depleted protein and lipid reserves. The relationship between alert behavior and brood size does not support a recent model of parental investment which predicts no such relationship (Lazarus and Inglis 1986).

**Key words:** *Monogamy; parental investment; behavior; Canada Goose; Branta canadensis minima.*

## INTRODUCTION

Geese form long-term pair-bonds, and in most populations pairs remain together throughout the year (Owen 1980), although in the smallest geese pair members may frequently be separated during fall migration and winter (Sedinger and Bolinger 1987, Johnson and Raveling 1988). Maintenance of pair-bonds is thought to be beneficial for defense of winter food resources (Hanson 1953, Raveling 1970, Black and Owen 1989) and earlier, and consequently greater, spring weight gain by females (McLandress and Raveling 1981a). Advantages of this social system accrue in part because female geese rely heavily on stored lipid and protein reserves to produce and incubate a clutch of eggs (Ankney and MacInnes 1978, Raveling 1979a), and females may require several weeks in spring to acquire sufficient reserves

for both migration and breeding (Raveling 1979b, McLandress and Raveling 1981a, Ankney 1982). Presumably, the presence of a mate during this period not only plays a role in stimulating hyperphagia in females (McLandress and Raveling 1981b), but also elevates their social rank (Hanson 1953, Raveling 1970), thus providing better access to food resources and more time for feeding than they could otherwise attain. Maintenance of family groups has also been shown to elevate the social status of juveniles (Hanson 1953, Fischer 1965, Raveling 1970, Black and Owen 1989), increasing their foraging time (Black and Owen 1984) and food availability (Black and Owen 1989).

During nesting, defense of territories may be related to female foraging requirements (Inglis 1976). Protection of paternity (Mineau and Cooke 1979a, 1979b; Welsh 1988), reduced harassment of females (Ewaschuk and Boag 1972, Inglis 1977, Mineau and Cooke 1979b), or reduced predation (Aldrich 1983) also contribute to the advantages of pair-bond maintenance for one or both members of pairs.

Because of the physiological demands of egg

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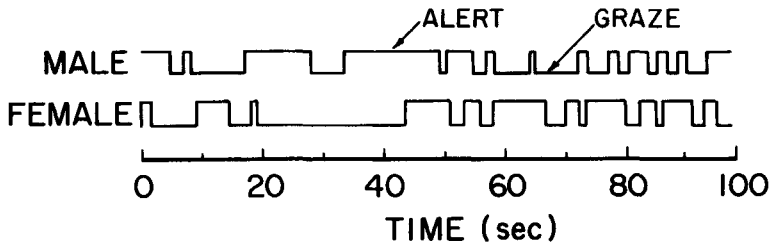


FIGURE 1. Typical pattern of grazing and alert periods for a pair of Cackling Geese.

production and incubation, female geese reach their lowest annual levels of carcass protein and lipid when clutches hatch (Ankney and MacInnes 1978, Raveling 1979a). Protein levels are restored following hatching during a period when vegetation of high protein content is available (McLandress and Raveling 1981a, Cargill and Jefferies 1984, Sedinger and Raveling 1986). Of course lipids must also be replenished prior to fall migration.

Geese have precocial young and consequently little attention has been given to their parental investment following hatching (but see Lazarus and Inglis 1978, Lessells 1987). Goslings are brooded regularly during their first 2 weeks (Ebbinge and Ebbinge-Dallmeijer 1975, pers. observ.), and both sexes may participate in vigilance for predators (Lazarus and Inglis 1978) and/or aggressive interactions. Vigilance potentially conflicts with feeding time necessary for adults, particularly females, to restore depleted protein and lipid reserves following hatching. To the extent that female condition at the end of brood rearing influences future survival or reproduction, males should adopt behaviors that allow their mates to restore depleted reserves because this likely will enhance their own fitness.

We studied the behavior of adult Cackling Canada Geese (*Branta canadensis minima*) on the Yukon-Kuskokwim Delta, Alaska, during brood rearing in 1978 and 1979. Our goals were to describe the proportion of time allocated to important activities, examine the roles of both members of pairs in vigilance, and determine the relationship between brood size and vigilant behavior. We reported on gosling behavior elsewhere (Sedinger and Raveling 1988).

#### METHODS

We observed adult Cackling Geese from an interconnected cabin and observation tower be-

tween 27 June and 8 August 1978, and 20 June and 9 August 1979. The tower was located within a 40.4-ha study area 10 km south of Old Chevak (61°N, 165°W), a U.S. Fish and Wildlife Service field station (see Mickelson 1975 for a general description of the area).

The peak of hatching occurred on 21 and 20 June in 1978 and 1979, respectively, and fledging began during the first week of August (Sedinger and Raveling 1984). Observations used in our analyses were made between 06:00 and 23:00.

Foraging adult geese alternated regularly between alert periods and grazing periods when they searched for, or consumed, food (Fig. 1). These behaviors corresponded to "head-up" plus "extreme head-up," and "graze," respectively, of Lazarus and Inglis (1978). We measured the duration of alert and grazing periods of males and females while foraging, to the nearest 0.5 sec. In a subsample of these measurements, durations of both behaviors were measured for the same individual. The ratio of the average length of grazing periods to the sum of the average lengths of grazing plus alert periods provided an estimate, for each individual, of the percentage of foraging time spent grazing, i.e., searching for, or consuming, food.

We assessed the independence of alert and grazing periods between members of pairs by examining the proportion of foraging periods that males and females simultaneously were alert (or grazing) compared to the proportional overlap in these behaviors expected by chance (i.e., the product of the proportions of time spent in a behavior by each member of a pair). If pairs coordinated their behaviors to minimize overlap in time spent alert we should have observed less overlap in alert behavior than expected by chance.

Individual pairs were observed for periods of 1 hr to 7 hr and the behavior of both members of the pair was assigned to one of the following

categories at 5-min intervals: foraging (which included grazing and alert behaviors), resting (sitting and not engaged in other activities), preening, bathing, moving (walking or running without engaging in other behavior), and agonistic activities. A single estimate of activity for each observation period was calculated as the percentage of 5-min sample points spent in each behavior during the period. We estimated the percentage of the total time budget spent grazing by multiplying the percentage of time spent foraging (from 5-min samples) by the proportion of total foraging time actually spent grazing by individuals for whom the lengths of alert and grazing periods were measured. Time spent alert was estimated as the product of foraging time and the proportion of foraging time spent in alert postures. Each of these samples (activity over an entire observation period) was treated as an independent estimate of behavior, although geese were unmarked and there was some potential for sampling some pairs more than once during a summer. We calculated approximate probabilities of repeatedly sampling pairs by counting all pairs within 400 m of the observation tower nearly daily in 1978 and 1979. The peak number present during a single count was used to calculate the probability of selecting a pair for observation in each year. We assumed that each pair was equally likely to be selected for an observation period and used the binomial distribution to estimate the probability of a pair being sampled more than once. We distinguished males from females based on the larger body sizes of males (Raveling 1978) and recorded size of broods for all pairs sampled.

For analysis of behavioral data we divided the brood-rearing period into two parts: (1) prior to the molt of adult remiges (pre-molt, first 23 days after hatching), (2) adult molt plus the gosling fledging period (molt-fledge, 24th–49th days after hatching) because adult behavior might depend on molt status either for nutritional (Raveling 1979a, Ankney 1984) or predator avoidance reasons. This criterion also divided the brood-rearing period at about its midpoint. The two time periods were separated by 15 and 14 July in 1978 and 1979, respectively.

Our estimates of the percentage of the total time budget spent grazing and alert were products of independent estimates of time spent foraging and the proportion of foraging time spent grazing or alert. We calculated the variance of

our estimates of percentage of time spent grazing and alert from the formula for the variance of the product of two random variables (Mood et al. 1974, p. 180).

Between-year and between-sex comparisons of percentage of time spent grazing and alert were made using *t*-tests because of the composite nature of the estimates. Other between-sex or between-time-period comparisons of percentage of time spent performing behaviors were made using Mann-Whitney *U*-tests. Comparisons between the sexes of percentages of foraging periods spent grazing were made using Mann-Whitney *U*-tests. We tested for diurnal variation in percentage of time spent in each of the behavioral categories using Kruskal-Wallis tests, with 2-hr time periods between 06:00 and 22:00 serving as treatment levels.

Individuals were repeatedly sampled to estimate the lengths of alert periods and feeding bouts. Therefore, some measures of these behaviors were not independent with respect to individuals. We analyzed between-sex differences in the duration of these periods using a nested ANOVA, with individuals as the nesting factor, to account for the lack of independence of samples collected from the same individual.

The relationships between brood size and percentage of time spent foraging or percentage of foraging time spent alert were examined for both males and females by linear regression. For analysis of the percentage of foraging time spent alert vs. brood size relationship, samples were combined across years and time periods (pre-molt, molt-fledge) after first testing for variation in adjusted mean levels of percentage of foraging time spent alert in each time period using ANCOVA. Analysis of covariance and nested ANOVA were performed using the BMDP Statistical Computing Package (Dixon 1985).

## RESULTS

As many as 100 broods were within 1 km of the observation tower in 1978 which provided a maximum estimate of the number of broods from which behaviors were sampled. The peak numbers of broods counted on the 40.4-ha study in 1978 and 1979 were 46 and 24, respectively, which provided a minimal estimate of the number of broods sampled. For 46 broods sampled 49 times (sample size for time budgets in 1978) the binomial probability of sampling any one brood more than once was 0.083 if broods dis-

TABLE 1. Lengths (sec) of grazing and alert periods ( $\bar{x} \pm SE$ ) of adult Cackling Geese with broods during 1978 and 1979.

Sex	Premolt				Molt-fledge			
	Grazing		Alert		Grazing		Alert	
	1978	1979	1978	1979	1978	1979	1978	1979
Males	7.11	8.07	7.93	7.71	7.52	10.27	7.95	8.54
	$\pm 0.44$	$\pm 0.45$	$\pm 1.95$	$\pm 1.10$	$\pm 0.37$	$\pm 0.47$	$\pm 1.09$	$\pm 1.52$
	(101) <sup>a</sup>	(150)	(107)	(63)	(246)	(219)	(184)	(95)
	**b	*	ns	*	*	ns	ns	
Females	12.11	11.10	5.32	4.05	9.24	11.06	5.84	6.45
	$\pm 1.16$	$\pm 0.87$	$\pm 0.84$	$\pm 0.48$	$\pm 0.48$	$\pm 0.54$	$\pm 0.90$	$\pm 1.39$
	(134)	(128)	(109)	(67)	(222)	(177)	(177)	(98)

<sup>a</sup> Number of feeding bouts or alert periods measured.

<sup>b</sup> Statistical comparison (nested ANOVA, see Methods) of males and females; \*\*,  $P < 0.001$ ; \*,  $P < 0.05$ ; ns, not significant.

tributed themselves randomly. The comparable probability for 1979 was 0.646. Therefore it is likely that we did sample some broods more than once. Even under the conservative assumption that only 24 broods were available for sampling, the probability that we sampled five broods more than once is 0.11 (0.646<sup>5</sup>). We believe these estimates are conservative because our peak counts underestimated the number of broods actually available for sampling over the course of a field season. It is therefore unlikely that our assumptions about sample size inflated the sensitivity of our statistical analyses sufficiently to have altered our hypothesis tests.

We detected significant diurnal variation in behavior in only two (bathing and resting of males in 1979) of 24 tests (six behavioral categories for two sexes in each of 2 years). Because of the small number of significant results, given the large number of statistical tests, and the absence of a discernible pattern, we attributed to sampling error the observed diurnal variation for two be-

haviors in 1979 males. We therefore performed subsequent analyses on behavioral data pooled across daily time periods.

While foraging, females had significantly longer grazing periods than males prior to the molt in both 1978 and 1979 and during the molt-fledge period in 1978 (Table 1). In contrast, males had longer alert periods than females both prior to and during the molt in both years, although the difference was significant only during the 1979 premolt period. Differences in the duration of grazing and alert periods resulted in females searching for, or consuming, food a larger percentage of foraging periods than did males during all four of the possible time periods, highly significantly so prior to the molt in both years (Table 2). We detected no systematic coordination of alert periods by pairs; 17 of 33 pairs for which we simultaneously observed behavior for the male and female overlapped in alert behavior less than expected by chance, while the remainder overlapped more than expected.

TABLE 2. Mean percentage ( $\pm SE$ ) of foraging periods actually spent grazing (searching for or consuming food) by adult Cackling Geese on the Yukon-Kuskokwim Delta.

Sex	Premolt		Molt-fledge	
	1978	1979	1978	1979
Males	50.9 $\pm$ 4.7	54.0 $\pm$ 4.4	55.9 $\pm$ 4.5	60.6 $\pm$ 4.6
	(10.8–86.2) <sup>a</sup>	(30.2–80.7)	(8.8–87.3)	(18.4–95.6)
	(17) <sup>b</sup>	(14)	(26)	(26)
	$P = 0.002^c$	$P < 0.002$	$P = 0.09$	$P < 0.054$
Females	73.0 $\pm$ 4.1	74.6 $\pm$ 3.4	66.9 $\pm$ 3.5	70.7 $\pm$ 4.4
	(40.3–95.3)	(45.4–92.1)	(18.2–92.4)	(7.0–97.5)
	(15)	(17)	(25)	(28)

<sup>a</sup> Range of observed values.

<sup>b</sup> Number of separate intervals in which % of time spent grazing and alert were determined.

<sup>c</sup> Statistical comparisons of males and females were made with Mann-Whitney  $U$ -tests.

TABLE 3. Time budgets of adult Cackling Geese during brood rearing.

Time period (n) <sup>a</sup>	Mean ( $\pm$ SE) percentage of time devoted to behaviors						
	Grazing	Alert	Resting	Preening	Bathing	Moving	Agonistic
1978 Premolt (25)							
Males	32.4 $\pm$ 3.7 <sup>b</sup>	31.2 $\pm$ 3.6	24.1 $\pm$ 3.7	6.2 $\pm$ 1.3	1.0 $\pm$ 0.5	3.5 $\pm$ 1.0	1.6 $\pm$ 0.5
Females	41.4 $\pm$ 3.6	15.3 $\pm$ 2.6	32.4 $\pm$ 3.8	6.4 $\pm$ 1.8	0.8 $\pm$ 0.4	3.4 $\pm$ 1.0	0.2 $\pm$ 0.2
1978 Molt-fledge (24)							
Males	40.6 $\pm$ 3.7	32.0 $\pm$ 3.6	11.6 $\pm$ 1.8	9.9 $\pm$ 1.5	1.2 $\pm$ 0.4	4.7 $\pm$ 1.0	0.1 $\pm$ 0.1
Females	46.1 $\pm$ 3.0	22.8 $\pm$ 2.6	14.1 $\pm$ 1.8	10.7 $\pm$ 1.3	1.4 $\pm$ 0.6	4.8 $\pm$ 1.0	0.1 $\pm$ 0.1
1979 Premolt (23)							
Males	34.5 $\pm$ 3.1	29.3 $\pm$ 3.0	22.6 $\pm$ 2.1	8.0 $\pm$ 1.2	1.2 $\pm$ 0.5	3.8 $\pm$ 1.7	0.6 $\pm$ 0.3
Females	43.4 $\pm$ 2.6	14.8 $\pm$ 2.3	28.0 $\pm$ 2.3	8.9 $\pm$ 1.9	1.0 $\pm$ 0.4	3.9 $\pm$ 1.8	0.0 $\pm$ 0.0
1979 Molt-fledge (29)							
Males	35.5 $\pm$ 3.1	23.0 $\pm$ 2.9	23.9 $\pm$ 2.0	10.2 $\pm$ 1.1	2.6 $\pm$ 0.7	4.7 $\pm$ 0.8	0.2 $\pm$ 0.1
Females	40.4 $\pm$ 2.9	16.8 $\pm$ 2.6	24.0 $\pm$ 2.2	11.3 $\pm$ 1.2	2.8 $\pm$ 0.8	4.7 $\pm$ 0.8	0.1 $\pm$ 0.1

<sup>a</sup> Both members of pairs were sampled simultaneously so sample size represents both males and females.

<sup>b</sup> SE for grazing and alert was estimated as the ratio of the SD (estimated from Mood et al. 1974; see Methods) and the square root of the minimum sample size of estimates used in the calculation.

Grazing was the dominant behavior of females, while males spent similar amounts of time grazing and alert, before the molt in both years of the study (Table 3). There was no between-year difference in percentage of time devoted to grazing by either sex prior to the molt ( $P > 0.10$ , both sexes), but females spent a greater percentage of time grazing during this period than males (significant in 1979,  $P < 0.05$ ). Males were alert significantly more of the time than females before the molt ( $P < 0.005$ , both years). We detected no significant variation in alert or grazing time between the premolt and molt-fledge periods for either sex ( $P > 0.05$ , all comparisons). Nevertheless, shifts in behavior by both sexes between premolt and molt-fledge eliminated differences between the sexes in time devoted to alert or grazing during molt-fledge ( $P > 0.05$ , both behaviors).

Females rested a greater (but not significantly so,  $P > 0.18$ ) percentage of the time than males prior to the molt (average from both years 30% for females vs. 23% for males). Males were involved in aggressive interactions a greater percentage of time than females ( $P < 0.03$ , both years), but there were no other significant between-year or between-sex differences in behavior before the molt.

During the molt-fledge period, females reduced the time devoted to resting from that of the premolt period in both years but the difference was significant only in 1978 ( $P < 0.005$  in 1978,  $P > 0.2$  in 1979) (Table 3). Males reduced

their resting time in 1978 ( $P < 0.02$ ) but not in 1979 ( $P > 0.68$ ). Time involved in aggressive encounters by males also declined between the premolt and molt-fledge periods during 1978 ( $P < 0.005$ ) and 1979 but the difference was not significant in the latter year ( $P > 0.1$ ). As a result of differential changes in behavior by males and females between the premolt and molt-fledge periods there were no significant differences in the time budgets of the two sexes during the molt-fledge period ( $P > 0.30$ , all behaviors).

The percentage of foraging periods spent in the alert posture was significantly related to brood size for males ( $P < 0.001$ ) and females ( $P < 0.05$ , Fig. 2). The relationship was not significant for females when broods of zero were excluded from the analyses ( $P > 0.50$ ) but remained so for males ( $P < 0.05$ ).

## DISCUSSION

### ADULT VIGILANCE, DIVISION OF LABOR AND FEMALE BODY CONDITION

Goslings of arctic nesting geese suffer high rates of predation following hatching, particularly during their first 2 weeks of life (e.g., MacInnes et al. 1974, Mickelson 1975). Parental protection is important in reducing predation, and we have observed increased vulnerability to predation for goslings separated from their parents. Parental behavior by Cackling Geese reduces predation either by direct defense of the brood (primarily against Parasitic Jaegers, *Stercorarius parasiticus*, and Glaucous Gulls, *Larus hyperboreus*) or

by leading the brood to a safe environment, which is the principal response to arctic foxes (*Alopex lagopus*). Vigilance by the adults presumably increases the effectiveness of their defense of the brood. Martin et al. (1985) reported a significantly lower recapture rate for web-tagged goslings of "widowed" female Lesser Snow Geese (*Chen. c. caerulescens*) than for goslings of pairs, suggesting that lone females compared to intact pairs were either less vigilant or less capable of defending their broods, or both. Females might compensate for the loss of a mate during brood rearing by increasing their own vigilance as do incubating Lesser Snow Geese (Martin et al. 1985). However, this would reduce the females' feeding time and possibly, therefore, the restoration of their protein and lipid reserves before autumn migration.

Males may directly contribute to gosling survival or growth by maintaining brood integrity or by excluding other broods from the immediate foraging area (pers. observ.), in addition to their role in predator detection and defense. The investment in alert behavior by males is associated with their loss of carcass protein and body mass following hatching (Raveling 1979a). Male investment in vigilance allows females to spend more time grazing, thus restoring depleted protein and lipid reserves.

We believe that adult males would gain little by abandoning broods because males undergo smaller fluctuations in carcass protein content than do females (Raveling 1979a) and, therefore, have less need than females to consume large amounts of protein between hatching and fledging. Males that abandoned their mates and broods and attempted to form new pair-bonds the next winter would risk reduced reproductive success (Cooke et al. 1981).

PARENTAL INVESTMENT

Lazarus and Inglis (1986) proposed for species with precocial young that when parental investment is "unshared" among brood members there should be no relationship between investment and brood size. In Lazarus and Inglis' terminology, vigilance by adults is an unshared investment because benefits experienced by one gosling do not diminish benefits experienced by siblings and they predicted there should be no relationship between investment in this behavior and brood size.

Lazarus and Inglis (1978) and Lessells (1987)

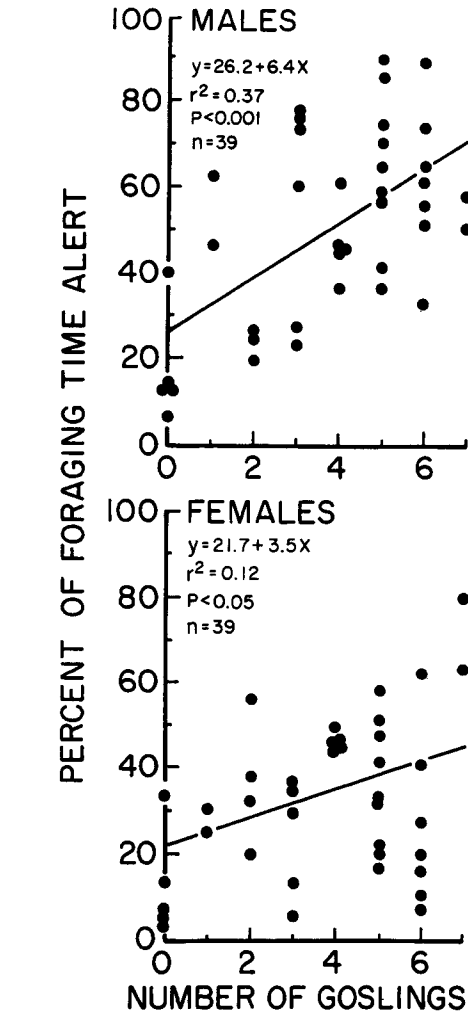


FIGURE 2. Relationship between percentage of foraging periods spent alert and brood size. Regression equations include data from pairs with no goslings.

did not detect a relationship between adult behavior and brood size in Pink-footed Geese (*Anser brachyrhynchus*) and Lesser Snow Geese, respectively. In contrast, Schindler and Lamprecht (1987) observed several positive correlations between alert and aggressive behaviors and brood size, and negative correlations between foraging time and brood size in semicaptive Bar-headed Geese (*Anser indicus*). Body masses of adult female Canada Geese when their goslings fledged were negatively correlated with brood size (Lessells 1985). Our observation that adult vigilance increased with brood size is consistent with those

of Schindler and Lamprecht (1987) and Lessells (1985), and these studies are inconsistent with the hypothesis of Lazarus and Inglis (1986).

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