BEHAVIOR OF CACKLING CANADA GEESE DURING BROOD REARING¹

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Abstract. We studied behavior of Cackling Canada Goose (Branta canadensis minima, cacklers) broods between 1992 and 1996 on the Yukon Delta National Wildlife Refuge in western Alaska. An increase in time spent foraging by goslings during our study was weakly correlated with an increase in the size of the local breeding population. Amount of time spent feeding by adults and goslings increased throughout the brood rearing period. Overall, goslings spent more time feeding than either adult females or males, and adult males spent the most time alert. Time alert varied among brood rearing areas and increases in feeding or alert behaviors were at a cost to time spent in all other behaviors. We suggest that there is not a simple trade-off between feeding and alert behaviors. We suggest that time spent feeding and alert are optimized against all other behaviors. We suggest that forage quality and availability determines the amount of time spent feeding, whereas the threat of predation or disturbance determines the amount of time spent alert.

Key words: Cackling Canada Goose, Branta canadensis minima, feeding behavior, vigilance, brood rearing, brood density.

INTRODUCTION

Adult geese must balance time spent feeding with the need to protect their goslings from predators (Trivers 1974, Lazarus and Inglis 1986). An increase in vigilance behavior may decrease the amount of time available to adults to restore depleted reserves during brood rearing (Lazarus and Inglis 1986). After hatch, males are in better condition than females (Raveling 1979, Ankney 1984) and they invest more time in vigilance behaviors while females spend more time feeding (Forslund 1993, Williams et al. 1994, Sedinger et al. 1995a). Time spent in vigilance behaviors by males also is positively correlated with brood size (Schindler and Lamprecht 1987, Williams et al. 1994, Sedinger et al. 1995a). These studies contrast with the prediction of Lazarus and Inglis (1986) that investment (vigilance) for precocial birds should be independent of brood size (Astrom 1993, Seddon and Nudds 1994).

In addition to brood size effects, forage quality and availability likely influence behavior during brood rearing (Sedinger and Raveling 1986). As forage quality decreases, adult geese and their goslings increase forage intake until they are limited by gut volume and food pro-

cessing rate (Sedinger and Raveling 1988). In response to lower availability of preferred forage plants, broods spend more time searching for forage and feeding (Sedinger and Raveling 1988, Sedinger et al. 1995a). In contrast, in areas with higher biomass of preferred food species, geese may spend less time feeding which is likely due to higher intake rates (Mulder et al. 1995). An increase in these foraging activities may decrease the proportion of time adults spend alert or in other vigilant behaviors (Sedinger et al. 1995a). At high brood densities, foraging behavior cannot compensate for lowered food quality and availability, leading to lower gosling growth rates (Cooch et al. 1991, Gadallah and Jefferies 1995a) and survival (Williams et al. 1993, Larsson and Forslund 1994, Sedinger et al. 1995b).

Adult geese and their goslings need to quickly acquire nutrients to regain condition and grow during a period when their preferred forage species are declining in quality and availability (Cargill and Jefferies 1984, Sedinger and Raveling 1986, Gadallah and Jefferies 1995b). Nitrogen levels in forage plants are highest just prior to or at peak gosling hatch, after which time nitrogen levels begin to decline (Sedinger and Raveling 1986, Gadallah and Jefferies 1995b). Geese can maintain high nitrogen levels in forage plants through grazing

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(Cargill and Jefferies 1984, Hik et al. 1991), but preferential selection of high quality plants tends to decrease their available biomass (Sedinger and Raveling 1986). At high brood densities, geese may have long-term negative impacts on their forage (Williams et al. 1993, Srivastava and Jefferies 1996).

Cackling Canada Goose (Branta canadensis minima, hereafter cacklers), the smallest subspecies of Canada Goose, breed exclusively on the outer fringe of the Yukon-Kuskokwim Delta, Alaska. In recent years, the cackler population has undergone dramatic fluctuations in population size. The population has declined from an estimated 384,000 in 1965 to the lowest counts in 1984, approximately 26,000 geese, and was estimated at 161,000 geese during the winter of 1994-1995 (Trost 1996). We studied behavior of cacklers with broods on the Yukon-Kuskokwim Delta from 1992 to 1996. Our objectives were to examine variation in behavior across years, between brood rearing areas, and among females, males and goslings (sex/age classes). We also examined the effect of brood size on alert behavior. We compare our results with previous studies which were conducted in the same area. Our results are interpreted in terms of forage quality/availability and predation/disturbance.

METHODS

This study was conducted along the Kashunuk River (61°20'N, 165°30'W) on the Yukon Delta National Wildlife Refuge in western Alaska. The area has been described in detail by Mickelson (1975) and Babcock and Ely (1994). Our study area included a site used to monitor waterfowl productivity sporadically since 1969 (Mickelson 1975, Sedinger and Raveling 1986, 1988, 1990). The study area was dominated by extensive sedge (Carex sp.) meadows with numerous small (< 0.25 ha in size), shallow lakes. Cacklers commonly nested along shores or on islands within these lakes. Every year we intensively searched study plots for cackler nests. We timed our searches to discover nests during laying or early incubation. We walked all edges of water bodies and visited all islands. We recorded all active nests and also nests that had been depredated before our searches. These nesting areas overlap the areas in which geese rear their young. Adult cacklers and their goslings were captured in late brood rearing during the adult remige molt and marked with individually coded neck collars beginning in 1986. Thus, a population of marked individuals was available at the onset of this study.

We observed adults and goslings from blinds 3 m above the ground at 8 locations using $90 \times$ spotting scopes. We recorded behaviors for 30 min, noting the behavior of both parents and the most common behavior among goslings every 15 sec; each 30 min session represented a single data point. We monitored the behaviors of adults with at least one gosling and when at least one adult was marked. These marked families were chosen for observation opportunistically. If the brood was out of view for more than 5 min, the session was terminated. Behaviors were categorized as feed, alert, rest, maintenance (preening and other comfort behaviors), travel (walk, run, swim or fly), and aggression. We attempted to observe behaviors of adults and goslings throughout the day, however since few broods were observed before 08: 00 or after 24:00, data from these times were not used. We observed behaviors on two distinct brood rearing areas separated by several kilometers, which are referred to as the Kootuk and Onumtuk sites.

STATISTICAL ANALYSES

We used multivariate techniques to analyze these data because percent time spent in at least some behaviors were not independent. Because we were mainly concerned with variation in time spent in feeding and alert behaviors, we used categories of percent time spent feeding, alert and in all other behaviors (i.e. rest, maintenance, travel, and aggression) combined to simplify analyses and interpretation. To normalize data, percentages were arcsine transformed before analyses. Times were grouped into 2-hr intervals for time-of-day analyses.

Behaviors from 1993, the year with the greatest number of multiple observations of individual broods (adults and goslings), were used to test for bias associated with repeated sampling of broods. We used a multivariate analysis of covariance (MANCOVA) with brood, sex/age class (males, females or goslings), and time of day as main effects, and average gosling age (measured as number of days following peak hatch) as a covariate. If brood had a significant effect, we randomly selected one observation from each brood from each

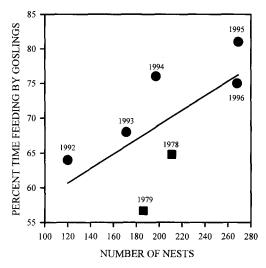


FIGURE 1. Correlation between number of cackler nests on study plots and percent time spent feeding by cackler goslings on the Yukon Delta National Wildlife Refuge. Percent time spent feeding in 1978 and 1979 are average values from Sedinger and Raveling (1988), and number of nests from 1978 and 1979 are from D. Raveling and C. Ely (unpubl. data) and C. Dau (unpubl. data).

year for use in subsequent analyses. To examine relationships between behaviors, we used a MANCOVA with year, sex/age, time of day and area as main effects, and average gosling age and brood size as the covariates. We included interactions among the independent variables but removed them when the type III F-tests were not significant. When the overall model was significant, we examined relationships between individual behaviors and the independent variables using analysis of covariance (Sedinger et al 1995a). We used Bonferroni's adjustment, which accounts for multiple means comparisons, for tests of individual behaviors (Johnson and Wichern 1988, Sedinger et al. 1995a). Spearman rank correlation coefficient (Zar 1984) was used to test for correlation between percent time feeding and nesting density. All analyses were performed with SAS (SAS Institute 1988).

RESULTS

Number of cackler nests found on our study plots doubled between 1992 and 1996 (Fig. 1). This local trend approximated the increase in the overall cackler population size (Trost 1996). The nesting density on study plots in 1993 and 1994 for an increasing population was similar to the number of nests found during a previous study in 1978 and 1979 while the population was declining (Fig. 1).

Using multiple observations of individual broods, behavior varied among broods ($F_{54,522}$) = 2.66, P < 0.001), thus we excluded multiple samples. When multiple observations were excluded from the analysis, behavior during brood rearing varied among years ($F_{12,1106}$ = 3.41, P < 0.001), among sex/age classes ($F_{6.836}$ =186.54, P < 0.001), and between brood rearing areas $(F_{3.418} = 5.31, P < 0.001)$, but we detected no variation in behavior with time of day ($F_{24,1212} = 0.84$, P > 0.67). Additionally, we detected variation in behavior with respect to covariates brood size ($F_{3,418}$ = 3.46, P = 0.01) and average gosling age ($F_{3,418} = 2.60, P$ = 0.05). None of the interactions were significant, so they were excluded from the final model.

Percent time spent feeding varied annually (Tables 1 and 2). Feeding increased from 1992 to 1995, but only 1995 was different from previous years (P < 0.001, adjusted $\alpha = 0.002$). Time spent feeding in 1996 was not different from any other year. Percent time feeding was

TABLE 1. Mean percent (\pm SE) time spent feeding, alert and in all other behaviors by cacklers along the Kashunuk River, Yukon Delta National Wildlife Refuge. Means are adjusted for average gosling age and brood size.

		Feed			Alert			Other		
	n	Females	Males	Goslings	Females	Males	Goslings	Females	Males	Goslings
1992	21	32 ± 4	34 ± 4	64 ± 5	32 ± 3	35 ± 4	1.9 ± 1	37 ± 5	31 ± 4	33 ± 5
1993	30	37 ± 3	34 ± 3	68 ± 4	33 ± 3	38 ± 3	2.9 ± 1	30 ± 4	28 ± 3	26 ± 4
1994	23	42 ± 4	30 ± 4	76 ± 5	26 ± 3	41 ± 4	2.3 ± 1	32 ± 5	29 ± 4	21 ± 5
1995	46	51 ± 3	41 ± 3	81 ± 3	30 ± 2	40 ± 3	2.6 ± 1	20 ± 3	19 ± 3	16 ± 3
1996	26	44 ± 4	36 ± 4	75 ± 5	34 ± 3	44 ± 4	1.6 ± 1	22 ± 5	19 ± 4	23 ± 5

	Feed		Alert		Other	
	F	Р	F	Р	F	P
Year	6.97	< 0.001	0.66	0.62	7.27	< 0.001
Sex/age	167.22	< 0.001	615.94	< 0.001	3.15	0.44
Area	2.10	0.14	8.29	0.004	11.45	< 0.001
Brood size	2.16	0.14	4.84	0.03	5.91	0.02
Average gosling age	7.60	0.006	0.28	0.59	4.94	0.03

TABLE 2. Analysis of covariance results of individual behaviors of cacklers during brood rearing along the Kashunuk River, 1992–1996 (n = 146). Only factors determined to be significant from the multivariate analysis of covariance were included in the model.

weakly correlated with number of nests found on our study plots (r = 0.67, P = 0.09, Fig. 1). Percent time spent feeding varied among sex/age classes (Tables 1 and 2). Goslings spent more time feeding than either adult females or males (P < 0.001, adjusted $\alpha = 0.008$), and females spent more time feeding than males (P = 0.01). There was variation in amount of time spent feeding by adults and goslings relative to average gosling age (Table 2); over the 30 day observation period, time spent feeding increased by about 15%. We did not detect any variation in percent time spent feeding between brood rearing areas (Table 2).

Time spent alert did not vary annually, although there was variation in behavior among sex/age classes (Tables 1 and 2). Adult males spent the most time alert (P < 0.001, $\alpha =$ 0.008), females spent less time alert (P <0.001) and goslings were rarely alert (P <0.001). There was a difference in time spent

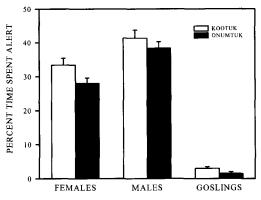


FIGURE 2. Percentage of time spent alert by cackler adult females, adult males, and goslings on two brood-rearing areas on the Yukon Delta National Wildlife Refuge, 1992–1996 (n = 57 for the Kootuk area and n = 89 for the Onumtuk area).

alert on the two brood rearing areas (Table 2); broods using the Kootuk spent more time alert than broods using the Onumtuk (Fig. 2). Amount of time spent alert increased with brood size (Table 2). Percent time spent in other behaviors besides feeding and alert varied among years, among sex/age class and between areas (Tables 1 and 2).

DISCUSSION

We found that individual broods accounted for a significant amount of the variation in behavior. We used only marked individuals, so we were able to resample the data and randomly select a single observation for each brood. Behavioral studies that fail to control for this variation may have biased results depending on the frequency of resampling. Our data suggest that individuals are consistent in behavior patterns within years. This variation in behavior among broods may influence fitness, and hence may represent variation in reproductive strategies.

Changes in percent time spent feeding has been correlated with changes in population sizes of cacklers and Black Brant (Branta bernicla nigricans; Sedinger and Raveling 1986, Sedinger et al. 1995a,). Grazing by geese reduces the availability of their preferred forage plants (Cargill and Jefferies 1984, Sedinger and Raveling 1986, Williams et al. 1993). For cacklers, there was a weak correlation between nesting density and the subsequent increase in brood density (unpubl. data), and percent time feeding by goslings. Goslings would most likely be influenced by declining food availability because they spend more time feeding than adults (Sedinger and Raveling 1988, Sedinger et al. 1995a). If an increase in time spent feeding is indicative of a reduction in availability of forage (Mulder et al. 1995), then our data suggest that the local population of cacklers may have increased to the point of influencing forage availability.

Cackler and Black Brant broods on the Yukon-Kuskokwim Delta increased the amount of time spent feeding throughout the brood rearing period (Sedinger and Raveling 1988, 1990, Sedinger et al. 1995a). For goslings, this increase may be related to an increase in gut capacity combined with a higher total demand for nutrients to meet basic metabolic requirements (Sedinger and Raveling 1988). Alternatively, geese may reduce the availability of preferred forage plants throughout the brood rearing period by selective foraging at a time when forage quality is declining as well (Sedinger and Raveling 1986). To compensate for these declines in quality and availability, adult cacklers and their goslings may be forced to increase percent time foraging to maintain a constant level of nutrient intake (Sedinger and Raveling 1988, Mulder et al. 1995).

Behaviors of adult female and male cacklers differed during brood rearing as reported for other northern-nesting geese (Sedinger and Raveling 1990, Astrom 1993, Forslund 1993, Williams et al. 1994). It is likely that these differences in behavior are related to presence of goslings because adults without broods typically show no differences in behavior (Astrom 1993, Williams et al. 1994). Males spent more time alert and females tended to feed more than males; females need to spend more time feeding to restore reserves that were lost during egg laying and incubation (Raveling 1979, Ankney 1984).

Contrary to other studies, our data do not suggest that geese trade-off between time spent feeding and time spent alert. We found that time spent feeding varied annually but not between areas, while time spent alert varied between areas but did not vary annually. Sedinger yet al. (1995a) found time spent alert decreased as time spent feeding increased for Black Brant. The Black Brant population has increased three-fold (Sedinger et al. 1993) and brood densities are much higher than for cacklers (pers. observ.); these greater numbers of broods present on brood rearing areas may compensate for the reduction in vigilance by adults with individual broods (Sedinger et al. 1995a). Williams et al. (1994) studied Lesser Snow Geese and found an inverse relationship between adult feeding and alert behaviors. Adults feed between 80 and 90% of the time and may reduce behaviors other than alert to minimum levels and therefore must trade-off between feeding and alert behaviors; this could be the case for Black Brant as well (Sedinger et al. 1995a). Our data suggest that cacklers do not simply trade-off time spent feeding for time spent alert, but adjust all other behaviors. If there are further increases in time spent feeding, cacklers may lose their ability to adjust other behaviors and trade-off increases in feeding with alert behavior.

It is evident that alert behavior mainly serves for protection of young and different requirements for that protection may explain differences between time spent alert on brood rearing areas. Forslund (1993) documented higher rates of vigilance in geese in brood rearing areas with higher gull (Larus spp.) predation rates. We observed few predation events, but the Kootuk area has traditionally had higher levels of nest predation (Ely, unpubl. data). Also, the Kootuk area was subject to more human disturbance because it was closer to the Kashunuk River than the Onumtuk area and located along a section of the river with more boat traffic (pers. observ.). Differences in time spent alert between areas are likely related to differences in frequency of disturbance by both humans and predators.

There is conflicting evidence concerning the relationship between brood size and time spent in alert behaviors. Similar to our results, some researchers have found that alert behavior of adults was positively correlated with brood size (Schindler and Lamprecht 1987, Forslund 1993, Williams et al. 1994), whereas others have supported the hypothesis that alert behavior is unrelated to brood size (Astrom 1993, Seddon and Nudds 1994). Sedinger et al. (1995a) hypothesized that variation among studies may be due to species-specific differences in the costs and benefits of increased alert behavior relative to increased foraging time. We suggest a more complicated situation for cacklers. We suggest that the threat of predation (which increases with brood size) and/or disturbance may determine the amount of time spent alert, whereas forage quality and availability may determine the amount of time spent feeding. Feeding or alert behaviors are increased at a cost to time spent in all other behaviors, such as travel, rest or maintenance. Thus, we propose a three way trade-off where time spent feeding, alert, and in all other behaviors combined are simultaneously influenced by forage quality and availability and predation and/or disturbance. The cost of reducing the amount of time spent in other behaviors is unknown.

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