VARIATION IN BROOD BEHAVIOR OF BLACK BRANT[1]

James S. Sedinger, Michael W. Eichholz and Paul L. Flint[2]
Institute of Arctic Biology and Department of Biology and Wildlife,
University of Alaska Fairbanks, Fairbanks, AK 99775-7000

Abstract. We studied behavior of broods of Black Brant (*Branta bernicla nigricans*) during five summers between 1987 and 1993, a period in which the local breeding population increased > 3-fold. Goslings spent more time foraging than adults of either sex, while adult males spent more time alert and less time foraging than adult females. Percentage of time spent alert was positively correlated with brood size for adult males but not adult females. Foraging time for all age and sex classes increased with date following hatch within years. Foraging time increased and time spent alert decreased between 1987 and 1993 for both adult males and adult females. The trend in foraging behavior for adults is consistent with an hypothesis of declining food availability at higher brood densities and declining alert behavior by adults has implications for prefledging survival of young.

Key words: Black Brant; Branta bernicla nigricans; brood-rearing; behavior; population density; Alaska.

INTRODUCTION

Geese are strictly herbivorous during the brood-rearing period (Owen 1980, Sedinger and Raveling 1984, Manseau and Gauthier 1993). Plants eaten by geese contain about 50% cell wall, composed primarily of structural carbohydrate and lignin (Sedinger and Raveling 1984), which are relatively indigestible by geese (Marriott and Forbes 1970, Sedinger et al. 1989). Plant foods also contain lower concentrations of protein, which is deficient in some essential amino acids (Sedinger 1984), compared to animal foods. Gosling growth rate is closely associated with food quality and availability (Lieff 1973, Wurdinger 1975, Cooch et al. 1991, Sedinger and Flint 1991, Larsson and Forslund 1991), likely because of the relatively poor nutritional quality of plant foods. Maximal rates of food intake are limited by time required to process fibrous plant foods (Sedinger and Raveling 1988), which limits the ability of goslings to compensate for low nutrient concentration in foods by increasing food intake. At higher brood densities, when biomass of preferred foods is reduced by grazing, food intake may be influenced by search time required to locate preferred foods (Sedinger and Raveling 1988) or by small bite size (Trudell and White 1981). Foraging behavior may be an important

indicator of food abundance under such circumstances.

While gosling behavior is likely determined by selection pressure to maximize growth rate (Cooke et al. 1984; Cooch et al. 1991; Sedinger, unpubl.), adult behavior is probably influenced by the requirement for nutrient intake and the conflicting demands of brood care and protection. Adult geese commit a substantial proportion of their time budgets to vigilance, because predation is an important source of gosling mortality (Sargeant and Raveling 1992, Bruggink et al. 1994). Female geese deplete nutrient reserves during egg formation and incubation (Ankney and MacInnes 1978, Raveling 1979, Ankney 1984) and must partially restore these reserves during the brood-rearing period (Ankney 1984, Sedinger 1986). In other species of geese, this requirement for females to restore depleted reserves has been associated with males being more vigilant and females spending more time feeding (Lazarus and Inglis 1978, Lessells 1987, Bregnballe and Madsen 1990, Sedinger and Raveling 1990).

In Cackling Canada Geese (*Branta canadensis minima*) (Sedinger and Raveling 1990) and Bar-headed Geese (*Anser indicus*) (Schindler and Lamprecht 1987), vigilance by adults was positively correlated with brood size, in contrast to predictions by Lazarus and Inglis (1986) that such correlations between behavior and brood size should not exist in species with precocial young. Female Canada Geese (*B. canadensis atlantica*) with larger broods had lower mass and nested later the next year than females with smaller

broods, implying that larger broods were associated with a greater investment (Lessells 1986), but no such relationship was observed in Lesser Snow Geese (*Chen caerulescens caerulescens*) (Lessells 1987). Lessells (1986) interpreted the delay in the next nesting attempt as a relatively minor cost to large brood size, but recent studies indicate that even delays in hatch of a few days can result in substantial reductions in fitness (Cooke et al. 1984; Cooch et al. 1991; Sedinger and Flint 1991; Prop and de Vries 1993; Sedinger, unpubl.). Cooch et al. (1991) observed a positive relationship between brood size and growth rate of Lesser Snow Goose goslings, implying that larger broods experienced superior foraging conditions, possibly resulting from higher social status.

We collected data on behavior of Black Brant (*B. bernicla nigricans*) (hereafter brant) broods during five years over a seven year period, when the population increased more than three-fold (Sedinger et al. 1993). We analyze variation in behavior across the years of the study. We also examine differences in behavior between adult males and females and between adults and goslings, to determine the extent to which brant pairs divide the investment in brood care. Finally, we studied the relationship between brood size and behavior to determine whether adults increased their vigilance as brood size increased.

METHODS

This study was conducted on brood-rearing areas used by brant nesting in the Tutakoke River colony near the mouth of the Kashunuk River (Sedinger et al. 1993) on the Yukon-Kuskokwim (Y-K) Delta, Alaska. Brant have been studied continuously at this site since 1984 and an intensive color-marking program has been conducted since 1986. Currently, approximately 30% of the adults in the colony are individually marked. This area is <1 m above mean high tide and is inundated several times each decade by storm surges, usually in fall. Broods feed heavily in the salt marsh community dominated by *Carex subspathacea* and *Puccinellia phryganodes* (see Kincheloe and Stehn 1991 for a description of vegetation structure). This community is the same as that used by Lesser Snow Geese on the west coast of Hudson Bay (Jefferies 1989), although patches of *C. subspathacea* and *P. phryganodes* are smaller on the Y-K Delta (R. F. Rockwell, pers. comm.). Vegetation shifts abruptly from a

community of highly salt tolerant species to a community dominated by *Elymus arenarius, Potentilla edgedii* and *Carex ramenskii,* which is a few centimeters higher in elevation (Kincheloe and Stehn 1992). *Triglochin palustris* (arrowgrass) an important food plant for geese on the Y-K Delta (Sedinger and Raveling 1984, Laing and Raveling 1993) occurs in the community dominated by *E. arenarius.* A major brood-rearing area, from which much of our data were collected, consisted of the *Elymus* community, interdigitated with large expanses of bare mud. Salt marsh plants bordered nearly all vegetated areas. Glaucous Gulls (*Larus hyperboreus*) are important predators on goslings on the Y-K Delta (J. Schmutz, unpubl.). Arctic foxes (*Alopex lagopus*) also prey on goslings but predation on goslings by foxes is likely less important than that of Glaucous Gulls.

We observed broods from four 5–7 m high observation towers with observation blinds at the top. Observers entered the blinds in the evening (generally after 22:00 hr) and did not collect data until the following morning to allow broods to resume normal activities. Observers remained in blinds for 2–3 days to minimize disturbance of broods. At one tower, the blind was too small to sleep in and the observer slept in a tent at the base of the tower. At this tower, the observer remained in the tower from entry in the morning until late evening (usually after 24:00 hr).

Broods were observed through 20–80× spotting scopes. We attempted to record behavior from at least three different broods from each tower each day. Observations were separated in time and we attempted to observe broods in which at least one adult was color-banded to minimize the probability of unknowingly repeatedly sampling the same brood. The proportion of marked adults in our sample increased from 12% in 1987 to 98% in 1991–1993. We included only a single observation period in the analysis for each marked brood. The likelihood of repeatedly sampling unmarked broods was low because we did not collect data from more than 94 unmarked broods in any year (1987) from areas that supported between 500 and 1,000 broods.

We attempted to record behavior for 1 hr from each brood because prior experience (Sedinger and Raveling 1988, 1990) had indicated that this was the approximate time required for a brood to complete an entire cycle of behavior. Geese usually undergo regular cycles of foraging, alter-

nating with other behaviors (Sedinger and Raveling 1988). By increasing the probability that each brood in our sample performed a full range of behaviors we reduced variance among broods associated with sampling error, thereby increasing the power of our hypothesis tests. This sampling design also reduced bias associated with the behaviors broods were engaged in at the time observations began. Behaviors were recorded into handheld computers or a field notebook from the male, female and goslings at 1 min intervals. We recorded the behavior of the majority of the goslings in a brood as gosling behavior at each 1 min sample. Behaviors were categorized as forage, preen, bathe, sit alert, stand alert, run, walk, swim, rest and aggression. Definitions of these behaviors correspond to those in Sedinger and Raveling (1988, 1990) and Welsh and Sedinger (1990). For analysis, we combined sit alert and stand alert into a single "alert" category, while bathe and preen were combined into a "maintenance" category, and run, walk and swim were combined into "travel." We recorded behavior as unknown when broods were out of view and if broods were out of view for more than five consecutive minutes we terminated the session. These unknown behaviors were not included in our calculation of percentage of time spent in each behavior. We recorded behavior from broods during all daylight hours. No observations were recorded between 02:00 and 03:00 when it was too dark to observe broods and geese were generally inactive (Sedinger and Raveling 1988). Fifty percent of observations were between 12:00 and 19:00, while 25% of our observations were earlier and later than these respective times.

For each brood, we calculated the proportion of each observation period spent in each behavior, which produced a six dimensional vector of behaviors for each observation period. The vector for each observation period, thus, provided an independent data point for analysis. The percentages themselves were correlated, however so it was necessary to analyze the data using multivariate techniques. Because data for several of the less common behaviors were not normally distributed, we arcsine transformed all data before analysis.

We tested for diurnal variation in behavior within the three age-sex classes (males, females, goslings) using a two-way multivariate analysis of covariance (MANCOVA) on behavior vectors

(Johnson and Wichern 1988) with time of day and year as main effects and brood size and days following peak of hatch as covariates. Time of day was partitioned into 2-hr time periods for these analyses. To test for annual and sex/age related variation in behavior, we performed a two-way MANCOVA on behavior vectors with year and sex-age class as main effects and brood size and days following peak of hatch as covariates. When the overall MANCOVA was significant we examined the relationship between individual behaviors, e.g., foraging, and the independent variable in question. We used Bonferoni adjustments for the tests of individual behaviors to account for the multiple tests (Johnson and Wichern 1988). Finally, to test the specific hypothesis that alert behavior of adult male and female brant was correlated with brood size (Lazarus and Inglis 1986) we used a one-way analysis of covariance with percentage of time alert as the dependent variable, year as the fixed factor and brood size and days following peak of hatch as covariates.

RESULTS

We detected no variation in behavior with time of day ($F \leq 1.16$, df = 36, 1,451, $P \geq 0.23$ all ages/sexes), so we did not include time of day in subsequent analysis. Overall, behavior varied significantly as a function of year (F = 9.24, df = 24, 3,779, $P < 0.00001$), sex-age class ($F = 144.8$, df = 12, 2,166, $P < 0.00001$) and days following peak of hatch ($F = 7.68$, df = 6, 1,084, $P < 0.00001$) (Table 1). There was also a significant interaction between year and sex/age-class ($F = 2.19$, df = 48, 5,333, $P < 0.00001$) (Table 1) which resulted from the very low rates of aggression and alert behavior by goslings. These behaviors, therefore, did not change among years for goslings (they were always near zero), whereas they did vary for adults. Brood size did not influence the overall behavior of brant ($F = 1.48$, df = 6, 1,084, $P = 0.18$), although in a univariate analysis of covariance with year as the main effect and brood size and days following hatch as covariates, adult males spent more time alert when their broods were larger ($F = 8.06$, df = 1, 359, $P = 0.005$). There was no significant relationship between brood size and percent time spent alert by females ($F = 0.44$, df = 1, 359, $P > 0.5$).

Time spent foraging increased significantly through the brood rearing period for each age

TABLE 1. Multivariate analysis of variance for the effects of date, year and sex/age on behavior of broods of black brant.[a]

Behavior	Adjusted date[b,c]			Year[b]			Sex/Age[b]			Year-sex/age[b]		
	MS	F	P	MS	F	P	MS	F	P	MS	F	P
Forage	1.15	20.81	<0.00001	0.54	9.72	<0.00001	15.12	272.59	<0.00001	0.06	1.06	0.3884
Aggression	0.10	11.63	0.0007	0.12	14.25	<0.00001	1.07	123.7	<0.00001	0.04	4.52	<0.00001
Rest	0.64	9.09	0.0026	0.15	2.13	0.0745	1.41	20.19	<0.00001	0.06	0.84	0.5659
Maintenance	0.12	4.39	0.0361	0.31	11.62	<0.00001	0.85	32.21	<0.00001	0.04	1.45	0.1708
Travel	0.11	2.97	0.0846	0.16	4.35	0.0017	0.02	0.58	0.5593	0.02	0.46	0.8857
Alert	0.05	2.32	0.1276	0.50	24.56	<0.00001	35.07	1,731.64	<0.00001	0.09	4.31	<0.00001

[a] Statistics reported for individual behaviors.
[b] d for date = 1, 1089; year = 4, 1089; sex/age = 2, 1089; year-sex/age interaction = 8, 1089.
[c] Adjusted date is a covariate, controlling for date within years.

TABLE 2. Mean annual percentages of ($\bar{x} \pm$ SE) of time spent in various behaviours, adjusted for date and brood size, by Black Brant in brood-rearing areas surrounding the Tutakoke River colony.

| Year	n	Forage			Alert			Aggression			Rest			Maintenance			Travel		
		Male	Fem.	Gos.	Male	Fem.	Gos.	Male	Fem.	Gos.	Male	Fem.	Gos.	Male	Fem.	Gos.	Male	Fem.	Gos.
1987	106	28 ±1.7	43 ±2.0	70 ±2.1	48 ±1.5	27 ±1.3	<1 ±1.5	1.7 ±0.4	1.1 ±0.3	0	4.6 ±1.0	8.6 ±1.5	13.6 ±2.0	7.8 ±0.8	8.4 ±0.9	4.4 ±0.4	11.1 ±1.2	10.4 ±1.2	10.0 ±1.2
1988	104	34 ±1.6	49 ±2.0	70 ±2.1	42 ±1.5	22 ±1.3	<1 ±1.5	1.9 ±0.4	0.8 ±0.3	0	5.1 ±1.0	10.6 ±1.5	16.5 ±1.9	4.3 ±0.7	5.0 ±0.9	2.2 ±0.5	13.2 ±1.2	13.1 ±1.2	12.0 ±1.2
1991	44	35 ±2.5	51 ±3.0	73 ±3.2	41 ±2.2	19 ±2.0	<1 ±2.4	5.7 ±0.6	3.7 ±0.5	0	5.2 ±1.5	18.0 ±2.3	15.4 ±3.0	3.3 ±1.1	4.9 ±1.4	1.9 ±0.7	9.2 ±1.8	8.7 ±1.8	9.6 ±1.8
1992	64	40 ±2.1	59 ±2.6	75 ±2.8	34 ±1.9	16 ±1.7	<1 ±2.1	2.4 ±0.6	0.9 ±0.4	0	5.9 ±1.3	9.9 ±2.0	13.3 ±2.6	3.0 ±1.0	3.7 ±1.2	2.1 ±0.6	9.9 ±1.5	9.6 ±1.6	9.6 ±1.6
1993	48	36 ±2.4	51 ±2.8	74 ±3.0	34 ±2.2	13 ±1.8	<1 ±2.2	3.4 ±0.6	1.9 ±0.5	0	9.7 ±1.5	15.1 ±2.2	14.6 ±2.8	7.8 ±1.1	7.9 ±1.3	1.4 ±0.6	9.6 ±1.7	8.9 ±1.7	8.4 ±1.7

[a] Number of observation periods.
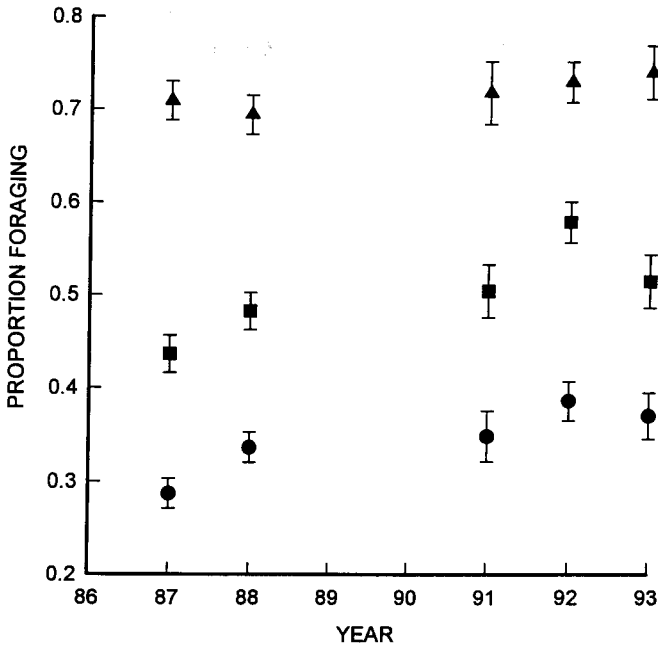
FIGURE 1. Percentage of active period spent foraging by Black Brant adult males (circles), adult females (squares) and goslings (triangles) from the Tutakoke River colony during brood-rearing, 1987–1993.

and sex class (Table 1). In contrast, time spent in aggressive interactions declined through the brood-rearing period for adult males and females. No aggressive interactions involving goslings were recorded. Female brant and goslings spent significantly less time resting as brood-rearing progressed.

Goslings spent an average of between 70 and 75% of daylight hours foraging among years of this study, after adjusting for date within years (Table 2). This represented a significantly greater proportion ($P < 0.0005$) of their daily time budgets than adult females (43–59%) who spent more time foraging ($P < 0.0005$) than males (28–40%). Alert was the most common behavior of adult males, representing 34–48% of their total time budget, after adjusting for date. Alert and foraging together represented 75% of the total time budget of adult males. Adult females spent significantly less time ($P < 0.0005$) in alert behavior (13–27%) than adult males (34–48%), while goslings spent less than 1% of the time in this behavior. Males spent between 2–6% of the time in aggressive interaction which was significantly greater than the 1–4% spent by adult females ($P < 0.0005$). Adult males and females did not differ in the proportions of time spent in mainte-

nance activities, which represented between 3 and 8% of adult time budgets. Goslings spent significantly less time in maintenance behavior (1–4%, $P < 0.0005$) than adults. Adult males rested less (5–10%) than females (9–15%) and goslings (3–16%) ($P < 0.0005$). Not surprisingly, there was no variation among age or sex classes in time spent traveling because these behaviors were conducted in unison by family groups.

Time spent foraging increased significantly between 1987–1988 and 1991–1993 for both adult males and females ($P < 0.0005$) (Fig. 1). Goslings also tended to forage more during the later years of the study but the change was relatively small (70% versus 75%) and not significant. In contrast, time spent alert declined steadily for both adult males and females across years of the study (Fig. 2). Both sexes of adults also spent more time in aggressive interactions during the 1990s than in 1987–1988, but the trend was less consistent than that for alert behaviors.

DISCUSSION

ANNUAL AND GEOGRAPHIC VARIATION

Density of nesting pairs on the Tutakoke River colony increased more than three-fold between
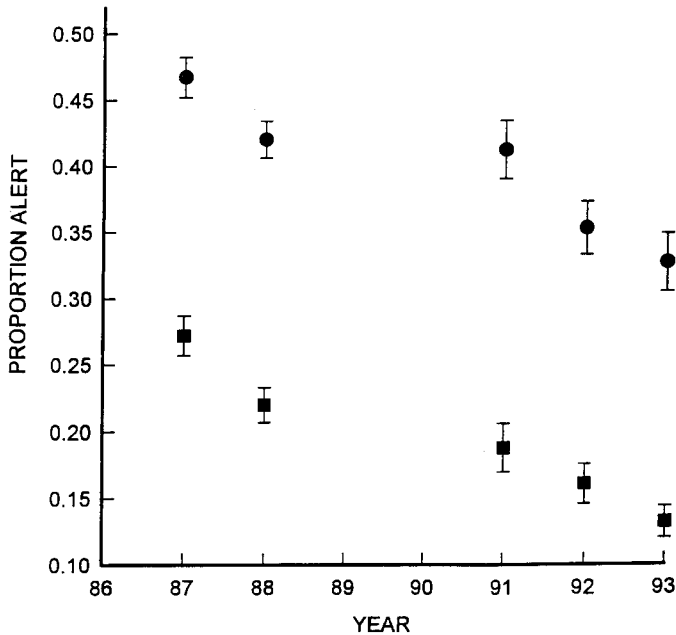
FIGURE 2.   Percentage of active period spent alert by adult male (circles) and adult female (squares) Black Brant from the Tutakoke River colony during brood-rearing, 1987–1993.

1985 and 1991 (Sedinger et al. 1993, Sedinger et al. 1994), but was variable between 1991 and 1993 (R. M. Anthony, unpubl.). Geese significantly reduce the standing crop of their preferred foods during brood rearing (Cargill and Jefferies 1984, Sedinger and Raveling 1986, Hik and Jefferies 1990). Food intake is apparently limited by a digestive bottleneck in the processing of their plant foods (Sedinger and Raveling 1988), which should increase foraging time as food abundance declines because rates of food intake are lower. Cackling Canada Geese exhibit such a pattern; more time is spent foraging at higher brood densities and later in the brood-rearing period (Sedinger and Raveling 1988). The data from this study are consistent with an hypothesis that food abundance declines and foraging time increases as brood density increases.

Corresponding with the substantial increase in foraging time, brant adults significantly reduced time spent alert between 1987 and 1993. Alert behavior by adults serves principally as vigilance against predation (Lazarus and Inglis 1978). Therefore, reduction in alert behavior may have increased vulnerability of goslings to predators in the 1990s compared to 1987–1988. It is possible, however, that the greater number of broods present partially compensated for reduced vigilance on the part of individual broods.

Adult brant spent the most time in aggressive interactions during 1991, the year with the largest number of nesting pairs during the years of our study (R. M. Anthony, unpubl.). Generally, aggressive interactions occupied more of the total time budget in the 1990s when brood densities were higher than in 1987–1988.

Other behaviors did not vary significantly among years. Lack of significant annual variation in other behaviors may have resulted from low statistical power associated with the relatively small proportion of the total time budget represented by these behaviors, and a correspondingly large relative variance. Alternatively, brant may require minimum times spent in these behaviors, eliminating their flexibility to adjust these behaviors in response to environmental variation. Nevertheless, we observed a direct tradeoff between time spent foraging and in alert behavior, the two most common behaviors of adults.

Lack of diurnal variation in behavior during the normal active period (03:00–01:00 hr) is consistent with earlier findings for Cackling Canada Geese (Sedinger and Raveling 1988) and Light

Bellied Brant (*B. b. hrota*) on Svalbard (Bregn-balle and Madsen 1990). Time devoted to for-aging by adult brant during the 1980s in this study was similar to that of Light Bellied Brant (*B. b. hrota*) breeding on Svalbard (Bregnballe and Madsen 1990) in the 1980s (46% of the time budget by females in both areas and 31% and 33% by males in Alaska and Svalbard, respec-tively). Increases in time spent foraging by adult brant in Alaska during the 1990s resulted in them spending a larger portion of the time budget feed-ing compared with Svalbard Brant during the 1980s. Brant goslings in Alaska spent a substan-tially larger proportion of their time budgets for-aging (> 70%) than did brant goslings on Sval-bard (55%). These differences in time budgets between Black Brant in Alaska during the 1990s and Brant on Svalbard are consistent with lower food abundance for Alaskan Brant in the 1990s compared to that experienced by Brant on Sval-bard (Bregnballe and Madsen 1990).

DATE WITHIN YEARS

Time spent foraging increased through the brood-rearing period for adult males and females and goslings. Adults were less aggressive later in brood rearing and adult males reduced time spent alert. These patterns are generally consistent with those observed in Cackling Canada Geese (Sedinger and Raveling 1988, 1990). Increased foraging time later in brood-rearing is consistent with de-clining availability of high quality food later in brood-rearing (Sedinger and Raveling 1986), which coincided with slower growth rates of gos-lings hatching later in the season (Sedinger and Flint 1991). Greater time spent foraging as brood-rearing progressed could be attributed to in-creased gut capacity in goslings (Sedinger and Raveling 1988). This hypothesis cannot explain seasonal increases in foraging time by adult brant, however, nor can it explain the general increase in foraging time during later years of this study.

DIVISION OF LABOR

Consistent with all other studies of geese (Lessells 1987, Schindler and Lamprecht 1987, Sedinger and Raveling 1990, Gauthier and Tardif 1991), male brant spent more time in alert and aggres-sive behavior than did female brant. In contrast, females spent more time foraging than males. As for other geese, we interpret this pattern as the requirement for female brant to restore depleted nutrient reserves used during egg laying and in-cubation (Ankney 1984). Of interest, female brant spent about 50% more of their time budgets for-aging than did sympatric female Cackling Can-ada Geese, but gained less mass between hatch and fledging of young (6% in brant between 1987 and 1989 [Sedinger, unpubl.] versus > 20% in cackling geese [Sedinger and Raveling 1986]). This difference between species may reflect the relatively poorer foraging conditions experi-enced by brant compared to Cackling Canada Geese but we require measures of food abun-dance for brant to further test this hypothesis.

BROOD SIZE

We detected only a weak association between behavior and brood size in brant. Only alert be-havior by adult males was positively correlated with brood size in brant. The association be-tween male alert behavior and brood size is con-sistent with that in Cackling Canada (Sedinger and Raveling 1990) and Bar-headed (*Anser in-dicus*) Geese (Schindler and Lamprecht 1987). Lazarus and Inglis (1986) predicted no relation-ship between brood size and adult behavior be-cause vigilance represented a "shared" behavior among members of a brood. That is, increased vigilance was not required by larger broods be-cause a given level of vigilance benefits all brood members equally. Lazarus and Inglis' (1986) hy-pothesis ignores the spatial structure of goose broods, however; if larger broods cover a larger area, greater vigilance may be required to ensure the same level of security for members of larger versus smaller broods. Furthermore, broods oc-cupying a larger area may elicit attacks at higher frequency (Mendenhall and Milne 1985), which would favor greater vigilance.

We cannot rule out two alternative hypotheses for a positive correlation between male behavior and brood size. The first hypothesis is that high quality males are both more vigilant and asso-ciated with larger broods (Lessells 1987) so the relationship between male behavior and brood size is spurious. Second, more vigilant males may be associated with larger broods because greater vigilance is associated with higher gosling sur-vival rates and consequently larger brood sizes. Per capita survival is actually lowest for goslings from large broods in brant (Flint 1993) and Less-er Snow Geese (Rockwell et al. 1987), which is inconsistent with the hypothesis that larger broods have higher survival rates. We note that the re-lationship between brood size and survival should

favor the relationship between male behavior and brood size we observed. Rigorous tests of both hypotheses will require observations of broods whose size has been experimentally manipulated. Such experiments will not be feasible for many populations, owing to the low detection probabilities for individual broods during brood-rearing.

Substantial variation in the relationship between brood size and adult behavior has been observed in geese (Lazarus and Inglis 1978, Lessells 1987, Schindler and Lamprecht 1987, Sedinger and Raveling 1990, this study). Such variation might reflect shifts in the tradeoffs between the costs of increased alert behavior (reduced foraging) and the benefits of increased vigilance (reduced predation on goslings). In habitats where goose grazing most reduces food abundance for adults (e.g., for brant and Lesser Snow Geese) we predict a weaker relationship between adult behavior and brood size because adults must increase foraging time to meet their own nutritional requirements. In habitats where avian predators that prey on goslings are abundant, we predict adult alert behavior will be more closely correlated with brood size. For brant both conditions hold which could explain the intermediate relationship between adult behavior and brood size we observed.

ACKNOWLEDGMENTS

LITERATURE CITED

ANKNEY, C. D. 1984. Nutrient reserve dynamics of breeding and molting Brant. Auk 101:361–370.

ANKNEY, C. D., AND C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 101:361–370.

BREGNBALLE, T., AND J. MADSEN. 1990. Post-hatching behaviour of Light-bellied Brant Geese *Branta bernicla hrota*. Wildfowl 41:27–34.

BRUGGINK, J. G., T. C. TACHA, J. C. DAVIES, AND K. F. ABRAHAM. 1994. Nesting and brood-rearing ecology of Mississippi Valley population Canada Geese. Wildl. Monogr. No. 126.

CARGILL, S. M., AND R. L. JEFFERIES. 1984. The effects of grazing by Lesser Snow Geese on the vegetation of a sub-arctic salt marsh. J. Appl. Ecol. 21:669–686.

COOCH, F. G., D. B. LANK, A. DZUBIN, R. F. ROCKWELL, AND F. COOKE. 1991. Body size variation in Lesser Snow Geese: seasonal variation in gosling growth rate. Ecology 72:503–512.

COOKE, R., C. S. FINDLAY, AND R. F. ROCKWELL. 1984. Recruitment and the timing of reproduction in Lesser Snow Geese (*Chen caerulescens caerulescens*). Auk 101:451–458.

FLINT, P. L. 1993. Prefledging survival and reproductive strategies in Black Brant. Ph.D.diss., Univ. of Alaska Fairbanks, Fairbanks, AK.

GAUTHIER, G., AND J. TARDIF. 1991. Female feeding and male vigilance during nesting in Greater Snow Geese. Condor 93:701–711.

HIK, D. S., AND R. L. JEFFERIES. 1990. Increases in the net above-ground primary production of a salt marsh forage grass: a test of the predictions of the herbivore optimization model. J. Ecol. 78:180–195.

JEFFERIES, R. L. 1989. Pattern and process in arctic coastal vegetation in response to foraging by Lesser Snow Geese, p. 281–300. *In* M.J.A. Werger, P.J.M van der Aart, H. J. During and J.T.A. Verhoeven [eds.], Plant form and vegetational structure. Adaptation, plasticity and relationship to herbivory. SPB Academic Publishing, The Hague.

JOHNSON, R. A., AND D. W. WICHERN. 1988. Applied multivariate statistical analysis. 2nd ed. Prentice Hall, Englewood Cliffs, NJ.

KINCHELOE, K. L., AND R. A. STEHN. 1991. Vegetation patterns and environmental gradients in coastal meadows on the Yukon-Kuskokwim Delta, Alaska. Can. J. Bot. 69:1616–1627.

LAING, K. K., AND D. G. RAVELING. 1993. Habitat and food selection by Emperor Goose Goslings. Condor 95:879–888.

LARSSON, K., AND P. FORSLUND. 1991. Environmentally induced morphological variation in the Barnacle Goose, *Branta leucopsis*. J. Evol. Biol. 4:679–686.

LAZARUS, J., AND I. R. INGLIS. 1978. The breeding behaviour of the Pink-footed Goose: parental care and vigilant behaviour during the fledging period. Behaviour 65:62–88.

LAZARUS, J., AND I. R. INGLIS. 1986. Shared and unshared parental investment, parent-offspring conflict and brood size. Anim. Behav. 34:1791–1804.

LESSELLS, C. M. 1986. Brood size in Canada geese: a manipulation experiment. J. Anim. Ecol. 55:669–689.

LESSELLS, C. M. 1987. Parental investment, brood size and time budgets: behaviour of Lesser Snow Goose *Anser c. caerulescens* families. Ardea 75: 189–203.

LIEFF, B. C. 1973. Summer feeding ecology of Blue and Canada Geese at the McConnell River, NWT. Ph.D.diss., Univ. Western Ontario, London.

MANSEAU, M., AND G. GAUTHIER. 1993. Trade-off

between food quality and food abundance in Greater Snow Geese. Ecology 74:2045–2055.

MARRIOTT, R. W., AND D. K. FORBES. 1970. The digestion of lucerne chaff by Cape Barren Geese, *Cereopsis novaehollandiae* Latham. Aust. J. Zool. 18:257–263.

MENDENHALL, V. M., AND H. MILNE. 1985. Factors affecting duckling survival of Eiders *Somateria mollisima* in northeast Scotland. Ibis 127:148–158.

OWEN, M. 1980. Wild geese of the world. Batsford, London.

PROP, J., AND J. DE VRIES. 1993. Impact of snow and food conditions on the reproductive performance of Barnacle Geese *Branta Leucopsis*. Ornis Scand. 24:110–121.

RAVELING, D. G. 1979. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. Auk 96:234–252.

ROCKWELL, R. F., C. S. FINDLAY, AND F. COOKE. 1987. Is there an optimal clutch size in snow geese. Am. Nat. 130:839–863.

SARGEANT, A. B., AND D. G. RAVELING. 1992. Mortality during the breeding season, p. 396–422. *In* B.D.J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec and G. L. Krapu [eds.], Ecology and management of breeding waterfowl. Univ. of Minnesota Press, Minneapolis.

SCHINDLER, M., AND J. LAMPRECHT. 1987. Increase of parental effort with brood size in a nidifigous bird. Auk 104:688–693.

SEDINGER, J. S. 1984. Protein and amino acid composition of tundra vegetation in relation to nutritional requirements of geese. J. Wildl. Manage. 48:1128–1136.

SEDINGER, J. S. 1986. Growth and development of Canada goose goslings. Condor 88:169–180.

SEDINGER, J. S., AND P. L. FLINT. 1991. Growth rate is negatively correlated with hatch date in Black Brant. Ecology 72:496–502.

SEDINGER, J. S., AND D. G. RAVELING. 1984. Dietary selectivity in relation to availability and quality of food for goslings of Cackling Geese. Auk 101:295–306.

SEDINGER, J. S., AND D. G. RAVELING. 1986. Timing of nesting by Canada Geese in relation to the phenology and availability of their food plants. J. Anim. Ecol. 55:1083–1102.

SEDINGER, J. S., AND D. G. RAVELING. 1988. Foraging behavior of Cackling Canada Goose goslings: implications for the roles of food availability and processing rate. Oecologia 75:119–124.

SEDINGER, J. S., AND D. G. RAVELING. 1990. Parental behavior of Cackling Canada Geese during brood rearing: division of labor within pairs. Condor 92:174–181.

SEDINGER, J. S., C. J. LENSINK, D. H. WARD, R. M. ANTHONY, M. L. WEGE, AND G. V. BYRD. 1993. Status and recent dynamics of the black brant breeding population. Wildfowl 44:49–59.

SEDINGER, J. S., D. H. WARD, R. M. ANTHONY, D. V. DERKSEN, C. J. LENSINK, K. S. BOLLINGER, AND N. K. DAWE. 1994. Management of Pacific Brant: population structure and conservation issues. Trans. N. Amer. Wildl. Nat. Res. Conf. 58:50–62.

SEDINGER, J. S., R. G. WHITE, F. E. MANN, F. A. BURRIS, AND R. A. KEDROWSKI. 1989. Apparent metabolizability of alfalfa components by yearling Pacific Black Brant. J. Wildl. Manage. 53:726–734.

TRUDELL, J., AND R. G. WHITE. 1981. The effect of forage structure and availability on food intake, biting rate, bite size and daily eating time of reindeer. J. Appl. Ecol. 18:63–81.

WELSH, D., AND J. S. SEDINGER. 1990. Extra-pair copulations in Black Brant. Condor 92:242–244.

WURDINGER, I. 1975. Vergleichend morphologische untersuchungen Zur Jugendentwicklung von Anser-und Branta Arten. J. Ornithol. 116:65–86.