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An Experimental Study

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# DOMINANCE, BROOD SIZE AND FORAGING BEHAVIOR DURING BROOD-REARING IN THE LESSER SNOW GOOSE: AN EXPERIMENTAL STUDY<sup>1</sup>

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**Abstract.** We investigated the relationship between brood size and social dominance during the brood-rearing period in Lesser Snow Geese (*Anser caerulescens caerulescens*) by experimentally manipulating food availability to create high-biomass food patches. A total of 128 social interactions were subsequently observed in experimental areas; the rate of interactions was significantly higher in experimental high-biomass plots (9.6 hr<sup>-1</sup>) than in control, low-biomass, areas (0.4 hr<sup>-1</sup>).

During social interactions families (pairs with one or more goslings) were always dominant over pairs without goslings. However, there was no clear dominance hierarchy among families in relation to brood size. Neither aggressiveness (the number of interactions initiated) nor the proportion of successful interactions varied consistently with brood size. We conclude that, during brood rearing, dominance ranking is determined more by individual variation in aggressiveness of adult (parent) birds, rather than by any "motivational" effect of offspring or by brood size per se.

Geese fed longer in the high biomass plots (mean 19.2 min per visit) than in control plots (2.9 min), and birds "defended" high biomass areas: 32% of all interactions involved a social unit inside the experimental plot driving off a social unit which was trying to enter the plot from outside. This suggests that geese derived benefits from monopolization of good quality food patches. The behavior of foraging geese varied in relation to food availability: birds took fewer steps per minute during both feeding and non-feeding bouts in the experimental plots and females, but not males, had shorter feeding bouts in experimental plots, i.e., they adopted the vigilant head-up posture more frequently. We suggest that the benefits of utilizing high biomass food patches during brood-rearing include higher intake rates, decreased energetic costs of foraging and reduced predation risk through increased vigilance behavior by parents and greater cohesion of the family unit.

**Key words:** *Anser caerulescens caerulescens*; brood size; dominance; foraging behavior; Lesser Snow Goose.

## INTRODUCTION

Dominance hierarchies play an important role in the social organization of animals living in groups (Rowell 1974, Brown 1975, Gauthreaux 1978). Hierarchies may promote stability within social groups as individuals learn to recognize other individuals that can defeat them, and those that they can defeat, and modify their behavior accordingly. Dominant individuals can thus obtain the benefits associated with a higher social rank (typically better access to resources, e.g., food or mates [Clutton-Brock et al. 1986, Richner 1989]) using only threats and displays and without becoming involved in potentially damaging physical fights (Wilson 1975, Hand 1986).

Dominance hierarchies may also influence habitat use and dispersal patterns, e.g., low-ranking individuals may be forced to disperse greater distances when resources are scarce (e.g., Ekman and Askenmo 1984), thus increasing the survival probability of more dominant individuals (Morse 1980). Dominant individuals have been shown to have higher survival rates than subordinates in many avian species (e.g., Baker et al. 1981, Arcese and Smith 1985).

Dominance hierarchies have been widely reported to occur among foraging geese (e.g., Collias and Jahn 1959; Lamprecht 1986a, 1986b; Black and Owen 1987; Gregoire and Ankney 1990), and numerous benefits of high rank or dominant status have been identified. Access to the richest feeding areas or the most profitable food types is positively related to the rank of individuals or families in Barnacle Geese (*Branta leucopsis*, Prop et al. 1984) and Brent Geese (*Branta bernicla*, Prop and Deerenberg 1991).

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Furthermore, increased access to, or monopolization of, resources by dominant individuals or families on the wintering grounds has been related to increased breeding success in the following season in several species (Collias and Jahn 1959, Teunissen et al. 1985, Lamprecht 1986a, Black and Owen 1987). Nevertheless, the factors that determine social dominance in geese are still unclear. Gregoire and Ankney (1990) demonstrated that there was a positive covariance between rank and the presence of young in Lesser Snow Geese (*Anser caerulescens caerulescens*) and suggested that family or brood size was a major determinant of dominance. Many studies have found that large families dominate small families in geese while foraging (Boyd 1953; Hanson 1953; Raveling 1970; Prop et al. 1984; Black and Owen 1984, 1989). Raveling (1970) pointed out, however, that there were several cases in Boyd's (1953) study where small families dominated larger families. In addition, Cloutier and Bedard (1992) failed to find a relationship between brood size and dominance among Greater Snow Geese (*Anser caerulescens atlantica*) held under captive conditions. Raveling (1970) suggested that, in addition to family size, individual variation in aggressiveness of adult males affected dominance in his study. Lamprecht (1986b) also found that ranking among families of semi-captive Barn-headed Geese (*Anser indicus*) was primarily determined by the behavior of the male parent rather than by brood size.

One proposed cause of the relationship between family size and dominance is co-operation between parents and their offspring during aggressive or social interactions (Hanson 1953, Raveling 1970). For example, Black and Owen (1989) showed that throughout the winter offspring of Barnacle Geese contributed increasingly to vigilance behavior and assisted in aggressive interactions. The number of young (brood size) might also affect a parent's rank if larger broods having a greater motivational effect on parents (Boyd 1953, Hanson 1953).

All studies that have demonstrated a relationship between brood size and dominance in foraging geese have been carried out on the wintering grounds or spring staging areas. Conversely, studies that have failed to observe an effect of brood size on dominance have dealt with breeding geese on the brood-rearing grounds or geese held in captivity during the breeding season. In

spite of this, several advantages of large brood size have been proposed for brood-rearing geese (assuming that brood size is related to dominance, Prop et al. 1984). These include better growth and survival of goslings (Cooch et al. 1991, Williams et al. 1994) and better access to areas of higher food availability (Prop et al. 1984). On the brood-rearing grounds during summer, goslings feed almost continuously and do not assist their parents during interactions as they do on the wintering grounds (Lessells 1987). Thus, a positive relationship between number of goslings and their parent's ranking or dominance on the breeding grounds could only be due to a motivational effect of offspring on the male and/or female parents. Alternatively, if brood size does not affect parental motivation (which we equate to individual variation in aggressiveness) there should be no relationship between dominance and brood size during brood rearing.

In this paper we investigate the relationship between brood size and social dominance during brood-rearing in the Lesser Snow Geese by experimentally manipulating food availability. In addition, we consider possible benefits of social dominance in relation to use of food resources by comparing feeding behavior and parental care (vigilance) in geese foraging in patches of differing food availability.

## METHODS

Fieldwork was carried out during July 1992 at La Pérouse Bay, Manitoba (54°43'N 93°27'W). To induce otherwise infrequently observed social interactions between Lesser Snow Goose broods we manipulated vegetation on salt marsh brood-rearing areas using exclosures. Exclosures prevented geese from grazing experimental plots, allowing an increase in biomass compared to areas outside the plots. Six 5 × 5 m experimental plots were exclosed, using chicken wire and garden netting, prior to the arrival of the geese and their newly-hatched young. A 5 × 5 m, non-exclosed, control plot was marked with corner stakes adjacent to each of the experimental plots. Plots were sited so that the vegetation in all the plots was homogeneous and consisted of the main vegetation types used by Lesser Snow Geese at La Pérouse Bay (*Puccinellia phryganoides* and *Carex subspathacea*). Experimental plots were placed 50–75 m from an observation tower such that two experimental plots and their corre-

sponding control plots could be observed from the tower at the same time. The two experimental plots in each pair were separated from each other by a small stream to discourage geese from moving back and forth between plots during the experiment.

Vegetation in the first pair of exclosures was made available to foraging geese on 11 July, two weeks after the first families arrived on the feeding grounds. The other two pairs of exclosures were made available at weekly intervals thereafter (on 18 and 25 June respectively). Four corner stakes were left to mark the position of the plot during subsequent observations. Plots were observed from dawn (before which no geese fed on the salt-marshes); as soon as the first geese encountered the newly released plots we continuously recorded the arrival and departure times for all birds visiting the plot, and all social interactions, for 4–5 hr. All social units (lone birds, pairs or families) were individually recognizable, due either to uniquely coded and colored leg bands or from distinct plumage characteristics; males were sexed by their larger size, females being notably thinner immediately after hatch. For each social interaction where at least one individual was inside the experimental plot, we recorded: (1) the number of young in the social units involved, (2) which social unit initiated the interaction, and (3) the nature and outcome of the interaction. An individual, pair or family was defined as having won an interaction if it displaced its opponent, or if it was not displaced by an opponent who initiated the interaction. These observations were subsequently used to construct dominance matrices for each plot following the method described by Brown (1975). This method was chosen because it allows for the separate treatment of each experimental plot and takes into account multiple encounters and reversals in outcome between the same two social units. The results obtained from the dominance matrices were used to determine the number of dyads (two social units interacting) in which a particular social class (a pair, a small family, or a large family) dominated another social class. Pairs with one or two young were classified as small families and those with three or four young as large families (no pair observed in experimental plots had more than four young). Binomial tests were used to determine whether one particular social class dominated another more

often than vice versa. The aggressiveness (number of interactions initiated) and frequency of success of the different social classes were compared using the Mann-Whitney *U*-test.

To measure food availability in experimental and control plots, six 10 × 10 cm turves were cut from each plot at the time of release (before grazing). Three more turves were collected from each experimental plot at the end of the 4–5 hr observation period (after grazing). Turves were taken from areas representative of the entire plot and above-ground biomass ( $\text{g m}^{-2}$ ) was determined following the method described in Williams et al. (1993). Values obtained in this way for control plots were the same as those for a larger sample of randomly selected plots over the entire salt-marsh area, suggesting we did not significantly over- or underestimate the homogeneity of vegetation in the plots (R. L. Jefferies, pers. comm.). There were no significant differences in above-ground biomass between pairs of plots released at the same time ( $P > 0.05$ ) so data were pooled for each weekly period.

To investigate differences in foraging and parental (vigilance) behavior we observed a sample of adult geese, as described in Williams et al. (1994), while they were foraging in experimental plots. Focal individuals were observed for 2–3 min periods (longer observations were not possible due to the time required for recording the high level of activity and interactions between social groups) and the following parameters recorded: (1) number of steps taken while feeding (with head down), (2) number of steps taken while not feeding (head-up, the vigilant posture), and, (3) the number of feeding bouts (defined as the period of continuous feeding between two head-ups). These data were used to calculate feeding bout duration and the percentage time spent feeding. All behavioral observations took place within the first half hour of a visit by a social unit to the plot, and when there were at most two other units present in the plot. For comparison, behavioral observations were also carried out on adult geese feeding in other non-enclosed areas of the salt-marsh (not the exclosure control plots) throughout the brood-rearing period (see Williams et al. 1994 for further details). Since goslings feed almost continuously while on the brood-rearing grounds (personal observations) they were not included in the study. Results are given as means  $\pm$  SE unless otherwise stated.

TABLE 1. Above-ground biomass ( $\text{g} \cdot \text{m}^{-2}$ ) of vegetation in experimental plots before and after grazing, and in control plots. Values are means  $\pm$  SE. Replicate plots within each treatment have been pooled for each week.

Week	Above-ground biomass ( $\text{g} \cdot \text{m}^{-2}$ )			Cont vs. expt before grazing		Before vs. after grazing (expt)	
	Control plots ( $n = 12$ )*	Experimental plots		<i>t</i>	<i>P</i>	<i>t</i>	<i>P</i>
		Before grazing ( $n = 12$ )*	After grazing ( $n = 6$ )*				
1	22.92 $\pm$ 1.78	38.61 $\pm$ 1.68	22.45 $\pm$ 2.57	6.41	<0.001	5.40	<0.001
2	26.11 $\pm$ 1.99	55.64 $\pm$ 3.76	35.10 $\pm$ 3.50	6.93	<0.001	3.47	<0.01
3	34.61 $\pm$ 0.99	80.86 $\pm$ 2.54	53.21 $\pm$ 2.41	16.97	<0.001	6.91	<0.001

\*  $n$  = number of  $10 \times 10$  cm turves.

## RESULTS

Experimental plots had significantly higher mean above-ground biomass compared to paired control plots at the time of release in all three weeks (Table 1). At the end of the 4–5 hr observation period grazing had significantly reduced above-ground biomass in all experimental plots (Table 1). Release of exclosed plots resulted in a large number of geese feeding in a relatively small area, with a maximum of six social units (pairs without young or families) feeding in a plot at the same time. In comparison, at most only two social units were seen in control plots at the same time. Mean duration of visits was significantly greater for experimental plots ( $19.2 \pm 3.0$  min,  $n = 31$ ) than for control plots ( $2.9 \pm 0.5$  min,  $n = 33$ ;  $P < 0.01$ ), and individuals and families re-entered

TABLE 2. Brood sizes of dominant and subordinate social units in dyads of families (pairs with young) versus pairs (without young), and in dyads of different-sized families.

Dyad composition	Brood size of social unit		No. of interactions
	Dominant	Subordinate	
Family vs. pair	1	0	8
	3	0	6
	1	0	7
	1	0	11
	2	0	6
	2	0	1
	2	0	2
	2	0	2
	1	0	2
	1	0	3
	1	0	2
Family vs. family	1	3	4
	2	1	16
	3	2	2
	1	4	1
	1	2	1
	4	1	1
	4	1	1

the experimental plots repeatedly. A total of 128 interactions were observed in experimental plots during 13.4 hr of observations (9.6 interactions/hr). Of these, 41 interactions (32%) involved a social unit inside the experimental plot driving off a social unit which was trying to enter the plot from outside. In comparison, 34 interactions were noted in non-experimental areas during the routine observation period which totalled approximately 90 hours and covered a much larger area (0.4 interactions/hr). No social interactions were recorded in the exclosure control plots even though these plots were observed continuously at the same time as the experimental plots.

Pairs without goslings (i.e., social units with brood size of zero) always ranked lowest in the 11 observed dyads of pairs and families (i.e., social units with brood size of one or more) interacting (Table 2). Families were thus significantly more dominant than pairs (Binomial test,  $P = 0.001$ ,  $n = 11$ ). However, amongst families with one or more goslings, there was no clear ranking with respect to the size of families (Table 2). There were seven observed dyads of different-sized families that interacted with each other; in three dyads the larger family dominated the smaller family, but in the other four dyads the reverse was true (three different one-gosling families were involved in the three dyads where small families were dominated by large families). Large

TABLE 3. Percent of interactions initiated and interactions won by pairs without goslings, small families (brood size = 1 or 2), and large families (brood size = 3 or 4).

Social unit type	No. of interactions	Percent (%) of interactions	
		Initiated	Won
Pairs ( $n = 12$ )	122	31%	30%
Small families ( $n = 9$ )	104	63%	64%
Large families ( $n = 3$ )	30	70%	80%

TABLE 4. Feeding behavior of parental and non-parental Lesser Snow Geese in experimental plots and non-manipulated salt-marsh areas (data for each three week period have been pooled, see text). Values are means  $\pm$  SE. Sample sizes: experimental plots, parent males and females  $n = 5$ , non-parent males  $n = 8$ , and non-parent females  $n = 9$ ; control plots, parent males and females  $n = 54$ , non-parent males and females  $n = 10$ .

Feeding behavior	Sex	Status	Control	Experimental	<i>t</i>	<i>P</i>
No. feeding steps $\cdot$ min <sup>-1</sup>	Male	Parent	23.5 $\pm$ 0.9	13.8 $\pm$ 4.7	3.07	0.003
	Female	Parent	23.2 $\pm$ 0.9	17.7 $\pm$ 4.0	1.80	0.078
	Male	Non-parent	23.2 $\pm$ 2.6	17.3 $\pm$ 2.1	1.69	NS
	Female	Non-parent	24.0 $\pm$ 1.6	12.8 $\pm$ 1.7	4.79	<0.001
No. non-feeding steps $\cdot$ min <sup>-1</sup>	Male	Parent	53.5 $\pm$ 4.8	1.7 $\pm$ 1.1	10.43	<0.001
	Female	Parent	47.2 $\pm$ 5.3	4.7 $\pm$ 3.0	6.91	<0.001
	Male	Non-parent	63.5 $\pm$ 18.5	68.6 $\pm$ 35.0	0.14	NS
	Female	Non-parent	38.1 $\pm$ 14.1	6.5 $\pm$ 5.3	2.11	0.058
Feeding bout duration (min)	Male	Parent	0.54 $\pm$ 0.08	0.44 $\pm$ 0.15	0.38	NS
	Female	Parent	0.85 $\pm$ 0.12	0.33 $\pm$ 0.08	3.48	0.002
	Male	Non-parent	0.82 $\pm$ 0.16	0.76 $\pm$ 0.20	0.24	NS
	Female	Non-parent	1.16 $\pm$ 0.19	1.11 $\pm$ 0.21	0.18	NS
Percent (%) time spent feeding	Male	Parent	87.1 $\pm$ 1.3	81.3 $\pm$ 6.0	1.23	NS
	Female	Parent	91.8 $\pm$ 1.0	86.9 $\pm$ 4.2	1.50	NS
	Male	Non-parent	95.6 $\pm$ 0.9	91.7 $\pm$ 4.0	1.19	NS
	Female	Non-parent	96.8 $\pm$ 1.6	97.6 $\pm$ 0.8	0.52	NS

families were therefore not dominant significantly more often over smaller families than vice versa (Binomial test,  $P = 0.773$ ,  $n = 7$ ).

Families won more interactions than pairs without goslings (Mann Whitney  $U$ -test,  $Z = -1.91$ ,  $P = 0.055$ ,  $n = 11$  pairs, 13 families). However, there was no difference in percent interactions won between large (brood size 3 or 4) and small (brood size 1 or 2) families (Mann Whitney  $U$ -test,  $Z = -0.34$ ,  $P = 0.734$ ,  $n = 10$  small families, 3 large families; Table 3). Similarly, families were more aggressive than pairs without goslings, as measured by the percentage of interactions they initiated (Mann Whitney  $U$ -test,  $Z = -2.15$ ,  $P = 0.032$ ,  $n = 12$  pairs, 13 families); whereas small and large families did not differ in aggressiveness (Mann Whitney  $U$ -test,  $Z = -0.68$ ,  $P = 0.497$ ,  $n = 10$  small families, 3 large families; Table 3).

For comparison of feeding behavior in experimental plots and non-experimental areas data for all three weeks were pooled; Williams et al. (1994) found no significant variation in behavior among weeks over the same period using the larger data set from the non-experimental areas. Males and females were examined separately, however, since they do differ in their feeding behavior during the brood-rearing period (Lessells 1987, Williams et al. 1994). Adult parent geese behaved differently in experimental plots compared to control areas (Table 4). Male par-

ents took fewer steps per minute when feeding in experimental plots than when feeding in control areas ( $P < 0.01$ ). The same trend was apparent for female parents ( $P = 0.08$ , Table 4). Similarly, when not feeding (i.e., with their head up) both male and female parents exhibited significantly lower step rates in experimental plots than in control areas ( $P < 0.0001$ ). In addition, female parents, but not male parents, had shorter feeding bouts in experimental plots than in control areas, i.e., they adopted the vigilant head-up posture more frequently ( $P < 0.01$ ). The percent time spent feeding did not, however, differ between experimental plots and control plots for either male or female parents (Table 4). Differences between experimental and control plots in feeding behavior of pairs without young were not as pronounced. The only significant difference was the number of feeding steps per minute in females, which was lower in experimental plots as compared to control areas ( $P < 0.0001$ , Table 4). Feeding behavior in non-parent males did not differ among plots. Overall, differences in feeding behavior between experimental plots and control areas tended to be more pronounced among females than among males (Table 4).

## DISCUSSION

Lesser Snow Geese were clearly attracted to the high-biomass experimental plots created in this study, as was apparent by the large number of

geese feeding simultaneously in the plots, the prolonged duration of their visits, and their frequent return or re-entry to the plots. The marked effect of grazing over a very short period (4–5 hr) on above-ground biomass in experimental plots was also indicative of their attractiveness to the geese. The high densities of geese in the experimental plots increased the likelihood of individuals encountering each other and resulted in a high frequency of social interactions as compared to control areas.

On this brood-rearing area, Lesser Snow Goose pairs without goslings had a lower status in the observed dominance hierarchy than pairs with goslings. This result is consistent with other goose studies on the wintering grounds and during spring migration (Boyd 1953, Hanson 1953, Raveling 1970, Black and Owen 1989, Gregoire and Ankney 1990). However, dominance status or ranking among pairs with at least one offspring did not appear to be affected by brood size during the brood-rearing period at La Pérouse Bay: large families did not dominate small families more often than vice versa, and neither the number of interactions initiated nor the proportion of successful interactions varied in relation to brood size. These results are consistent with other studies of brood-rearing geese which also failed to find a relationship between brood size and dominance (Lamprecht 1986b, Cloutier and Bedard 1992), though these previous studies involved semi-captive or captive geese. Although Prop et al. (1984) suggested that a dominance hierarchy related to family size did occur on the summer brood-rearing grounds in Barnacle Geese, they provided no data in their paper to support this statement.

On the summer brood-rearing grounds, parental "status," i.e., whether a goose has goslings (one or more) or not, appears to play a strong role in determining dominance, since parents always dominated pairs without young. However, our results and those of Lamprecht (1986b) and Cloutier and Bedard (1992) do not support the hypothesis that brood size per se is involved in maintenance of dominance hierarchies amongst geese during the brood-rearing period. This is perhaps not surprising, in that goslings feed almost continually on the brood-rearing areas and do not assist their parents in social or agonistic interactions, in contrast to behavior on the wintering grounds (goslings fed on average for 93% of the time at La Pérouse Bay in 1991, with no

social interactions being observed,  $n = 42$  goslings, 1,008 focal observations; T. D. Williams, unpubl. data; see also Lessells 1987). The lack of a positive relationship between family size and dominance also fails to support the hypothesis that increased brood size causes increased parental motivation during social interactions which indirectly determines dominance ranking. Rather, it seems most likely that individual variation in aggressiveness of adult birds is responsible for the dominance hierarchies of foraging geese during brood-rearing (as has been suggested in other situations, e.g., Raveling 1970, Lamprecht 1986b).

We obtained direct evidence that geese attempted to remain within, and monopolize, high-biomass food patches. Firstly, the duration of visits to experimental plots was much greater than that in control areas (which had much lower above-ground biomass), and birds continually reentered experimental plots. Prop and Loonen (1988) similarly reported increased residence time in Brant Geese feeding in areas of high food availability. Secondly, a significant proportion (32%) of the social interactions recorded involved geese inside the experimental plots ("residents") preventing other birds from entering these plots, i.e., they "defended" the high-biomass resource. This suggests that geese obtained some benefit from remaining within, and continuing to feed on, the high-biomass food patches.

Foraging behavior of parental Lesser Snow Geese differed significantly between experimental plots and control areas. In contrast, changes in feeding behavior of geese without young were not as pronounced in the experimental plots confirming that differences observed in parent geese were directly related to the presence of offspring. Although there was no difference in the proportion of time spent feeding in experimental and control plots, geese would have achieved a higher intake rate in the high-biomass areas due to the greater blade length of the forage plants in these areas, leading to greater intake per peck (Teunissen et al. 1985, Prop and Loonen 1988; see also Drent and Swierstra 1977). This represents the most obvious advantage of feeding in good food patches. The lack of any increase in time spent feeding in relation to increased food availability suggests that the geese were already feeding for the maximum amount of time possible in control areas. Consistent with this, the per-

centage of time spent feeding in Lesser Snow Geese at La Pérouse Bay (87–92%) is much higher than has been reported in other studies of brood-rearing geese (e.g., 50–75%, Sedinger and Raveling 1990; 30–60%, Eberhardt et al. 1989). This may reflect the generally poor feeding conditions caused by the long-term decline in food availability which has occurred at this site (Williams et al. 1993; M.J.J.E. Loonen, unpubl. data). In fact, both male and female Lesser Snow Geese tended to spend less time feeding in the high-biomass areas (Table 4), though this difference was not significant.

Feeding bout duration was significantly shorter in female Snow Geese in experimental plots, that is, they stopped feeding and adopted the vigilant head-up posture more frequently than when in control (low-biomass) areas. Thus, an additional benefit of feeding in areas of higher biomass might be improved parental care by females: birds are alert more frequently, thus affording their offspring better protection from predators (e.g., Safriel 1975). This pattern was not apparent in males, perhaps because males are in better condition post-hatching and can afford to feed less and be more vigilant regardless of intake rate and feeding conditions (Ankney and MacInnes 1978, Sedinger and Raveling 1990). This suggests that increased vigilance was related to better feeding conditions per se, rather than simply being a consequence of the greater density of birds in experimental plots as, if the latter were the case, increased vigilance would have been expected in both sexes. A difference in male and female body condition post-hatching would also explain why, in general, changes in behavior in response to high biomass in the experimental plots tended to be more pronounced among females than males.

Lesser Snow Geese in experimental plots also adjusted their walking rates during feeding bouts. In both sexes parents walked more slowly while feeding in the high-biomass plots compared to control areas, though the difference was not quite significant for females. Similarly, both males and females walked significantly more slowly in experimental areas when not feeding (i.e., between feeding bouts), suggesting they had to move around less in search of good vegetation patches. This should lead to a decrease in the energetic costs of foraging. Several other studies have shown that geese feeding in areas of higher food availability decrease the number of steps taken

per minute (Prop et al. 1984, Teunissen et al. 1985, Prop and Loonen 1988). During brood-rearing this decreased walking rate in high-biomass is likely to have another advantage in relation to parental care: families which move less rapidly will maintain greater cohesion and reduced adult-gosling distances. This, in turn, is likely to reduce the risk of predation of goslings which will be higher in more dispersed broods (Safriel 1975, Lessells 1987).

Feeding in good (high-biomass) food patches might provide several benefits to dominant geese capable of monopolizing such areas. These benefits include higher intake rates, decreased energetic costs of foraging, increased time spent in vigilance behavior, and greater cohesion of the family unit. However, on the brood-rearing grounds, dominance is probably more closely related to individual variation in aggressiveness of adult (parent) birds, rather than to family or brood size per se.

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