AGONISTIC BEHAVIOR AND DOMINANCE RELATIONSHIPS AMONG LESSER SNOW GEESE DURING WINTER AND SPRING MIGRATION

PAUL E. GREGOIRE[1] AND C. DAVISON ANKNEY[2]

Department of Zoology, University of Western Ontario, London, Ontario N6A 5B7, Canada

ABSTRACT.—We studied dominance and aggression among family and nonfamily groups of Lesser Snow Geese (*Chen caerulescens caerulescens*) in salt marshes and rice fields in Louisiana, from January to March 1984, and in corn fields during the subsequent spring migration. Some proximate costs and benefits of family unity were examined by comparing the behavior of adults and juveniles among different family and nonfamily groups. We also determined if habitat differences influenced agonistic behavior among social groups of foraging Snow Geese.

Lesser Snow Geese had a well-defined dominance hierarchy. Large families dominated small families, which in turn dominated pairs, lone adults, and lone juveniles. Single-parent families and crippled geese were less successful in aggressive interactions than were their normal counterparts. Family groups initiated and won more interactions than nonfamily groups. Individual aggression decreased as family size increased among juveniles in salt marshes. Aggression differed among habitats and was three times more frequent in corn fields than in marshes or rice fields. However, more intense aggression and more within-group aggression were observed in salt marshes as compared with rice or corn fields. *Received 26 May 1988, accepted 26 January 1990.*

DOMINANCE relationships figure prominently in the social behavior of wild birds. Dominant individuals enjoy access to limited resources, such as food and space (Jenkins 1944, Raveling 1970, Welty 1975). Dominance hierarchies also provide stability in a group by reducing the intensity and frequency of altercations (Raveling 1970, Welty 1975, Kaufmann 1983). Individuals learn to identify group members by their position in the hierarchy. Thus, displays or threats can replace more costly interactions, thereby saving time, energy, and injury.

Wild geese are social birds, goose families remain together from one breeding season to at least the beginning of the next (Eisenhauer and Kirkpatrick 1977, Bellrose 1980, Prevett and MacInnes 1980), and pair bonds often remain intact until one adult of the pair dies (Bellrose 1980, Prevett and MacInnes 1980). A dominance hierarchy related to group size accompanies these social bonds. Large families dominate small families, which in turn dominate pairs and single geese (Boyd 1953, Hanson 1953, Raveling 1970). Although larger families dominate smaller families, it is unclear if the larger families actually benefit from their position (Lazarus and Inglis 1978). We assumed a dominance hierarchy exists for Lesser Snow Geese (*Chen caerulescens caerulescens*; hereafter called Snow Geese), and one aim of this study was to examine how group size influences aggression. A second was to determine if more dominant family groups benefit from their position in the social hierarchy.

The dominance status of single-parent families and crippled geese has not been examined. Hunting and disturbance are major contributors to the disruption of families (Prevett and MacInnes 1980) and to the injury of birds. Boyd (1953) and Raveling (1970) showed that dominance position is related directly to the number of individuals in a family at a particular time. Therefore, members of single-parent families would be expected to occupy a lower position in the dominance hierarchy and to experience more interference and displacement. Likewise, crippled geese may be less able to defend themselves or attack other geese. Consequently they occupy a status lower than that of their uninjured counterparts. We attempted to determine how these handicaps affect a bird's status in the flock.

Habitat type may influence how much

[1] Present address: 6207 41 Avenue, Camrose, Alberta T4V 2W5, Canada.

[2] To whom reprint requests should be sent.

aggression occurs in geese. Raveling (1970) observed a higher frequency of interactions among feeding Canada Geese (*Branta canadensis*) than among those at a roost. He showed also that more conflicts occurred where food was concentrated (millet) than where it was evenly dispersed (wheat). Snow Geese frequent several different habitats during winter and spring (Bellrose 1980). In winter, Snow Geese uproot grass rhizomes (mainly *Spartina* spp. and *Scirpus* spp.) in coastal marshes (McIlhenny 1932, Lynch et al. 1947), and they expend much time and energy to bring the rhizomes to the ground surface (McIlhenny 1932). They may protect newly established feeding sites from intruding conspecifics. Snow Geese also feed on inland rice fields (Hobaugh 1984) and graze on waste rice and young herbaceous shoots, which are rather evenly distributed over the ground surface. Snow Geese frequent corn fields during spring migration (Bellrose 1980) and feed on waste corn that is often on cobs or in clumps of loose kernels. An additional aim of our study was to determine if aggression was more prominent in habitats where food was distributed unevenly (e.g. marshes and corn fields).

During spring migration geese store nutrient reserves essential for breeding in the north (Alisauskas 1988), and food-related aggression may be more prominent. Aggression may be increased by hormone production associated with increased day length, which triggers courtship and mating behavior. New pair bonds are formed then (Bellrose 1980, Prevett and MacInnes 1980), and higher aggression by newly formed pairs may be evident (Raveling 1970). Also, family bonds may weaken as juveniles mature, although family breakup often does not occur until the geese reach the breeding grounds (Prevett and MacInnes 1980). A final aim was to determine how agonistic behavior changed among Snow Geese during spring migration.

Study Area and Methods

The winter portion of the study was done from January to early March, 1984, in southwestern Louisiana. We observed Snow Geese in salt marshes in the Cameron Parish within 5 km of the Gulf coast, and in rice fields in the Jefferson Davis Parish, ca. 65 km inland. Observations during spring migration were collected from mid-March to mid-May, in corn fields, at Fremont and Mills counties, Iowa; Brown, Marshall, and Kingsbury counties, South Dakota; and areas 30 km west and south of Portage La Prairie, Manitoba.

We observed the following groups (abbreviations in parentheses):

Family: an adult pair with one to six offspring (Fam 3–8; includes all family members).
Single-parent family: an adult with one or two offspring (S P Fam 2–3).
Pair: two adults with an apparent strong social bond (Pr).
Crippled pair: a pair with one crippled member (Crip Pr).
Lone adult: a lone goose older than one year (L Ad).
Crippled lone adult: a lone adult with at least one lame leg, sometimes also with an injured wing, but capable of flight (Crip L Ad).
Lone juvenile: a lone goose younger than one year (L Juv).

Pairs with no offspring and lone individuals were referred to collectively as nonfamily groups. Juvenile Snow Geese are readily distinguishable from adults by their darker (grayish) head and neck plumage. Adult blue- and white-phase geese have a white head and upper neck.

We determined family size by the coordinated behavior and proximity of family members (e.g. family members moved as a unit, and conspecifics that came too close to the family were pecked at or chased). Cooperative aggression and the fact that landing geese separated into their respective family groups immediately before alighting (Raveling 1968, Prevett and MacInnes 1980) were also useful to identify families. No attempt was made to capture and mark individuals.

All observations were made of birds on the outer edge of a flock. Boyd (1953) and Owen (1972, 1976) noted that goose families tend to occur at the edge of a flock, and birds at the periphery of a flock are more vigilant than other members (Drent and Swierstra 1977, Lazarus 1978, Jennings and Evans 1980). We therefore attempted to control for the effect of position within a flock. Because vigilant behavior decreases with increasing flock size in small aggregations of geese (Drent and Swierstra 1977, Lazarus 1978, Inglis and Lazarus 1981), flocks with <300 birds were not observed.

Snow Geese were observed from a 5-foot platform erected in the back of a truck. This enabled us to observe more than 95% of interactions. Geese were accustomed to vehicular traffic and were not disturbed by the truck as long as the observer remained with the vehicle. We used 8–24 × 50 zoom binoculars to observe geese. We recorded data on a portable tape recorder or directly onto data sheets. We alternated 10-day observation periods in salt marsh and in rice fields. This was repeated until the geese began to migrate.

A flock was scanned in search of a predetermined group size. That is, to sample all group sizes equally, we searched for a group with the smallest sample size

TABLE 1. Outcomes of interactions between social groups[a] of Snow Geese during winter and spring migration (all habitats combined).

	Losers												
Winners	L Juv	Crip L Ad	L Ad	Crip Pr	Pr	S P Fam 2	S P Fam 3	Fam 3	Fam 4	Fam 5	Fam 6	Fam 7 & 8	Total
L Juv	40	4	2		1			1					48
Crip L Ad	16	1	6		1								24
L Ad	50	9	20	1	1			2	1		1		85
Crip Pr	7	1	5		10								23
Pr	108	41	63	14	100	1	2	10	2	4	1		346
S P Fam 2	7	1	11		11			1					31
S P Fam 3	2		13		26	2		3					46
Fam 3	38	4	30	1	80	2	6	10	5	3	2		181
Fam 4	69	3	56	1	63	2	4	23	6	1			228
Fam 5	40	2	23		49			19	3	3		1	140
Fam 6	21		14		23			3	8	1			70
Fam 7 & 8	5		3		6			1	6	5			26
Total	403	66	246	17	371	7	12	73	31	17	4	1	1,248

[a] Abbreviations: family (Fam 3–8), single-parent family (S P Fam 2–3), pair (Pr), crippled pair (Crip Pr), lone adult (L Ad), crippled lone adult (Crip L Ad), and lone juvenile (L Juv).

for that particular time of day. Once located, a social group was observed for up to 20 min and all aggressive interactions were recorded. Observations of <5 min were discarded from the frequency data to remove an observed negative correlation between the number of interactions per minute and the duration of observation (Gregoire unpubl. data). Wins and losses for each altercation were determined by following the basic threat and escape postures described for the genus *Anser* by Boyd (1953) and for the genus *Branta* by Raveling (1970). We categorized aggressive encounters by decreasing levels of intensity: *fight* (where two individuals faced each other with their chests pushed against one another, some biting, wings often flapping), *peck* (a quick extension of the head and neck to hit an individual with the bill or to deliver a bite), *attempted peck* (same as peck, without physical contact), and *threat* (head and neck extended vertically or horizontally while standing, walking, or running toward an individual, often calling). The most intense form of aggression observed during an encounter determined its category. Fighting geese were very active and never hidden from view.

An aggressive interaction occurred when behavior fitting one of the above categories was manifested by individual(s) from one social group on individual(s) usually from a second social group. Interactions that occurred within a social group were recorded separately.

A *win* was tallied when individuals from one social group displaced individuals from a second social group (and retaliations were unsuccessful). A *loss* occurred when individuals from one social group were not displaced by advances from individuals in a second social group. A loss also occurred when the second social group backed out of striking distance or departed. A *tie* occurred when the two social groups neither retreated nor became displaced after one or more confrontations. Ties were uncommon.

We calculated involvement in aggressive interactions per adult bird by summing the number of interactions that involved 1 adult only, 2 adults only (multiplied by 2), ≥1 adult and ≥1 juvenile, and all members (multiplied by 2). The sum from these four categories was divided by twice the total number of interactions. Several categories were multiplied by 2 to account for the number of adults involved in the interactions (single-parent family interactions were not multiplied by 2). Involvement in aggressive interactions per juvenile bird was calculated similarly. Interactions per hour per adult and per juvenile were calculated by multiplying involvement in interactions by the frequency of aggressive interactions observed for that social group.

RESULTS

Dominance hierarchy.—We found a dominance hierarchy, based upon group size, in Snow Geese (Tables 1 and 2). Large families dominated smaller families, which in turn dominated pairs, lone adults, and lone juveniles ($P < 0.05$ for each comparison). Single-parent families won most of their interactions with pairs ($P < 0.01$), but lost most interactions with two-parent families ($P < 0.05$). Overall, crippled geese won fewer interactions against their uninjured counterparts, but not at statistically significant levels.

Sources of conflict.—Most aggressive interactions (>75%) observed in salt marshes and corn

TABLE 2. Agonistic encounters between selected social groups of Snow Geese. The analysis (Group 1 vs. Group 2) was based on the assumption that each group[a] had an equal probability of winning (data from Table 1); * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS = not significant ($P > 0.05$).

Group 1	No. of wins	Group 2	No. of wins	χ^2
Fam >4	17	Fam 4	1	12.50***
Fam 4	23	Fam 3	5	10.32**
Fam 3	80	Pr	10	52.90***
Pr	63	L Ad	1	58.14***
L Ad	50	L Juv	2	10.62**
Fam 3 & 4	14	S P Fam 2 & 3	4	4.50*
S P Fam 3	26	Pr	2	18.90***
S P Fam 2	11	Pr	1	6.75**
Pr	14	Crip Pr	10	0.38 NS
L Ad	9	Crip L Ad	6	0.75 NS
Crip L Ad	16	L Juv	4	6.05*

[a] See Table 1 for explanation of abbreviations.

fields appeared to be food related. Conflicts arose when social groups were protecting their food from intruding conspecifics or when individuals attempted to take over the food patch of another social group. Only individuals within a social group were permitted to feed on the same patch of food. Most aggressive interactions observed in rice fields, and the remainder of interactions observed in marshes and corn fields, appeared to be initiated by intrusions into a goose's *individual space* (the area immediately around a bird, which moved with the bird and included its family members). Birds in rice fields moved constantly and thus approached other social groups more frequently.

Family and nonfamily groups.—Success in aggressive interactions differed among social groups (Table 3). In salt marshes and rice fields, family groups of all sizes won most of their conflicts, but nonfamily groups won fewer than one half of interactions in which they were involved. In corn fields, pairs won just over one half of the interactions in which they were involved. There was also a trend for larger fam-

TABLE 3. Percent success in all aggressive interactions observed for each social group of Snow Geese, in each habitat (wins divided by [wins + losses + ties]). Asterisks indicate significant differences (Chi-square analyses) between the numbers above and below the asterisks; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

	Marsh		Rice		Corn	
	Success (%)	n[a]	Success (%)	n	Success (%)	n
L Juv[b]	7	45	12	139	10	415
					***	
Crip L Ad			9	23	27	131
L Ad	14	57	18	50	30	288
	**				***	
Crip Pr					53	68
Pr	35	88	27	75	52	681
	*		***		**	
S P Fam	63	30	70	53	88	60
					*	
Fam 3	64[c]	87	65[d]	82	75[e]	192
					**	
Fam 4	74	62	80	65	87	225
Fam 5	72	29	80	51	91	179
Fam >5	85[c]	39	95[d]	38	95[e]	82

[a] Number of interactions.
[b] See Table 1 for explanation of abbreviations.
[c] Fam 3 vs. Fam >5, $P < 0.05$.
[d] Fam 3 vs. Fam >5, $P < 0.01$.
[e] Fam 3 vs. Fam >5, $P < 0.001$.

TABLE 4. Percentage of interactions initiated and of those initiated won, for each social group of Snow Geese in each habitat (of the total number of interactions observed for each social group). Asterisks indicate significant differences (Chi-square analyses) between the numbers above and below the asterisks; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

	Marsh			Rice			Corn		
	Init. (%)	Init. won (%)	n[a]	Init. (%)	Init. won (%)	n	Init. (%)	Init. won (%)	n
L Juv[b]	9	75	44	16	77	134	11 ***	84	400
Crip L Ad				10	100	21	28	94	128
L Ad	18 *	90	57	22	82	50	30 ***	90	288
Crip Pr							54	95	68
Pr	35 **	90	86	31 ***	83	75	55 ***	92	681
S P Fam	69	100	29	77	86	53	88	96	60
Fam 3	73	80	86	71[c]	88	80	76 ***	93	192
Fam 4	76	89	62	83	94	60	90	95	223
Fam 5	79	91	29	90[c]	92	51	94	95	175
Fam >5	86	88	36	94	100	36	97	96	86

[a] Number of interactions.
[b] See Table 1 for explanation of abbreviations.
[c] Fam 3 vs. Fam 5, $P < 0.05$.

ilies to be more successful than were smaller families.

Unlike nonfamily groups, family groups initiated most interactions in which they were involved (Table 4). Pairs in corn fields were an exception as they initiated more than half of the interactions in which they were involved. There was also a trend for large families to initiate more interactions than smaller families did. Any group that initiated an interaction was likely to be successful.

Frequency of aggressive encounters varied between family and nonfamily social groups (Fig. 1). Lone adults and pairs were involved in fewer interactions than were family groups in marshes and rice fields. Lone juveniles were involved in more interactions than other nonfamily groups in rice fields and marshes. In corn fields, frequency of aggression was high and extremely variable, and no significant differences occurred between groups. Although pairs were involved in fewer interactions in marshes and rice fields, their involvement in corn fields exceeded that of most other groups. Frequency of interaction did not differ significantly among family sizes in any habitat. However, adults in families (Table 5) were involved in more interactions per hour than were adults in pairs in marshes ($Pr = 0.8 \cdot Ad^{-1} \cdot h^{-1}$) and rice fields ($Pr = 1.4 \cdot Ad^{-1} \cdot h^{-1}$) (Mann-Whitney tests $P < 0.05$). Family juveniles (Table 5) were involved in fewer interactions than lone juveniles (Fig. 1), in all habitats (Mann-Whitney tests $P < 0.01$).

Parents and offspring.—Parent geese took part in significantly more interactions than did their offspring in encounters initiated by families (Table 5). Most of these encounters involved only one adult. At least 75% of the interactions involving only juveniles involved one juvenile, regardless of family size or habitat type. Approximately 50% of encounters that involved some adults and juveniles included both adults, but most often only one juvenile. Involvement in interactions per parent goose varied little with family size, but adults of single-parent families were involved in a greater proportion of encounters than were adults of two-parent family groups (Chi-square $P < 0.05$ for each habitat). There was a trend for involvement in interactions per juvenile bird to decrease as family size increased, in all three habitats (Chi-square tests $P < 0.05$; Marsh Fam 3 > Fam >5 and Corn Fam 3 > Fam 5). When we accounted for the frequency of interactions observed for each social group, the number of interactions per hour per juvenile goose also decreased as family size increased, in the salt marshes and rice fields, but no change was observed in corn fields (Table 5). (Juveniles in marshes; Kruskal-Wallis test $P = 0.02$; Multiple Comparison Procedures (Conover 1980), Fam 4 < Fam >5, $P < 0.05$; Fam 3 < Fam >5, $P = 0.10$). Variation in

frequency of interactions was too great to identify statistical differences among single-parent and two-parent families.

Habitat comparisons.—Frequency of aggressive interactions differed significantly among all three habitat types. We combined all social groups in each habitat and counted an average frequency of 4.7 interactions per hour in salt marshes, 8.7 per hour in rice fields and 29.7 per hour in corn fields (Marsh < Rice < Corn, Kruskal-Wallis test and Multiple Comparison Procedures, $P < 0.001$; $n = 165$, 147, and 192, respectively). Aggressive interactions in corn fields were three times more frequent than in the other habitats and did not differ among the three corn study sites (one-way ANOVA $P > 0.50$).

Aggressive intensity also differed among habitats (Fig. 2). We observed more fights in salt marshes than in either rice or corn fields (marsh vs. rice, $\chi^2 = 6.42$, $P < 0.025$; marsh vs. corn, $\chi^2 = 4.81$, $P < 0.05$). A greater proportion of encounters involved attempted pecks in rice fields and corn fields than in marshes ($\chi^2 = 7.47$ and 6.7, respectively; $P < 0.01$). Pecks and threats did not differ in proportion among habitats.

Within-group aggression.—On 33 occasions we observed a Snow Goose lightly peck or attempt to peck its offspring, mate, or sibling. These within-group interactions occurred when a bird attempted to feed on the food item of another group member or when individuals' heads came close together while they were feeding. The resulting peck appeared to be of low intensity and the pecked individual did not retreat, but either moved its head out of the way or did not respond. Twenty-two interactions were between parents and their offspring, six were between siblings, and five were between members of pairs. Parents often tolerated having their food pulled away several times before they delivered a peck. We observed within-group aggression only in salt marshes and corn fields, but it occurred significantly more frequently in marshes ($\chi^2 = 22.93$, $P < 0.001$). Within-group aggression represented 9.0% ($n = 220$) of interactions in salt marshes and 1.5% ($n = 992$) in corn fields.

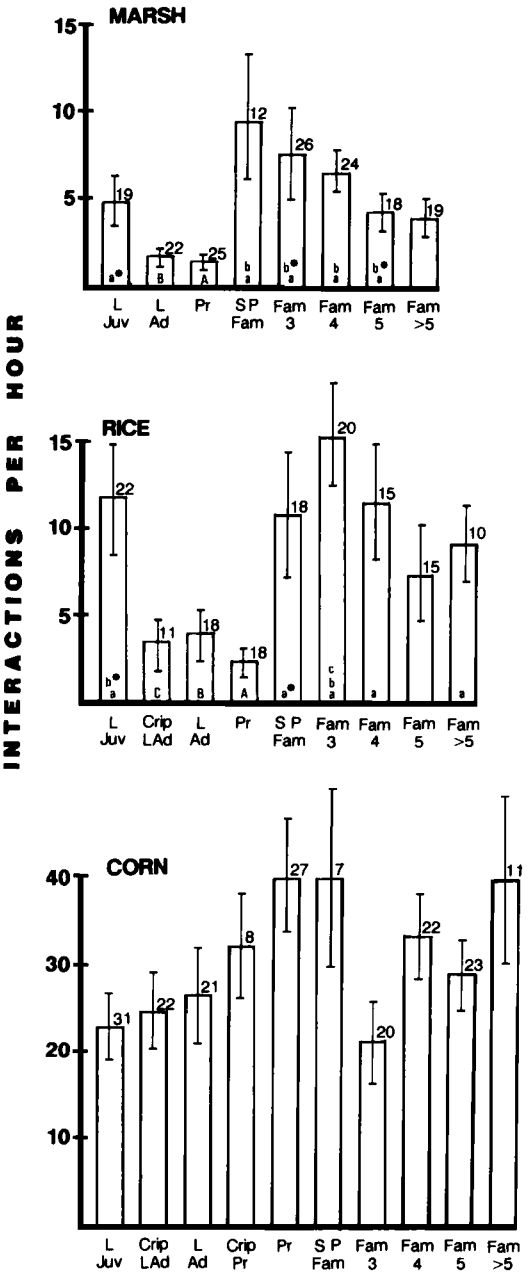

Fig. 1. Frequency of aggressive interactions ($\bar{x} \pm$ SE) among social groups of Snow Geese in marshes, rice fields, and corn fields. Columns with upper-case letters are significantly different from those with equivalent lower-case letters, within each habitat (Kruskal-Wallis and multiple comparison procedures; $P < 0.05$). Asterisks indicate $P < 0.10$; sample sizes are above each bar. See Table 1 for explanation of abbreviations.

Discussion

Dominance hierarchy.—Snow Geese have a well-defined dominance hierarchy which is positively correlated with group size. This is

TABLE 5. Involvement of family members (adults [ad] and juveniles [juv]) in interactions initiated by those families by habitat. All values are percentages except the *n* column and Interactions per hour column.

Habitat/ Groups	Family members: 1 Ad only	2 Ads only	Juv(s) only	Ad(s) & Juv(s)	All	*n*[a]	No. Ad vs. No. Juv Chi-square[b]	Involvement in interactions: Per Ad	Per Juv	Interactions per hour: Per Ad	Per Juv
Marsh											
S P Fam[c]	73		20	7	0	15	Ad***	80	14	7.5	1.3
Fam 3	61	10	19	2	8	59	Ad*	50	29	3.8	2.2
Fam 4	75	2	8	2	13	48	Ad***	54	18	3.5	1.2
Fam 5	58	8	25	4	4	24	Ad***	43	14	1.9	0.6
Fam >5	76	9	9	3	3	34	Ad***	53	6	2.1	0.2
Mean[d]	68	7	15	3	7			50	17	2.8	1.1
Rice											
S P Fam	76		17	2	5	41	Ad***	83	16	8.9	1.7
Fam 3	58	12	15	2	13	48	Ad**	55	30	8.4	4.6
Fam 4	54	15	15	4	12	52	Ad***	57	21	6.6	2.4
Fam 5	58	9	11	9	13	45	Ad***	58	22	4.3	1.6
Fam >5	56	0	22	19	3	32	Ad***	48	14	4.4	1.3
Mean[d]	56	9	16	9	10			55	22	5.9	2.5
Corn											
S P Fam	50		35	4	11	54	Ad***	64	29	25.7	11.6
Fam 3	62	8	11	7	12	152	Ad***	54	30	11.7	6.5
Fam 4	60	6	19	6	9	205	Ad***	49	21	16.4	7.0
Fam 5	52	6	21	14	8	168	Ad***	49	19	14.0	5.5
Fam >5	44	6	30	15	5	86	Ad***	43	19	17.1	7.6
Mean[d]	54	7	20	10	8			49	22	14.8	6.7

[a] Number of interactions.
[b] * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$. Significant values indicate greater parent involvement.
[c] See Table 1 for explanations of abbreviations.
[d] Excludes single-parent families.

consistent with reports for Canada Geese (Raveling 1970) and Greater White-fronted Geese (*Anser albifrons*; Boyd 1953). Physical contact occurred in <15% of all conflicts, indicating that there is an awareness of status and that threats usually suffice to reinforce rank (Raveling 1970). Fights that did occur were usually among closely ranked groups (Gregoire unpubl. data). Any group that initiated an interaction was likely to be successful; even lone juveniles had at least a 75% success rate in interactions that they initiated. Boyd (1953) found a 93% success rate among individual Greater White-fronted Geese that initiated interactions. Presumably geese are able to identify and evaluate social groups before challenging them.

Single-parent families with one adult and one juvenile were able to dominate pairs. Intuitively, we expected that two adults would dominate an adult with a juvenile because unattached adults clearly dominated unattached juveniles (Boyd 1953, Hanson 1953, Raveling 1970, Gregoire 1985). We suggest that the presence of offspring stimulates parent Snow Geese to be more aggressive, making them more likely to win an encounter. The trend for larger families to initiate more interactions and to be more successful overall than smaller families also provided evidence that the brood (and brood size) is a stimulus that motivates parents. Parents initiated most interactions (Table 5). Hanson (1953) first proposed that presence of the brood stimulates Canada Goose parents and stated that strength of the stimulus may be proportional to brood size. Raveling (1970) argued that success in aggression decreased immediately upon separation, and increased upon reunification, of family members. Hanson (1953) and Raveling (1970) proposed that higher hormone levels may be responsible for more intense displays of parents. There is a positive relationship of hormonal production with aggressive behavior and social rank (see reviews by Hinde 1973, Balthazart 1983). Parent geese may be more aggressive to enhance the survival and competitive ability of their offspring.

Crippled geese and single-parent families.—Crippled lone adults and pairs with a crippled adult won fewer interactions against their uninjured counterparts, which may be related directly to the injury. Leg injuries restricted mobility and made it more difficult for a goose to strike back and defend food or its individual space. Most crippled geese were observed alone (Gregoire unpubl. data), and those with mates had difficulty keeping up with them. Crippled adults are more likely to become separated from mates and less adamant in defense of prospective mates.

Adults of single-parent families were involved in more interactions than were adults in two-parent families. A greater effort by the single parent appeared to compensate for a missing mate because rate of involvement of their offspring in aggressive encounters was similar to that of juveniles in other family groups, except during spring migration. Single-parent families were as successful in aggressive interactions as small family groups, which indicates compensation for loss of a parent. What influence the sex of the single parent or the size of the brood had on their behavior is unknown.

Social group costs and benefits.—Family groups (including S P Fam) benefited from their more aggressive behavior by taking over food patches from nonfamily groups. They protected their food patches from intruding conspecifics more successfully. Also, family groups defended their individual space more successfully. This stresses the value of a parent to juveniles with respect to access to food and space, and freedom from conspecific interference. Nonfamily groups, especially lone juveniles, initiated less than one third of the interactions in which they were involved. This indicates that they were the individuals being attacked and displaced. Lone juveniles were attacked when too close to other social groups, and they often had their food stolen. Juveniles in families were involved in fewer interactions than were Lone Juveniles and were more free from conspecific interference. Juveniles in families were often aided by their parents when they attacked or were attacked by conspecifics. We did not determine whether lone juveniles have lower body mass and are less likely to breed successfully than are juveniles in families.

Parents of Canada Geese (Raveling 1970) and Greater White-fronted Geese (Boyd 1953) participated in more conflicts than did their offspring, and most conflicts involved the male. Our findings corroborate this as we also found greater parental involvement, particularly by one parent, in interactions initiated by Snow Geese. Snow Goose families on the wintering grounds were also involved in more aggressive interactions than most nonfamily groups. Because parents were involved in most encounters, this may reflect the parents' investment in their offspring. Lone adults and pairs with no young to protect were less aggressive.

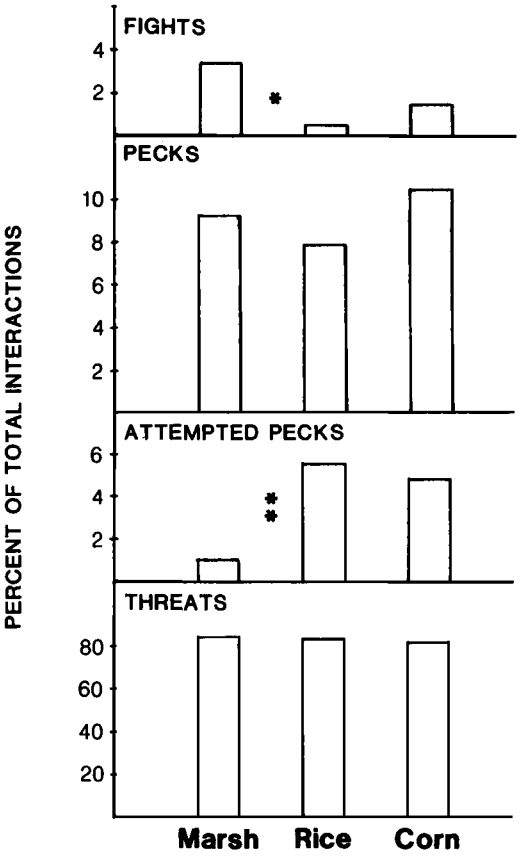

Fig. 2. Intensity of aggressive behavior of Snow Geese by habitat type (* = $P < 0.05$; ** = $P < 0.01$). There were 257 events in marsh, 381 in rice fields, and 1,465 in corn fields.

Family members initiated 75% of all interactions, and we believe this is representative of the entire Snow Goose population. Therefore, the proportion and frequency of interactions observed per juvenile bird (Table 5) implies that juveniles in larger families, in salt marshes and rice fields, may have benefited by fewer conflicts per individual than juveniles in smaller

families did. Perhaps because smaller social groups actively avoided larger families, more time is available for other activities, such as feeding, resting, and preening by juveniles in large families.

The proportion of interactions per juvenile in families feeding in corn fields decreased as family size increased (Table 5). Larger families were involved in more conflicts so that we observed no difference in the frequency of interactions per individual among family groups. The high level of activity in corn fields may have contributed to confusion, making it more difficult for a bird to identify another bird's status.

The frequency of encounters increased with brood size in wintering Canada Geese (Raveling 1970) but not in Snow Geese. The lower frequency of encounters we observed for larger families may be related to a poor Snow Goose breeding season in 1983 (Anonymous 1983), which resulted in few large families to compete with each other.

Aggression and habitat type.—Several factors may be responsible for the higher frequency of aggressive interactions in corn fields than in marshes and rice fields. First, cobs of corn and clumps of loose kernels are a patchy food resource, which all groups vigorously defended. Raveling (1970) observed more conflicts among Canada Geese in an area where food was concentrated and noted that aggressive encounters in winter corn fields were so frequent that they were impossible to record accurately. Second, waste corn (unlike rhizomes in marsh habitat) was visible at the ground surface, and provided a stimulus which apparently promoted attempts of birds to steal from each other. Geese depleted patches quickly and moved frequently in search of other food. Third, the birds were on spring migration, a time when they must acquire sufficient nutrient reserves to breed (Ankney 1982). Time of year may be only partially responsible for the high rate of aggression. Raveling (1970) reported a high frequency of conflicts in corn fields during winter. We found no evidence that frequency of aggression (in corn fields) increased during spring migration (Gregoire unpubl. data).

Geese showed more aggressive interactions in rice fields than in marshes. Although feeding areas in salt marshes were vigorously defended, the birds were more dispersed than in other habitats, and the uneven terrain restricted their movements. This reduced opportunity for contacts and consequent aggression. The food patches in marshes were not quickly depleted, and geese stayed in one spot for periods up to 20 min or more. Although food (green vegetation; Alisauskas et al. 1988) was not distributed patchily in rice fields, the substrate was flat and the geese were closely spaced and moved continually (Gregoire 1985). This provided more opportunity for aggressive interactions.

Geese in salt marshes fought more. They were reluctant to give up their food patches to intruders. Geese often fed in one spot for long periods. They grubbed and pulled rhizomes to the ground surface, which opened the area, and facilitated access to other rhizomes. Although food patches were defended in corn fields, corn was readily available at the ground surface obviating any investment to make the resource accessible. Geese in rice fields primarily grazed upon evenly distributed grass shoots, which reduced the potential for food-related confrontations. The low number of attempted pecks, a weak form of aggression, may be related to the nature of the salt marsh substrate. It was easier to avoid pecks in rice and corn fields, and attempted pecks were less successful in those habitats.

Spring migration.—The frequency and success in aggressive interactions for pairs increased in spring. Males become more protective of their mates upon breakup of the family in spring (Jenkins 1944) and chase potential rivals. This protection may allow the female to acquire the nutrient reserves needed to breed successfully (Ankney and MacInnes 1978). The high level of aggression by paired geese during spring migration may involve some geese which had recently formed pair bonds (Raveling 1970). The higher frequency of aggressive interactions observed in all social groups in corn fields, as compared with salt marshes and rice fields, appeared to be more a function of the habitat type than of time of year.

Within-group aggression.—Raveling (1970) observed within-family aggression in Canada Geese and noted that pecks were less forceful and not followed by escape or attack behavior. We found similar conditions in Snow Geese. Aggression among group members was restricted and often appeared to serve a disciplinary role. Within-group aggression and fighting among group members occurred only in coastal marshes and corn fields, where food was dis-

tributed unevenly. We suggest that habitat type and nature of the food resource influence aggression among Snow Geese.

Dominance and aggression play an important role in the social life of Snow Geese. Juveniles clearly benefited by remaining in families, as parents assumed the protective role and were involved in more interactions than were their offspring or nonfamily groups. Individuals in larger, more dominant families may benefit from fewer interactions than individuals in smaller families. We also suggest that the type of habitat (particularly the distribution of food) influences frequency and intensity of aggression.

ACKNOWLEDGMENTS

We thank B. Brown of the Lacassine National Wildlife Refuge, the staff of the Rockefeller State Wildlife Refuge, the Sand Lake National Wildlife Refuge, and S. Davis, for their hospitality during the field season. J. Haggeman helped with data collection, and R. Alisauskas, K. Somers, and S. Barry provided valuable advice. L. Brodsky and J. Lazarus gave many useful comments on the manuscript. Special thanks to J. Amery for preparing the figures and typing the paper. This research was funded by the Delta Waterfowl and Wetlands Research Station and a Natural Sciences and Engineering Research Council of Canada research grant to Ankney.

LITERATURE CITED

ALISAUSKAS, R. T. 1988. Nutrient reserves of Lesser Snow Geese during winter and spring migration. Ph.D. thesis, London, Ontario, Univ. Western Ontario.

———, C. D. ANKNEY, & E. E. KLAAS. 1988. Winter diets and nutrition of the midcontinental population of Lesser Snow Geese. J. Wildl. Manage. 52: 403–414.

ANKNEY, C. D. 1982. Annual cycle of body weight in Lesser Snow Geese. Wildl. Soc. Bull. 10: 60–64.

———, & C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 95: 459–471.

ANONYMOUS. 1983. 1983 status of waterfowl and fall flight forecasts. U.S. Fish and Wildlife Service and Can. Wildlife Service.

BALTHAZART, J. 1983. Hormonal correlates of behavior. Pp. 221–365 *in* Avian biology, vol. #7. (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.

BELLROSE, F. C. 1980. Ducks, geese and swans of North America. Harrisburg, Pennsylvania, Stackpole Books.

BOYD, H. 1953. On encounters between wild White-fronted Geese in winter flocks. Behaviour 5: 85–129.

CONOVER, W. J. 1980. Practical nonparametric statistics, second ed. New York, J. Wiley and Sons.

DRENT, R., & P. SWIERSTRA. 1977. Goose flocks and food finding: field experiments with Barnacle Geese in winter. Wildfowl 28: 15–20.

EISENHAUER, D., & C. KIRKPATRICK. 1977. Ecology of the Emperor Goose in Alaska. Wildl. Mono. 57: 1–62.

GREGOIRE, P. E. 1985. Behavior of family and other social groups in wintering and migrating Lesser Snow Geese. Unpubl. M.S. thesis, London, Ontario, Univ. Western Ontario.

HANSON, H. M. 1953. Inter-family dominance in Canada Geese. Auk 70: 11–16.

HINDE, R. A. 1973. Behavior. Pp. 479–535 *in* Avian biology, vol. 3. (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.

HOBAUGH, W. C. 1984. Habitat use by Snow Geese wintering in southeast Texas. J. Wildl. Manage. 48: 1085–1096.

INGLIS, I. R., & J. LAZARUS. 1981. Vigilance and flock size in Brent Geese: the edge effect. Z. Tierpsychol. 57: 193–200.

JENKINS, D. W. 1944. Territory as a result of despotism and social organization in geese. Auk 61: 30–47.

JENNINGS, T., & S. M. EVANS. 1980. Influence of position in the flock and flock size on vigilance in the Starling, *Sturnus vulgaris*. Anim. Behav. 28: 634–635.

KAUFMANN, J. H. 1983. On the definitions and functions of dominance and territoriality. Biol. Rev. 58: 1–20.

LAZARUS, J. 1978. Vigilance, flock size and domain of danger size in the White-fronted Goose. Wildfowl 29: 135–145.

———, & I. R. INGLIS. 1978. The breeding behaviour of the Pink-footed Goose: parental care and vigilant behaviour during the fledging period. Behaviour 45: 62–68.

LYNCH, J., T. O'NEIL, & D. LAY. 1947. Management significance of damage by geese and muskrats to Gulf coast marshes. J. Wildl. Manage. 11: 50–76.

MCILHENNY, E. A. 1932. The Blue Goose in its winter home. Auk 49: 279–306.

OWEN, M. 1972. Some factors affecting food intake and selection in White-fronted Geese. J. Anim. Ecol. 41: 79–92.

———. 1976. The selection of winter food by White-fronted Geese. J. Appl. Ecol. 13: 715–729.

PREVETT, J. P., & C. D. MACINNES. 1980. Family and other social groups in Snow Geese. Wildl. Monogr. 71: 1–46.

RAVELING, D. G. 1968. Can counts of group sizes of Canada Geese reveal population structure? Pp. 589–595 *in* Waterfowl ecology and management:

selected readings (J. T. Ratti, L. D. Flake, and W. A. Wentz, Eds.). 1982. Bethesda, Maryland, The Wildlife Society.

———. 1970. Dominance relationships and agonistic behavior of Canada Geese in winter. Behaviour 37: 291–319.

WELTY, J. C. 1975. The life of birds, second ed. Philadelphia, W. B. Saunders Co.

100 Years Ago in The Auk

From *The Auk*, Volume 7, July 1890

[The following is the complete listing of what we would consider "regular articles." Of 28 "General Notes," 20 were on range extensions or new local records. We at least improved the variety of our journal.—Ed.]

AN ACCOUNT OF FLAMINGOES (*PHOENICOPTERUS RUBER*) OBSERVED IN THE VICINITY OF CAPE SABLE, FLORIDA. By *W. E. D. Scott.*

CAPE COD BIRD NOTES. By *G. S. Miller, Jr.*

ADDITIONAL NOTES ON THE BIRDS OF ONEIDA COUNTY, NEW YORK. By *William and Egbert Bagg.*

NOTES ON THE NESTING HABITS OF SEVERAL BIRDS AT SAN JOSE, COSTA RICA. By *George K. Cherie.*

NOTES ON THE FRINGILLIDAE OF WESTERN ILLINOIS. By *Otho C. Poling.*

DESCRIPTIONS OF A NEW SPECIES AND THREE NEW SUBSPECIES OF BIRDS FROM ARIZONA. By *Dr. Edgar A. Mearns, U.S.A.*

OBSERVATIONS ON THE AVIFAUNA OF PORTIONS OF ARIZONA. By *Dr. Edgar A. Mearns, U.S.A.*

TWO SPECIES OF SWALLOW NEW TO NORTH AMERICA. By *W. E. D. Scott.*

A LIST OF BIRDS OBSERVED AT SANTAREM, BRAZIL. By *Clarence B. Riker.*