Dominance relations and agonistic behaviour of Tundra Swans (*Cygnus columbianus columbianus*) during fall and spring migration

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Abstract: Social interactions and agonistic activities of Tundra Swans (*Cygnus columbianus columbianus*) were documented at Long Point, Ontario, to determine (*i*) dominance relations among social groups and (*ii*) the frequency and intensity of agonistic acts by swans. Families were involved in one-third as many interactions as were nonfamily groups. Nonfamily groups initiated interactions with other nonfamily groups more often than they did with family groups, but families initiated the same relative numbers of interactions with family and nonfamily groups. Further, families won nearly all conflicts with nonfamily groups, which suggests that they generally dominated nonfamily groups. Tundra Swans also showed a dominance hierarchy based largely on family or group size. To reduce conflict and energy expenditure, swans may use a simple "decision rule" during interactions: larger groups and initiators win. Two results supported this: (1) swans initiated interactions more often with smaller groups and (2) groups that initiated won interactions more often than did recipients. Swans used low-intensity agonistic acts more frequently than higher intensity ones when engaging members of other social groups, but intensity of aggression was independent of group status. Dominance based on the use of simple cues may be especially beneficial in unstable social environments at major staging areas.

Résumé : L'étude des interactions sociales et des activités agonistiques chez les cygnes siffleurs (*Cygnus columbianus columbianus*) à Long Point en Ontario a servi à déterminer (*i*) les relations de dominance entre les groupes sociaux et (*ii*) la fréquence et l'intensité des actes agonistiques. Les familles sont impliquées dans un tiers de plus d'interactions que les groupes non familiaux. Les groupes non familiaux entreprennent des interactions plus souvent avec d'autres groupes non familiaux qu'avec des familles; en revanche, les familles amorcent le même nombre relatif d'interactions avec les autres familles et avec les groupes non familiaux. De plus, les familles gagnent presque tous les conflits qui impliquent des groupes non familiaux, ce qui laisse croire qu'elles dominent généralement les groupes non familiaux. Les cygnes siffleurs ont une hiérarchie de dominance qui est en grande partie basée sur la taille de la famille ou du groupe. Afin de réduire les conflits et les dépenses d'énergie, il se peut que les cygnes utilisent une « règle de décision » simple, e.g., que les groupes plus grands ou que les instigateurs de l'interaction gagnent. Deux de nos résultats vont dans ce sens : (1) les cygnes amorcent des interactions plus fréquemment avec les petits groupes et (2) les groupes instigateurs des interactions en sortent plus souvent vainqueurs que les groupes récepteurs. Les cygnes siffleurs utilisent des actes agonistiques de faible intensité plus fréquemment que ceux de forte intensité lorsqu'ils confrontent des membres d'autres groupes sociaux, mais l'intensité de l'agression est indépendante du statut du groupe. La dominance basée sur l'utilisation de signaux simples peut être particulièrement bénéfique dans les environnements sociaux instables sur les sites importants de parade.

[Traduit par la Rédaction]

Introduction

Dominance hierarchies and agonistic activities are important features of sociality for many animals. Dominant individuals or groups can gain greater access to scarce or valuable resources, such as food, preferred feeding or resting sites, safe refuges, and mates, than can subordinates

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(Huntingford and Turner 1987). Dominance relations and hierarchies ultimately serve to reduce the intensity and frequency of aggressive interactions, thereby providing group stability and optimizing time available for other activities (Kaufmann 1983). Dominance hierarchies not only benefit dominant individuals, but also may benefit subordinates by reducing time spent interacting with others, thus reducing risk of injury and increasing time available for other important activities (Huntingford and Turner 1987).

Social hierarchies have been documented in numerous species of geese (Bar-headed Goose (*Anser indicus*), Lamprecht 1986; Barnacle Goose (*Branta leucopsis*), Black and Owen 1989; Canada Goose (*Branta canadensis interior*), Raveling 1970; Lesser Snow Goose (*Chen caerulescens caerulescens*), Gregoire and Ankney 1990; White-fronted Goose (*Anser albifrons*), Boyd 1953) and two species of swans

(Bewick's Swan, *Cygnus columbianus bewickii*, Scott 1980, 1981; Whooper Swan (*Cygnus cygnus cygnus*), Kakizawa 1981). In most geese and in Whooper Swans, larger families are dominant to smaller families and family groups have higher social standing than do all nonfamily groups, while among nonfamily groups, pairs dominate single birds and single adults are dominant to lone juveniles (Raveling 1970; Kakizawa 1981; Black and Owen 1989; Gregoire and Ankney 1990). In Bar-headed Geese and Bewick's Swans, however, family size is not an important determinant of dominance even though family groups are dominant to nonfamily groups (Scott 1980, 1981; Lamprecht 1986). To my knowledge, there is only one published study of agonistic interactions or dominance structure among social groups of Tundra Swans, *Cygnus columbianus columbianus* (Earnst and Bart 1991).

Thus, the objectives of this study were to document (*i*) intraspecific interactions among different-sized social groups of Tundra Swans and (*ii*) the frequency, type, and intensity of agonistic acts by Tundra Swans on a major staging area during migration. Ultimately, I used these data to test the following predictions based on other studies of dominance or sociality in waterfowl. First, if family groups are dominant over nonfamily groups, then family groups will win interactions more often than do nonfamily groups. Second, if Tundra Swans exhibit a dominance hierarchy based on group size, then larger Tundra Swan groups will win interactions more often than do smaller groups. Third, if swans use a simple signal such as group size as a general guide to assess probability of success during interactions (Raveling 1970; Gregoire and Ankney 1990), group members will initiate interactions with members of relatively smaller groups, and when groups initiated interactions, they will win more often than they will lose, regardless of the size of the group that they challenge. Finally, a general feature of animals having a social dominance system, whether related to group size or not, is a reduced reliance on high-intensity and potentially harmful and energy-demanding acts during social interactions (Kaufmann 1983). Given this, swans should use lower intensity acts more often than higher intensity acts. I also wanted to determine if the intensity of interactions differed between family and nonfamily groups. Specifically, I tested whether family members used higher intensity acts such as chases and fights at a lower frequency than did nonfamily-group members.

Materials and methods

This study was conducted during fall (1998 and 1999) and spring (1999) migration at a globally important waterfowl staging area, Long Point, Ontario (42°38′N, 80°24′W) (Petrie 1998[2]; Petrie et al. 2002). Over the three staging seasons, a total of 227.5 diurnal hours (fall 1998: 38.7 h at Bouck's Pond and 54.5 h at Little Rice Bay; spring 1999: 21.3 h at Biosphere Pond, 14.8 h at Inner Long Point Bay, and 21.4 h at Crown Marsh Pond; fall 1999: 59.4 h at Big Creek North Pond and 17.3 h at Inner Long Point Bay) were amassed observing Tundra Swan activities from observation blinds over-

looking six (see above) shallow, open-water habitats or ponds bordered by emergent wetland plants. There was considerable variation in the number of Tundra Swans present during an observation period, but usually several hundred swans were available to interact with each other at a location during any given day (fall 1998: Bouck's Pond, mean = 115 (range = 41–195); Little Rice Bay, mean = 753 (range = 346–1337); spring 1999: Biosphere Pond, mean = 196 (range = 47–530); Inner Long Point Bay, mean = 718 (range = 88–1331); Crown Marsh Pond, mean = 100 (range = 18–301); fall 1999: Big Creek North Pond, mean = 227 (range = 5–560); Inner Long Point Bay, mean = 172 (range = 18–424).

Intraspecific interactions and agonistic acts among Tundra Swan social groups were recorded opportunistically or while using scan- or focal-group sampling techniques (Altman 1974) to determine diurnal activity budgets of swans and other waterfowl (S.S. Badzinski, unpublished data). Diurnal observation periods lasted either from 0.5 h before sunrise until noon (morning; approximately 5–6 h) or from noon until 0.5 h after sunset (afternoon; approximately 5–5.5 h). Two pairs of workers (an observer and a recorder) performed daily observations at the above-mentioned six locations from Tundra Swan arrival (fall: mid-October – early December; spring: early March – mid-April) until their departure. To reduce bias, the same two people (S.S. Badzinski and K. Patton in fall 1998 and spring 1999; S.S. Badzinski and S. Meyer in fall 1999) observed swan activity throughout each season. However, recorders often drew the observer's attention to additional intraspecific interactions occurring on ponds. Thus, because of the nearly constant scan- and focal-group sampling of waterfowl (S.S. Badzinski, unpublished data), combined with observations by recorders, almost all of the most conspicuous interactions (e.g., fights, chases, or vocal displays) likely were recorded during an observation period. Less conspicuous interactions (e.g., threats, pecks, or bites) were often detected during 294 fifteen-minute focal-group observations that were conducted during spring ($N = 149$) and fall ($N = 145$) field seasons (S.S. Badzinski, unpublished data).

Information recorded during intraspecific interactions included age (adult or juvenile) of the initiating individual, size or classification of the aggressor and recipient social group, type of agonistic act used by the aggressor, and outcome (win, loss, tie) of the interaction. Adults were distinguished from juveniles by differences in plumage characteristics (Scott 1980). Group membership was determined from social displays, proximity, or coordinated movements of individuals before, during, or after interactions (Scott 1980). Social groups were classified as lone juveniles (without parents), lone adults, paired adults, and families. Families were further classified by their size, which ranged from 3 (2 adults + 1 juvenile) to 6 (2 adults + 4 juveniles) individuals. Agonistic acts were categorized by decreasing level of intensity based on energy expended and likelihood of physical harm (Black and Owen 1989), as follows: fight (in which individuals of the two social groups faced each other and engaged in physical combat, often with wing flapping, pecking, or

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[2]S.A. Petrie. 1998. Waterfowl and wetlands of Long Point Bay and Old Norfolk County: present conditions and future options for conservation. Unpublished report, Norfolk Land Stewardship Council, Long Point Waterfowl and Wetlands Research Fund, Port Rowan, Ontario.

Table 1. Numbers of interactions between social groups of Tundra Swans (*Cygnus columbianus columbianus*) during fall and spring migration at Long Point, Ontario.

	Loser							
Winner	Family 6	Family 5	Family 4	Family 3	Pair	Lone adult	Lone juvenile	Total[a]
Family 6	1		1					2
Family 5		1	4	1	3	3	1	13
Family 4			4	7	9	5	1	26
Family 3		1	1	6	12	8		28
Pair		1		1	26	8	2	38
Lone adult					3	47	8	58
Lone juvenile					3	1	3	7
Total	1	3	10	15	56	72	15	172

[a]Ties are not included in totals: 1 (family 5 – family 4), 2 (family 3 – family 3), 3 (pair–pair); total interactions = 178.

Table 2. Percentages of agonistic encounters between different-sized social groups of Tundra Swans that were won during fall and spring migration at Long Point, Ontario.

Social group 1	Percentage of wins	Social group 2	Percentage of wins	G	P[a]
Family ≥5	83 (4)	Family 4[b]	0 (0)	12.936	<0.001
	50 (1)	Family 3	50 (1)		
	75 (3)	Pair	25 (1)		
	100 (3)	Lone adult	0 (0)		
	100 (1)	Lone juvenile	0 (0)		
Family 4	88 (7)	Family 3	12 (1)	28.543	<0.001
	100 (9)	Pair	0 (0)		
	100 (5)	Lone adult	0 (0)		
	100 (1)	Lone juvenile	0 (0)		
Family 3	92 (12)	Pair	8 (1)	25.774	<0.001
	100 (8)	Lone adult	0 (0)		
	—	Lone juvenile	—		
Pair	73 (8)	Lone adult	27 (3)	7.134	<0.01
	67 (2)	Lone juvenile	33 (1)		
Lone adult	89 (8)	Lone juvenile	11 (1)	9.206	<0.01

Note: Numbers in parentheses are sample sizes.
[a]Based on df = 1 from G test on total wins for social groups below 1; analyses are based on equal chances of a win or loss.
[b]There was one tie (see Table 1).

biting), chase ("purposeful" following of another swan, often in conjunction with threat postures), peck/bite (a quick extension of the head and neck to hit an individual with the bill or deliver a bite), threat (one swan facing another and extending its head and neck forward in a bobbing motion, vocalizing and (or) posturing while swimming or walking toward another individual, or extending the head and neck with the mouth held open, or attempting to peck). The act of highest intensity employed by individuals (or groups) during a confrontation was recorded because swans often used a graded series of acts during interactions. A win was recorded when individuals in the initiating social group displaced individuals from a recipient group (and retaliations by the latter group were unsuccessful). A loss occurred when individuals from a recipient social group were not displaced by the actions of the initiating individuals. A loss also was recorded when the initiating group backed out of striking distance or departed the immediate vicinity of the recipient group, which thereby received a win. A tie occurred when neither social group retreated or was displaced

during a confrontation; this outcome was very uncommon, so most interactions ended in a clear win or loss. Because interactions were documented between unmarked individuals it was impossible to know whether the same individuals were involved in more than one interaction, but the probability of this seems minimal because (*i*) there were usually hundreds of individual swans at a location (see above) and (*ii*) usually, few interactions were observed at a site each day (approximate mean per observation day = 4) and most involved groups with different size combinations.

Wins and losses among social groups were arranged in a matrix to show the total number of interactions and to aid in visualizing the structure of dominance relations among social groups (Martin and Bateson 1993). Log-likelihood-ratio goodness-of-fit tests and contingency-table analyses, both using the G statistic, were employed to assess whether counts of observed interactions or agonistic acts deviated from those expected with respect to the categories of interest (Zar 1996). To aid in describing differences among groups, I report the percentages and actual counts of interactions and agonistic

Table 3. Percentages of interactions that were initiated with larger and smaller groups of Tundra Swans and percentages of interactions initiated that were won by each social group with relatively larger, similar-sized, and relatively smaller groups during fall and spring migration at Long Point, Ontario.

	Percentage initiated[a]		No. initiated and percentage won[b,c]			
	Larger groups	Smaller groups	Larger groups	Similar-sized groups	Smaller groups	Overall
Family 6	—	100 (1/1)	—	100 (1/1)	100 (1/1)	100 (2/2)
Family 5	0 (0/0)	60 (9/15)	0 (0)	100 (1/1)	89 (8/9)	90 (9/10)
Family 4	33 (2/6)	87 (20/23)	0 (0/2)	25 (1/4)	100 (20/20)	81 (21/26)
Family 3	30 (3/10)	81 (17/21)	67 (2/3)	63 (5/8)	94 (16/17)	89 (23/28)
Pair	15 (4/26)	56 (9/16)	25 (1/4)	76 (22/29)	100 (9/9)	76 (32/42)
Lone adult[d]	22 (6/27)	78 (7/9)	50 (3/6)	96 (45/47)	100 (7/7)	92 (55/60)
Lone juvenile	37 (7/16)	—	57 (4/7)	100 (3/3)	—	70 (7/10)
Total	26 (22/85)[e]	74 (63/85)[e]	45 (10/22)	84 (78/93)	97 (61/63)	84 (149/178)

[a]Numbers in parentheses show number of interactions initiated / total number of group interactions.
[b]Numbers in parentheses show number of wins / total number of initiated interactions.
[c]The following tests were done assuming an equal probability of winning or losing an interaction: larger groups: 45% (10) wins, $G = -9.400$, df = 1, $P > 0.05$; same-sized groups: 84% (78) wins, $G = 80.692$, df = 1, $P < 0.001$; smaller groups: 97% (61) wins, $G = 80.628$, df = 1, $P < 0.001$.
[d]Lone juvenile is included in "smaller" and is based on age and lower social standing (see Table 1).
[e]Total number of interactions initiated / total number of group interactions.

Table 4. Comparisons of the relative frequencies of agonistic acts used by Tundra Swan groups when initiating social interactions during the fall and spring migration at Long Point, Ontario.

	Percentage of agonistic acts		
Comparison	Low intensity	High intensity	Total
Overall[a]			
Family	80 (53)	20 (13)	(66)
Nonfamily	74 (83)	26 (29)	(112)
Total no. of acts	136	42	178
Juveniles[b]			
Family	89 (8)	11 (1)	(9)
Nonfamily	80 (8)	20 (2)	(10)
Total no. of acts	16	3	19
Adults[c]			
Family pair	79 (45)	21 (12)	(57)
Nonfamily pair	79 (33)	21 (9)	(42)
Nonfamily single	70 (42)	30 (18)	(60)
Total no. of acts	120	39	159

Note: Numbers in parentheses show the number of acts.
[a]$G = 0.901$, df = 1, $P > 0.05$.
[b]$G = 0.287$, df = 1, $P > 0.05$.
[c]$G = 1.537$, df = 1, $P > 0.05$.

acts performed by social groups. When employed, the results of statistical analyses were considered reliable and worthy of discussion if $P \leq 0.10$.

Results

In total, 178 intraspecific interactions between Tundra Swan social groups were documented during fall and spring migration (Table 1). Families were involved in far fewer interactions (29%, or 104 of 356) than were nonfamily groups (71%, or 252 of 356; $G = 23.401$, df = 1, $P < 0.001$). The most commonly observed interactions were between pairs of adults (15%) and between lone adults (26%), which likely reflected the greater relative abundance of these groups at observation locations. Families initiated 17% (30 of 178) and 20% (36 of 178) of interactions with other families and nonfamily groups, respectively; nonfamilies, however, initiated a much higher percentage of interactions with other nonfamily groups (58%, or 104 of 178) than with family groups (5%, or 8 of 178). When family and nonfamily groups interacted, families won 95% (42 of 44) of the confrontations.

Tundra Swans appeared to have a dominance hierarchy based largely on group size (Table 2). Larger families generally dominated smaller families, which in turn dominated pairs, lone adults, and lone juveniles. Among nonfamily groups, paired adults won most interactions with lone birds and lone adults generally dominated lone juveniles.

Overall, individuals that initiated interactions did so most often with members of social groups that were smaller (74%, or 63 of 85) as opposed to larger (26%, or 22 of 85) than their own group; the same pattern was also observed within each social group (Table 3). Even though individual swans (or groups) initiated interactions more often with relatively smaller groups, whenever an interaction was initiated, the aggressor(s) had a high probability of success (84%, or 149 of 178 wins) (Table 3). Further, aggressors usually won if the recipient group was the same size or relatively smaller, but they won only as many interactions as they lost when they challenged relatively larger groups (Table 3).

Overall, Tundra Swans used low-intensity agonistic acts (35% threats and 41% pecks/bites) much more frequently than they used acts of higher intensity (17% chases and 7% fights) during social interactions (76%, or 136 of 178 (low) vs. 24%, or 42 of 178 (high)) (Table 4). Fights occurred relatively infrequently during interactions and were observed most often between similar-sized groups. For example, most fights (69%, or 9 of 13) were between nonfamily groups, e.g., lone adults (46%, or 6 of 13), pairs (15%, or 2 of 13), or pairs and lone adults (8%, or 1 of 13), but families were involved in only 31% (4 of 13) of all fights. Juveniles, whether or not they had parents, were never (0 of 19) observed initiating fights with other swans. Employment of low- and high-intensity agonistic acts did not differ between family and nonfamily groups (Table 4). Further, in a comparison controlling for age (juvenile and adult), the use of high-

and low-intensity agonistic acts did not differ between family and nonfamily juveniles, nor were there differences among family pairs, nonfamily pairs, and single adults (Table 4).

Discussion

Tundra Swans using aquatic habitats during fall and spring migration displayed a dominance hierarchy based largely on family or group size, and it was reinforced or maintained by the use of relatively low-intensity interactions. These main findings were consistent with the reported social structure and mechanism used to establish or maintain such dominance hierarchies in several species of geese (Boyd 1953; Raveling 1970; Black and Owen 1989; Gregoire and Ankney 1990; but see Lamprecht 1986) and Whooper Swans (Kakizawa 1981). The results of this study, however, did not agree entirely with those of an investigation of sociality in Bewick's Swan, a subspecies of *Cygnus columbianus* found in Europe and Asia.

Bewick's Swan families were clearly dominant to nonfamily groups (Scott 1980, 1981), and this generally supports the results of studies of other swans (Kakizawa 1981; Earnst and Bart 1991; this study) and numerous other waterfowl (see above). However, there was no relation between group size and dominance in Bewick's Swan. Rather, social status of dominant individuals in groups was the main determinant of intergroup dominance relations, as the social status of a male usually determined his group's dominance (Scott 1980, 1981). This difference in social organization between Tundra and Bewick's swans could be related to how and when data were collected during the annual cycle and possibly to differences in social environment during migration and winter.

The influence of social status of individuals on the dominance structure observed among Bewick's Swans may partly be due to Scott's (1980, 1981) ability to identify and follow specific individual swans or groups throughout the study period. By using bill markings unique to each swan, she was able to document repeated interactions between known individuals or groups of individuals. The opportunity to do so was further facilitated by observing a relatively stable flock of swans (i.e., the same birds) during winter that were feeding at an artificially concentrated food source (see also Lamprecht 1986); in contrast, in my study, data were collected on unknown birds in relatively dynamic flocks and under natural conditions during migration (see below). The heightened frequency and intensity of interactions at artificial feeding sites also likely allowed the effects of social status to be detected independently of those of family or group size, and this type of dominance structure may actually be beneficial when food availability is high and predictable and flock composition is relatively constant (Lamprecht 1986). However, Kakizawa (1981) observed known individuals and groups of Whooper Swans during four winters at artificial feeding sites and, consistent with the results of this study, reported a dominance structure based largely on family and group size. In Kakizawa's (1981) study and mine, lower ranking (smaller) groups occasionally won interactions with apparently higher ranking (larger) groups. Such deviations were not surprising, but did suggest that factors in addition to family or group size influenced intergroup dominance

structure in Tundra and Whooper swans. Factors that can influence dominance in social animals include age (Lamprecht 1986; Black and Owen 1987), sex (Scott 1980; Lamprecht 1986), body size (Scott 1980; Black and Owen 1987), arrival chronology (Kakizawa 1981; Scott 1981), and hormone levels (Huntingford and Turner 1987).

Dominance based on group or family size may be favoured when the social environment that individuals typically encounter is relatively unpredictable and unstable. Such an environment may be common at major waterfowl staging areas. Unfortunately, data on characteristics of Tundra Swan flocks during migration, such as composition, membership, and cohesion, are lacking. Nevertheless, I think that the social environment at staging areas is much less stable than that on most wintering areas (Scott 1981; Lamprecht 1986), owing to influx and departure of migrant flocks and shorter overall stay (Thorson and Cooper 2002). Human disturbance may also cause instability of waterfowl social environments at many staging (Korschgren et al. 1985; Petrie et al. 2000) and wintering areas (Hohman and Rave 1990; Dahlgren and Korschgren 1992). At Long Point, for example, diurnal disturbance during fall and spring forces large Tundra Swan flocks (often up to 2000 or more) from feeding areas that they frequent each night and causes them to disperse among numerous smaller undisturbed ponds with low food availability (S.S. Badzinski, unpublished data). During diurnal observations I often observed that when one or several newly arriving Tundra Swan social groups joined existing flocks, the frequency of interactions and vocalizations (at night) increased markedly upon their arrival, and subsequently declined. In this type of social environment, the use of group size as a simple signal of dominance would enable migrant Tundra Swans to easily avoid confrontation or injury and maximize time spent in feeding or other important nonsocial activities.

Findings of this study also suggested that when interacting at staging areas, Tundra Swans employ a simple decision rule: larger groups and initiators win. There were two lines of evidence that Tundra Swans use such a mechanism. First, like several species of geese (Raveling 1970; Black and Owen 1989; Gregoire and Ankney 1990), Tundra Swans initiated interactions with smaller groups more frequently than with larger groups. Also, any group that initiated an interaction was likely to be successful, especially if they engaged a similar-sized or smaller group. Even the lowest ranking social group, lone juveniles without parents, were successful in 70% of interactions that they initiated, which agrees with the results of studies on Barnacle Geese (Black and Owen 1989), White-fronted Geese (Boyd 1953), and Lesser Snow Geese (Gregoire and Ankney 1990). Besides suggesting that the Tundra Swans followed a simple decision rule during conflicts, my results also indicate that they were aware of the dominance or social status of other groups or individuals (Raveling 1970; Gregoire and Ankney 1990).

In general, Tundra Swans most often used relatively low intensity agonistic acts when initiating an interaction with another individual or social group, which suggests that they used the lowest intensity interactions necessary to reinforce or maintain dominance. This agrees with the findings of other waterfowl studies (e.g., Boyd 1953; Raveling 1970;

Black and Owen 1989) and is a common manifestation of dominance hierarchies in most animals (Kaufmann 1983; Huntingford and Turner 1987). Contrary to the findings of some other waterfowl studies (Boyd 1953; Raveling 1970; Black and Owen 1989), I found that the intensity of agonistic acts employed did not differ between adults with and without young (or between juveniles with and without parents). It is interesting to note, however, that fighting was most common among nonfamily (adult) groups, especially those that were identical in size. This may reflect the greater relative abundance of nonfamily groups at observation sites. Alternatively, it may indicate that swans without young are more willing to escalate interactions to higher intensities when they interact with groups that are perceived to have similar social status. Thus, the existence of a dominance structure in Tundra Swans generally reduced the need for energetically expensive and potentially harmful fighting, which may be especially beneficial for such large and powerful birds.

In summary, I propose that Tundra Swans use simple signals (e.g., presence of young, larger group size, or willingness to initiate) to recognize the dominance of unfamiliar swans and thereby reduce conflict on the staging grounds. The resulting dominance structure may function so well that it reduces intensive aggression among swans of all social and age groups and allows reinforcement of dominance through relatively low intensity acts that are less energy demanding or less harmful to the interacting individuals. Recognition of dominance based on simple cues may be especially beneficial for Tundra Swans in the relatively unstable social environment characteristic of Long Point, and perhaps other major staging areas, if it allows them to maximize time spent feeding to acquire the nutrients necessary for migration or breeding.

Acknowledgements

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