

# Social Influences on Tundra Swan Activities During Migration

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**Abstract.**—Diurnal activities and foraging methods of juvenile, parent (adults with young), and non-parent (adults without young) Tundra Swans (*Cygnus columbianus*) were measured during autumn and spring migration at Long Point, Ontario, to evaluate: 1) age-related differences in activities and feeding methods of family members, 2) potential short-term behavioral costs and benefits of prolonged parent-offspring association, and 3) several predictions based on predation risk and swan social structure. Vigilance of inactive parents and juveniles declined as flock size increased at observation sites. However, other evaluations of vigilance in active (and inactive parent/non-parent) swans and use of risk-prone foraging methods did not support the hypothesis that swans respond to reduced risk of predation resulting from membership in larger flocks. These results may be due to their use of inaccessible aquatic habitats and their large relative size, both of which relate to their lack of natural predators, at staging areas. Both parents and young used sub-surface feeding methods to the same amount, but parents “treadled” more than did juveniles and juveniles “dabbled” more on the surface than did parents. These findings suggest that some degree of resource partitioning exists between parents and young or possibly parents indirectly facilitate feeding activities of their young. Parents were more vigilant and interacted with other social groups more than did juveniles, but their feeding activity was unaffected as both parents and juveniles spent similar time foraging. Time spent vigilant, in intraspecific interactions, and feeding was similar between parents and non-parents. Based on this evidence, parents did not appear to incur short-term behavioral or energetic costs of prolonged association with young. However, both parents and juveniles likely benefited from higher social standing associated with family status or larger family size. Received 10 February 2005, accepted 23 April 2005.

**Key words.**—Activity, behavior, *Cygnus columbianus*, dominance, family size, flock size, parental investment, social status, staging, Tundra Swan.

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The Tundra Swan (*Cygnus columbianus*) is among the most social of waterfowl species. Large numbers congregate at staging and wintering areas where they display well-developed dominance hierarchies and prolonged parent-offspring associations (Scott 1980; Earnst and Bart 1991; Petrie *et al.* 2002; Badzinski 2003a). Because Tundra Swans also have delayed sexual maturity, several social and age groups are present and interact during the non-breeding season (Limpert and Earnst 1994; Badzinski 2003a). Thus, many different social factors, including flock size, inter-group dominance relations, and group or age-class membership may influence behavior and activities of these and other social waterfowl outside the breeding season (Lazarus 1978; Scott 1980; Black and Owen 1989b; Siriwardena and Black 1999).

Outside of the breeding season, the Tundra Swan and other social waterfowl congregate in flocks of varying size. One explanation for flock formation and group

association relates to reduction of predation risk (Roberts 1996). Hypothetically, as group size increases the number of individuals capable of observing a predator also increases, which should result in decreased vigilance of individuals in larger groups (Pulliam 1973). Many studies have shown that time spent alert by an individual decreases with increased flock size (Lazarus 1978; Bertram 1980; Brown and Brown 1987; Pöysä 1994; Roberts 1995). Decreased individual vigilance may enable each group member to spend more time feeding (Lipetz and Bekoff 1982; Beauchamp and Livoreil 1997), which is especially beneficial for migrating birds that must replenish energy stores. Feeding by waterfowl in aquatic habitats can conflict with vigilance because when their eyes are below water they cannot scan the environment for potential threats (Pöysä 1987; Guillemain *et al.* 2001). Thus, if minimizing predation risk is a strong factor influencing foraging behavior, then use of these types of

feeding methods should decrease with increasing flock size.

Family status and size figure prominently in structuring Tundra Swan societies during the non-breeding season (Scott 1980; Limpert and Earnst 1994; Badzinski 2003a). Family groups (often the largest ones) typically obtain advantages, such as more time to feed, access to higher quality territories or resources, or reduced intraspecific competition, due to their higher social standing (Huntingford and Turner 1987). Dominant individuals or groups, however, can incur apparent short-term costs due to increased vigilance, aggression, or energy expenditure (Black and Owen 1989b; Black *et al.* 1992; Siriwardena and Black 1999). Parental time allocation among activities may vary with family size and could be related to factors other than dominance, including parental investment (Trivers 1974; Lazarus and Inglis 1986).

Unlike most other bird species, the Tundra Swan (and geese) has a prolonged parent-offspring association that lasts throughout the first winter and often dissolves during spring before arrival on arctic breeding areas (Kear 1970; Earnst and Bart 1991; Limpert and Earnst 1994). In such extended associations, conflict might arise between parents and offspring over the amount, duration, or type of parental care given until young become independent (Trivers 1974). During the non-breeding season, parents of precocial birds do not expend energy directly in feeding or brooding young, but Tundra Swan parents may provide assistance during foraging bouts (Earnst and Bart 1991), and in social interactions (Scott 1980), or possibly reduce risk of predation through protection and vigilance as do parents of other social waterfowl (Sedinger and Raveling 1990; Sedinger *et al.* 1995). Thus, parents of social waterfowl could be more vigilant and aggressive than other groups or age-classes (Siriwardena and Black 1999) and adults with more young often invest more in vigilance and aggression than do those with smaller families (Sedinger *et al.* 1995; Fowler and Ely 1997; Siriwardena and Black 1999; but see Lazarus and Inglis 1986). Increased vigilance and intraspecific interaction during the non-breeding season, howev-

er, may conflict with time necessary for parents to feed and replenish fat stores (Siriwardena and Black 1999), thus representing a cost to extended association with young.

Young Tundra Swans are not fully-grown when they depart from the arctic in autumn or at departure from wintering grounds in spring (Limpert and Earnst 1994). Young birds also generally have higher metabolic requirements for growth and thermoregulation than do adults (Ricklefs 1983) and usually display relatively undeveloped social and foraging skills (Scott 1980; Earnst and Bart 1991). Thus, juveniles often spend more time feeding and less time in alert and aggressive activities than do other social groups, especially their parents, during the post-fledging period (Scott 1980; Austin 1990; Earnst and Bart 1991; Bélanger and Bédard 1992; Caithamer *et al.* 1996).

In this study, the activities of inactive and active Tundra Swan family groups (parents and juveniles) and adults (parents and those without young) were documented to assess general differences in behavior of staging birds, but also to test several specific hypotheses related to parental investment and predation risk. To do this, I first determined if Tundra Swan activities were influenced by numbers of conspecifics present; specifically testing whether vigilance and frequency of surface feeding decreased with increasing flock size and if social status (e.g., age or parental status) influenced those flock size effects. I also evaluated if activities and feeding methods of parents and juveniles differed and if adult (or juvenile) activities were influenced by family size. In particular, I assessed whether: 1) parents showed increased vigilance and intraspecific interaction (with possible reductions in feeding by adults) relative to juveniles, but particularly to adults without young, 2) apparent parental investment (vigilance and interaction) into young increased with family size, 3) age-related differences in foraging methods existed among family members that were consistent with parental investment or resource partitioning, 4) juveniles showed increased feeding activity relative to adults. Comparison of parents and non-parents was done to assess behavioral differences resulting

from association/retention of young during migration, which may identify potential short-term behavioral costs (increased vigilance, intraspecific interaction, locomotion or reduced feeding) or benefits (increased feeding) to parents. Similar comparisons of young with and without parents were not possible because juveniles were rarely observed without parents (Badzinski 2003a).

## METHODS

### Study Area and Observation Locations

This study was made during autumn and spring migration at Long Point, Ontario (42°38'N 80°24'W). Long Point is a 32-km sand-spit extending east from the southern shore of Ontario into Lake Erie. This landform facilitated the formation of the Inner and Outer Long Point Bays and their associated marsh complexes, which are among the most important staging areas for Tundra Swans and ducks in eastern North America (Petrie 1998; Petrie *et al.* 2002).

Diurnal activities were documented during autumn 1998 (11 November-1 December 1998), spring 1999 (7 March-31 March 1999). During autumn, data were collected from an observation blind in the Long Point National Wildlife Area (LPNWA). However, few Tundra Swans used the LPNWA location during spring, so observations at that time were collected on large numbers of swans using the shallow water margin of Inner Long Point Bay (ILPB). The same observers made all behavioral observations at each location each season. Observation sites were both classified as emergent marsh and had similar habitat characteristics such as, water depths and aquatic vegetation types. Water depths in areas used by active and feeding swans in this study were less than 1 meter (Badzinski 2003b). Specifically, both locales were characterized by open water areas entirely (LPNWA, autumn) or partially (ILPB, spring) surrounded by emergent marsh plants including *Typha* spp. and *Scripus* spp. Both locations also supported diverse and similar aquatic plant communities. Dominant submerged and floating-leaved plants, included Musk Grass (*Chara vulgaris*), Wild Celery (*Vallisneria americana*), Coontail (*Ceratophyllum demersum*), Waterweed (*Elodea Canadensis*), naiads (*Najas* spp), Sago Pondweed (*Potamogeton pectinatus*), Yellow Pond Lily (*Nuphar variegata*), and arrowheads (*Sagittaria* spp). The vegetative and subterranean parts of many of these plants are important foods for migrant swans (Beekman *et al.* 1991; Limpert and Earnst 1994; Nolet and Drent 1998).

### Behavioral Observations

Observations each season were divided mainly into two diurnal time blocks: 1) one half hour before sunrise until 12.00 h and 2) 12.00 h to one half hour after sunset. To determine when to sample, two 15-minute observation sessions were chosen randomly each hour within a time block. Before starting an observation session, a family group (parents and juveniles) or a pair of adults without young (non-parents) was selected from within the larger flock. Focal groups were identified by proximity, coordinated activity, and social displays of individu-

als, whereas age was determined from plumage characteristics (Scott 1980). Group status (non-parent, parent, or juveniles) and family size (2 parents + young) were recorded for each focal group. Family groups of six were present but were rarely observed during the study, which precluded their inclusion in analyses. Because uniquely marked individuals were rarely observed, data were collected for social groups of different size or status only once within distinct areas at each observation location each day to reduce pseudo-replication. Given the large number of swans present at locations (mean = 500) each day, combined with the seasonal turnover of migrant birds, it was unlikely that the same focal groups were sampled more than once each day (or over longer time periods). Tundra Swan flock size was determined each hour from scan samples of all birds visible at each observation location (Badzinski 2003b); those data were then recorded for each corresponding sample period.

Eight general categories of behavior, including intraspecific interaction, alert, head-up, locomotion, maintenance, preening, sleeping, and feed, were identified and recorded for each bird in a focal group during a sampling period. Intraspecific interactions included threat displays, pecks, chases, and fights directed at conspecific individuals or social groups, as well as triumph ceremonies performed following a social encounter (Limpert and Earnst 1994; Badzinski 2003a). "Alert" was an extreme head-up posture with the neck extended straight up. "Head-up" was when a swan was not in motion and the head was up and in a relaxed position with a curved neck. "Locomotion" included swimming or walking in shallow water. "Maintenance" included preening, bathing, drinking, scratching, stretching, and other uncommon activities in active swans. "Preening" was the use of the bill to manipulate feathers while inactive. "Sleeping" was an inactive swan with its head resting on its back. "Feeding" originally was recorded as four distinctive and specific acts used by swans to obtain aquatic foods, including treadling, dabbling, head-under feeding, and tipping-up, that were later combined into a general feeding category for active birds. *Treadling* is a relatively energy demanding activity characterized by a swan remaining stationary and assuming a posture resembling head-up above, but accompanied by a rocking motion of the body resulting from pumping their feet into the marsh substrate to uncover tubers of aquatic plants (Earnst and Bart 1991). *Dabbling* was feeding on the water's surface or with only the bill submerged. *Head-under* feeding was when the head and neck were submerged while the body remained parallel to the water surface. *Tipping-up* was when the head and neck were submerged and the rear end of the bird lifted from the water and represented maximum swan foraging depth. To evaluate relations between predation risk and foraging methods, feeding acts where the swan's eyes were above water and scanning for threats (treadling and dabbling) were combined into a variable called "surface feeding"; those where the eyes were below water (head-under and tip-up) were combined into a variable called "subsurface feeding".

Behavior and specific feeding acts used by each focal group member were recorded instantaneously at 15-second intervals for 15 minutes (Altman 1974). Because swans were observed over a relatively short period of time, their general activity state also was classified as either active/foraging or inactive. Samples were included in the active/foraging data sets only if the swans were mobile or performed at least one feeding act during the 15 minutes. Inactive swans were birds that did not feed

and were stationary for the entire sampling period. Partitioning subsequent statistical analyses in this way controls for potential differences in some activities that may arise from these two distinct phases of diurnal swan activity at observation sites.

#### Statistical Analyses

To ensure independence of social groups, activity data for juveniles, parents, and non-parents within focal groups were averaged (Earnst and Bart 1991). Statistical analyses were made using those means and sample sizes were the number of social groups observed. Activities were converted to proportions by dividing the counts of each activity by the total number of observations for each social group. Specific feeding methods were converted to the proportion of all feeding acts employed during a foraging bout. Error distributions generated from statistical models using behavior as proportional data were not normally distributed. Thus, an arcsine square root transformation was applied, which improved, but did not entirely normalize, error distributions of these data (Zar 1996). Nonparametric analyses were not used because parametric statistics are robust to deviations from normality (Johnson 1995; Smith 1995; Stewart-Oaten 1995) and they allow for use of covariates to obtain more precise estimates of effect sizes.

Arcsine transformed variables were used in multivariate analysis of covariance (MANCOVA; PROC GLM, SAS Institute Inc. 1990) were used to evaluate the influence several aspects of Tundra Swan social structure had on behavior and feeding methods. Multivariate models containing all relevant covariates and effects of interest were reduced in a backward, stepwise manner after assessing statistical significance ( $P < 0.05$ ) of effects using Wilks' criterion as an approximation of the F-statistic. Univariate F-tests, based on type III sums of squares, were then evaluated for each response variable within reduced MANCOVA models. Behavioral acts of active (feed, vigilance, locomotion, intraspecific interaction, and maintenance) and inactive (vigilance, preen, and sleep) Tundra Swan families were investigated to test predictions of parental investment and predation risk and to investigate age- and group size-related differences in foraging methods (surface and subsurface feeding) of the Tundra Swan. Thus, the following effects were evaluated for both active (foraging) and inactive family groups: Age (adult vs. juvenile), Season (autumn vs. spring), Day (days since swan arrival each season, continuous), Family size (continuous), Flock size (continuous), Age  $\times$  Season, Age  $\times$  Family size, Age  $\times$  Flock size. I also used MANCOVA to identify important sources of variation in the behavior of adults with and without young during periods when swans were active and inactive by specifying the following main effects and interactions: Status (parent vs. non-parent), Season (Autumn, Spring), Days (continuous), Flock size (continuous), Status  $\times$  Season, Status  $\times$  Flock size.

In all analyses, the "Season" effect could not be interpreted because different observation sites were used by swans in autumn and spring. So, this factor was included in models to control for any potential variation in behavior associated with both season and location. Days since swan arrival (Day) was interpretable, but was mainly included in models to control for potential changes in behavior due to environmental factors that were correlated with advancing date during autumn and spring (e.g., seasonal changes in habitat/food or physiological state of swans). Thus, "Season" and "Day" effects will not be dis-

cussed at length in this paper. Unless otherwise noted, the least-squares mean  $\pm$  one standard error of non-transformed (i.e., percentages) estimates generated from the final models are reported in the text, tables, and figures.

## RESULTS

### Behavior of Tundra Swan Families

*Inactive Tundra Swans.* Behavior of inactive Tundra Swan families were only influenced by the total number of Tundra Swans present at observation sites (Flock size: MANCOVA,  $F_{3, 138} = 3.52$ ,  $P < 0.02$ ); age, family size, days since swan arrival, season/location and age  $\times$  season, age  $\times$  family size, and age  $\times$  flock size effects were not included in the final MANCOVA model (Fig. 1a). Vigilance of both adults and juveniles decreased ( $\beta = -0.003\% \pm 0.001\%/swan$ ,  $P < 0.005$ ), whereas preening ( $\beta = 0.012\% \pm 0.005\%/swan$ ,  $P < 0.01$ ) and sleeping ( $\beta = 0.015\% \pm 0.006\%/swan$ ,  $P < 0.005$ ) increased, with increasing flock size.

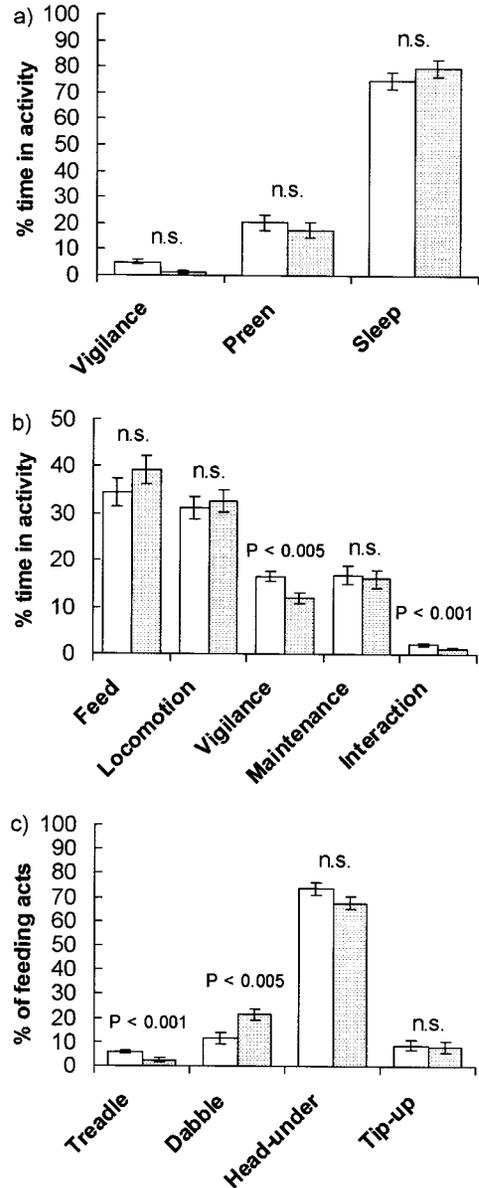
*Active Tundra Swans.* Behavior of active Tundra Swan families were influenced by both season (MANCOVA,  $F_{5, 208} = 8.18$ ,  $P < 0.001$ ) and within season temporal (day) effects (MANCOVA,  $F_{5, 208} = 5.31$ ,  $P < 0.001$ ), but age also explained a significant amount of variation in their activities (MANCOVA,  $F_{5, 208} = 4.38$ ,  $P = 0.001$ ); family size and flock size, along with age  $\times$  season, age  $\times$  family size, and age  $\times$  flock size, effects did not account for substantial variation in behavior of active family groups.

Season explained significant variation in locomotion ( $12.5\% \pm 3.5\%$  higher in autumn,  $P < 0.003$ ), vigilance ( $2.7\% \pm 1.0\%$  higher in autumn,  $P < 0.01$ ), and interspecific interactions ( $1.0\% \pm 0.3\%$  higher in spring,  $P < 0.001$ ) of active swan family groups. Locomotion decreased ( $\beta = -0.9\% \pm 0.3\%/day$ ,  $P < 0.01$ ) and maintenance activities increased ( $\beta = 0.9\% \pm 0.3\%/day$ ,  $P < 0.005$ ) throughout each season. After accounting for season effects and within-season temporal variation, no significant age-related differences were observed in feeding, locomotion, or maintenance activities, but adults spent more time vigilant ( $4.6\% \pm 1.1\%$ ,  $P < 0.005$ ) and in interspecific interactions ( $0.8\% \pm 0.2\%$ ,  $P < 0.001$ ) than did juveniles (Fig. 1b).

**Foraging methods.** Foraging methods used by Tundra Swan families at observation locations were influenced by season (MANCOVA,  $F_{4,162} = 20.2$ ,  $P < 0.001$ ), days since swan arrival (MANCOVA,  $F_{4,162} = 12.89$ ,  $P < 0.001$ ), age (MANCOVA,  $F_{4,162} = 4.15$ ,  $P < 0.005$ ), and flock size (MANCOVA,  $F_{4,162} = 8.80$ ,  $P < 0.001$ ). Season accounted for some variation in surface ( $28.6\% \pm 3.5\%$  higher in spring,  $P < 0.001$ ), and head-under ( $30.5\% \pm 3.9\%$  higher in autumn,  $P < 0.001$ ) feeding acts used by foraging swans. Most major feeding methods used by swans were influenced by within season temporal effects; treadling ( $\beta = 0.4\% \pm 0.1\%/day$ ,  $P < 0.001$ ) and head-under ( $\beta = 2.1\% \pm 0.4\%/day$ ,  $P < 0.001$ ) feeding increased, whereas use of surface feeding decreased ( $\beta = -2.5\% \pm 0.4\%/day$ ,  $P < 0.001$ ), the longer swans remained at each observation site. Two of the four feeding methods were affected by numbers of swans present; dabbling ( $\beta = 0.016\% \pm 0.004\%/swan$ ,  $P < 0.001$ ) increased, but feeding with the head-under decreased ( $\beta = -0.020\% \pm 0.004\%/swan$ ,  $P < 0.001$ ), with increasing flock size. Controlling for temporal effects, adults treadled more during foraging bouts than did juveniles ( $3.3\% \pm 0.8\%$ ,  $P < 0.001$ ; Fig. 1c). After accounting for variation due to season, date, and flock size, juveniles dabbled more often than did parents ( $10.0\% \pm 3.4\%$ ,  $P < 0.005$ ), but parent and juvenile use of head-under feeding did not differ (n.s.; Fig. 1c). Parents and young did not differ in their use of tipping-up to feed (n.s.). Contrary to predictions, surface feeding methods (i.e., all feeding acts where swan's eyes were above water) increased ( $\beta = 0.014\% \pm 0.004\%/swan$ ,  $P < 0.001$ ), and subsurface feeding methods decreased ( $\beta = -0.014\% \pm 0.004\%/swan$ ,  $P < 0.001$ ), with increasing flock size (MANOVA, Season:  $F_{1,166} = 76.0$ ,  $P < 0.001$ ; Day:  $F_{1,166} = 23.5$ ,  $P < 0.001$ ; Flock size:  $F_{1,166} = 18.5$ ,  $P < 0.001$ ).

#### Behavior of parent and non-parent Tundra Swans

**Inactive Tundra Swans.** The reduced MANCOVA model describing variation in behavior of inactive adult swans (parents [ $N = 68$ ] vs. non-parents [ $N = 18$ ]) contained only a



**Fig. 1.** Age-related differences in behavior of inactive (a), active (b), and foraging (c) Tundra Swan families at Long Point, Ontario. Number of family groups observed ( $N$ ) are as follows, Inactive: family 3 = 27, family 4 = 28, and family 5 = 16; Active: family 3 = 41, family 4 = 37, and family 5 = 30; Foraging: family 3 = 31, family 4 = 32, and family 5 = 22. White (adult) and gray (juvenile) bars are least-square (adjusted) means  $\pm$  SE from reduced Multivariate Analysis of Covariance (MANCOVA) models. Fitted MANCOVA models are as follows, inactive:  $Y_{1-3} = \text{Age}$  ( $F_{3,137} = 2.12$ , n.s.), Flock size ( $F_{3,137} = 3.59$ ,  $P < 0.02$ ); active:  $Y_{1-5} = \text{Age}$  ( $F_{5,208} = 4.38$ ,  $P < 0.001$ ), Season ( $F_{5,208} = 8.18$ ,  $P < 0.001$ ), Day ( $F_{5,208} = 5.31$ ,  $P < 0.001$ ); foraging methods:  $Y_{1-4} = \text{Age}$  ( $F_{4,161} = 4.18$ ,  $P < 0.005$ ), Family size ( $F_{4,161} = 2.29$ , n.s.), Flock size ( $F_{4,161} = 8.94$ ,  $P < 0.001$ ), Season ( $F_{4,161} = 19.52$ ,  $P < 0.001$ ), Day ( $F_{4,161} = 11.98$ ,  $P < 0.001$ ).

significant within-season date effect (MANCOVA,  $F_{3,82} = 3.13$ ,  $P < 0.05$ ); parental status and flock size main effects and the status  $\times$  flock size and season  $\times$  status interactions were not retained in the final MANCOVA model. Thus, there were no differences between parents and non-parents in any activity and there were no relations between behavior and numbers of Tundra Swans. Vigilance (Intercept:  $8.0\% \pm 1.9\%$ ) of adults decreased ( $\beta = -0.3\% \pm 0.1\%/day$ ,  $P < 0.02$ ), but preening (Intercept:  $20.1\% \pm 6.8\%$ ) and sleeping (Intercept:  $71.9\% \pm 7.9\%$ ) did not change appreciably throughout each season.

*Active Tundra Swans.* Season (MANCOVA,  $F_{5,119} = 6.51$ ,  $P < 0.001$ ) and days since swan arrival each season (MANCOVA,  $F_{5,119} = 2.42$ ,  $P < 0.04$ ) both explained variation in behavior of active adult ( $N_{\text{parent autumn}} = 40$ ,  $N_{\text{non-parent autumn}} = 11$ ,  $N_{\text{parent spring}} = 56$ ,  $N_{\text{non-parent spring}} = 19$ ) Tundra Swans; parental status, flock size, and associated interactions (i.e., status  $\times$  flock size and season  $\times$  status) were not retained in the final MANCOVA model. Thus, there were no differences in feed, vigilance, locomotion, intra specific interaction, and maintenance activities between parents and non-parents nor were there any changes in activities attributable to flock size (Table 1). Season effects were significant for feed, vigilance, locomotion, and interspecific interaction (Table 1). Feeding and intraspecific interactions both increased throughout the autumn and spring, whereas locomotion declined as each season progressed (Table 1).

*Foraging methods.* Flock size (MANCOVA,  $F_{4,112} = 8.09$ ,  $P < 0.001$ ), season (MANCOVA,

$F_{4,112} = 9.35$ ,  $P < 0.001$ ), and days since swan arrival ( $F_{4,112} = 6.40$ ,  $P < 0.001$ ) all explained variation in feeding methods used by adult Tundra Swans; the parental status main effect and status  $\times$  flock size and season  $\times$  status interactions were not included in the final model. Thus, there were no differences in use of feeding methods between parents and non-parents. Use of dabbling and head-under feeding differed between seasons/locations, but use of treading and tip-up feeding did not (Table 2). Adult use of treading and head-under feeding increased, but dabbling decreased, throughout each season (Table 2). Dabbling and feeding with the head-under water decreased, whereas tipping-up to feed increased, with increasing flock size (Table 2). However, adult use of all feeding methods where swans's eyes were above water increased ( $\beta = 0.013\% \pm 0.004\%/swan$ ,  $P < 0.005$ ), while use of all sub-surface feeding methods decreased ( $\beta = -0.013\% \pm 0.004\%/swan$ ,  $P < 0.005$ ), with increasing flock size (MANCOVA: Season:  $F_{1,115} = 33.79$ ,  $P < 0.001$ ; Day:  $F_{1,115} = 6.78$ ,  $P < 0.01$ ; Flock size:  $F_{1,115} = 9.81$ ,  $P < 0.005$ ).

## DISCUSSION

### Flock Size and Vigilance

A negative relationship between group size and vigilance is common in social vertebrates (Roberts 1996). One explanation for this group-size effect, the "many-eyes" hypothesis (Pulliam 1973), is based on the premise that as group size increases more individuals are watching for predators. Thus, each indi-

**Table 1.** Behavioral acts of active parent and non-parent Tundra Swans during autumn and spring at Long Point, Ontario. Overall season (MANCOVA:  $F_{5,119} = 6.51$ ,  $P < 0.001$ ) and day ( $F_{5,119} = 2.42$ ,  $P < 0.04$ ) effects were significant. Sample sizes (N) are as follows: 40 parents and 11 non-parents were observed during autumn; 56 parents and 19 non-parents were observed during spring.

Behavior (%)	Intercept	Season		Days since arrival	
		Autumn vs. spring <sup>a</sup>	P	$\beta$	P
Feeding	$23.3 \pm 6.8$	$12.6 \pm 5.1$	$<0.02$	$1.2 \pm 0.5$	$<0.02$
Vigilance	$16.9 \pm 2.6$	$2.5 \pm 1.9$	$<0.05$	$-0.3 \pm 0.2$	n.s.
Locomotion	$44.0 \pm 6.0$	$-10.2 \pm 4.6$	$<0.05$	$-1.0 \pm 0.4$	$<0.02$
Interaction	$0.7 \pm 0.5$	$-1.1 \pm 0.4$	$<0.001$	$0.1 \pm <0.1$	$<0.03$
Maintenance	$15.0 \pm 4.3$	$-3.7 \pm 3.3$	n.s.	$<0.1 \pm <0.1$	n.s.

<sup>a</sup>Positive values indicate activity was x % higher in autumn than spring, whereas negative values denote activity was x % lower in autumn as compared to spring.

**Table 2.** Foraging methods used by parent and non-parent Tundra Swans during autumn and spring at Long Point, Ontario. Overall flock size (MANCOVA:  $F_{4,112} = 8.09$ ,  $P < 0.001$ ), season ( $F_{4,112} = 9.35$ ,  $P < 0.001$ ), and day ( $F_{4,112} = 6.40$ ,  $P < 0.001$ ) effects were significant. Sample sizes (N) are as follows: 40 parents and 11 non-parents were observed during autumn; 50 parents and 18 non-parents were observed during spring.

Behavior (%)	Intercept	Flock size		Season		Days since arrival	
		$\beta$	P	Autumn vs. spring <sup>a</sup>	P	$\beta$	P
Treadle	2.2 ± 1.8	-0.001 ± 0.001	n.s.	-0.9 ± 1.2	0.628	0.4 ± 0.1	<0.001
Dabble	34.0 ± 5.8	0.014 ± 0.004	<0.002	-19.1 ± 3.7	<0.001	-1.7 ± 0.4	<0.002
Head-under	62.8 ± 6.6	-0.026 ± 0.005	<0.001	22.8 ± 4.2	<0.001	1.0 ± 0.4	<0.04
Tip-up	1.1 ± 5.4	0.013 ± 0.004	<0.003	-2.8 ± 3.5	0.359	0.2 ± 0.4	n.s.

<sup>a</sup>Positive values indicate activity was x % higher in autumn than spring, whereas negative values denote activity was x % lower in autumn as compared to spring.

vidual can devote less time to vigilance, and presumably spend more time feeding, as group size increases without decreasing the group's ability to detect a predator. This study provides some support for this hypothesis, given that vigilance of inactive parent and juvenile Tundra Swans decreased with increasing flock size. This result also agrees with findings of several other waterfowl studies evaluating vigilance and group size (Lazarus 1978; Lazarus and Inglis 1978; Inglis and Lazarus 1981; Black *et al.* 1992; Pöysä 1994).

However, most other evidence compiled did not support that risk of predation was a strong influence on the behavior of staging Tundra Swans. First, when family group members were active and feeding, vigilance did not systematically change with flock size. Second, vigilance of adults (parents and non-parents) during both active and inactive periods also was independent of flock size. Further, some waterfowl alter foraging strategies in relation to predation risk by increasing use of foraging methods that allow their eyes to remain above water so they can still scan for potential threats (Pöysä 1987; Guillemain *et al.* 2001). However, Tundra Swans predominately used foraging acts where their eyes were below the water and use of surface feeding generally did not increase when fewer swans were present at locations. Overall, it seems predation risk was not a major factor in Tundra Swan flock formation or membership while staging at Long Point.

Tundra Swans have few natural predators and resultantly high survival rates once they depart arctic breeding grounds (Bart *et al.*

1991; Limpert and Earnst 1994). During migration, these birds use the largest and most isolated aquatic habitats and wetlands (Earnst 1994), which provide safety from those terrestrial predators capable of killing swans. Tundra Swans are no longer totally dependent on aquatic habitats and use agricultural fields extensively during the migration (Petrie *et al.* 2002). A comparison of vigilance and foraging activities in relatively risk-averse aquatic habitats and relatively risk-prone terrestrial habitats may better elucidate the role that predation risk has in Tundra Swan flocking and foraging behavior.

#### Parental investment and family size

Trivers (1972) first used the term parental investment for any investment by a parent in an individual offspring that increases the offspring's chance of surviving, and thus reproducing, at the cost of the parent's ability to invest in other offspring. Aggression, vigilance, and some specialized feeding methods often have been cited as acts of parental investment in swans and other waterfowl with extended parent-offspring relations (Scott 1980; Sedinger and Raveling 1990; Earnst and Bart 1991; Limpert and Earnst 1994). Lazarus and Inglis (1986) later suggested that "unshared" parental investment, which is investment that simultaneously benefits some or all of the young, (e.g., vigilance) should be independent of brood size in precocial birds.

Results of this study supported Lazarus and Inglis' (1986) hypothesis because vigilance of Tundra Swan parents was not corre-

lated with numbers of young present during the migration periods. These results contradicted those of several other waterfowl (non-swans) studies showing parental vigilance increased with family size during the pre fledging (Schindler and Lamprecht 1987; Sedinger and Raveling 1990; Forslund 1993; Sedinger *et al.* 1995; Fowler and Ely 1997; Loonen *et al.* 1999; but see Lazarus and Inglis 1978; Lessells 1987; Seddon and Nudds 1994) and post-fledging (Siriwardena and Black 1999; but see Caithamer *et al.* 1996) periods.

The most plausible explanation for the positive relationship between vigilance and brood size found in most other studies is that larger broods, especially of small and flightless birds, are more vulnerable to predators and more difficult for parents to watch and protect (Sedinger and Raveling 1990; Forslund 1993; Fowler and Ely 1997). At staging and wintering areas, juvenile Tundra Swans (and Canada Geese, *Branta canadensis*) are among the largest waterfowl present. Staging Tundra Swans also usually inhabit inaccessible aquatic habitats (Earnst 1994), making them susceptible to very few predators. These two factors may explain why vigilance of Tundra Swan parents in this study, and possibly Canada Goose parents studied by Caithamer *et al.* (1996), did not increase with family size.

Among Tundra Swan families staging at Long Point, dominance is positively correlated with group size (Badzinski 2003a). Because dominance often conveys foraging advantages to individuals with such social standing (Scott 1980; Black and Owen 1989a, b), it was expected that swans in larger groups might spend less time in social interactions, vigilance, or swimming, and thus spend more time feeding. However, family size had no measurable effect on any of these activities in adult or juvenile swans. Future studies quantifying actual dietary selection, forage intake, and caloric assessments of foods among swans in families of differing size would provide a much better evaluation of family size or dominance-related costs and benefits.

Although Tundra Swan parents did not show predicted increases in "parental" activities with increased family size, active, but not inactive, parents spent more time in vigilance

and in intraspecific interactions than did juveniles. Parents, relative to adults without young, did not show reductions in feeding, increased mobility or use of treadling, suggesting that extended association with young has minimal costs to parents during the migration period. Maintaining a social bond with young throughout migration is probably beneficial to parents given that family status and group size are important determinants of dominance among staging Tundra Swans (Badzinski 2003a). The decreased vigilance and low involvement in intraspecific interactions within staging juveniles, relative to adults, implies they are still socially inexperienced and remain dependent upon the parents for social assistance and protection during migration. Other studies made on wintering or staging areas also found that juveniles were involved in fewer social interactions and their parents most often initiated acts or intervened during physical conflicts on their behalf (Scott 1980; Earnst and Bart 1991; Badzinski 2003a). Thus, it is likely that parents incur some added costs (e.g., higher risk of injury) through aggressive interaction with other swans (Scott 1980; Badzinski 2003a), which shows some degree of investment into young during migration.

In Tundra Swans, treadling has been cited as an act of parental investment, at least at some times and places during the annual cycle (Earnst and Bart 1991). In this study, Tundra Swan parents treadled more than did their young, but parents and non-parents did not differ in their use of this foraging method. Within this context, treadling does not appear to be an intentional act used by parents to facilitate foraging of their young. Treadling is an energetically demanding activity used to excavate and dislodge tubers of aquatic plants from the marsh substrate (Limpert and Earnst 1994), so it may simply be less prevalent among juveniles because they have not yet attained physical maturity during autumn and spring migrations (Limpert and Earnst 1994).

The divergent foraging patterns for adults and juveniles observed in this study suggest some age-related resource partitioning may exist in staging Tundra Swans. While feeding

below the water, parents treadled more than did juveniles, whereas juveniles dabbled more on the water surface. These results confirm observations that young often exploited treadling and subsurface feeding activities of parents by eating aquatic plant parts that had floated to the surface. Foraging adults were rarely aggressive toward their own offspring, but threatened or chased off non-related young (Badzinski 2003a), indicating parents allowed their young to forage close to them and to exploit their foraging efforts. Juveniles often would remain to feed at the crater their parent had created even after the adult had departed (S. Badzinski, pers. obs.). Thus, parent-offspring foraging associations probably reduce energy expenditure of young Tundra Swans. The actual costs to parents of such a foraging relationship (i.e., mutualism, commensalism, or parasitism) remain to be determined, but based on behavioral assessments in this study, costs appear to be minimal.

Although most behavioral patterns documented in this study did not provide strong evidence for benefits associated with extended parent-offspring association for young (e.g. no increase in time spent foraging), behavioral data presented herein do not adequately quantify advantages associated with higher social standing that family membership conveys to staging swans. For example, dominant groups or individuals typically have access to higher quality feeding areas (Scott 1980; Black and Owen 1989a, b), which is particularly important for both parent and juvenile swans that are attempting to build up reserves for migration. Membership in a dominant social group is probably the most important benefit to juvenile Tundra Swans because without parents they are the lowest ranking social group at staging areas (Badzinski 2003a). Given this, it might be expected that without parental attendance, juveniles would have spent considerably more time in social interactions, vigilance, or locomotion and, likely, much less time feeding than other swans. Because juvenile Tundra Swans were almost never observed without parents (Badzinski 2003a), further illustrates that the prolonged affiliation between parents and young is important in this waterfowl species.

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