Costs and benefits of extended parental care in Tundra Swans *Cygnus columbianus columbianus*

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Short-term costs and benefits of extended parental care were studied in Tundra Swans feeding on tubers of aquatic vegetation on an autumn migratory stopover and feeding on clams on the wintering grounds. In both seasons, families were dominant over non-parents and may have maintained access to better feeding sites as a result. Parents fed less intensively than non-parents during both seasons. Parents and cygnets did not differ from non-parents in frequency of, or time spent in, agonistic interactions in either season. Cygnets appeared to exploit the foraging behaviour of their parents in two ways: 1) cygnets copied parents' feeding sites in both seasons; and 2) during the autumn, cygnets dabbled for vegetation churned to the surface by parents. When feeding on clams during the winter and being kleptoparasitized by gulls, cygnets sought protection from gulls by approaching parents, and parents threatened gulls more than did non-parents.

Unlike most avian species, many species of geese and swans exhibit parental care throughout the offsprings' first winter (reviewed in Scott 1980a, other exceptions include helpers-at-the-nest, Brown & Brown 1984, and many seabirds, Burger 1980). Two broad categories of short-term benefits to young and costs to parents resulting from extended parent-offspring association in waterfowl have been documented: 1) those related to agonistic interactions, and 2) those related to foraging strategies.

In several species of waterfowl, families are dominant to non-families, and parents appear to protect offspring from competition with conspecifics (e.g. Boyd 1953, Raveling 1970, Scott 1980a,b, Black & Owen 1989a,b). In the two best documented cases, Barnacle Geese *Branta leucopsis* (Black & Owen 1989a,b) and Bewick's Swans *Cygnus columbianus bewickii* (Scott 1980a), parental protection allowed young to win more interactions, be attacked less often, and spend more time feeding than those offspring not receiving protection. Also, young Barnacle geese attached to families had access to more plant biomass and were fatter than unattached young. Parents in both species incurred a short-term cost of less time spent feeding and more time spent in vigilance and aggression than non-parents.

Short-term benefits and costs in the second category, those related to foraging strategies, have been documented in geese, but have not been previously investigated in swans. Parental Snow Geese *Chen caerulescens atlantica* and Barnacle Geese allowed offspring to take over feeding sites where they had been digging for rhizomes (Snow Geese; Turcotte & Bedard 1989) or grazing (Barnacle Geese; Black & Owen 1989a).

Objectives

In this study of Tundra Swans *Cygnus columbianus columbianus* feeding on natural aquatic foods during the autumn and winter, we quantify the short-term costs and benefits related to agonistic interactions and foraging strategies, and we introduce a third category of costs and benefits related to kleptoparasitism by gulls during the winter.

Costs of parental care were investigated through comparisons of parents and non-parental pairs. Benefits to young were investigated through comparisons of young and non-parental pairs. Unfortunately, the more meaningful comparison of young with and without parents is not possible in Tundra Swans because young are almost never without their parents. An alternative analysis, which will be pursued after further data collection, is to compare young receiving various amounts of parental care.

Short-term measures of costs and benefits are useful in investigating the adaptive significance of extended parental care if they are related to long-term measures (in terms of future reproductive success, Trivers 1972). Such a relationship is difficult to document logistically and is complicated conceptually by the positive feedback between having young and being dominant (e.g., Lamprecht 1986, Black & Owen 1989b). Despite these difficulties, short-term costs and benefits are useful in identifying the potential functions of parent-offspring associations during post-breeding seasons, and they indicate the behavioural mechanisms by which long-term costs and benefits are achieved.

Study sites

Tundra Swans of North America's Eastern Population, numbering near 90,000, breed along the north coast of Alaska and Canada and winter on the east coast of the United States, primarily on the Chesapeake Bay (the winter study site) and in North Carolina (Serie & Bartonek 1991). Several important migratory stopovers have been identified in Canada and the United States (Bellrose 1976), including the prairie pothole region of North Dakota (the autumn study site).

The autumn study site, in Kidder County, North Dakota, (47° 05′ N, 99° 40′ W), consists of more than 150 wetlands which support over 4,000 Tundra Swans during the peak of migration. Swans feed primarily on lakes of intermediate salinity in which sago pondweed, *Potamogeton pectinatus*, is the dominant submerged vegetation (Earnst, unpub. data, Stewart & Kantrud 1971).

The winter study site, Eastern Neck National Wildlife Refuge (39° 02′ N, 76° 12′ W), is located on the eastern shore of the Chesapeake Bay in Queen Annes County, Maryland. Several hundred Tundra Swans feed near the observation point during low tide, and up to 2,000 use the area as a night roost. There is little submerged vegetation, and the swans appear to eat only molluscs, probably primarily *Mya arenaria* although *Macoma baltica* are also eaten (Stewart & Manning 1958). Although extensive consumption of molluscs has not been previously reported for any swan, a combination of aerial and ground surveys revealed that an average of 95% of swans in the surrounding five county area were feeding on molluscs (Earnst, unpub. data). Swans feeding on clams were attacked by gulls; Ring-billed Gulls *Larus delawarensis* attacked most often, while Herring Gulls *L. argentatus* and Great Black-backed Gulls *L. marinus* were present but rarely attacked.

Methods

Focal units, consisting of a family or a non-parental pair, were chosen systematically from the foraging swans on a wetland. We attempted to observe each focal unit only once, thus we consider our samples to be independent. In North Dakota, the focal units on a given wetland were observed sequentially during one visit, and each wetland was visited only once. Location and brood size aided our attempt to distinguish among units. In Maryland, observations on a given section of coastline on a given day were continued only until we believed all units had been observed once on that day (again, using location and brood size as distinguishing characteristics). Although we do not know to what extent the same individuals were sampled on different days in Maryland, several hundred swans were present at a given time and there was substantial opportunity for exchange with the additional hundreds which used the area as a night roost.

During the autumn (7-31 Oct.) in North Dakota, 40 families and 23 non-parental pairs were observed; during the winter (7-29 Feb.) in Maryland, 24 families and 31 non-parental pairs were observed. Observation periods usually lasted 1 hr (1988), 0.5 hrs (1989), or until the swan began sleeping or left the wetland.

Time budgets were constructed from instantaneous focal animal sampling (Altmann 1974). At one-minute intervals, for each individual in the focal unit, we recorded behaviour and distance to parent or mate. All interactions with conspecifics or gulls were described, and in Maryland each clam brought to the surface was counted.

Definitions of behaviours

Active periods were partitioned into interaction bouts and foraging bouts. An interaction bout included all consecutive instantaneous samples, preceding and following an interaction, on which non-foraging behaviours were recorded. Foraging bouts included all other intervals in the active period. The per cent of time spent foraging during foraging bouts provided an estimate of foraging intensity. Bouts defined in this way provided independent estimates of feeding intensity and time spent on interactions, and avoided ambiguity about which behaviours should be considered part of an interaction. Active periods terminated at the onset of six consecutive resting (i.e., preening, standing, or sleeping) observations. Estimates of time spent in active and resting periods were obtained from scan samples of flocks and will be presented elsewhere.

Agonistic interactions ranged from subtle displacements to prolonged calling and wing-flapping matches sometimes involving contact. The loser of an interaction was defined as the social unit which was displaced or which changed its direction of movement away from the opponent. If any member of a family or non-family was involved in an interaction, then all members were counted as having had an interaction, although members could spend different amounts of time in the interaction bout. Sequential encounters with the same opponent were considered one interaction unless the focal swan was recorded as feeding between the interactions.

Foraging swans most often used neck-under and up-ending postures (defined in Owen & Kear, 1972); other foraging modes were dabbling on the water's surface, mandibulating clams, and treadling, i.e., churning with the feet to dislodge rhizomes, tubers, and clams. Treadling was easily identified by the forceful, pumping motion of the upper legs. Non-foraging behaviors during foraging bouts consisted mostly of swimming and sitting on the water in a non-resting position (resting defined as head placed on back).

A swan was considered to have copied the feeding site of another swan if it approached from more than two swan-bodylengths away and immediately began foraging within one bodylength. This operational definition, although somewhat arbitrary, was based on the approximate size of feeding craters (produced by treadling) observed while walking through wetlands. In Maryland, a clam was considered to be obtained as a result of copying if it was obtained within the next one-minute sampling interval.

Most gull attacks were obvious attempts to dislodge a clam from a swan's bill. The most subtle attacks involved sudden approaches to within one swan-bodylength which produced evasive action by the victim. A swan was considered to have sought protection from another swan if it approached from more than two bodylengths away to within one bodylength, did not feed immediately after approaching, and approached during an interval in which a gull was present.

Statistical analysis

Focal units were considered independent primary sampling units (Cochran, 1977). Thus, statistical tests (two-tailed t-tests) were performed on the means of focal units (i.e. the data for broodmates were averaged, and the data for pair members were averaged) and therefore the sample sizes were the number of focal units observed.

Results

Agonistic interactions

In both autumn and winter, families appeared to dominate non-parents. Families won a significantly larger per cent of interactions against non-parents than expected by chance (autumn, 88%, $n = 24$, $P < 0.00001$; winter, 86%, $n = 14$, $P = 0.0006$).

Benefits to cygnets. Two lines of anecdotal evidence suggest that parents were protecting cygnets from competition with conspecifics. Parents intervened in interactions which an offspring was losing; and an apparent orphan attempting to feed was attacked 0.20 times per minute (compared to the average of 0.07 for young in families) and was bitten twice during a 30-minute observation period.

Although our comparison of cygnets to non-parents is indirect, cygnets receiving protection might be expected to do as well as, or better than, non-parents. Cygnets did not differ from

Table 1. Percent of active period spent in agonistic interactions on a migratory stopover and during winter. N = number of focal units.

	Migratory stopover[1]			Winter[1]		
Focal unit	N	%	SE	N	%	SE
Broods	40	12.5	2.7	14	12.9	3.8
Non-parents	23	19.5	4.0	21	9.2	1.7
Parents	40	14.1	2.5	14	14.5	5.4

[1]None of the differences within seasons was significant; all P-values > 0.27.

Table 2. Foraging success of Tundra Swans feeding on clams and being kleptoparasitized by gulls. Table entries are means.

Measure of success[1]	Broods	Non-parents	Parents
No. clams obtained/min	0.22	0.24	0.18
No. gull attacks/clam	0.33	0.33	0.24
Prop. attacks successful	0.52	0.51	0.49
No. clams consumed/min	0.19	0.20	0.16
N, number of focal units	23	31	18

[1]None of the differences for a given measure of success was significant; all P-values >0.10.

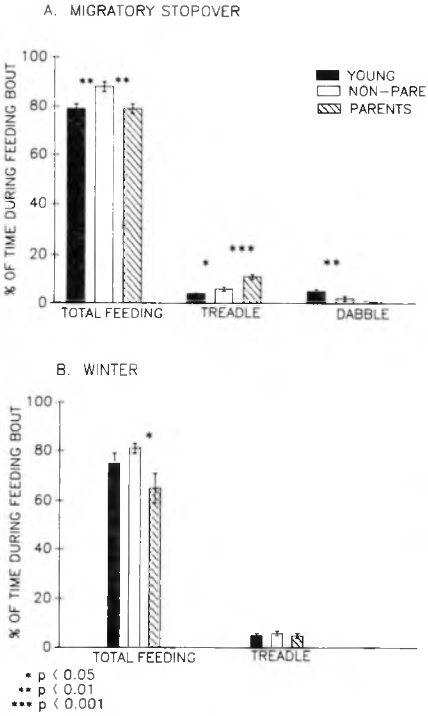

Figure 1. Percent of time during feeding bouts spent in feeding behaviours by Tundra Swan broods (n=40A,24B), non-parents (n=23A,31B), and parents (n=40A,18B) on a migratory stopover (A) and during the winter (B). Bars are standard errors.

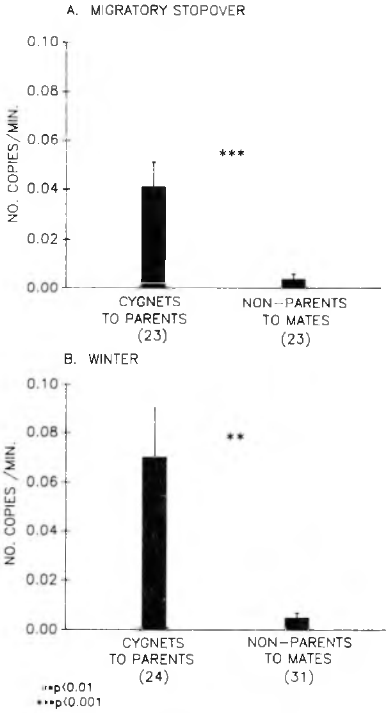

Figure 2. Rate at which Tundra Swan cygnets copied the feeding site of their parents, and non-parents copied the feeding site of their mates, on a migratory stopover (A) and during the winter (B). N, the number of focal units observed, is given in parentheses. Bars are standard errors.

non-parents in time spent in interaction bouts in either season (Table 1), or in number of clams consumed during the winter (Table 2). However, cygnets spent less time foraging during foraging bouts than non-parents, particularly during autumn (Fig. 1), but less time feeding does not necessarily imply a disadvantage (see **Discussion**).

Costs to parents. Parents did not spend more time in interaction bouts than non-parents in either season (Table 1) or interact more frequently than non-parents in either season (autumn, families 0.06 interactions/minute, non-parents 0.09, $P = 0.10$; winter, families 0.07 and non-parents 0.07, $P = 0.58$). However, parents spent less time foraging during foraging bouts in both seasons (Fig. 1).

Foraging strategy.

Benefits to cygnets. During the autumn, cygnets appeared to benefit by exploiting the treadling behavior of their parents (Fig. 1). Cygnets dabbled on the water's surface more than did non-parents ($P = 0.004$), even though cygnets treadled somewhat less than did non-parents ($P = 0.05$). Cygnets usually dabbled directly behind parents, and parents treadled more and dabbled less than non-parents (see below).

On the winter feeding grounds, because there was no submerged aquatic vegetation, neither adults nor cygnets dabbled on the water's surface. Treadling was apparently used during winter to partially excavate clams which were then brought to the surface with the bill. In contrast to

Table 3. Percent of all clams obtained by a focal unit which was obtained by copying a feeding site and by stealing directly from another swan. N = number of focal units.

	Clams obtained by					
	Copying			Stealing		
Focal unit	N	%	SE	N	%	SE
Broods	11	14.4	6.3	17	1.9	0.9
Non-parents	21	0.7	0.6	31	0.2	0.2
	$P = 0.005$			$P = 0.02$		

autumn, cygnets and non-parents did not differ in amount of time spent treadling (Fig. 1).

The most striking way in which cygnets exploited their parents' foraging behaviour in both autumn and winter was by copying their parents' feeding site. Copying was performed 10 times more frequently by cygnets than by non-parents in North Dakota ($P = 0.0008$), and 14 times more frequently than by non-parents on the wintering grounds ($P = 0.002$; Fig. 2). During the winter, cygnets obtained 14% of their clams as a result of copying and stole an additional 2% directly from their parents (Table 3).

Costs to parents. If parents were actively providing parental care by treadling, rather than simply allowing cygnets to consume a surplus product of treadling, then one might expect parents to treadle more than non-parents. During the autumn, when treadling served to excavate food and bring it to the water's surface, parents treadled significantly more often than did non-parents ($P < 0.0001$; Fig. 1). This foraging strategy is consistent with the increased dabbling of their offspring. Interestingly, even though parents were evidently bringing more vegetation to the surface, they dabbled somewhat, but not significantly, less than non-parents ($P = 0.27$).

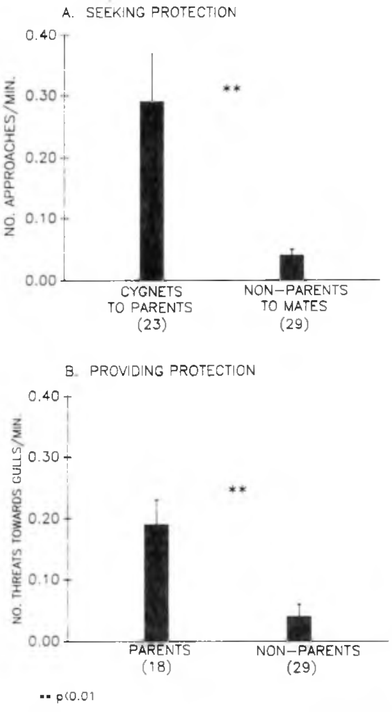

Figure 3. Rate at which Tundra Swan cygnets approached parents in the presence of gulls (A) and rate at which parents threatened gulls (B) during winter compared to the rates of non-parents. N, the number of focal units observed, is given in parenthesis. Bars are standard errors.

During the winter, when treadling was used solely to excavate clams, parents did not spend more time treadling than did non-parents ($P = 0.48$; Fig. 1).

Kleptoparasitism

Benefits to cygnets. Focal cygnets approached parents in the presence of gulls significantly more often than focal non-parents approached their mates ($P = 0.003$; Fig. 3). (The number of approaches was standardized by the number of parents/mates available to be approached.) Focal cygnets were not victims of gull attacks more often than non-parents, nor were gulls more successful when attacking cygnets (Table 2).

Costs to parents. Focal parents threatened gulls significantly more often than did non-parents ($P = 0.002$; Fig. 3). Focal parents and non-parents were victims of gull attacks nearly equally often, and gulls were nearly equally successful when attacking parents and non-parents (Table 2).

Discussion

Agonistic interactons

During both autumn and winter, families dominated non-families, as is true in many species of geese and swans (e.g. Scott 1980a, Black & Owen 1989a). Because most interactions were feeding displacements (Earnst, unpub. data), higher relative dominance probably allowed families to acquire and maintain better feeding sites (e.g. Black & Owen 1989a,b). Dominance may be particularly advantageous in swans feeding on natural aquatic foods rather than terrestrial or supplemented foods. A displaced swan feeding on submerged (and often buried), patchily distributed foods probably incurs substantial searching and travelling costs. Perhaps more importantly, it is likely to lose its feeding crater which contains exposed tubers or clams, and which is probably energetically expensive to reconstruct (see below).

If parents were protecting cygnets from competition with conspecifics, then cygnets receiving parental care should spend less time in interaction bouts and feed more intensively than cygnets not receiving parental care (e.g. Scott 1980a,b, Black & Owen 1989a,b). Our comparison between cygnets and non-parents does not allow us to address this question directly. Without parental care we might expect cygnets to have done much worse than non-parents, since lone cygnets are subordinate to non-parents (Scott 1980a). Cygnets receiving care did not differ from non-parents in time spent in interaction bouts in either season, or in feeding intensity or number of clams obtained during the winter.

If parents were providing protection, they may have incurred a cost of more frequent interactions (e.g. Black & Owen 1989b). On the other hand, parents need only win more often, not fight more often, to maintain their family's dominance status (Hinde 1974). In this study, parents did not spend more time in interaction bouts, or have more frequent interactions, than non-parents in either season.

Tundra Swan parents fed less intensively than non-parents in both seasons (and therefore spent more time in head-up, potentially vigilant, behaviours). A lower feeding intensity has been considered a cost of protecting young from competition in other species (winter: Scott 1980a,b, Black & Owen 1989a,b; breeding season: Lamprecht 1986, Schindler & Lamprecht 1987). However, it is difficult to interpret a difference in time spent feeding as either a benefit or a cost. It is possible that birds which forage less simply require less food, consume food more quickly, or consume higher quality food.

Foraging strategy

Treadling has not previously been investigated as a form of parental care during post-breeding seasons (although see Bailey & Batt 1974, Scott 1977). During the autumn, cygnets dabbled more frequently than did non-parents, and perhaps as a consequence of their parents' higher treadling rate, they treadled less themselves. The advantage gained is one of obtaining food at a lower cost. Dabbling on the water's surface is probably less expensive, and treadling is probably more expensive (in so far as it resembles waddling, Pinshow *et al.* 1977), than the more common foraging methods of neck-under and up-ending. When feeding on clams during the winter, parents did not differ from non-parents in per cent of time spent treadling. One plausible, but untested, explanation for the decrease in parental treadling to the level exhibited by non-parents is that a difference in the distribution of clams and tubers made treadling for clams a less efficient means of helping offspring than was treadling for tubers.

Copying

Potential benefits of copying a feeding site include acquiring a rich food patch, a feeding crater, and a specific food item. We observed one family foraging for clams at very low tide. The cygnet repeatedly placed its bill in the exact position from which its parent's bill had just been removed and frequently displaced its parent from an approximately 30-cm-deep crater and began treadling itself.

Cygnets also successfully took clams directly from their parent's bill, a behaviour never observed between adults. Cygnets (and rarely adults) stole clams dropped by their parents (or mates) during gull attacks. Both copying and stealing sometimes provoked threats from parents, but cygnets attempting to copy almost always succeeded in gaining their parents' foraging site.

Parents probably incurred a cost of increased searching and travelling time as a result of being displaced from their feeding site, and this may partially explain why they spent less time foraging during foraging bouts than did non-parents (but see arguments under *Agonistic interactions*).

Kleptoparasitism

Cygnets that approached parents in the presence of gulls may have profited simply from the parent's proximity. Barnard & Thompson (1985) have shown that Golden Plovers, *Pluvialis apricaria*, and Lapwings, *Vanellus vanellus*, decrease the chance of losing prey to an attacking Black-headed Gull, *Larus ridibundus*, by increased vigilance, and thus increased chance of detecting the gull during its attack. Parent swans may have been more vigilant for gulls than non-parents in general, based on the higher proportion of time they spent in non-feeding behaviours during feeding bouts.

Sometimes offspring approached parents immediately after bringing a clam to the surface and before an attack, or sometimes during an attack. It is therefore likely that such cygnets were seeking more than the added vigilance of the parents' presence. Parents threatened gulls, including threats in direct response to attacks on offspring and themselves, more often than did non-parents. Although gulls rarely stayed away for long after a parental threat, the threats may have deterred future attacks or decreased the success of attacks.

Barnard & Thompson (1985) have shown that Black-headed Gulls kleptoparasitize those individuals upon which they are most likely to be successful. Because foraging ability increases with age and experience in several bird species (e.g. Sullivan 1988, Barnard & Thompson 1985, Burger 1980), it seemed likely that cygnets would not avoid gull attacks as well as adults, and thus would be attacked more often. However, in this study, gulls did not attack focal cygnets more successfully or more frequently than they attacked focal adults. It is possible that this result is due to the parental care received by cygnets. We are currently investigating relationships between measures of parental care and the degree to which cygnets are kleptoparasitized.

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