

Parental Care in Tundra Swans During the Pre-fledging Period

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Abstract.—Among studies that have quantified the care of precocial young, few have investigated forms of parental care other than vigilance. During the pre-fledging period, Tundra Swan (*Cygnus columbianus columbianus*) parents provided simultaneous biparental care by foraging near each other and their cygnets, and cygnets spent more time foraging during bouts in which both parents were foraging nearby than when only one parent was foraging nearby. Parents spent nearly twice as much foraging time on land than did non-parents, a habitat in which cygnets foraged more intensely than parents (i.e., spent more time foraging during foraging bouts) and could graze on protein-rich sedges rather than use more difficult below-water foraging methods. Parents also spent more than twice as much time being vigilant and more than three times as much time defending their territory than non-parents, behaviors that presumably benefited cygnets by decreasing predation risk and indirect foraging competition, respectively. Parents therefore incurred the costs of foraging less intensely during foraging bouts, spending more time interacting, more time in vigilance, and less time sleeping/preening than non-parents.

Key words.—Alaska, breeding grounds, *Cygnus columbianus*, foraging, habitat use, parental care, Tundra Swan.

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Among avian species with self-feeding, precocial young, parental care was traditionally assumed to require little time and energy (e.g., Emlen and Oring 1973; Parmelee and Payne 1977). However, most studies of precocial young that have quantified parental care (i.e., behavior likely to increase the survival and productivity of offspring, Clutton-Brock 1991, p. 8) during the pre-fledging period have found that it substantially constrains the time and energy of parents (Table 1). Despite such studies, the parental care of self-feeding, precocial young remains less understood than that of altricial young.

Care of precocial young is often subtle and thus difficult to investigate; indeed, few studies have investigated forms of care other than vigilance (Table 1). An exemplary exception is the study of lapwings (genus *Vanellus*) in which Walters (1982) documented vigilance, leading and following young, showing food to young, and foraging away from young as care-giving behavior.

Most studies of parental care during pre-fledging have identified behavioral adaptations that benefit offspring by comparing (1) parental behavior to adult behavior in non-breeding years or seasons, or (2) examining parental behavior in relation to brood age or brood size (Table 1). However, comparisons of behavior between breeding and non-

breeding seasons are complicated by social and ecological differences among seasons, and there are conflicting interpretations of differences in parental care with brood size and brood age (Clutton-Brock 1991, chapter 9; Sedinger *et al.* 1995). Tundra Swans (*Cygnus columbianus columbianus*) provide an ideal opportunity to compare parent and non-parent behavior under similar ecological and social conditions because, in the northern-breeding swans, many pairs hold territories in years in which they do not raise cygnets (Rees *et al.* 1991; Henson and Cooper 1994).

Among many shorebirds and waterfowl, proximate measures of costs to parents indicate that there is a trade-off between time spent in parental care and time spent resting or foraging (Table 1). The longer-term fitness consequences of parental care in waterfowl have been measured only in relation to differences in current brood size, and most of these studies suggest that there are no meaningful fitness costs of raising larger broods (Rohwer 1985; Lessells 1987; Rohwer and Heusmann 1991; Williams *et al.* 1994; Loonen *et al.* 1999). However, Lessells (1986) found that Canada Geese (*Branta canadensis atlantica*) that raised experimentally enlarged broods had lower body mass at the end of the rearing period, molted later, and laid eggs later the following year. Delayed breeding

Table 1. Studies that have quantified parental care and its proximate costs during the pre-fledging period in shorebirds and waterfowl. Three forms of parental care are considered: vigilance (VG), maintaining proximity (PX), and defending a foraging area or protecting young from foraging competition (DF). "X" = behavior varied as expected (i.e., more effort expended by parents than non-parents, and on larger and younger broods); "-" = behavior did not vary as expected; blank = comparison not quantified.

Species	Form of care				Reference
	Comparison	VG	PX ^a	DF ^b	
Trumpeter Swan <i>Cygnus buccinator</i>	Non-parents	X			Henson and Cooper 1992
Pink-footed Goose <i>Anser brachyrynchus</i>	Non-parents	X		X	Lazarus and Inglis 1978
	Brood age	X			
Greater Snow Goose <i>A. caerulescens atlantica</i>	Non-parents	X			Giroux <i>et al.</i> 1986
Lesser Snow Goose <i>A. caerulescens caerulescens</i>	Non-parents	X			Lessells 1987
	Brood size	-	X		
Lesser Snow Goose	Non-parents	X			Williams <i>et al.</i> 1994
	Brood size	X			
Light-bellied Brant <i>Brania bernicla hrota</i>	Non-parents	X			Bregnballe and Madsen 1990
Black Brant <i>B. bernicla nigricans</i>	Brood size	X			Sedinger <i>et al.</i> 1995
Cackling Canada Goose <i>B. canadensis minima</i>	Brood size	X		X	Sedinger and Raveling 1990
Giant Canada Goose <i>B. canadensis maxima</i>	Brood size	X			Seddon and Nudds 1994
	Brood size	X			
Canada Goose <i>B. canadensis atlantica</i>	Non-parents	-	X		Lessells 1986
Barnacle Goose <i>B. leucopsis</i>	Brood size	X			Forshlund 1993
	Brood size	X			
	Brood size	X			Loonen <i>et al.</i> 1999
Bar-headed Goose <i>A. indicus</i>	Brood size	X		X	Schindler and Lamprecht 1987
Cape Barren Goose <i>Cereopsis novaehollandiae</i>	Brood size	X			Pellis and Pellis 1982
Northern Pintail <i>Anas acuta</i>	Brood age	X			Rushforth Guinn and Batt 1985
Australian Wood Duck <i>Chenonetta jubata</i>	Brood age	X			Kingsford 1990
	Brood size	-			
Killdeer <i>Charadrius vociferus</i>	Brood age	X			Lenington 1980
Semipalmated Sandpiper <i>Calidris pusilla</i>	Brood age	X			Ashkenazie and Safriel 1979
Southern Lapwing <i>Vanellus chilensis</i>	Non-breeding season	X			Walters 1982
Long-toed Lapwing <i>V. crassirostris</i>	Non-breeding season	X			Walters 1982
Blacksmith Plover <i>V. armatus</i>	Non-breeding season	X			Walters 1982

^aProximity measured as frequency with which parents approached young in Bar-headed Geese, as time spent following brood in Northern Pintails, and as parent-brood distance in Killdeer, Giant Canada Geese, and Barnacle Geese. ^bDefense of foraging area measured as dominance over non-parents in Pink-footed Geese, dominance of families relative to all other social units in Barnacle Geese, and as attacks on conspecifics in Bar-headed Geese and Light-bellied Brant. ^cFemales only. Females with experimentally enlarged broods also delayed laying in following years but their fecundity and survival to next year was not affected. ^dRather than costs to parents, the benefits of increased social dominance and better female body condition during molt were associated with increased brood size. ^eData appear to show difference, but author does not give direct statistical comparison of time spent foraging by parents and non-parents.

has substantial fitness costs in northern-breeding geese because late-hatching goslings grow more slowly and have lower survival rates (Cooch *et al.* 1991a; Sedinger and Flint 1991; Prop and de Vries 1993; Lindholm *et al.* 1994).

Although other studies have investigated parental care in Tundra Swans during the non-breeding seasons (Earnst and Bart 1991), this is the first field study of parental care in Tundra Swans during the pre-fledging period, a time when they are wary and sparsely distributed. The aims of this study are to document and quantify parental care in Tundra Swans during the pre-fledging period, and to investigate its proximate costs to parents. To achieve these aims, the following forms of parental care were quantified: vigilance, territory defense, foraging intensity (measured as proportion of time spent foraging during a foraging bout), proximity to the brood during foraging bouts, habitat use while foraging, and use of an activity cycle assumed to be beneficial to cygnets (measured as average length of foraging periods).

METHODS

Study Site and Phenology

Tundra Swans were studied during May–August, 1987–1990, on the Colville River Delta, 90 km east of Prudhoe Bay, on the northern coast of Alaska. The 500-km² Delta supports an average of 31 breeding pairs, 53 non-breeding pairs, and several non-breeding flocks each year (Bart *et al.* 1991). Territories were approximately 1 km² and included a large waterbody and usually numerous polygonal ponds. Swans fed on aquatic and terrestrial vegetation in and around both types of waterbodies (Earnst 1992a). Breeding pairs arrived in late May when most wetlands were ice-covered and began egg-laying soon after. The brief arctic summer places severe time constraints on the development of cygnets which typically hatch around 8 July and fledge 65–75 days later, shortly before wetlands freeze for the winter (Bellrose 1980; Earnst 1992a).

Observations

Behavioral observations of breeding pairs with cygnets were compared to those of non-breeding pairs after 8 July (the average hatching date). Most observations (90%) had been made by the fifth week after hatching (2 August), and the remainder were made before August 28. The behavior of undisturbed swans was recorded from three enclosed blinds located 2–4 km apart in an area known to support numerous breeding territories. Blinds were built on a tower or ridge, providing a viewing platform 2–4 m above the swan habitat, and

were accessible with minimal disturbance to swans. Focal swans were usually 0.5 to 1.0 km from the blind and were observed through a 60–90× telescope.

Instantaneous, focal-animal sampling (Altman 1974) was used on pairs and families occupying known territories within viewing distance from the blinds. Observations were made from one blind per day and focal pairs and families were chosen systematically (i.e., from left to right) from those that were visible, while attempting to achieve similar total observation hours per focal unit. Observation period length was determined prior to approaching the blind to avoid bias arising from any unintentional association with swan behavior. Swans usually appeared unaware of movement to the blind but, if they were disturbed, data collection was postponed until they resumed their previous behavior or assumed a relaxed posture, typically after 15–30 minutes. For each focal pair or family, the following parameters were recorded at one-minute intervals: behavior and habitat of each mate, distance between mates, and behavior and distance-to-nearest-parent (in adult body-lengths) for each cygnet. A continuous count-down timer with alarm was used to notify the observer at each one-minute interval. Distance was recorded in adult swan body-lengths. Specific behavior was recorded and later categorized into five behavioral types (in order of precedence): feeding, interacting agonistically with non-family members, preening, traveling (walking, running, swimming, and flying), and resting (sleeping, sitting, standing, floating). If swans were engaged in two behavioral types simultaneously (e.g., feeding and standing), the behavior was categorized into the type having higher precedence. Specific feeding behaviors included up-ending, neck-under, head-under, dabbling, treadling (paddling the feet to scrape vegetation to the surface), and grazing (see Owen and Kear 1972 for definitions). Swan posture was recorded at each one-minute interval as head-up (the plane of the neck being above horizontal), alert (the extreme head-up, as defined by Lazarus and Inglis 1978), or neither. Feeding habitat was categorized as aquatic (surface water present) or terrestrial (no surface water). Continuous sampling was used for observations of territorial interactions and encounters with predators. Swans were out of sight on 5% of the instantaneous samples (range 0 to 9%) and appeared to be approximately equally visible when engaged in each of the five behavior types. Thus, recorded observations are considered a representative sample of each focal animal's behavior.

Bout Definitions

Observations made at consecutive one-minute intervals were pooled into behavioral bouts in order to address questions of foraging intensity and foraging period length. Five bout-types, corresponding to the five behavioral types listed above (feeding, interacting, preening, traveling, and resting), were identified. The following set of rules was used to determine bouts: (1) a new bout-type began on a one-minute interval if it was the first of six consecutive intervals in which at least three of the six were of a single behavioral type; (2) once begun, a bout-type continued if the interval behavior matched the bout-type or if the interval was the first of six consecutive intervals in which at least two of the six intervals matched the bout-type; and (3) if an interval did not meet the criteria for continuing a bout or initiating a new bout-type, it was coded as transitional.

Subsequently, to simplify analysis, preening and resting bouts were combined, traveling bouts that directly preceded or followed an interaction bout were added to the interaction bout (this type of traveling usually resulted from a bird moving towards an intruder and back to its original position), and transition intervals were added to the preceding bout. Thus, four bout-types (feeding, interacting, traveling, and resting) were used in the final analysis. This set of rules was chosen because it avoided production of short resting and traveling bouts, minimized the number of transitional intervals, and produced bouts in which most behaviors were of the bout-type (e.g. foraging comprised 73% of intervals within foraging bouts), and because time spent in each bout-type was similar to time spent in the respective behavior categories over all bout types (e.g., 47% vs. 41% foraging; 42% vs. 46% resting). In addition to the set of rules described here, analyses using four other sets of bout rules (i.e., criteria used to identify a bout) revealed that bout lengths and the estimated time spent in each bout-type were similar among bout rules, indicating that the choice of this set of rules over others likely had little affect on subsequent analyses.

Bouts were assigned only for those periods in which the identity of adults could be kept separate. Foraging intensity was defined as the proportion of intervals during a foraging bout recorded as foraging. Foraging time spent in proximity to the mate was measured as the proportion of an individual's foraging bout in which it was within six adult body-lengths of its mate (Scott 1980). The foraging intensity of cygnets was used to determine whether cygnets gained any advantage of foraging near both, rather than only one, parent. Because the identity of cygnets could not be kept separate, their behavior was not assigned to bouts. Thus, the foraging intensity of each cygnet was defined as the proportion of intervals in the nearest parent's foraging bout in which the cygnet's behavior was also recorded as foraging. The foraging intensities of all cygnets within a brood were averaged to obtain a mean foraging intensity for each brood. Except for an occasional moment immediately before or after a parental foraging bout, cygnets were never seen foraging unless at least one parent was in a foraging bout.

To investigate activity cycles, two types of periods were distinguished: those in which foraging was the predominant activity and those in which resting, and thus food digestion, was predominant. Thus, foraging periods were defined as foraging bouts plus any interacting, traveling, floating, and standing intervals that were of short duration (<5 min) and interrupted an otherwise continuous foraging bout. Defining foraging periods in this way was also appropriate because cygnets continued to forage during brief interruptions in their parents' foraging bouts. The inter-foraging period was the time between foraging periods. Only foraging bouts completed within the observation period were used in calculating foraging period length. The potential for bias in estimating the length of the foraging period is minimal because the average foraging bout was substantially shorter than the average observation period (36 and 204 min, respectively).

Statistical Analysis

In the four years of this study, nine different territories were visible from blinds during the brood-rearing period. One or both members of four focal pairs wore neck collars containing individually identifiable codes

in at least one year of study. Studies on northern-breeding swans indicate that breeding pairs typically occupy the same territory in consecutive years (Whooper Swans, *Cygnus cygnus*, Einarsson and Rees 2002; Bewick's Swans, *Cygnus columbianus bewickii*, Rees pers. comm.). Similarly, in this study, five breeding pairs were banded on territory (two in the observed area, three elsewhere on the Delta), both members were known to be alive in subsequent seasons, and their territories were checked thoroughly enough to provide resightings of banded birds. In all five cases, the pair occupied its same territory in subsequent years, irrespective of whether it bred. Thus, as a conservative approach to avoid pseudoreplication, data from pairs present as breeders in more than one year (three pairs) or as non-breeders in more than one year (two pairs) were pooled across years (see also Henson and Cooper 1992; Grant *et al.* 1994). Analyses were based on means per pair or brood. The proportion of time spent on each behavior by a focal pair was calculated for each observation period and then averaged across observation periods. Average proportions for each focal pair were weighted by the total time it was observed (analogous to weighting by sample size; Cochran 1977) then averaged with the weighted means of other focal pairs. Statistical comparisons were made using independent t-tests unless noted otherwise. Standard errors are reported with means throughout the text, tables, and figures.

RESULTS

Of the nine territories visible from blinds, seven were breeding territories in at least one year of the study. Analyses were based on seven breeding pairs observed for a total of 156 h during ten pair-years, and five non-breeding pairs (three of which were also observed as breeders) observed for a total of 76.1 h during six pair-years. However, some parameters could not be quantified for social units with territories far from the blind, thus degrees of freedom differ among tests. Pairs were observed for an average of 3.4 h per observation period, 6.1 observation periods, and 20.7 total hours each.

Maintaining Proximity

Parents spent nearly twice as much of their foraging time in proximity (within six body-lengths) to one another as did non-parents ($P < 0.001$, Table 2). Because cygnets were, on average, only 1.3 (± 0.2) adult body-lengths from their nearest parent, parents near one another were also both near their brood.

Cygnets fed significantly more intensely (i.e., spent more time foraging during their parent's foraging bout, see Methods) when

Table 2. Mean proportion of time spent in parental care behaviors, and mean length of foraging and inter-foraging intervals, by parents and non-parents during the brood-rearing period. Standard errors in parentheses. N = 7 parental pairs and 4 non-parental pairs, except where noted otherwise, and statistical significance based on independent t-tests.

Form of parental care	Measure	Parents	Non-parents	t	P <
Proximity	Proportion of foraging time <6 body-lengths	0.58 (0.05)	0.30 (0.01)	5.57	0.001
Foraging habitat	Proportion of foraging time on land ^a	0.41 (0.02)	0.24 (0.05)	3.19	0.02
Vigilance	Proportion of time alert ^b	0.05 (0.007)	0.02 (0.007)	3.43	0.01
	Proportion of time head-up ^b	0.48 (0.04)	0.37 (0.07)	1.39	n.s.
Territory defense	Proportion of time interacting ^b	0.014 (0.004)	0.004 (0.002)	2.24	0.05
Activity cycle	Length of foraging period (min)	41.6 (3.7)	26.1 (2.1)	3.64	0.005
	Interval between foraging periods (min)	40.7 (3.8)	49.1 (8.6)	0.89	n.s.

^aN = 6 parental pairs, 4 non-parental pairs. Alert posture is defined as the neck being held rigidly vertical.

^bN = 7 parental pairs, 5 non-parental pairs. Head-up posture includes all behaviors in which the plane of the neck is above horizontal.

both parents were foraging nearby than when only one parent was foraging nearby ($P < 0.01$, Table 3).

Parents did not appear to incur costs, as measured by decreased feeding intensity, when foraging in proximity to one another. In fact, when both parents were foraging and near one another, they fed significantly more intensely than during other feeding bouts ($P < 0.001$, Table 3).

Activity Cycle and Foraging Habitat

Parents engaged in foraging periods about 1.5 times longer than those of non-parents ($P < 0.01$) and did not differ from non-parents in length of intervals between foraging periods (n.s., Table 2). Parents spent nearly twice as much foraging time on land as did non-parents ($P < 0.01$, Table 2) and cygnets always foraged in the same habitat as their parents. The one pair for which sufficient data were available used terrestrial habitat significantly more during a breeding

than a non-breeding year ($\bar{x} = 0.45 \pm 0.12$ and 0.10 ± 0.07 , respectively, with the observation periods as the sampling units, $t_{11} = 2.53$, $P < 0.05$).

When feeding on land, cygnets fed with nearly twice the intensity as their parents ($t_{10} = 4.31$, $P < 0.01$, Fig. 1). When feeding on water, cygnets did not forage significantly more intensely than parents ($t_{12} = 1.33$, n.s., Fig. 1), and rarely used the below-surface foraging methods (head-under, neck-under, and up-end) that were commonly used by their parents ($\bar{x} = 0.12 \pm 0.02$ and 0.49 ± 0.07 , respectively, $t_{12} = 4.96$, $P < 0.001$). Although cygnets foraged 81% of the time during foraging bouts on land and 64% on water, the SE on land was large, and the difference was not significant (Fig. 1). In contrast, the foraging intensity of adults (non-parents and parents combined) was significantly lower, rather than higher, on land than on water ($P < 0.05$, Fig. 1). The pattern was similar when considering parents only, but was not statistically significant.

Table 3. Foraging intensity (i.e., proportion of time spent foraging during a foraging bout) of broods and parents when both parents were foraging and near the brood (<6 body-lengths) compared to foraging intensity when only one parent was foraging near the brood. N = 7 parental pairs and 4 broods; statistical significance based on paired t-tests. SEs given in parentheses.

	Both parents foraging and near brood	One parent foraging near brood	t	P <
Broods	0.76 (0.03)	0.65 (0.03)	5.67	0.01
Parents	0.69 (0.02)	0.44 (0.02)	6.67	0.001

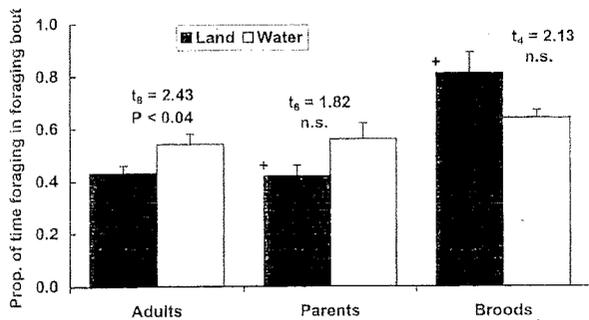


Figure 1. Foraging intensity of all adults (parents and non-parents combined), parental pairs, and broods, when foraging on land and water. Error bars denote one SE and + denotes a significant difference between parents and broods. Total sample sizes were nine pairs, seven parental pairs, and seven broods, but foraging intensity of some broods could not be quantified on land due to poor visibility (thus d.f. varies among tests). Statistical tests of behavior on land compared to water were paired t-tests (shown on graph); tests comparing parents to broods were independent t-tests. Broods foraged more intensely than parents on land ($t_{10} = 4.31$, $P < 0.01$) but not on water ($t_{12} = 1.33$, n.s.)

Vigilance and Territory Defense

Parents spent more than twice as much time alert ($P < 0.01$) and more than three times as much time in agonistic interactions with other adult swans ($P < 0.05$) than did non-parents during the brood-rearing period (Table 2). Interactions included threatening or chasing intruders from the territory either in the air or on the ground (especially during molt). During interactions, one parent engaged the intruder while the other, sometimes in a hiding posture, remained with the brood. As a result, parents were in synchrony during interaction bouts (i.e., both interacting) significantly less often than were non-parents ($\bar{x} = 0.61 \pm 0.08$ and 0.84 ± 0.03 , respectively, $t_7 = 2.59$, $P < 0.05$). The division of labor did not appear to be sex-specific: male and female parents were observed in each role and spent similar amounts of time interacting ($\bar{x} = 0.7 \pm 0.5$ and 0.7 ± 0.6 , respectively, $t_5 = 0.0$, n.s.).

Parents spent less time sleeping/preening than non-parents ($\bar{x} = 0.18 \pm 0.02$ vs. 0.32 ± 0.05 , $t_{10} = 2.50$, $P < 0.05$). Parents also fed less intensely during foraging bouts than did non-parents ($\bar{x} = 0.62 \pm 0.05$ vs. 0.73 ± 0.02 , $t_9 = 2.29$, $P < 0.05$), but parents did not spend less time foraging overall ($\bar{x} = 0.34 \pm 0.04$ vs. 0.31 ± 0.02 , $t_{10} = 0.77$, n.s.).

DISCUSSION

Comparison of behavior of parents and non-parents revealed several forms of parental care in Tundra Swans during the pre-fledging period. Tundra Swan parents spent more time being vigilant, defending their territory, foraging in proximity to one another, and foraging on land than non-parents. In addition to the energetic costs of vigilance and territory defense, parents incurred costs related to foraging less intensely during foraging bouts and spending less time sleeping/preening, but did not spend a lower proportion of time foraging overall.

Maintaining Proximity

Parents foraging near one another provide their brood with simultaneous biparental care. Any benefits that cygnets gain from foraging near a parent (such as assistance in finding food and protection from predators) are presumably greater when two parents, rather than one, are nearby. Other studies of waterfowl that have identified maintaining proximity as a form of parental care have found that parents maintain greater proximity when brood size is smaller (Schindler and Lamprecht 1987; Forslund 1993), offspring are younger (Seddon and Nudds 1994), and when foraging in high quality patches (Eberhardt *et al.* 1989; Mulder *et al.* 1995). This study's finding that parents spent more foraging time in proximity with one another than did non-parents, and that cygnets benefited from these behaviors by having increased foraging intensity when both parents, rather than only one, were foraging nearby, suggests that these behaviors are components of parental care in this species. Cygnets have been shown to copy the precise foraging location of their parents and to forage on vegetation paddled to the surface by parents on migratory stopovers and wintering grounds (Earnst and Bart 1991), and although not quantified here, these are likely advantages of foraging near parents in this study also, particularly when foraging on water. An alternate explanation, that parental territories had richer patches of food that allowed clos-

er proximity while foraging, raises the possibility that maintaining high quality territories, rather than maintaining proximity, may be the parental behavior under selection.

Any cost to parents of foraging near one another was not detectable in feeding intensity, and in fact, parents may have benefited from proximity to one another since parents fed more intensely when feeding near their mate than at other times.

Activity Cycle

Data from Trumpeter Swans (*Cygnus buccinator*) and geese indicate that, compared with adults, young have longer foraging bouts (Giroux *et al.* 1986; Grant 1991) and spend more time foraging (Giroux *et al.* 1986; Bregnballe and Madsen 1990; Grant 1991; Sedinger *et al.* 1995). Tundra Swan parents had longer foraging periods than non-parents, which suggests that parents may adjust their activity cycle according to cygnets' needs. The longer foraging bouts of cygnets may result from their lower foraging efficiency and greater nutritional requirements. Nutrient intake of geese and swans is limited by processing rate and gut capacity as well as by time available for foraging (Sedinger and Raveling 1988; Squires 1991; Manseau and Gauthier 1993), so individuals often respond to decreased food availability or foraging efficiency by increasing foraging bout length (Drent and Swierstra 1977; Sedinger and Raveling 1988).

Foraging Habitat

Differences between parents and non-parents in habitat use during foraging bouts suggest that habitat use by parents corresponds to the foraging needs of cygnets. Parents spent nearly twice as much time foraging on land as did non-parents.

Several lines of evidence suggest that grazing on terrestrial vegetation is more beneficial to cygnets than foraging on aquatic vegetation. First, cygnets have poorer access to submerged plants than adults because their necks are shorter and they are inefficient at neck-under and tip-up postures for

the first few weeks of life (Owen and Keeney 1972, pers. obs.). In this study, cygnets dabbled for floating vegetation or grazed on emergent vegetation, but used below-surface foraging methods only one-fourth as often as parents (12% vs. 49% of foraging time on water). Similarly, Grant *et al.* (1994) found that Trumpeter Swan cygnets foraged on submerged vegetation less than adults, and Monda *et al.* (1994) found that young Tundra Swan cygnets grazed on terrestrial vegetation more than older cygnets. The poor foraging performance of cygnets on water is also illustrated by parents treading vegetation to the surface where cygnets dabbled for it (Earnst 1992a).

Second, cygnets foraged with about the same intensity as their parents during foraging bouts on water, but foraged substantially more intensely than their parents during foraging bouts on land. Similarly, when foraging in nutrient rich patches, goslings of Canada Geese and Lesser Snow Geese (*Chen caerulescens caerulescens*) spent more time foraging and less time moving than when foraging elsewhere (Eberhardt *et al.* 1989; Mulder *et al.* 1995). A direct comparison of cygne foraging intensity on land ($\bar{x} = 0.81$) compared to water ($\bar{x} = 0.61$) was hampered by the high variation in foraging intensity on land, suggesting that further study of a large sample of broods and territories is needed to understand the benefits to cygnets of foraging on land.

Third, grazing on terrestrial plants involves less search time (Grant *et al.* 1994, pers. obs.) and less energetic cost (Wooley and Owen 1978; Coleman and Boag 1987) than foraging beneath the water's surface and the protein content of terrestrial forage is probably high shortly after hatching (Sedinger and Raveling 1986). These advantages are presumably more important to rapidly growing cygnets than adults because cygnets have higher protein demands, and their growth rate and survival may be limited by plant nutrient levels, as is true of arctic-breeding geese (Sedinger and Raveling 1986; Cooch *et al.* 1991a,b; Larsson and Forslund 1991; Sedinger and Flint 1991; Lindholm *et al.* 1994). Although the caloric

and protein content of aquatic and terrestrial forage have not been compared at this study site, results from other studies suggest that aquatic plants, although high in caloric content, lack the protein content of newly grown sedges (*Carex* spp.) (Clausen 1994; Prop and Deerenberg 1991).

When feeding on land, parents did not accrue any advantage in foraging intensity relative to foraging on water. In fact, parents fed less intensely and spent more time in head-up behaviors than when foraging on water, probably due in part to (1) the need for greater vigilance on land where cygnets are more vulnerable to predators, and (2) greater forage quality allowing more time for parental care. Similarly, Mulder *et al.* (1995) found that when Lesser Snow Geese foraged in high-biomass patches compared to control plots, parents fed for shorter periods, spent more time vigilant, and moved less rapidly which likely reduced distances between adults and goslings, and that these differences were more pronounced in parents than non-parents.

Vigilance

Parents were in an alert posture more often than non-parents and tended to spend more time in head-up behaviors. Parents are known to be more vigilant than non-parents in several species of waterfowl and shorebirds (Table 1). Vigilance probably functions to detect conspecific territorial intruders and predators. Cygnets were primarily at risk of predation by Snowy Owls (*Nyctea scandiaca*), Arctic Foxes (*Alopex lagopus*), and Parasitic Jaegers (*Stercorarius parasiticus*). Vigilance presumably enabled parents to detect predators earlier, allowed more time to respond appropriately, and thus decreased the risk of predation to cygnets.

In most studies reviewed in Table 1, increased time spent vigilant by parents relative to non-parents was accompanied by decreased time spent feeding or resting, suggesting that there is a trade-off being made by parents. Similarly, when parents encountered higher food availability, they tended to reduce time spent foraging while increasing

time in vigilance (Sedinger *et al.* 1995; Mulder *et al.* 1995). In this study, parents spent more time in vigilance and less time sleeping/preening. Parents did not spend less time in feeding behaviors or feeding bouts, but they fed less intensely during foraging bouts than did non-parents.

Territory Defense

Tundra Swan parents, like those of other northern-breeding swans, typically maintain territories throughout brood-rearing. One advantage of territoriality during brood-rearing is thought to be the exclusive use of a foraging area for cygnets. In breeding populations of Black Swans (*Cygnus atratus*) and Black-necked Swans (*Cygnus melancoryphus*) where parents do not defend exclusive foraging areas, young are continually driven from foraging sites by conspecifics, and incur high mortality as a result (e.g., Braithwaite 1981; Schlatter *et al.* 1991).

Parents spent significantly more time interacting with other swans than did non-parents. This larger effort by parents can be interpreted as a form of parental care (given the probable benefit to cygnets). Increased time spent interacting by parents may be influenced, in part, by higher quality territories and therefore greater attractiveness of their territories to intruders, but the need to maintain a high quality territory is also a form of parental investment. In other studies of geese and swans, parents attacked or threatened conspecifics more frequently than did non-parents (Schindler and Lamprecht 1987; Bregnballe and Madsen 1990) and were dominant to non-parents during breeding (Lazarus and Inglis 1978; Mulder *et al.* 1995) and non-breeding seasons (Boyd 1953; Raveling 1970; Scott 1980; Black and Owen 1989a,b; Earnst and Bart 1991).

Although exclusive use of a foraging area is likely beneficial to cygnets, they may also incur costs of territoriality if left alone during interactions. Unattended cygnets are at risk of predation but may also risk being separated from their parents and adopted by the intruding pair as has been reported in Whooper Swans (Rees *et al.* 1990) and Mute

Swans, *Cygnus olor* (Minton 1968; Bacon 1980). Tundra Swan parents minimized these threats by a clear division of labor during interactions: one parent, sometimes in a hiding posture, remained with the brood while the other engaged the intruder. The division of labor did not appear to be sex-specific since male and female parents were observed in each role and spent similar amounts of time interacting. During segments of the brood-rearing period during which one mate was undergoing complete wing molt and the other was not (six days on average), the fully-feathered parent assumed all territory defense (Earnst 1992b). The division of labor was evident in the larger proportion of time that parents spent in asynchrony during interactions compared to that of non-parents.

In conclusion, comparisons with non-parents indicated that parents provided young with substantial parental care during the pre-fledging period. Parents spent more time in vigilance and in territory defense, more foraging time on land where cygnets foraged more efficiently than their parents, and more of their foraging time near one another and thus near their cygnets.

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