Breeding behaviour of wild Whistling Swans

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Introduction

In most ducks (Anatinae), males and females are only paired during part of the year, and females are left with sole responsibility for incubation and care of the young. This contrasts the situation in geese and swans (Anserinae) which form life-long pairs, and where both sexes remain with the young for extended periods of time. But even in these species the female is still usually responsible for sitting on the eggs. The role of the male at this time is not clear. Various authors have suggested that division of labour is involved, with the male maintaining defence of the territory or immediate vicinity of the nest against conspecifics and predators (Ewaschuk & Boag 1972; Ryder 1975; Inglis 1976), or that both parents are necessary for antipredator defence (Maynard-Smith 1977). But few studies have investigated this quantitatively in geese (see Ewaschuk & Boag 1972; Lazarus & Inglis, in press), while no detailed studies have been made on swans in the wild, and only limited ones on captive swans (Evans 1975, 1977).

The present study aimed to investigate the roles of male and female parent in incubation, territorial defence and care of the young, with a view to understanding their functional significance in wild Whistling Swans *Cygnus columbianus columbianus*.

Study area

The study area was located at Old Chevak, the U.S. Fish and Wildlife Field Station in the Clarence Rhode National Wildlife Range, an area of prime Whistling Swan habitat within the Yukon-Kuskokwim delta, Alaska. The tundra is characterized by a mosaic of pools interspersed with lowland tundra (dominated by sedges *Carex*) and upland tundra (dominated by mosses *Sphagnum*). Previous observations (C. Lensink, pers. com.), indicated that the swans nest on raised ground, islands or promontories beside large lakes, at an average density of one pair per 2·6 square kilometres. Non-breeding birds were also known to be present in the area.

Methods

Between 8th May and 13th June 1976, the conditions on the Kashunuk River prevented aerial access to Old Chevak, so all survey work had to be done on foot, covering as large an area as possible on account of the low density of breeding pairs. Conditions for observation were not ideal and the swans were easily frightened at distances of less than 100 metres. The terrain was such that it was hardly ever possible to look down on the birds, but a chain of portable hides across the riverine flats and three towers in upland tundra provided access to small non-breeding groups on several days, and a 2 m square tent made long periods of observation on one breeding pair feasible.

Over the first three weeks, observations were made on pairs and groups of swans in which aggression, courtship, copulation, incipient nest building and signs of territoriality were recorded. The first breeding pair (code-named DQ) was located on 1st June and 24-hour watches to a total of 150 hours were maintained on them until hatching (27th June). Two further nests (HA and GS) were watched for short periods towards the end of incubation. During 24-hour watches the identity of the bird on the nest, its position and activity, and the activity, distance and location of its mate were recorded every 15 minutes.

After hatching, three families (DQ, HA, HS with broods of 4, 4 and 3 cygnets) were watched until the third week while they were visible feeding on open water. They then moved to small ponds with tall vegetation. Within samples (one minute every other minute for up to 2 hours), frequencies were recorded with which parents and cygnets approached or left (a distance of 3 metres from each other) or followed (behind and in the same direction); so was the duration of parental trampling (a paddling movement while feeding which probably stirs up food items in the water and may have some signal function (Heinroth 1911)). At the end of sample minutes the activity and relative position of each member of the family was recorded. Throughout all the observation periods a continuous record was made of the presence and activity of other swans in the area and of potential predators and the pair's reaction to them. Observations on non-breeding birds continued sporadically until mid-June when the main flock moved away.

Results

Pre-nesting

At the beginning of May, swans collected in pairs or small groups on the few ponds or lowland meadows with open water. Over the first two weeks there was a steady passage of birds flying north, some of which landed for short periods in the Old Chevak vicinity. Frequencies of aggression and courtship behaviour were high but it was seldom possible to determine the social status of the birds involved. No obvious family units were observed, nor was there any evidence of expulsion of yearlings by their parents, but since individuals could not be followed for long periods, these relationships might not have been detected. Flocks averaged 12–20 individuals and comprised up to 60% first-year birds.

Throughout May and the first half of June frequencies of courtship and aggression in non-breeding flocks remained high in comparison with winter flocks. Aggressive displays were more conspicuous and more frequently aerial. Courtship displays also differed in having longer durations and greater intensity, and often included elements of aggression (pecks and low intensity threats), suggestive of pair formation rather than pair maintenance. There was some indication that non-breeding pairs defended small tundra pools for feeding throughout the season.

Between 13th and 19th May, pairs were observed copulating on open water, usually away from other groups of swans. Nest building behaviour, still unoriented, became increasingly common while pairs were feeding on the riverine flats. Nest site selection behaviour by females was seen twice on 21st and 22nd May, after which there was no further evidence of breeding activity in the immediate Old Chevak area, except 13 inferred territorial establishment fights viewed at a distance. By 1st June, when a nest was located, territories were established, nests built and incubation was beginning. An aerial survey on 20th June gave a density of 0·14 breeding pairs per square kilometre.

Incubation

Data from 24-hour watches of DQ showed a clear difference in the time male and female spent sitting on the eggs. The female was on the nest 81·3% of the time, the male only 15·9% of the time, while the eggs were uncovered during the changeovers (Table 1a). The female also sat for longer periods, with a mean bout length of 6·9 hours (range 2·0–17·2) compared with 1·3 hours (range 2·5–3·5) for the male (Table 1b). Over the course of incubation the female's bout lengths appeared to decrease at first and then to increase to a maximum just before hatching, but this is not significant. She would remain longer on the nest in bad weather (rain or snow), and would not rise when the male returned to the vicinity of the nest. No obvious diurnal pattern in incubation was apparent.

Nest relief was silent except on one occasion when the female returned with a triumph display after an encounter with a neighbouring pair. Otherwise it was similar to that in captive swans, the relieved parent standing poking downwards into the nest-bowl a few times before walking off and the relieving bird then walking on and settling.

Table 1. Division of incubation between the sexes

(a) Percentage of time spent sitting on eggs (per day).

Nest	Male	Female	Uncovered	No. of hours observed
DQ	15·9	81·3	2·8	141
HA	9·5	89·4	1·1	17
GS	27·0	72·2	0·8	18

(b) Average bout lengths of incubation (in hours).

Nest	Male			Female		
	Av.	Range	Sample	Av.	Range	Sample
DQ	1·33	0·25–3·5	19	7·00	2·0–17·15	20
HA	(0·67)	—	1	5·15	4·75–5·67	3
GS	(1·0)	—	1	2·67	—	1

Typically, the male was more reluctant to rise from the eggs than the female, and whereas the female flew off to feed within one minute of rising, he spent an average of 6·1 minutes adding material to the base of the nest before leaving.

While the male did most of the addition of material around the sides and base after a changeover, the female spent more time rearranging material around the nestbowl (titivating), especially after settling or shifting position. The activities off the nest also differed, the female spending a greater proportion of the time feeding than the male (Table 2). Over the incubation period, the frequency with which other birds were audible or visible in the area was low (at 0·45 per hour). The pair reacted by hiding, by looking alert, by displaying or by chasing (Table 3), and the male did more displaying, particularly aerial chasing, than the female; the commonest response was looking alert. Reactions were more frequent to birds audible or visible within 400 m, and throughout incubation there were few 'territorial survey' flights. Hiding was not confined to the bird on the nest, where it takes the form of a flattening of head and neck forwards over the nest rim, and could be shown by either sex when elsewhere.

Table 2. Percentage time spent feeding when off nest (DQ)

Date (June)	Male	Female
5/6	87·3	77·8
7/8	55·6	94·7
11/12	77·5	91·7
14/15	63·0	75·0
18/19	50·0	88·0
22/23	61·3	100·0
24/25	65·6	100·0

Defence against predators was only witnessed once when an Arctic Fox *Alopex lagopus* passed and hesitated within 4 m of a nest. The female rose from the eggs, and hissed with wings half open, and the fox continued on its way. The male was not visible. Otherwise when foxes passed within 50 m both parents would usually become alert.

After hatching

Parents of all three families feeding on open water spent around 20% of the time trampling. This continued without decline for the period of observation, with no overall difference between sexes (Table 4). Similarly there was no significant difference in the time each parent spent in vigilant posture; neither were differences in feeding rates apparent. Males would sometimes feed alone in mid-pond, while the female brooded the young on the bank, often when neighbours were visible, and especially preceding or following territorial clashes.

The frequency with which other swans were audible or visible in the area seemed to be greater (1·16 per hour) after hatching, with an apparent increase in the frequency of aggressive display by parents. The roles of male and female parent in defence were not as distinct as during incubation but the male usually performed more aerial displays and chases (Table 3). Only he was involved in physical attack; only the female ever responded by hiding. A typical interaction

Table 3. Frequency of reactions per hour to other swans (DQ)

	Incubation		After hatching	
	Male	Female	Male	Female
Hiding	0·03	0·07	0·00	0·05
Looking alert	0·15	0·18	0·39	0·38
Display	0·16	0·07	0·47	0·43
Aerial display or chase	0·18	0·01	0·26	0·13
Physical fight	0·00	0·00	0·06	0·00

Table 4. Percentage time spent while 'feeding' in other activities

Pair	Trampling		Vigilant posture		Sample
	male	female	male	female	
DQ	26·0	24·7	17·8	15·7	13
HA	27·2	24·6	23·5	21·5	8
HS	22·5	27·7	23·5	19·3	6

might begin with the parents responding to a neighbour's territorial survey flight with display, the cygnets bunching together beneath their parents' outspread wings. The male might then take off in pursuit while the female led the cygnets to the shore. Only once did both parents become involved in aerial battle and the cygnets were left together on open water. No encounters between families and predators were observed.

Cygnets follow parents more often than vice versa, but this difference might decrease with time (Table 5a). Also, cygnets both approach and leave their parents more often than parents approach or leave them, indicating that parents are in attendance while the cygnets are making exploratory forays when feeding. Paternal and maternal relations with the cygnets were most distinct in DQ and HS, the cygnets being followed by and following the female more frequently than the male (Table 5b). In HS there was also a tendency for the cygnets to keep closer to the female.

Conflict between siblings in the form of bill-wrestling was observed in the first three days. These conflicts became progressively more one-sided, until the wrestling stage was rapidly followed by prolonged chases of one cygnet by another. Inability to recognize individual cygnets made it impossible to discover whether a dominance order was established.

Environmental Factors

Copulation and nest initiation are only possible once there is open water and suitable nest sites are snow free. Late springs resulting in reduced clutch sizes have a significant effect on productivity (Lensink 1974). Furthermore in this study it became clear that bad weather during incubation could influence bout lengths of sitting by the female. It also apparently affected the passage of other swans in the area and so perhaps influenced the frequency of defence necessary by parent birds. The abundance of insects on which newly-hatched cygnets feed was clearly weather-dependent. At the end of the breeding season the timing of the freeze-up is crucial for the survival of the cygnets and is a period of high mortality (A. Helmericks, pers. com.), but this is also partly related to the relative maturity of the cygnets at this time which in turn relates to spring conditions.

Predators commonly responsible for mortality of swans on the Yukon/Kuskokwim delta include foxes, mink *Mustela vison*, gulls *Larus* spp. and humans. Observations suggested that in normal circumstances none of the first three would be successful against a defending parent but parents are occasionally induced to leave the eggs or young. This might be due to interference by other swans or humans, or lack of experience and synchrony between the parents. The overall impression is that failure due to predation is small.

Comparison with captive pairs

Despite the small number of breeding pairs of Whistling and Bewick's *Cygnus columbianus bewickii* Swans watched either in captivity (Evans 1975, 1977) or in the wild, parental roles appear similar in both situations. In captivity, the male likewise spent less time on the nest than the female during incubation, and after hatching showed more aggressive display. Bewick's cygnets were also found to interact more with the female (both following and being followed by her). Bout lengths of incubation were shorter in captivity and the female maintained closer contact with the cygnets. It is possible that the first difference is associated with the short distance to the feeding area (with super-abundant food) and the continual proximity of the captive male to the nest.

Discussion

In all birds, parental investment functions to ensure the development of the eggs to

Table 5. Leader/follower relationships (Frequency per hour)

Pair	5(a) Cygnets follow parents (male, female or both)	Parents follow cygnets	5(b) Cygnets follow male only	Cygnets follow female only	Cygnets are followed by male only	Cygnets are followed by female only
DQ	25·8	3·6	8·4	13·2	1·2	2·4
HA	25·2	1·2	12·0	10·2	0·0	1·2
HS	24·6	4·2	7·2	12·0	1·2	3·0

hatching and the survival of the young to fledging. Behaviour identified in this study as parental care included incubation (sitting on the eggs and turning them), nest-building and maintenance, trampling, brooding, vigilance, hiding, defensive display and territoriality, but the relative importance of each in terms of costs to parents and benefits to cygnets could only be inferred. However, especially after hatching, the frequency of interaction with neighbouring pairs, and the necessity for territorial defence, which may be costly, plus the increase in trampling to 20% of the time spent feeding, indicate that parental care at this time is particularly related to protection against intraspecific competition and to ensuring an adequate food supply for the young.

The relative importance of the male's role in swans and geese is difficult to evaluate except in relation to its absence in ducks. The ecological significance of this difference between the two groups may lie in differing levels of intraspecific competition: the continued presence of the male appears to be necessary in anserines to ensure adequate food for the young. Studies of wintering geese and swans suggest that at this time too, the male plays an important part in protecting the young from feeding competition with other adults, and in establishing their social rank within the flock (Raveling 1970; DS, unpub. data). The relative importance of the male's role in protection against nest predators seems more doubtful (Maynard-Smith 1977).

In monogamous species, parental investment should take the form of equality in amount of parental care by male and female (Trivers 1972). Examples of this are common among birds, especially where parents feed their offspring directly. But Trivers has also suggested on the basis of studies by Kluijver (1933) and Verner and Wilson (1969) on passerines, where males were found to incubate less than females, that in some monogamous species the male is actually doing less. The study described here suggests that division of labour may be more important than is superficially apparent.

The results show a clear difference in the nature of parental roles during incubation which is maintained to a lesser extent after hatching. The female is mostly concerned with maintaining the correct nest conditions for egg development, spending more time sitting, while the male is responsible for defence, and covering the eggs while the female is off. After hatching the only separation is in frequency and type of defence display (the male) and in brooding (the female). Other aspects of parental care are shared equally.

Parental roles are thus similar to those in geese (Ewaschuk & Boag 1972; Lazarus & Inglis, in press) though are less distinct. The most marked difference is that in these swans the male may sit on the nest. In the other northern swans (Trumpeter *Cygnus c. buccinator* and Whooper *C. c. cygnus*) males do not take part. It is possible that levels of territorial defence can be lower in Whistling and Bewick's Swans and that this allows males to spend more time on the nest while the female is off feeding. In addition, his participation may allow faster development of the eggs. Speed of development in these large birds is at a premium due to the short duration of the arctic summer (see Kear 1970; Lack 1968).

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Summary

This paper describes a study of the behaviour of wild Whistling Swans *Cygnus columbianus columbianus* on their breeding grounds on the Yukon-Kuskokwim delta, Alaska, from May to July 1976. There was a separation of roles of male and female parents during incubation: the female was mainly responsible for incubation, the male for defence. This difference largely disappeared after hatching and subsequent parental care was more equally shared. These results are compared with studies on captive pairs. Observations on non-breeding birds and some of the important environmental influences on the swans during the breeding season are described.

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At the opposite end of the range of the Whistling Swan *Cygnus c. columbianus*, on the wintering grounds in Chesapeake Bay, Maryland, a flock is baited into a trap for ringing. (*Philippa Scott*).