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Preflight Signalling in Swans:
A Mechanism for Group Cohesion and Flock Formation

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With 3 figures

Abstract

The preflight behaviour of whooper swans *Cygnus cygnus* and Bewick's swans *Cygnus columbianus bewickii* was examined to determine the adaptive significance of the ritual. Analysis of the preflight sequence revealed that the rate of signalling became significantly faster as the time of take-off approached. This provides the first quantitative evidence that a threshold of excitability is responsible for triggering synchronised flight in social units. Two ultimate and two proximate factors that affect this threshold were uncovered. They are: 1) Maintaining proximity to partners — flight was delayed by birds with non-attentive mates and signalling lasted on average four times longer than those whose mates showed more interest. 2) Maintaining flock cohesiveness — birds which performed signals for longer periods while swimming among uninterested birds were successful in attracting followers 61 % of the time. 3) The bird's feeding performance related to dominance status — less successful feeders (potentially hungry birds), flew after little time and few signals. 4) The type of feeding opportunity at the eventual destination — birds which flew to provided feeds (nutritious barley) spent less time performing preflight signals than when they flew to forage on grass fields.

Introduction

This paper deals with the description and function of the ritualised head and neck movements which are performed by northern swans prior to take-off. The investigation was carried out from the premise that ritualised signals have co-

evolved through the manipulation of conspecific behaviour by the sender of signals and through detecting the intentions by the reactors to signals, e.g. the mind-readers (KREBS & DAWKINS 1984).

Two descriptive studies of the visual signals that Canada geese *Branta canadensis* perform prior to locomotion suggest that the function of pre-locomotor signalling is to keep mates and progeny from becoming separated (RAVELING 1969; BLACK & BARROW 1985). There are numerous energetic and social benefits in maintaining family association in large waterfowl (SCOTT 1980 a; BLACK & OWEN 1984; 1988 a, b). Continual and long-term association with the same mate yield selective advantages for geese and swans since a substantial reduction in lifetime reproductive success is realised if re-pairing occurs (OWEN et al. 1987; SCOTT, in press).

In addition to manipulating a mate, KREBS & DAWKINS (1984) suggest that visual signals may have evolved for an equally selfish reason; that of manipulating other flock members for individual gain. Given that an individual is at less risk of predation when in a group of neighbours and that food finding and exploitation can be more efficient in flocks (PERRINS & BIRKHEAD 1983; PULLIMAN & CARACO 1984), flock members may benefit by watching others' preflight movements and decide whether or not to follow. Some birds may be more at risk than others given their social and energetic states and would therefore benefit more from a flock situation. In goose flocks an individual's ability in obtaining the best food is related to its dominance rank according to social class; single, pair or family member (BLACK & OWEN 1988 b). In swans dominant birds feed for longer periods (SCOTT 1980 b; BLACK & REES 1984).

When partners perform preflight movements in rapid succession it has been assumed that take-off will result as soon as a threshold of excitement is reached (RAVELING 1969). It is also thought that different partners may exercise varying degrees of leadership in this ritual (RAVELING 1969; REES 1987). In order to discover the mechanism and reasons for the evolution of the swan's preflight ritual and how it might be effective in manipulating pair, family and flock members I observed the behaviour in whooper swans *Cygnus cygnus* and Bewick's swans *Cygnus columbianus bewickii* under different feeding regimes. These species are ideal subjects for studying visual signals because of their exaggerated movements and vocalisations and because they readily frequent baited ponds where observations can be made at close quarters.

Methods

The swans were observed at the Caerlaverock Wildfowl Refuge, Scotland. The flock has been encouraged to visit the reserve since 1979 by a daily provision of barley. A ringing programme that used individually coded leg bands was also initiated at this time (BLACK & REES 1984). During this study between 20—40 kg of barley was provided at 08.30 and 14.00 h on one pond and 16.30 h on another. The food was thrown from a barrow along a 50—100 m length of the pond's edge. Two or three weeks after the swans' arrival they became accustomed to the regime and flew onto the ponds up to 2 h before the feeding time and floated on the water in front of the gate where the barrow was wheeled. Depending on the number of birds on the pond (between 50 and 200), and the amount

provided, it took between 40—90 min before the food was eaten. All the birds' rings were recorded each day; the majority of the individuals were present for the entire season between October and April (BLACK & REES 1984).

Flocks were scanned for preflight sessions after the scheduled feeds using a tally counter and a stop watch. A swan needed a runway on which to run and flap its wings to get enough lift for flight. The usual situation on the pond was for a signalling bird or birds to swim to the far end of the pond which was free of loafing or feeding flock members. At other times birds would climb out of the water and walk some distance on land before they turned, facing the wind, to take-off. Some signalling also occurred by birds which swam into a group of loafing neighbours but flight did not commence until birds had enough room to physically take-off. The following aspects were recorded during as many sessions as possible for two winter seasons: the signaller's ring number and social class, the identity of a mate and cygnets, the number of head and neck movements performed by each, position relative to other flock members, the initiator of signalling, the initiator of flight, the time elapsed before the mate and neighbours joined the sequence, the order of departure, the date, and the destination of the flight. Preflight sequences began with the first head movement and ended when the swan crouched and opened its wings prior to running and taking flight. Some sequences were recorded on a cassette tape and later transferred to an event recorder to analyse the frequency of various types of movements and to record which individual was performing the signals. In order to ensure independence of data, duplicate sequences from the same individuals in the same situations were averaged. Often swans which left the pond formed a group with other units which made it more difficult to examine the factors that influence preflight behaviour. Therefore, most analyses were performed on discrete unit departures of singles, pairs and families. Data was also collected on unringed birds that were identifiable by unique facial characteristics (REES 1981).

The majority of preflight movements consist of a single upward thrust of the head (headbobs) until it could be raised no further; the movement ended with the head held in its highest upright position. The only difference between the species is that Bewick's swans sometimes had a bouncier culmination of the final rising of the head to its upright position giving the appearance of one and a half headbobs movements. Apart from this slight difference in display there were no other differences between the species' preflight behaviour; the rate and duration of signalling were not statistically different. Thus, data from the two species was combined to increase sample sizes where applicable.

After the food was dispensed, individual performance (of whooper swans only) in feeding was measured by recording the frequency of aggressive interactions and the time spent feeding during 5 min continuous watches. Only those threat/attacks which caused a subordinate to turn its head or flee to a new area were recorded. Since I was interested to determine how feeding performance affected flight and preflight behaviour, birds which did not take part of the provided food were not included in the analysis.

Spearman rank correlation (SRC), Mann-Whitney U test (MWU), binomial and chi square tests were used (two tailed tests) (SIEGEL 1956).

Results

Preflight Movements

The movements that occur during a preflight sequence include head-bobbing — a vertical movement of the head and neck, head-shaking — a lateral movement, and wing-flapping (JOHNSGARD 1965; SCOTT 1978; BRAZIL 1981). Head-bobs made up 91.5 %, head-shakes 7.8 % and wing-flaps 0.6 % of the movements given during preflight sequences (N = 60 pairs and family sequences, 3939 movements). Head-bobbing occurred in 100 % of the sequences; head-shakes in 81 % and wing-flaps in only 23 %. The frequency of head-bobs and head-shakes were positively correlated (SRC, rs = 0.51, t = 4.48, df = 58, p < 0.001). Head-bobbing and wing-flapping were not correlated in this manner (SRC, rs = 0.11, t
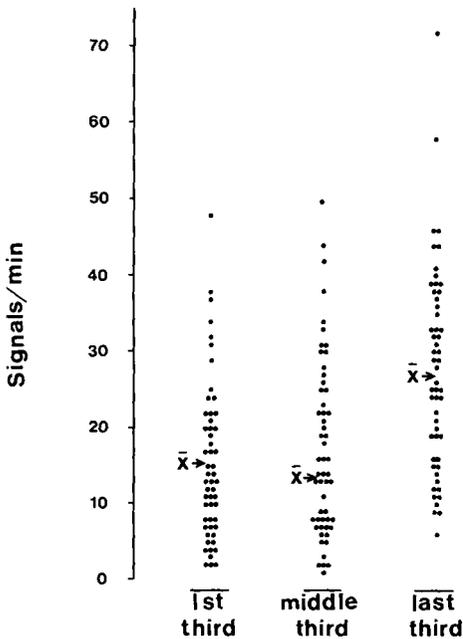
Fig. 1: Rate of signalling in the first, second and last thirds of preflight sequences

= 0.81, df = 58, ns). I therefore assumed that head-bobbing was the primary movement, head-shaking was a secondary but significant movement and wing-flapping was not a contributor to the signalling process. Wing-flapping was, therefore, not included in the remaining analyses.

Head-bobbing was performed with varying intensities; shallow and deep neck dips and moderate and extreme head raising. The movement may also serve as a contact signal (SCOTT 1978). In this study I distinguished a preflight head-bob from other types by the distinct four syllabic vocalisation which accompanied each raising of the head. Both the movements and the loudness of the calls became. more exaggerated as the end of sequence approached. The call changed when flight was initiated to a more high pitched sound.

Preflight Mechanism

The number of preflight signals increased with the length of the sequence (SRC, rs = 0.78, t = 9.8, df = 61 pair data, p < 0.001). In 93 % of the preflight sequences the bird which performed the most signals also initiated flight (binomial test, N = 71 pair and family data, p < 0.001). The individual which initiated signalling also initiated flight more than a chance effect would permit; in 60 out of 88 cases the initiator of signalling and flight were the same (binomial test, p < 0.001). There was no significant tendency for one of the sexes to initiate more of the flights (females 40, males 59) or to perform more signals (females 36, males 40); there was no sex ratio bias in the flock (BLACK & REES 1984). Parents, however, initiated significantly more flights than cygnets even though there were fewer parents in the flock (binomial test, N = 41, x = 9, p < 0.001).

Fig. 2: Mean signal frequency during the mi-
nute prior to flight for 11 pairs; bars indicate
SE
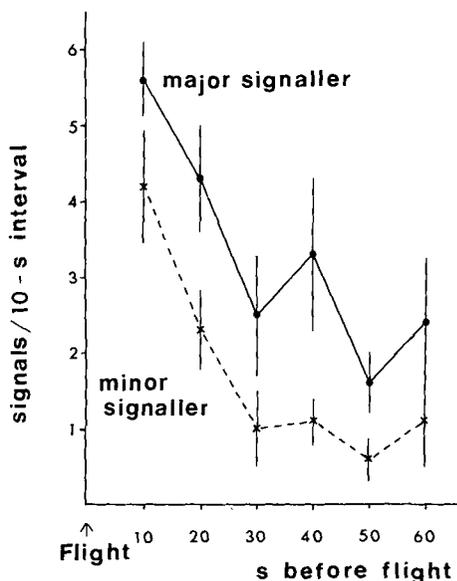
Threshold of Excitability Concept

Flight was triggered neither after a specific number of signals nor after a certain length of time. The number of signals for all classes ranged between 0 and 687 prior to flight and sequences lasted between 0 and 42.2 min. To investigate whether take-off was triggered by a certain rate of signalling I divided 54 sequences from pairs and families, that had more than 25 signals in them, into first, second and last thirds. If a threshold of excitability exists it would be expected that the period closest to take-off would have the highest rate of signals. Fig. 1 depicts the results. The rate of signals in the first and second thirds was not significantly different from each other (first mean 15.5 signals/min, SE 1.4; second mean 13.5, SE 3.3) (MWU, $z = 0.64$, ns). The last third contained significantly more signals per min than either the first or second third (last mean 26.7 signals/min, SE 1.7) (MWU, first vs third $z = 4.96$, $p < 0.001$; second vs third $z = 4.27$, $p < 0.001$). Fig. 2 shows that the rate of signalling increases rapidly from about 30 s before take-off. The figure also shows that although one member of a pair performs more signals both members increase their signalling simultaneously. However, the actual rate of signalling that triggered take-off differed with various social and ecological situations (see below).

Manipulating Pair and Family Members

Many preflight sequences were abandoned to other activities such as resumed preening or feeding. This usually occurred when only one member of a pair or family was performing signals while the other was engaged in the other activity. Single birds performed fewer signals and left quicker than birds with

Table 1: Preflight data for different classed birds according to their partners' attentiveness. SE in parentheses

Class/ type	Duration (s)	No. of signals	Sample sizes
Singles[a])	32.5 (7.0)	2.7 (0.5)	24
Pairs with attentive mate	100.9 (9.4)	35.4 (5.2)	36
Pairs with inattentive mate	445.0 (66.1)	95.3 (12.4)	18
Parent with attentive mate	106.6 (18.1)	31.0 (3.8)	20
Parent with inattentive mate	589.5 (155.5)	174.3 (74.1)	6
Cygnet with inattentive parent	317.1 (55.4)	69.9 (10.6)	14

[a]) Data excludes cases of neighbour pulling. All data excludes first leavers (see text).

mates (Table 1); on four occasions they flew without performing any preflight signals. From these observations it seemed possible that preflight signalling functioned in synchronising take-off and thus reducing the risks of pair separation. This hypothesis was tested by comparing the time till take-off when the sequence was initiated by both members of a pair and when it was not. In this comparison pairs were considered to start their preflight sequence together when a mate performed at least one preflight signal or if it swam or walked with the signalling mate while it maintained an alert posture, rather than continuing its previous activity within 55 s of the partner's first signal.

Pairs that started the preflight sequence together left more than four times faster than when the mate was not attentive from the start (Table 1). This difference is highly significant (MWU, pair-data, $n_1 = 36$, $n_2 = 18$, $z = 5.71$, $p < 0.001$) (MWU, parent-data, $n_1 = 20$, $n_2 = 6$, $z = 3.34$, $p < 0.01$). When a mate performed signals alone it either remained close to the loafing mate or temporarily joined other signalling birds. Birds which started the sequence without their mates performed more than twice as many signals as those which were signalling with the mate's cooperation. This difference is also highly significant (MWU, pair-data, $n_1 = 36$, $n_2 = 18$, $z = 4.49$, $p < 0.001$).

Because there was no significant difference between pair and family preflight duration or the number of signals (MWU, $n_1 = 36$, $n_2 = 20$, duration $z = 0.10$, ns, signals $z = 0.08$, ns) it appeared that an attempt at synchronising flight in this study was between mates rather than between parents and offspring. If parents initiated a preflight sequence their take-off was determined by the mate's attentiveness rather than by the offsprings. Cygnets on the other hand rarely initiated flights but continued signalling until their parents joined the sequence.

Fig. 3: Frequency of first departures in relation to the amount of food potentially available per swan
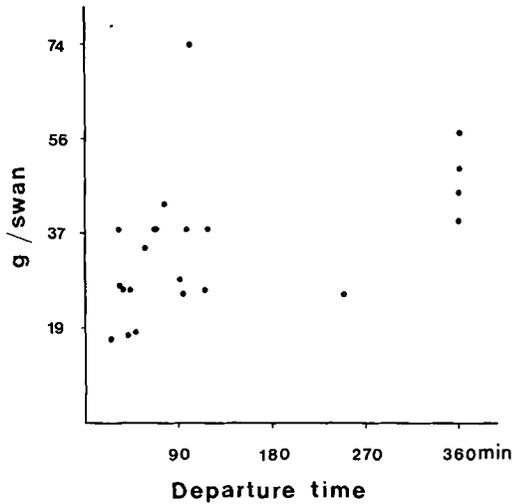
Preflight Signalling and Destination

Because the birds consistently flew to a pond before the provided feeds it seemed apparent that they were aware of the feeding schedule on both sites. I expected that signalling investment would be less when preparing to fly to a predictable site (a provisioned feed) than it would be if they were about to fly to a site of which they had less experience and/or which was less "safe" and nutritious (grass fields). This was tested by comparing the sequences prior to flights to non-refuge areas (flights of 5—20 min away) and flights from one refuge pond to another where food was about to be provided. The result was as predicted. Preflight sequences took on average 3 min longer before flying to non-refuge sites (pair begin with mate data, mean 4.9 min, N = 10, SE 1.4) than to a provided feed on the refuge (mean 1.7 min, N = 36, SE 0.2). This difference is statistically significant (MWU, z = 2.78, p < 0.006). In addition pairs performed significantly more signals prior to flying off the refuge than to a provided feed (flying far mean 93.6, N = 10, SE 19.0; flying to feed mean 35.4, N = 36, SE 5.2) (MWU, z = 3.16, p < 0.002).

Effect of Dominance Relationships and Feeding Performance

Flight from the pond normally occurred after all the grain was eaten and after the birds had rested or preened on the pond banks (BLACK & REES 1984). The time of the first flight was significantly correlated to the amount of food that was put out per bird (SRC, rs = 0.52, t = 2.64, df = 19, p < 0.02, Fig. 3). This suggests that although all birds acquired enough grain to afford time to rest or preen, flight from the pond was related to a bird's relative success at obtaining food, i.e. their hunger after a period of not feeding. SCOTT (1978; 1980 b) established in a similar artificial feeding regime that a dominance rank order exists between different classed swans; families rank highest, then pairs, then singles. In

Table 2:   Outcome of aggressive conflicts during provided feeding periods for different classed birds
and mean number of days birds were in attendance at the·site. SE in parentheses

Class	Displaced others per 5 min	Displaced by others per 5 min	% time feeding	Attendance (mean days)
Single adults N = 13	3.4 (0.88)	5.5 (0.68)	89.0 (0.01)	48.5 (11.71)
Paired adults N = 12	6.7 (2.01)	3.5 (0.92)	90.5 (0.02)	70.9 (5.15)
Family cygnets N = 9	5.3 (0.94)	4.0 (1.21)	82.6 (0.05)	73.3 (2.85)
Family adults N = 8	8.1 (2.52)	3.3 (1.06)	76.0 (0.07)	60.3 (5.32)

a comparison between species BLACK & REES (1984) showed that a larger propor-
tion of the dominant whooper swans continued to eat provided food until it was
gone, whereas the Bewick's swans and mute swans *Cygnus olor* gave up sooner.
Thus, the following analyses were on whooper swan data only.

Table 2 lists the feeding competition results from the 5-min continuous
watches for different classed birds. Single birds were displaced significantly more
than pair and family adults (MWU, $n_1 = 13$, $n_2 = 20$, U = 63.5, p < 0.05). The
time that birds actually fed was inversely proportional to the number of displace-
ments they suffered (SRC, rs = -0.38, t = -2.63, df = 40, p < 0.02) as well as
to the number of threats they performed at others (SRC, rs = -0.35, t = -2.36,
df = 40, p < 0.05). However, since each threat resulted in a displacement the
birds that performed threats and which were infrequently displaced monopolised
the same patch of usually dense grain, whereas, subordinate birds tended to be
pushed to areas of less dense grain. Food intake was measured by counting the
time it took for birds to pick up 50·grains from the ground. In areas of dense
grains swans picked up 92.9 grains/min (SE 1.7, N = 10), in intermediate areas
58.5 grains/min (SE 3.5, N = 10) and less dense areas 40.6 grains/min (SE 1.9, N
= 10). It can therefore be assumed that the birds that were displaced more
acquired less food due to lower grain density and time lost feeding.

In addition SCOTT (1978) found that late arrivals to the wintering site were
less likely to achieve dominance and that dominance was related to the time that
birds spent in the area where food was dispensed. I tested this by looking at birds
on 14—15 January (about the 107th day of the season) which had been on the
study site for more and less than 70 days. In this comparison birds which had
more experience of the site suffered fewer displacements (mean 1.9 displacements
per 5 min. SE 1.0 compared to 4.4 displacements SE 0.9) and fed longer (mean
92.1 % SE 1.7 % compared to 77.6 % s SE 6.0 %) (MWU, $n_1 = 9$, $n_2 = 10$
displacements, U = 20, p < 0.05; feeding time, U = 19.5, p < 0.05).

In review, less successful feeders in this study tended to be unpaired
individuals and birds with less experience of the site. If departure from the site

Table 3: Who joined whom in preflight signalling sequences and the percentage of flights that each
class left alone, joined others and attempted neighbour pulling

Departure status	Singles	Pairs	Families
Left alone	69	84	76
Joined singles	8	2	2
Joined pair	32	30	1
Joined family	4	11	1
Joined group	15	43	3
Total[a])	132	203	98
% left alone	52 %	41 %	78 %
% joined others	45 %	42 %	7 %
% of attempted	44 %	63 %	6 %
neighbour-pulling	(N = 18)	(N = 32)	(N = 16)

[a]) Total includes flights alone and flights when others joined and when others were joined.

was related to feeding performance (i.e. hunger) these bird categories should predominate among the first leavers. I determined the identity of 27 individuals which were the first birds to leave the pond on different occasions. In only five cases (N = 27) did good feeders and/or birds which were well established at the site fly from the pond first (binomial test, p = 0.002). The other swans that left first were identified as new to the site (less than 10 days), low ranking in aggressive encounters and/or poor feeders. It should be stated that some birds, not included in the analysis, did not attempt to feed on the dispensed grain probably because they were not used to the regime. They seemed not to be willing to afford time to rest and preen with the others, rather they left the pond with very little interaction. These non-feeders are considered in the discussion.

Manipulating Flock Members

When signallers swam into a group of loafing neighbours they were postponing their departure since flight was normally only possible from a "clear" runway. Since they continued to perform signals it appeared that they were attempting to induce others to follow. I tested the effectiveness of these "neighbour pulling" attempts by recording if any flock members joined the signaller on the runway. Birds were considered as having joined a session if they followed the signaller(s) to the runway, maintained alert head-up postures and especially if they too performed signals. Because of the confounding effect of different departure tendencies between species the data was limited to whooper swans.

Neighbour pulling was successful in attracting followers in 61 % of 31 attempts compared to only 35 % when the behaviour was not employed (N = 37). This difference is statistically significant (χ^2 = 4.63, df = 1, p < 0.05). It can therefore be assumed that preflight signalling does affect the behaviour of flock members.

Large group departure was not uncommon during this study. If joining another unit or investing in getting others to join a group is adaptive, in terms of benefits from flock foraging, I would expect the first birds to leave a site to put more effort into preflight signalling (when they were preparing to fly to the same location — in this test — to a predictable site). Table 3 lists the frequency that different classed birds left alone, joined others and attempted neighbour pulling. Several things are notable in this table. Singles, which tend to be less successful feeders, were rarely joined by other classes (binomial test, p < 0.001). The frequency with which the different classes attempted neighbour pulling varied significantly (χ^2 = 13.6, df = 2, p < 0.01); families made the least and pairs the most attempts. Families flew significantly more times alone than when they joined others (binomial test, p < 0.001). It was my impression that families were able to leave without others by attacking would-be followers or they would simply walk away from the pond out of view from the flock before take off. The implications of these findings are discussed below.

All of the swans in the study area attended the provided feeds, so when the first birds left the pond they had no other flocks to join. They were, in effect, initiating a new flock and were, therefore, taking the greatest risks. Pairs which left first signalled for significantly longer before taking off (10.1 min, N = 6, SE 3.7) than those which followed others (1.7 min, N = 36, SE 0.2) (MWU, z = 2.19, p = 0.03).

Neighbour pulling attempts were usually performed by the first birds to leave after a feed. I tested if preflight sequences which involved neighbour pulling attempts were significantly longer than those without. Single birds had no mate with which to synchronise take-off so the preflight signals and calls they gave near uninterested neighbours could only be intended for flock members. In sequences with neighbour pulling attempts singles took on average 4.5 min (N = 14, SE 1.1) to leave the pond which is significantly longer than when they left without mingling with others (mean 0.54 min, N = 24, SE 0.1). This difference is statistically significant (MWU, n_1 = 14, n_2 = 24, z = 4.82, p < 0.001). Singles also performed significantly more signals during sequences with neighbour pulling attempts (mean 29.9 signals, SE 6.2 with neighbour pulling; mean 2.7, SE 0.5 signals without neighbour pulling, MWU, z = 5.1, p < 0.001). Furthermore, when single birds joined a group they invested significantly more time and effort in preflight than when they left on their own (singles in a group N = 24: mean time 2.2 min, SE 0.3, mean signals 14.7, SE 2.4; singles' lone departure means in Table 1) (MWU, time comparison z = 4.71, p < 0.001; signal comparison z = 4.34, p < 0.001). Unlike the preflight behaviour of pair and family units, group members sometimes left before all members were ready. It was not uncommon for a group of twenty birds to be performing signals after which only a discrete unit (a single or pair) flew, leaving the rest of the group to continue signalling.

Discussion

I have shown that at the end of a preflight sequence the rate of signalling becomes more rapid. Within pairs, signalling is increased simultaneously by both

members in the last 30 seconds before take-off. This provides the first quantitative evidence that a threshold of excitability exists as the mechanism for triggering synchronised flight. But why has such a mechanism evolved and what influences the threshold? In this study four factors that affect preflight behaviour have been uncovered. They are the mate's attentiveness, the effort or need to maintain flock cohesiveness through manipulating flock members, a bird's energetic state relating to dominance status and the eventual destination of the signaller.

The fact that the initiators of preflight sequences invest in substantially more signals and wait until the mate joins them before flying indicates how swans are able to maintain continual proximity to mates; a mating system in which partners benefit from mate protection, increased feeding success and offspring care (SCOTT 1980 a; BLACK & OWEN 1987; 1988 a, b). In other monogamous birds which do not maintain continuous proximity to mates no preflight intentions have evolved so the burden of maintaining contact lies on one or other of the sexes to follow its mate soon after it leaves (TEACHER & ROBERTSON 1986; GOWATY & PLISSNER 1987). In the present study the longest preflight session that was recorded was for a family of Bewick's swans, initiated by the female when her mate and two of the three cygnets were sleeping. After 680 preflight signals and 42 min the mate finally stood up and gave three head-bobs after which the family left together. This shows the extent to which these swans will go to synchronise flight. During this study period I observed only three cases of a partner flying without its mate. In one of these cases the mate immediately ran in the direction of the mate's departure and took off giving distress calls. In the other situations the birds immediately returned if a mate did not follow. Besides the risk of becoming separated, the fact that take-off and flight are energetically expensive for the large bodied swan may act in reducing such mistakes in leaving before a mate is ready.

If a mate is unwilling to leave a site the only way it is able to influence a displaying partner is not to follow or join the sequence. This strategy is risky only if the mate's degree of attachment is misjudged. In the kittiwake *Rissa tridactyla* calls and postures have evolved that serve to control or extinguish a partner's flight intentions (DANIELS et al. 1984). Such specialised counter measures have probably developed to deal specifically with the fact that kittiwakes do not maintain continuous proximity to mates, and thus may not be as aware of a mate's fidelity, as well as with the dynamics of cliff-nesting. I suggest that the evolution of ritualised signals in long lived species that stay together continuously, like swans, are closely linked with a pair's mutual experience. REES (1987) showed that members of established pair-bonds each performed similar preflight signalling rates, whereas, the rate for newly paired birds was less proportionate.

However, if selection acted only on an individual's success in attracting the attention of a mate in the development of the preflight ritual such dramatic movements of the head and neck and vocalisations would probably have been reduced or nonexistent. KREBS & DAWKINS (1984) suggest that "cooperative communication, in which manipulator (the sender of signals) and mind-reader (the reactor to signals) roles share a common interest (such as a pair's reproductive success), should lead to cost-minimising, muted signals . . ." The other factors which appear to influence preflight behaviour and which were probably favoured

by selection in its development may best be discussed under three categories using the approximate terminology of KREBS & DAWKINS (1984).

Active manipulator is a bird which actively attempts to attract flock members to its preflight sequence. This may be done by either performing the ritualised movements and calls for extended periods, as in the case of the first birds to leave a site (after feeding on the provided grain), or by postponing departure and swimming into a flock of uninterested swans while performing signals, e.g. neighbour pulling. It was shown that extended signalling and neighbour pulling were successful in attracting others to join. In house sparrow flocks *Passer domesticus* departure from foraging flocks was thought to be a result of reduced feeding rates due to subordinates being supplanted to less dense patches (BAR-NARD 1980). This was the case in this study where feeding competition was high and food was limited. Each time a bird lost an encounter it was pushed to less dense grain where feeding rates were lower. As a result first leavers were found to be unpaired birds and those with lower attendance at the site. These categories are linked with low success in encounters and poorer feeding performance.

EVANS (1982) found that the contact call performed by black-billed gulls *Larus bulleri* were effective in attracting flock members to follow and that birds initiating a departure performed more calls than the followers. This is consistent with my findings in that first birds performed significantly more signals than subsequently departing birds and that birds which performed signals while near other flock members successfully attracted them to join them in the preflight process. I agree with EVANS' suggestion that such a strategy probably functions in maintaining or establishing a flock for benefits in group foraging (see BRAZIL 1981).

But if feeding success is related to dominance why do poorer feeders attract others who would compete with them? This can be approached from two directions. First leavers (poorer feeders) may invest in attracting others to follow because their main food source is highly divisible. The swans in this study fed almost entirely on grass fields when they were not on the provisioned site (BLACK & REES 1984). According to ELGAR (1986) sparrows which were feeding on divisible foods (bread crumbs) attempted to attract others to the site whereas those which fed on non-divisible food items (one piece of bread) did not. Assuming that swans benefit from flock foraging and that a field of grass is a highly divisible food then it would not be ill-adaptive for first leavers to try and attract others to follow. In fact, this may be why the investment in attracting followers to grass fields is greater than it is to less divisible food items at the provided feeds; aggression is higher when swans feed on barley than on grass (BLACK & REES 1984).

Alternatively, the first leavers' degree of hunger may not have been high enough to warrant lone departure and thus feeding alone. If the birds mentioned earlier which did not acquire any food during the provided feeds are included in the departure analysis they would be categorised as extremely poor feeders. These birds performed very few signals (sometimes no signals) and never attempted neighbour pulling prior to leaving. In their case it may have been more adaptive to quickly find another food source where competition was less daunting than it was

to maintain a flock situation. The criterion, however, for first leavers in this study was that a bird had to take part in the provided food and loaf on site for a time before departing. For these birds, therefore, it was probably less risky to continue to compete in a flock since their hunger was at least partially satisfied. The hunger hypothesis may provide an additional explanation why such a high percentage of first leavers were singles (48 %) and why they left with the least preflight investment of all classes.

The second category, *active mind-readers*, are birds which join and follow signallers which have already initiated a preflight sequence. The identity of this category has yet to be fully uncovered but the available data suggests that they are made up of poorer and intermediate feeders. Table 3 shows that 45 % and 42 % of singles and pairs, respectively, join flock members prior to departure, whereas the more successful food competitors, the families, tend to leave alone and make few neighbour pulling attempts. It was shown that single birds invested more in preflight signals when they joined a group departure. Presumably birds which allow others to join them or which try to attract others have little to lose and something to gain by maintaining a flock situation. In the "information centre" theory debate it has been hypothesised that the subordinates are the mind-readers of the good feeders' intentions (WEATHERHEAD 1987). If this is the case then why do not singles try to follow families which are known to be good feeders?

This brings us to the third category of *unwilling victims*. It appears that families try not to attract others by performing their preflight signals away from flock members and by threatening would-be followers. By adopting these counter measures families usually fly on their own (78 %). They presumably would not benefit as much from decreased vigilance and increased feeding inherent in a flock situation. Data recently obtained on the composition of whooper swan flocks in an international census (SALMON & BLACK 1986) confirmed that there is a tendency for families to be in small flocks often as discrete units whereas singles and pairs tend to be in larger flocks (HEWSON 1964; BRAZIL 1981).

Another assumption in the "information centre" theory (WARD & ZAHAVI 1973) is that followers act as if they realise that leaders know in advance that they are going to a good food source. In this study I show that swans changed their preflight behaviour according to where they went. If they were going to a known food source of good quality (a provided feed) the number of signals and the time till take-off were significantly less than in those sequences prior to flights destined for a less profitable site, suggesting that destination was known prior to take-off. Besides a known food situation this finding could have been related to the distance of flight and/or the relative predictability of whether other flock members were or would be present at the new site.

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