The behaviour of Bewick's Swans at the Welney Wildfowl Refuge, Norfolk, and on the surrounding fens: a comparison

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Introduction

Studies of the social behaviour of individual wild animals are frequently made at provisioned sites, where the animals are easily observed (e.g. McHugh 1958; Sabine 1959; Kikkawa 1961; Sade 1967; Van Lawick-Goodall 1968; Hrdy 1977; Kurland 1977). However, it is seldom possible to assess the effects of the 'artificiality' of such sites by studying behaviour in more natural situations as well (but see Grant 1973; Clutton-Brock *et al.* 1976). In this paper, the behaviour of wintering Bewick's Swans *Cygnus columbianus bewickii* at the Welney Wildfowl Refuge, on the Ouse Washes, Norfolk, where the swans are fed, is compared with their behaviour on surrounding fenland, and on flooded meadows in the vicinity. In particular, the following variables are investigated, flock sizes, daily activities, flock densities, interaction frequencies, dominance relationships between individuals, parent-offspring relationships, mortality and breeding success. To assist the comparison, some fen data from the work of others are reviewed (e.g. Cadbury 1975; Owen & Cadbury 1975). Before making this comparison, however, the general behaviour of the swans at Welney is described and compared with that observed at another feeding site at the Wildfowl Trust, Slimbridge, Glos. where wild Bewick's Swans have been studied in detail since 1964 (P. Scott 1966; Evans 1978). Here it was discovered that individuals could be recognized, both within winters and from one winter to the next, by differences in the pattern of black and yellow on the bill (P. Scott 1966). The first section of the paper thus describes flock structure, return rates, mortality and reproductive success, numbers, activities, densities, interaction frequencies and weather effects, and relates the results to those obtained at Slimbridge (Evans 1978, 1979a, b, c).

Study sites

The Ouse Washes and surrounding fens have been an important wintering ground for Bewick's swans since the 1940s (Nisbet 1955; Ogilvie 1969). At first the swans were found distributed irregularly along the marshes feeding on flooded areas in small flocks, but in 1970 when the washes were both flooded and frozen, they were first observed feeding on agricultural crops on the fens, a habit which has since continued and become widespread. The effect of this change in food habits on the distribution of the swans could not be ascertained since the situation changed further in the winter of 1971–1972, when the Wildfowl Trust began to provide grain (wheat or barley) two or three times a day (0930, 1530 and sometimes 1900 h), in front of the main observatory at the Welney Wildfowl Refuge. The refuge also provided an undisturbed roost for the birds, since access for walking and shooting was prohibited. The result was that the swan usage of the area immediately around Welney was significantly greater over 1972–1973 than in 1969–1971 (Cadbury 1975). However, during the mild winters of 1974–1975 and 1976–1977 the Washes were flooded over long periods, the roosting area in front of the observatory severely diminished, and the swans spread out again to other areas in the vicinity, so that the proportion of the Ouse Washes population at Welney was reduced. Detailed observation of the swans' behaviour were made both from the main observatory at Welney and on surrounding fenland and flooded meadows.

At the Wildfowl Trust at Slimbridge, Glos., Bewick's Swans were originally attracted in the early 1960s to the grain provided for birds in the collection, and in 1964 were lured to the small pond in front of the Director's house by the calls of some captive swans (P. Scott 1966). In 1964, 24 different individuals were identified. Subsequently, numbers increased to 626 in 1970–1971, after which there was a decline until 1978–1979, when a maximum 721 was recorded. Although at first the swans at Slimbridge roosted on the river, in more recent years they have roosted around the small pond 'Swan Lake' where they are floodlit each evening. At Welney, the birds are floodlit until 2100 h.

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Methods

In the course of this study, during the winters of 1974–1975 and 1975–1976, 583 different individuals were identified by bill pattern, drawn and named. The methods used to record and file information on individual swans have been described in detail elsewhere (P. Scott 1966; Evans 1977; D. Scott 1978b).

Individuals were classified according to age (up to 3½ years), sex and paired status. Cygnets (first winter birds) have grey plumage, while yearlings (second winter birds) retain traces of grey feathering on the head and neck. In this study all third winter birds identified had been recorded the previous winter as yearlings. Sex was estimated from body size, males being around 13% bigger than females (Evans & Kear 1978). The accuracy of such estimates was checked at Slimbridge, where individuals whose sex had been estimated were subsequently caught and examined cloacally. The accuracy for paired birds was slightly greater (95%, n = 100 paired birds from 100 different pairs) than for single individuals (78%, n = 50). Whether an individual was single (S), or had a mate (P), or a mate and cygnets (F), was usually immediately obvious or could normally be ascertained after several minutes watching. Pairs and families formed particularly coherent units during aggressive encounters involving displays (D. Scott 1978a).

To obtain basic data on flock structure, return rates and lengths of stay of different classes of individual, a register of all known individuals present was kept each day. Total numbers of swans present were recorded by making counts at hourly intervals, except during periods of observation on the fens. Although, unlike at Slimbridge, not all individuals that visited the lagoon in front of the observatory during the winter were identified, all regular visitors were known, including 200–300 birds which always came to the feeds.

To make a direct comparison of activities and interaction rates of birds in front of the observatory and on the fens, flock scan samples lasting one hour were made at 1030 h in each situation usually on alternate days. During these samples, the total number of swans, and the number engaged in different activities (standing alert, preening, sleeping swimming, feeding) were recorded at 15-minute intervals, while the number, duration and intensity of all aggressive encounters involving display (bugling and neck-stretching: see D. Scott 1978a) were recorded continuously. Such encounters rarely occurred simultaneously. Their conspicuousness, both visual and vocal, made them easy to record in this way and the only necessary equipment was a pocket tape recorder, a stop-watch and normal watch.

To investigate daily activities on the fens, for comparison with Cadbury's (1975) data, two all-day watches were kept in 1975–1976 recording in the same manner as during flock scan samples.

Comparison of flock density in the two situations was made using focal animal samples, in which one individual was followed continuously and nearest neighbours recorded. In front of the observatory, focal samples were made during feeds, and during the hour-long period before feeds when the birds were loafing. Due to the difficulty of following individuals at feeding time, samples during feeds lasted one minute, during which all interactions were recorded, and, at the end, the distance to three nearest neighbours. During loafing, the same items were recorded in samples of one minute every ten minutes, made on particular chosen individuals. This schedule allowed a rota of five swans to be observed in the following way: A was watched for one minute, then after a gap of one minute, B was watched for a minute and so on for C, D and E, and then A was found again. In an hour's session, each individual was watched for a total of five minutes. This method enabled comparison of the behaviour of different individuals in front of the observatory even though the situation was continually changing. Focal swans were chosen from all social classes (families, pairs, singles) and most were watched in five sessions each during the winter of 1975–1976.

On the fens, focal samples could not be made in this way due to the problem of finding the same bird more than once when heads were down feeding. So individuals were watched for periods of ten minutes. Thirteen known individuals were observed for two or more such samples and 42 for one. Interactions were recorded continuously during samples. At the end of each minute, activity and distance to three nearest neighbours, and distances to mates and relatives were recorded. Distances were recorded in swan lengths (s.l.) (one swan length is approximately 0·67 m). Density in flocks on the fens was also recorded by estimating nearest neighbours

Table 1. Flock composition at Welney (%)

	Paired birds with cygnets	Paired birds without cygnets	Single adults (3rd winter or older)	Second winter birds (yearlings)	Cygnets	Total number of individuals
1974–1975	11·8	53·2	13·0	8·6	13·4	184
1975–1976	19·8	44·4	11·7	4·9	19·8	285

through the flock. This was done at the beginning of a flock scan sample by making a transect in the following way: starting at one side of the flock, the distance to the nearest individual within the forward two quadrants (180°) was recorded (Figure 1).

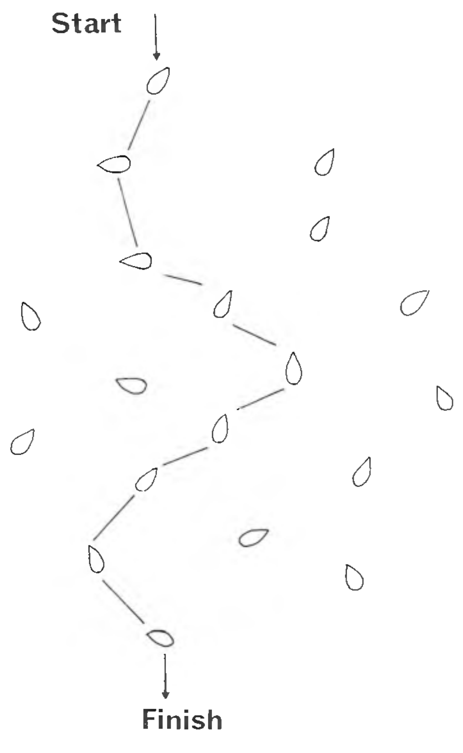

Figure 1. Estimating nearest neighbour distances through the flock.

This individual was taken and the procedure repeated and so on across the flock. If two nearest neighbours were equidistant, the one closest to the direction of the end point was taken. This method of determining density was rather inaccurate due to the difficulties of estimating distances on flat country.

General behaviour and ecology of Bewick's Swans on Welney Wildfowl Refuge

Flock structure

Throughout this study there were no obvious differences in the structure of the flock observed at Welney from that discovered at Slimbridge (P. Scott 1966). The family was still the largest stable unit, comprising a pair with 1–5 accompanying cygnets, and sometimes up to four offspring of previous years. The proportions of parents, pairs without offspring, single adults, yearlings and cygnets in the regular flock at Welney are shown in Table 1. These were similar to those at Slimbridge, except that fewer single birds and yearlings were regular visitors at Welney (see Evans 1979b).

Return rates and length of stay: class and sex differences

The proportion of known individuals at Welney that returned the following winter was generally higher than that at Slimbridge. But this was probably because at Welney, only regular visitors were known, while at Slimbridge all individuals were recorded. Table 2 shows data on return rates of different classes of individual from 1974–1975 to 1975–1976. As at Slimbridge (Evans 1978, 1979c), the highest return

Table 2. Class and sex differences in return. (% of 1974–1975 birds that returned in 1975–1976)

Class	%of males	(n)	% of females	(n)
Paired birds without cygnets	80·2	(81)	76·5	(81)
Paired birds with cygnets	69·0	(58)	65·5	(58)
Single adults	56·0	(25)	61·1	(18)
Yearlings	55·6	(9)	54·5	(11)

rate was among pairs, especially those without cygnets in the previous winter, while single adults and yearlings showed lower return rates.

At Slimbridge, the longest stays during the winter were by single birds and yearlings (Evans 1978, 1979c). This was not apparent at Welney, (Table 3), but it was impossible to record all individuals present. As at Slimbridge, parents with cygnets were present in front of the observatory on fewer days than pairs without cygnets. This was true for pairs which came with cygnets one year but not the other: 12 of 15 pairs ($p < 0{\cdot}05$ Sign Test) spent fewer days in front of the observatory when they had cygnets than when they did not.

Table 3. Mean number of days present in front of the observatory for different classes in 1975–1976. (Standard error in brackets). Birds arriving in October and November only.

Parents and cygnets	$n = 34, \bar{x} = 80{\cdot}3$ (14·3)
Pairs without cygnets	$n = 41, \bar{x} = 96{\cdot}2$ (7·4)
Singles (including yearlings)	$n = 21, \bar{x} = 91{\cdot}2$ (17·3)

Families also spent a smaller proportion of days between arrival and departure in front of the observatory than did pairs without cygnets, or singles ($X^2 = 9{\cdot}99$, df $= 1$, $p < 0{\cdot}01$, Median test). Parents with cygnets also showed greater tendency to stay through March before departure. On this point, data collected in front of the observatory in both 1974–1975 and 1975–1976 agree with Cadbury's analysis of the winters between 1969 and 1975 (Cadbury 1975).

In 1975–1976 fewer families tended to arrive after November than did pairs ($X^2 = 2{\cdot}78$, df $= 1$, $p < 0{\cdot}1$), or singles ($X^2 = 10{\cdot}98$, df $= 1$, $p < 0{\cdot}001$) and more singles arrived after November than pairs ($X^2 = 4{\cdot}34$, df $= 1$, $p < 0{\cdot}05$) (Table 4).

Table 4. Percent of individuals or units in different classes arriving in different months.

	Families	Pairs	Singles
October	21·2	33·3	31·4
November	68·1	47·1	34·3
December	3·6	10·3	11·4
January	5·4	3·5	7·2
February	1·7	5·8	7·1
March	0	0	8·6
	55	87	70

Sex ratio

As among birds sexed in the hand at Slimbridge (Evans & Kear 1978), adult birds at Welney, whose sex was estimated by eye, had a preponderance of males (Table 5). At Welney, this did not appear to be the case among yearlings.

Table 5. Sex ratio among birds identified in front of the observatory at Welney.

Welney flock 1975–1976	Number of males	Number of females
Single adults	25	18
Yearlings	9	11

Mortality and injury

During the two winters at Welney, one known and three unknown birds died of lead poisoning in front of the observatory, one known bird showed the symptoms but recovered and returned the next year. Two unknown birds were injured by shooting, and a known male parent was seriously lame but later recovered.

Several unknown birds were picked up beneath overhead wires. Owen & Cadbury (1975) gave winter mortality of cygnets at 2·4%, but cygnets disappeared from known families at a higher rate, 10·4% before February in 1974–1975 and 7·3% in 1975–1976. At Slimbridge, 8·1% of all cygnets recorded were lost in the winters between 1963–1978 (Evans 1979b). It cannot be assumed that all these cygnets died. Lone cygnets were infrequently seen in front of the observatory and never stayed more than one or two days.

Reproductive success

In 1974–1975, the maximum proportion of cygnets in the flock visiting the lagoon was 14·2%. The difference between this and Cadbury's (1975) figure of 17·6% obtained from monthly counts of the Ouse Washes area may be partly due to the mild weather which did not bring many of the fen families to visit the lagoon. At Slimbridge an overall 20·5% of cygnets were registered throughout that winter (Evans 1978). In 1975–1976, the maximum proportion of cygnets on the lagoon on one day was 20·2% while at Slimbridge the overall figure was 16·7%.

Data collected in front of the observatory in 1974–1975 on brood sizes did not differ from Cadbury's (1975). Table 6 also shows the data for 1975–1976, and 1976–1977.

Table 6. Brood size distribution (known parents).

Number of cygnets in brood	Number of families 1974–1975	1975–1976	1976–1977
1	14	12	5
2	13	19	10
3	17	16	6
4	10	8	3
5	0	1	0
Mean brood size	2·43	2·40	2·29

Number of swans visiting the lagoon in front of the observatory

Figures 2 and 3 show the changes in numbers over the seasons 1974–1975 and 1975–1976 when hourly counts were made. Three measures are illustrated: the mean number observed in each week at 0900 h when birds were loafing before the feed, the maximum number in each month, and the total along the Ouse Washes. While the first gives some idea of the numbers of regular visitors, the second indicates the number of birds in the area, which could only be estimated when birds feeding on the fens were disturbed and came into the lagoon for refuge.

The fewer numbers of birds present in 1974–1975 may have been partly associated with the longer floods which made the refuge a less suitable roosting site. However, numbers were also low at Slimbridge in that year and this may have been due to mild weather (Evans 1979a, b). In both years, maximum numbers occurred in the second half of the winter.

Although maximum numbers in each month were considerably greater than at Slimbridge, the mean number at 0900 did not always exceed numbers at this time at Slimbridge. However, numbers dropped off much more rapidly in January and February at Slimbridge than at Welney, and the swan season was thus shorter at Slimbridge.

Activities

Since regular visitors always roosted around the lagoon and many other birds

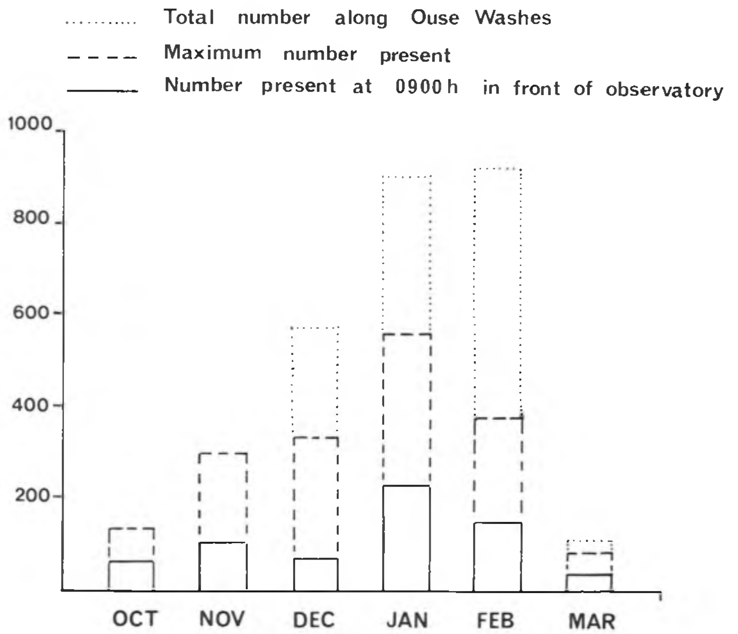

Figure 2. Number of swans during the winter 1974–1975 in front of the observatory.

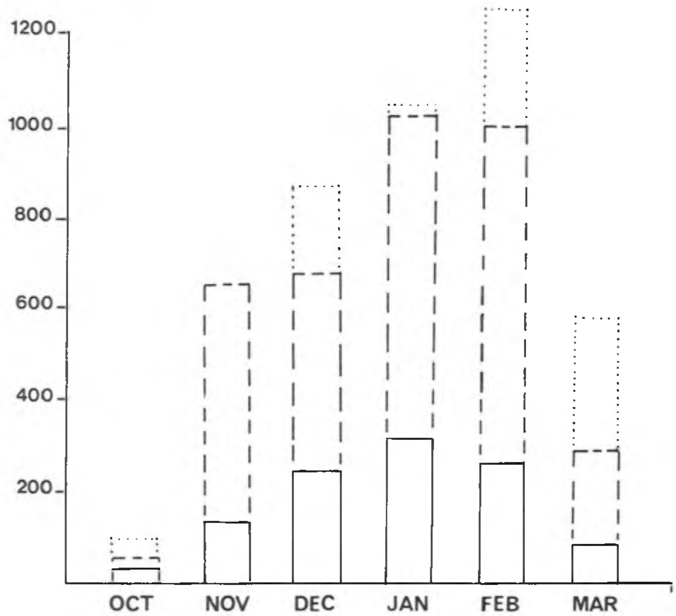

Figure 3. Number of swans during the winter 1975–1976 in front of the observatory. Key as for Figure 2.

came there only to roost, the pattern differed slightly from that on Swan Lake at Slimbridge where few come just to roost. In 1975–1976, at Welney, around 60% of individuals left for the fens at dawn and the remaining birds would gradually move across to loaf in front of the observatory for around one hour before the feed at 0930 h. Then, as at Slimbridge, when the food has been distributed, individuals remained in the feeding area for periods up to 30 minutes, after which they typically went to the shore to preen for a while, and then slept. Again as at Slimbridge, birds would leave throughout the morning to feed on nearby farmland. They started to return as early as 1400 or returned for short periods to drink. Those that did not go out, usually remained inactive until 1430, when they approached and loafed in front of the observatory before the 1530 h feed. After this feed, when it was dark, they again went to roost and remained roosting until dawn, unless there was another feed at 1900 h. If the grass on neighbouring washes was good, the swans tended to graze during part of the morning and early afternoon and sometimes after the evening feed.

Density

Irrespective of flock size, nearest neighbour distances were always smallest during the feed, when the birds jostled over each other (Figure 4). As the food was consumed, density decreased.

During loafing before feeds, density increased as feeding time approached. At first, distances of around 4 swan lengths to unrelated neighbours were maintained, but these decreased to around 2 swan lengths just before the feed. For four of seven hour-long continuous watches on particular individuals before feeds, significant positive correlations ($p < 0.01$) were obtained between mean distance to three nearest neighbours (within a five-minute block) and time before feed, while the other three were positive but not significant. But even at maximum densities, nearest neighbours were never within 0·5 s.l. during loafing.

Density during loafing was also apparently influenced by the number of swans present and by weather. For six focal paired birds, observed for six or more sessions between November and February in 1975–1976, there were negative correlations between the average distance to nearest neighbours and the number of swans present at the beginning of the session ($n = 6$, $p < 0{\cdot}05$, Sign test). During the cold spell at the beginning of February 1976, records were taken on five paired birds and in each case mean density was higher than in other sessions when similar numbers of swans were present (150–200).

Density during grazing on the lagoon wash was lower than during loafing, for six focal individuals compared in each situation. Again nearest neighbour distance appeared to be negatively related to the number of swans in the group ($n = 4$ focal parents, $r_s = -1{\cdot}0$, $p < 0{\cdot}1$, $n = 5$ focal pairs, $r_s = -0{\cdot}9$, $p < 0{\cdot}1$: parents and pairs were treated separately because parents tended to be further away from nearest unrealted neighbours than did pairs). During roosting, density tended to be lower than during loafing and more similar to grazing

Interaction frequencies

In front of the observatory during loafing, rates of all communicative behaviours increased with density, including agonistic (threats, head-bobs, vocalizations, display, avoidance) and non-agonistic behaviours (head-bobs and vocalizations). The combined frequency of all signals was positively related to density in different sessions for eight of nine focal pairs, although only five of these were significant ($p < 0{\cdot}05$). Similarly, during grazing, the frequency of agonistic interactions (threats and avoidance combined) was positively related to density ($n = 13$ sessions, $r_s = 0{\cdot}49$, $p < 0{\cdot}1$). In addition, during the feed, when density was highest, threat frequencies were significantly higher than during loafing ($n = 6$ focal individuals observed in both situations, $x = 0$, $p < 0{\cdot}05$ Sign test: Table 7).

Weather

Both cold and wet weather affected the number of swans present in front of the observatory (and in the area), their activities and interaction rates. As already mentioned, floods on the Washes caused the swans (including regular visitors to the lagoon) to move elsewhere. On frosty

Figure 4. The afternoon feed in front of the observatory. (*Philippa Scott*)

Table 7. Threat frequencies and nearest neighbour distances for focal individuals in different situations.

Focal swan (F = Parent) (P = Pair)	Threat frequency on fens (and total number of minutes observed)	Mean distance to nearest neighbour (NN) across minutes	Threat frequency in feed in front of observatory	Nearest neighbour distances estimated	Threat frequency during loafing	Mean distance to nearest neighbour across mins and across sessions
ALDE (♂ F)	0·08 (25)	5·1	2·7 (3)	0–1·5	0·69 (31)	3·40
BAAY (♂ F)	0·10 (20)	3·2	1·4 (41)	0–1·5	0·96 (64)	4·82
HORN (♂ F)	0 (5)	3·1	2·0 (19)	0–1·5	0·86 (28)	2·46
ALOE (♀ F)	0·30 (10)	4·5	4·8 (8)	0–1·5	0·80 (45)	3·89
HERN (♀ F)	0 (8)	5·5	2·0 (7)	0–1·5	0·68 (44)	3·37
CHIT (♂ P)	0 (30)	4·2	0·5 (5)	0–1·5	1·07 (39)	4·34
TOWE (♂ P)	0 (9)	4·5	1·9 (13)	0–1·5	? (0)	?
Median	0·04	4·5	2·0	0·7	0·83	3·65
Median threat frequency / Median NN distance	0·009		2·86		0·23	

days, the number of birds at the morning feed was higher than on milder days, and the proportion of those roosting around the lagoon that stayed until mid-day was also higher. The effect became most apparent during the cold spell between 25 January and 5 February 1976, when the number of birds in front of the observatory between 0900 and 1000 h exceeded 500. The lack of open water elsewhere in the area also brought many more swans to roost around the lagoon which otherwise roosted further down the Washes, so that the total number roosting in front of the observatory reached 1,200 (on 31 January 1976).

During this cold spell, it appeared that fewer birds than usual went out to feed on the first day of snow cover (26 January 1976), many spending the whole day asleep on the ice at high density. On subsequent days an increasing number went out each day until the proportion going out was as high as on a milder day.

Cold weather also affected the composition of the flock: since a smaller proportion of roosting birds went out to the fens, the flock in front of the observatory contained a higher proportion of families than on milder days ($n_1 = 5$ cold days, $n_2 = 11$ milder days, $U = 0{\cdot}5$, $p < 0{\cdot}001$).

Individuals spent more time asleep or preening and less time loafing during the day when it was windy for periods when the washes were flooded, although the difference was less apparent at other times (Table 8).

Discussion

The results described above suggest that the behaviour of Bewick's swans in front of the observatory at Welney is similar to that on Swan Lake at Slimbridge. The main difference was in the earlier departure of swans from Slimbridge than from Welney in the spring, the reason for which is not yet clear (Evans 1978).

As found in many studies (Myers *et al.* 1971; Tingay 1974), interaction rates were positively correlated with density, and were also greater during feeding (including grazing) than during roosting (Tingay 1974; Lazarus & Inglis 1978).

It was apparent that in cold weather, a greater proportion of roosting birds stayed in front of the observatory through the day. One explanation for this is that individuals remain because they may gain access to higher quality food (grain) in front of the observatory, especially if fen food sources are frosted. This, however, does

Table 8. Activities on windy versus still days

	Still/light wind (no. of days)	Strong wind	Probability of difference
% Asleep at mid-day			
No flood	62·2 (7)	69·7 (8)	n.s.
Floods	21·7 (4)	43·8 (6)	$U = 3$, $p < 0{\cdot}07$
% Swimming at mid-day			
No flood	12·3 (7)	9·7 (8)	n.s.
Floods	37·2 (4)	11·1 (6)	$U = 0$, $p < 0{\cdot}01$

not explain the striking phenomenon of more than 500 fen birds which usually only roosted there, spending the first day of snow cover in a cold spell asleep on the ice. One possibility is that the swans were conserving energy on the first day, on the chance that it might be a short cold spell. When this turned out not to be the case, they started to go out in increasing numbers in the following days.

Comparison of behaviour on the fens with that in front of the observatory

Introduction

With the general behaviour of the swans in front of the observatory at Welney in mind, we may now investigate their behaviour in a 'more natural' situation on surrounding agricultural land, and compare the two situations.

Some limitations on collection of data on the fens and on flooded meadows account for the relatively small sample sizes. It is seldom possible to recognize known individuals on the fens: either because the birds were too far away or because those that were present had mud-covered bills and were therefore unrecognizable. Disturbance was sometimes so frequent that many focal animal and flock scan samples had to be terminated before complete. Finally the small field of view of the telescope meant that it was often difficult to monitor the position of the mate of a focal animal.

Those problems were especially acute on flooded meadows where the occurrence of swans was unpredictable and access was frequently difficult. So observations in this situation were largely qualitive.

Activities

The most immediately apparent difference between the behaviour of individuals in front of the observatory and those on the fens was in the relative amounts of time spent feeding, preening, and sleeping. Birds on the fens spent a larger proportion of the time feeding. Data from two all-day watches show a pattern similar to that observed by Cadbury (1975). The mean percentage of birds in the flock feeding on each hour throughout the day was 60%, while the highest percentage was at the beginning of the day with some evidence of a second peak towards the end of the day.

It was not possible to compare the behaviour of those that spent all day on the fens with those that only spent part of the day there and that returned for feeds in front of the observatory. In addition, since birds did not loaf on the fens it was not always possible to compare aspects of behaviour (density, interaction rates) in fen and in observatory situations.

Flock sizes

Mean flock size on the fens was somewhat smaller and was similar to that on flooded meadows in the period January–February 1976 (when data were collected in all three situations) (Table 9).

Table 9. Flock sizes in different situations in January–February 1976.

Location	Mean flock size	Standard error	Number of flocks
In front of observatory	294·7	53·7	19
On fens	150·4	43·5	20
On flooded meadows	157·5	39·3	8

Density

Density in front of the observatory was exceptionally high during the feed. (Figgures 4 and 5). On the fens, feeding birds maintained a mean distance of 5·1 s.l. ($\pm 0{\cdot}7$: n = 58 ten-minute focal samples) to three nearest neighbours. However, when birds were feeding on unharvested potatoes, the density tended to be lower than on winter wheat ($X^2 = 19{\cdot}96$, df = 3, $p < 0{\cdot}001$).

On the fens density tended to be higher when a large proportion of the flock was sleeping or preening, and these roosting densities did not differ from those in front of the observatory. On the fens, however there was no obvious relationship between density and flock size, above 50 individuals. On flooded meadows, nearest neighbour distances tended to be slightly greater than on the fens and more variable: individuals were usually distributed unevenly over the meadow, often linearly along shores at a certain depth of water.

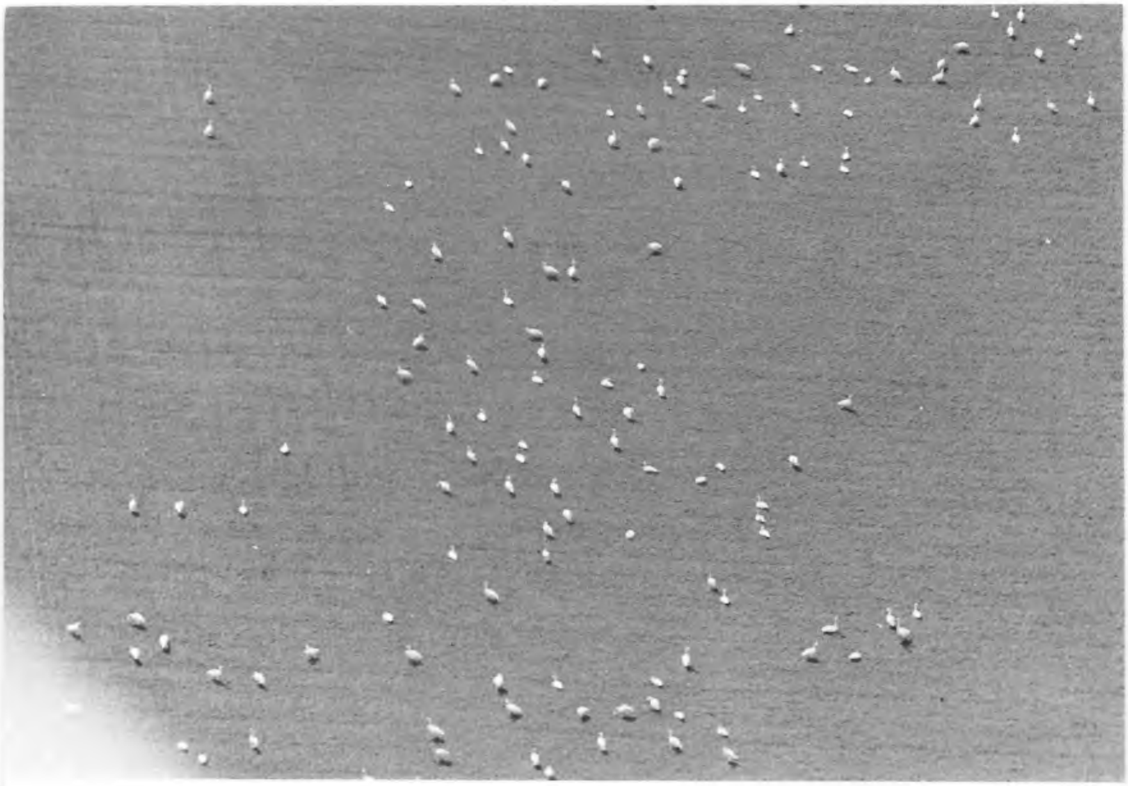

Figure 5. Swans feeding on winter wheat on the fens (aerial view). (*Marion Zunz*)

Interaction frequencies

During the feed in front of the observatory, simple threat frequencies were around ten times greater than in feeding flocks on the fens; but density was also higher. During loafing before the feed, densities were only slightly greater, frequencies of head-bobs and vocalizations were similarly elevated compared with those on the fens (Table 7). The greatest difference was in the frequency of aggressive displays which was more than ten times greater during loafing in front of the observatory (Table 10). However, there was no difference in frequency of aggressive displays between fen and observatory situations between 1030 and 1130 h, and all differences were restricted to the relatively short periods of loafing and feeding in front of the observatory.

Table 10. Mean frequency of aggressive display (mean number of bouts of neck-stretching per minute).

On fens	During loafing in front of observatory
0·07	1·15

Probability of difference: $n = 12$ focal animals observed in both situations, $x = 0$, $p < 0{\cdot}01$, Wilcoxon Matched Pairs Test.

On the fens also, aggressive encounters were more common during feeding than during roosting. Thus there was a negative relationship between the number of display encounters per hour and the proportion of the flock preening or sleeping ($n = 20$ hours, 1030–1130, $r_s = -0{\cdot}6$, $p < 0{\cdot}02$). Aggression rates also varied with density. All aggressive interactions tended to be more frequent at high densities when birds were feeding on wheat (Table 11). However, the relationship was less obvious on potatoes. Then despite maintaining greater distances to nearest neighbours, they also tended to show higher interaction rates ($n_1 = 11$ sessions on focal birds, $n_2 = 14$, $U = 24{\cdot}5$, $p < 0{\cdot}02$).

On flooded meadows, interaction rates appeared to be lower than in front of the observatory, but higher than on the fens, taking density into account.

Dominance

Dominance relationships between individuals and units are described in detail elsewhere (D. Scott 1978a, in press, b). They were very similar between fen and observatory situations, both between different classes of individuals and between particular individuals. As in geese (Boyd 1953; Raveling 1970), families tended to dominate pairs which dominated single individuals and relationships between were extremely constant over the winter. For six pairs of opponents observed encountering each other both in front of the observatory and on the fens, the outcome was the same in both situations. In addition, the proportion of opponents beaten by different focal individuals on the fens was comparable with that for the same birds in front of the observatory although numbers of opponents on the fens were small due to the low frequency of interactions.

The only apparent difference between fen and observatory situations was in the overall success of different sized units in aggressive encounters. On the fens, pairs less often beat families ($X^2 = 7{\cdot}1$, df = 1, $p < 0{\cdot}01$) and singles less often beat pairs ($X^2 = 6{\cdot}1$, df = 1, $p < 0{\cdot}02$) than in front of the observatory (Table 12).

Parent-offspring relationships

Variations in parent-offspring relationships are described and analysed in statistical detail elsewhere (D. Scott, in press, a).

In front of the observatory during the feeds, family members became separated in the melée. Cygnets were within 4 s.l. of their parents on only 15% of occasions and were seldom among the latter's nearest neighbours. This contrast all other feeding situations where cygnets spent more than 80% of their time within 4 s.l. of their parents.

Otherwise, in both the observatory and fen situations parents and cygnets were usually each others' nearest neighbours. They were closest together in dense flocks, during roosting, and also during aggressive encounters involving displays; the cygnets of subordinate parents were generally

Table 11. Variation in frequency of agonistic interaction with density on the fens on wheat and potato fields.

Wheat: Focal individuals	Freq. of agonistic interactions per minute	$\bar{x}$ distance to 3 nearest neighbours during sample	Potatoes: Focal individual	Freq. of agonistic interactions per minute	$\bar{x}$ distance to 3 nearest neighbours during sample
CHIT	0·13	4·1	BRYW	0·20	2·2
CRAC	0	11·0	DKYL	0·30	3·9
LATE	0	7·5	JOEY	0·10	6·1
LUCR	0	3·5	LTWD	0·60	5·3
ILIA	0	3·7	MULL	0·30	4·1
JOSH	0	10·8	PANE	0·10	2·8
MARS	0·30	2·9	SORR	0·20	3·2
MIMS	0	3·4	SPOT	0·17	3·8
MOSA	0·40	3·2	WOMB	0·20	4·3
OXLO	0	2·5	742	0·12	2·9
PERS	0·10	3·6	744	0·10	2·9
SMIT	0	4·7			
THER	0·03	5·5			
TOWE	0	4·5			
$n = 14$, $r_s = 0{\cdot}617$, $p < 0{\cdot}1$			$n = 11$, $r_s = 0{\cdot}380$, $p > 0{\cdot}1$		

Table 12. Number of encounters between different classes in different situations

	Pairs (P) v Singles (S)		Families (F) v Pairs (P)		Families with n + 1 cygnets v families with n cygnets	
	P beat S	S beat P	F beat P	P beat F	F + (n + 1) beat F + n	F + n beat F + (n + 1)
Fens 1030–1130	67 (90·5%)	7 (9·5%)	22 (88%)	3 (12%)	4 (66·7%)	2 (33·3%)
	$p < 0{\cdot}001$		$p < 0{\cdot}001$		n.s.	
In front of observatory 1030–1130	33 (73·3%)	12 (26·7%)	74 (60·2%)	49 (39·8%)	19 (59·4%)	13 (40·63%)
	$p < 0{\cdot}01$		$p < 0{\cdot}05$		n.s.	

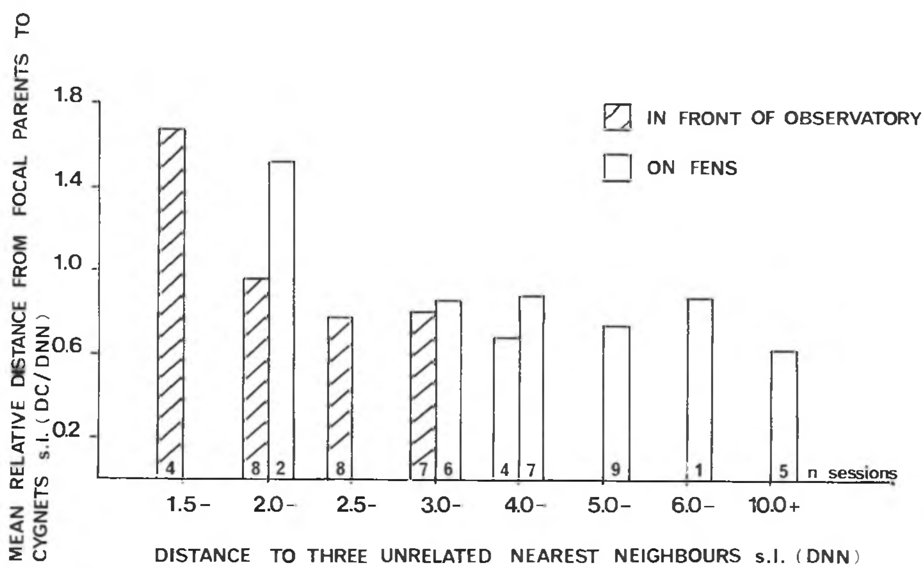

Figure 6. Relationship between density (i.e. distance to unrelated flock members) and relative distance to cygnets (distance to cygnets, DC,/distance to nearest neighbours, DNN).

closer to their parents than those of dominant parents. In addition, cygnets tended to be closer to their parents in flocks feeding on potatoes than on winter wheat.

There was a slight tendency for cygnets to be closer to their parents (relative to the distance to nearest neighbours) in front of the observatory than on the fens over a range of densities (Figure 6). However, this may be a product of the different activities.

Movements of parents and cygnets relative to each other (i.e. frequencies with which they approached to within 4 s.l. or left each other) were greater in front of the observatory during loafing than on the fens or on flooded meadows, and greater when the birds were feeding on flooded meadows or potatoes than on wheat. These differences were associated with the overall rate of movement of individuals in the flock, which was particularly slow on wheat.

Mortality and breeding success

There was no evidence between 1975–1976 and 1976–1977 of any differential mortality or reproductive success between known individual pairs spending a large and those spending a small part of the time in front of the observatory. Of 131 regular pairs in 1975–1976, 9·9% brought cygnets the following year, while of 36 pairs spending less than 60% of time in front of the observatory, 11·1% brought cygnets. This difference is not significant.

Discussion of behaviour on the fens

As has been found in a number of waterfowl species that feed diurnally, feeding activity tended to be greater in the morning and late afternoon than in the middle of the day (e.g. Blue-winged Teal *Anas discors*, Miller 1976; Mandarin Ducks *Aix galericulata*, Bruggers & Jackson 1977). The data from swans feeding on the fens agree with those of Owen & Cadbury (1975). However, these authors found that when feeding on flooded washes, the swans spent more time feeding before dusk.

Feeding competition is likely to be greater where resources are in potentially defensible patches than where they are evenly distributed (e.g. Jarman 1974; Wrangham 1977), and, indeed, aggressive interactions were more frequent on potatoes than on wheat despite a lower density of swans.

Differences in feeding interference may also explain the smaller distances between neighbours during roosting than during feeding, as found also in Pink-footed Geese *Anser brachyrhynchus* (Lazarus & Inglis 1978).

Concluding discussion

It is frequently suggested that provisioning flocks of wild birds has harmful effects on them, which may operate through the increased density which such provisioning induces. The effects include increased likelihood of disease transmission, and increased stress, with implied consequent mortality.

Although disease transmission is likely to increase with density and turnover of birds, to date there has been no evidence of ill-effects resulting from disease at Welney. In addition, at similar sites in Japan where swans are provisioned and where numbers may be even greater (e.g. Odaito: Ohmori, in press and Horiuchi, in press) outbreaks of disease have not been observed (see also Hatakeyama, in press). There was no evidence of differential mortality or reproductive success among birds spending large amounts of time in front of the observatory compared with those spending little time there.

The existence of stress caused by high densities has not been demonstrated in wild populations of birds, although it has been demonstrated in a wild mammal, the arctic lemming (e.g. Christian & Davis 1964). However in the latter case, densities are usually chronically high over an extended period before emigration and associated mortality occur. Furthermore, densities are high in surrounding areas and the pay-offs of emigration are small, whereas at provisioning sites for birds, densities are not uniformly great in surrounding areas.

Although the greater density during feeding in front of the observatory than on the fens was associated with higher interaction rates, the period of feeding was much shorter (c. 20 minutes three times a day), compared with around six hours (Owen & Cadbury 1975). This means that over a whole day, an individual in front of the observatory might be involved in around four times more interactions than on the fens. Any effect of stress was not apparent in obvious behavioural differences between fen and observatory birds.

The absence of significant differences between fen and observatory flocks in types of interaction, in overall success in interactions of individuals, and in spatial relations of members of pairs or families is important in another way. It provides some justification for making generalizations about these variables and their interrelationships from data collected in front of the observatory to 'more natural' situations, and thus for functional explanations of characteristics observed in front of the observatory.

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Summary

This paper describes the general behaviour of Bewick's Swans *Cygnus columbianus bewickii* at the Welney Wildfowl Refuge, on the Ouse Washes, Norfolk, and compares this with the behaviour of the swans on surrounding fenland. On the fens, the swans were at lower densities and interacted aggressively less often during feeding than in front of the observatory, although, on the fens, they spent more time feeding throughout the day. In addition, fen flocks contained more cygnets than those in front of the observatory. This was because pairs spent more time on the fens in years when they had cygnets than when they did not. However, there were few differences in other aspects of social behaviour, and no evidence of differential mortality or breeding success between swans spending much time on the refuge and those spending little time there.

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