Detailed aspects of time-budgeting, feeding and reproductive behaviour of breeding and non-breeding birds were also investigated.

M A BRAZIL
Department of Psychology
University of Stirling
Stirling FK9 4LA
Scotland

# THE BEHAVIOURAL ECOLOGY OF *CYGNUS CYGNUS CYGNUS* IN CENTRAL SCOTLAND

## M BRAZIL

## Observation areas

Area 1 (see Fig 1), to the east, lies between the A91 road to the north and the A905 road to the south and extends to Monument Hill in the west and to Alva and Alloa in the east. Area 2, to the west, lies between the A84 and the A811 as far west as the B8075 and extending to Stirling in the east. All observations were made from a vehicle, mostly at a range of 100 m or more.

## The distribution and size of flocks

During the period from 31 October 1977 to 7 May 1979, 142 flocks were recorded from the study areas, the term 'flock' being used for all numbers including single-tons. Each flock is given an identification number. This number is retained if the flock remains the same size during consecutive observations, although it may move to a different locality.

During the same period, birds were present for a total of 5123 bird-days, 40.5% (2075 bird-days) in winter 1977/78 and 59.5% (3048 bird-days) in 1978/79. Of a total of 26 localities used, only nine contributed more than 200 bird-days each, only four of which received similar usage over two winters. The remainder each contributed fewer than 100 bird-days (see Table 1 and Fig 1).

Flocks ranged in size from 1 to 134, the mean being 26.9 (24.8 winter 1, 27.3 winter 2). However, if localities contributing more than 200 bird-days are considered separately, the mean flock size is 40 (n = 119: 40.8 winter 1, 39.5 winter 2) while for the remaining localities it is 18.2 (18.6 winter 1, 17.6 winter 2). Over two thirds (70.4%) of all flocks are of fewer than 50 birds (Fig 2). Large
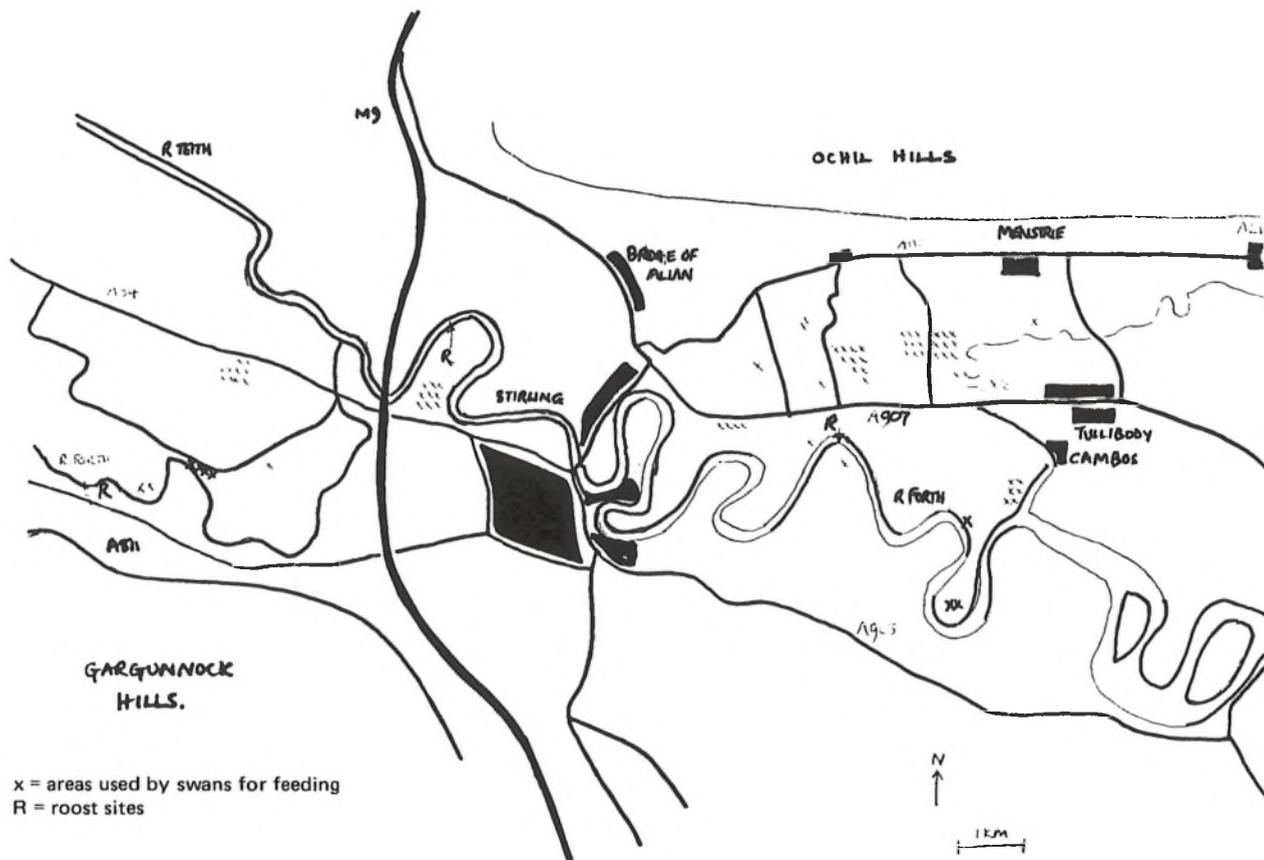
x = areas used by swans for feeding
R = roost sites

Fig 1. The study areas east and west of Stirling.

Table 1.   Habitat use (expressed in bird-days) by *Cygnus cygnus cygnus* in the Stirling area.

| Month | 1977/78 | | | 1978/79 | |
|---|---|---|---|---|---|
| | Stubble | Grass | Flood water | Stubble | Grass |
| October | | | | 6 | |
| November | 671 | | 2.25 | 1372 | |
| December | 506 | | | 284 | 317 |
| January | 138 | 65 | 45.25 | 174 | |
| February | 31 | 71 | 215 | 69 | 412.5 |
| March | | 207.25 | | | 43 |
| April | | 85.75 | | | 356.75 |
| May | | | | | 14 |
| Total | 1346 | 429 | 262.5 | 1905 | 1143.25 |

flocks of over 30 birds are much more common between October and the end of the year, while small flocks of fewer than 20 are much more common between the beginning of the year and departure in the spring. Central Scotland is a stop-over area; there is good feeding but birds readily move on, especially during hard weather. Autumn arrivals are large but gradually larger flocks move on or split up into smaller units. The advantages of larger flock sizes are discussed later. Sites with higher usage support a larger mean flock size. During the second winter there was an increase of 1000 bird-days, yet mean flock size did not increase.

## Flock structure

The number of swans using or passing through the Stirling area is only a small part of the Scottish wintering population, so the proportion of young present in flocks in this area does not necessarily indicate the general level of breeding success.

Including flocks both from the study area and the immediate vicinity, 160 flocks were recorded, of which 93 contained first-year birds. The number of yearlings was determined accurately for 85 of these flocks, the mean number per flock being 5 and the mean percentage 20.2. A total of 153 broods was counted for 26 flocks. Since all broods of zero are missed, it is not possible to calculate the proportion of adults which bred. Poor breeding success is as likely to be due to failure to hatch or rear any young (Boyd and Eltringham 1962) as to reduced brood size. The mean brood size was 1.86 in winter 1977/78 and 2.77 in winter 1978/79. Although the most frequent brood size was 2 in both winters, larger broods were commoner in winter 1978/79. Bell (1979) made a similar observation for northeast Scotland. Bulstrode *et al* (1973) found that 56% of pairs had young with a mean brood size of 3 and Hewson (1964) found that in large flocks the mean percentage of first-year birds was 15.1 and 26.4 in smaller flocks. Both these previous studies showed
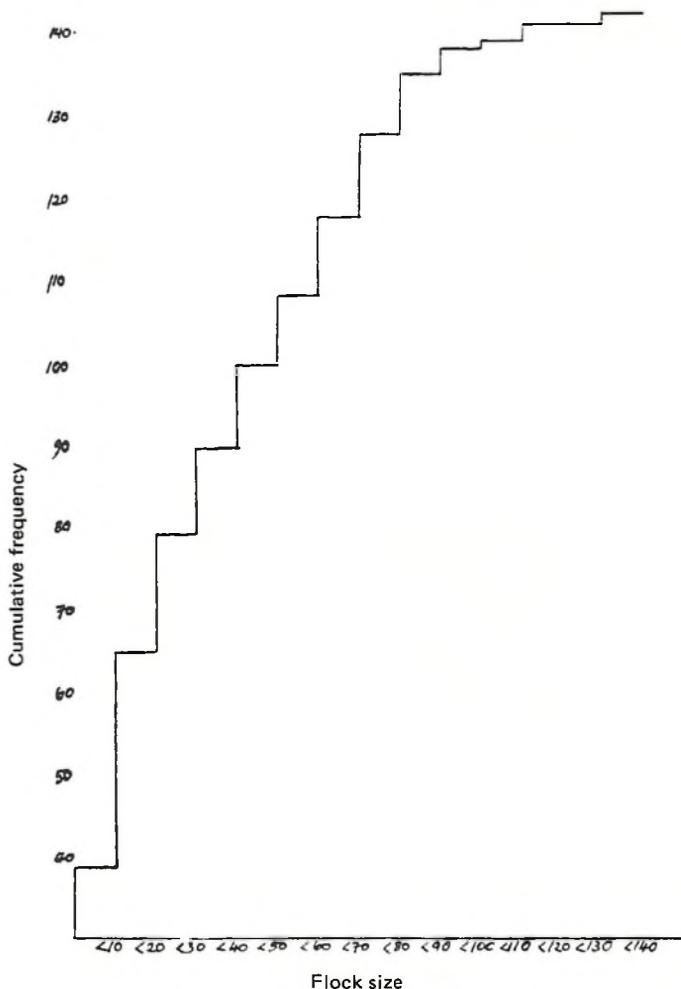
Fig 2. Cumulative frequency distribution of *Cygnus cygnus cygnus* flocks.

a similar breeding success to the present study. The weather in Iceland in summer 1979 was very bad and a census of *Cygnus cygnus cygnus* in Britain that winter showed that over large areas the percentage of young was less than 5% (J Kirk pers comm).

## The pattern of behaviour in winter

*C. c. cygnus* began to use agricultural land for foraging after the series of hard

winters in the 1940s (Owen and Kear 1972). In adapting to a new feeding habitat it has adopted a similar daily pattern to that traditionally shown by geese, ie it commutes between a night roost and a day foraging site. Unlike geese, swans do not normally feed by moonlight. In the first half of the winter, from late October until January/February, the swans feed at stubble fields on waste grain and some late-growing grass. In January or February they switch to feeding on grass (Table 1). When the swans are feeding on stubble fields they use the area east of Stirling and roost on the tidal Forth near Manorneuk. When eating grass, they change foraging area, moving to the west, and roost on a stretch of the River Forth near Kildean (Fig 1).

The area west of Stirling has about 10% more stubble than that to the east. In spite of the inevitable decline due to ploughing, by April the proportion of stubble to the west was still two thirds of that to the east in October. The swans could thus feed on stubble all winter. Feare *et al* (1974) found that in stubble fields used by *Corvus frugilegus* grain density declines rapidly from September until November and thereafter more slowly until March. Murton (1965) found that, for *Columba palumbus,* stubble fields became exhausted 'some time between November and early January'.

In October and December, over 40% of both areas was down to grass, whereas stubble at its maximum in October contributes only 24.3% of the western area and 15.3% of the eastern area. Birds are therefore active in their selection of stubble in the autumn and of grass in the spring. Root crops are not common in this area and the use of them by swans is rare and confined to potatoes. Many species, eg geese and sheep (Owen 1971), are capable of selecting those foods with a higher nutritional value.

The availability of grassy vegetation declines only slightly during the winter, from 42.2% to 39.5% between October and April in the west and from 45.9% to 39.8% in the east area. Some is lost to ploughing and some gained owing to the sprouting of winter wheat. Winter wheat and the early spring growth of grass leys is of greater nutritional value than old grass, which becomes less palatable as it gets longer. Autumn grass is presumably of less value than grain, while in late winter new grass is growing as grain densities are being depleted, hence the switch for feeding.

The overall preference for stubbles in autumn and grass in spring has been observed in Aberdeenshire and Dumfriesshire (J Kirk pers comm).

## Weather conditions

Prolonged cold weather reduces the areas of fresh water available to swans while snow cover prevents them from grazing. For instance, the extremely cold weather of January 1979 drove birds from the study area. The weather was severe through-out Scotland and most inland waters were frozen for long periods. Swans became

scarce in central areas while larger numbers were reported in the southwest. A sighting of swans there flying out to sea (G Sheppard pers comm) on 19 January 1979 suggests that some moved through to Ireland.

## Winter movements

Previous observations by Henty (1977) suggested that swan flocks utilizing the area east of Stirling were small, moved regularly between fields and sometimes used separate roost sites. Since 1977, however, it has been rare to find swans other than in a single flock and this tended to use a single field over a period of several days and also a single roost site.

Swans leaving a roost, either river or loch, must climb above tree and powerline height before flying out to the fields. From this height (circa 30 m) they are able to see the variety of fields available to them, as well as where earlier departing birds have landed. Abandonment of previously favoured fields may be due to disturbance or reduced food density. Where birds have been seen to be disturbed, they have moved to another field of the same type.

## Diurnal behaviour

Where light intensity is the controlling factor, weather factors such as cloud, mist and frost (Owen 1977) would be expected to delay morning flight and advance evening flight. Seibert (1951) working on Ardeidae found that they left the roost at a lower light intensity than that at which they arrived, while Siegfried (1971) suggested that with *Bubulcus ibis* a specific light intensity threshold for roosting is modified by environmental constraints and physiological needs. Hein and Haugen (1966) found that there was least change in the start of morning flight and the end of evening flight. The end of morning flight and the duration of evening flight changed most. They also found that on dark or foggy days morning flights were delayed and evening flights were prolonged.

## Departure time

The time of departure for each subflock and the light reading at that time were recorded. A standard Weston light meter was used in the field. This was later calibrated against a 40x opto-meter to convert light readings into foot-candles. Light readings (zenith) were also taken at regular intervals in the final half hour of daylight. Times GMT were converted to minutes after local sunset (Glasgow minus 2 minutes) and a 50% departure time (shown by Davis (1956) with *Sturnus vulgaris* to be the endpoint least influenced by chance variation) was used. Data are available for 39 evenings for day-lengths from 7 hours to 15½ hours (time between sunrise and sunset).

There is a wide scatter of post-sunset departure times for days of similar length

and any relationship is masked. Examining the data from midwinter alone shows a tendency towards earlier departure relative to sunset on longer days.

Some other waterfowl have also been shown to exhibit this relationship, eg Hein and Haugen (1966) found both light intensity and season to be important to *Aix sponsa.* Morning flight began when illumination reached 1 foot-candle in August, whereas by November it began at illumination levels of less than ¼ foot-candle. Evening flights were similarly affected, birds arriving at the roost between 70 and 2 foot-candles in August and between 4 and ¼ foot-candles by late October. Martin (1957), also working on *A. sponsa,* found that flight times were linked with sunset and sunrise (seasonally variable). Morning flights began about half an hour before sunrise and evening arrivals concentrated mostly between 15 and 30 minutes after sunset. Siegfried *et al* (1977) found marked seasonal variation in arrival time at the roost in *Anas sparsa.*

In the present study, frequency of departures increases markedly with falling light intensities (Fig 3). Few departures occur above 0.1 to 0.25 foot-candles, the majority at less than 0.08 foot-candles. Very heavy cloud reduces illumination levels. It was expected that at low temperatures the birds would feed for longer to make up for greater energy loss but the present study does not support this. The swans sometimes remain well after sunset at any time during the winter. Assuming that there is enough light for them to see to fly safely even below the sensitivity of the light meter, the question still remains: why do they remain on the fields after dark? On most evenings, often the last ten minutes are not spent feeding. Waves of 'head-up' positioning pass through the flock and wing-flapping becomes more frequent. Some birds begin head-bobbing and calling and frequently form small groups walking about through the flock. Eventually all members of the flock will stop preening or feeding and adopt the 'head-up' position. Then, finally, departure will occur. Where subgroups depart separately, it is normally the birds which have recently been head-bobbing that leave first. In the time that all this takes place, visibility often becomes very poor. Unless such social behaviour is crucial to the flock members in some way, it seems a dangerous and unnecessary delay, in view of flight obstacles and the risk from flight predators.

It is possible that, for much of the winter, swans feeding and roosting in such an area are not under extreme energetic stress and can afford to spend time on the foraging grounds not feeding. Henty (1977) found 'no noticeable effect of frost during the preceding 24 hours although continued hard weather disrupted the whole commuting system'. If the swans were already under physiological stress, cold weather would be expected to exacerbate this. The effects of low temperatures at night, the critical period at high latitudes (Kendeigh 1961), can be ameliorated in several ways. Communal roosting in *C. c. cygnus* may serve several functions such as both an anti-disturbance strategy and as an information centre but it could well aid in thermo-regulation. Aquatic species roosting on a river will receive some wind shelter from river banks and vegetation. Even when the wind direction is
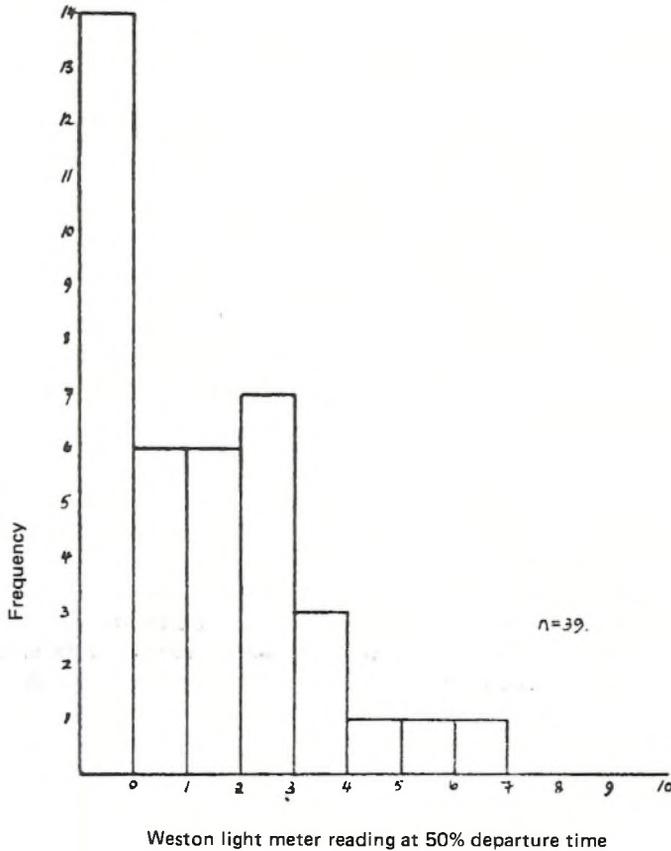
Fig 3. Departure of *Cygnus cygnus cygnus* to the roost in relation to light intensity.

parallel to the section of the river, roosting in a flock will aid thermo-regulation by decreasing wind speed. Some members of the flock will always be in the lee of others. Wind velocity has been shown by many studies directly to affect heat loss and hence energy uptake.

Feeding regime

It is assumed that swans do not feed at night. Casual observations at the roost site after dark and at dawn showed that, when it was possible to make out the birds, drinking and preening are important activities in the evenings. In the mornings head-up and calling are most common.

Monthly activity budgets were compiled for winter 1977/78. Scans were made every 15 minutes and the proportion of the flock engaged in feeding, preening, roosting and head-up was recorded. The term 'feeding' includes birds obviously pecking and those between pecks, ie with the head below the level of the body and close to the ground. 'Preening' is used for all comfort movements including wing-flapping and defaecation. 'Roosting' includes birds standing or sitting with the head resting on the back and tucked into the feathers, whether the eyes are open or closed, and also birds with the neck curved so that the head lies almost horizon-tally on the lower neck. 'Head-up' includes birds standing or sitting with the head and neck raised above the level of the body. Subjectively, 'head-up' is used by birds which are generally 'vigilant', as opposed to 'extreme head-up', which occurs when a specific stimulus has been perceived and is directed towards it, such as a disturbance or birds joining or leaving the flock. Mean activity level and hence the proportion of time spent in these activities are calculated from the sample scans (Table 2).

Table 2. The activity budget of *Cygnus cygnus cygnus* in the Stirling area 1977/78.

| | | November | December | Fields January/ February | Water January/ February | March |
|---|---|---|---|---|---|---|
| Feeding | mean per daylight hour (%) | 70.8 | 72.7 | 61.6 | 31.5 | 75.3 |
| | mean per hour (%) | 26.5 | 27.3 | 28.2 | 14.4 | 40.8 |
| Preening | mean per daylight hour (%) | 2.1 | 1.7 | 3.7 | 8.7 | 4.4 |
| | mean per hour (%) | 0.8 | 0.7 | 1.7 | 4.0 | 2.6 |
| Roosting | mean per daylight hour (%) | 12.7 | 9.0 | 18.8 | 29.6 | 4.1 |
| | mean per hour (%) | 67.3 | 65.9 | 62.7 | 67.8 | 47.9 |
| Head-up | mean per daylight hour (%) | 14.5 | 16.5 | 16.1 | 30.0 | 16.1 |
| | mean per hour (%) | 5.4 | 6.2 | 7.4 | 13.7 | 8.7 |

As is to be expected, feeding is the most time-consuming activity (between 60% and 75% of time). Ecologically, foraging is the most important behavioural com-ponent of the time/activity budget and non-foraging daytime activities are influenced by feeding intensity, except head-up, the second most important behaviour in terms of time investment (14.5% to 16.5%).

Many animals show a bimodal pattern of activity, with morning and afternoon peaks. This is true of geese, eg Owen (1972) and Ebbinge *et al* (1975), and of dabbling ducks (Henty 1975).

There is a marked feeding pattern between November and February (Fig 4), with
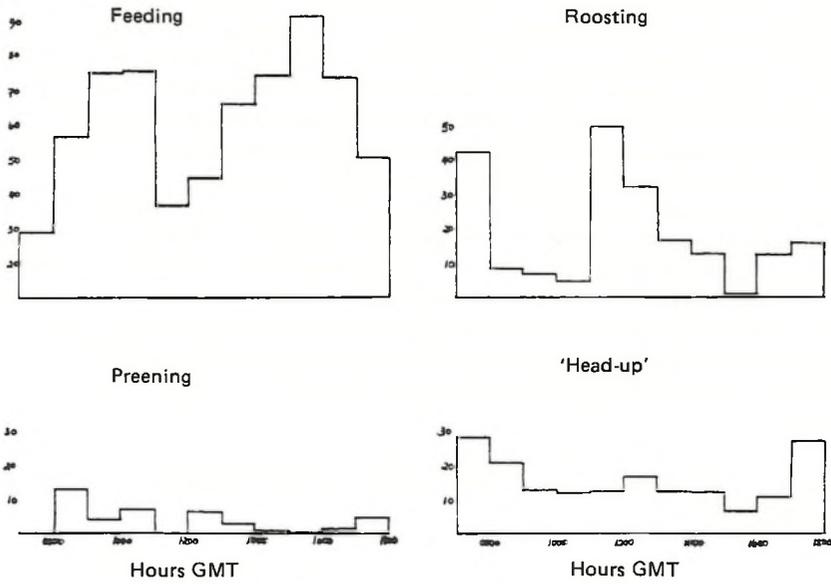
Fig 4. Activity budget: January/February 1978. Grass.
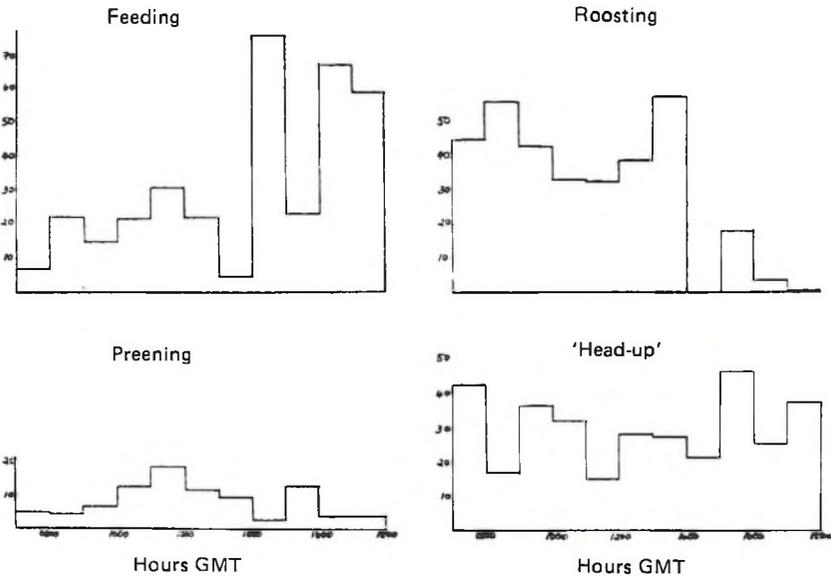


Fig 5. Activity budget: January/February 1978. Water.

high morning and afternoon peaks. By March (Fig 6) this pattern has changed somewhat, with birds feeding at a higher rate for longer and the midday lull has almost disappeared. Excepting March, roosting peaked during the feeding lull and was otherwise at a very low level. Some head-up occurs throughout the day but with noticeable increases occurring usually at the beginning and towards the end of the day. Preening occupies least time and occurs at low levels throughout the day.

The pattern observed for swans feeding on land is distinctly different from that of birds feeding on water (see Figs 4 and 5). Owen and Cadbury (1975) found that for both *C. olor* and *C. columbianus bewickii* the basic pattern of activity was for feeding to begin at a low level at sunrise, for it to increase steadily, reaching a plateau three hours after sunrise in *C. olor* and six hours after in *C. c. bewickii*, and continuing until dark. Intensive feeding continued for one hour after dark in *C. c. bewickii*. For the latter half of January and the first week of February 1978, the *C. c. cygnus* flock within the study area spent its time on flooded meadows by the River Forth near Cambus. The meadows drained between 8 and 15 February owing to a breach in the retaining bank and the flock moved back to the fields. The pattern observed for aquatically feeding swans was very similar to that seen by Owen and Cadbury (1975). There was a steady rise in feeding until between seven and eight hours after sunrise, ie an hour later than that for *C. c. bewickii*. Roosting is the dominant activity in the morning, preening reaches its maximum (18%) between 1100 and 1200 hours, while head-up occurs throughout the daylight period at between 18% and 47%.

This major difference in feeding activity pattern is attributable to the fact that birds feeding on fields must fly to and from the roost and are unable to feed during the hours of darkness. Birds on water, on the other hand, do not have the extra energy requirements of flight and can continue to feed after dark.

The requirements immediately before the spring migration, when fat reserves must be laid down for the migration and, in the case of females, for egg production and the incubation period, are likely to be greatest. Any differences in feeding between the sexes should be most marked at this time.

*C. c. cygnus* being herbivorous is limited by a low energy diet. As far as is known, there is no cellulose digestion by geese (Marriott and Forbes 1970; Mattocks 1972) and it is reasonable to assume the same for swans. Swans, like geese, counter these factors by a rapid throughput of a large volume of food. Grazing is limited by the gizzard's capacity to process food. For any given energy requirement, therefore, there is a fixed lower time in which the necessary food quantity can be processed. When daylight is equal to this minimum necessary foraging time, the birds will be at starvation level and will lose weight. Such weight loss can be accepted if the overall energy budget is balanced in the long term.

## Feeding rate

Time spent foraging is dependent on several proximate factors such as: a) energy requirements, in turn dependent on each individual's weight and metabolic rate, b) daylength, c) weather factors such as low temperature. The ultimate factors involved may be the risk of mortality from predators or from collision during flight due to remaining on the fields after dark. Without changing to a higher energy food supply swans under physiological or environmental stress could: a) feed faster, b) feed longer, c) feed faster and longer. As can be seen from the winter time budget data (Table 2), the time spent feeding increases even though daylength is also increasing. In November and December the feeding day is of approximately nine hours. This increases to 11 hours by February and 13 by March. The cumulative percent of time feeding for any given number of hours after dawn is generally similar except in January/February, eg nine hours after dawn the cumulative percent feeding is 636.4 in November, 654.12 in December, 551.96 in January/February and 696.96 in March. However, the cumulative totals for each month increase progressively. As daylength increases, more time is spent feeding (Table 3).

Table 3. Cumulative percent of time feeding, winter 1977/78.

| Time | November | December | January/February | March |
|---|---|---|---|---|
| 06⁰⁰–07⁰⁰ | | | | 85.91 |
| 07⁰⁰–08⁰⁰ | | | 29.1 | 170.41 |
| 08⁰⁰–09⁰⁰ | 72.27 | 82.65 | 86.25 | 246.86 |
| 09⁰⁰–10⁰⁰ | 139.62 | 170.33 | 161.95 | 321.86 |
| 10⁰⁰–11⁰⁰ | 225.47 | 247.47 | 237.78 | 391.06 |
| 11⁰⁰–12⁰⁰ | 311.14 | 312.69 | 274.55 | 461.98 |
| 12⁰⁰–13⁰⁰ | 340.04 | 367.29 | 318.75 | 534.48 |
| 13⁰⁰–14⁰⁰ | 398.49 | 433.64 | 385.34 | 619.76 |
| 14⁰⁰–15⁰⁰ | 481.12 | 523.25 | 459.9 | 696.96 |
| 15⁰⁰–16⁰⁰ | 562.82 | 605.95 | 551.96 | 769.31 |
| 16⁰⁰–17⁰⁰ | 636.4 | 654.12 | 626.12 | 845.56 |
| 17⁰⁰–18⁰⁰ | | | 677.42 | 907.44 |
| 18⁰⁰–19⁰⁰ | | | | 979.23 |

Not only is the length of the feeding day extended by March but the mean hourly level of feeding is also highest. Time spent feeding is only a relative measure of feeding intensity. The quantity of food ingested and hence the energy gained during a day is also dependent on the rate of feeding. The pecking rate of adults, yearlings and parents was measured whenever possible by the method used by Owen (1971). Birds were selected randomly and the number of pecks made during one minute was measured directly between 1977 and 1979. A different method was used in 1979/80 because within a minute's sample there was a high chance that another behaviour would interrupt feeding. This involved measuring the time taken to make 20 pecks. Pecks per minute were then calculated.

The increase in time spent feeding in March 1978 was not correlated with a
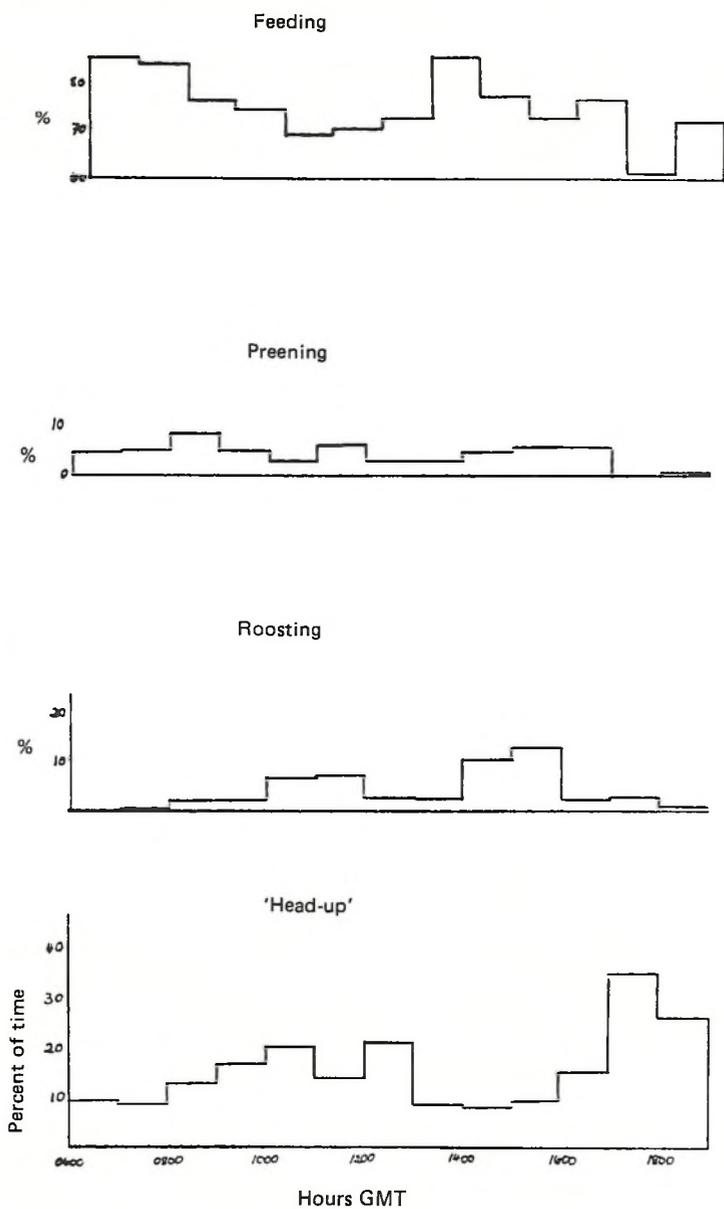
**Feeding**

**Preening**

**Roosting**

**'Head-up'**

Hours GMT

Fig 6.   Activity budget: March 1978.

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decrease in peck rate. The latter is assumed to be equivalent to ingestion rate as no peck should be unsuccessful. This suggests that, overall, more food is ingested per day in late winter, because the birds' physiological requirements have changed.

The effect of time of day on pecking rate was also studied. Several observations were usually made within a period of ten to 15 minutes. In three consecutive winters the relationship was very similar. Peck rate increased linearly throughout the day, eg January 1980 (r = 0.5, p < 0.01) to a maximum of over 65 pecks per minute (Fig 7). This is exactly the same relationship as that found by Owen (1972)
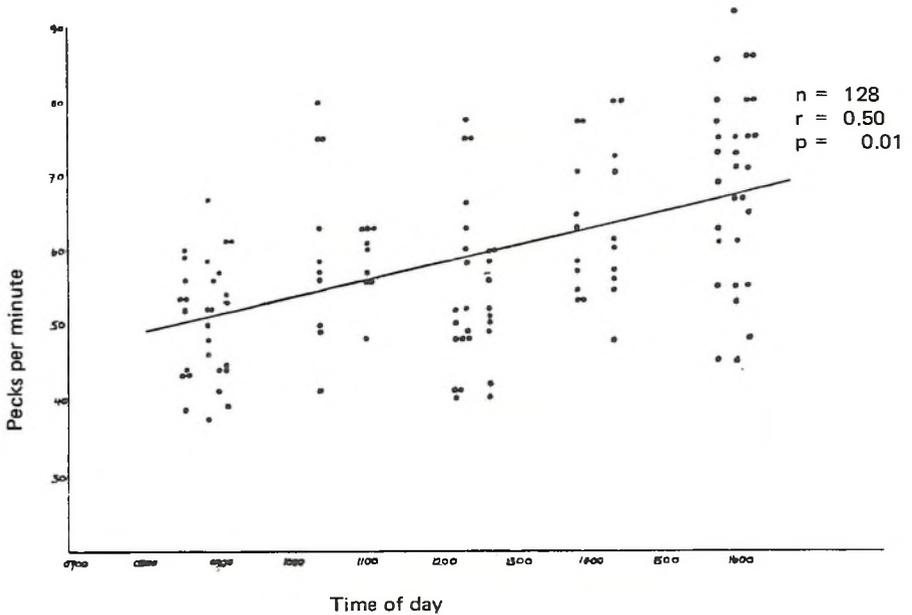


Fig 7.  Peck rate of adults, January 1980.

for *Anser albifrons,* although its pecking rate was over twice as high. In *A. albifrons* there is evidence that the increased rate of feeding towards evening leads to an accumulation of grass in the long elastic oesophagus because the gizzard is unable to process it fast enough. It seemed very likely that this would occur in field feeding *C. c. cygnus,* and a yearling bird which flew into powerlines on its way to the roost had an oesophagus full of small pieces of grass.

In March 1978 both adults and yearlings showed the same linear increase through the day in pecking rate. The slope of the regression lines is very similar (r = 0.318 adult, r = 0.321 yearlings) but that of the yearlings lies above that of the adults. Adult peck rate begins in the morning at about 45 ppm and increases to about 55 ppm, while yearling peck rate begins at about 55 ppm and rises to about 65 ppm.

In contrast to *A. albifrons* which rests more on the longer days, *C. c. cygnus* uses the latter to feed for longer. There is a slight increase in preening, time spent roosting during the day is reduced and head-up remains constant.

## Vigilant behaviour

At any one time there is usually at least one flock member in head-up position and looking around. Since a flock is a heterogeneous mixture of birds of different reproductive status and since birds of different status will have differing motivation for feeding and 'vigilance', then it is to be expected that there should be some behavioural differences between such classes.

Parents, having expended a great deal of energy during the summer in terms of egg production, nest building, incubation, nest and territorial defence and attention to the young, will be in relatively poor condition by the autumn. Non-breeders, having expended no energy in reproductive effort, should be in good condition. Young birds of the year are still growing and have recently migrated and have a great deal of weight to gain. Therefore, parents should ingest more food than non-breeding adults. Young should ingest more food than adults. However, these expectations will be confounded by the conflicting requirements of vigilant behaviour. There is likely to be some behavioural investment by parents in their offspring and this is likely to take the form of vigilance directed towards those offspring and more time generally alert for potential dangers to them. Adults without offspring should spend less time in head-up position than parents. There is no evidence that second-year birds rejoin or nelp their parents. Young birds may not have fully developed the normal pattern of vigilant behaviour. They can rely on their parents being vigilant but can feed only by their own efforts, hence they will spend less time head-up than either their parents or adults.

If parents have both the greatest energy requirements and the greatest motivation for head-up of the three classes, then they may feed faster in between bouts of head-up. Young birds, on the other hand, may spend longer feeding and less time alert or longer feeding and feed faster.

Birds were chosen at random and followed until they became vigilant. The interval between this first bout of head-up and the next was timed with one stop-watch and the length of the following bout of head-up was timed with a second. Parents raise their heads for a mean time of 10.1 sec, adults for a mean time of 9.2 sec and young birds for 7.2 sec. Although the differences between the bout lengths of head-up for the different reproductive classes are not significant (using the Mann Whitney U test), the trend of the means, with parents spending longest and young birds spending shortest times head-up, is, as was expected, when considering the likely relative motivation for this behaviour.

Although the lengths of bouts of head-up do not differ significantly between the

three classes, the period from one bout of head-up to the next does. The inter head-up period for parents had a mean length of 40 sec, for adults 77 sec and for young birds 175 sec. The differences between parents and adult and between parent and young were significant ($p = 0.002$, $p = 0.00003$, Mann Whitney U test) but not that between adults and young ($p = 0.389$). Parents, then, are head-up more frequently than either adults or young, although not for longer, again as anticipated.

Frequency and length of bouts of head-up are factors having direct effects on feeding, since these behaviours are mutually exclusive. It follows that parents have less time to feed than either adults or young. If they have to make up condition lost during the breeding season, then they must feed faster or select foods of higher energy values. As yet, there is no evidence on these points. Immatures spend less time head-up less frequently than other birds, thus providing extra feeding time, but they also feed faster than adults. This would enable them to increase in weight rapidly during the winter. Feeding time might also be extended in young birds because they may be less efficient feeders than adults.

It is expected that parental vigilance will decline during the winter as their offspring become larger and older. During winter 1977/78 for all months except November and January there was no significant difference between the lengths of bouts of head-up for the three classes but in November, just after arrival when young birds are relatively small, parents spent longer head-up than they did ($p < 0.01$, Mann Whitney U test). In January young spent longer alert than adults ($p < 0.05$, Mann Whitney U test). It is not known why. The longer bout lengths of head-up in November shown by parents agree with the assumption that parental investment is in the form of vigilance and this declines through the winter. The difference may be increased at this time since the young will need to feed more at this stage and will not have fully developed the adult behavioural sequence of regular head-up interspersed with feeding.

By March all birds spend longer on the foraging grounds and spend longer feeding. This increase in feeding prior to the migration leads to the disappearance of any differences in the inter head-up bouts between the three classes.


Flock size and behaviour

It is evident that flock size affects some aspects of individual behaviour, especially vigilance. Where vigilance increases, other behaviours must decrease and there will be some reduction in feeding time which might be compensated for by a faster feeding rate. The levels of vigilance for a range of flock sizes from 1 to 150 was measured to test for *C. c. cygnus* the hypothesis as stated by Lazarus (1978): 'If flocking reduces the individual's risk of capture by a predator, then the time spent by individuals in vigilance will decline as flock size increases, since the benefit to be gained from such vigilance also declines'.

Scans of the flocks were made, one every minute. At each scan the proportion of birds head-up was recorded and after ten scans the results were combined to produce a mean proportion of head-up. The number of birds vigilant was significantly correlated with flock size ($r = +0.85$, $n = 86$, $p < 0.001$). The percentage of birds vigilant declined significantly as flock size increased ($r = -0.40$, $n = 89$, $p < 0.001$), declining rapidly at first before levelling out at a flock size between ten and 20 (Fig 8). Individuals in larger flocks thus spend less time in vigilant behaviour and therefore have more time available for other activities such as feeding.
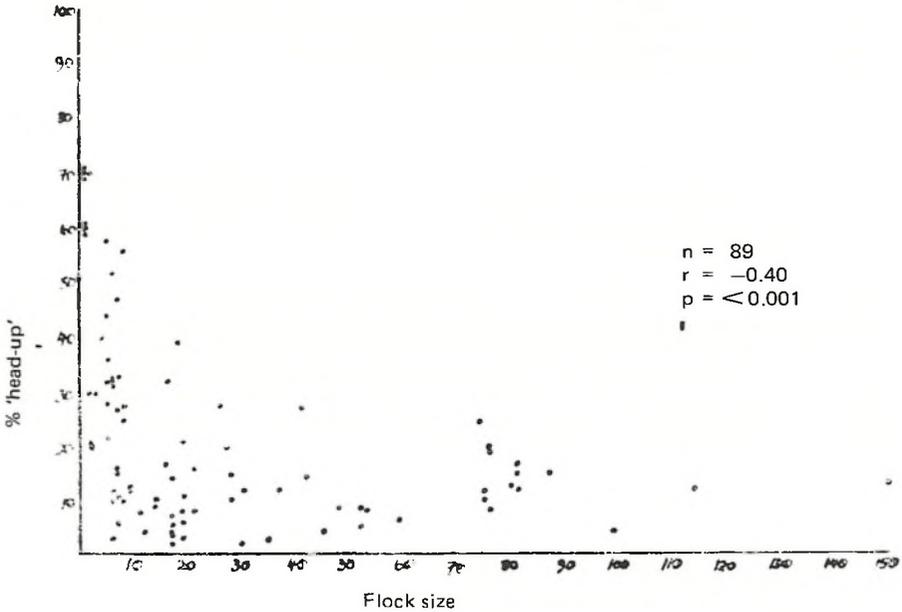


Fig 8. The relationship between flock size and the proportion of the flock which is 'head-up'.

It could be that individuals assess the size of the flock they are in and adjust their behaviour accordingly or that, because of the 'peripheral predation' phenomenon (Lazarus 1978), individuals on the edge would be expected to be more vigilant, as suggested by Drent and Swierstra (1977). As flock size increases, the periphery will represent a reduced proportion of the flock. The structure of swan flocks is different from that of geese. The flocks are usually smaller and flock shape is far less regular. It is not possible, therefore, to assess whether individuals are peripheral or central and in small flocks it seems unlikely that this factor would be important. Nearest neighbour distance could well be an important factor in regulating vigilant behaviour.

The important implication of reduced vigilance by individuals in larger flocks is that more time is available for feeding. This was conclusively demonstrated by Abramson (1979) working on *Numenius arquata*. He showed that look-up decreased significantly as the number of birds increased, while the number of prey captured per individual increased.

## Acknowledgements

## Summary

In central Scotland the size and structure of flocks and their use of agricultural land and patterns of movements between roosting and foraging sites are examined. Birds in autumn feed on waste grain from stubble fields and switch to young grass in January/February. This switch also involves a change in roost site.

Feeding occupies between 62% and 73% of time during autumn and midwinter. Diurnal and seasonal feeding patterns are described and comparisons drawn between aquatic and terrestrially feeding swans. The former slowly increase the proportion of time spent during the day, the latter have distinct morning and afternoon peaks. Feeding as a proportion of the daylight hours increases prior to the spring migration and feeding rate increases prior to evening roost flights. Their behaviour in winter is discussed with reference to environmental and physiological stresses imposed upon them throughout the year.

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M BRAZIL
University of Stirling
Department of Psychology
Stirling
Scotland FK9 4LA

# FOOD SELECTION BY *CYGNUS OLOR* IN CHESAPEAKE BAY, MARYLAND

## G H FENWICK

The food habits of non-native *Cygnus olor* in Chesapeake Bay were examined between 1975 and 1978 to determine their effects on the aquatic food supply of native wintering waterfowl. Swan food preferences and daily intake were determined by faecal and gizzard analysis, floral analysis of swan nesting and moulting areas and testing with captive birds.

Preference for submerged vascular vegetation by *C. olor* was demonstrated by