FEEDING BEHAVIOUR OF WIGEON *ANAS PENELOPE* ON VARIABLE GRASSLAND SWARDS

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Wigeon in winter have a specialised grazing behaviour which involves repeatedly returning to the same feeding areas of short grassland. Two experiments are described which examined their behavioural adaptations to this type of grazing. A study on captive birds showed that they exhibited highest peck rates on grass of 30 mm height and peck rates declined on both taller and shorter grassland. Wild birds were shown to concentrate their grazing on high quality fertilised grassland, through slower walking speeds and increased peck rates.

Keywords: Wigeon, Feeding Behaviour

Wigeon are the smallest species of grazing waterfowl, being half the size of the smallest British goose, the Brent *Branta bernicla*. Their size imposes constraints on their behaviour because Wigeon need to feed for about 14 hours a day in order to obtain their daily energy requirements (Mayhew 1988). A feature of Wigeon feeding is that they do not use extensive areas of grassland like geese, but repeatedly return to the same areas of short grass swards (Owen 1973, Cadwallader & Morley 1974), and it has been shown that this repeated, intensive grazing stimulates grass growth and results in an elevated protein content (Mayhew & Houston, 1999). A consequence is that Wigeon often feed on grass that has previously been intensively cropped, and this paper considers the way in which grassland height and quality influence feeding behaviour of Wigeon.

For many herbivores it has been shown that there is an almost linear increase in food intake with increasing sward height, until a point is reached beyond which there may be no further increase, or a decline, in feeding rate (Crawley 1983). This relationship is called the functional response. The small size of Wigeon makes it likely that the type of grassland that provides them with favourable grazing conditions may differ substantially in height from that chosen by geese. We examine how peck rate varies with grass height in a captive flock of birds. We also consider how wild birds alter their behaviour so that they graze most intensively in sites where they can maximise energy intake. While birds are feeding they will experience patches of high and low quality grassland. To forage efficiently they need to maximise the time they spend in good quality habitat and minimise the time spent in poorer quality patches. We therefore considered the effect of grassland quality on the peck rate and speed of walking of birds.

Methods

Captive bird experiment to record how peck rate varied with grass height

Ten (six male, four female) pinioned wigeon, all first year birds, were obtained from The Wildfowl & Wetlands Trust Martin Mere reserve, where they had been bred. The experiment was conducted at the WWT Caerlaverock reserve on the north shore of the Solway Firth, Scotland, during April/May 1981. The birds were housed overnight in a fox and mink-proof exclosure and fed solely on grass. The experiment was conducted in a grazing enclosure (6 m x 2.5 m) into which the birds were gently herded each day. They were left to settle for 1.5 hours before any observations commenced, from a hide about 10m away. A focal bird was chosen at random and then timed for 25 pecks with a stop watch (Owen 1972). If a bird stopped grazing for more than 5 s the result was discarded. For shorter breaks, the watch was stopped till grazing resumed. The data were collected over 17 days (about 25 sets of peck rate observations were recorded each day) so that the grass height in the enclosure was gradually grazed down. Grass height was calculated each morning from the mean of a sample of 35 random measurements of the length of the longest grass blade touching a vertical ruler held at soil ground level.

Fertiliser experiment to record how wild birds responded to changes in grassland quality

This experiment was also carried out at the Caerlaverock reserve. About 800 birds winter at this site feeding on the agricultural grasslands adjacent to man-made ponds (Mayhew & Houston 1989). In late September 1982, 10 grassland strips, 3 m wide were marked with short coloured bamboo posts. Alternate strips were fertilised with standard agricultural fertiliser (22N: 11K:11P) applied at the rate of 20 gm^{-2}. A warm, damp autumn resulted in obvious biomass differences by late October and data on site use and grass quality differences were collected during November. Differential use of the strips by Wigeon was assessed by 14 droppings quadrats (Mayhew & Houston 1989), randomly placed on the fertilised and unfertilised strips - all within 5 m of water. Biomass of the strips was measured adjacent to the 14 quadrats using a spectrophotometer (Mayhew *et al.* 1984). Protein content of the grass was assessed by hand-grazing grass from an approximate 15 cm x 15 cm plot, chosen at random, on each strip. Samples from each treatment (fertilised/unfertilised) were pooled, thoroughly mixed, and protein content assessed using an automatic Kjeldahl analyser (Kjel-Foss 16200; a factor of 6.25 was used to convert nitrogen to protein values). Grass height was not measured, though casual observation suggested little difference between strips. Peck rate (time for 50 pecks) and step rate (time for 20 steps) were measured as in the captive bird experiment. A minimum of 35 peck or step rates were recorded for each treatment, *ie* fertilised/unfertilised. If a bird moved out of a strip during the observation, the result was discarded.

Results

We examined the data in both experiments for differences between the sexes (Mayhew 1987) but found none, so observations have been combined.

Captive bird experiment

Figure 1 shows the relationship between grass height and peck rate on a range of grassland heights. Grass height of 30 mm gave rise to the highest rate of feeding and, above this height, there was a highly significant relationship between the rate of pecking and grass height, such that feeding rate was progressively slower on taller grass (r^2 = 0.22, df = 363, P<0.001). Grass heights of 25 mm or less, however, resulted in a greatly reduced peck rate, primarily because green grass biomass was so low that it took longer for birds to locate edible grass blades.

Fertiliser experiment

The application of fertiliser to the grassland resulted in differences between fertilised and

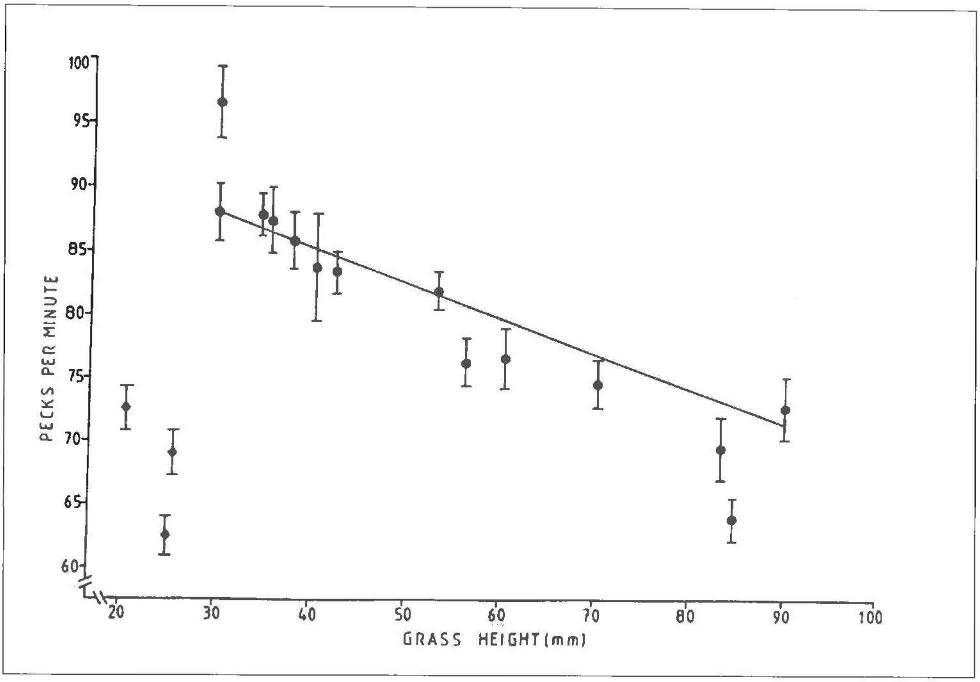

Figure 1. Mean peck rate (± s.e.) of captive Wigeon on grass of varying height. Regression for points above 30 mm y = -0.271x + 96.07, *n* = 365.

unfertilised strips for both green grass biomass (84.4 ± 4.8 (s.e.) and 62.0 ± 3.1 gm^{-2}; t_{12} = 3.93; $P<0.01$) and protein content (24.4 and 18.3%; single analysis of pooled sample). Grazing use of the fertilised strips was almost three times that of unfertilised strips (20 ± 2.1 and 7.7 ± 2.1 droppings/quadrat; t_{12} = 4.24; $P<0.01$).

Peck rate was highest on the fertilised strips (99.1 ± 2.1 and 86.2 ± 2.0 pecks per minute on fertilised and unfertilised respectively, d = 4.38; n = 37, 35; $P<0.001$) while step rate was lower on fertilised strips (25.0 ± 2.1 and 37.8 ± 2.6 steps per minute respectively, d = 3.82; n = 33, 34; $P<0.001$).

Discussion

This study used observations on captive and wild birds. The use of captive birds always raises the problem that they may behave differently from wild birds. Two main factors are responsible. Firstly the birds may be stressed. However, our birds were born in captivity, were tame, and were allowed a settling period before any observations were carried out. Secondly, it is well known that the gut morphology of captive birds can differ from those in the wild (Moss 1972, Owen 1975) in response to the change in diet quality. In these trials we kept the birds on a completely natural diet (grass) and it is unlikely that their digestive physiology differed sufficiently to influence the behaviour observations.

Previous studies (Mayhew 1987, Mayhew & Houston 1989, 1999) have suggested that the Wigeon's habit of repeatedly grazing short grass swards adjacent to water could have two main advantages - predator avoidance and increased protein intake in late winter. The disadvantage of this behaviour is the lost opportunity of feeding in taller, higher biomass areas (Mayhew & Houston, 1999) which, theoretically, should be advantageous to a bird with relatively high energy demands (Mayhew 1988). The results presented here support the view that Wigeon, with their short broad bills, are able to, at least in part, maintain their rate of food intake on short, intensively grazed grassland, by increasing their peck rate.

Clearly the recording of pecking frequency does not directly measure food intake, because birds may alter the size of bite taken according to the speed of feeding. If they take a larger leaf size when feeding on taller grass then higher peck rates may not lead to higher intake rates, and this is known to occur in Barnacle Geese *Branta leucopsis* (Drent & Swierstra 1977). However, peck rate is an important factor influencing food intake and Kenward & Sibly (1978) found in Woodpigeons *Columba palumbus* that although the size of leaf taken at each peck varied with the peck rate, the rate of intake was still correlated with peck rate. There is evidence that this also applies to Wigeon. Jacobsen (1992) studying breeding Wigeon in Norway, found that, while peck rate decreased with increasing vegetation height through the spring, there was no coincident increase in bite size, which remained at about 2-2.3 cm. He also found an inverse relationship between peck rates and defecation intervals, coincident with constant dropping weight. He concluded that intake rate increased with peck rate.

Clearly there will be a threshold on heavily grazed grassland, at which peck rate cannot compensate for reduced biomass and intake rates begin to fall, particularly in late winter (Mayhew & Houston, 1999). Further work is required to determine this threshold and thus clarify the trade-offs between energy intake, protein intake and predator avoidance.

A change in walking speed with grassland quality is known to occur in geese (Harwood 1975) and results in birds spending longer periods in the better feeding areas (Teunissen *et al.* 1985). Wigeon clearly show this behaviour, and wild birds which moved between fertilised and unfertilised grass altered their peck and step rate resulting in increased time and more intensive grazing on higher quality grassland. This behaviour will help them to forage efficiently in a mosaic of patches of grassland of varying quality. A practical application of this technique would be to use fertiliser to concentrate Wigeon feeding in particular reserve areas and to improve the quality of grazing available in such areas.

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