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ORIGINAL ARTICLE

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Variation of pecking rate with sward height in wild wigeon *Anas penelope*

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Abstract We examined how pecking rate changed with sward height in wintering European wigeon *Anas penelope* in a nature reserve of the French Atlantic coast. Pecking rates were recorded as the time taken to perform 10 or 50 pecks. We found a negative correlation between pecking rate and sward height over a range of heights from 1.0 to 3.5 cm, but no sex effect. Equations based on the time taken to perform 10 or 50 pecks were slightly different, suggesting that scanning (scans of the surroundings) and moving (search for plant items of good quality) had an effect on pecking rate. However, these costs were lower (i.e. a decrease of 6–10% of pecking rate) than the effect of handling time, which remained the dominant foraging process constraining pecking rate (i.e. a decrease of 24% with each 1-cm increase in sward height).

Keywords Foraging efficiency · Functional response · Handling time · Wigeon *Anas Penelope*

Introduction

Following studies on mammalian herbivores, the functional response (i.e. the relationship between intake rate and food quantity; Holling 1959) has been the focus of an increasing number of papers in herbivorous birds in the last 10 years (Hewitt and Kirkpatrick 1996; Rowcliffe et al. 1999; Hassall et al. 2001; Lang and Black 2001; Durant et al. 2003). The functional response is important in explaining the birds' spatial and temporal distributions, and thus habitat use (Piersma et al. 1995). Indeed, intake rate has been shown to be one of the crucial factors in patch choice in herbivorous ducks and geese in combination with parameters of food quality, i.e. nitrogen content (Riddington et al. 1997; Hassall et al. 2001; Durant et al. 2004).

One of the methods used to estimate the instantaneous intake rate (IIR) of birds is to record pecking rate (i.e. the frequency of pecks per minute) and peck size (i.e. the mass of plant tissue taken per peck) independently from each other. IIR is then calculated as the product of these two components (Prop and de Vries 1993; Durant et al. 2003). Pecking rate is recorded by a direct method of observation, and is defined as the time for an individual to perform a given number of pecks (Owen 1972; Madsen 1988; Mayhew and Houston 1993). Peck size is less easy to measure accurately, but can be obtained from the ingestion rate of food using captive birds. The ingestion rate in itself is defined from the mass of droppings collected by correcting for food assimilation efficiency using an internal marker (see Durant 2003 for a review). Peck size is then estimated by dividing the amount of ingesta by the number of pecks taken per minute (Owen et al. 1992; Durant et al. 2003). Intake rate can also be estimated in the wild, from the measurement of dropping rates (Prins et al. 1980; Van der Wal et al. 1998), when plant digestibility is known.

Many studies on foraging of herbivorous Anatidae have reported measurements of pecking rate in a large range of species (Prins et al. 1980; Madsen 1988; Kotrschal et al. 1993; Therkildsen and Madsen 2000). Factors affecting pecking rate are numerous; for instance, it varies from one species to another (Fox et al. 1992; Durant et al. 2003), or according to the sex (Jacobsen and Ugelvik 1994). The grazing rate of geese was also reported to vary markedly over the daylight period (Owen 1972; Ebbinge et al. 1975; Owen et al. 1992), and according to the season (Jacobsen 1992; Owen et al. 1992). Pecking rates vary with sward height

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and/or biomass (Drent and Swierstra 1977; Sedinger and Raveling 1986; Meire and Kuijken 1991; Black et al. 1992; Jacobsen 1992; Mayhew and Houston 1998; Hassall et al. 2001). As in mammalian herbivores, some Anatidae species have been shown to respond to a decrease in sward height by increasing their feeding rate, i.e. their pecking rate, in order to compensate for a smaller peck size thereby aiming to maintain a high rate of intake (Durant et al. 2003).

In this study, we examined how pecking rate changed with sward height in wintering European wigeon *Anas penelope*. Mayhew and Houston (1998), as well as Durant et al. (2003) in a recent study, found a negative correlation between pecking rate and vegetation height in captive wigeon. But, to our knowledge, only one study has focused on this species in the wild during the winter season (Mayhew 1985). Such investigations are, however, crucial to estimate intake rate of wigeon in the wild and the variation of feeding components in relation to grass characteristics.

Methods

The study was carried out in the nature reserve of Moëze-Oléron, on the French Atlantic coast (Charente-Maritime, 45°53′N, 1°05′W) from December 1999 to February 2000. This reserve is a wintering area of national importance for wigeon (Deceuninck and Maillet 1998), where an average of 3,000–3,500 individuals can be observed. The observations were performed on a former salina of 58 ha, constituted of a series of ridges and flooded depressions with brackish water. Observations were made within flocks of wigeon (10–100 individuals) visiting a set of ten plots (8×8 m squares, the corners of which were marked with white stones). Plots were set out on ridges grazed by highland ponies. The sward height (dominated by the grasses *Lolium perenne*, *Dactylis glomerata*, and the herb *Medicago arabica*) in each plot was estimated as the mean of 30 random measurements taken with a sward stick, i.e. a 4-cm square of polystyrene and a graduated stick (Summers and Critchley 1990). This was done after each observation session, at night in order to avoid disturbance of the birds. Plots varied in mean sward height from about 1.0 to 3.5 cm. We could not measure pecking rate on taller swards since wigeon showed a preference for short grass areas, and repeatedly returned to these areas.

The pecking rate was defined as the time taken by an individual to perform 10 or 50 pecks (measured with a stop-watch) and expressed as pecks/min (Madsen 1988). A combination of the two measures renders us information on scanning and moving times. Vigilance costs as well as costs for locomotion were neglected for all measurements of 10 pecks as birds pecked without scanning and did not walk (or only one to two paces, but pecks occurred in the same feeding station). With 50 pecks, however, scans of the surroundings by birds occurred (in general scans lasted about 1 s), and birds were moving from one feeding station to another, which was associated with the need for the bird to search for plant items of good quality. If a bird did not perform these pecks continuously, e.g. when long interruptions by head-up postures occurred, the measure was discarded. Pecking rates were recorded during the morning and afternoon feeding times (1100–1800 hours), and on several different individuals (males and females) selected randomly.

Results

We first tested for the effects of sward height and sex and the interaction term (sward height × sex) on the pecking rate calculated on the basis of 10 or 50 pecks (MANOVA). There were no differences in pecking rates between males and females (on the basis of 10 pecks: $F=0.48$, $df=1$, $n=80$ females, $n=61$ males, $P=0.49$; 50 pecks: $F=0.21$, $df=1$, $n=35$ females, $n=38$ males, $P=0.65$). For both 10 and 50 pecks, the interaction was not significant, showing that the slope of the relationship between pecking rate and sward height was not different between males and females. We found a negative correlation between pecking rate and sward height over the range of heights measured. Pecking rate strongly decreased from about 140 pecks/min on 1-cm-high swards to 80 pecks/min on sward of 3.5 cm in height. The equations are: $y=-27.8x+175.6$, $df=13$, $n=141$, $r^2=0.40$, $F=12.74$, $P<0.001$; and $y=-27.2x+167.9$, $df=10$, $n=73$, $r^2=0.61$, $F=16.52$, $P<0.001$ (Fig. 1), for relationships established from the time taken to perform 10 and 50 pecks, respectively. There was a significant difference between those two relationships ($F=4.45$, $df=1$, $n=217$, $P=0.036$), but the interaction sward height × pecking rate measurement method (10 or 50

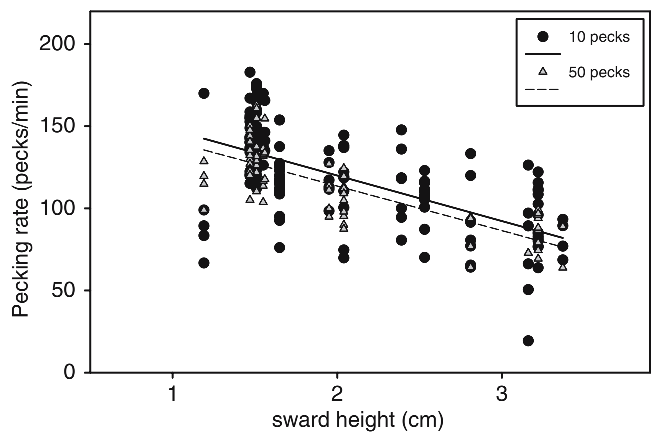

Fig. 1 Relationship between pecking rate (pecks/min) and sward height (cm) in wild wigeon *Anas penelope*. Data are from measurements on the basis of 10 pecks (equation: $y=-27.8x+175.6$, $n=141$, $r^2=0.40$, $F=12.74$, $P<0.001$), or 50 pecks (equation: $y=-27.2x+167.9$, $n=73$, $r^2=0.61$, $F=16.52$, $P<0.001$)

pecks) was not significant ($F=0.53$, $df=10$, $n=217$, $P=0.87$), and thus the slopes were not different.

Discussion

Our results of pecking speed (80–140 pecks/min) fell partly within the range of those reported in Mayhew and Houston (1998) in captive wigeon. For example, at 3.5-cm sward height they found a pecking rate of 85–90 pecks/min against 80–85 pecks/min in this study. However, the mean pecking rate was much higher than that found in captive birds by Durant et al. (2003) especially for very short grass (1–2 cm high). In wild birds, pecking rates reached a mean of about 140 pecks/min, which has never been recorded in wigeon before (Jacobsen 1992; Jacobsen and Ugelvik 1994). This can be explained by several factors. First, the methods used were not exactly the same: the mean pecking rate was calculated on a basis of the time taken to perform 10 or 50 pecks in this study, and 25 pecks in Mayhew and Houston (1998). Anyhow, there was only about a 10 pecks per minute difference between our two methods, which could not explain the difference observed by Mayhew and Houston (1998). In Durant et al. (2003), the authors divided the total number of pecks given by birds by total grazing time of about 20 min (however, not including long vigilance bouts). This difference in methodology is thus likely to produce lower pecking rates with the latter method (i.e. due to the time taken by birds to search for patches of good quality). Second, captive birds may behave differently from wild birds, i.e. with a lower pecking speed. Third, it may be linked to differences in sward density and species composition of pastures between studies, which has been shown to affect biting rates in mammalian herbivores (Black and Kenney 1984), and has been supposed also to affect pecking rates in grazing Anatidae (Black et al. 1992; Lang and Black 2001).

We found a negative relationship between pecking rates of wigeon and sward height, as reported elsewhere for this species (Jacobsen 1992; Mayhew and Houston 1998; Durant et al. 2003). Following the reasoning developed by Durant et al. (2003), who adapted the Spalinger–Hobbs model (Spalinger and Hobbs 1992) of mammalian herbivores to herbivorous Anatidae for resources (grasses) being spatially concentrated and apparent (process 3 of the model), this negative relationship is characteristic of handling limited foraging. As sward height increases peck size also increases (even if moderately in wigeon; see Durant et al. 2003). The handling time per peck (i.e. time to peck, to handle leaves in the bill and to swallow them) increases accordingly, which lowers pecking rates. Vegetation processing (handling time) is thus an important foraging process constraining pecking rate.

The 50 peck method gave a slower pecking rate compared to the 10 peck one (7–8 pecks/min of difference; Fig. 1). This suggests that scanning and moving had an effect on pecking rate, here irrespective of the sward height. This was in agreement with Fritz et al. (2002) who showed that scan rate in Mallards *Anas platyrhynchos* certainly decreases IIR through a decrease in peck frequency. These costs were however lower (amounting to a decrease in pecking rate of 6–10%) than the effect of handling time, which remained the dominant foraging process constraining pecking rate (i.e. a decrease of 24% with each 1-cm increase in sward height). Our observations show that the wigeon, with its short and narrow beak, is able to graze efficiently on swards as short as 1 cm. This species is able to compensate a deficiency in bite size, given by the length of the sward, by a quite pronounced increase in pecking rate (up to 24%; see also Durant et al. 2003). This mechanism can explain why wigeon in the nature reserve of Moëze showed a strong preference for very short swards of 1–4 cm in height; D. Durant et al., unpublished data). Maintaining an almost constant intake rate by means of this compensation mechanism, wigeon should thus select short grass, which is of better quality than taller swards (Summers and Critchley 1990). We say *almost* since on very short grass, peck size decreases to a level where the fastest possible pecking rate cannot completely compensate, and thus intake rate shows a slight decrease (Durant et al. 2003). By preferring short swards, wigeon thus maximise their nutrient (in particular protein) intake rate (Durant et al. 2004).

In conclusion, despite the narrow range of sward heights covered, this study shows the effect of sward height on bird grazing efficiency, i.e. a negative relationship between pecking rate and vegetation height. Recording of peck frequency does not directly measure food intake (because birds can change the size of their bite according to peck frequency). However, combined with peck size measurements on captive birds, observations of that type are useful to understand the general mechanisms of food intake in herbivorous Anatidae.

Zusammenfassung

Abhängigkeit der Pickrate von der Grashöhe bei der Pfeifente (Anas penelope)

In einem Schutzgebiet an der französischen Atlantikküste untersuchten wir, wie die Pickrate überwinternder Pfeifenten *Anas penelope* von der Grashöhe bestimmt ist. Als Pickrate wurde die Zeit genommen, die die Enten brauchten, um 10 oder 50 Picks durchzuführen. Bei einer Grashöhe von 1–3,5 cm war die Pickrate negativ korreliert mit der Grashöhe. Unterschiede zwischen den Geschlechtern bestanden nicht. Unterschiede zwischen 10 und 50 Picks werden auf vermehrte Beobachtung der Umgebung und der Suche nach qualitativ guten Pflanzen zurückgeführt. Die Kosten hierfür waren aber geringer (Abnahme der Pickrate von 6–10

%) als der Aufwand für die Handhabung der Nahrung, die der dominante limitierende Faktor bei der Nahrungsaufnahme ist (Abnahme der Pickrate von 24 % mit jedem zusätzlichen cm Graslänge).

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