The functional response in three species of herbivorous Anatidae: effects of sward height, body mass and bill size

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Summary

1. The functional response, i.e. the quantity of food consumed per unit of time as a function of food availability, is a central process in foraging ecology. The application of this concept to foraging by mammalian herbivores has led to major insights into the process of resource acquisition, but it has so far been little used to understand foraging in avian herbivores.

2. In this study, we describe the functional responses of three grazing Anatidae, the wigeon *Anas penelope* L. (mean body mass in this study 620 g), the barnacle goose *Branta leucopsis* B. (2000 g), and the greylag goose *Anser anser* L. (3500 g). We measured instantaneous intake rates on eight grass heights from 1 cm to 12 cm, as well as pecking rates and peck sizes, and used the Spalinger–Hobbs model developed for mammalian herbivores to explore the mechanisms limiting intake in these three species.

3. Greylag geese increased their intake rate with increasing food availability (a Type II response), wigeon showed a weak quadratic (Type IV) response, and intake rate by barnacle geese did not vary significantly across the range of variability we offered the birds.

4. Intake rates differed markedly between individuals, especially in greylag geese, where body mass explained much of the variation. For individuals in all three species, peck sizes strongly influenced instantaneous intake rates, and the size of the bill (width in particular) appeared to be an important determinant of peck size.

5. Peck sizes increased with sward height (although only very weakly in wigeon), but so did cropping time for wigeon and barnacle geese, which led to a significant decline of intake rates on the tallest grass, at least in the small wigeon. For these very selective small herbivores, the time to crop a mouthful was therefore a significant limiting factor for the birds' instantaneous intake rate (in addition to peck size and swallowing time). This differs markedly from the situation in mammalian herbivores where bite size (through chewing time) is the principal controlling process in food concentrated patches, a result that we found in greylag geese. We discuss the differences in foraging between the three species in relation to their principal food resources, body mass and bill morphology.

Key-words: body size, functional response, grass height, grazing, herbivorous Anatidae.

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Introduction

The functional response, the quantity of food consumed by an animal per unit of time as a function of food availability (Holling 1959), is one of the central processes in foraging ecology and this concept has helped to understand predator–prey and plant–herbivore interactions in many systems (Noy-Meir 1975; McNaughton 1984; Wanink & Zwarts 1985; Spalinger & Hobbs 1992; Goss-Custard *et al.* 1995a). This is particularly true for mammalian herbivores where functional responses have been described for many species. In herbivores, the consumption rate generally increases with the amount of available food, until an asymptote (a Type II response, Gross *et al.* 1993). In mammalian herbivores intake rates are commonly affected by body mass and mouth morphology (Illius & Gordon 1987; Demment & Greenwood 1988; Andersen & Saether 1992). Because the intake rate increases with bite size

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(Spalinger, Hanley & Robbins 1988) and larger herbivores obtain larger bites from their larger mouths (Gordon, Illius & Milne 1996), when the availability of food is not limiting, larger herbivores are able to ingest more plant biomass per unit time than are smaller animals. Functional responses are also affected by characteristics of the vegetation such as its structure, density and spatial distribution through the effects of these variables on the size and frequency of bites (Wickstrom *et al.* 1984; Spalinger *et al.* 1988; Spalinger & Hobbs 1992; Gross *et al.* 1993). The elucidation of these mechanisms has provided a useful framework to develop predictions on diet selection, habitat choice and competition for food between sympatric species (Illius & Gordon 1987).

Little is known about the mechanisms controlling intake rates in grazing Anatidae (ducks, geese and swans). The studies of mammalian herbivores foraging provide a conceptual framework for studying the mechanisms underlying functional responses of herbivorous birds (Hewitt & Kirkpatrick 1996). Pecking rates and peck sizes have been described in a number of goose and duck species (Prop & Deerenberg 1991; Black *et al.* 1992; Mayhew & Houston 1998). Vegetation characteristics are known to affect feeding behaviour (e.g. Rowcliffe, Sutherland & Watkinson 1999 for peck sizes and pecking rates; Van der Wal, Van de Koppel & Sagel 1998 for short-term intake rates). Charman (1979) found a Type II functional response for daily intake in brent geese *Branta bernicla* L. feeding on *Zostera*, and Rowcliffe *et al.* (1999) found a linear one for instantaneous intake by brent on green algae. As the shape of the functional response is an essential element for recent models relating the behaviour of wildfowl to the carrying capacity of wet grasslands and *Zostera* beds (Sutherland & Allport 1994; Percival, Sutherland & Evans 1996), more work is thus needed on this aspect of wildfowl foraging.

Interspecies differences in the processes limiting intake rate may help to understand resource partitioning in herbivorous Anatidae, as has been the case for mammals. The effects of variations in body and bill size on intake rates in different species of herbivorous Anatidae are not known. Because larger birds have larger bills, peck sizes and thus intake rates should scale with body mass as in mammals both at the interspecific (Shipley *et al.* 1994) and intraspecific (Gordon *et al.* 1996) level. In this study, we used three species covering a wide range of body sizes amongst Anatidae: wigeon *Anas penelope* L. (mean body mass in our study was *c.* 620 g), barnacle goose *Branta leucopsis* B. (*c.* 2000 g) and greylag goose *Anser anser* L. (*c.* 3500 g). The three species use swards of grass of varying heights (Rijnsdorp 1986; Jacobsen 1992), although only the barnacle goose is considered as a specialized grazer (Marchant & Higgins 1990), while for wigeon, *Zostera* beds on mudflats are also a major food resource (Mathers & Montgomery 1997), and greylag geese use tubers and rhizomes from *Scirpus* species when these

are available (Amat 1986). These species–specific preferences are likely to be a function of the rate of food intake that can be achieved on different sward heights: as data on functional responses are difficult to obtain in the field, we investigated the functional response of these three species experimentally.

We used the approach of Spalinger & Hobbs (1992) to explore the functional response of these grazing Anatidae: among the three processes described by Spalinger and Hobbs (S–H), Process 3 generally applies for grazers, where the resources (grasses) are spatially concentrated and apparent. It is primarily handling time (i.e. the time needed to crop and process a peck) that limits the intake rate. In S–H Processes 1 and 2, the food items are dispersed in space, detectable (Process 2) or not (Process 1) from a distance. In both processes, item density is low enough that one peck can be processed before the next is encountered. Thus in these cases, it is travel time or encounter rate between pecks that limits the intake rate.

Pecking rate (B, pecks min^{-1}) is the inverse of handling time (H, min peck^{-1}):

$$B = 1/H \qquad \text{eqn 1}$$

Handling time was defined as the time needed to crop a peck (T_C, min peck^{-1}) and to swallow a mouthful (T_S, min peck^{-1}) (Hewitt & Kirkpatrick 1996):

$$H = T_C + T_S \text{ (equivalent to } T_h = h + T_p \text{ in S–H 1992)} \qquad \text{eqn 2}$$

T_S increases with peck size, and thus,

$$T_S = S/R_{max} \qquad \text{eqn 3}$$

where, S is the peck size (mg) and R_{max} is the maximum swallowing rate (mg min^{-1}). Thus, substituting eqn 3 for T_S in eqn 2, and rearranging terms, the pecking rate can be written as:

$$B = 1/H = R_{max}/(S + T_C \times R_{max}) \qquad \text{eqn 4}$$

The pecking rate, B, should therefore decrease asymptotically with peck size, and H should increase linearly with peck size:

$$H = 1/B = T_C + (S/R_{max}) \qquad \text{eqn 5}$$

There are no measures of grass availability in these equations: in ungulate foraging under Process 3, it is the relationship between sward height and bite size that links instantaneous intake rate to the available grass biomass. However, for a very selective small herbivore, the increase in sward height could also reduce the accessibility of suitable bites, leading to an increase in the time to crop a mouthful, T_C.

The aims of this paper are: (i) to describe the functional responses of these three grazing Anatidae, i.e. to

determine instantaneous intake rate as a function of grass height (and biomass); (ii) to determine the relationships between instantaneous intake rate, peck size and pecking rate, and to identify the mechanisms leading to the functional responses; (iii) to investigate how body and bill size affect intake rates and peck sizes within and between species; and (iv) to determine whether Process 3 of S–H is applicable to herbivorous Anatidae, and to discover which component of handling time (T_C and/or T_S) limits intake rate in the three species.

Materials and methods

EXPERIMENTAL DESIGN

The experiments were performed from 26 October 1999 to 22 March 2000 at the Centre d'Etudes Biologiques de Chizé, using 10 European wigeon (five males, five females), 10 greylag geese (two males, eight females) and six barnacle geese (four males, two females). The wigeon and greylag geese were descendants of individuals caught in the wild and the barnacle geese came from the Parc zoologique de Clères (Muséum National d'Histoire Naturelle, in northern France) but were kept at Chizé for 6 months before the start of the experiments. During the daytime the birds had access to grass, poultry pellets, wheat and water *ad libitum*; at night they were kept in an aviary with a pool of water.

After a training period of 3 weeks, food intake was measured in an enclosure (15 × 10 m, made of green mesh wire 1 m high) set up in the grassland dominated by rye grass *Lolium perenne* L. where the birds normally fed. The trials were run in the early morning and the late afternoon with animals which had been fasted for 10–12 h to empty their gut. This fasting period is commonly used in this type of experiments (Van der Wal *et al*. 1998) and is unlikely to affect the behaviour of birds, provided that ducks have supplementary food and resting period after it. Each species was tested separately from the others, and the individuals were tested in small flocks of 6–10 birds.

The enclosure was divided by a fence into two sections (each 7·5 × 10 m) with different grass heights (treatments, i.e. from 1 cm to 12 cm). The animals were tested in one section while the other section was prepared for the following treatment. The grass grew throughout the experiment, so to attain shorter swards, it was cut to ground level with a mower or electric shears and then allowed to regrow, so the plants were in an immature growth stage and stems were not over-represented. We alternated trials on short and tall treatments, so that any time effect would not be confounded with a treatment effect. Before the beginning of each experiment, the grass height was estimated as the mean of 30 measurements taken at chance to the nearest 0·5 cm using a 'drop disc', i.e. a sliding square of polystyrene (4 × 4 cm, i.e. about the size of the head of a duck; 360 mg) on a graduated stick. Four 25 × 25 cm quadrats were clipped and the aerial parts of the plants were dried at 60 °C to constant mass and weighed. The apical halves of blades (the part of the plant consumed by birds) were harvested and analysed for contents of acid detergent fibre (ADF: cellulose + lignin) at the laboratory of the Institut National de la Recherche Agronomique de Lusignan using the Van Soest method (Van Soest 1982). Ash content was measured after incineration at 550 °C for 3 h. The results are expressed as percentage of ash-free dry matter (AFDM).

INTAKE MEASUREMENTS

There have been few studies of functional responses in herbivorous Anatidae (but see Drent & Swierstra 1977; Therkildsen & Madsen 2000), perhaps because it is difficult to quantify short-term intake rates. As the amounts eaten are relatively small, it is important that the birds have empty guts before the experiments (to avoid errors through variable amounts of gut contents) and that all droppings were collected. Caecal turnover is slow in herbivorous Anatidae, e.g. for the barnacle goose, 4% of droppings produced daily are caecal (Ebbinge, Canters & Drent 1975), and in our case, the three species produced only 1–3 caecal droppings in 10–12 h. We thus assumed that no grass enters the caeca (Mattocks 1971). If this assumption is wrong, any error is likely to be acceptable because, for wigeon for example, 1·7 caecal droppings on average (i.e. 0·07 g DW, *n* = 149 trials; which represents 11% of the mean mass of droppings) were excreted during the whole fasting period plus experiments.

The birds could move and graze freely in the enclosure, where fresh water was provided in two bowls. One observer watched a single individual continuously (two to four individuals were observed at a time depending on the number of trained observers available) at a distance of a 5–10 m; the birds were tame, and appeared undisturbed. The total time spent feeding by an individual (i.e. vigilance periods excluded), and the cumulative number of pecks given were measured by direct observation. The mean time of appearance of the first dropping is short, i.e. about 30 min in wigeon (Mayhew & Houston 1993; personal observation), so the experiments were stopped after 25 min from the beginning of active foraging, and birds were then put in individual boxes with a moveable tray beneath a 1-cm plastic mesh floor for at least 6 h to collect all the faeces. Because the mean throughput time of grass in wigeon is 70–75 min (Mayhew & Houston 1993) and 120 min in greylag and barnacle geese (Mattocks 1971; Prop & Vulink 1992), this ensures that all droppings produced from food eaten in the foraging period were collected. Faeces of caecal origin were collected separately since they contain residues from food consumed a few days before (Mattocks 1971). Droppings were dried at 60 °C for 2 days, weighed and ground through a 1-mm screen. Before release, the birds were weighed to the nearest
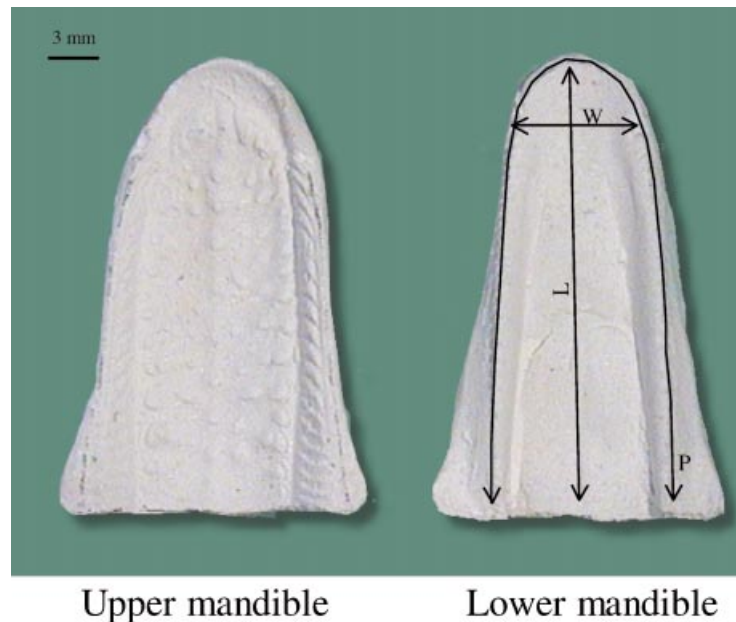
Fig. 1. Views of the upper (left) and lower (right) mandibles of a barnacle goose showing the three measurements taken from each mandible: P, perimeter of the bill; W, width at the lamellae insertion point and L, mandible length.

gram. Each bird was tested 1–4 times on eight different height treatments, with at least 1 day between two experiments.

ADF is a reliable marker to measure the digestibility of food in Anatidae (Summers & Grieve 1982; Prop & Deerenberg 1991; Manseau & Gauthier 1993). We calculated the digestibility of organic matter (ash free dry weight = AFDW) as:

$$\text{Digestibility (\% AFDW)} = [1 - (Mg/Md)] \times 100$$

where Mg and Md are ADF contents of grass and droppings, respectively (% AFDW). For each treatment we determined the mean digestibility for each bird by pooling approximately equal dry weights of droppings from each test ($n = 3$, range 1–4). Analyses of ADF and ash contents of faeces were done on a single subsample per replicate. Some of the estimates of digestibility were negative, 12 out of 69 for wigeon, 16 out of 53 for greylag geese and 11 out of 46 for barnacle geese. Because this is biologically impossible, the values were set to zero (see Gadallah & Jefferies 1995 for a similar correction). Knowing the digestibility of AFDW of each bird, the quantity of grass ingested was calculated as:

$$\text{Intake (g AFDW)} = \text{mass of faeces (g AFDW)}/ \\ (1 - \text{digestibility})$$

with the digestibility expressed as a proportion.

The dry weight (DW) of grass ingested was then calculated from the ash free measures using the measured ash content of the grass. Instantaneous intake rate (IIR, mg DW min^{-1}) and peck size (i.e. the mass of tissue removed per single peck, mg DW peck^{-1}) were estimated by dividing the amount of grass consumed (g

DW) by the total grazing time and the total number of pecks, respectively. Pecking rate (number of pecks min^{-1}) was calculated by dividing total number of pecks by total grazing time (not including periods of vigilance). The three replicates were averaged to give a single value of IIR, peck size and pecking rate per individual and per treatment. The use of an average value also minimized any effects of inter-individual interactions that could have caused subtle variations in the grazing behaviour of our birds as they were tested in flocks, although very few interaction were recorded.

BILL MORPHOLOGY

We made impressions of the upper and lower mandibles of each bird with dental impression material (Vival–Vivadent), and then made models of the bill with plaster. Because grass blades are taken into the bill lamellae and cut with a scissor-like action, and the lower mandible is slightly smaller than the upper one, the size of mouthfuls is determined by the size of the lower mandible. We therefore measured the following properties lower mandibles (to the nearest 0·1 mm, each repeated three times) using an ocular scale in a binocular microscope: (i) the perimeter of the mandible (P), (ii) the width at the insertion point of the lamellae (W), and (iii) the mandible length (L) (Fig. 1). The greylag geese had the largest bills on all measures, while the barnacle geese were intermediate for width but smallest for bill length and bill perimeter (Table 1).

STATISTICAL ANALYSES

As a first step, we tested for the effect of grass height (HEIGHT) on IIR using a random maximum likelihood

Table 1. Mean values ($\pm \Sigma\Delta$) of the lower mandible measurements of the three species. P, perimeter of the bill (mm); W, width at the lamellae insertion point (mm); L, mandible length (mm). Significant interspecific differences in P, W and L are indicated by values with different letters, Mann–Whitney *U*-test, $P > 0.05$

Variables	Wigeon ($n = 10$)	Barnacle geese ($n = 6$)	Greylag geese ($n = 10$)
P	$75.62 \pm 3.05a$	$66.23 \pm 6.11b$	$127.41 \pm 11.88c$
W	$7.74 \pm 0.57a$	$8.99 \pm 0.59b$	$12.29 \pm 1.03c$
L	$35.01 \pm 1.23a$	$29.99 \pm 2.90b$	$59.31 \pm 5.23c$

procedure (REML, Patterson & Thompson 1971) in the SAS MIXED procedure (SAS Institute 1999), which deals with the problem of pseudoreplication and allows variation due to individuals (IND) and experimental periods (PERIOD) to be evaluated and accounted for. The experiments were spread over 5 months, so the day of an experiment was classed into four periods of approximately 1 month, with only three periods for greylag geese. In the REML, HEIGHT was classed as a fixed effect; PERIOD and IND as random effects.

We then tested for the Type II functional response, the most frequently observed in herbivores (birds: Murton 1968; Hewitt & Kirkpatrick 1996; mammals: Allden & Whittaker 1970; Wickstrom *et al*. 1984; Spalinger & Hobbs 1992) using Holling's (1959) model:

$$\text{Intake} = a \times x/(1 + a \times H \times x),$$

where *x* is the grass height or biomass, *a* the search efficiency, and *H* the handling time. Under this model, intake increases to an asymptote as a decelerating function of grass availability. Because intake may decrease in tall swards (Van der Wal *et al*. 1998), we also tested a quadratic equation (Intake = $a + b \times x - c \times x^2$). Data for males and females were pooled. We fitted Holling's disc and the quadratic equations using a SAS NONLIN procedure (SAS Institute 1999), and we compared the fit with linear regression by comparing the coefficient of determination, R^2, coefficient of variation, CV, using the biological relevance of parameter values and their standard errors if necessary (Juliano & Williams 1987; Lundberg 1988). The R^2 were calculated with corrected sum-of-squares (Motulsky & Ransnas 1987) and we used all individual points to allow a better estimate of parameter values. The use of the biological criteria is crucial to discriminate between models that generate similar R^2 and CV (Lundberg 1988; Fritz, Durant & Guillemain 2001). The intercept of the quadratic curves was not forced through the origin though the IIR must tend to zero as grass heights approach zero values.

The hypothesis that intraspecific variations in IIR and peck size can be explained by body mass and bill size (P, W and L) was tested by linear and multiple regression analyses using SAS STEPWISE procedure

(SAS Institute 1999). For this, we used the average values of the feeding variables obtained from the sward where each individual was at its maximum IIR. Individual body masses were calculated by averaging body mass measurements taken throughout the study. Although bill measurements and body size were sometimes correlated, we always included one bill measurement and body mass in the multiple regression: despite the collinearity of the two independent variables, the regression estimates are more reliable (Freckleton 2002). We used stepwise Type III sum-of-square regression and Type I sum-of-square regression for which we manually permuted the first independent variable entered to assess which of the variable would explain most of the variance in cases were the high level of correlation between two variables would not allow the determination of a hierarchy. This was necessary for greylag geese.

A REML was then performed in order to investigate the influence of grass height on the relationship between the inverse of pecking rate (handling time) and peck size (eqn 5). PECK SIZE, HEIGHT and the interaction PECK SIZE × HEIGHT were considered fixed effects, and IND a random effect. The interaction tested the difference between slopes (i.e. $1/R_{max}$) for the different grass heights, and HEIGHT tested for differences in the *y*-intercepts, i.e. differences in T_C between sward heights.

Results

VEGETATION CHARACTERISTICS

Grass biomass ranged from 24 g to 160 g DW m^{-2} for mean grass heights of 1 cm and 12 cm, respectively, and these variables were highly correlated ($r = 0.94$, $n = 9$, $P = 0.0002$). ADF content increased slightly with grass height (from about 18–23% as height increased from 1 cm to 12 cm, $r = 0.73$, $n = 8$, $P = 0.040$). The fibre content of the grass therefore did not vary much over the height range (1–12 cm) in this study.

FUNCTIONAL RESPONSES

The functional response curves were based on 50–60 trials per species. PERIOD had no significant effect on IIR (all *P* values > 0.05). The greylag geese had higher average IIR ($F_{1,83} = 11.75$, $P < 0.001$), and wigeon had lower IIR ($F_{1,106} = 59.28$, $P < 0.001$) than barnacle geese.

In wigeon IIR varied strongly among individuals ($F_{9,59} = 3.35$, $P = 0.002$). After controlling for IND, IIR still varied significantly with HEIGHT (REML: $F_{7,59} = 2.41$, $P = 0.031$). A type II functional response did not fit the data ($F_{1,75} = 0.17$, $P = 0.67$), but a quadratic equation accounted for some of the variance in the relationship between IIR and HEIGHT ($y = 94.62 + 14.24x - 1.27x^2$, $F_{7,59} = 5.62$, $P = 0.005$, $r^2 = 0.13$; Fig. 2). IIR increased slightly to a maximum of 140 mg DW
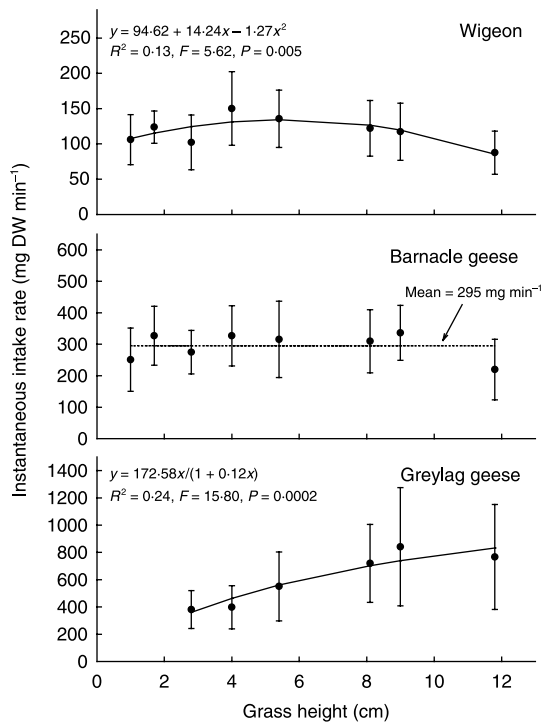
Fig. 2. The relationships between grass height (cm) and mean IIR ($\pm$ SD, g DW min^{-1}) in wigeon, barnacle geese and greylag geese. DW = dry weight. The regression analyses were performed on the raw data ($n = 77$ for wigeon; $n = 46$ for barnacle geese and $n = 53$ for greylag geese) but mean values are presented for clarity.
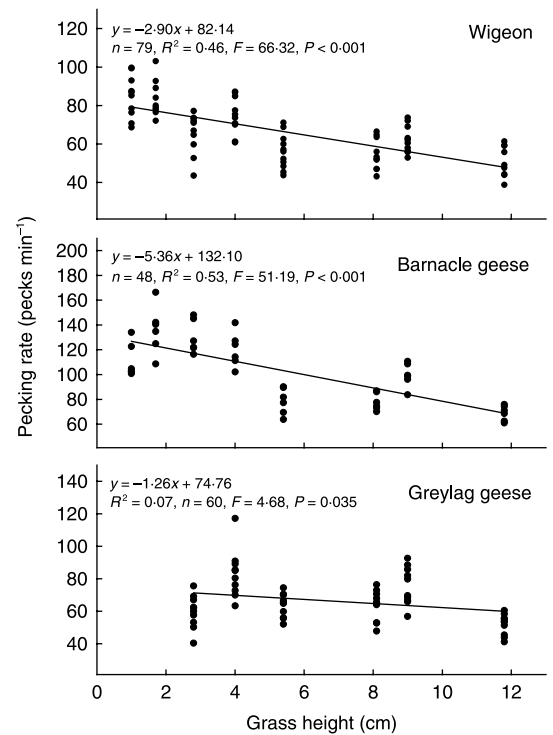

Fig. 3. The relationships between grass height (cm) and pecking rate in wigeon, barnacle geese and greylag geese. DW = dry weight. Each dot represents the mean value of 1–4 replicates for each individual.

min^{-1} at a grass height of 5–6 cm and then declined. In general, the individual curves followed this pattern but none fitted the quadratic equation significantly because of the variability in IIR values.

A significant IND effect on IIR was also found in barnacle geese ($F_{5,33} = 8\cdot02$, $P < 0\cdot001$). HEIGHT had no significant effect on IIR after controlling for IND ($F_{7,33} = 2\cdot10$, $P = 0\cdot072$), but was close to significance. The shape of the functional response tended to be quadratic (Fig. 2), but not significantly, so barnacle geese had a mean IIR of 295 mg DW min^{-1} for grass heights between 1 cm and 12 cm.

Greylag geese also showed a significant individual effect ($F_{9,38} = 7\cdot81$, $P < 0\cdot001$), and after controlling for IND, IIR still varied significantly with HEIGHT (REML: $F_{5,38} = 8\cdot78$, $P < 0\cdot001$). The greylag geese refused to feed on short grass (height < 3 cm); their functional response fitted the disc equation of Holling (Type II, Fig. 2). This explained about a quarter of the variance in IIR ($R^2 = 0\cdot24$, $P = 0\cdot0002$). IIR increased from 360 mg DW min^{-1} to a maximum of nearly 830 mg DW min^{-1} on 12 cm grass. The shape of individual curves were generally of this type, but the equation fitted significantly only three out of 10.

Pecking rates decreased as grass height increased for wigeon and barnacle geese, but showed little variation for greylag geese (Fig. 3). The slopes of these three regressions were significantly different (wigeon/greylag geese: $F_{5,125} = 2\cdot43$, $P = 0\cdot038$; greylag geese/barnacle

geese: $F_{5,94} = 13\cdot79$, $P < 0\cdot001$; wigeon/barnacle geese: $F_{7,111} = 9\cdot28$, $P < 0\cdot001$). The relationships between peck size and grass height showed an asymptotic increase for wigeon and barnacle geese, and a linear increase for greylag geese (Fig. 4).

FACTORS DETERMINING IIR AND PECK SIZE

The maximum IIR (IIR max) was positively correlated with body mass in greylag geese ($r_S = 0\cdot65$, $P = 0\cdot04$), but not in barnacle geese ($r_S = 0\cdot26$, $P = 0\cdot62$) (Fig. 5). In wigeon, this relationship was significantly negative ($r_S = -0\cdot70$, $P = 0\cdot02$).

After controlling for the individual effect, a REML showed that IIR was positively related to peck size in wigeon ($F_{1,66} = 106\cdot89$, $n = 77$, $P \le 0\cdot0001$, Fig. 6a), in barnacle geese ($F_{1,39} = 19\cdot51$, $n = 46$, $P \le 0\cdot0001$, Fig. 6b) and in greylag geese ($F_{1,42} = 146\cdot61$, $n = 53$ $P \le 0\cdot0001$, Fig. 6c). IIR was unrelated to peck rate for the three species (all $P > 0\cdot05$). This suggests that peck size was the primary determinant of IIR.

Both in wigeon and barnacle geese, most of the variance in the maximum peck size was accounted for by the width of the bill at the insertion point of the lamellae, W ($F_{1,8} = 12\cdot35$, $P = 0\cdot008$; $r^2 = 0\cdot61$ and $F_{1,4} = 31\cdot38$, $P = 0\cdot011$; $r^2 = 0\cdot95$, respectively).

In greylag geese, W was also related to maximum peck size ($F_{1,8} = 7\cdot96$, $P = 0\cdot026$; $r^2 = 0\cdot52$), as well as body mass ($F_{1,8} = 6\cdot28$, $P = 0\cdot041$) depending which of the variables was entered first in the multiple regression.
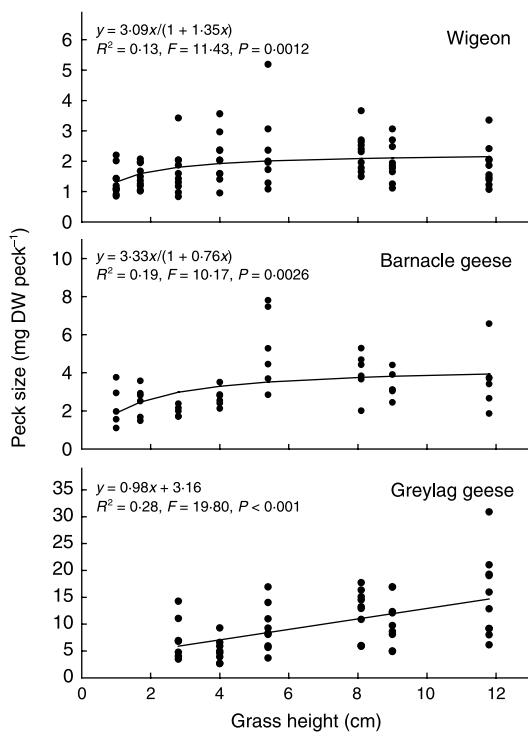
Fig. 4. The relationships between grass height (cm) and peck size in wigeon, barnacle geese and greylag geese. DW = dry weight. Each dot represents the mean value of 1–4 replicates for each individual.

Once one of these two variables was fitted, the second did not improve the model significantly. This is certainly the consequence of the strong correlation between body mass and W in greylag geese ($r_s = 0.81$, $P < 0.01$), which did not exist in wigeon and barnacle geese (all $P > 0.05$). In greylag geese, peck size is also determined by bill size, but this morphological trait may in fact be primarily conditioned by body size.

MECHANISMS REGULATING THE FUNCTIONAL RESPONSE

To identify the mechanism governing the changes in intake rate we fitted to our data eqn 5, $H = T_C + (S/$

$R_{max})$, the relationship between handling time, H, and peck size, S, with sward height as a covariate. In this equation, the slope, $1/R_{max}$, is the processing time and the y-intercept, T_C, the cropping time. Sward height had no significant effect on the slope in any species (PECK SIZE × HEIGHT: wigeon, $F_{1,64} = 0.35$, $P = 0.52$, barnacle geese, $F_{1,37} = 0.00$, $P = 0.98$, and greylag geese, $F_{1,41} = 0.00$, $P = 0.95$).

In the analysis without the interactions, as expected from eqn 5, H increased linearly with peck size in all three species (Table 2, Fig. 7), which means that the handling time increased with peck size, probably through an increase in time to swallow. However, the y-intercept (i.e. T_C) increased significantly with grass height for wigeon and barnacle geese, but not for greylag geese (Table 2, Fig. 7). In greylag geese, the mechanism is very similar to that observed in mammalian herbivores, where bite size (through chewing time) is the principal controlling process in food concentrated patches. In wigeon and barnacle geese, time to crop is the key variable limiting food intake.

Discussion

FUNCTIONAL RESPONSES

Our calculations of intake rate depend partly on the measure of digestibility for each bird. The calculation of digestive efficiency of birds using the ADF contents of grass and droppings sometimes leads to negatives values (Gadallah & Jefferies 1995). Our negative values are from individuals whose droppings had lower ADF content than the others. This could have been due to errors in the chemical analysis, but there was no evidence for this. Alternatively, these birds may have selected plant parts of higher quality than the average value found in our control plots. Some birds may also have digested some of the fibres. However, no single bird showed a systematic bias in its digestibility values. The mean digestibility of grass for our species ranged from 18% (barnacle geese) to 24% (greylag geese). Although low, they fall within the range of digestibility
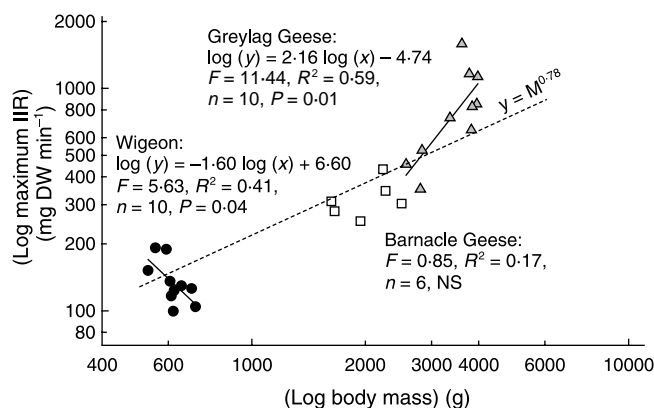

Fig. 5. The relationship between maximum IIR (mg DW min^{-1}) and body mass (g) for the three species. Both scales are logarithmic. NS = not significant.

(a) Wigeon

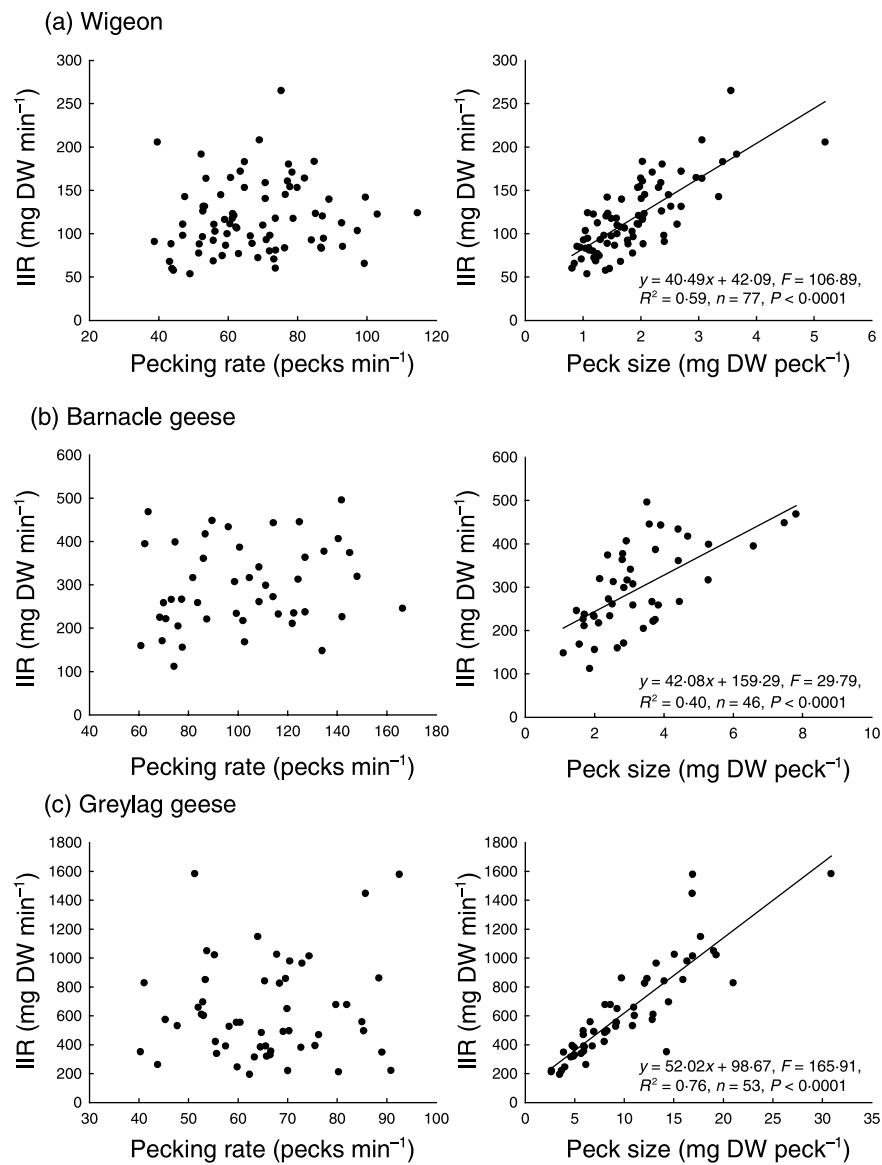
(b) Barnacle geese

(c) Greylag geese

Fig. 6. The effects of peck size and pecking rate on IIR for the three species: (a) wigeon, (b) barnacle geese and (c) greylag geese.

Table 2. Results of the REML on Handling time, with Size and Sward height as explanatory variables, and values of the model equations (these values were used to draw the graphs for wigeon and barnacle geese, see Fig. 7)

	F	P	Coef	Model equation
Wigeon				
SIZE (S)	$F_{1,65} = 14 \cdot 24$	0·0004	0·00151	$H = 0 \cdot 00151 \times S + 0 \cdot 00061 \times Sh + 0 \cdot 00947$
HEIGHT (Sh)	$F_{1,65} = 52 \cdot 33$	0·0001	0·00061	$R^2 = 0 \cdot 54$
Barnacle geese				
SIZE (S)	$F_{1,38} = 17 \cdot 03$	0·0002	0·00077	$H = 0 \cdot 00077 \times S + 0 \cdot 00046 \times Sh + 0 \cdot 00531$
HEIGHT (Sh)	$F_{1,38} = 41 \cdot 70$	0·0001	0·00046	$R^2 = 0 \cdot 71$
Greylag geese				
SIZE (S)	$F_{1,41} = 6 \cdot 72$	0·01	0·0002	$H = 0 \cdot 0002 \times S + 0 \cdot 0135$
HEIGHT (Sh)	$F_{1,41} = 0 \cdot 55$	0·46	–	$R^2 = 0 \cdot 14$

found in herbivorous Anatidae are generally between 20% and 40% (Buchsbaum, Wilson & Valiela 1986; Gadallah & Jefferies 1995; Van der Wal *et al*. 1998). Thus, it is possible that our estimates of intake rates and peck sizes are also slightly under-estimated, but they

are broadly consistent with those of other studies (barnacle goose: Drent & Swierstra 1977; Black *et al*. 1992; greylag goose: Van Eerden, Slager & Soldaat 1998). These values are thus not likely to have affected the observed functional response nor the mechanisms causing them.
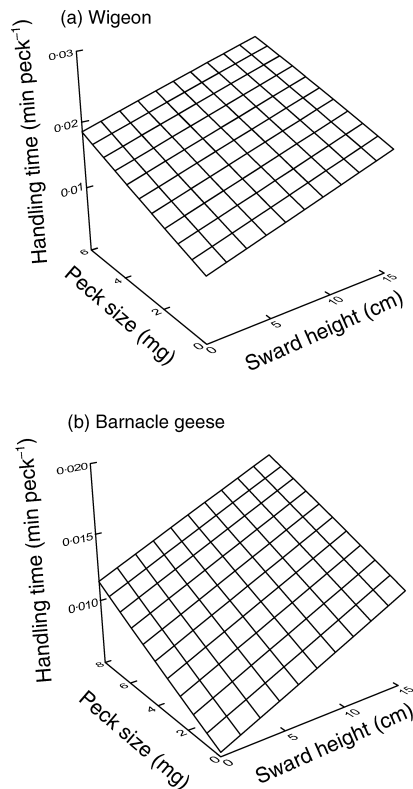
Fig. 7. The effects of handling time, H, peck size, S, and sward height, Sh, for (a) wigeon and (b) barnacle geese. The increase in peck size is associated with an increase in time to process the peck, and the increase in sward height is associated with an increase in time to crop. See Table 2 for the model equations.

Greylag geese clearly had low intake rates on short grass, and showed a functional response which was probably of Type II, but the range of heights offered was too small to be sure. Such a pattern has been described in the ruffed grouse *Bonasa umbellus* L. (Hewitt & Kirkpatrick 1996) and in the brent goose (Charman 1979). The smaller species, wigeon and barnacle geese, showed near constant instantaneous intake rates across the wide range of grass heights. Wigeon showed a Type IV functional response, and the same trend was found in barnacle geese: a similar result was obtained in the pink-footed goose *Anser brachyrhynchus* B. which showed a quadratic curve of instantaneous intake rate when primary leaf length increased (Therkildsen & Madsen 2000) and in barnacle geese feeding on swards with biomass up to 90–95 g m^{-2} (Van der Wal *et al.* 1998). For the smallest species, the additional effect of the increase in time to crop (T_C), seemed to cause the final decline in the functional response. This result suggests that in the tallest swards wigeon (and perhaps barnacle geese) have more difficulty in locating and/or cropping the best bites (the most digestible leaves) than in shorter swards. At high plant biomasses, some birds also appeared to have difficulty in manipulating the long leaves with their bills (as evidenced by their gaping bills, the 'spaghetti effect' of R. Drent, personal communication, see also Bignal 1984).

This phenomenon may only occur at very high biomass and hence is difficult to detect through standard general linear model. However, wigeon and barnacle geese rarely took very long leaves. Our results thus suggest that T_C may in fact have played a greater role than T_S (time to swallow) in shaping the functional responses on our experimental swards. Conversely, greylag geese showed a Type II functional response, which was mainly determined by bite size (i.e. processing time, in fact swallowing time for greylag geese), as in most mammalian species (Gross *et al.* 1993). However we expect that intake also decreases in very tall swards (> 20 cm) in this species. In the wigeon and barnacle geese, feeding on apparent and aggregated items, time to crop increased faster with sward height than did processing time with peck size. These birds seem to be at the boundary of Process 3 and Process 2 as defined by Spalinger & Hobbs (1992): although principally limited by peck size and processing time (Process 3), they approach being limited by time to crop, i.e. encounter rate (Process 2). This transition between processes occurs at high biomass and not at low biomass as described in mammalian herbivores (Spalinger & Hobbs 1992), which explains the Type IV functional response. These results suggest that Process 2 and 3 can in fact be described by the same equation, if time to crop is allowed to vary with plant characteristics as well as bite size, and thus processing time. This calls for further experiments on more extreme sward conditions in order to confirm whether or not the three species all have Type IV functional response.

The bills of the three species are not equally adapted to eating grass. The wigeon belongs to the Tribe Anatini of the Subfamily Anatinae (Marchant & Higgins 1990) and is adapted primarily to feeding on eel-grass *Zostera* (Charman 1977). These birds typically remove only the ends of the leaves with the tip of their bill, so peck size varies little (1–2 mg, Fig. 4). Greylag geese and barnacle geese belong to the Tribe Anserini (Marchant & Higgins 1990) in which the lamellae are transformed into horny 'teeth' along the edges of the mandible. Greylag geese feed principally on underground rhizomes and tubers (e.g. *Scirpus* species; Amat 1986), and had difficulty in grazing short swards with the sides of their bills. IIR decreased strongly with peck size: so very short swards were unprofitable for greylag geese, and they refused to feed on them (< 3 cm, Fig. 2). Barnacle geese, on the other hand, eat mainly grass (Marchant & Higgins 1990): they have a shorter bill than the wigeon and greylag geese, especially when corrected for body mass. It has been shown that the length of the bill is the main determinant of the time to swallow in birds that peck (Kooloos & Zweers 1991): in herbivorous Anatidae (which peck) there is therefore strong selection in favour of short bills. A short bill also allows barnacle geese to select small, high quality items, even in medium to tall swards. Ultimately peck sizes tended to asymptotic values, limited by bill size or by the maximum size of an item that can be handled:

in the smaller species the asymptote occurred between 4 cm and 6 cm, while in the greylag geese peck size was still increasing on 12 cm swards.

It is a general rule that herbivores compensate for small bite sizes by increasing bite rates (mammals: Trudell & White 1981; Wickstrom *et al.* 1984; Spalinger *et al.* 1988; birds: Drent & Swierstra 1977; Hewitt & Kirkpatrick 1996; Mayhew & Houston 1998). However, some species have a higher compensatory capacity than the others. For instance, barnacle geese have much higher pecking rates than wigeon or greylag geese (Fig. 3); this presumably requires specific morphological adaptations. We did not measure the size of the neck muscles, but it is likely that this differs among the three species. This fully compensatory mechanism allows the smaller species to maintain IIR on short swards better than larger ones (see also Allden & Whittaker 1970; Wickstrom *et al.* 1984). These differences in functional responses may explain why small species prefer grazing on short swards (wigeon and 'dark geese'), whereas larger ones ('grey geese') graze on taller grass (see Vickery & Gill 1999 for a review). Furthermore, the smaller species may be able to competitively exclude the larger ones from swards through the maintenance of very short sward heights, as in mammals, or would be less susceptible to the effects of depletion than larger ones, and hence remain longer on swards with lower grass biomass provided that it remains of sufficient quality (see Illius & Gordon 1987 for ungulates).

The results for these three Anatidae also suggest that maximum instantaneous intake rates in birds scale allometrically with body mass with an exponent of $M^{0.78}$ (Fig. 5) which is close to the scaling coefficient of metabolisable energy intake found by Bruinzeel *et al.* (1998). This is also close to the interspecific exponent for intake in mammals ($M^{0.70}$, Shipley *et al.* 1994). However, data on more species of herbivorous birds are required before the principles underlying interspecies differences in intake rates can be established with certainty.

VARIATIONS IN IIR WITHIN SPECIES

The fact that the birds were tested in flocks rather than individually could have created some intraspecific variation in IIR due to dominance interactions, and even if IIR was calculated from the grazing time excluding vigilance time, some birds could still have adjusted their feeding behaviour to the presence of dominant flock members. As these birds would not feed alone, it was not possible to obtain individual data. In fact there were very few interactions, so these measures should be reliable.

Body mass varied only slightly among wigeon (530·0–708·3 g; coefficient of variation CV = 8·9%), and was more variable in barnacle and greylag geese (1623·8–2497·7 g; CV = 17·4% and 2567·1–3978·5 g; CV = 15·4%, respectively). Within greylag geese, but

not in barnacle geese, body mass accounted for much of the variance in IIR (59%). The negative relationship found in wigeon is inexplicable, and certainly should require further investigation. In the three species IIR was sensitive to peck size, which seemed principally determined by bill size. For all three species, the maximum peck size was best related to the width of the lower mandible (W), but bill length was also correlated to maximum peck size. This is consistent with studies in grazing ruminants which showed that the breadth of the incisor arcade accounts for more variability in the bite size and rate of food intake than does body mass (Shipley & Spalinger 1992; Gordon *et al.* 1996). However, the strong correlation between bill size and body size in greylag geese does not allow for clear conclusions in this species.

A striking example of the ultimate role of mouth parts has been found in Soay sheep (*Ovis aries* L) of St Kilda (Scotland): when the vegetation is severely depleted because of high densities of sheep, individuals with wide incisor arcades have higher intake rates, and survive better than individuals with narrow arcades (Illius *et al.* 1995). Our study is among the few which shows that individual birds differ in their intake rates (e.g. Partridge 1976; Goss-Custard *et al.* 1995b; Caldow *et al.* 1999; Fritz *et al.* 2001), and that these differences are due to variations in morphology, particularly bill size. This has important implications for intraspecific competition. Individual variations in foraging efficiency is the main determinant of competitive ability and hence fitness in birds (e.g. Lemon & Barth 1992; Caldow *et al.* 1999), so individuals with larger bills should be better competitors and should survive better where feeding competition occurs, with all the consequences that this may have for population dynamics (Goss-Custard *et al.* 1995b). However, in time of low food abundance, smaller bills may allow the selection of more nutritious food items, hence enable individuals to survive better. This could explain the maintenance of some polymorphism in the bill size of birds (see Illius *et al.* 1995 for ungulates). These results call for more research on the effects of variations in morphological traits on individual foraging efficiency in grazing ducks and geese, as in other animal species, and their consequences for population dynamics.

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