

Size-related consumption of *Scirpus maritimus* tubers by greylag geese *Anser anser* explained by their functional response

Daphné Durant^{a,b,*}, Laurent Desnouhes^{a,c}, Hervé Fritz^{d,1}, Matthieu Guillemain^b, François Mesléard^a

^a Centre de Recherches de la Tour du Valat, Le Sambuc, 13200 Arles, France

^b Office National de la Chasse et de la Faune Sauvage, CNERA Avifaune Migratrice, La Tour du Valat, Le Sambuc, 13200 Arles, France

^c CPIE Sèvres et Bocage, Maison de la vie rurale, 85700 la Flocellière, France

^d CEBC/CNRS, UPR 1934, 79360 Villiers-en-Bois, France

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ABSTRACT

To explain the preference of wintering greylag geese *Anser anser* for small *Scirpus maritimus* tubers (<10 mm) over larger ones, our hypothesis was that the former would provide higher intake rates. This 'consumption rate hypothesis' was tested experimentally by deriving the functional responses of geese feeding on tubers of three contrasting sizes. Goose consumption rates were measured as: (i) feeding rate (tubers/min) and (ii) instantaneous intake rate (g fresh weight/min) on various tuber densities (5–200 tubers/tray). Geese had linear functional responses over the range of tuber densities offered, and tuber size affected their consumption rate. The results were then used to re-examine intake rates according to relative biomass of tubers found in the wild. In support of our hypothesis, the larger tubers allowed the lower intake rates. Foraging mechanisms that possibly control the tuber ingestion rate of geese were explored. After controlling (through chemical analyses) that nutritional components of tubers do not differ between sizes, it was concluded that geese preference is mainly due to size-related constraints (i.e. handling time) on their ingestion rates. Additional limiting factors (tuber extraction, digestion capacity) which are likely to constrain food intake of wild geese are also discussed.

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1. Introduction

The relationship between the consumption rate of an animal and its prey density, called the functional response, has been described of various types, i.e. shapes (from linear Type I to dome-shaped type IV; Holling, 1959; Begon et al., 1996). Many studies have linked behavioural and ecological mechanisms to the shape of the functional response, e.g. to elucidate the mechanisms regulating intake rate in predators (Colton, 1987), mammalian herbivores (Spalinger and Hobbs, 1992; Laca et al., 1994) or birds (Hewitt and Kirkpatrick, 1996; Durant et al., 2003). This concept has also been central to the development of studies on diet selection and patch choice (Fryxell and Doucet, 1993; Norris and Johnstone, 1998; Durant et al., 2004). Indeed, the understanding of not only the shape, but also the sources of variations of the functional response (e.g. food item size,

Fritz et al., 2001) allowed the testing of hypotheses related to the consumption of various food types and sizes, playing an important part in elaborating optimal foraging theory (Stephens and Krebs, 1986).

Some Anatidae species show a strong preference for feeding on underground storage organs, e.g. tubers, of rhizomatous aquatic plants (ducks: Anderson and Low, 1976; swans: Beekman et al., 1991; geese: Desnouhes and Lepley, 2004), in which they show size-related consumption (van Eerden et al., 1998a). For instance, in the marshes of Guadalquivir (Spain), wintering greylag geese *Anser anser* prefer small (<10 mm) *Scirpus maritimus* tubers over larger ones (Amat, 1986, 1995). This was confirmed by preliminary results on gizzard samples in the Camargue, Rhône delta, southern France (Desnouhes L., unpublished data).

If greylag geese largely select small tubers, it can be assumed that birds benefit from consuming them preferentially. Several hypotheses have been formulated to explain this preference. Amat (1995) suggested that small tubers may be easier to digest, i.e. to break down in the gizzard, than larger ones. Moreover, since herbivorous Anatidae have high nitrogen requirements and avoid fibre-rich diet (Buchsbaum et al., 1986; Hassall et al., 2001), this author proposed that nutritional quality may vary with tuber size as the protein:fibre ratio would be higher in the younger, smaller

* Corresponding author at: Centre de Recherches de la Tour du Valat, Le Sambuc, 13200 Arles, France. Tel.: +33 4 90 97 20 13.

E-mail address: daphne.durant@wanadoo.fr (D. Durant).

¹ Present address: Université Lyon 1, CNRS UMR 5558, Laboratoire de Biométrie et de Biologie Evolutive, 43 Bd du 11 novembre 1918, 69622 Villeurbanne Cédex, France.

tubers (Amat, 1986; hereafter called the 'nutrient hypothesis'). However, two constraints associated with tuber consumption in geese may also greatly and more directly influence their selection: (i) extraction of tubers from the mud by strong head/bill movements (Amat et al., 1991; Desnouhes and Lepley, 2004), and (ii) handling, i.e. disconnecting rootlets and rhizomes from the tuber, and breaking it into pieces before ingesting it. Tubers of increasing size may need more time to be extracted and handled, resulting in higher energy costs (Amat, 1986, 1995). To our knowledge none of these hypotheses has yet been tested in geese, but some studies on Bewick's swans *Cygnus columbianus bewickii* foraging on Sago pondweed *Potamogeton pectinatus* tubers could provide an adequate framework to compare with. For instance, it has been demonstrated that the spatial variation in resource depletion by swans was due to differences in foraging energy costs related to water depth and the silt content of the sediment (Nolet et al., 2001). This lack of knowledge is however unfortunate as a better understanding of size-selective tuber consumption by greylag geese and underlying factors explaining this selection is the essential first step (i) to understand goose distribution (see e.g. Piersma et al., 1995; Iason et al., 2002), (ii) to assist the development of models relating feeding behaviour of water birds to 'foraging quality' of protected areas, with the aim of establishing suitable management strategies (Percival et al., 1996, 1998; Goss-Custard et al., 2002; West et al., 2005), and (iii) to investigate the structure and dynamics of *Scirpus* populations (e.g. trade-off between sexual and vegetative reproduction) in response to grubbing (Clevering and Gulik, 1997; Miller et al., 1997).

The functional response of greylag geese feeding on *Scirpus* tubers has never been derived either, as opposed to other food types (van Eerden et al., 1998b; Durant et al., 2003). In recent laboratory experiments, functional responses of herbivorous Anatidae and changes in their associated parameters have been used to explain patch selection (Durant et al., 2003, 2004). van Eerden and Munsterman (1998) also demonstrated, through a functional response study, that teal *Anas crecca* prefer seed species providing higher intake rates. In line with these studies, we believe that the establishment of the functional responses of greylag geese on tubers may help understanding of their feeding preferences since, if they prefer small tubers, we would expect their intake rate – considered here as a measure of profitability – to be higher on small tubers than on larger ones (hereafter called the 'consumption rate hypothesis').

This study was thus designed to test the 'consumption rate hypothesis' by deriving the functional responses of greylag geese feeding on tubers of three contrasting sizes. An alternative hypothesis is that there are differences in chemical composition of tubers depending on their size, which could also influence size selection by geese. This potential effect was controlled for by performing chemical analyses of tuber components. We depart from Amat's hypothesis (Amat, 1986) by exploring not only proteins and fibre, but also other potentially influential components in tuber selection by geese, i.e. water-soluble carbohydrates, and lipids to a lesser extent as they are much less abundant. It was predicted that, under the 'nutrient hypothesis', the proportions of proteins and carbohydrates (+lipids) would be higher, and that of fibre would be lower in small rather than large tubers thus explaining the selection of small ones.

As this study implied obvious logistical problems in natural *Scirpus* communities, an experimental approach was used, with tame geese searching for *S. maritimus* tubers in customised patches. In order to dissociate the relative influence of extraction and handling costs on geese selectivity, extraction costs were suppressed by performing the experiment with tubers disconnected from shoots and rhizomes in a mixture of sand and water. Because the experiments

were not conducted in conditions similar to those found in the wild, our aim was to obtain relative values of the functional response on the three tuber sizes and not to determine absolute *in situ* values of the consumption rate. It was thus expected to test the extent to which their comparison predicts goose selectivity for small tubers. The second aim was to explain how functional response parameters (e.g. handling time) changed with tuber size, and thus approach the foraging mechanisms regulating tuber ingestion by geese.

2. Materials and methods

2.1. Experimental design

The experiments were performed in July–August 2004 and 2005 at the Tour du Valat (Rhône delta - Camargue), using 6 greylag geese (3 males and 3 females; mean body mass 3470 g). Geese were descendants of individuals caught in the wild, and had been kept in captivity ever since. Between experiments, geese were held in an enclosure where they had access to grass, poultry pellets and water *ad libitum*. *Scirpus maritimus* tubers were collected in the nearby Saint-Seren marsh, where an increasing number of greylag geese, ca. 1000 individuals since 5–6 years (Desnouhes et al., 2003), mainly feed on tubers (Desnouhes and Lepley, 2004). Tubers were collected a maximum of 8 days before experiments and kept in fresh conditions. Tubers were disconnected from shoots and rhizomes, and sorted by size with a calliper. Three size classes were distinguished: (i) small (S: 0.3 g fresh weight on average ± 0.03 S.D.; 5–6 mm), (ii) medium (M: 0.8 g ± 0.07 S.D.; 10–11 mm), and (iii) large (L: 2.0 g ± 0.12 S.D.; 15–16 mm).

Foraging observations were conducted in a bare ground subdivision of the enclosure (6.3 × 9 m), where geese were offered 6 trays (15 cm long × 10 cm width × 9 cm high) filled with a mixture of sand and water (50:50). Each tray contained the same density of tubers of the same size (randomly chosen before the trials), trays therefore represented replicates. In 2004, trials were conducted with 20, 45, 60, 75, 105, 135, and 165 tubers/tray, and were completed in 2005 with 5, 10, 150 and 200 tubers/tray. To ensure achieving asymptotic intake rates (if any), higher tuber densities than those encountered in the wild were used. The trays were fixed every 30 cm on a wooden structure (2.50 m long, 10–15 cm high). Geese were fasted for ca. 10 h prior to experiments to encourage feeding. As they refused to eat individually, they were tested all together. Trials were ran early in the morning (before 08:00) or late in the afternoon (after 17:00), and for no more than 5 consecutive days. Experiments were performed on an instantaneous basis (ca. 20 min) so as to limit the negative consequences of depletion on intake rate. A video camera recorded the experiments.

After each trial, the remaining tubers were counted, which allowed the determination of the consumption of tubers by geese in each tray by difference. From the video tapes, the total foraging time was measured in each tray with a stopwatch, i.e. the cumulative time spent feeding by one or several successive individuals (vigilance periods excluded). Tuber ingestion rate was then estimated, i.e. feeding rate (in number of tubers/min), and the (instantaneous) intake rate (in g fresh weight/min) by dividing the number of tubers and the biomass consumed, respectively, by total foraging time. When all tubers in a tray were consumed (which only occurred for one tray), the data was excluded as there was no way to know when all tubers had been consumed. Geese often changed the tray in which they fed. It was however rare to observe two individuals feeding simultaneously in the same tray (when this happened, it never lasted more than a few seconds). Consequently, as a feeding rate or intake rate measurement could not be assigned to each individual, and since trays were not independent from each other,

the six replicates were averaged, providing a single value of feeding rate and intake rate per tuber density and per size.

2.2. Functional response models

Functional responses are mainly affected by two consumer traits: (i) attack rate (a), also called searching efficiency, i.e. the mean instantaneous area searched during the entire foraging trial (in distance units per time unit), and (ii) handling time (Th), the time needed to handle each prey item, i.e. disconnect tuber from the rhizomes, and breaking it into pieces before ingestion (in seconds). These are the parameters of the Holling's disc equation (Holling, 1959):

$$\text{Intake} = \frac{a \times x}{1 + aTh \times x},$$

where x is prey density or biomass. As being common in Anatidae (Charman, 1979; Fritz et al., 2001; Durant et al., 2003), a type II functional response was first tested to fit the experimental data with a non-linear least-square procedure (STATISTICA 6.0). Fit quality was then compared (coefficient of determination R^2) with a linear regression:

$$\text{Intake} = a' \times x + b',$$

where the slope a' represents the consumer's attack rate (Begon et al., 1996). The F test comparison of curves macro of Sigmaplot 8.0 based on Abramowitz and Stegun (1972) was also used to determine if the disc equation provided a statistically better fit.

To test the 'consumption rate hypothesis', the most relevant measure of goose consumption rate is the biomass consumed per time unit, i.e. the relationship between intake rate and tuber biomass (in g DW/m²). However, functional responses were also constructed as the relationship between feeding rate and tuber density (in tubers/m²). Tuber biomass was calculated by multiplying tuber density by the mean dry weight of a tuber, as field measurements provided the following relationship between tuber fresh and dry weights: DW = 0.340 FW – 0.007, $R^2 = 0.82$, $p < 0.01$; Gouraud et al., 2008.

2.3. Other behaviour parameters and measures

Under our experimental conditions, tubers were not visible (i.e. mixed with sand and water), and geese therefore had to search for them. Searching (+ collecting) and handling were mutually exclusive, i.e. searching for tubers could not occur simultaneously to handling (pers. obs.). Total foraging time (T) was defined as: $T = \sum Ts + \sum Th$. Ts (in seconds) represents search time, the time from when a goose puts its bill in the water until it finds a tuber. Th (handling time; see above) is defined as the time from when the goose found a tuber until that tuber was swallowed. These behavioural parameters were measured from the videotapes. For L and M tubers, the distinction between searching and handling was obvious because, having found a tuber, geese raised the head and started handling it by a sort of breaking process, possibly aiding in crushing the item into pieces before it was swallowed. Small tubers, conversely, were generally consumed under water. It was consequently impossible to clearly distinguish Ts from Th for this tuber size, and none of them could therefore be estimated.

2.4. Chemical composition of tubers

In January–February 2006, tubers were collected in the Saint-Seren marsh at three different sites commonly exploited by greylag geese (L. Desnouhes, pers. com.). From each site, twelve samples

were collected, i.e. clusters of several tubers connected by rhizomes. In the laboratory, tubers were disconnected and sorted by size. Each sample was composed of 20–30, 15–20, and 3–5 tubers matching the S, M and L sizes, respectively, to ensure enough material for chemical analyses. Tubers were carefully washed and then oven-dried at 60 °C to constant mass. They were then ground (<1 mm sieve), and analysed for crude protein content (Duma method $\times 6.25$). Ash content was obtained after incineration at 550 °C for 3 h. The fibre contents, that is to say NDF (neutral detergent fibre, i.e. hemicellulose + cellulose + lignin) and ADF (acid detergent fibre, i.e. cellulose + lignin) were estimated by the Van Soest method (Van Soest, 1982). Chemical analyses were performed in two laboratories of *Institut National de la Recherche Agronomique*. The hemicellulose content was obtained by the difference between NDF and ADF. Water-soluble carbohydrates + lipids content were deducted as: 100% – proteins% – NDF% – ash%. Fat content however represents only a small percentage, e.g. 0.8% from Kantrud (1996).

2.5. Statistical analyses

The effects of size and tuber density, as well as those of size and tuber biomass, were tested on feeding rate and intake rate, using a residual maximum likelihood procedure (REML, Patterson and Thompson, 1971) with the SAS MIXED procedure (SAS Institute, 1999). When data failed to satisfy the assumption of normality or homogeneity of variances, the square-root transformation was applied. As trials were performed over 2 years, REML allowed variation due to years to be evaluated and accounted for (if any). In the models, size and tuber density or tuber biomass were thus entered as fixed effects, and year was classed as a random factor. The interactions tuber density \times size and tuber biomass \times size were also tested, but as they were not significant in any analysis, results are presented without interactions. To compare, two by two, feeding rate and intake rate means according to sizes, the post hoc t -tests associated with REML analyses were used.

Potential effects of (a) tuber size and (b) tuber density on Ts and Th means were tested using non-parametric tests (Mann–Whitney and Kruskal–Wallis tests, respectively) since the assumption of homogeneity of variances was not satisfied and a log-transformation had no improving effect. Size was also tested as an effect on carbohydrates (+lipids), proteins and fibre contents, but as we also wanted to control for a possible effect of the site where tubers were collected, a nested ANOVA was performed for each tuber component, with size as a fixed factor, site nested within size, i.e. site(size), as a random factor, and samples as the residual. These analyses were performed with STATISTICA 6.0.

3. Results

3.1. Functional responses

Linear regressions significantly fitted the relationships between feeding rate and tuber density, as well as the relationships between intake rate and tuber biomass, and this for the three tuber sizes (all $p < 0.01$; Figs. 1 and 2). This explained ca. 40–60% of the variation in consumption rates. Feeding rate and intake rate values showed great variances, which initially rendered the distinction among models (i.e. linear or disc equation) problematic. Linear models were however used to express the functional responses because they provided a better fit to the data than nonlinear ones within the range of experimental tuber densities. Indeed, testing a type II functional response, we found that this equation did not always significantly fit the data, and when it did (4 out of 6 cases), the curves were very close to linear. When evaluating the fit of the disc equation, it was very similar to that of a linear functional response

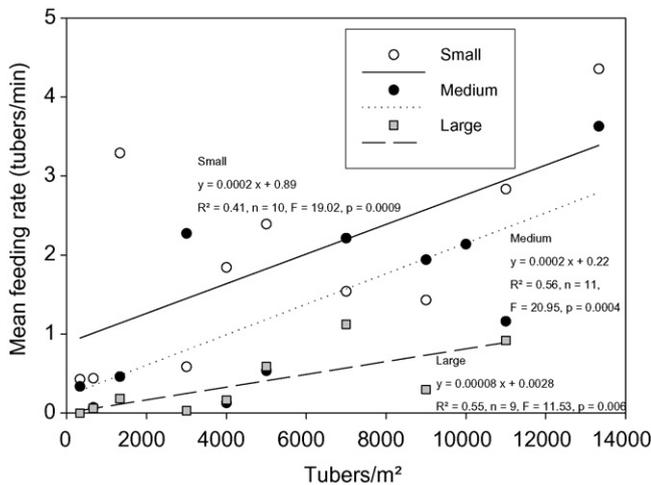


Fig. 1. Relationships between feeding rate (tubers/min) and tuber density (tubers/m²) for the three tuber sizes (S, M, and L).

(for Fig. 1 relationships: $R^2 = 0.56$ compared to $R^2 = 0.55$ for a linear functional response, and $R^2 = 0.54$ compared to $R^2 = 0.56$ for large and medium tubers, respectively; for Fig. 2 relationships: $R^2 = 0.57$ compared to $R^2 = 0.56$ for a linear functional response, and $R^2 = 0.47$ compared to $R^2 = 0.49$ for large and medium tubers, respectively).

Curves were not forced through the origin since we believe that it is better to have a model that fits the observed data well rather than one that goes through the origin but provides a poorer fit. Indeed, in our situation, the fit of a linear model with an intercept was similar ($R^2 \sim 0.50$ – 0.55) or, in the case of two models, was even better than that of a model without an intercept ($R^2 = 0.41$ versus $R^2 = 0.22$ for the $y = a \times x$ equation, and $R^2 = 0.56$ versus $R^2 = 0.26$). For the needs of the analyses however, we forced the linear equations through the origin before comparing the two types of equations using an F test for comparison of curves. The results showed that, in the majority of cases, the disc equation did not show a statistically better fit (for Fig. 1 relationships: $F = 0.096$, $p = 0.76$; $F = 0.0003$, $p \leq 0.05$; $F = 0.91$, $p = 0.37$ for large, medium and small tubers; for Fig. 2 relationships: $F = 0.061$, $p = 0.80$; $F = 0.043$, $p = 0.82$; $F = 0.98$, $p = 0.35$ for large, medium and small tubers). As having positive feeding and intake rates at zero tuber density is not biologically satisfactory, this suggests that the relationships between tuber density

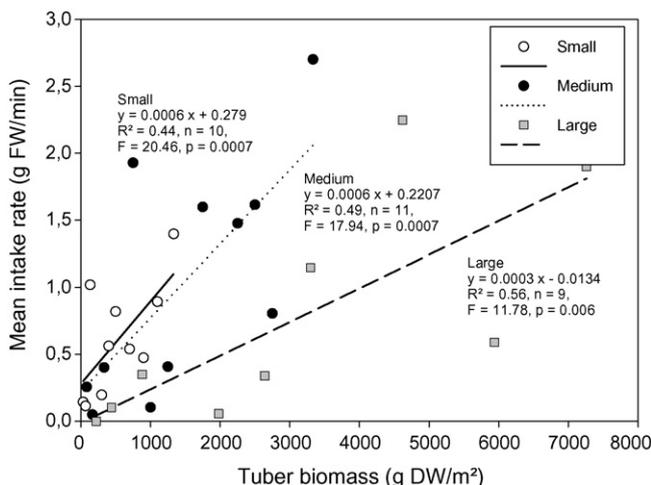


Fig. 2. Relationships between intake rate (g FW/min) and tuber biomass (g DW/m²) for the three tuber sizes (S, M, and L).

and consumption rates may be nonlinear for very low densities but is linear within the range of experimental densities (see Quinn and Keough, 2002, p. 99 for a similar discussion).

Even if complete depletion occurred once (data excluded from the analyses), patch depletion during trials was generally low (most depletion rates $\leq 10\%$). However, it reached 30–50% for S tubers when densities were < 3000 tubers/m², which could have conceivably biased feeding rate and intake rate values. Apart from these latter values which could have been slightly lowered, we considered that the effect of tuber depletion on consumption rates could be ignored, and we see no *a priori* reason to doubt our functional response results.

3.2. Effect of tuber size on functional responses

After controlling for year as a random effect, feeding rate was observed to vary significantly and linearly with tuber density (REML: $F_{1,25} = 28.59$, $p \leq 0.001$; Fig. 1). Tuber density accounted for 41, 56 and 55% of the variance for S, M and L tubers, respectively. Size also had a significant effect on feeding rate ($F_{2,25} = 10.69$, $p \leq 0.001$): geese had a higher feeding rate on S than on L tubers (t -test: d.f. = 25, $t = -4.61$, $p \leq 0.001$); M tubers provided a higher feeding rate than L tubers did (d.f. = 25, $t = -2.79$, $p \leq 0.01$), and there was a tendency for feeding rate on S tubers to be higher than that on M ones (d.f. = 25, $t = -1.97$, $p = 0.06$). Geese ingested from about 1.0 to 3.5, from 0.3 to 2.9 and from about 0 to 0.9 tubers/min on S, M and L tubers, respectively.

Converting tuber consumption rate in intake rate, a linear relationship between intake rate and tuber biomass was also clearly exhibited ($F_{1,25} = 26.22$, $p \leq 0.001$, Fig. 2), tuber biomass accounting for 44, 49 and 56% of the variance for S, M and L tubers, respectively. Size, adjusted for covariate tuber biomass, also showed a significant effect ($F_{2,25} = 6.13$, $p \leq 0.01$). Geese had higher intake rates on S and M tubers than on L ones (t -test: d.f. = 25, $t = -2.99$, $p \leq 0.01$; and d.f. = 25, $t = -3.30$, $p \leq 0.01$). Conversely, intake rates on S and M tubers did not differ significantly from each other (d.f. = 25, $t = -0.10$, $p = 0.92$).

3.3. Feeding behaviour parameters

From slopes of linear relationships in Fig. 1, a' , the attack rate or searching efficiency was deduced for S, M and L tubers (Begon et al., 1996). The values of a' were not significantly different, as the tuber density \times size interaction (testing differences between slopes) had no effect on feeding rate. Estimated a' was similar for S and M tubers (a'_S and $a'_M = 2$ cm²/min), but appeared smaller for L ones ($a'_L = 0.8$ cm²/min; Table 1), which suggests that variance around estimates was too large to allow discrimination between slopes.

Values of time spent searching, T_s , and handling, T_h , obtained from the videotapes, are reported in Table 1 (except for S tubers for which it was impossible to clearly distinguish T_s and T_h , see methods). T_s did not differ between L and M tubers (Mann–Whitney U test: $U = 9445$, $p = 0.31$). The density of tubers had a significant effect

Table 1

Estimations of a' , attack rate, T_s , search time, and T_h , handling time (from video tapes; mean \pm S.D.). Values with different letters are significantly different ($p < 0.05$) after Mann–Whitney U tests, except for a' (results of the non-significant tuber density \times size interaction, see text for explanations).

Size	a' (cm ² /min)	T_s (s)	T_h (s)
Small	2.0b	No data	No data
Medium	2.0b	4.3 \pm 2.5 (n = 143)b	9.7 \pm 5.5 (n = 79)b
Large	0.8b	4.9 \pm 4.9 (n = 142)b	20.3 \pm 14.4 (n = 26)c

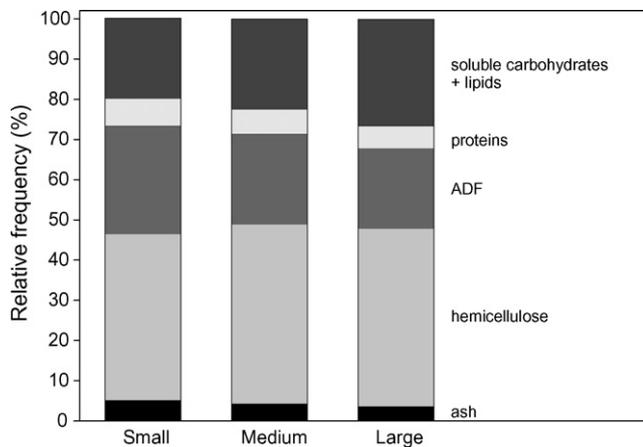


Fig. 3. Mean relative frequency ($n = 36$) of chemical components of tubers (% of dry matter) in relation to tuber size (S, M, and L). ADF = Acid Detergent Fibre.

on T_s (Kruskal–Wallis test: for L tubers: $H = 28.5$, $n = 136$, $p < 0.001$; for M tubers: $H = 17.4$, $n = 143$, $p = 0.015$), but we did not observe that T_s decreased with tuber density, as it would have been expected. Geese significantly spent more time handling L tubers than M ones ($U = 540.5$, $p < 0.001$), but this did not differ between tuber densities (for L tubers: $H = 2.9$, $n = 26$, $p = 0.58$; for M tubers: $H = 9.3$, $n = 79$, $p = 0.23$).

3.4. Effect of tuber size on chemical composition

Tubers had a high proportion of fibre (ca. 65–70% hemicellulose and ADF) and water-soluble carbohydrates (ca. 25%), the remainder being made of proteins and ash (Fig. 3). Percentages of ash (ca. 4–5%), hemicellulose (ca. 41–45%), and proteins (ca. 6–7%) were similar between tuber sizes. ADF seemed to decrease with tuber size (from 26.9 to 20.0%), and carbohydrates + lipids to slightly increase (from 19.9 to 26.5%). However, the nested ANOVA revealed that size had no significant effect on water-soluble carbohydrate (+lipids) (d.f. = 2, $F = 2.66$, $p = 0.15$), protein (d.f. = 2, $F = 3.18$, $p = 0.11$) and fibre contents (d.f. = 2, $F = 1.33$, $p = 0.33$).

4. Discussion

4.1. Shape of functional responses

Greylag geese consuming *S. maritimus* tubers showed linear functional responses (Figs. 1 and 2). This is in contrast with the type II and III (i.e. sigmoid) relationships described for this species when foraging on grass (Durant et al., 2003) and seeds (van Eerden et al., 1998b), respectively. Nevertheless, linear relationships have been reported in mammals (Batzli et al., 1981; White et al., 1981) as in other Anatidae, e.g. teals (van Eerden and Munsterman, 1998; Arzel et al., 2007), brent geese *Branta bernicla* (Rowcliffe et al., 1999) and barnacle geese *Branta leucopsis* (Van der Wal et al., 1998).

Linear functional responses indicate that geese ingested tubers at a rate that is proportional to their availability. Consumption rates result from the complex interaction of (i) bite size (i.e. tuber mass, as geese consume only one tuber at a time), (ii) attack rate (a'), and (iii) tuber density (or biomass). For a given tuber size, as tuber density increases, bite size remains the same, but it becomes easier to find a tuber since encounter rate (defined as: $a' \times$ tuber density or biomass) increases, and thus feeding rate and intake rate increase as well. In our experimental conditions a non-saturated process, based on changes in encounter rates with increasing tuber densities, thus seems to drive the goose foraging mechanism. There is no doubt

however that a maximum consumption rate exists in greylag geese (i.e. saturation), and these curves could also be considered as the beginning of type II functional responses.

4.2. Effect of tuber size on functional response

We found that food item size negatively affects feeding rates in greylag geese (the difference between small and medium tubers only tending, however, to be significant), as Fritz et al. (2001) showed in Mallards *Anas platyrhynchos* foraging on pellets. We interpret this size effect as representing a longer time spent handling tubers when size increases, and provide the following lines of evidence that support this hypothesis:

- (1) Handling time (Th) is an increasing function of tuber size. This was at least demonstrated in medium and large tubers, as it took twice as long to handle large tubers as medium ones (ca. 20 s versus 10 s, respectively). Although we could not quantify Th in small tubers, geese seemed to take less time to handle them (pers. obs.). On the contrary, the time required to find a tuber did not change with tuber size (T_s ca. 4–5 s). Since Th took an increasing proportion of time when size increases, we expect total search time (as well as a') to be reduced. Consequently feeding rate decreased. This was supported by the fact that tuber size tended to affect a' , which was 2.5 times shorter (although not significantly) in large tubers than in small and medium ones (Table 1). Although foraging mechanisms differ between mammals and birds, this phenomenon looks quite similar to that described in mammalian herbivores where plant fibrousness affects feeding rates through its effects on handling time (i.e. at similar bite sizes, more chewing effort is needed to cope with more fibrous bites; Shipley and Spalinger, 1992).
- (2) The nature of Th differs somewhat between sizes. Small tubers were generally rapidly consumed under water, and Th seems mainly composed of the time implicated in the transport of the tuber in the bill and in swallowing. Conversely, geese systematically raised the head when feeding on medium and large tubers. In addition to the time cost of transport and swallowing, Th was also characterised by a breaking process similar to chewing, i.e. a reduction by mandibles of the tuber into pieces before its swallowing (pers. obs.). This may also imply that handling can be part overlap with searching, and that short handling times associated with small tubers may well fall within this overlap in processes. Such overlap between searching and handling has been documented in large herbivores (e.g. Fortin et al., 2004).

Geese were reluctant to consume large tubers and many (ca. 80%) were rejected (versus ca. 30% of medium ones). As some were apparently too hard to be broken into pieces and too big to be ingested as a whole, size may not be the only attribute that affects goose ingestion rates and tuber hardness may in some way play a role (these two factors however possibly covary positively). The lower feeding rate on large tubers compared to small and medium ones (Fig. 1) is thus likely to reflect (i) handling time costs, and (ii) additional costs associated with handling those tubers not consumed (i.e. wasted handling time).

4.3. Do functional responses explain size-related consumption of tubers by geese?

The chemical analyses performed on tubers collected in the Saint-Seren marsh showed percentages of proteins (ca. 5–10%) similar to those reported in the literature (ca. 8%); fibre content was relatively higher (ca. 65–70%) and carbohydrates thus lower (ca. 20–25%) than the ca. 45% and 45% values obtained by Amat et al.

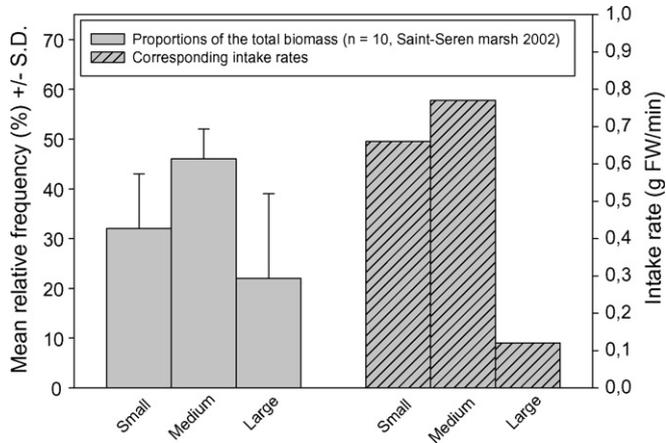


Fig. 4. Mean relative frequency of the total biomass of each tuber size (S, M, and L) from the grazed Saint-Seren marsh (Desnouhes, unpubl. data) in 2002, and corresponding potential computed intake rate (g FW/min). Intake rates were calculated for a given tuber biomass of 2000 g DW/m², based on equations in Fig. 2 and corresponding frequencies of each tuber size.

(1991). Amat (1986) proposed nutrient considerations to explain goose preference for small tubers. Our results do not support this hypothesis, as we found no differences in chemical components between the three tuber sizes. Instead, they suggest that the reason why greylag geese consume small tubers preferentially has to do with size-related constraints (i.e. handling time) on their ingestion rates. Handling time as a factor influencing food preferences has already been reported in mammals (Kaufman and Collier, 1981), or birds (Clark et al., 1986). Expressing food availability as tuber biomass and considering intake rate values corresponding to natural tuber biomasses (1100–2800 g DW/m²; Podlejski, 1981; Esselink et al., 1997; Charpentier, 1998; Gouraud et al., 2008), intake rates of small (and medium) tubers were 2–3 times higher than that of large tubers (Fig. 2). However, we cannot conclude, simply on this basis, that both small and medium tubers may be more profitable than large ones (in terms of intake rates). Indeed, in *S. maritimus* stands, a variety of tuber sizes are all inter-mingled in the soil, and they differ in their abundance (Gouraud et al., 2008). For this reason, intake rates were re-examined, but this time according to the relative biomasses of the three tuber sizes. Fig. 4 illustrates this for a mean tuber biomass of 2000 g DW/m² in the grazed Saint-Seren marsh in 2002. This biomass was multiplied by the proportion of tubers of each size (Gouraud et al., 2008) to derive the corresponding estimated biomasses (i.e. 640, 920 and 440 g DW/m² for small, medium and large tubers) which were then used to calculate intake rates according to equations in Fig. 2. We found that small and medium tubers constitute ca. 75–80% of the total tuber biomass. Assuming that tubers are evenly distributed, corresponding intake rates would be approximately seven and eight times higher, respectively, than that of large tubers. The ‘consumption rate hypothesis’ is thus not completely validated since medium tubers provided (though slightly) higher intake rates than small ones. However, making reference to Amat’s work, which suggests that 10 mm is the threshold tuber diameter above which geese get increasingly reluctant to forage on (Amat, 1986, 1995), one may consider that medium tubers in our study have a relatively close diameter (10–11 mm) to this upper limit, and can in some way correspond to the ‘small’ category defined by Amat. This implies that, in the present study, tuber size would be represented only in a two-phase state, i.e. high intake rate: ‘small’ tubers, and lower intake rate: large tubers, without however undermining our finding that geese would effectively rely (at least partly) on intake rate considerations for their tuber choice.

Considering the higher abundance of small (as well as medium) tubers compared to large ones, this could simply be the reason of the biased tuber size consumption by geese (without postulating preference), although Amat (1995) argued that birds ingested small tubers in higher proportions compared to their availability (the commonly admitted definition for preference). Additional constraints, intentionally ignored in our experimental study, are also likely to influence goose intake rates in the wild and could be supplementary arguments for them to forage preferentially on small tubers. Two constraints commonly invoked are: (i) digestive capacity (processing constraint), and (ii) tuber extraction (procurement constraint) (Amat, 1986, 1995). Indeed, in birds foraging on hard-to-digest food such as tubers, the throughput rate of food in the gut may be an important factor governing daily intake rate. As shown in other birds (Sedinger and Raveling, 1988; Kersten and Visser, 1996), a slow throughput rate (i.e. a digestive bottleneck) could limit intake rate by constraining geese to regularly interrupt their foraging periods until their gut is empty, which was indeed observed in greylag geese foraging on tubers (L. Desnouhes, pers. obs.). Moreover, small tubers are generally assumed to be less firmly attached to the substrate and to develop at lower depths, which would make them easier to extract than larger tubers. This remains however to be demonstrated, as e.g. Esselink et al. (1997) found no relationship between *S. maritimus* tuber size and tuber depth. Rather, goose digestive capacity appeared to be a more important factor influencing tuber choice as small tubers are presumably easier to break down in the gizzard, and may have a shorter processing time (digestion and passage). These costs could be considered as components of the ‘true’ handling time (i.e. handling tubers *per se*, breaking them into pieces and digesting them), so that tuber profitability may decrease rapidly with increasing size. Thus, digestive processing may well be the ultimate factor determining the optimal size of tuber on which to feed.

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