

Instantaneous intake rate in horses of different body sizes: Influence of sward biomass and fibrousness

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ARTICLE INFO

Article history:

Accepted 21 November 2008

Available online 3 January 2009

Keywords:

Biomass

Body size

Functional response

Grazing

Horses

Sward quality

ABSTRACT

The functional response, that is the relationship between the food intake rate of a forager and the availability of food items, has been subject to numerous investigations in ruminants. In horses however, the functional response has been poorly studied despite of the importance of grazed forage in horse nutrition and the increasing role of horses in the management of grasslands in Europe. Large differences in body size can be found in adult horses of different breeds and intake rates are commonly affected by body size and mouth morphology in mammalian herbivores. This study describes the functional response of horses using, for the first time, natural swards offering a wide range of biomass (from 82 to 513 gDM m⁻², i.e. heights from 3 cm to 63 cm) and varying in quality (NDF: 53–68%), and animals of different body sizes (ponies: 253 kg, saddle horses: 602 kg, heavy horses: 953 kg). Instantaneous intake rate was the product of bite size measurements on sward trays and bite rate values obtained on the same swards while horses were grazing at pasture. Using the Spalinger and Hobbs [Spalinger, D.E., Hobbs, N.T., 1992. Mechanisms of foraging in mammalian herbivores: new model of functional response. *Am. Nat.* 140, 325–347] model developed for mammalian herbivores, we found that Type II functional responses (i.e. asymptotic curve) provided a satisfactory fit to the intake rate by horses of contrasting body sizes on the range of biomass tested. As has been found in ruminants, handling time (i.e. the time needed to crop and to process a mouthful) increased linearly with bite size in the three sizes of horses. The maximum processing rate increased with body size, indicating that smaller horses are more constrained when bite size increases. Taking into account the fibrousness of swards did not improve the estimation of handling time which means that horses were relatively unaffected by the range of fibrousness in our study.

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1. Introduction

The functional response, that is the relationship between the intake rate of a foraging animal and the availability of food items (Holling, 1959), has been subject to numerous investigations because it is central in understanding predator–prey and plant–herbivore interactions (Noy-Meir, 1975; Spalinger and Hobbs, 1992). In

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mammalian grazing herbivores, for which the rate of forage intake has consequences for fitness and production (Smallegange and Brunsting, 2002), the intake rate has commonly been found to increase asymptotically with grass biomass or grass height on uniformly leafy swards, as a Type II functional response (Gross et al., 1993). Spalinger and Hobbs (1992) provided a theoretical explanation of the asymptotic curve through the competing processes of cropping and processing food in the mouth of grazers foraging on food-concentrated patches. Because larger bites need to be chewed for longer than smaller ones, bite size and bite rate are negatively related. Until recently, less attention has been given to the intake rate by mammalian grazing herbivores faced with mature swards which consist of complex mixture of various plant parts (e.g. leaves and stems), characterized by different structural and chemical properties (Van Soest, 1982) (but see Benvenuti et al., 2006, 2008; Drescher et al., 2006; van Langevelde et al., 2008).

Across species and individuals in mammalian herbivores, intake rates are also commonly affected by both body size and mouth morphology (Illius and Gordon, 1987; Demment and Greenwood, 1988; Gordon et al., 1996). Because intake rate increases with bite size (Spalinger et al., 1988) and larger herbivores obtain larger bites from their larger mouths (Gordon et al., 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, both at the interspecific (Shipley et al., 1994) and intraspecific (Gordon et al., 1996) level. Theoretically, this scaling would be between 1 (scaling of buccal volume) and 0.75 (scaling of metabolic rate). However, when swards are limiting then large herbivores are more constrained and intake rate will reduce to scale at around 0.33 (Illius and Gordon, 1987).

It is well known that horses at pasture create and maintain patches of short grass where they spend most of their grazing time (Ménard et al., 2002) within a matrix of tall swards contaminated with faeces which are avoided for feeding (Ödberg and Francis-Smith, 1976; Edwards and Hollis, 1982; Putman et al., 1991). The usual explanation was that this feeding behaviour is an adaptation to reduce infection by gastrointestinal parasites (Taylor, 1954) but recent studies suggest that this could also result, at least partially, from a nutritional strategy (Fleurance et al., 2005, 2007). A better understanding of the mechanisms of food acquisition by horses, obligate grazers (Martin-Rosset et al., 1984), would further contribute to unravel the processes determining grazing behaviour. The application of the concept of functional response has led to major insights into the process of resource acquisition by grazing ruminants, but has been poorly investigated in horses (but see Gross et al., 1993). The influence of body size of horses on their functional response has never been investigated experimentally, nor has the influence of sward quality.

In this study, we tested for the Type II functional response, the most frequently observed in mammalian herbivores, in horses (*Equus caballus*) varying in body size (ponies: 253 kg, saddle horses: 602 kg, heavy horses: 953 kg). We analysed the response of horses when

presented with a wide range of biomass and quality in natural swards. As in Durant et al. (2003), we used the approach of Spalinger and Hobbs (1992) to explore the functional response of horses. According to the Process 3 of Spalinger and Hobbs (1992), which generally applies for grazers where the resources are spatially concentrated and apparent, it is primarily handling time that limits the intake rate. Handling time (H , min bite⁻¹), the inverse of bite rate (B , bites min⁻¹), is defined as the time needed to crop a bite (T_c , min bite⁻¹) and to process (chew and swallow) a mouthful (T_s , min bite⁻¹):

$$H = \frac{1}{B} = T_c + T_s$$

T_s increases with bite size (S , gDM bite⁻¹), constrained by the maximum processing rate (R_{max} , gDM min⁻¹), thus:

$$T_s = \frac{S}{R_{max}}$$

Thus, handling time should increase linearly with bite size:

$$H = \frac{1}{B} = T_c + \left(\frac{S}{R_{max}} \right)$$

The objectives of this paper were (i) to test if the Type II functional response describes the intake rate of horses of contrasting body sizes, (ii) to determine whether Process 3 of Spalinger and Hobbs (1992) is applicable to horses (i.e. if handling time increases linearly with bite size), (iii) to investigate the influence of sward fibrousness on handling time and (iv) to discuss the influence of body size on the rate of intake by horses.

2. Material and methods

The experiment was performed from 14 June 2005 to 06 October 2005 at the field station of the French National Stud, the Station Expérimentale des Haras Nationaux (Chamberet, France).

2.1. Animals

Nine non-reproductive female horses, between 6 and 11 years old, were used for this experiment: 3 ponies (Welsh breed; 252.8 ± 14.9 kg S.E.), 3 saddle mares (Anglo-Arab and French saddle breeds; 602.1 ± 39.8 kg S.E.) and 3 heavy mares (Breton breed; 952.8 ± 66.3 kg S.E.). From the beginning of the training period (one month prior to the start of the experiment) to the end of the experiment, the different sizes of horses were maintained in 3 enclosures at pasture sown in 1991 (9.1 ha; 30% English ryegrass *Lolium perenne*, 30% tall fescue *Festuca arundinacea*, 20% white clover *Trifolium repens*, 15% cocksfoot *Dactylis glomerata*, 5% alfalfa *Medicago sativa*). Here they were faced with a large range of vegetation varying in height and maturity as they grazed the pasture heterogeneously. During the training period, the nine animals were trained to graze from sward trays (see below) of various heights (between 2.5 and 49.5 cm) by presenting them, on a daily basis, alternating short and tall treatments. The sward trays were prepared (see below) the morning before the training test from another heterogeneous pasture previously grazed by horses, offering a large range of sward heights. The nine horses were held in individual horse boxes for 5 h before being presented the trays in the test box at 13:30 p.m. to ensure that they ate from the swards offered to them. The horses were then offered an experimental tray from which they were allowed to take 20 bites and then returned to pasture.

2.2. The swards

During the experiment, the horses were presented with swards from the experimental area of the same pasture where they were maintained

throughout the experiment, prepared to offer a wide range of sward heights and maturities typical of that eaten by horses. Nine sward types with sward heights of 2.9, 4.6, 6.6, 8.5, 13.3, 20.4, 43.3, 54.6 and 62.7 cm were prepared on the pasture by mowing the grass to a height of 2 cm. Nine strips (10 m × 90 m each) were mowed every 2 weeks from the end of March and then allowed to grow for 2, 3, 19, 28, 35, 44, 59, 55 and 83 days before the tests to achieve the nine sward heights. Each strip was divided into 4 areas: 1 area (10 m × 12 m) was devoted to the preparation of the sward trays for indoors bite size measurements and 3 areas (ponies: 10 m × 19 m, saddle mares: 10 m × 24 m, heavy mares: 10 m × 34 m) were devoted to the outdoor bite rate measurements of the 3 sizes of horses.

2.3. Experimental design

The 9 sward types were offered to the horses over 9 periods on 3 consecutive days. We alternated tests on short and tall treatments so that any time effect would be included in the treatment effect.

The morning before the tests, rectangles of the sward type to be tested, including the top 10 cm of soil and roots, were cut to the dimensions of the subtrays composing the tray offered to the animal. Each tray was composed either of 2 (ponies), 4 (saddle mares) or 8 (heavy mares) subtrays (560 mm × 360 mm, depth × 108 mm). Rectangles of the sward were wedged in the subtrays with two horizontal metal bars (5 mm diameter) at the level of the soil surface to prevent the horses from pulling the swards out of the subtrays. We conducted preliminary trials to choose the dimensions of the trays to ensure that they were large enough to allow the animals to take 20 bites without noticeable depletion of the sward that could have affected bite size.

The 9 animals were brought indoors at 08:30 a.m. and fasted for 5 h to ensure that they ate from the trays at the beginning of the tests that started at 13:30 p.m. Each horse was then brought from its box to the test box and the sequence in which the individual animals were offered trays was modified each day. We presented the trays to the horses, restrained with a halter by an observer, on a metal table (70 cm high, to prevent trampling) and the animals were allowed to graze from the trays until they had taken 20 bites. On days 1 and 2, the 9 horses returned immediately to their enclosure at pasture at the end of the test. On day 3, the horses were lead to the experimental area in the outdoor pasture that corresponded to the same sward type that they had been presented with in the trays so that bite rate measurements could be made. These horses were then returned to their enclosures.

2.4. Measurements

2.4.1. Vegetation

Every morning we measured 90 sward heights (45 on each diagonal) (drop disc; i.e. a sliding square of polystyrene, 2.7 g; see Ménard et al., 2002) on the strip corresponding to the sward type to be tested before constructing the sward trays. Every 3 sward height measurements (15 on each diagonal), the sward was cut to the ground level in a 25 cm × 25 cm square and dried at 60 °C to constant weight to estimate dry matter content of the sward and biomass offered. For each sward type, 6 biomass samples were randomly selected and analysed for neutral detergent fiber (NDF).

2.4.2. Bite size

Prior to each test, we weighed each tray (sum of the subtrays). Two extra subtrays were used to measure the mass loss resulting from evapo-transpiration during the test. We kept these subtrays in the test area and weighed them at the same time as the trays presented to the horses. The mass loss resulting from evapo-transpiration during the test was subtracted from the total mass loss of the sward tray, to give herbage consumption. This was then divided by the number of bites (i.e. $n = 20$) taken from the tray to give the mean bite size in wet mass (WM) (gWM bite^{-1}). Across the experiment, the evapo-transpiration loss from the two extra subtrays averaged 6.5 ± 0.3 g (\pm S.E.). After each test, we cut the vegetation that remained on the tray to the grazing height and used this sample to determine the dry matter (DM) of the sward ingested (dried at 60 °C to constant weight). This was then multiplied to the mean bite size (gWM bite^{-1}) to express it in dry matter (gDM bite^{-1} , dry mass). The 3 replicates (3 days) per individual and per sward type were averaged to give a single value of bite size (S).

2.4.3. Bite rate

The 3 horses of a given body size grazing one of the 9 sward types were simultaneously observed by one observer for each horse. 5 measurements of bite rate (bites min^{-1}), alternated with 5 measurements of chew rate (chew min^{-1}) were recorded per individual during 1 min of uninterrupted feeding. The 5 replicates per individual per sward type were averaged to give a single value of bite rate (B). 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 horses as they were tested in groups (with the other individuals of their body size).

2.4.4. Instantaneous intake rate

To determine the effect of the availability of material on the swards (i.e. sward biomass) on dry matter instantaneous intake rate (DMIIR, gDM min^{-1}), we estimated intake rates using the following equation for each sward type and each individual:

$$\text{DMIIR} = S \times B$$

2.5. Statistical analyses

We first tested for the type II functional response in the 3 sizes of horses using the model of Holling (1959): $\text{DMIIR} = a \times \text{biomass} / (1 + b \times \text{biomass})$. Under this model, instantaneous intake rate increases to an asymptote as a decelerating function of sward availability. We fitted the equation using a SAS NON-LIN procedure (SAS Institute, 1999) and we compared the fit with linear regression using the coefficient of determination R^2 . The intercept of the quadratic curves was not forced through the origin though the DMIIR must tend to zero as grass biomasses approach zero values. In this paper we present both the asymptotic intake rate given by the model (a/b) and the maximum intake rate measured on the range of sward biomasses tested as well as the influence of body size on them.

We then investigated if the Process 3 of Spalinger and Hobbs (1992) was applicable for the 3 sizes of horses by fitting the linear equation (SAS Institute, 1999):

$$\text{Handling time} = T_c + \left(\frac{S}{R_{\max}} \right),$$

where T_c is the time needed to crop a bite (min bite^{-1}), S is the bite size (gDM bite^{-1}) and R_{\max} is the maximum processing rate (gDM min^{-1}). Comparison of equation parameters between body sizes was performed using non-parametric tests.

Finally, a Mixed Maximum Likelihood model was performed in order to investigate the influence of sward fibrousness (NDF) on the relationship between handling time and bite size. This analysis allows the specific effects of covariates and factors, the “fixed variables”, to be tested while accounting for the variance explained by potentially confounded variables, which are included as “random variables”. This prevents the variance due to these random variables, here the variable “individual”, being erroneously incorporated in the error term of the analysis. We used model selection methodologies based on AIC values to test if handling time in the different types of horses was better explained by i) bite size only, ii) bite size and NDF, iii) bite size, NDF and $\text{NDF} \times \text{bite size}$. The best models were considered as those with AIC values smaller than the others by 2 units (Burnham and Anderson, 1998). The variables were transformed when necessary to normalise their distribution.

3. Results

3.1. Vegetation characteristics

Sward biomass ranged from 82 to 513 gDM m^{-2} and was highly correlated with sward height (2.9–67 cm) ($r = 0.96$, $n = 9$, $p < 0.0001$). NDF content increased with sward biomass (from 53 to 68%, $r = 0.86$, $n = 9$, $p = 0.003$).

3.2. Applicability of the Type II functional response to horses

For the three body sizes, a type II functional response produced a satisfactory fit to the relationship between

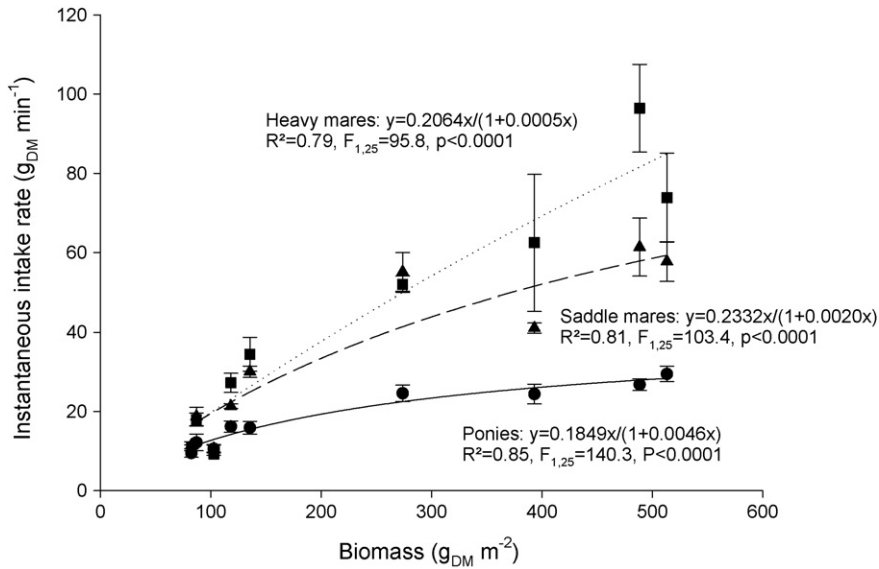


Fig. 1. The relationships between sward biomass (g DM m^{-2}) and mean instantaneous intake rate (\pm S.E., g DM min^{-1}) in ponies (circles, solid line), saddle mares (triangles, dashed line) and heavy mares (squares, dotted line). The regression analyses were performed on the raw data ($n = 27$ for each size of horses); mean values are presented for clarity.

instantaneous intake rate and sward biomass in horses (Fig. 1). The asymptotic values of DMIIR given by the model $y = a \times \text{biomass} / (1 + b \times \text{biomass})$ were $40.2 \text{ g DM min}^{-1}$ for ponies, $116.6 \text{ g DM min}^{-1}$ for saddle horses and $412.8 \text{ g DM min}^{-1}$ for heavy horses. Among the heavy horses, one individual (No. 8) showed a less asymptotic functional response than the two others: $\text{IIR} = 0.2253 \times \text{biomass} / (1 + 0.0001 \times \text{biomass})$. This individual was not the heaviest and did not have the largest mouth dimensions but she had the highest bite sizes and bite rates on

tall swards. When this horse is removed from the analysis, the asymptotic value of DMIIR given by the model (a/b) for heavy horses drops to $250.0 \text{ g DM min}^{-1}$.

Bite size (g DM bite^{-1}) increased linearly with sward biomass (g DM m^{-2}) on the range tested (Ponies: $y = -0.0350 + 0.0031x$, $R^2 = 0.83$, $F_{1,25} = 122.0$, $p < 0.0001$; Saddle mares: $y = -0.1972 + 0.0055x$, $R^2 = 0.92$, $F_{1,25} = 304.0$, $p < 0.0001$; Heavy mares: $y = -0.3507 + 0.0080x$, $R^2 = 0.88$, $F_{1,25} = 176.3$, $p < 0.0001$) and heavier horses increased their bite size faster than the smaller ones

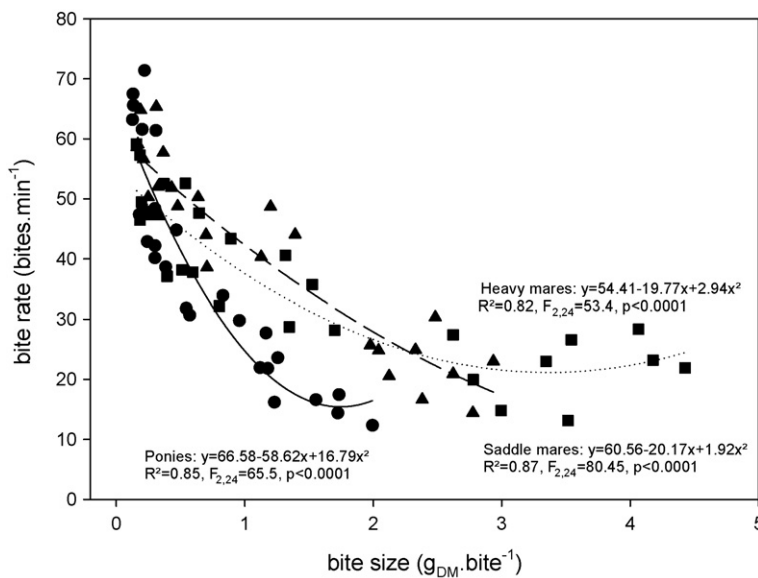


Fig. 2. The relationships between bite size (g DM bite^{-1}) and bite rate (bites min^{-1}) in ponies (circles, solid line), saddle mares (triangles, dash line) and heavy mares (squares, dotted line). Each dot represents the mean value for one individual.

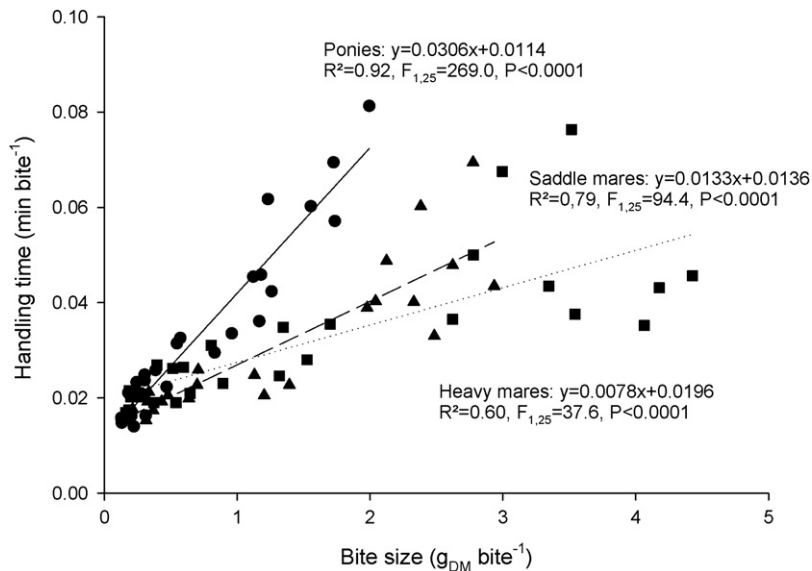


Fig. 3. The relationships between bite size (gDM bite^{-1}) and handling time (min bite^{-1}) in ponies (circles, solid line), saddle mares (triangles, dash line) and heavy mares (squares, dotted line). Each dot represents the mean value for one individual.

(Kruskal–Wallis, $p = 0.027$, $n = 9$ individuals). However, increasing bite size reduced the rate of increase in intake because cropping rate declined (Fig. 2).

3.3. Mechanisms regulating the functional responses

For all body sizes, handling time increased linearly with bite size in horses (Fig. 3). We also tested for the influence of sward fibrousness on handling time in the 3 sizes of horses. We compared the model of Spalinger and Hobbs (1992) where handling time is fully explained by bite size (i) with models where fixed effects were bite size, NDF (ii) and bite size, NDF, bite size \times NDF (iii). Taking into account the sward fibrousness did not improve significantly the estimation of handling time compared to the model of Spalinger and Hobbs (1992) (Table 1). In ponies, however, the interaction bite size \times NDF was significant and with a negative coefficient (Table 1), which means that the slope of the relationship between handling time and bite size increased less steeply with increasing fibrousness, for a given bite size. Thus, the ponies seemed to reduce their handling time as sward fibrousness increased.

3.4. Scaling of maximum instantaneous intake rate

The maximum processing rate ($R_{\text{max}} \pm \text{S.E.}$, gDM min^{-1}) increased strongly with body size (ponies: $R_{\text{max}} = 36.0 \pm 4.0 \text{ gDM min}^{-1}$, saddle mares: $R_{\text{max}} = 76.2 \pm 9.6 \text{ gDM min}^{-1}$, heavy mares: $R_{\text{max}} = 129.4 \pm 27.9 \text{ gDM min}^{-1}$) (Kruskal–Wallis, $p = 0.027$, $n = 9$ individuals). The time needed to crop a bite ($T_c \pm \text{S.E.}$, min bite^{-1}) tended to increase with body size (ponies: $T_c = 0.0126 \pm 0.0010 \text{ min bite}^{-1}$, saddle mares: $T_c = 0.0135 \pm 0.0013 \text{ min bite}^{-1}$, heavy mares: $T_c = 0.0189 \pm 0.0008 \text{ min bite}^{-1}$) (Kruskal–Wallis, $p = 0.055$, $n = 9$ individuals). Similar conclusions are obtained if the heavy mare No. 8 is removed from the

analysis (Heavy mares: $R_{\text{max}} = 101.5 \pm 0.5 \text{ gDM min}^{-1}$, $T_c = 0.0200 \pm 0.0007 \text{ min bite}^{-1}$).

Whatever the body size considered, the DMIIR max given by the model $y = a \times \text{biomass} / (1 + b \times \text{biomass})$ (Ponies: $40.2 \text{ gDM min}^{-1}$, Saddle mares: $116.6 \text{ gDM min}^{-1}$, 1, Heavy mares with/without No. 8: $412.8 \text{ gDM min}^{-1} / 250.0 \text{ gDM min}^{-1}$) was higher than our estimation of the maximum processing rate (R_{max}) (Fig. 4).

The maximum values of intake rate calculated from the measurements on the two highest sward biomass levels (mean \pm S.E.; Ponies: $28.1 \pm 1.6 \text{ gDM min}^{-1}$, Saddle mares: $59.5 \pm 4.4 \text{ gDM min}^{-1}$, Heavy mares: $85.1 \pm 9.8 \text{ gDM min}^{-1}$) were much lower than the asymptote given by the model and a bit lower than the R_{max} estimates (Fig. 4), as expected from the theoretical models.

4. Discussion

4.1. Vegetation characteristics

Here we describe, for the first time, the instantaneous intake rate in horses of different body sizes which were offered a wide range of sward types typical of natural sown pastures. Gross et al. (1993) tested the influence of a range of sward biomasses similar to that used in this study ($11\text{--}467 \text{ gDM m}^{-2}$) on intake rate in saddle horses but the sward quality was higher and less variable as these authors used alfalfa (*M. sativa*) only, chosen for its consistence in quality between the study locations. Naujeck and Hill (2003) measured the bite dimensions in saddle horse, on swards with a range of biomass/height that was smaller than that used in our study ($59\text{--}399 \text{ gDM m}^{-2}$, 3–19 cm), and the sward quality was probably lower (perennial ryegrass, *L. perenne*) as the vegetation was allowed to grow to 19 cm tall before it was cut to the height to be presented in the test, hence having a higher stem to leaf ratio.

Table 1

Influence of the explanatory variables (i) Bite size, (ii) Bite size, NDF, (iii) Bite size, NDF, Bite size \times NDF on handling time (H) in the 3 sizes of horses (Mixed Maximum Likelihood model). The variable Individual was incorporated as a random effect; sq rt = square root.

Effects on sq rtH	F	p	Coeff	Model AIC
Ponies				
(i) Bite size (S)	$F_{1,24.7} = 399.84$	<0.0001	0.07621	-154.4
(ii) Bite size (S)	$F_{1,25.7} = 175.45$	<0.0001	0.07897	
arcsine NDF	$F_{1,25} = 0.34$	0.5632	-0.00070	-152.7
(iii) Bite size (S)	$F_{1,24} = 9.75$	0.0046	0.29580	
arcsine NDF	$F_{1,24.6} = 2.80$	0.1071	0.00348	
Bite size \times arcsine NDF	$F_{1,24} = 5.28$	0.0305	-0.00432	-155.4
Effects on H				
Saddle mares				
(i) sq rt Bite size (S)	$F_{1,27} = 79.65$	<0.0001	0.02709	-183.5
(ii) sq rt Bite size (S)	$F_{1,27} = 25.55$	<0.0001	0.02514	
arcsine NDF	$F_{1,27} = 0.24$	0.6256	0.00041	-181.7
(iii) sq rt Bite size (S)	$F_{1,27} = 0.03$	0.8703	0.01431	
arcsine NDF	$F_{1,27} = 0.00$	0.9571	0.00013	
sq rtBite size \times arcsine NDF	$F_{1,27} = 0.02$	0.9014	0.00022	-179.7
Effects on sq rtH				
Heavy mares				
(i) sq rtBite size (S)	$F_{1,24.1} = 78.43$	<0.0001	0.05351	-128.1
(ii) sq rtBite size (S)	$F_{1,24.2} = 33.10$	<0.0001	0.05288	
arcsine NDF	$F_{1,24.1} = 0.01$	0.9288	0.00017	-126.1
(iii) sq rtBite size (S)	$F_{1,24.4} = 1.28$	0.2682	0.24230	
arcsine NDF	$F_{1,24.4} = 0.76$	0.3913	0.00550	
sq rtBite size \times arcsine NDF	$F_{1,24.4} = 0.79$	0.3840	-0.00379	-124.9

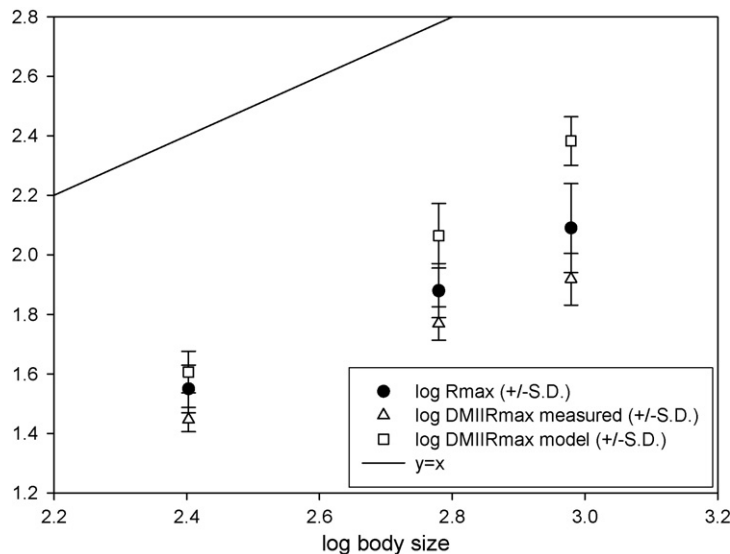


Fig. 4. Influence of body size on Rmax (gDM min⁻¹), DMIIIRmax measured (gDM min⁻¹, calculated as the mean, for each individual, of the two highest DMIIIR values obtained on the two highest biomasses) and DMIIIRmax given by the model (DMIIIR = $a \times \text{biomass} / (1 + b \times \text{biomass})$; gDM min⁻¹). For heavy horses, the DMIIIRmax given by the model was estimated without the data from individual No. 8 (see Section 3.2).

4.2. Functional responses

The relationship between bite size and sward biomass increased linearly on the range of biomass tested (as in ruminants, Burlison et al., 1991; Laca et al., 1992; Gong et al.,

1996) and bite size increased faster with sward biomass for large horses (Illius and Gordon, 1987). On a lower range of biomass of perennial ryegrass, saddle horses increased their bite size exponentially (Naujeck and Hill, 2003). In that study the range of bite size was 0.2–2.1 gDM bite⁻¹ which is

very similar to the result found in our study for saddle horses on comparable biomasses ($0.1\text{--}2.0\text{ gDM bite}^{-1}$). In the study of Gross et al. (1993), the saddle horses achieved a maximum bite size of 8 gDM bite^{-1} on plant biomass of 467 gDM m^{-2} (i.e. $10.5\text{ gDM plant}^{-1}$), which is much higher than the maximum value found in our study. This difference might be explained by the vegetation species used. Alfalfa is a forb with easily harvested stems, and in the Gross et al. (1993) study its quality was consistent and high. This limited structures that could potentially reduce bite size such as poor-quality grass stems (Flores et al., 1993; Ginnett et al., 1999; Benvenuti et al., 2006), with high fiber levels (Spalinger et al., 1988).

It is a general rule that herbivores compensate for small bite sizes by increasing bite rates (Trudell and White, 1981; Wickstrom et al., 1984; Spalinger et al., 1988); in this study the horses increased bite rate to a maximum of about 1 bite sec^{-1} on the shortest swards (Fig. 2) but this was not enough to maintain instantaneous intake rate (Fig. 1). Similar maximum values for bite rate were found in cattle (Gross et al., 1993). On taller swards, bite rate decreased as bite size increased, as in ruminants (Black and Kenney, 1984; Penning, 1986; Penning et al., 1991a, 1991b), which lead to the Type II functional response observed in most mammalian herbivores (Gross et al., 1993). A decrease in intake rate at high biomass (type IV functional response) has been observed in cattle as stem density increased in an artificial sward (sub-tropical guinea grass *Panicum maximum* Jacq.) (Drescher et al., 2006; Benvenuti et al., 2006), indicating that the slope of the functional response curve may decrease for large herbivores in extreme sward conditions. On these swards, stem density had a negative asymptotic effect on bite area, bite mass and instantaneous intake rate for both mature cattle (3-year-old; 605 kg) and younger ones (1-year-old; 324 kg) but this effect was greater for the older cattle (Benvenuti et al., 2008). The authors cautioned, however, that the negative effects of grass stems on bite size and forage intake could be less pronounced in softer grass species.

4.3. Mechanisms regulating the functional responses

According to the Process 3 of Spalinger and Hobbs (1992) handling time limits the intake rate in herbivores. As sward height increases, bite size also increases and the handling time per bite increases accordingly, which lowers bite rates. In our study, handling time increased linearly with bite size which confirmed our hypothesis.

Taking account of sward fibrousness did not improve the estimation of handling time, which suggests that horses are relatively tolerant to the range of fibrousness tested. In saddle horses, Brøkner et al. (2006) did not find any effect of grain NDF content (11–31% NDF) on chewing time. Nonetheless, we did find a significant effect of the bite size \times NDF interaction in ponies (Table 1) which suggests that horses of small body size would be more affected by sward fibrousness than the heavier ones. Interestingly, the response by ponies was not to compensate for a lower quality by increasing their effort in handling but conversely they increased their handling time to a lesser extent as compared to heavier horses. Our

findings suggest that, when the sward fibrousness is high, the ponies limit their investment in chewing activities ($\text{chew/gDM} = 17.447 - 0.221 \times \text{NDF}(\%)$, $R^2 = 0.43$, $F_{1,25} = 18.92$, $p = 0.0002$) which may be relatively costly as compared to the nutritional benefits and we hypothesize that they compensate by increasing passage rate of digesta through the digestive tract.

4.4. Scaling of maximum instantaneous intake rate

Maximum instantaneous intake rate was found to scale allometrically with body size ($0.63\text{BS}^{0.71}$) for mammalian herbivores in a multispecies data set (Shipley et al., 1994). In our study, the DMIIR max given by the model $a \times \text{biomass}/(1 + b \times \text{biomass})$ were much higher than those predicted by Shipley et al. (1994): Ponies: 31.8 gDM min^{-1} , Saddle mare: 59.1 gDM min^{-1} , Heavy mares: 81.9 gDM min^{-1} . These values were also very high compared to the maximum processing rate (R_{max}) (Fig. 4). As in the study of Gross et al. (1993), the time needed to crop a bite (T_c) was weakly influenced by body size, while R_{max} significantly increased with body size, indicating that smaller horses are more constrained when bite size increases. Shipley et al. (1994) proposed an allometric relationship between R_{max} and body size ($0.71\text{BS}^{0.70}$); our R_{max} values at the intraspecific level scaled isometrically with body size (Fig. 4). This would be consistent with the study of Heuermann (2007) who found an isometric relationship between maximum intake rate and body size in different sub-species of Canada geese (*Branta canadensis*). This would imply that large animals ingest the same proportion of their body size as smaller ones do, while they require less energy per unit body size to meet their metabolic requirements. The smaller ones would, therefore, need to compensate for the lower intake by selecting food of higher quality, and/or are less tolerant for decrease in intake rate and thus select patches where they are always at the maximum value of IIR (Demment and Van Soest, 1985; Illius and Gordon, 1992). According to Illius and Gordon (1992), the upper limit to body size in ungulate herbivores may be imposed by restricted nutrient intake rate under conditions of resource depletion. The absence of equids at or above the present maximum size of ruminants in the extant fauna may, therefore, arise from their lower tolerance of food shortages than ruminants and from seasonality in the food supply (Janis, 1989).

In the context of herbivore foraging under process 3, it is clearly not possible for DMIIRmax to be higher than R_{max} . Therefore, in our study, we have overestimated the DMIIR max values with our model because of a lack of data for higher biomasses. Indeed, if the values of DMIIR at the tallest sward tested in our study were already the asymptotic value of DMIIR, our fitted model would not be able to detect it. This is particularly true for the bigger horses for which there is no real sign of any levelling off of the functional response curve (Fig. 1). When considering the maximum measured values we actually obtained more realistic estimates. Initially, we tried to use taller swards (i.e. biomass: 965 gDM m^{-2} , sward height: 88 cm) but we faced methodological limitations because the vegetation did not stand up in the trays. Consequently, the feeding

behaviour by horses was not consistent between indoor (bite size) and outdoor (bite rate) measurements: on trays, horses took larger bites than at pasture where they fed mainly on ears and leaves of the grass. In the study of Gross et al. (1993), the horses (432 kg) reached a plateau of intake rate (40 gDM min⁻¹) for a bite size of 3 gDM bite⁻¹ and on a sward biomass (~180 gDM m⁻²) which was much lower than the maximum value tested in our study. Again this may be due to the type of sward (i.e. alfalfa) and here, saddle horses (600 kg) achieved maximum intake rate (59.5 gDM min⁻¹) and maximum bite size (2.4 gDM bite⁻¹) on the highest biomasses tested (488–513 gDM m⁻²). An alternative but not exclusive explanation of the difference between DMIR_{max} given by the model and R_{max} is that the R_{max} is an underestimate as would occur if T_c also varied with bite size (S) (see also Ginnett and Demment, 1995). T_c would then be composed of a fixed fraction (T_{cf}) and a variable fraction function of bite size (T_{cv}). The equation would become:

$$H = T_{cf} + \left(T_{cv} + \frac{1}{R_{max}} \right) \times S$$

hence the estimated slope would be (T_{cv} + 1/R_{max}) and not R_{max}, and thus because (T_{cv} + 1/R_{max}) is always higher than 1/R_{max}, the value of R_{max} would be underestimated since the slope of the regression between H and S is taken to be only a measure of 1/R_{max}.

It is well known that horses maintain patches of short grass (Ménard et al., 2002) and our results go against the dry matter intake-rate maximisation prediction (Belovsky, 1978; Owen-Smith and Novellie, 1982; Ungar and Noy-Meir, 1988; Thornley et al., 1994; Newman et al., 1995) which has been verified in a few experimental studies (Black and Kenney, 1984; Illius et al., 1999). Fryxell (1991) suggests instead that grazing animals would make a trade-off between sward availability and quality and select intermediate swards where they would maximise their intake rate of digestible nutrients (Forage Maturation Hypothesis). A number of studies confirmed this hypothesis in ruminants (Wilmshurst et al., 1995, 1999a, 1999b) but this has never been tested in horses, even though some studies have shown the role that the rate of digestible energy intake may have in the diet selection in horses (van Wieren, 1996). A recent study suggests that horses may respond to an interaction between a nutritional and an anti-parasite strategy i.e. they avoid patches of tall grass of low quality and areas contaminated with parasite larvae leads horses to select patches of short grass far from faeces more frequently than would be expected from the proportion of these patches in the pasture (Fleurance et al., 2007).

5. Conclusion

This study provides new insights on the mechanisms of food acquisition in horses of different body sizes. The functional responses of the three sizes of horses tested fitted the Type II model found in many species of mammalian herbivores. Handling time, which limits intake rate, increased linearly with bite size but was not affected by the fibrousness of swards. This suggests that

horses were relatively tolerant of forage fibrousness in the range tested. The maximum processing rate of forage increased with body size, confirming that the intake rate of smaller horses was more constrained when bite size increased than was that of larger horses.

Acknowledgments

This work was funded by Les Haras Nationaux, Direction des Connaissances. Particular thanks to colleagues from the experimental farm of the French National Stud at Chamberet, especially Claude Larry, and to Amélie Cauvin who helped with the collection of data.

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