Mechanisms of functional response and resource exploitation in browsing roe deer

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Summary

1. The functional responses of roe deer were examined using 11 plant species. A technique to discriminate between encounter-and handling-limited processes was used, and it can be concluded that the functional response applicable to patch browsing by roe deer is governed not by the rate of encounter but by the rate of oral processing.

2. The large differences between plant species were due to variations in both parameters of the functional response: h, the time lost in biting, and R_{max}, the maximum processing rate. Removing the thorns from three of the species affected these parameters differently, according to the size and density of thorns.

3. Animals took larger bites from larger patches (branches), and bite mass declined as patch exploitation progressed, implying that animals were selecting the larger items to eat first. It was demonstrated experimentally that depletion of the larger bites does occur first, and it was concluded that prey selection is an important component of herbivore foraging behaviour.

4. The gain curves for deer feeding on the different plant species are calculated as being virtually linear. Patch depression did not, in general, occur because increasing bite rate compensated for declining bite mass. Our mechanistic approach is contrasted with other approaches to describing the gain curve in the literature.

5. *A priori* and empirical grounds are presented for rejecting the hypothesis that resource exploitation by browsing mammals is governed by optimal patch use. Diet optimization, involving a trade-off between diet quality and quantity, offers a better explanation of herbivore foraging behaviour.

Key-words: functional response, herbivore, marginal value theorem, patch depression, spinescence.

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Introduction

Knowledge of the mechanisms of resource exploitation is fundamental to our understanding of the population ecology of consumers. Important processes in resource exploitation include the way a forager's intake rate responds to resource abundance (the functional response), diet optimization and optimal patch use in cases where short-term intake rate declines as exploitation of food patches proceeds (patch depression). This paper examines the implications of recent advances in describing the functional response of mammalian herbivores for our recognition of the predominant processes in resource exploitation by browsing ungulates.

Our understanding of the mechanisms of functional response in mammalian herbivores was transformed by the work of Spalinger & Hobbs (1992), who recognized that handling can overlap to some degree with searching, unlike the constraint of exclusive searching and handling conventionally assumed to apply to foragers. This is because, although herbivores have to finish chewing one bite before they can take the next, they can use the time spent chewing to search for the next bite. Thus, separate functional responses apply to the cases where intake rate is limited by the time taken to search for the next bite and by the time taken to chew ingested forage. Spalinger & Hobbs (1992) derived equations for the functional response under conditions where intake rate is limited by one of three processes:
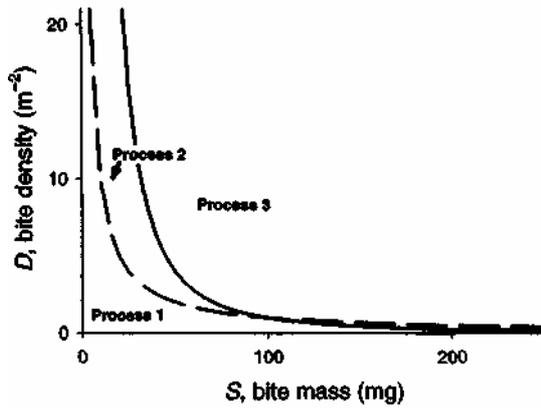
Fig. 1. Boundary conditions distinguishing three mechanisms of functional response as functions of bite density and bite mass (Spalinger & Hobbs 1992). The dashed line separates Processes 1 and 2, and is $D^* = \dfrac{R_{max}}{SV_{max}W}$; the solid line separates Process 2 and 3, and is $D^* = \left[\dfrac{R_{max}}{SV_{max}}\right]^2$, with $R_{max} = 100$ mg s^{-2}, $V_{max} = 1$ m^{-2}, $W = 1$ m. Parameters are defined in the Analysis section.

rate of encounter with cryptic food items (Process 1); rate of encounter with apparent items (Process 2); and rate at which food can be chewed and swallowed (Process 3). Spalinger & Hobbs (1992) defined the boundary conditions between encounter-limited and handling-limited foraging in terms of the density of bites *(D,* m^{-2}) and bite mass *(S),* as illustrated in Fig. 1. There are good *a priori* grounds for thinking that patch exploitation by browsers is governed by either process 2 or 3: food items are apparent rather than cryptic and may be encountered at a sufficiently high rate for oral processing rate to be the most likely constraint on intake rate. Gross *et al.* (1993) applied the Process 3 model to analysis of functional response by mammalian herbivores feeding on artificial patches of lucerne (or alfalfa, *Medicago sativa).* Farnsworth & Illius (1998) considered the implications of these new functional responses for prey choice in herbivores, and the present paper addresses empirically the implications of these mechanisms for patch depression in browsing European roe deer *(Capreolus capreolus).*

Under the simple assumptions of uniform prey size, of mutually exclusive searching and handling, and non-systematic searching, the successive removal of prey from a patch by the forager causes a decline in encounter rate, and this reduces intake rate. This would occur in herbivores if the combination of encounter rate and item size was below the boundary (see Fig. 1), and foraging was thus encounter-limited. On the other hand, if the combination of encounter rate and prey size exceeded the boundary condition, intake rate would be determined by oral processing rate and not by encounter rate, and would not therefore decline as prey became more scarce. The examples illustrated in Fig. 2 show that a herbivore would not experience patch
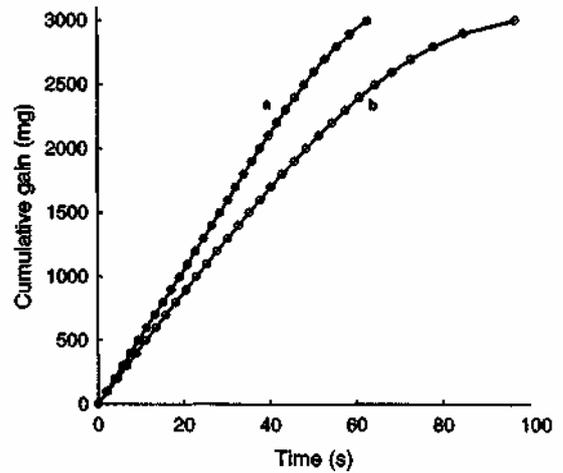
Fig. 2. Patch depression. (a) A herbivore whose intake rate is described by the Spalinger-Hobbs equations (see text for details). The example, using the same parameter values as in Fig. 1, shows the progressive depletion of a patch of 30 items each of 100 mg distributed over 10 m^2 (b) A conventional predator that searches randomly, that cannot simultaneously is represented by a Holling-type function: $I = \dfrac{aD}{1 + aDT_h}$, where I is intake rate, $a = 1$ is search efficiency and $T_h = \left(h + \dfrac{S}{R_{max}}\right)$ is handling time. Open symbols denote the part of the gain curve where intake rate is limited by encounter rate.

depression until a patch of uniformly sized prey had become almost totally depleted; a greater degree of patch depression would be experienced by a conventional forager with mutually exclusive handling and searching. In either case, there would be no patch depression if searching was systematic and encounter rate thus remained constant. A further possibility is that, as Vivås, Saether & Andersen (1991) showed with moose, browsers select the largest items first and deplete patches in order of item size. Then, provided item size and encounter rate continue to exceed the boundary conditions, depression in intake rate could result from declining bite mass not being fully compensated for by increasing bite rate, according to the Process 3 functional response. Therefore, the type of functional response that applies during browsing, the uniformity or otherwise of bites selected and the existence of prey selection during patch depletion will determine whether depression in intake rate will occur. The elucidation of these mechanisms is the object of our study.

European roe deer *(Capreolus capreolus)* are the most abundant European browsing ungulate. The botanical composition of their diets is well known: they use a wide range of plant species, but are highly selective (see Duncan *et al.* 1998 for a review). We used 10 common native species of trees and shrubs typical of the deciduous woodlands of western Europe, together with lucerne, which has been widely used in other

studies of herbivore foraging. The leaves of the plants naturally eaten by roe deer vary in size by more than an order of magnitude from the 15 mg leaves of blackthorn *(Prunus spinosa)* to the 600 mg ones of oak *(Quercus robur/pedunculata);* and three of the species are protected against mammalian herbivores by spines (blackthorn and hawthorn, *Crataegus monogyna)* or thorns (brambles, *Rubus fruticosa).* Leaf size has been found previously to have a positive effect on intake rates in goats (Koerth & Stuth 1991), and fibrousness (Spalinger *et al.* 1988) and thorniness reduce intake rates in African and American browsers (Cooper & Owen-Smith 1986; Haschick & Kerley 1997; see also Myers & Bazely 1992).

Materials and methods

THE ROE DEER

We used members of two groups of seven and eight tame roe deer at the Centre d'Études Biologiques de Chizé, aged 1-3 years of age, which came from a variety of sources in north and west France. All had been bottle-reared, but had fed on natural vegetation from their first summer. They lived in a large woodland pen, and seven had been used for observations on food selection and five for measurements of food intake rates, using hand-held plants (see Tixier *et al.* 1997). Supplementary food was provided (goat pellets [CAPRIVAL] in wheat chaff), but the goats obtained much of their food from the natural vegetation, especially in spring and summer when these data were collected.

The members of these groups had similar feeding behaviour. When foraging in natural plant communities in spring, though there were significant differences among individuals in their diets (analysis of variance, $F_{6,1152} = 2.47$, $P = 0.022$), these concerned only two species of minor importance (<3% of the diet) among the 62 plant species present. The three tamest animals used for the studies reported here fed readily on hand-held branches. They showed significant differences in their rates of food intake. Though these were slight (<10% of the mean value) we took account of individual effects in the analysis. During the experiments they were not deprived of food; two were adult, breeding animals and the third a yearling. Their median body mass was 22 kg.

THE PLANTS

We used branches from 10 bushes and trees which are commonly eaten by roe deer in deciduous temperate woodland, and lucerne which is also used by roe deer and is widely used in studies of feeding by mammalian herbivores. The species were chosen to provide a wide range of leaf sizes, and included the three species in our area with thorns (blackthorn and hawthorn) and spines (brambles). The branches were cut near the

enclosures, immediately before the experiments. These species are used by the deer to varying extents: *Carpinus, Cornus, Quercus* and *Crataegus* are commonly the main components of the diet in spring or summer; *Acer campestris* is sometimes a principal species; and *Prunus* and *Fagus* are minor components of the diet, and often avoided (Tixier & Duncan 1996; Tixier *et al.* 1997). Distances between thorns in *Crataegus, Prunus* and *Rubus* were measured on six branches of six individuals of each species. A thorn was selected at random, and the distance to its nearest neighbour measured.

EXPERIMENTS

In a preliminary experiment, we examined the effects of plant size and depletion on the bite mass deer obtained in trial periods during which the deer were allowed to take 15 bites from branches (i.e. patches). Three different plant species were used, separately. Three treatments were imposed: the effect of patch size was examined by comparing bite mass from small branches with that from large branches, neither of which had previously been browsed, and the effect of depletion was assessed by then offering the large branches a second time for a further 15 bites to be taken from them by the deer. Two animals were used, and each treatment for each plant species was repeated 10 times, giving a total of 180 trials. The results were analysed using the method of residual maximum likelihood (REML, Genstat 5.3.2, Genstat 5 Committee, 1993), fitting animal and branch as random effects, to account for the repetition of measures.

In the main experiment, branches of 11 plant species varying widely in mass (by a factor of about 10) were offered to the animals individually. The observations ceased when the animal stopped feeding, or when about half of the leaves had been eaten, whichever occurred first (between 5 and 50 bites).

In the third experiment we studied the effects of thorns on parameters of the functional response by offering to the animals branches of the two spiny species, hawthorn and blackthorn *(Crataegus and Prunus),* and the thorny brambles *(Rubus)* which were presented to the animals either intact or after the thorns had been removed.

OBSERVATIONS

Two observers recorded information on the duration of feeding (from the first movement of the head towards the branch to the last chew), the number of bites and the total number of chews. Before and after each trial, the mass of each branch was weighed, and the dry matter concentration of the leaves was estimated by drying at 60 °C samples obtained by simulating browsing. Control branches were weighed before and after the experiments to correct for water losses due to transpiration. The dry mass eaten per bite could thus be calculated.

PHYSICAL AND CHEMICAL CHARACTERISTICS OF THE PLANTS

The mean mass, surface area and length of the leaves of the woody species were measured, and neutral detergent fibre (NDF), acid detergent fibre (ADF) and Van Soest lignin concentrations were determined by the INRA Station at Lusignan (France), using standard techniques.

ANALYSIS

Spalinger & Hobbs (1992) derived equations for the functional response under conditions where intake rate is limited by one of two processes that are likely to be relevant to patch exploitation by browsing herbivores. The process limiting biting rate will be either the rate of encounter with apparent items (Process 2 in Spalinger-Hobbs terminology), or the rate at which food can be chewed and swallowed (Process 3). Given an animal with a maximum foraging velocity V_{max} (m s^{-1}), maximum eating rate R_{max} (mg s^{-1}), minimum handling time per bite in the absence of chewing *(h,* s), foraging on plants offering bites at density D (m^{-2}), and offering a size of bite S (mg), then the rate of biting B (bites/s) can be written as:

$$\text{Process 2: } B_2 = \frac{V_{max}\sqrt{D}}{1 + hV_{max}\sqrt{D}} \qquad \text{eqn 1}$$

$$\text{Process 3: } B_3 = \frac{R_{max}}{(R_{max}h + S)}. \qquad \text{eqn 2}$$

The actual rate at which animals bite, B, in a given context will be the minimum of *(B₂, B₃)*. The equations can be rearranged to give the time taken per bite, T_b:

$$T_{b2} = h + \frac{1}{V_{max}} \cdot \frac{1}{\sqrt{D}} \qquad \text{eqn 3}$$

$$T_{b3} = h + \frac{1}{R_{max}} S. \qquad \text{eqn 4}$$

These are in forms convenient for linear estimation, which has the advantage over nonlinear estimation of giving unbiased estimates of the parameters in cases where S varies within a single experiment.

The difficulty in actually applying such an analysis to a set of data is that it is not known when either process will apply, that is, whether it takes longer to find the next bite or to chew the previous one. We cannot assume that Process 3 applied merely because deer were feeding in patches. One possible solution to this problem is to fit both equations 3 and 4 simultaneously, using an optimizing procedure (Fitnonlinear, Genstat 5.3.2; Genstat 5 Committee, 1993), and allowing the maximum of (T_{b2}, T_{b3}) to define the Process that applies to each case. We had not estimated D, but by assuming that V_{max} is an animal constant and that D is constant within each plant species, equation 3 becomes $T_{b2} = h + c$. The function to be estimated is thus:

$$T_b = \max\left(h + \frac{1}{R_{max}}S, \ h + c\right). \qquad \text{eqn 5}$$

The threshold value of bite mass, S^*, below which Process 2 applies is therefore cR_{max}.

The weakness of this approach is that it is difficult to take account of the repeated measures on experimental animals, and so the standard errors of the parameters will tend to be underestimated. It is also difficult to fit the function to all plant species at once. Slightly reduced accuracy of estimation of the parameters will therefore result from having to analyse separately the data on each species. The method was therefore used just to detect which of Process 2 or 3 applied. Thereafter, the relevant equation (i.e. 3 or 4, above) was fitted to the whole data set, and fitting plant species as a factor, using REML to account for the repeated measures on each animal by ensuring that covariate effects were assessed against the correct error term.

The mean number of leaves taken per bite of was estimated by simulation. It was assumed that the distribution of leaf masses in a typical bite was the same as that of the leaves weighed, whose mean and Ð are given in Table 3. Given successive leaves of mass m_1, m_2, etc. drawn at random from a normal distribution, the number of leaves, n, taken per bite of mass M is the highest number that satisfies:

$$\left(\sum_{i=1}^{n-1} m_i + \frac{m_n}{2}\right) \leq M. \qquad \text{eqn 6}$$

The mean and SD of 500 estimates of n was calculated.

Results

PATCH DEPLETION: PRELIMINARY TRIAL

The effects of branch size and previous defoliation on bite mass in three browse species were assessed first. Bite mass differed significantly between treatments (Table 1; $F_{2,62} = 47$, $P < 0.001$) and between plant species $(F_{2,62} = 101$, $P < 0.001)$ and with a significant interaction $(F_{4,62} = 3.18$, P $< 0.05)$. The effect of branch size on bite mass was positive but weak: bite mass increased by about 10% on average for a doubling of branch size, and was significant only in the case of common maple $(t_{62} = 2.04$, $P < 0.05)$. There was strong evidence for an effect of depletion on bite mass, since the average mass of the first 15 bites removed from large branches was significantly greater than that of the subsequent 15 bites (181.2 vs. 108.3 mg, respectively, $P < 0.001$).

FUNCTIONAL RESPONSES OF ROE DEER TO THE 11 PLANT SPECIES

The wider range in branch size and bite numbers used in this experiment achieved wide variation in bite mass, as intended. Bite mass varied between 10 and 650 mg

Table 1. Mean branch mass (g, fresh) and bite mass (mg, dry) taken from three plant species in experiment 1

Species	Treatment 1: Small branches		Treatment 2: Large branches		Treatment 3: Large branches depleted by 15 bites	
	Branch mass	Bite mass	Branch mass	Bite mass	Branch mass	Bite mass
Carpinus	36·2	158·9[a]	73·3	168·8[a]	65·0	112·4[d]
A. monspessulanus	42·7	239·9[b]	95·37	272·5[c]	82·7	161·1[e]
Cornus	34·8	94·1[d]	73·29	102·2[d]	66·9	51·4[e]

Means of bite mass with different superscripts differ with $P < 0.05$. SED between bite masses is 15·96, except for comparisons between treatments 2 and 3 within, for which SED = 13·34. The equivalent values for branch mass are 5·07 and 0·429, respectively.
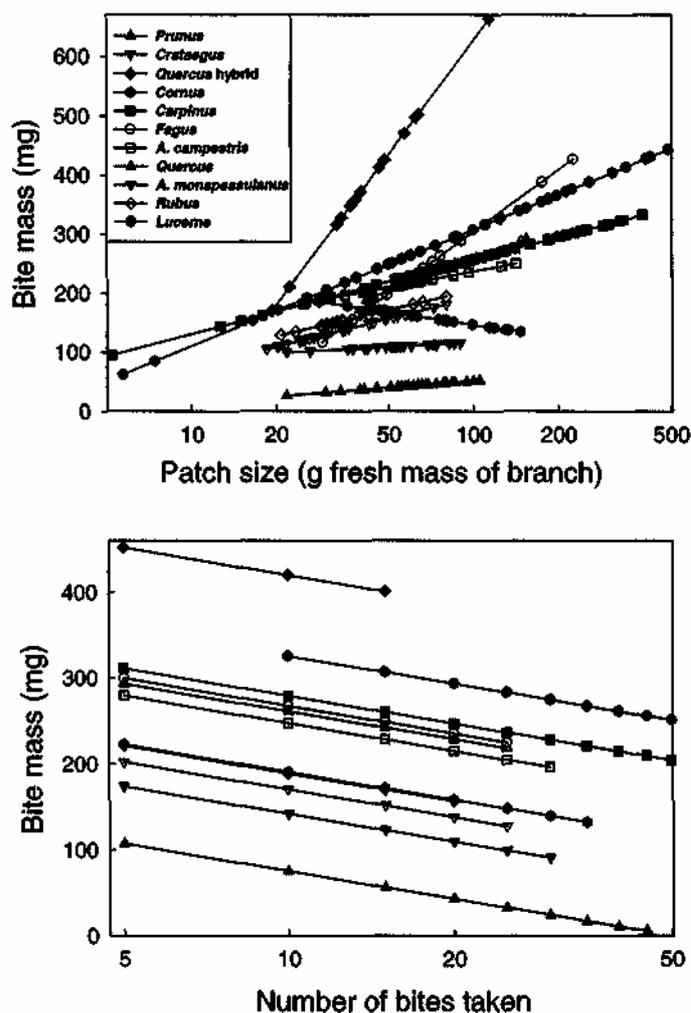
Fig. 3. Bite mass is higher in larger patches and declines as patch exploitation proceeds. Fitted curves show (top) the effect of patch size on bite mass, after 20 bites have been taken, and (bottom) the effect of bite numbers on bite mass, for patches of the average size for each plant species. Note the logarithmic axes for the independent variables.

(Fig. 3), and bite rates (0.1–0.9 per s) decreased as bite size increased, in the manner expected when intake rate is limited by processing rate. There were significant differences in bite mass between species $(F_{10,248} = 49, P < 0.001)$; after accounting for this, mean bite mass increased with branch mass $F_{1,248} = 106$, $P < 0.001$), and declined as bite numbers on a branch increased $(F_{1,248} = 51, P < 0.001)$. There was a significant inter-action between species and branch mass $(F_{10,248} = 6.8, P < 0.001$; Fig. 3a), but no other interactions were

significant. These results corroborate those obtained in the preliminary trial. This combination of fixed effects, together with the random term for animal, accounted for 76% of the variation in bite mass. The random term for animal significantly reduced residual deviance $(P < 0.005)$. The fitted values excluding animal effects were highly correlated with observed bite mass $(r = 0.86)$.

To analyse the functional response, we first tested whether Process 2 or 3 (see *Analysis)* applied in each

Table 2. Parameter values (SE) estimated from equation 5 for 11 species of browse in experiment 2

Species	c	h	R_{max}	r^2	P
Prunus	2·28 (0·756)	−0·48 (0·746)	31·24 (7·20)	0·56	0·001
Crataegus	0·27*	1·265 (0·288)	102·2 (19·6)	0·49	0·001
Quercus hybrid	2·41 (1·80)	3·73 (1·27)	87·1 (21·5)	0·58	0·003
Cornus	1·31 (0·580)	0·21 (0·424)	73·4 (10·6)	0·70	0·001
Carpinus	1·24 (0·624)	2·02 (0·496)	120·8 (27·0)	0·33	0·001
Fagus	4·12*	0·16*	68·5*	0·04	0·32
A. campestris	1·96 (0·839)	0·50 (0·759)	98·9 (26·8)	0·42	0·001
Quercus	0·23*	3·79 (0·829)	327 (288)	0	0·54
A. monspessulanus	1·96 (0·615)	0·52 (0·582)	63·0 (12·9)	0·60	0·001
Rubus	2·42*	0·92*	53·2*	0·25	0·072
Lucerne	0·11*	2·58 (0·256)	192·6 (35·4)	0·46	0·001

*SE could not be estimated.

experiment using equation 5. Parameter estimates for each species are given in Table 2. It was estimated that in only 47 of the 280 trials the animal would have spent more time searching for the next bite (i.e. Process 2) than it spent chewing the previous one (Process 3). Most of the trials with Process 2 foraging were on *Primus* and *Fagus*. Although bites from *Prunus* were small enough (see Table 3) to suggest that Process 2 might truly have applied in some trials, the larger mean bite size for *Fagus* suggests that description of foraging as Process 2 is an artefact of the imprecise parameter estimates (see Table 2). Accordingly, intake rate was assumed to be governed, in general, by Process 3. The data were reanalysed by fitting equation 4, using REML to account for repeated measures on the three animals, and allowing greater accuracy of estimation of parameter values and standard errors (Table 3). Estimates of *h* and R_{max} using the two techniques agree reasonably well for most of the plant species (Table 2, cf. Table 3), which supports the conclusion that Process 3 is the appropriate one. When these more reliable estimates of h and R_{max} were substituted into equation 5 and *c* was re-estimated, Process 2 was found to have applied in only 17 of the 280 trials, and none in *Fagus*.

There were significant differences between species in both the time taken by animals to crop each bite *(h)* and in their processing rate R_{max} $(F_{10.256} = 88.1$ and $F_{11.256} = 16.54$, respectively), and these species differences are illustrated in Fig. 4(b). There was a tendency for h and R_{max} to be positively correlated (r = 0.596, $r_{crit} = 0.602$; d.f. = 9). The estimated value of *h* varied from 0.7 to 4.7 s, and was significantly shorter on *Cornus, Rubus* and *Prunus* than on the two varieties of Q*uercus, Fagus* and lucerne. Most of the variation in *h* in the woody plants was accounted for by leaf size, particularly leaf mass (Table 3; $r^2 = 0.72$), with larger leaves taking longer to crop. The maximum processing rate (R_{max}), varied from 214 mg s^{-1} in lucerne down to 49 mg s^{-1} in *Rubus*. The estimate of R_{max} for *Rubus* was significantly lower than all others *(P < 0.05)* except for *Cornus* and *A. monspessulanus*, while the estimate for *Prunus* was significantly lower
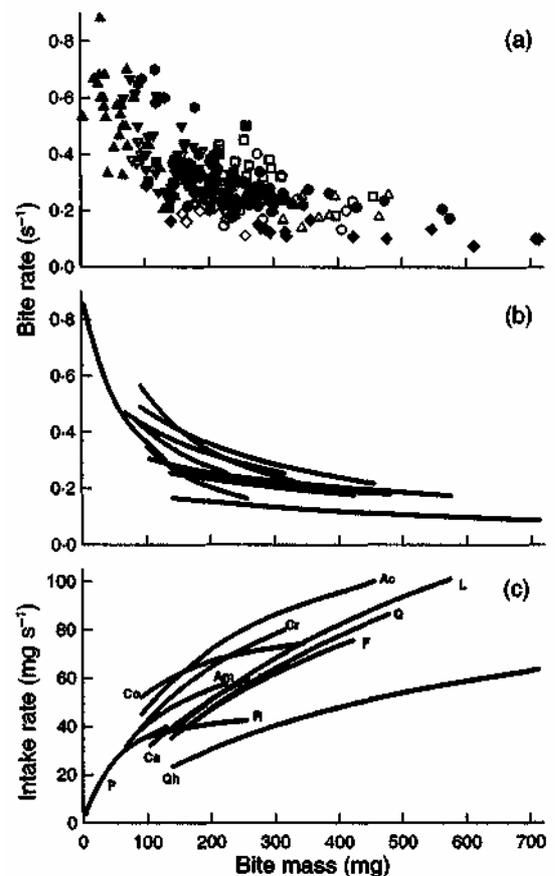

Fig. 4. Bite rates (data and fitted) and intake rate (fitted) in relation to bite mass in 11 browse species. Symbols as in Fig. 3. See Table 2 for species names.

than that for *Fagus, Quercus* hybrid and lucerne. R_{max} was not significantly related to any of the leaf physical or chemical parameters among the woody plants, but tended to increase with fibrousness, against expectations.

Intake rate was calculated as the product of bite mass and bite rate, using equation 4 and the fitted parameter estimates for *h* and R_{max}, and plotted in Fig. 4(c). The highest rates of intake were observed on the common maple *(Acer campestris),* and the lowest on *Primus, Rubus* and hybrid *Quercus.*

Table 3. Estimated parameter values of the Spalinger–Hobbs Process 3 functional response (h, R_{max}) together with leaf dimensions and fibre concentration in experiment 2

Species	h (s)	R_{max} (mg s^{-1})	Bite mass (mg)	Leaf length (cm)	Leaf area (cm^2)	Leaf mass (SD) (mg)	NDF (g kg^{-1})	ADF (g kg^{-1})	ADL (g kg^{-1})
Prunus	1·10	60·4	58·3	2·40	1·87	14·8 (5·63)	320	120	52
Crataegus	1·63	136·1	140·8	1·12	7·10	40·8 (13·44)	406	286	199
Quercus hybrid	4·71	109·7	339·3	12·99	52·75	604 (284·98)	419	195	77
Cornus	0·72	88·2	200·6	7·72	21·13	121·1 (59·64)	163	70	20
Carpinus	2·54	146·2	245·7	6·52	19·09	93·0 (137·91)	375	164	45
Fagus	3·10	170·6	283·2	7·66	24·66	164·4 (57·92)	583	304	118
A. campestris	1·40	144·2	248·2	6·31	29·28	176·7 (103·53)	386	184	75
Quercus	3·27	211·6	300·3	9·15	27·71	279·0 (114·41)	446	214	98
A. monspessulanus	1·27	85·7	162·3	2·59	4·76	31·0 (15·56)	345	198	77
Rubus	0·77	48·7	183·2	–	–	–	–	–	–
Lucerne	3·01	214·3	276·6	–	–	–	–	–	–
Mean	2·14	128·7		6·171	18·64	136·4	365	185	835
Average SED	0·772	52·45							
Correlation with h	–	0·596**	0·80**	0·76*	0·78*	0·85*	0·64	0·43	0·17
Correlation with R_{max}	0·596**	–	0·50	0·35	0·36	0·25	0·66	0·59	0·40

*Correlation coefficient is significant at 5% when $r \geq 0·666$ (d.f. = 7) or **when $r \geq 0·602$ (d.f. = 9).
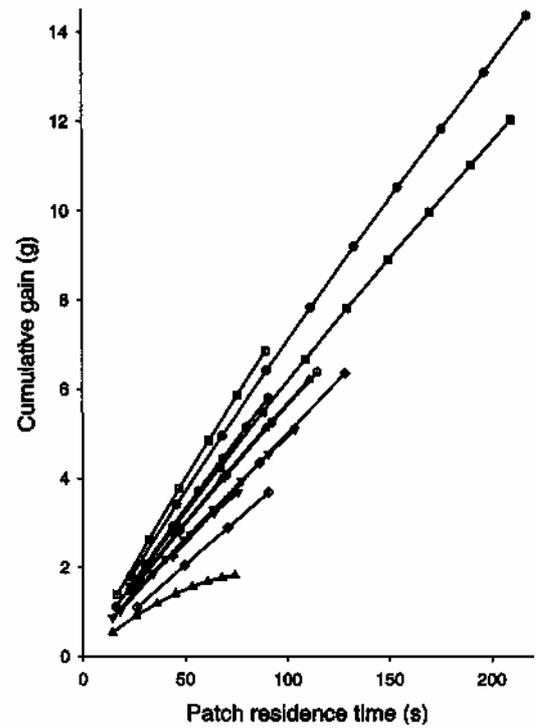

Fig. 5. Calculated gain curves for 11 browse species, assuming the mean patch size for each species. The points are plotted at intervals of five bites along each curve. Symbols as in Fig. 3.

PATCH DEPLETION AND DEPRESSION

We can now combine the effects of patch depletion and the functional response, and the resulting gain curves are shown in Fig. 5. These were calculated up to the maximum number of bites observed in each plant species using the fitted values for h and R_{max} (derived above) and using the regression estimates to predict the bite mass that would be taken from the average-sized branch for each species, and including the depletion effect of increasing bite number. The gain curves were therefore built up from the established mechanisms at play during patch exploitation. As can be seen, they are virtually linear, except in the case of *Prunus*. As the deer successively depleted each branch, the animals wholly or partially compensated for the declining bite mass by increasing the rate of biting, under Process 3.

EFFECTS OF THORNS ON FUNCTIONAL RESPONSE PARAMETERS

The third experiment examined the effect of thorns on the functional response by comparing three thorned species *(Primus, Rubus* and *Crataegus)* with or without the thorns removed. As before, we first tested whether Process 2 or 3 was the most appropriate description of the functional response, and found that 134 of the 137 trials appeared to be governed by Process 3. We subsequently analysed the data by fitting equation 4, using REML. Estimated values of h and R_{max} are given in Table 3. There were large effects of plant species

($F_{3,123}$ = 157, P < 0·001) and bite mass ($F_{1,123}$ = 44, P < 0·001) on time per bite, with no interaction ($F_{2,123}$ = 0·9). There was a significant effect of the presence of thorns (P < 0·01), but an effect that depended on the plant species (species–thorns interaction: $F_{2,123}$ = 12·4, P < 0·001). In *Prunus,* there was no significant effect of the presence of thorns on h ($F_{1,49}$ = 0·1) or R_{max} ($F_{1,49}$ = 0·6). In *Crataegus* the removal of thorns led to a slight but significant decrease in h (1·43 vs. 1·22 s, $F_{2,48}$ = 10·65, P < 0·001) but there was no effect on R_{max} ($F_{1,48}$ = 0·6). In *Rubus* there was a strong and significant increase in R_{max} when the spines were removed (48·7 vs. 323 g s^{-1}, $F_{2,25}$ = 17·5, P < 0·001). As well as having spinescent stems, *Rubus* also carries spines on the midrib of the leaf, and these would normally be consumed. The removal of thorns allowed the deer to process bites more rapidly. Thorn removal had the unexpected effect of increasing h in *Rubus* (1·01 vs. 3·22, $F_{1,25}$ = 5·9, P < 0·025).

The deer took smaller bites from intact branches (59·7 vs. 76·2 mg; P < 0·05, after accounting for significant effects of bite numbers and plant species) with no difference between plant species ($F_{2,130}$ = 1·4). Intake rate was higher in de-thorned *Rubus* (41·2 vs. 55·5; t = 2·33) but not in Crataegus (53·2 vs. 61·7; t = 1·6) or *Prunus* (29·55 vs. 31·0; t = 0·41).

Distances between thorns on the stems of each species were significantly different ($F_{2,15}$ = 106, P < 0·001) with *Rubus* having smaller distances than *Crataegus* (1·46 vs. 2·66 cm, t_{15} = 4·4, P < 0·001), which in turn had smaller distances than *Prunus* (2·66 vs. 5·34 cm, t_{15} = 9·8, P < 0·001).

Discussion

Our experiments elucidate the mechanisms of resource exploitation in browsing herbivores in a number of ways, and raise doubts about the relevance of the patch optimization for this mode of foraging. The work of Spalinger & Hobbs (1992) provides a systematic means of analysing functional response and evaluating biologically meaningful parameters. We employed an optimization technique to discriminate between encounter- and handling-limited processes, and conclude that the functional response applicable to patch browsing of most plant species by roe deer is governed by the rate at which animals can process each bite. The relevant parameters of the functional response, describing the time required to take bites and the rate of processing them, differs widely between plant species commonly browsed by roe deer, and is affected to some degree by spinescence. Although bite mass, the driving variable in this mode of foraging, declined as patch exploitation progressed, there was little evidence of any reduction in intake rate (i.e. patch depression) because increasing bite rate largely compensates for declining bite mass.

Instantaneous rate of food intake in roe deer was controlled by the time taken to prehend and chew bites

in virtually all the trials. Much of the difference between plant species in the estimated mean cropping time per bite, h, was accounted for by variation in leaf size (Table 3). The deer required about 1 s to take a bite from the small-leaved species such as *Prunus,* about 3 s for *Fagus* or *Quercus,* and they fed particularly slowly on the large leaves of the hybrid *Quercus* (4.7 s/bite). Similar results have been obtained on white tailed deer (Koerth & Stuth 1991) and African browsers (bushbuck, *Tragelaphus scriptus,* and goats, Haschick & Kerley 1997). The extreme case was the hybrid oak, which provided very large bite sizes but was clearly difficult for them to eat, and this species had the lowest intake rate. Rather surprisingly, maximum chewing rate (R_{max}) was not significantly correlated with physical or chemical characteristics of the leaves. R_{max} did not decline with fibrousness, but tended rather to increase, which is the opposite of the results obtained by Shipley & Spalinger (1992).

Intake rates varied widely between plant species, when compared at equal bite mass (Fig. 4c). The highest values were seen in the maple *(Acer campestris),* and the lowest values for a given bite mass were observed in the hybrid oak, *Rubus* and *Prunus.* High values of h reduce intake rate, particularly at low bite mass, and high values of R_{max} increase intake rate at high bite mass. Species differences in these parameters (Table 3) thus cause the differences in intake rate observed.

The removal of thorns from branches of woody species leads to significantly increased ungulate herbivory (Milewski *et al.* 1991). Thorns have been found to reduce rates of food intake in a range of mammalian herbivores, usually through a decrease in bite size (Cooper & Owen-Smith 1986; Belovsky *et al,* 1991; Myers & Bazely 1992; Haschick & Kerley 1997; present study). Intake rate was found to be negatively correlated with spine density by Gowda (1996). Evidently, the effect of thorns on the functional response depends on the thorn characteristics of each plant species. Thus, the different responses of roe deer to the plant species in our experiment support the suggestion of Cooper & Owen-Smith (1986) that animal size and thorn spacing interact in a way that may allow small-bodied animals to evade or mitigate the effects of thorns on reduce intake rate. *Prunus* has few, widely spaced, thorns that the small-mouthed roe deer were apparently able to avoid while foraging, and hence there was no significant effect of the presence of thorns on either parameter of the functional response. In contrast, the effect of thorns in *Crataegus* was to increase the time taken to prehend bites *(h),* implying that evasion of the thorns had a time cost. Thorns in this species are more densely packed than in *Prunus,* and very sharp. Lastly, in *Rubus,* there are many thorns on the midribs of the leaves and the deer were obliged to eat considerable amounts of them. The thorns appear painful to chew, which may have slowed the chewing process, resulting in lower R_{max}. The higher value for h in de-thorned *Rubus*
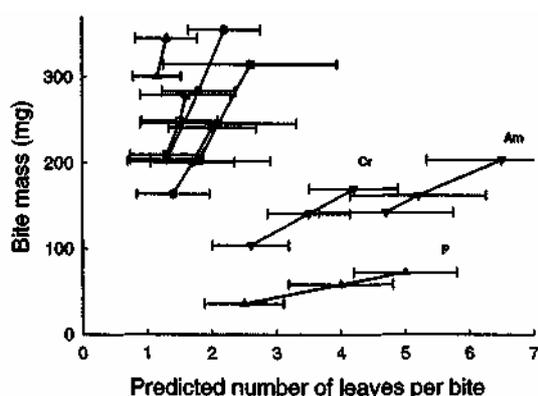
Fig. 6. Predicted number of leaves contained in the lower quartile, median and upper quartile bite mass (SD). Symbols as in Fig. 3.

is, we believe, an artefact of the statistical procedure. *h* is estimated as the intercept of the regression of time per bite on bite mass, and where the data do not extend close to zero bite mass, it is necessarily extrapolated, and therefore cannot be estimated precisely. In summary, application of the Spalinger-Hobbs functional response shows the different ways that thorns may affect intake rate, depending on thorn characteristics.

MECHANISMS OF PATCH EXPLOITATION AND PATCH DEPRESSION

The larger bite masses initially taken from larger branches and the decline with the number of bites as the animals fed on a patch (Fig. 3) demonstrate that animals were selective during patch exploitation. Given that bite mass exceeds leaf mass in many of the species, and therefore animals must have been selecting bunches of leaves for each bite, the largest bunches must have been selected first. An estimate of this effect (Fig. 6) shows how the mean number of leaves per bunch would have declined as bite mass declined over the course of patch exploitation. Item selection by browsers has previously been noted by Edenius (1991) who found that moose *(Alces alces)* selected larger twigs and obtained larger bites on their first visit to Scots pine *(Pinus sylvestris)* and aspen *(Populus tremula)* trees than on subsequent visits.

In grazing ungulates, bite mass decreases as animals bite deeper into grass swards, but often without concomitant increases in bite rate (Laca *et al.* 1994; Ginnett *et al. 1*999). Increasing fibrousness of the grass ingested or increasing time spent prehending each bite may explain the lack of compensation by bite rate for declining bite mass in these studies. Nevertheless, patch depression results solely from decreasing bite mass in these two studies of grazing cattle.
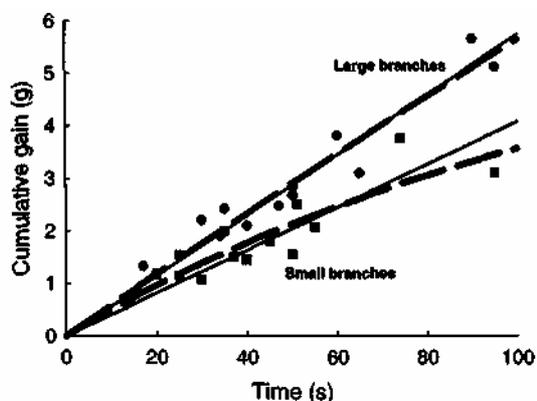
The decline in bite mass during patch exploitation suggests a possible mechanism of patch depression in browsers. However, it is evident that the gain curves in our experiment are virtually linear for each plant spe-

cies, with the exception of *Primus* (Fig. 5). The decline in bite mass in this species was proportionately greater than in other species: from over 100 mg to about 50 mg over the course of 20 successive bites (Fig. 3). In the other species, an increase in bite rate apparently compensated for the decrease in bite mass, according to the Process 3 functional response (see equation 2). Because intake rate was limited by processing rate rather than by encounter rate, the explanation of patch depression by lengthening encounter intervals would not apply until the patch was severely depleted (see Fig. 2). Note that the range of bite mass obtained during patch depletion generally remained well above the estimated threshold $(S^* = cR_{max})$ at which Process 2 would take over. Secondly, given the selection of bites by browsers during patch depletion, it seems evident that they systematically search branches for prey items. This would also have the effect of avoiding patch depression, because encounters between successive items would not be increased. In terms of the different functional responses developed by Spalinger & Hobbs (1992), systematic search is described by Process 2, where animals move directly between apparent food items. The overlap of handling and searching that underlies what we argue is the applicable Process 3 functional response offers an alternative mechanism whereby the same effect can be achieved: no time is wasted in searching. As a consequence, diminishing bite mass as the larger items become depleted in our experiments with roe deer appears to be the only potential source of patch depression, and one that is generally too small to have such an effect.

We argue that browsers have linear gain functions and that published evidence of patch depression is a mistaken inference. Patch depression in browsers has previously been reported by Åström, Lundberg, & Danell (1990). Using a function that implicitly assumes patch depletion and depression while foraging, they analysed intake in relation to exploitation time by moose feeding on trees of two species: Scots pine, *Pinus silvestris,* and Norway spruce, *Picea abies.* One of the parameters of their function represents the total available biomass of the patch (tree), and although this was continuously distributed in their, data set, it was necessary to divide the trees between five size-classes for the analysis. The fitted function was nearly linear in all cases, with considerable scatter about the fitted line, and the statistical improvement over a linear function was marginal at best in most cases. Shipley & Spalinger (1995) measured cumulative gain in relation to foraging time in white-tailed deer *(Odocoileus virginianus)* and moose feeding on uniform artificial patches of red maple, *Acer rubrum.* They fitted a power function to the data, but comment on the fact that the fitted line was nearly linear and that the scatter around it was large. When we examined whether our roe deer data were best described by the Åström function or by a linear gain function, we found that a straight line, usually without an intercept, gave as good a fit in almost all

Table 4. Regression statistics comparing the gain curve of Aström *et al.* (1990) with a linear regression for each browse species (data from experiment 2). Where an improvement was obtained by separating the data into large and small branches, the relevant statistics are shown

Species	No. observations	Åström *et al.* (1990) gain function: Intake = $s[1 - 1/(1 + kT/s)]$		Linear function: Intake = $c + dT$ or, Intake = dT		Improved by separating large from small branches?
		R^2	Residual mean square	R^2	Residual mean square	
Prunus	27	0·559	0·174	0·562	0·173	No
Crataegus	27	0·760	0·317	0·755	0·322	No
Quercus hybrid	14	0·591	0·815	0·658	0·682	Yes
Cornus	27	0·878	0·233	0·880	0·231	No
Carpinus	52	0·810	2·168	0·814	0·2125	No
Fagus	13	0·790	0·4071	0·785	0·417	Yes
A. campestris	24	0·666	0·810	0·593	0·987	No
Quercus	23	0·565	0·906	0·574	0·887	No
A. monspessulanus	25	0·879	0·168	0·876	0·173	Yes
Rubus	15	0·692	0·149	0·609	0·189	No
Lucerne	33	0·671	6·43	0·682	6·22	No

Fig. 7. Gain curves for branches of *A. monspessulanus* obtained by fitting either the function of Åström *et al.* (1990) (dashed lines) or linear functions (solid lines) to large (●) or small (■) branches (i.e. those above or below the median branch size).

cases (Table 4). An example (Fig. 7) shows that a linear gain function certainly applies in the case of larger branches, and that there is little to choose between linear and curvilinear functions for smaller branches. Individual animal effects also accounted for some variation, and on average increased the correlation of fitted and actual values from 0.872 to 0.914 (average of all browse species).

There are several problems in attempting to use statistical comparisons to detect nonlinearity and compare different functional forms. Animal experiments usually generate widely scattered data, and the source of variation due to individual differences is seldom accounted for. It is hard to control the uniformity of patch size. Generating data over a sufficient range of patch residence times usually depends on the animal choosing to exploit patches for different times. These should, in theory, be a function of travel times or patch characteristics, but in practice generally depend on departures from the optimal residence time rather than adherence to it. This raises the question of whether the animal is responding to some unmeasured or uncontrolled property of the environment or of the patch, such as accessibility of the food items or variation in their digestibility, that has no relevance to patch exploitation.

A further reason for the apparent curvilinearity of published gain functions could be an artefact of the methodology. Animals occasionally pause momentarily during patch depletion experiments, perhaps because they are disturbed or because they habitually scan for predators while foraging. If pauses are randomly distributed during feeding, then the mean number of pauses will increase with time and will be Poisson-distributed. Depending on how pause length is distributed, the accumulated increase in patch residence time due to pauses will have some form of skewed distribution. Gathering together data on food intake and residence time from a number of trials and fitting some form of gain function, as is a normal procedure, inevitably tends to bias the gain function towards the more curvilinear, owing to the skewness of the data. Simulation shows that curvilinear functions of the type used by Åström *et al.* (1990) arise from data generated from trials in which the underlying rate of food intake is constant, but with random pauses (Illius & Fryxell, in press). Such an effect might be mistaken as a *bona fide* cause of patch depression, but its origin is distinct from food-related mechanisms and is contingent on the degree of disturbance or other environmental influences such as predation risk.

Rather than apply statistical or phenomenological criteria to select a gain function, it is preferable to derive the function from known mechanisms. Our application of the theory of the functional response in mammalian herbivores seeks to do this, and the gain curves derived from fitted functional response parameters are, for the reasons discussed above, virtually linear (Fig. 5). Shipley & Spalinger (1995), analysing the same problem, regarded possible sources of patch

depression to be declining R_{max} or increasing h as successive bites become more fibrous, or a decline in bite mass. We argue that, given bites of homogeneous quality, patch depression in browsing herbivores should only occur in the final stages of patch depletion (see Fig. 2). The same mechanisms as we have demonstrated in browsers must apply in grazing herbivores, but the greater decline in bite mass during progressive defoliation of grass patches at a single feeding station (e.g. from 800 to 200 mg; Ginnett *et al.* 1999) is apparently sufficient to cause patch depression. Differences between the characteristics of the food patches used by grazers and browsers (i.e. grass swards vs. branches) explain the virtual absence of patch depression experienced by browsers, whose bite mass declines only slightly over the course of patch exploitation.

IMPLICATIONS FOR OUR UNDERSTANDING OF UNGULATE HERBIVORY

Obvious feature of patch use by browsers in the studies of Åström *et al.* (1990) and Shipley & Spalinger (1995) are the wider range of patch exploitation times and lower patch depletion observed than would be predicted from nearly linear gain functions. The near linearity of gain functions in browsers demonstrated by these authors and by us suggests that optimal patch use would involve nearly complete defoliation, according to the reasoning of the Marginal Value Theorem (MVT, Charnov 1976). Yet Åström *et al.* (1990) observed that patches were 'far from depleted', and other studies of browsing show similarly low amounts of biomass removal. For example, Fritz & de Garine-Wichatitsky (1996) observed that increasing group size in impala *(Aepyceros melampus)* reduced the number of bites that individuals took from acacia bushes. It can be estimated from their data that biomass removal per bush was maximized at intermediate group size, when it was between 11% of total browseable biomass from large and 40% from medium or small bushes. This is less than would be expected to cause patch depression (see Fig. 2). Solitary impala would only have removed about 2, 6 or 24% of browseable biomass from large, medium or small bushes, respectively. Given the response of defoliation intensity to group size, we must reject the hypothesis that patch depression and patch optimization were significant features of impala foraging behaviour. Incomplete biomass removal could be explained by solitary herbivores' unwillingness to stay in one place for long enough to be stalked by predators (Brown 1988), but if group foraging confers some protection against predators, then individuals in larger groups should be prepared to stay longer at each bush. The opposite was observed by Fritz & de Garine-Wichatitsky (1996). Of course, one reason for suboptimal patch residence times in published studies of browsing could be that the error costs little, in terms of reduced long-term energy intake rate, if the gain function is linear and provided that travel time is

short. However, we regard the deviations of observed behaviour from predictions of the patch model to be sufficient to warrant rejection.

The fact that patch-use by browsers is hard to predict with any accuracy is in contrast to the success in predicting diet optimization at the bite scale (e.g. Vivås & Sæther 1987; Vivås *et al.* 1991; Shipley *et al.* 1999). Shipley *et al.* (1999) successfully predicted browse selection from considerations of diet quality, and it has been noted that browsers respond to both food quality and availability by eating a higher-quality diet and taking less from each plant at high food densities (Vivås & Sæther 1987; Andersen & Sæther 1992; Shipley & Spalinger 1995). This suggests that diet optimization under digestive constraints may be the fundamental process in browser foraging, as it appears to be in other mammalian herbivores (Belovsky 1978; Lundberg & Åström 1990; Fryxell 1991; Doucet & Fryxell 1993; Wilmshurst, Fryxell & Colucci 1999). As Fortin, Fryxell & Pilote (2002) make clear, the important question is one of time-scale. Foraging behaviour that would maximize energy intake rate over the short-term cycle of patch residence and interpatch travel (typically minutes) would not necessarily maximize energy intake rate over the longer time-scale at which digestive constraints operate (typically hours to days). The model of Shipley *et al.* (1999) can be used to show that the patch residence time that maximizes daily energy intake under digestive constraints is generally shorter than the residence time that maximizes energy intake rate under ingestive constraints, especially in small-bodied animals and when diet quality declines with increasing intensity of patch utilization. Therefore, short-term optimization based on MVT may well be subordinated to long-term optimization of diet quality, regardless of the fact that successive removal of food items in order of diet quality is a patch depletion process. In summary, there are *a priori* and empirical grounds for the propositions that optimal patch use is not an appropriate model of resource use by browsing mammalian herbivores, and that longer-term diet optimization, i.e. the trade-off between diet quality and daily intake rate, is a more likely explanation of their foraging behaviour.

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