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The allometry of patch selection in ruminants

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An axiomatic feature of food consumption by animals is that intake rate and prey abundance are positively related. While this has been demonstrated rigorously for large herbivores, it is apparent from patch selection trials that grazers paradoxically tend to prefer short, sparse swards to tall, dense swards. Indeed, migratory herbivores often shift from areas of high to low sward biomass during the growing season. As nutritional quality is an inverse function of grass abundance, herbivores appear to sacrifice short-term intake for nutritional gains obtainable by eating sparse forage of higher quality. Explicit models of this trade-off suggest that individual ruminants maximize daily rates of energy gain by choosing immature swards of intermediate biomass. As body mass is related positively to both ruminant cropping rates and digestibility, there should be an allometric link between grass abundance and energy maximization, providing a tool for predicting patterns of herbivore habitat selection. We used previously published studies to develop a synthetic model of trade-offs between forage abundance and quality, predicting that optimal sward biomass should scale allometrically with body size. The model predicts size-related variation in habitat selection observed in a guild of grazing ungulates in the Serengeti ecosystem.

Keywords: constraints; foraging; functional response; herbivore; resource partitioning; Serengeti

1. INTRODUCTION

Due to the positive relationship between bite size and plant biomass, cropping rates (grams of grass ingested per unit time) for herbivores of all sizes increase with sward biomass (Black & Kenney 1984; Short 1985; Lundberg 1988; Gross *et al.* 1993; Laca *et al.* 1994). This occurs even when the negative relationship between sward density and grass quality resulting from phenological maturation of the sward is considered (Illius & Gordon 1987). However, field observations suggest that many grazing herbivores prefer low biomass grass patches when high biomass patches are available (Vesey-Fitzgerald 1960; Gwynne & Bell 1968; Jarman 1974; Langvatn & Hanley 1993; Wilmshurst *et al.* 1995). This suggests that the current allometric theory of patch selection for grazers is at odds with observed behaviour.

What is rarely incorporated into models is the interaction of the poor nutritional quality of grass and the rate at which that grass can be processed in the gut (Illius & Gordon 1992). As grass swards mature, they increase in biomass and decrease in quality as they accumulate structural carbohydrates (Waite 1963). Mature, poorly digestible grass requires longer retention in the rumen and/or reticulum to reduce particle sizes sufficiently to pass to the hind gut (Illius & Gordon 1992). Faster passage of high-quality grass means that it can be consumed in greater quantity by ruminants than can low-quality grass (Baile & Forbes 1974). Poor digestibility and slow passage of mature grass are particularly problematic for small ruminants for which a gut filled with slowly fermenting grass both prevents further intake and provides little maintenance energy (Wickstrom *et al.* 1984). This constraint is eased for large ruminants with larger guts and relatively lower per unit mass metabolic demands (Illius & Gordon 1987). As body mass is related positively to ruminant cropping rates, voluntary intake and digestibility, there should be an allometric link between grass abundance and energy maximization, providing a tool for predicting patterns of herbivore habitat selection. We modelled this trade-off across a range of body sizes to detect possible patterns in habitat selection for a guild of grazing herbivores in Serengeti National Park, Tanzania.

2. METHODS

(a) *The model*

Daily intake of metabolizable energy (ME) for grazing ruminants is regulated by opposing functions that we assume to be constraining under average conditions (Owen-Smith 1993). These functions are a cropping constraint (I_1: MJ of ME day^{-1}) that links forage digestibility to the grazer's functional response, and a digestion constraint (I_2: MJ of ME day^{-1}) that links forage digestibility to the grazer's daily voluntary intake (DVI). These lines cross for most parameter combinations and the point of intersection indicates maximum daily energy intake (figure 1). In general the model predicts that ruminants should maximize daily energy intake on low-to-intermediate biomass swards (Fryxell 1991).

Rates of dry matter intake increase with plant height, leaf size and leaf bulk density in food-concentrated patches (Spalinger & Hobbs 1992; Gross *et al.* 1993). Using grass biomass (V: g m^{-2}) as a surrogate for these plant features, we modelled daily dry matter intake applying the Michaelis–Menten form of the instantaneous functional response multiplied by the maximum daily feeding time ($t_{\max}$: 13 h for all species). We multiplied daily dry matter intake by the maturational decline in forage quality (Q: MJ g^{-1}) (Rittenhouse *et al.* 1971) to predict daily digestible energy intake constrained by cropping:

$$I_1(M) = Q(M) \times \frac{R_{\max} \times V}{b + V} \times t_{\max}, \qquad (1)$$

where M (kg) is body mass, $R_{\max}$ (g min^{-1}) is maximum instantaneous cropping rate and b (g m^{-2}) is grass biomass at which intake is half maximum (figure 1).

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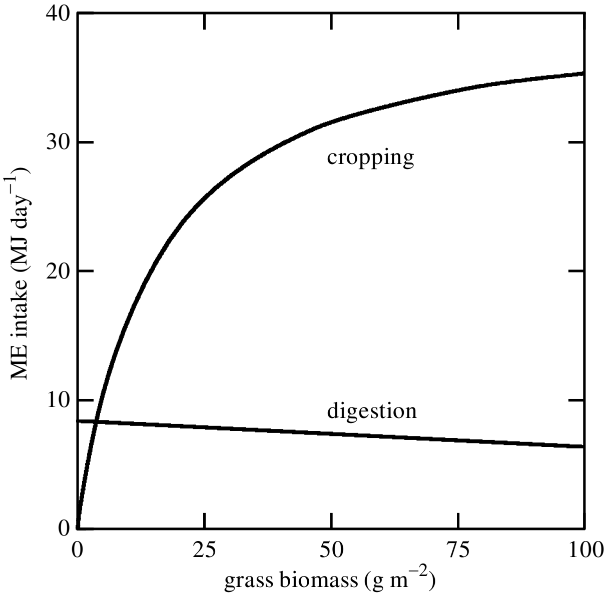

Figure 1. Daily ME intake constraint curves for Thomson's gazelle grazing on complex swards (parameters given in table 1). The cropping constraint (I_1) is the maximum amount of energy an individual can consume daily in the absence of digestion constraints and the digestion constraint (I_2) is the maximum amount of energy an individual can process daily in the absence of cropping constraints. Realized daily ME intake as a function of sward biomass tracks the minimum of the two constraint lines. The point of intersection identifies the maximum daily ME intake on the ordinate and the optimal grass biomass on the abscissa.

Model parameters for the cropping constraint were taken from 15 studies of functional responses of 12 ruminant species ranging in size from 20 to 750 kg (table 1). We recorded parameters that measured intake on two types of swards: simple swards composed solely of grass leaf or forbs and complex swards using whole grass tillers or intact grass communities.

In studies where Michaelis–Menten parameters were not reported, we calculated them using available information. Gross *et al.* (1993) report cropping rates relative to plant size using the Spalinger & Hobbs (1992) form of the functional response. We calculated b from their data by multiplying $R_{\max}$ by $\bar{h}$ (average minutes per plant) and plant density (plant m^{-2}). Murray & Brown (1993) reported cropping rates as a multiple regression of green-leaf biomass, crude protein and stem density. We calculated cropping rates relative to green-leaf biomass alone by substituting mid-range values for crude protein and stem density they report and determined Michaelis–Menten parameters from their data using nonlinear regression.

We modelled daily intake on swards ranging from 0 to 300 g m^{-2} using a typical data set from the Serengeti ecosystem relating grass quality to grass biomass (Wilmshurst *et al.* 1999). This data set is also relevant to our subsequent empirical test of habitat use by the guild of Serengeti grazers. Within this range of grass biomass, digestible energy (DE) content is a linear function of its *in vitro* digestible organic matter (IVDOM) content (Rittenhouse *et al.* 1971) that is, in turn a function of forage neutral detergent fibre (NDF) content and animal body mass ($\mathrm{IVDOM} = 90.1 - 0.53 \times \mathrm{NDF}(\%) + 0.013 \times M$, $F_{2,297} = 78.6$, $p < 0.001$, $r^2 = 0.35$; H. Meissner personal communication). NDF also varies linearly with biomass up to 300 g m^{-2} ($F_{1,23} = 7.5$, $p = 0.01$, $r^2 = 0.25$), although this relationship tends to be nonlinear across broader ranges of grass biomass due to saturating NDF content on dense swards (Breman & de Wit 1983; Hobbs & Swift 1985; Gordon 1989). Hence, across the range of sward biomass we modelled, $\mathrm{DE}(\%) = 65.6 - 0.27 \times$ biomass (g m^{-2}). ME content of the forage was calculated as 82% of DE (Van Soest 1982). Given a standard combustible energy content per gram of grass, $Q(M)$ is calculated as $\mathrm{ME}(\%) \times 17.1$ (MJ g^{-1}) (Golley 1961).

We calculated the digestion constraint as daily dry matter consumption under *ad libitum* feeding conditions multiplied by forage quality. Digestion constraints relative to body size were derived from a study of DVI for six ruminant species ranging in size between 30 and 550 kg (Meissner & Paulsmeier 1995). While voluntary intake may not always represent maximum daily intake due to variation in animal state or behaviour (Baile & Forbes 1974) it is a useful estimate of *ad libitum* daily intake. Meissner & Paulsmeier (1995) reported that DVI scaled isometrically to forage quality but allometrically ($M^{0.9}$) to body mass. We modelled digestion constraints as a multiple regression equation relating both per cent NDF of grass and animal body mass to DVI (kg dry matter day^{-1}):

$$\mathrm{DVI} = 2.5 - 0.049 \times \%\mathrm{NDF} + 0.061 \times M^{0.9}, \qquad (2)$$

($r^2 = 0.95$) (H. Meissner, personal communication). Kilograms DVI were converted as above to DVI of ME. From this function we calculated I_2:

$$I_2(M) = \mathrm{DVI} \times Q(M). \qquad (3)$$

To account for phylogenetic relationships, we created dummy variables to represent family and tribe classifications (Harvey & Pagel 1991). Model predictions of optimal grass biomass and maximum energy intake for each species listed in table 1 were tested for dependency to body mass, sward type and phylogeny using stepwise multiple regression. Relationships among significant effects were determined using ANCOVA.

(b) *Field data*

The Serengeti ecosystem of East Africa provides an excellent setting to test model predictions. Due to a complex pattern of localized rainfall, a substantial range of grass densities is available to the diverse guild of Serengeti grazers in a small area. To measure local herbivore densities, we drove twenty-five 220-km long ground transects on the Serengeti plain (2°32.1′ S, 34°57′ E to 2°56.1′ S, 34°21′ E) during the growing seasons of 1994 to 1996. All large herbivores visible within an arc extending 200 m to the sides and front of the driver were counted at two random locations in each kilometre of transect. At each location the height and percentage cover of green vegetation was measured using visual estimation (Daubenmire 1959). These measurements were calibrated to grass biomass (g m^{-2}) using clip-plots from which quality relationships were also determined (Wilmshurst *et al.* 1999). Five herbivore species were found in sufficient abundance for analyses: Thomson's gazelles (*Gazella thomsoni*), Grant's gazelles (*Gazella granti*), hartebeest (*Alcelaphus buselaphus*), wildebeest (*Connochaetes taurinus*), and topi (*Damaliscus lunatus*). Grant's gazelles have a 50 kg body mass (Estes 1991); body masses of the other species are listed in table 1.

3. RESULTS

Predicted optimal sward biomass was dependent on body mass and on the complexity of the sward on which functional response parameters were measured, but not on phylogeny. On simple swards, cropping constraints

Table 1. *List of species parameters used to model constraint curves*

species	mass (kg)	$R_{\max}$ (g min^{-1})	b (g m^{-2})	sources
Thomson's gazelle[a] (*Gazella thomsoni*)	20	6.42	16.6	Wilmshurst *et al.* (1999)
sheep[a] (*Ovis aries*)	42	7.02	30.8	Black & Kenney (1984)
mule deer[a] (*Odocoileus hemionus*)	42	2.22	1.97	Wickstrom *et al.* (1984)
white-tailed deer[b] (*Odocoileus virginianus*)	45	9.17	3.03	Gross *et al.* (1993)
axis deer[b] (*Axis axis*)	53	8.42	2.27	Gross *et al.* (1993)
reindeer[a] (*Rangifer tarandus*)	70	6.37	31.7	Trudell & White (1981)
topi[b] (*Damaliscus lunatus*)	75	17.0	10.6	Murray & Brown (1993)
hartebeest[b] (*Alcelaphus buselaphus*)	92	11.9	8.54	Murray & Brown (1993)
wildebeest[b] (*Connochaetes taurinus*)	97	20.2	9.94	Murray & Brown (1993)
caribou[b] (*Rangifer tarandus*)	104	16.3	7.82	Gross *et al.* (1993)
wapiti (yearling)[a] (*Cervus elaphus*)	170	31.2	160.4	Wilmshurst *et al.* (1995)
bison (yearling)[b] (*Bison bison*)	180	54.8	99.2	Bergman *et al.* (2000)
elk[b] (*Cervus elaphus*)	266	47.4	71.2	Gross *et al.* (1993)
cow[b] (*Bos taurus*)	548	74.6	24.6	Gross *et al.* (1993)
cow[a] (*Bos taurus*)	750	129.5	688.6	Laca *et al.* (1992, 1994)

[a] Complex sward trials.
[b] Simple sward trials.

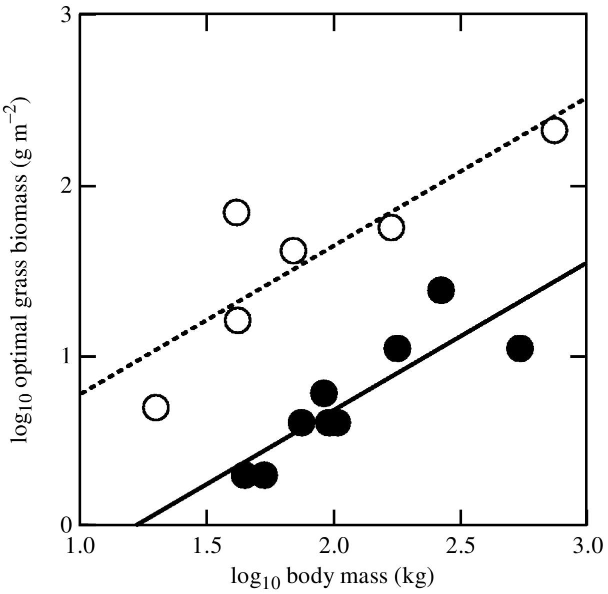

Figure 2. Optimal grass biomass relative to body mass for modelled ruminants listed in table 1. The open points represent trials conducted on complex grass swards, described by the function $\log_{10} y = -0.088 + 0.86 \times \log_{10} x$ (dashed line). The filled points represent trials conducted on simple, leafy swards, and are described by the function $\log_{10} y = -1.05 + 0.86 \times \log_{10} x$ (solid line). Slopes are homogeneous ($F_{1,11} = 0.27, p = 0.87$ for heterogeneity) and multiple regression including body mass and sward complexity confirmed the significance of linear functions ($F_{2,12} = 32.8$, $p < 0.001, r^2 = 0.86$).

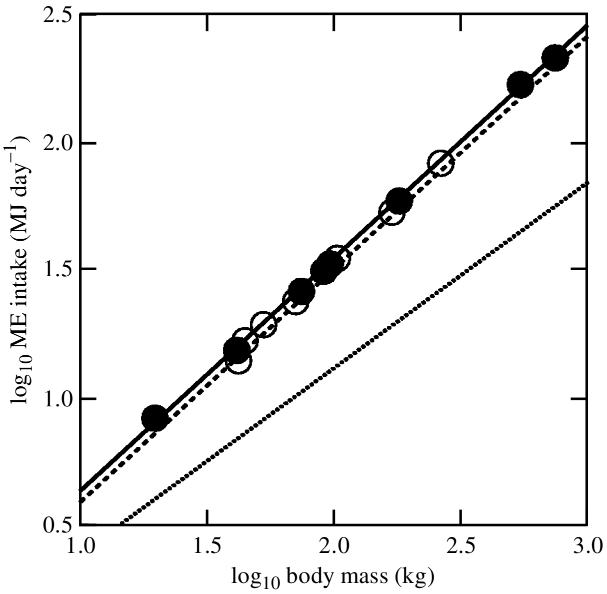

Figure 3. Maximum daily ME intake relative to ruminant body mass. The open points represent cervids, described by the function $\log_{10} y = -0.302 + 0.91 \times \log_{10} x$ (dashed line). The filled points represent bovids, described by the function $\log_{10} y = -0.29 + 0.91 \times \log_{10} x$ (solid line). Slopes are homogeneous ($F_{1,11} = 0.24, p = 0.63$ for heterogeneity) and multiple regression including body mass and family confirmed the significance of linear functions ($F_{2,12} = 9524.7, p < 0.001$, $r^2 = 0.99$). The dotted line is the basal (ME) requirements relative to body mass (MJ day^{-1} $= 0.45 \times \mathrm{kg}^{0.73}$) (Konoplev *et al.* 1978).

increased steeply, intersecting the digestion constraint at low biomass (figure 2). On complex swards, functional responses increased more gradually, causing the constraints to intersect at an order of magnitude higher biomass (figure 2). This effect of sward structure has been shown using experimental manipulation of sward complexity in trials featuring grazing bison (Bergman *et al.* 2000).

Predicted maximum energy intake rates were a positive linear function of body mass and phylogenetic relatedness but were not related to sward type (figure 3). The energy function scaled to $M^{0.86}$ indicating a stronger link between energy maximization and digestion constraints, which scaled to $M^{0.90}$ (Meissner & Paulsmeier 1995), than to cropping constraints, which scaled to $M^{0.73}$ (Shipley *et al.* 1994). The realized metabolic rate for mammals is approximately two to three times the basal metabolic rate (Peters 1983), suggesting that our estimates of maximum metabolic energy gain (approximately 3.5 times the daily metabolic requirement for Artiodactyla (figure 2)), realistically predict maximum daily values.

Biomass of patches on which Serengeti grazers were observed was a function of their body mass. Treating the density of each species in each year independently, there was a significant positive relationship between body mass and mean sward biomass of patches they occupied ($\log_{10}$ biomass (g m^{-2}) $= 1.5 + 0.22 \times \log_{10}$ body mass (kg), $F_{1,13} = 5.4$, $p = 0.04$, $r^2 = 0.3$). The observed pattern better matched the predictions derived from complex swards than those from simple swards; nevertheless the slope of the observed relationship among species was shallower than predicted by the model (0.22 compared with 0.86).

4. DISCUSSION

The sward biomass on which ruminants optimize energy gain is a positive, decelerating function of body mass. This reflects a gradual shift in the intersection of the digestion constraint and the cropping constraint from low biomass swards for small ruminants, to swards of higher biomass for large ruminants with commensurately larger gut capacity. Thus, the positive relationship between optimal sward biomass and ruminant body mass is the result of both a relaxation of digestion constraints (Meissner & Paulsmeier 1995) and increasing bite size (Gross *et al.* 1993) in larger ruminants.

Our assumption that energy gain by ruminants is a hump-shaped function of grass abundance (Fryxell 1991) makes our work fundamentally different from previous allometric models. We found that body mass-related habitat selection can result purely from individual energy maximization, independent of either plant species selectivity or interspecific competition and that, in general, ruminant herbivores should prefer short, intermediate biomass swards over tall, high biomass swards. In Illius and Gordon's (1987) allometric model of energy function in ruminants, daily energy gain is a positive function of grass abundance, thus predicting that tall, high biomass patches should be preferred by grazing ruminants regardless of body size. They predict a positive relationship between ruminant body mass and grass biomass, as do we, but resulting from competition for tall, high biomass swards. Their model cannot explain the selection by ruminants of low biomass swards when tall, high biomass swards are available (McNaughton 1984; Langvatn & Hanley 1993; Wallis DeVries & Schippers 1994; Wilmshurst *et al.* 1995, 2000; Bradbury *et al.* 1996).

It is interesting that we found no impact of phylogeny on predicted optimal sward biomass, as this prediction is strongly affected by the form of the functional response, which is presumably under morphological control. Nevertheless, we did find a slight difference between cervids and bovids with respect to maximum daily energy gain (figure 3). This suggests at least marginal phylogenetic linkage between muzzle architecture and body mass, which has been postulated in other analyses of ruminant foraging strategies (Gordon & Illius 1988).

The positive relationship we found between herbivore body mass and sward biomass in the surveys of Serengeti herbivores lends qualitative support to the idea that allometric scaling in gut passage and cropping in ruminants is linked to patch selection. There is a tendency for small ruminants to be found on lower biomass patches than larger ruminants during the growing season as predicted by our model. Several processes could account for the deviation of our model from the Serengeti observations. If sward complexity is positively related to grass biomass then predictions of optimal grass biomass for small ruminants would conform to the simple sward regression model and predictions of optimal grass biomass for large ruminants would conform to the complex sward regression model (figure 2). Thus, the effects of sward complexity would predict a much shallower slope than predicted by either model. In addition, by choosing relatively simple representations of forage intake constraints, we ignore processes such as competition and predation that influence on herbivore distributions in the Serengeti (Sinclair 1985; Hofer & East 1993; Durant 1998). Indeed we found an inverse relationship between body mass and how closely their observed patch choice matched that predicted, perhaps the result of larger animals excluding smaller animals from preferred patches.

These results lend theoretical and empirical support to the hypothesis that there is size-specific ecological separation among grazing herbivores on the basis of differential foraging efficiency (Murray & Brown 1993). The gradient between optimal patch and body mass suggests that herbivores of similar body size and feeding style may be competing. Our work also suggests that large ruminants should perform better on more productive grasslands than do small ruminants, with the converse true of low-productivity grasslands. In highly productive grasslands in which tillers grow and lose quality rapidly (Braun 1973), large-bodied ruminants are favoured.

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