

WHAT CONSTRAINS DAILY INTAKE IN THOMSON'S GAZELLES?

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Abstract. We tested whether cropping or digestion by Thomson's gazelles (*Gazella thomsoni*) constrains daily energy intake under sward conditions normally encountered during the growing season. Distinguishing between these alternatives is important in understanding grass-grazer interactions and modeling grazer energetics. Grazing trials on artificial swards showed that gazelles had a monotonically saturating functional response, but that relationships between grazing rate and forage density changed with grass height. Grazing rate was positively related to biomass on short swards, yet there was no significant relationship for tall swards. Bite mass and bite rate also differed in their relationship to biomass across sward heights, with the strongest relationships being found on short swards. Bite rate and bite mass were inversely related, as predicted by current theory for dense grass swards. Voluntary energy intake on a daily basis was a positive function of the digestible energy content of forage, but a negative function of sward biomass. Therefore, our results indicate that daily energy intake is constrained by digestive processes on swards with biomass >25 g/m², whereas intake is constrained by cropping processes at lower sward biomass. Our data additionally suggest that variation in bite rate and bite mass with sward height could permit a small ruminant to select high-quality grass, thereby achieving high energy gain on immature swards.

Key words: bite mass; bite rate; constraints, daily energy intake; digestibility; energetics; functional response; forage quality; *Gazella thomsoni*; grazer; Serengeti National Park, Tanzania; Thomson's gazelle.

INTRODUCTION

Grazing herbivores are confronted at every spatial and temporal scale with variation in forage quality and abundance (Banyikwa 1976, Senft et al. 1987, McNaughton 1988, O'Conner 1994, Tilman 1994). They must simultaneously satisfy demands for essential minerals, water, energy, and protein (Westoby 1978, Belovsky 1986a, Bazely 1989) from a nutritionally poor and variable food source. To track this variation, many large herbivores move continuously across landscapes, in both small-scale nomadic shifts and large-scale seasonal migrations (Hebert 1973, Maddock 1979, Fryxell et al. 1988, Fryxell and Sinclair 1988a, b, Albon and Langvatn 1992, Fryxell 1995, Murray 1995). One approach to understanding how herbivores distribute themselves relative to resources in heterogeneous environments has been to identify behavioral, morphological, and physiological characteristics that constrain food intake (Belovsky 1978, 1986b, Illius and Gordon 1991, Spalinger and Hobbs 1992).

Ruminant grazers are constrained either by the rate at which food can be cropped or by the rate at which food can be processed. On short, homogeneous swards, the quantity of grass cropped in each bite (bite mass)

is small (Black and Kenney 1984). As sward height increases, the bite mass also increases (Black and Kenney 1984, Laca et al. 1992a, Gross et al. 1993). Eventually, a point is reached at which the quantity of grass that could be cropped in a single bite exceeds mouth dimensions (Illius and Gordon 1987). At this point, the grazing rate (mass of grass cropped per unit time) is constrained by the rate at which grass can be chewed and swallowed (Spalinger and Hobbs 1992). For most grazing herbivores, this process results in a decelerating (Type II) functional response (Gross et al. 1993).

The incubator-type digestive system of ruminants necessitates long periods of retention of ingested material to permit fermentation of fibrous plant cell walls (VanSoest 1982). Retention is facilitated by a constriction at the base of the rumen-reticulum through which only small particles can pass (Hungate 1966). Hence, highly fibrous forage, resistant to particle breakdown, takes a prolonged period to digest, which itself can constrain the long-term rate of food processing due to limited gut capacity. For ruminants, this means that voluntary daily intake should be higher on highly digestible, low-fiber grass than on poorly digestible, fibrous grass (Ammann et al. 1973, Mould and Robbins 1982, Illius and Gordon 1991). Because forage quality is inversely related to abundance, due to the maturational accumulation of fiber in grass tissue (Waite 1963), voluntary daily intake should be a negative function of sward biomass.

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The relative importance of forage quality and abundance for nutrient intake by ruminant herbivores is poorly understood (Hanley 1997). Nevertheless, this relationship must be resolved if we are to understand herbivore distribution and abundance in resource-limited environments. Recently, Bradbury et al. (1996) compared grazing rates of free-ranging Thomson's gazelles (*Gazella thomsoni*) in southwestern Kenya relative to grass availability, using the foraging model of Spalinger and Hobbs (1992). In general, the Spalinger and Hobbs model predicts that as forage density in patches increases, the cropping rate by grazers should shift from being constrained by searching for grass to being constrained by chewing and swallowing mouthfuls of grass. In the study area of Bradbury et al. (1996), short swards consisted of widely spaced clumps of grass, whereas tall swards tended to have a more homogeneous spatial distribution. Consequently, the foraging behavior and grazing rate of Thomson's gazelles differed between tall and short swards. This suggests that gazelle distributions could be related to forage abundance in patchy environments.

Serengeti National Park in northern Tanzania lies south of the study area of Bradbury et al. (1996) and is the principal wet-season range of the migratory Thomson's gazelles that they studied. The grazing conditions in Serengeti differ from those in southern Kenya in that grass swards tend to be more spatially homogeneous, irrespective of height. As part of a larger study of the spatial dynamics of Serengeti herbivores, we conducted detailed foraging trials with captive Thomson's gazelles under grazing conditions typical of Serengeti grasslands. This provided the opportunity to test rigorously the cropping measures of Bradbury et al. (1996) as well as to develop a grazing model for Thomson's gazelles that synthesizes the effects of both forage quality and forage availability. Our objectives were (1) to measure the components of grazing and digestion in Thomson's gazelles, and (2) to determine whether digestion or cropping constraints limit daily rates of energy intake under conditions prevailing on the African savanna.

METHODS

The model

As grass matures, its digestibility for herbivores declines (VanSoest 1982). Coincident with maturational declines in grass quality, the sward increases in biomass, leading to a fundamental trade-off for grazers: low-biomass swards are highly digestible and high-biomass swards are poorly digestible. There are several possible methods for modeling this trade-off. The first is to incorporate grass digestibility as a function of grass biomass in the herbivore functional response. This can be achieved by converting handling time from a constant to a positive function of forage biomass in the disc equation, to simulate slow passage of fibrous

forage (Fryxell 1995). A second approach is to model intake and gut fill as independent functions of maturational variation in grass digestibility (Fryxell 1991). This is based on the idea that, although cropping is suspended in favor of rumination once gut capacity is reached, gut capacity is unlikely to limit cropping before this threshold is reached. Hence, the two constraints operate independently. Both approaches yield hump-shaped daily energy gain curves relative to grass biomass, but the former method tends to overestimate daily energy gain by not explicitly considering limits on gut capacity. Hence, we used the dual-constraint model in order to distinguish between the functioning of two separate processes: the active cropping of bites, regulated in part by the muzzle morphology of the herbivore (Gordon and Illius 1988, Janis and Ehrhardt 1988), and the amount of material that can be processed in the digestive system, which is regulated by the volume of the rumen-reticulum (VanSoest 1982).

The model, adapted from Fryxell (1991), contrasts daily intake of digestible energy constrained by both forage availability (cropping constraint) and physical capacity of the ruminant digestive system (digestion constraint) relative to a gradient of swards varying in grass biomass. We defined the cropping constraint (C , in megajoules of digestible energy intake per day) as the product of the instantaneous intake of grass (in grams of dry matter per minute), the digestible energy content (Q , in megajoules per gram of dry matter) of grass, and daily foraging time (t_{\max} , in minutes per day), all as a function of grass biomass (V , in grams per square meter):

$$C(V) = Q \frac{R_{\max} V}{b + V} t_{\max}. \quad (1)$$

We use the Michaelis-Menten (Michaelis and Menten 1913) form of the instantaneous intake function, where R_{\max} is the maximum rate of forage consumption (in grams per minute) and b is the grass biomass (in grams per square meter) at which intake is half maximum. Although this is not a mechanistically explicit reproduction of the herbivore functional response, such as Spalinger and Hobbs's (1992) formulation, it allows us to link our independent variable, grass biomass, to grass quality. Nevertheless, the Spalinger and Hobbs equation is mathematically equivalent to the Michaelis-Menten form in dense (food-concentrated) patches when competition between cropping and chewing limits intake rates, indicating that our model is comparable to their approach.

We defined the digestion constraint (D , in megajoules of digestible energy intake per day) as the product of the maximum daily food consumption (grams of dry matter per day) under ad libitum conditions and Q , both as functions of V :

$$D(V) = Q(c + dV). \quad (2)$$

Studies of domestic and wild ruminants have found that



PLATE 1. Thomson's gazelles (*Gazella thomsoni*) in Serengeti National Park, Tanzania.

daily voluntary intake is positively related to forage digestibility (Ammann et al. 1973, Mould and Robbins 1982, Illius and Gordon 1991, Meissner and Paulsmeier 1995). Although the shape of the positive relationship between daily voluntary intake and food digestibility can vary (Meissner and Paulsmeier 1995), we model it here as a linear function, with c being the intercept (in grams per day) and d being the slope (in square meters per day).

The model is solved graphically. Both constraints are plotted on the same axes (daily digestible energy intake vs. sward biomass) and the realized daily digestible energy intake tracks the minimum of the two lines (Fryxell 1991). Under most conditions of grass digestibility, maximum daily digestible energy intake will coincide with the intersection of the constraints (Fryxell 1991, Wilmshurst 1998), the point that also identifies optimal sward biomass.

Study area and animals

We conducted intake trials using captive Thomson's gazelles (see Plate 1) at the Tanzania Wildlife Corporation animal holding facility at Oldonyo Sambu, 40 km north of Arusha, Tanzania (3° 9.7' S, 36° 38.9' E). Two subadult Thomson's gazelles (one male, one female) being held temporarily as evidence in an illegal exportation trial were made available for our study. The animals were housed in a tree-shaded, 1000-m² pen that was devoid of low-level vegetation. They were fed daily with a combination of fresh-cut grass (predominantly *Cynodon dactylon*) and alfalfa (*Medicago* sp.) obtained locally.

Functional response

A functional response is the relationship between the instantaneous rate of intake by a consumer and some measure of food abundance (Solomon 1949). A recently developed method for measuring the functional response of grazing herbivores is to measure the mass

of forage removed in brief trials from swards assembled on perforated boards by a single grazer (Black and Kenney 1984, Laca et al. 1992b, Gross et al. 1993). We adapted this methodology to the conditions available at our holding facility.

We perforated a single sheet of 0.25-m² particle board with 1 cm diameter holes evenly spaced at 5-cm intervals. Bundles of grass (*Cynodon dactylon*) of known mass were inserted into each hole and held in place with tapered wooden pegs, hammered in from beneath. Following the terminology of Gross et al. (1993), these boards constituted food-concentrated patches, as the grass formed a continuous mat on the board. Once such patches are encountered by a forager, grazing rates should be constrained by handling rather than by searching for the next bite, i.e. process 3 foraging, sensu Spalinger and Hobbs (1992).

Trials were conducted at five grass densities (1–5 tillers per hole) and at two sward heights (5 cm and 15 cm). In 5-cm trials, only leaf and sheath tissues were exposed to grazing above the board, whereas in 15-cm trials, leaf, sheath, and stem were exposed to grazing, with the stem protruding 5 cm above the board to support the leaf tissue. Two boards were placed in the shade at the center of the animals' holding pen next to their feed bin, which was covered for the duration of the trial. An observer, positioned 30 m away on an elevated platform, observed foraging on the board with binoculars and recorded each bite, as observed, into a tape recorder. Data were later transcribed using a stopwatch to measure biting intervals and duration. The trial was terminated after a minimum of 20 bites were taken from each patch or the animals stopped foraging. Data were not used if more than one animal grazed from a single patch in a trial, or if two animals grazed simultaneously on adjacent patches. Failed trials, in which no foraging occurred, were used to calibrate for mass loss due to tiller desiccation during trials (water concentration was a constant 71% of grass wet mass,

$F_{1,11} = 560.7$, $P < 0.001$, $r^2 = 0.98$). At the end of each trial, the board was recovered and the height and mass of the forage remaining above the board were measured. In total, we observed 24 trials at 5 cm and 18 trials at 15 cm tiller height.

Voluntary intake

By manipulating the proportion of grass vs. alfalfa provided to the animals in their holding pen, we were able to vary dietary quality and measure variation in voluntary intake as a function of diet quality. We prepared five rations that varied in their quantity of highly nutritious alfalfa. This changed the proportion of dietary acid detergent fiber (ADF) and, hence, digestibility (VanSoest 1982). Each ration was provided in random order to the animals ad libitum for two consecutive weeks. Because the animals could not be isolated from each other and ate from the same feeder, we were unable to measure selection differences between individuals. Therefore, we provided sufficient food for two individuals. Fresh and previously weighed rations were provided each morning, with refusals from the previous day also collected and weighed. Separate weighed samples, placed under similar shade conditions but inaccessible to the animals, were used to calibrate daily mass loss of rations due to desiccation (water concentration was a constant 73% of grass wet mass, $F_{1,54} = 2216.2$, $P < 0.001$, $r^2 = 0.99$). Periodic grab samples were taken and preserved for subsequent quality analysis at the University of Guelph.

Digestibility

We measured grass digestibility relative to abundance using fecal collections taken from free-ranging Thomson's gazelles in Serengeti National Park, Tanzania in 1996. Individual gazelles were located and observed for one grazing/rumination cycle, and fresh droppings were collected simultaneously with the collection of a single grass sample. This is potentially problematic, because the feces were composed of grass ingested up to 72 h prior to sampling and may relate poorly to a single grab sample of grass. To address this problem, we only collected feces from territorial males who move little from day to day (Walther 1968). Samples from 21 individuals were collected on swards ranging widely in maturity. The samples were air-dried and returned to the lab at the University of Guelph for analysis.

Following the methods of Penning and Johnson (1983a, b) and Nelson et al. (1990), we measured the concentration of indigestible acid detergent fiber (IADF) in each fecal and grass sample. IADF acts as a natural indigestible marker and permits the estimation of dry matter digestibility (Nelson et al. 1990). Samples (0.5 g) of feces and grass, ground to pass a 1-mm screen, were measured into individual 80-mL culture tubes. Each was digested in vitro (Tilley and Terry 1963) in a 38°C water bath using rumen inocula from

a hay-fed steer. Following 24-h incubation in rumen fluid and 24-h digestion in pepsin, the samples were neutralized with NaCO_3 and were reinoculated with rumen fluid for a further 96-h incubation. At the end of this period, tube contents were transferred to 500-mL beakers, combined with 50 mL of acid detergent fiber (ADF) solution (Goering and VanSoest 1970), boiled for 1 h on a condensing rack, and rinsed through Whatman 54 filter paper (Whatman, Inc., Clifton, New Jersey, USA) with boiling distilled water. Samples were oven-dried overnight and the IADF content was calculated by difference. Percentage dry matter digestibility was calculated as $100 [1 - (\text{grass IADF}/\text{fecal IADF})]$. Digestible energy (DE) content was calculated by multiplying digestible dry matter by 17.1 J/g of energy in grass (NRC 1958:520–534).

Digestibility in these samples was related to the ADF content of the grass samples by linear regression. Percentage of ADF in grass relative to sward biomass was estimated from 2-m² exclosures erected over patches mowed at the beginning of the 1996 growing season on the Serengeti plain. Quadrat samples (0.25 m²) of known height were collected monthly and sorted into leaf, sheath, stem, and dead components. They were then dried, ground through a 1-mm screen, and returned to the University of Guelph for analysis. A leaf sample (0.35 g) was measured into individual culture tubes with 35-mL of ADF solution (Goering and VanSoest 1970), boiled for 1 h in a water bath, and rinsed through Whatman 54 filter paper. The samples were reweighed after drying overnight at 100°C to measure the quantity of ADF remaining after treatment. The digestibility of a grass sample of known biomass was calculated as a function of its ADF content. We collected 105 samples, covering a wide range of patch biomasses, for analysis.

Statistical analyses were performed with SYSTAT software (Wilkinson 1990). We report means \pm 1 SD and grass densities on a dry matter basis.

RESULTS

The results of our functional response trials revealed that intake increased initially with grass biomass and then reached an apparent asymptote (Fig. 1). The pooled results confirm what has been observed for virtually every other grazing herbivore tested on dense patches: a Type II functional response. For Thomson's gazelles, we calculated a maximum consumption parameter (R_{max}) of 6.42 g/min and a half-saturation constant (b) of 16.57 g/m² ($r^2 = 0.36$). Our estimate of R_{max} is higher than the value of 5.738 g/min predicted from the allometric prediction of Shipley et al. (1994) for a 20-kg Thomson's gazelle. In addition, mixed-effects ANOVA showed that both the biomass of prepared sward on the board and the sward height influenced grazing rate (biomass, $F_{1,38} = 25.1$, $P = 0.003$; height, $F_{1,38} = 6.35$, $P = 0.016$). This suggests that there are two separate, yet interacting, processes that influence grazing by Thomson's gazelles.

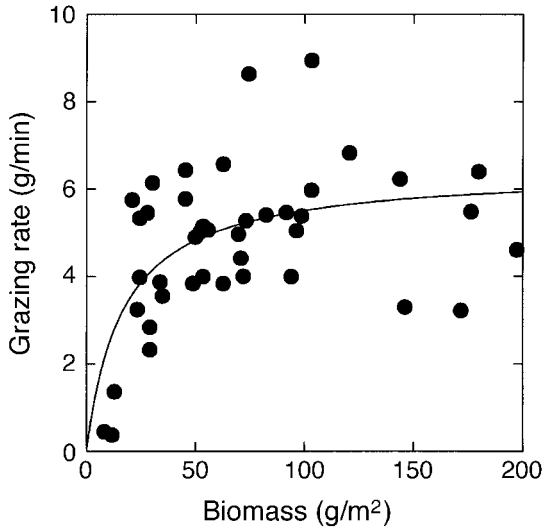


FIG. 1. Dry-matter grazing rate by Thomson's gazelles relative to biomass of hand-assembled grass swards.

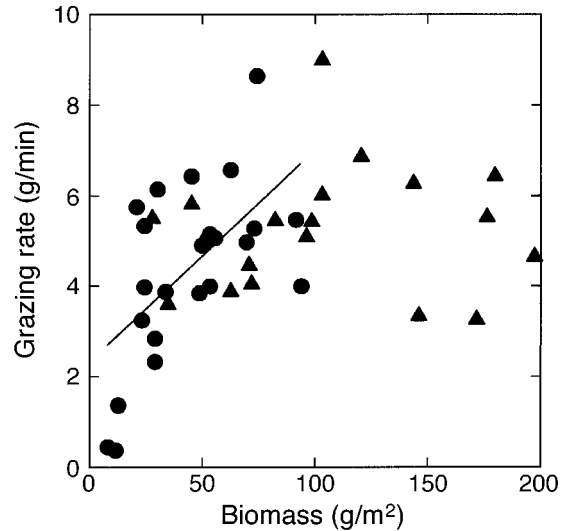


FIG. 2. Dry-matter grazing rate by Thomson's gazelles, differentiated by tiller height presented in foraging trials (●, 5-cm tillers; ▲, 15-cm tillers). On 5-cm swards, intake = $2.3 + 0.05(\text{biomass})$. There is no significant relationship between intake and biomass on 15-cm swards.

To illuminate these effects, we partitioned our intake data according to sward height. Grazing rate increased with grass abundance on short swards ($F_{1,22} = 11.76$, $P = 0.002$, $r^2 = 0.35$; Fig. 2), but we found no significant relationship between grazing rate and biomass on tall swards ($F_{1,16} = 0.07$, $P > 0.5$; Fig. 2). Partitioning these relationships by separating grazing rate into its components (bite mass and bite rate) further clarified the patterns. Bite mass on short swards increased linearly with increasing biomass ($F_{1,22} = 44.23$, $P < 0.001$, $r^2 = 0.67$; Fig. 3), whereas bite mass did not vary significantly with biomass on tall swards ($F_{1,16} = 1.96$, $P = 0.18$; Fig. 3). Bradbury et al. (1996) suggested that bite mass should change nonlinearly with forage density (bite mass = $g[\text{forage density}]^a$ where g and a are constants), and that a should fall between 0.15 and 0.5. Nonlinear parameter estimation for this function using our bite mass data at both heights yielded $g = 0.017$ and $a = 0.46$, providing a good fit to our observed pattern at both tiller heights ($r^2 = 0.59$) and to the prediction of Bradbury et al. (1996) (Fig. 3).

Bite rate on short swards decreased with increasing biomass ($F_{1,22} = 10.8$, $P = 0.003$, $r^2 = 0.33$; Fig. 4), whereas the relationship was much weaker on tall swards ($F_{1,16} = 4.09$, $P = 0.06$; Fig. 4). We tested both bite rate and bite mass relationships with biomass across heights for homogeneity of variance using analysis of covariance. We found significant heterogeneity (height \times biomass interaction with respect to bite mass $F_{1,38} = 5.812$, $P = 0.02$; with respect to bite rate $F_{1,38} = 12.35$, $P = 0.001$), indicating different relationships of bite mass and bite rate to sward biomass at each height tested. Bradbury et al. (1996) predicted that bite rate should be a hyperbolic function of forage protein density:

$$\text{bite rate} = \frac{5.7375}{g(\text{protein density})^a + 0.0738} \quad (3)$$

In their study area, forage protein density was a positive, accelerating function of forage biomass density (protein = $0.065[\text{biomass}]^{1.11}$; J. W. Bradbury, *personal communication*). Relative to forage biomass, their estimate of g becomes 0.043 and their estimate of a be-

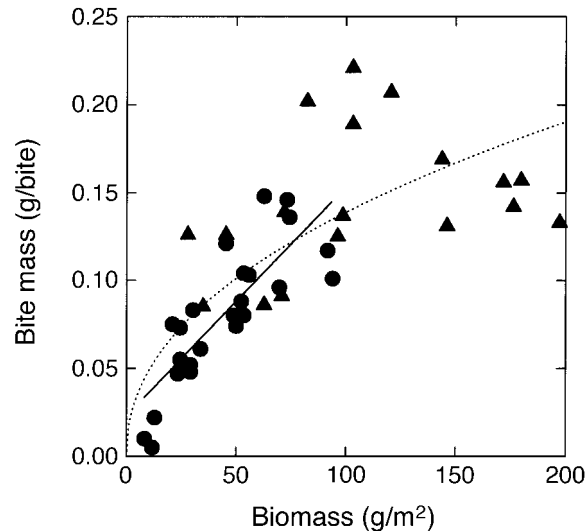


FIG. 3. Bite mass in relation to sward biomass on assembled swards at two heights (●, 5-cm swards; ▲, 15-cm swards). On 5-cm swards, bite mass = $0.023 + 0.001(\text{biomass})$. There is no significant relationship between bite mass and biomass on 15-cm swards. The dotted line is a function describing bite mass at both heights; bite mass = $0.017(\text{biomass})^{0.456}$.

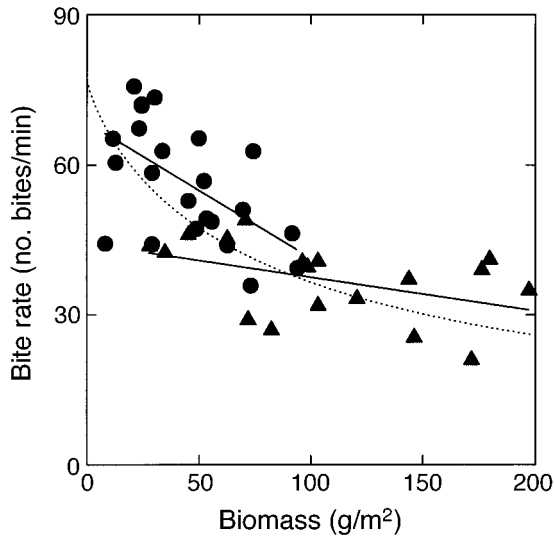


FIG. 4. Bite rate in relation to sward biomass on assembled swards at two heights (●, 5-cm swards; ▲, 15-cm swards). On 5-cm swards, bite rate = $1.14 - 0.005(\text{biomass})$. On 15-cm swards, bite rate = $68.5 - 0.271(\text{biomass})$. The dotted line is the bite rate estimated from the hyperbolic form of bite rate by nonlinear regression (bite rate = $6.42 / (0.002[\text{biomass}]^{0.832} + 0.013)$) from Bradbury et al. (1996).

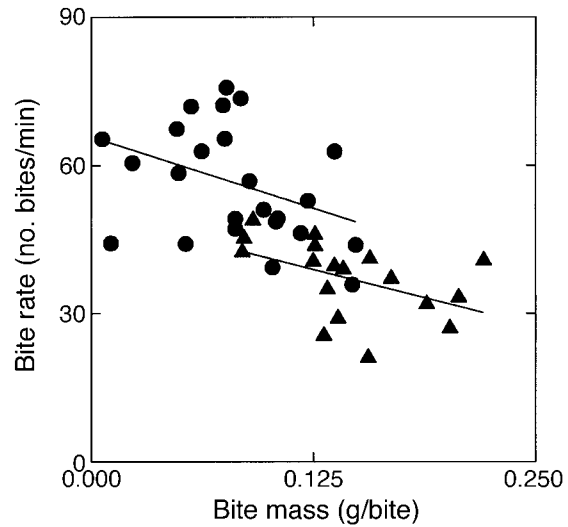


FIG. 5. Bite rate as a function of bite mass on assembled swards at two heights (●, 5-cm swards; ▲, 15-cm swards). On 5-cm swards, bite rate = $65.7 - 114.7(\text{bite mass})$. On 15-cm swards, bite rate = $50.4 - 91.8(\text{bite mass})$.

comes 0.243. Nonlinear regression of bite rate vs. forage biomass from our data yielded an estimate of $g = 0.002$ and an estimate of $a = 0.832$ ($r^2 = 0.51$; Fig. 4). Bradbury et al. (1996) calculated a maximum bite rate on dense swards (77.8 bites/min) that is comparable to our observed maximum (76.1 bites/min).

Spalinger and Hobbs (1992) suggested that bite rate and bite mass should be inversely related in dense swards. We found this to be generally true across grass heights ($F_{1,40} = 32.5$, $P < 0.001$), but the relationship became weaker when we considered sward heights separately (short swards: $F_{1,22} = 3.86$, $P = 0.06$; tall swards: $F_{1,16} = 4.62$, $P = 0.05$; Fig. 5).

Voluntary intake trials with the gazelles showed a positive relationship between the digestible energy content of the forage and ad libitum rates of energy consumption (consumption = $-6.4 + 2.6 \cdot \text{content}$; $F_{1,67} = 41.9$, $P < 0.001$, $r^2 = 0.39$). This indicates that forage digestibility constrains voluntary intake rates, as predicted on the basis of digestive kinetics (Illius and Gordon 1991).

Behavioral observations of free-ranging Thomson's gazelles suggest that they strongly select for grass leaf and sheath, which are the most digestible fractions of a tiller (Bradbury et al. 1996). To confirm these observations experimentally, we compared the height of the remaining stubble in board trials at the two sward heights (5-cm trials: mean stubble height 1.33 ± 0.35 cm; 15-cm trials: mean stubble height 5.5 ± 1.05 cm; $t_{26} = 17.8$, $P < 0.001$). Comparison of mean stubble height in the tall swards vs. the height of stem (5 cm) also showed a significant difference ($t_{21} = 2.4$, $P =$

0.03), showing that Thomson's gazelles cropped tillers slightly above the point of stem attachment. This presumably reduces consumption of small amounts of fibrous stem tissue. Given that Thomson's gazelles select for the leaf component, we considered only leaf and sheath fractions in both our calculations of energy and fiber content. Percentage digestibility measured from feces collected from free-ranging gazelles was a negative linear function of leaf-sheath biomass of the sward ($F_{1,19} = 6.31$, $P = 0.021$, $r^2 = 0.25$; Fig. 6).

We calculated daily energy intake constrained by grazing and digestion processes (Fig. 7). To be con-

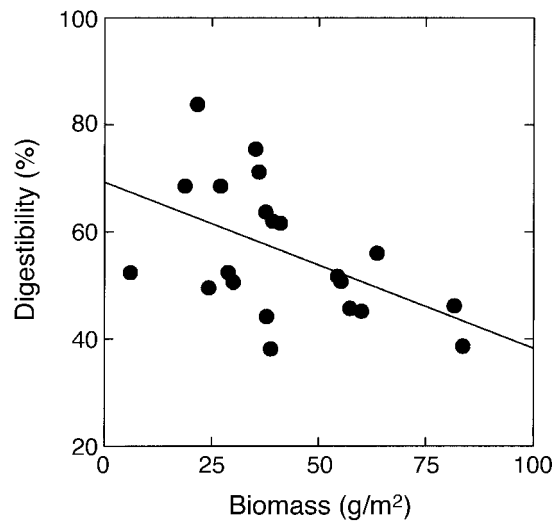


FIG. 6. Digestibility of leaf and sheath tissue for Thomson's gazelles as a function of the biomass of leaf and sheath in the sward; percentage digestibility = $65.5 - 0.29(\text{biomass})$.

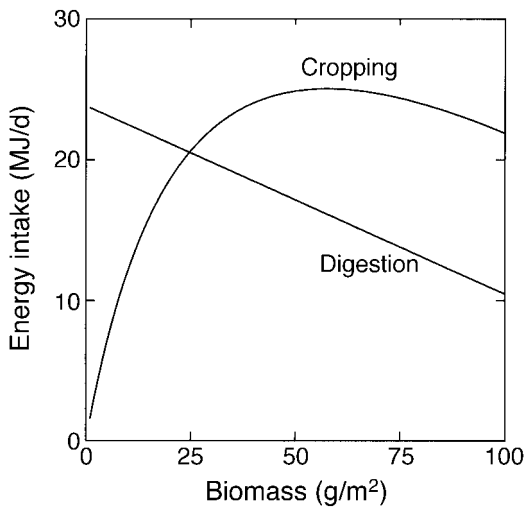


FIG. 7. Grazing and digestion constraints as generated by the forage maturation model. Maximum energy intake occurs at the junction of the two constraints at a sward biomass of 25 g/m².

sistent with our findings from the functional response trials, we restricted our analyses to variation in biomass associated with short swards. We found that daily energy intake is constrained by grazing rate on swards with biomass <25 g/m², but is constrained by digestion on swards with biomass >25 g/m². Peak energy intake is predicted to be 20 MJ/d for an individual Thomson's gazelle. This compares to an estimated range of 8 to 12 MJ/d average realized metabolic requirements for a 20-kg artiodactyl (Konoplev et al. 1978, Peters 1983).

DISCUSSION

In their natural range, Thomson's gazelles tend to aggregate on shortgrass plains during the growing season (Walther 1973, Maddock 1979, Borner et al. 1987, Bradbury et al. 1996). Although explanations such as predator avoidance (FitzGibbon and Lazarus 1995) or demands for mineral nutrients (Murray 1995) have been posed to explain avoidance of tall grasslands within their movement radius, our experimental work suggests a more direct, energetic explanation. Thomson's gazelles can maximize daily energy intake by foraging on swards of low-to-intermediate biomass, where grazing rates are not inhibited by either very short or very tall tillers, and where the forage digestibility remains acceptably high. Although other factors may certainly contribute to the distribution of Thomson's gazelles in the wild, we suggest that energy maximization offers the simplest explanation for their preference for short vs. tall grasslands.

Functional responses for grazing herbivores have been measured for a variety of taxa (Allden and Whitaker 1970, Short 1985, Lundberg 1988, Spalinger et al. 1988, Lundberg and Danell 1990, Gross et al. 1993, Wilmshurst et al. 1995), with the consistent finding of

positive, decelerating (Type II) relationships between forage abundance and grazing rate. This was our result for Thomson's gazelles, based on data pooled over two sward heights. However, subtle differences in consumption patterns between short vs. tall swards demand further explanation.

We found that grazing rates by Thomson's gazelles can vary as a function of biomass at a given height, a property also reported by Bradbury et al. (1996) for Thomson's gazelles, but this is not necessarily true for all grass heights. A sharp increase in bite mass with increasing biomass on short swards results in an increased intake rate under the same conditions. On tall swards, however, both bite mass and bite rate show little or no variation with biomass, resulting in no variation in grazing rate over a broad range of biomass. Because this effect is a function of variation in both bite rate and bite mass, it supports the assertion by Laca et al. (1992a) that both sward height and sward density interact to influence intake, even on homogeneous swards. The consistent underestimation of bite rate illustrated that these parameters appeared to vary with sward height, independently of bite mass. This is an important consideration for grazing herbivores, whose food resource often forms a dense grazing lawn under sustained herbivory (McNaughton 1984), yielding a superficial impression of homogeneity. Minor underlying variation in biomass can result in large variation in intake rates, which could contribute to heterogeneous spatial distributions of herbivores exploiting open, continuous grasslands.

A second noteworthy feature of our experimental results relates to the three processes of grazing by terrestrial herbivores identified by Spalinger and Hobbs (1992). Our functional response trials were designed to mimic food-concentrated patches (process 3 foraging) in which competition between cropping and chewing bites limits intake (Spalinger and Hobbs 1992, Bradbury et al. 1996). Pooled data for both sward heights showed an inverse relationship between bite rate and bite mass, as predicted by Spalinger and Hobbs' model, and as has been shown for similar data collected over a range of heights and densities (Black and Kenney 1984, Spalinger et al. 1988). This pattern was far weaker when the data were subdivided into the two trial heights. Despite significant relationships for both bite rate and bite mass relative to sward biomass on short swards, bite rate was relatively constant over a range of bite masses. On tall swards, where the relationships between bite rate and bite mass relative to biomass were weak, there was a significant but weak trend for declining bite rate relative to bite mass. This suggests that in process 3 foraging, bite rates are a more or less constant feature at a particular sward height, with strong variation in bite mass related to sward density. Saturating intake rates may stem not only from competition between bite mass and bite rate per se, but

also from plant part selection (resulting in lowered bite rates) on tall swards.

The relationship that we found between bite mass and sward height is consistent with the findings of Bradbury et al. (1996) on the dry-season range of migratory Thomson's gazelles. They found quantitative shifts in the grazing behavior of gazelles between searching for bites (process 1 and 2 foraging) on short, sparse swards vs. a trade-off between bite mass and bite rate (process 3 foraging) on tall, homogeneous swards. The behavioral shift was predictable using multivariate analysis of measures of grass greenness and height (Bradbury et al. 1996). From 5 to 15 cm high swards, Thomson's gazelles shifted from an 83% probability of process 1 or 2 foraging to only 14%, whereas the probability of process 3 foraging increased from 3% to 33% over the same range of sward heights (J. Bradbury, *personal communication*). We could not detect behavioral shifts among the three foraging processes proposed by Spalinger and Hobbs (1992) that corresponded to sward height, but found evidence for process 3 foraging at both heights. Given that variation in sward height itself was not sufficient to produce a foraging behavior shift in Thomson's gazelles, grass greenness or plant part selection may be responsible. Greater than 50% of short-sward biomass measured by Bradbury et al. (1996) was brown-leaf tissue of poor nutritional value. Such a mix of dead and live tissue creates a mosaic of palatable patches for which search time between bites would be considerable, resulting in process 1 or 2 foraging behavior. This contrasts with the wet-season condition on the Serengeti shortgrass plains where, in patches that have recently received rain, swards are short, concentrated, and almost entirely green tissue. Our finding of process 3 foraging on short grass therefore appears to be related to the lack of plant part selection on these swards. During the wet season in Bradbury et al.'s (1996) study area, dead grass declined to ~13% of sward biomass, creating food-concentrated patches and leading to process 3 foraging, as we found in our foraging trails. Our result adds strength to the finding of Bradbury et al. that switching among foraging processes is dominated by both grass height and, perhaps more significantly, the fraction of green tissue in the sward, both of which may influence bite mass.

Maximization of energy gain on grass swards of intermediate biomass is a feature of herbivory not limited to Thomson's gazelles (Wilmshurst 1998), and may have wider implications for understanding grass-herbivore dynamics (Fryxell 1991, Wilmshurst et al. 1995). To maximize daily energy intake, grazing herbivores should avoid very short or tall patches in their movement radius, but should deplete patches of intermediate biomass. This suggests that bimodal frequency distributions of grass biomass should develop where grazers are foraging optimally, a pattern for which there is some empirical evidence (Gibb and Ridout 1986,

1988, Gibb 1991, WallisDeVries and Daleboudt 1994). Across larger landscapes, in which many species are exploiting the grass resources, scarcity of patches of intermediate grass biomass could lead to habitat segregation as small grazers shift to more digestible short patches and larger grazers, more tolerant of fibrous forage (Illius and Gordon 1987), shift to tall patches. From the perspective of the grass, herbivore preferences for intermediate-biomass swards also offers opportunities to escape intense exploitation by either adopting a very short or dispersed growth form or, alternatively, achieving very rapid maturation, thereby defending against herbivory through low nutritive quality (Åström et al. 1990, Lundberg and Åström 1990).

Although limits to grazing rate may restrict energy intake on short swards, our model of constraints on daily energy intake suggested that, on swards of grass biomass >25 g/m², digestion constrains intake for Thomson's gazelles. Only on the sparsest swards was daily energy gain constrained by forage availability. This supports previous assertions that small ruminants should be sensitive to forage quality (Illius and Gordon 1991, Gordon and Illius 1994, Hanley 1997). Measures of instantaneous intake only tell us how quickly an individual will reach its daily dry matter intake limit, not what this limit will be. This is a subtle, but nevertheless important, feature of forage use by ruminants. It tells us that the instantaneous functional response is a rather poor index of daily energy gain, except when animals are grazing the sparsest of grass swards. As a consequence, we should expect to find Thomson's gazelles selecting patches with low-to-intermediate forage densities, rather than swards with high biomass.

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LITERATURE CITED

- Albon, S. D., and R. Langvatn. 1992. Plant phenology and the benefits of migration in a temperate ungulate. *Oikos* **65**:502-513.
- Allden, W. G., and I. A. McD. Whittaker. 1970. The determinants of herbage intake by grazing sheep: the interrelationship of factors influencing herbage intake and availability. *Australian Journal of Agricultural Research* **21**:755-766.
- Ammann, A. P., R. L. Cowan, C. L. Mothershead, and B. R. Baumgardt. 1973. Dry matter and energy intake in relation to digestibility in white-tailed deer. *Journal of Wildlife Management* **37**:195-201.

- Åström, M., P. Lundberg, and K. Danell. 1990. Partial prey consumption by browsers: trees as patches. *Journal of Animal Ecology* **59**:287–300.
- Banyikwa, F. F. 1976. A quantitative study of the ecology of the Serengeti short grasslands. Dissertation. University of Dar es Salaam, Dar es Salaam, Tanzania.
- Bazely, D. R. 1989. Carnivorous herbivores: mineral nutrition and the balanced diet. *Trends in Ecology and Evolution* **4**:155–156.
- Belovsky, G. E. 1978. Diet optimization in a generalist herbivore: the moose. *Theoretical Population Biology* **14**:105–134.
- . 1986a. Generalist herbivore foraging and its role in competitive interactions. *American Zoologist* **26**:51–69.
- . 1986b. Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. *Oecologia* **70**:35–52.
- Black, J. L., and P. A. Kenney. 1984. Factors affecting diet selection by sheep. II. Height and density of pasture. *Australian Journal of Agricultural Research* **35**:565–578.
- Borner, M., C. D. FitzGibbon, M. Borner, T. M. Caro, W. K. Lindsay, D. A. Collins, and M. E. Holt. 1987. The decline of the Serengeti Thomson's gazelle population. *Oecologia* **73**:32–40.
- Bradbury, J. W., S. L. Vehrencamp, K. E. Clifton, and L. M. Clifton. 1996. The relationship between bite rate and local forage abundance in wild Thomson's gazelles. *Ecology* **77**:2237–2255.
- FitzGibbon, C. D., and J. Lazarus. 1995. Antipredator behavior of Serengeti ungulates: individual differences and population consequences. Pages 274–296 in A. R. E. Sinclair and P. Arcese, editors. *Serengeti II: dynamics, management, and conservation of an ecosystem*. University of Chicago Press, Chicago, Illinois, USA.
- Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. *American Naturalist* **138**:478–498.
- . 1995. Aggregation and migration by grazing ungulates in relation to resources and predators. Pages 257–273 in A. R. E. Sinclair and P. Arcese, editors. *Serengeti II: Dynamics, management and conservation of an Ecosystem*. University of Chicago Press, Chicago, Illinois, USA.
- Fryxell, J. M., J. Greever, and A. R. E. Sinclair. 1988. Why are migratory ungulates so abundant? *American Naturalist* **131**:781–798.
- Fryxell, J. M., and A. R. E. Sinclair. 1988a. Causes and consequences of migration by large herbivores. *Trends in Ecology and Evolution* **3**:237–241.
- Fryxell, J. M., and A. R. E. Sinclair. 1988b. Seasonal migration by white-eared kob in relation to resources. *African Journal of Ecology* **26**:17–31.
- Gibb, M. J. 1991. Differences in the vertical distribution of plant material within swards continuously stocked with cattle. *Grass and Forage Science* **46**:339–342.
- Gibb, M. J., and M. S. Ridout. 1986. The fitting of frequency distributions to height measurements on grazed swards. *Grass and Forage Science* **41**:247–249.
- Gibb, M. J., and M. S. Ridout. 1988. Application of double normal frequency distributions fitted to measurements of sward height. *Grass and Forage Science* **43**:131–136.
- Goering, H. K., and P. J. VanSoest. 1970. Forage fiber analyses. USDA Agricultural Research Service Agriculture Handbook **379**.
- Gordon, I. J., and A. W. Illius. 1988. Incisor arcade structure and diet selection in ruminants. *Journal of Animal Ecology* **2**:15–22.
- Gordon, I. J., and A. W. Illius. 1994. The functional significance of the browser–grazer dichotomy in African ruminants. *Oecologia* **98**:167–175.
- Gross, J. E., L. A. Shipley, N. T. Hobbs, D. E. Spalinger, and B. A. Wunder. 1993. Functional response of herbivores in food-concentrated patches: tests of a mechanistic model. *Ecology* **74**:778–791.
- Hanley, T. A. 1997. A nutritional view of understanding and complexity in the problem of diet selection by deer (Cervidae). *Oikos* **79**:209–218.
- Hebert, D. M. 1973. Altitudinal migration as a factor in the nutrition of bighorn sheep. Dissertation. University of British Columbia, Vancouver, Canada.
- Hungate, R. E. 1966. The rumen and its microbes. Academic Press, New York, New York, USA.
- Illius, A. W., and I. J. Gordon. 1987. The allometry of food intake in grazing ruminants. *Journal of Animal Ecology* **56**:989–999.
- Illius, A. W., and I. J. Gordon. 1991. Prediction of intake and digestion in ruminants by a model of rumen kinetics integrating animal size and plant characteristics. *Journal of Agricultural Science* **116**:145–157.
- Janis, C. M., and D. Ehrardt. 1988. Correlation of relative muzzle width with dietary preference in ungulates. *Zoological Journal of the Linnean Society* **92**:267–284.
- Konoplev, V. A., V. E. Sokolov, and A. L. Zotin. 1978. Criterion of orderliness and some problems of taxonomy. Pages 349–359 in I. Lamprecht and A. L. Lotin, editors. *Thermodynamics of biological processes*. deGruyter, Berlin, Germany.
- Laca, E. A., E. D. Ungar, N. Seligman, and M. W. Demment. 1992a. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. *Grass and Forage Science* **47**:91–102.
- Laca, E. A., E. D. Ungar, N. G. Seligman, M. R. Ramey, and M. W. Demment. 1992b. An integrated methodology for studying short-term grazing behaviour of cattle. *Grass and Forage Science* **47**:81–90.
- Lundberg, P. 1988. Functional response of a small mammalian herbivore: the disc equation revisited. *Journal of Animal Ecology* **57**:999–1006.
- Lundberg, P., and M. Åström. 1990. Low nutritive quality as a defence against optimally foraging herbivores. *American Naturalist* **135**:547–562.
- Lundberg, P., and K. Danell. 1990. Functional response of browsers: tree exploitation by moose. *Oikos* **58**:378–384.
- Maddock, L. 1979. The “migration” and grazing succession. Pages 104–129 in A. R. E. Sinclair and M. Norton-Griffiths, editors. *Serengeti: dynamics of an ecosystem*. University of Chicago Press, Chicago, Illinois, USA.
- McNaughton, S. J. 1984. Grazing lawns: animals in herds, plant form and coevolution. *American Naturalist* **124**:863–886.
- . 1988. Mineral nutrition and spatial concentrations of African ungulates. *Nature* **334**:343–344.
- Meissner, H. H., and D. V. Paulsmeier. 1995. Plant compositional constituents affecting between-plant and animal species prediction of forage intake. *Journal of Animal Science* **73**:2447–2457.
- Michaelis, L., and M. L. Menten. 1913. Kinetics of invertase action. *Biochemische Zeitschrift* **49**:333–369.
- Mould, E. D., and C. T. Robbins. 1982. Digestive capabilities in elk compared to white-tailed deer. *Journal of Wildlife Management* **46**:22–29.
- Murray, M. G. 1995. Specific nutrient requirements and migration of wildebeest. Pages 231–256 in A. R. E. Sinclair and P. Arcese, editors. *Serengeti II*. University of Chicago Press, Chicago, Illinois, USA.
- Nelson, M. L., L. Motjope, J. W. Finley, and S. M. Parish. 1990. Ash-free indigestible acid detergent fibre as an internal marker to estimate digestibility with grazing ruminants. *Journal of Range Management* **43**:224–228.
- NRC (National Research Council). 1958. Composition of

- cereal grains and forages. National Academy of Sciences (USA), Washington, D.C., USA.
- O'Connor, T. G. 1994. Composition and population responses of an African savanna grassland to rainfall and grazing. *Journal of Applied Ecology* **31**:155–171.
- Penning, P. D., and R. H. Johnson. 1983a. The use of internal markers to estimate herbage digestibility and intake. 1. Potentially indigestible cellulose and acid insoluble ash. *Journal of Agricultural Science* **100**:127–131.
- Penning, P. D., and R. H. Johnson. 1983b. The use of internal markers to estimate herbage digestibility and intake. 2. Indigestible acid detergent fibre. *Journal of Agricultural Science* **100**:133–138.
- Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, UK.
- Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* **37**:789–799.
- Shiple, L. A., J. A. Gross, D. E. Spalinger, N. T. Hobbs, and B. A. Wunder. 1994. The scaling of intake rate in mammalian herbivores. *American Naturalist* **143**:1055–1082.
- Short, J. 1985. The functional response of kangaroos, sheep and rabbits in an arid grazing system. *Journal of Applied Ecology* **22**:435–447.
- Solomon, M. F. 1949. The natural control of animal populations. *Journal of Animal Ecology* **18**:1–32.
- Spalinger, D. E., T. A. Hanley, and C. T. Robbins. 1988. Analysis of the functional response in foraging in the sitka black-tailed deer. *Ecology* **69**:1166–1175.
- Spalinger, D. E., and N. T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. *American Naturalist* **140**:325–348.
- Tilley, M. A., and R. A. Terry. 1963. A two-stage technique for the in-vitro digestion of forage crops. *Journal of the British Grasslands Society* **18**:104–111.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* **75**:2–16.
- VanSoest, P. J. 1982. Nutritional ecology of the ruminant. O&B Books, Corvallis, Oregon, USA.
- Waite, R. 1963. Botanical and chemical changes in maturing grass and their effect on its digestibility. *Agricultural Progress* **38**:50–56.
- WallisDeVries, M., and C. Daleboudt. 1994. Foraging strategy of cattle in patchy grassland. *Oecologia* **100**:98–106.
- Walther, F. 1968. Verhalten der Gazellen. A. Ziemsen Verlag, Wittenberg Lutherstadt, Germany.
- Walther, F. R. 1973. Round-the-clock activity of Thomson's gazelle (*Gazella thomsoni* Gunther 1884) in the Serengeti National Park. *Zeitschrift für Tierpsychologie* **32**:75–105.
- Westoby, M. 1978. What are the biological bases of varied diets? *American Naturalist* **112**:627–631.
- Wilkinson, L. 1990. SYSTAT: the system for statistics. Systat, Evanston, Illinois, USA.
- Wilmshurst, J. F. 1998. Foraging behaviour and spatial dynamics of Serengeti herbivores. Dissertation. University of Guelph, Guelph, Canada.
- Wilmshurst, J. F., J. M. Fryxell, and R. J. Hudson. 1995. Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behavioral Ecology* **6**:209–217.