The Dynamics and Scaling of Foraging Velocity and Encounter Rate in Mammalian Herbivores

The dynamics and scaling of foraging velocity and encounter rate in mammalian herbivores

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Summary

1. We developed a simple model of foraging locomotion for mammalian herbivores that contains two parameters, maximum foraging velocity (V_{max}, $m\,s^{-1}$) and acceleration (a_o, $m\,s^{-2}$) and a single dependent variable, the distance between plants (d, m).

2. We examined predictions of our model by varying the distance between plants offered to nine mammalian herbivores ranging in mass from 0·05 to 533 kg.

3. Application of simple laws of motion were adequate to explain the dynamics of foraging locomotion. As the animals travelled between food items, they accelerated to a maximum foraging velocity, which they maintained until they approached the next food item. Acceleration was achieved by increasing both the length and the frequency of strides. Mean foraging velocity increased up to 10-fold as plant spacing increased, but as plant spacing increased, mean velocity was asymptotic with distance between plants.

4. V_{max} scaled in proportion to $M^{0.04}$, and a_o scaled as $M^{-0.17}$.

5. Our results suggest that small herbivores achieve similar maximum foraging velocities as do large herbivores, but can accelerate faster and therefore encounter plants more rapidly when plants are spaced closely together (<2 m apart). We conclude that foraging models that do not include the effects of acceleration will overestimate encounter rate and affect the model solution.

Key-words: Acceleration, body mass, locomotion, movement, travel speed

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Introduction

Rates of encounter with food items are an influential component of virtually all models of diet selection, functional response, and foraging behaviour (Holling 1959; Charnov 1976; Stephens & Krebs 1986; Getty & Pulliam 1991). For animals such as herbivores that feed on stationary food items, encounter rate is a function of the spatial distribution of foods, an animal's ability to perceive that distribution, and the animal's rate of travel among the items it perceives. An animal's rate of travel, in turn, depends in part on its size and leg morphology.

The mechanics of locomotion and its relationship to the body size of animals has been examined thoroughly at maximum running velocity and at gait changes (Taylor, Schmidt-Nielsen & Raalo 1970; Heglund, Taylor & McMahon 1974; Pennycuick 1975; Garland 1983; Alexander & Jayes 1983; Strang & Steudel 1990). However, the dynamics and scaling of travel while foraging may differ from that of maximum travel velocity because foraging animals must perceive resources and decide which ones to consume as they move (Speakman & Bryant 1993). Perception and decision making constrain the animal to travel at velocities that are less than its physiological maximum (Garland & Janis 1993; Senft *et al.* 1987; Bell 1991; Getty & Pulliam 1991). While foraging, animals may also travel at rates that enhance the net energy gain while foraging (Orians & Pearson 1979; Pyke 1981) and the feeding animal is constantly slowing and stopping to capture food items. Because herbivores spend up to 10 h per day searching for and consuming their relatively bulky and low-quality prey (Bunnell & Gillingham 1985), we believe that the

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dynamics and scaling of foraging velocity and thus encounter rate is relevant to the ecology of animals and warrants further attention.

Previous foraging models for herbivores assume that encounter rate (λ, plants s^{-1}) is a simple, linear function of plant density (D, plants m^{-2}) and therefore foraging velocity (V, m min^{-1}, rate of travel between food items) is assumed to be constant (Demment & Laca 1994; Getty & Pulliam 1991; Houston 1992; Spalinger & Hobbs 1992). However, recent studies suggest that foraging velocity is not constant, but rather varies as a function of the distance between plants (Wickstrom *et al.* 1985; Speakman 1986; Spalinger, Hanley & Robbins 1988; Shively 1989; Speakman & Bryant 1993). Gross *et al.* (unpublished manuscript) and Shively (1989) proposed that acceleration and deceleration upon departure and arrival at plants may contribute to the lack of fit between predicted and observed intake rates of herbivores. Likewise, Speakman & Bryant (1993) found that the searching speed of shorebirds was limited in part by acceleration after each encounter with food. Here, we develop a simple model predicting foraging velocity and encounter rate of mammalian herbivores. We tested this model with nine species of mammalian herbivores varying in locomotion styles (hopping and walking) and ranging over four orders of magnitude in body mass, and examined the scaling of model parameters with body mass to derive a general relationship for encounter rate.

Model development

Encounter rate with food items is a function of two time intervals – the time required to move between plants and the time spent eating them. In earlier works (Spalinger & Hobbs 1992; Gross *et al.* 1993) we considered the processes affecting eating rate. Here, we focus on the dynamics of movement while foraging. More specifically, we are concerned only with the time interval (T_t, s) that encompasses the departure of the animal from one plant and its arrival and subsequent contact with the next plant. Thus, we define λ (encounter rate, plants s^{-1}) as $1/T_t$.

We modelled encounter rate as a mechanical process operating in a simple environment, where a forager proceeds directly in a straight line from one food item to another. This means that food items are detected from a distance as the animal leaves each feeding position. Encounter rate with plants can thus be expressed as a simple function of foraging velocity and distance moved between plants (d, m plant^{-1}):

$$\lambda = \overline{V}/d, \qquad \text{eqn 1}$$

where $\overline{V}$ is the average foraging velocity (m min^{-1}) of the animal during the travel interval T_t. Typically, d is a complex function of the spatial distribution of plants. For simple spatial distributions, d can be easily determined. For example, where plants are uniformly distributed in space at a density D, $d = 1/\sqrt{D}$. Similarly, where plants are randomly distributed, the

expected value of d, $E(d)$, is determined by $E(d) = 1/(2\sqrt{D})$ (Clark & Evans 1954).

Although d is a property of the plant community, $\overline{V}$ is a function of the morphology of the herbivore and the physics of locomotion. Therefore the average foraging velocity is simply

$$\overline{V} = \frac{d}{T_t}. \qquad \text{eqn 2}$$

The time T_t is composed of three phases: (1) a time interval (T_a) in which the animal accelerates from rest when leaving a plant to a maximum foraging velocity, V_{max} (m s^{-1}); (2) a time interval (T_c) during which the animal maintains a constant velocity, V_{max}; and (3) a time interval (T_d) in which the animal decelerates to arrive at the next plant (Fig. 1). For parsimony, we make several simplifying assumptions. First, we assume the animal begins and ends the trip between food items at rest (i.e. instantaneous velocity is 0). Second, we assume that the animal accelerates at a constant rate, a_o (m s^{-2}), and decelerates at a constant rate, a_d. Finally, we simplify the process by assuming the rate of deceleration is equal but opposite to the rate of acceleration (i.e., $a_d = -a_o$). Thus, the acceleration and deceleration phases are mirror images of each other, and $T_d = T_a$. Equation 2 then becomes:

$$\overline{V} = \frac{d}{2T_a + T_c}. \qquad \text{eqn 3}$$

If we define $d_o/2$ as the distance required for an animal to accelerate at a constant rate from rest to V_{max}, then from the kinematic equation of straight line motion with constant acceleration,

$$\frac{d_o}{2} = 1/2 a_o T_a^2. \qquad \text{eqn 4}$$

Rearranging equation 4, we get

$$T_a = \left[\frac{d_o}{a_o}\right]^{1/2}. \qquad \text{eqn 5}$$

Similarly, we can derive V_{max} from the kinematic equation:

$$V_{max}^2 = 2 a_o \frac{d_o}{2}, \qquad \text{eqn 6}$$

and hence,

$$V_{max} = [a_o d_o]^{1/2}. \qquad \text{eqn 7}$$

The time spent moving at V_{max} is

$$t_c = \frac{d - d_o}{V_{max}}. \qquad \text{eqn 8}$$

Substitution of equations 5, 7, and 8 into equation 3 results in

$$\overline{V} = \frac{(a_o d_o)^{1/2}}{1 + \dfrac{d_o}{d}}, \qquad \text{eqn 9}$$

which reduces to

$$\bar{V} = \frac{V_{max}}{1 + \dfrac{d_o}{d}} \cdot \qquad \text{eqn 10}$$

By rearranging equation 7 and substituting it for d_o, we can also express $\bar{V}$ in terms of V_{max} and a_o,

$$\bar{V} = \frac{V_{max}d}{d + \dfrac{V_{max}^2}{a_o}} \cdot \qquad \text{eqn 11}$$

Although the form of equation 11 is not as reducible as either of its alternatives, it is more appropriate for the purposes of scaling its parameters with animal size, because V_{max} and a_o can be interpreted relative to the mechanics and morphometries of animals. Hence, we use this form to test our model.

When the distance between plants is such that $d < d_o$, then the animal cannot accelerate to V_{max}, and the time spent moving between plants is comprised of only the acceleration and deceleration phases. In these circumstances, the average velocity will be

$$\bar{V} = \frac{d}{2\left(\dfrac{d}{a_o}\right)^{1/2}} = \frac{(a_o d)^{1/2}}{2} \cdot \qquad \text{eqn 12}$$

Encounter rate is thus determined by substituting the appropriate equation for $\bar{V}$ (i.e. equations 11 or 12) into equation 1.

We expect the scaling of the two model parameters, V_{max} and a_o to be predictable from the mechanics of locomotion. If V_{max} is the product of stride length (L_s, m) and stride frequency (S_f, strides s^{-1}) (Hill 1950; Pennycuick 1975, 1992; Schmidt-Nielsen 1984), then the exponent for the scaling of velocity would logically result from the scaling exponents of L_s and S_f. Stride length is hypothesized to be proportional to leg length (L_l^1; Schmidt-Nielsen 1984), whereas stride frequency has been shown to conform to a mechanical model similar to the natural oscillation of a pendulum (Pennycuick 1975; Alexander & Jayes 1983;

McMahon 1984). Hence if leg length is the length of the pendulum, then S_f would scale with $L_l^{-0.50}$, and V_{max} will scale with $L_l^{0.50}$.

An animal's acceleration has been modelled as the quotient of the force produced by the muscles and body mass (Hill 1950; Lovvorn, Jones & Blake 1991; Katz & Gosline 1993). If muscle force is proportional to the cross-sectional area of the muscles (Alexander 1982), then we expect $a_o \propto L_d^2/M$, where L_d is leg diameter. We have thus far expressed the scaling of V_{max} and a_o as a function of leg length and diameter. To relate limb morphology to body mass we must use principles of similarity. The principle of geometric similarity (one of three similarity models) follows the concept of Euclidean geometry, where volume (and mass) $\propto$ area$^{3/2}$ $\propto$ length^3. Relative body proportions of an animal are expected to remain constant as body size changes, and thus $L_l \propto L_d \propto M^{0.33}$. Therefore we hypothesize that V_{max} will scale with $M^{0.17}$, and a_o with $M^{-0.33}$.

Materials and methods

MEASURING FORAGING VELOCITY

Our analysis of encounter rate proceeded in three phases. First, we examined the relationship between plant spacing and foraging velocity by conducting experiments with nine species of herbivores (Table 1). We fitted equation 11 to observed data to estimate the values of V_{max} and a_o for each herbivore species, and subsequently derived scaling relationships with body mass. Second, leg morphology and locomotion mechanics were measured to provide the basis for developing independent estimates of the scaling of V_{max} and a_o. Finally, we examined the correspondence between observed and predicted scaling relationships.

V_{max} and a_o were estimated from a series of experiments during which two to five individuals of each herbivore species (Table 1) foraged on hand-assembled arrangements of plants. Foraging trials were conducted at Texas Agricultural Experiment Station, Texas A&M University, Uvalde, TX, and Colorado State University, Ft Collins, CO. Fresh alfalfa plants were evenly arranged along runways that were scaled to the animals' size and devoid of any extraneous plant material. Plants were anchored to holes in plywood boards using the camming action of inverted rubber stoppers. Distances between plants were varied among trails to examine the relationship between spacing distance and the animals' foraging velocity. The runways in which the animals foraged were marked at regular distance intervals so that distance travelled between plants could be accurately measured.

For each animal, a minimum of five trials were conducted at no less than five different plant spacings, which ranged between 0·6 and 16 stride lengths of the animal. We video-taped each trial and measured
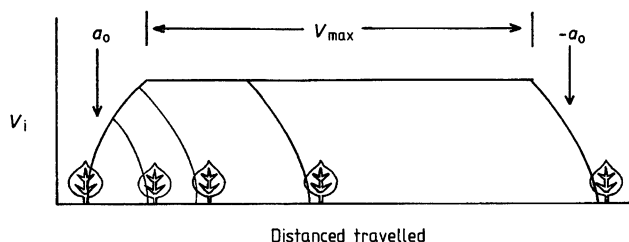

Fig. 1. A conceptual model of the change in instantaneous velocity with distance while animals travel between stationary food items. The animal accelerates at a constant rate (a_o) until it reaches a maximum sustainable foraging velocity (V_{max}). The animal maintains this velocity (V_{max}) until it approaches the next food item, and then decelerates to a stop at a rate equal in magnitude but opposite in sign to acceleration ($-a_o$). When the distance between food items is short, the animal may not reach V_{max} before it begins to decelerate for the next item.

Table 1. Characteristics of herbivores used in the foraging experiments

Animal species	No.	Body mass (kg) $\bar{X}$ (SE)		Leg length (m) $\bar{X}$ (SE)	
Collared Lemming (*Dicrostonyx groenlandicus* Traill 1823)	5	0·05	(0·001)	0·04	(0·0004)
Eastern Cottontail (*Sylvilagus floridanus* J.A. Allen 1890)	2	0·61	(0·010	0·18	(0·004)
Black-tailed Prairie Dog (*Cynomys ludovicianus* Ovd 1815)	5	0·75	(0·02)	0·09	(0·001)
Domestic Rabbit (*Oryctolagus cuniculus* Lilljeborg 1871)	4	3·12	(0·08)	0·27	(0·005)
Angora Goat (*Capra hircus* Linnaeus 1758)	3	19·2	(1·45)	0·49	(0·006)
White-tailed Deer (*Odocoileus virginianus* Mearns 1898)	4	54·7	(5·77)	0·76	(0·02)
Elk (*Cervus elaphus* V. Boiley 1935)	3	296	(3·65)	1·22	(0·02)
Domestic Horse (*Equus caballus* Linnaeus 1758)	2	435	(7·42)	1·60	(0·03)
Domestic Cattle (*Bos taurus* Linnaeus 1766)	3	533	(26·84)	1·22	(0·01)

movement rates from slow-motion replays of the video recordings. A trial commenced when we first detected (within one frame of the video tape, 1/30 s) that the reference point (base of the tail) on the animal first moved forward when leaving a plant. The trial ended when the reference point failed to move any further forward upon arrival at the next plant. Each segment of travel between two plants was considered an observation, and we did not include the time spent cropping bites from the plant in these observations. All animals were habituated to the experimental protocol before data were collected.

Mean velocity was estimated from the quotient of the time spent travelling between plants and the distance travelled. Time spent travelling was calculated from the number of frames of the video tape that elapsed between the beginning and ending of the trial, and distance travelled was measured as the difference between the location of the reference point at the beginning of the trial and its location at the end of the trial. V_{max} and a_o were subsequently determined by non-linear regression of distance on velocity according to equation 11. We evaluated the model fit by examining the residuals for normality and uniform scatter around the regression line and by calculating r^2 from the corrected sum of squares (Motulsky & Ransnas 1987).

For plants spaced at distances less than d_o, we hypothesized that equation 12 would be the appropriate velocity model. However, we suspected that the fits of equations 11 and 12 were likely to be qualitatively similar at these short distances, and that the added complexity of using two equations (i.e. 11 and 12) to determine $\bar{V}$ would be unwarranted for most circumstances. To determine whether equations 11 would adequately describe $\bar{V}$ for $d < d_o$, we substituted parameter values for a_o from the regression fit of equation 11 into equation 12, and visually com-

pared the differences in predicted $\bar{V}$ resulting from the two equations.

We examined each animal's instantaneous velocity (V_i) as it travelled from one plant to the next by plotting the animal's position (i.e. the reference point) in the runway at five-frame intervals (i.e. 0·17 s). For lemmings, which accelerated very rapidly, the interval was shortened to every three frames (0·10 s). In addition, we examined the changes in stride length (m), stride period (s), and the velocity (m s^{-1}) of each stride by measuring the displacement of the tip of each (both left and right) front hoof or toe and the time between successive footfalls of the same foot. The strides of domestic and cottontail rabbits were determined from the duration and displacement of the hind feet as the moved together.

SCALING MODEL PARAMETERS

To determine the scaling of mean stride length and frequency at V_{max}, we removed the first two and last two strides from each trial, to reduce any potential effect of acceleration and deceleration. Only trials during which the animals took at least five useable strides were included in the analysis of average L_s and S_f. Leg length was measured from the greater trochanter of the hip to the toe of the hind leg when extended back as in walking or hopping. Body mass of each animal was measured on an electronic or beam balance to the nearest 0·001 kg for lemmings, 0·01 kg for animals <5 kg, to the nearest 0·1 kg for animals between 5 and 100 kg, and to the nearest 1 kg for animals >100 kg.

We initially calculated the scaling coefficients of V_{max}, a_o, L_1, L_s, and S_f in relation to body mass using ordinary least-squares linear regression (SAS Institute, Inc. 1985) on $\log_e$-transformed data fit to the model $Y = aM^b$ (transformed to the linear model

$\log_e Y = \log_e a + (b)\log_e M)$. The scaling of V_{max}, a_o, L_s, S_f in relation to leg length was determined in the same manner. We used the mean value of model parameters for each herbivore species to determine scaling coefficients. If a significant relationship existed between M and the dependent variable, ordinary least-squares slopes were converted to reduced major axis slopes by dividing the ordinary least-squares slopes by the correlation coefficient (Rayner 1985; McArdle 1988; LaBarbera 1989). Standard errors of slopes estimated from reduced major axis regression were used to construct confidence estimates and test against the hypothesized slopes (Hayami & Matsukuma 1970).

SIMULATING ENCOUNTER RATE

The scaling of encounter rate relative to distance between plants was examined by first inserting the observed scaling relationships for V_{max} and a_o into equation 2 to determine $\bar{V}$, and then substituting $\bar{V}$ into equation 1 to simulate encounter rate for animals from 0·05 to 500 kg in body mass travelling between plants spaced 0·01 to 10 m apart.

Results

TEST OF THE VELOCITY MODEL

Mean foraging velocity ($\bar{V}$) of all nine species of herbivores increased about 10-fold with increasing

distance between plants, approaching an asymptotic velocity at the longest distances (Fig. 2). Using equation 11 for all distances, plant spacing accounted for 69–91% of the variation in foraging velocity (Fig. 2). The residuals around the predicted curve were normally distributed and uniformly scattered. For $d < d_o$, equation 12 provided a better fit to the data than equation 11, which underestimated the actual foraging velocity by a maximum of $0·03\,\mathrm{m\,s^{-1}}$ at the shortest distances between plants (Fig. 3). However, the slight improvement in model fit achieved by using both equations 11 and 12 does not seem to justify the additional complexity associated with the discontinuous, two-equation model for estimating $\bar{V}$.

Instantaneous velocity (V_i) increased rapidly as an animal departed a plant and decreased as it approached the next plant (Fig. 4). At the shortest distances between plants, animals did not reach V_{max}. Our simple model of foraging velocity described the V_i of our animals reasonably well (Fig. 4), and therefore approximates the mechanics of foraging velocity without undue complexity.

Stride length and frequency changed dramatically as the animals walked between plants (Figs 5 and 6). With successive steps between food items, stride length and stride velocity increased during the first few steps, remained relatively constant, and then declined during the last few steps. Likewise, stride period generally decreased and then increased
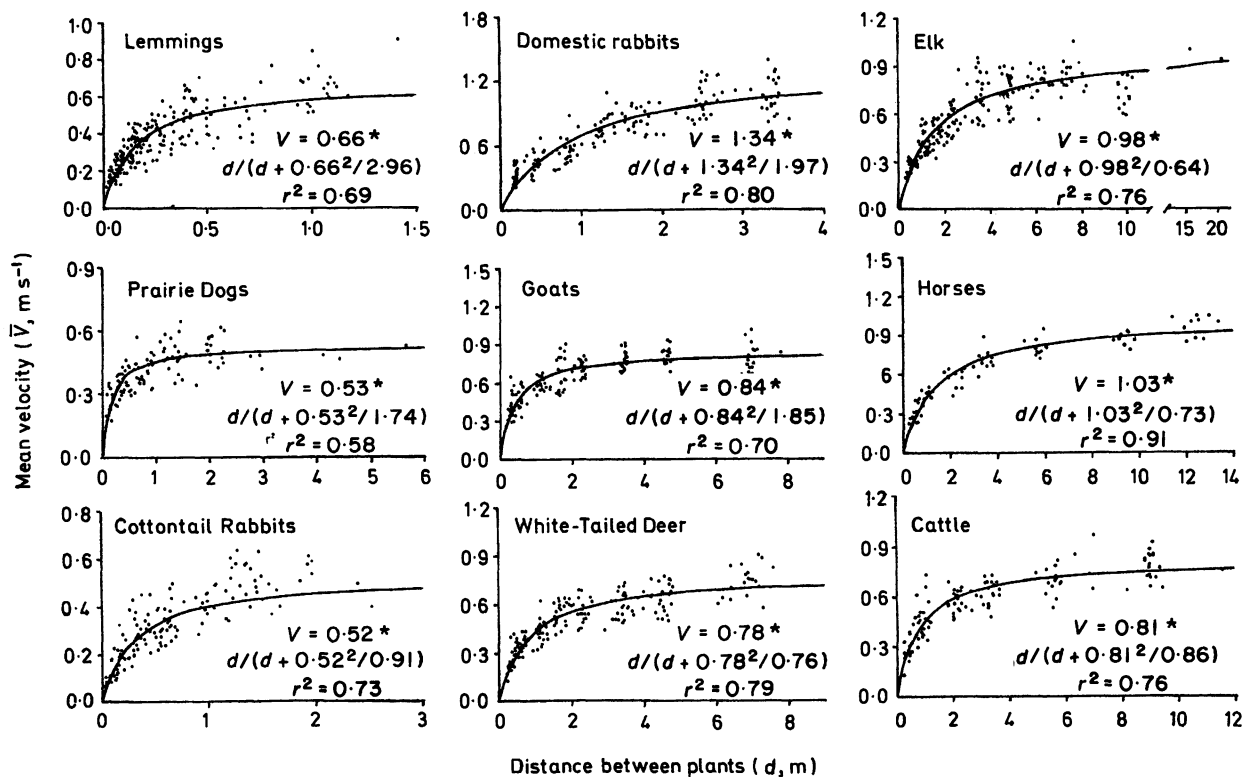

Fig. 2. The relationship between distance between plants (d) and mean foraging velocity, $\bar{V}$ ($\mathrm{m\,s^{-1}}$), of nine herbivore species, fit using the model $\bar{V} = V_{max}d/(d + V_{max}^2/a_o)$, where V_{max} is the maximum sustainable velocity while foraging and a_o is acceleration ($\mathrm{m\,s^{-2}}$).

again as the animals travelled between plants. Maximum stride length was generally achieved one to two steps after departing the plant, and stride length began to decline three or four steps before the next plant. Stride velocity increased with successive footfalls until it reached a maximum just before the animals decelerated to reach the next plant.

Estimates of encounter rate with plants (λ) were improved by accounting for the dynamics of acceleration and deceleration (Fig. 7). For example, if foraging velocity is assumed to be constant with plant density (i.e. the effects of acceleration and deceleration are ignored), and we assume a simple

inverse relationship between encounter rate and plant density (equation 1), then encounter rate observed for our animals is substantially over-estimated, especially at short distances between plants (Fig. 7). This discrepancy was greater for the larger animals that accelerated more slowly than for the smaller animals.

SCALING OF MODEL PARAMETERS

The parameter V_{max} was directly and strongly related to the product of L_s and S_f (Table 2, $V_{max} = 1.03 + 0.03(L_s S_f)$, $r^2 = 0.96$) as expected. The scaling exponent for V_{max} was 0.04 (ordinary least-squares regression), but was not significantly different from 0 (Fig. 8a, $t = 1.556$, $P = 0.16$). Maximum foraging velocity was therefore virtually independent of M within our nine herbivore species.

Stride length scaled with $M^{0.29}$ (Table 2), not significantly different from the scaling of leg length ($\alpha M^{0.38}$; $Z = 0.44$, $P = 0.33$; Fig. 8b). However, the scaling of leg length was different than expected from geometric similarity ($\alpha M^{0.33}$; $Z = 2.67$, $P\,0.004$). Stride frequency scaled with $M^{-0.24}$ and $L_1^{-0.64}$, which differed from the relationship predicted by the oscillation of a pendulum ($\alpha L_1^{-0.50}$, $Z = 2.83$, $P = 0.002$). Acceleration (a_o) scaled with $M^{-0.17}$ (Fig. 8c) confirming that small animals accelerate faster than do large animals. However, the scaling exponent was higher than that predicted from geometric similarity ($\alpha M^{-0.33}$, $Z = 4.00$, $P < 0.0001$).

Because a_o scaled with $M^{-0.17}$ and V_{max} was nearly independent of M, the scaling of encounter rate with plants depended upon both spacing distance (d) and herbivore body size. As distance between plants increased, the scaling exponent for encounter rate in relation to M increased (Fig. 9). Therefore, smaller animals encountered plants faster when $d < 2\,m$, whereas large animals encountered plants faster when $d > 2\,m$. Notice, however, that the scaling exponent for encounter rate remained close to 0 over the entire range of inter-plant distances simulated (Fig. 9).

Discussion

Our experiments demonstrated that foraging velocity of mammalian herbivores increases asymptotically as the distance between plants (d) increases and that our animals travelled at strikingly similar velocities while foraging, regardless of body size. Movement between stationary food items was described well by a simple kinematic model that describes the animal's acceleration to an asymptotic velocity when leaving a plant and subsequent deceleration when approaching another plant (equation 11, Figs 2 and 4). In deriving this model, we obtained two equations for the relationship between foraging velocity and d, one (equation 11) appro-
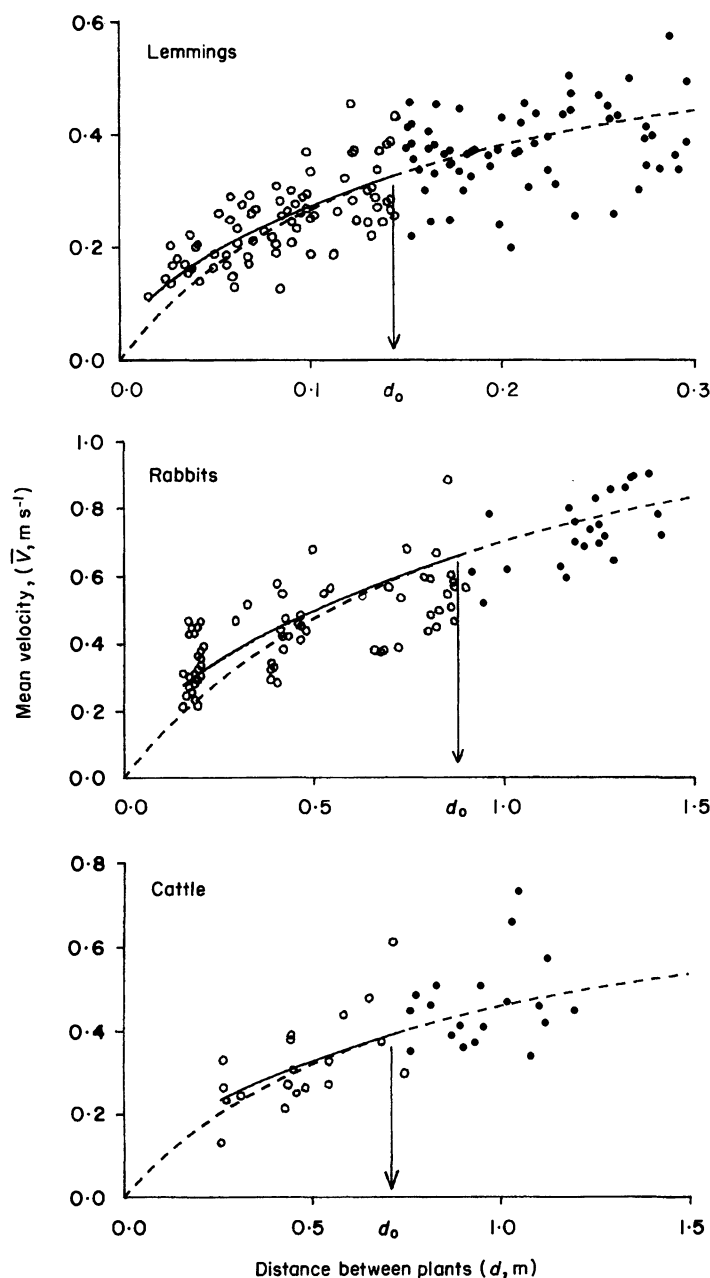

Fig. 3. By enlarging the lower left region of Fig. 1, the small difference in fit between equation 12 for distances less than d_o (unshaded circles and solid line) and equation 11 for all distances (shaded circles and dashed lines) is evident.

priate when d exceeds the distance required to fully accelerate and decelerate (d_o), and the other (equation 12) for the special case when $d < d_o$. We suggest, however, that because both equations give similar predictions for foraging velocity when $d < d_o$, equation 11 alone provides a suitable, simple model for estimating foraging velocity.

Animals accelerated upon leaving a plant by increasing the length of strides and reducing the time needed to swing the foot forward (Figs 4–6). Similar relations were observed in feeding shorebirds (Speakman & Bryant 1993). Although acceleration and deceleration were not mirror images of each other, they were relatively symmetrical (Figs 4–6), justifying the simplification used in the model.

Our results imply that models of encounter rate that ignore the dynamics of acceleration and deceleration will overestimate an animal's rate of encounter when plants are spaced relatively closely together (Fig. 7). This problem will be more severe for larger animals than for smaller ones because larger animals accelerate more slowly than do smaller ones (Figs 2 and 7). Our smaller animals reached their maximum foraging velocity more quickly than did the larger animals, enabling them to achieve higher encounter rates when plants were spaced closely together, and encounter rates nearly equivalent to the large herbivores when plants were dispersed. Therefore, accurately predicting functional response, diet selection, and foraging behaviour of herbivores of different sizes feeding in patchy environments requires that the acceleration and deceleration portions of travel be considered and included in models.

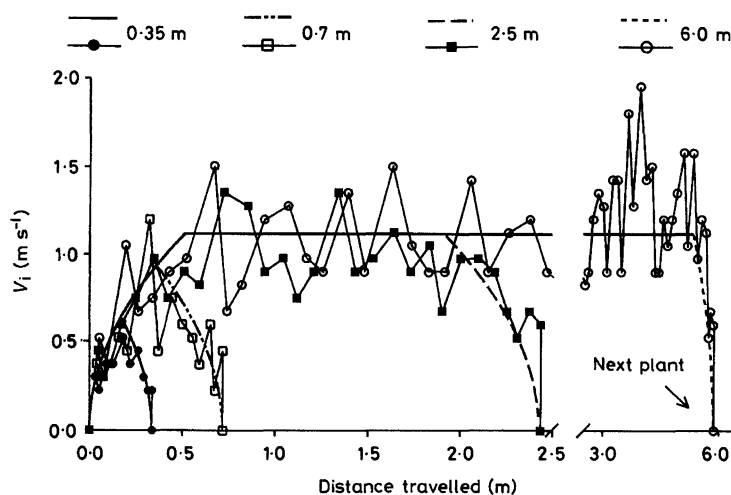Although our mechanical model was able to

describe and explain the dynamical pattern in foraging velocity in relation to plant density, it cannot explain the magnitude of maximum foraging velocity, V_{max}, and acceleration, a_o, achieved by animal species. We expected these values to vary between species in relation to body size, and within a species in relation to behavioural and perceptual constraints imposed by the habitat and the animal. However, we found that V_{max} scaled with $M^{0.04}$, which was not significantly different from M^0. Therefore we conclude that foraging velocity is largely independent of body mass. Our conclusions differ from observations of the scaling of travel velocity at the animal's physiological maximum (Peters 1983; Schmidt-Nielsen 1984) and at gait transitions (Pennycuick 1975).

We offer several specific explanations for this result. First, our scaling relationships were derived from only nine animal species. A different or larger collection of species would possibly result in slightly different scaling relationships. Our scaling exponent for leg length (0·38) fell at the high end of the range found in several studies that included a much larger number of mammalian species (i.e. 0·27 to 0·38, Alexander et al. 1979; Raich & Casinos 1991; Garland & Janis 1993). Therefore, our smaller animals were perhaps better suited to high foraging velocities than on average.

Second, the scaling relationships we found may be the outcome of leg proportions and locomotion mechanics that are different than we hypothesized. For example, Hill (1950) predicted our result that maximum travel velocity should be independent of body mass. However, his hypothesis is based on the idea that stride frequency should scale inversely with leg length (i.e. M^{-1}), whereas our hypothesis is based on the pendulum model which predicts $L^{-0.50}$ (McMahon 1977). Stride frequency in our animals scaled with an exponent of –0·64, which was between the two hypothesized values.

In retrospect, the absence of a significant relationship between body size and V_{max} is most likely caused by differences in perceptual, energetic, and behavioural constraints faced by animals. If we assume stride frequency has been adapted to exploit the forces of gravity and match the frequency of a pendulum as found by Pennycuick (1975) and Heglund et al. (1974), then we must conclude that while foraging, the smaller animals in our study purposely increased their stride frequency relative to their maximum frequency or frequency normally used at transitions between gaits. Smaller animals may be compelled to move more rapidly between plants than are larger animals for several reasons. First, small animals have a potentially higher risk of predation. Rapid locomotion tends to reduce the time spent foraging (Abrams 1984) in the open and increase the time available for vigilance (Berger & Cunningham 1988).
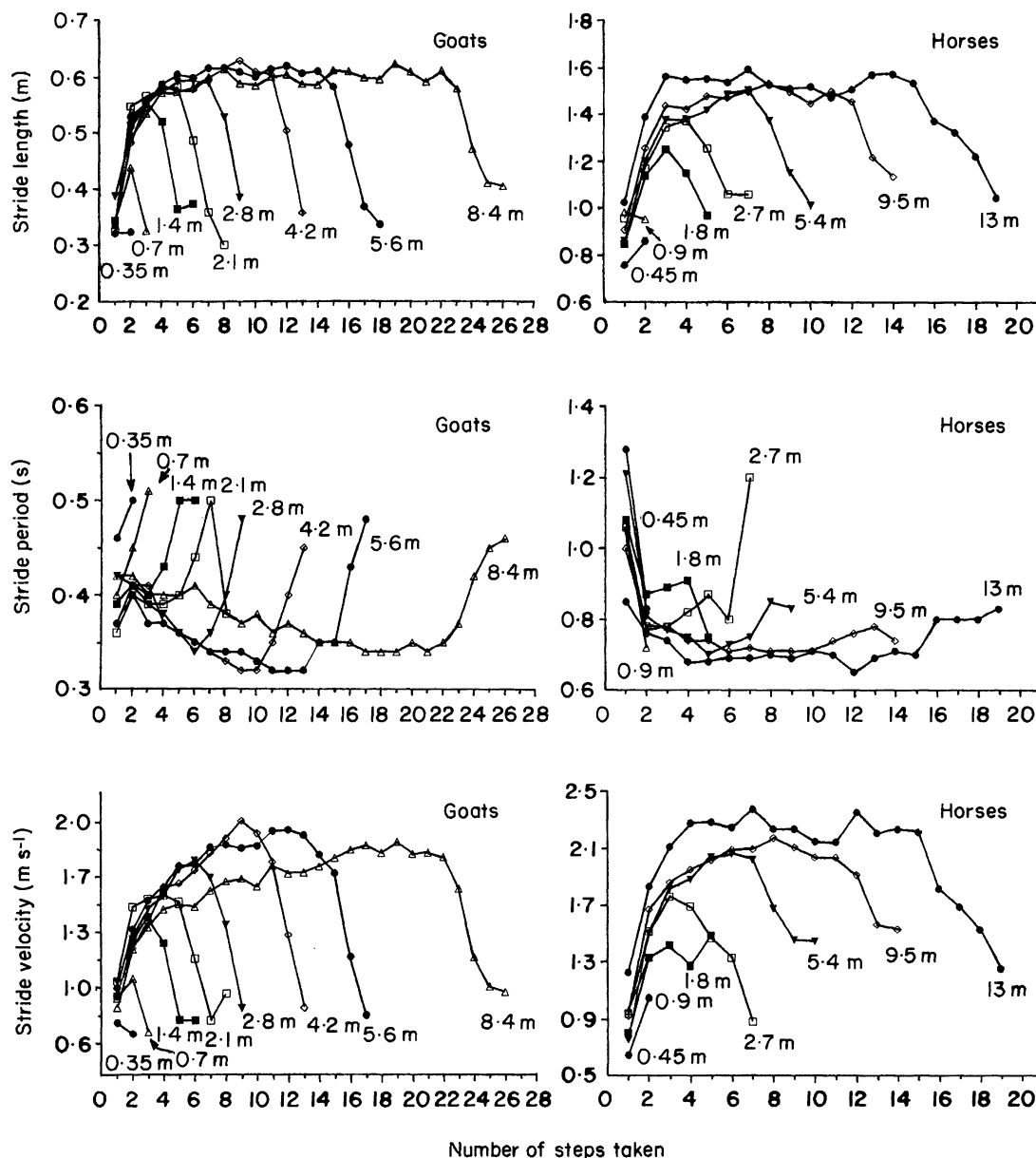

Fig. 4. An example of the relationship between instantaneous velocity (V_i) and cumulative distance between plants. Displayed are observations of instantaneous velocity averaged over intervals of 0·17 s for a White-Tailed Deer used in these experiments. Plant spacing distances were 0·35 m (shaded circles, solid line), 0·72 m (unshaded squares, dashed and dotted line), 2·5 m (shaded squares, dashed line), and 6 m (unshaded circles, dotted line).

Fig. 5. Changes in mean (a) stride length, (b) stride period, and (c) stride velocity (the quotient of stride length and stride period) in relation to the number of steps taken between plants spaced different distances apart.
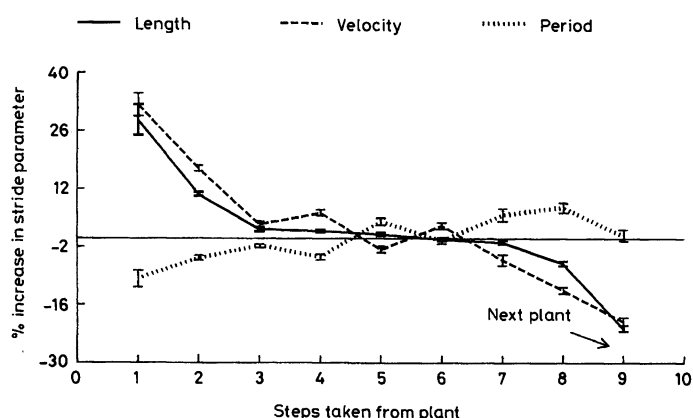

Fig. 6. The mean % increase in stride length (with standard error bars), stride period, and stride velocity for the nine herbivore species as they travelled between plants spaced nine steps apart.

Alternatively, a small animal's ability to decelerate quickly upon encountering a plant may allow it to move at a relatively higher velocity without the risk of 'overshooting' or missing plants in its foraging patch, especially if an animal's ability to detect plants is independent of the animal's size. Because the ability of the animal to detect food items declines with increasing velocity (Getty & Pulliam 1991), an animal faces trade-offs between encountering foods and detecting suitable food items. Large and small animals may require approximately the same foraging velocities to provide the best chance of detecting food items of a size scaled to that animal, while maintaining a high encounter rate.

Finally, small herbivores may move faster while foraging to optimize food intake relative to metabolic cost (Pyke 1981). When the energetic

cost of locomotion is considered, the optimal search rate is often lower than maximum walking speed (Gendron & Staddon 1983; Houston 1992). Small animals, however, must expend relatively more energy in travel than large animals because both net cost of locomotion (i.e. the energy expended above the cost of standing, $kJ\,ml^{-1}$) and energetic overhead (i.e. basal metabolic rate and the incremental cost of standing) are greater rela-

tive to size than that of large animals (Taylor *et al.* 1970; Robbins 1983). Hence, smaller animals may forage at relatively higher velocities to minimize energetic overhead cost of travel.

Differences in V_{max} observed among individuals within a species or while foraging in different plant communities is also undoubtedly shaped by predation risk, thermal constraints, perceptual acuity, and trade-offs between energy expense of travel and the energy gain of food items (Pyke 1981). Therefore we would expect both V_{max} and rate of acceleration to decline if travel becomes difficult or hindered by ground slope, vegetation, or snow. V_{max} should also vary with the apparency or detectibility of food items (Getty & Pulliam 1991). However, defining the detection ability of animals is difficult, and must include the relative ability to detect food in the perceptual radius around the head (Roese, Risentoover & Folse 1991), the contrast between the food item and the matrix (Blough 1989), and the process of forming 'search images' (Tinbergen 1960; Dawkins 1971; Reid & Shettleworth 1992). Although we have not specifically addressed detection in our experiments, relative values of V_{max} achieved by animals within a species may serve as a potential index of the apparency of food items in the foraging area.

Our results suggest that patchy distributions of food items can create non-linear changes in the foraging velocity and encounter rate of mammalian herbivores. In turn, the dynamics of foraging velocity may influence the way food patches are used by these animals. For example, if an animal must slow and stop to select a bite, and by doing so, increase foraging time and expend energy to overcome inertia when it leaves the plant, the animal may choose to exploit many bites at one 'feeding station' before moving on. Therefore the time and energy losses from acceleration and deceleration may justify the use of 'feeding station' as one possible functional definition of 'patch' for herbivores. Furthermore, scaling relationships for encounter rate, when coupled with the scaling of intake rates (Shipley *et al.* 1994), may provide a functional basis for defining patch hierarchies and resource scales for herbivore communities.
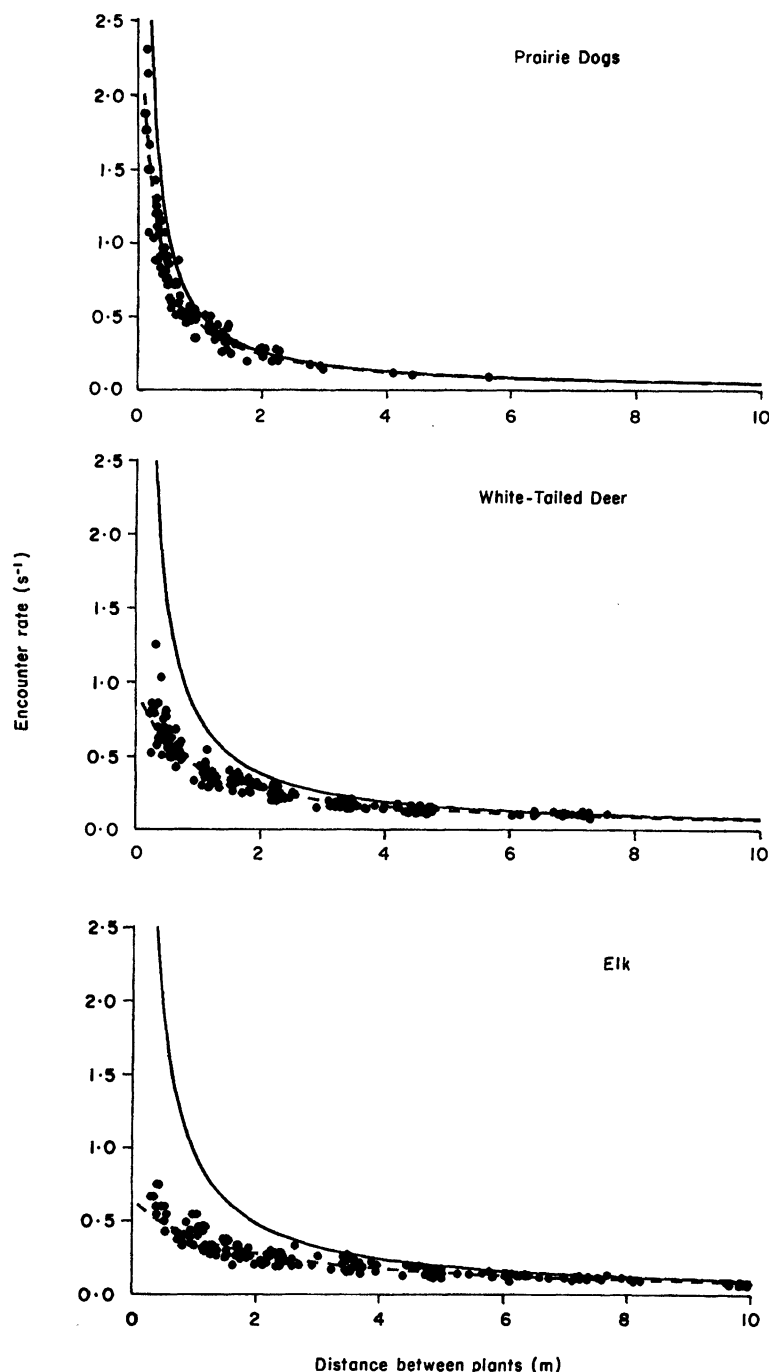

Fig. 7. Observed encounter rate (solid dots) compared with encounter rate predicted by the equation $\lambda = V_{max}/d$ (solid line) which does not account for acceleration and deceleration, and encounter rate predicted by the equation $\lambda = \bar{V}/d$, where $\bar{V}$ is calculated from equation 11 (broken line).

Acknowledgements

Table 2. Scaling of the components of foraging velocity of nine species of mammalian herbivores with body mass (M, kg) and leg length (L_1, m) using the $\log_e$ transformation of the model $Y = aM^b$

Component	Ordinary least-squares regression					Reduced major axis†
	$\log_e a$	(SE)	b	(SE)	r^2	$b + 95\%$ CI
α Body mass						
V_{max}, m s^{-1}	−0·14	0·05	0·04	0·03	0·26	–
a_o, m s^{-2}	0·22	0·07	−0·13	0·04	0·60	−0·17 ± 0·07
Stride length (L_s), m	−0·60	0·02	0·29	0·01	0·99	0·29 ± 0·02
Stride frequency (S_f), steps s^{-1}	0·43	0·04	−0·24	0·02	0·94	−0·24 ± 0·04
Leg length, m	−0·83	0·05	0·38	0·03	0·97	0·38 ± 0·04
$L_s S_f$, m s^{-1}	−0·17	0·06	0·05	0·03	0·35	0·08 ± 0·04
α Leg length						
V_{max}	−0·04	0·05	0·13	0·07	0·32	0·23 ± 0·12
a_o	−0·07	0·07	−0·35	0·13	0·65	−0·43 ± 0·20
L_s	0·04	0·03	0·76	0·04	0·98	0·77 ± 0·09
S_f	−0·09	0·05	−0·61	0·08	0·89	−0·64 ± 0·14

†Reduced major axis slopes may be calculated by dividing ordinary least-squares slopes by the correlation coefficient r (Rayner 1985).
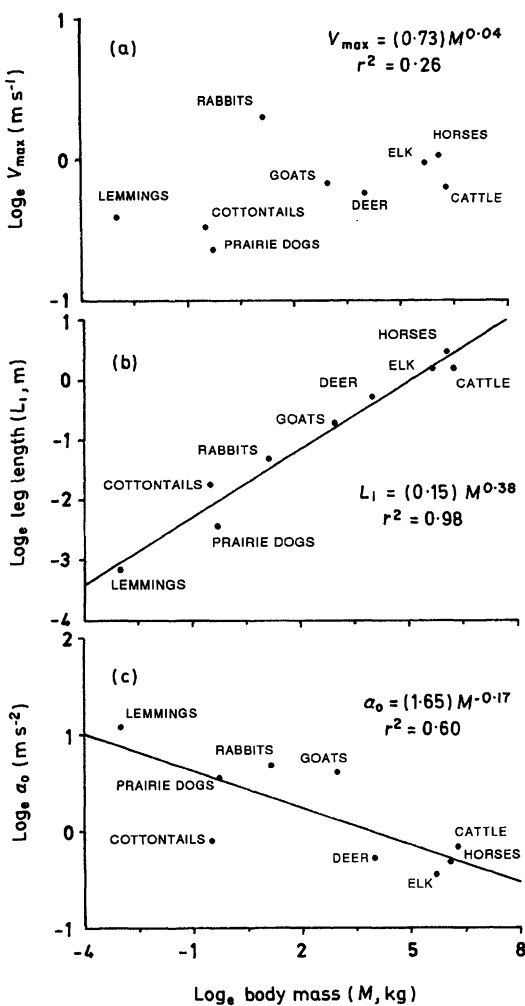

Fig. 8. Maximum sustainable foraging velocity, V_{max}, (a), leg length, L_1 (b), and acceleration, a_o (c) as a function of body mass.
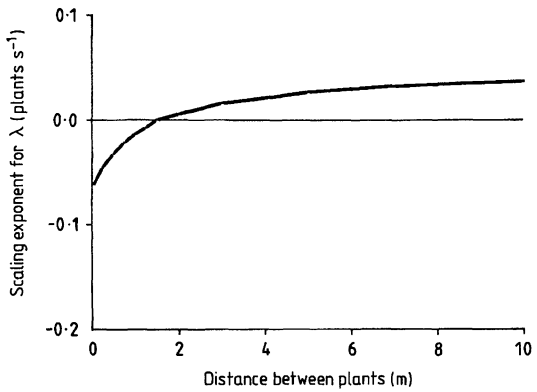

Fig. 9. The scaling exponent for encounter rate, λ as a function of the distance between plants.

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