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Interactions between the Fractal Geometry of Landscapes and Allometric Herbivory

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The scale at which herbivorous mammals forage is determined in part by home range area, population density, metabolic rate, movement speed, transport costs, and ingestion rate. These ecological, behavioral, and physiological characteristics that vary with body mass constitute the notion of allometric herbivory. In fractal landscapes, forage density varies with the scale at which animals perceive the resource. Interactions between scale-dependent resource density and allometric herbivory were investigated by using remotely sensed imagery to simulate fragmented distributions of forage biomass in an 810-ha landscape, and then simulating allometric herbivory for 2–6-kg animals. Between years, changes in landscape geometry altered foraging success. Within years, resource depletion resulted in increased aggregation among foragers followed by sudden increases in mobility and dispersion. Portions of the forage remained after the foragers shifted from the aggregation phase to one of mass dispersal. Spatial patterns of resources may regulate resource uptake and depletion rates within the landscape, with potential implications for demographics, intra-specific competition, and community assembly. © 1992 Academic Press, Inc.

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1. Introduction

Ecological phenomena such as foraging, nest parasitism, seed dispersal, and nutrient redistribution are affected by landscape pattern and dynamics (Risser *et al.*, 1984; Forman and Godron, 1986; Turner, 1989). Landscape pattern is regulated by biotic and geophysical processes (e.g., seedling establishment, fire, land use practices, and erosion) that vary with scale (Urban *et al.*, 1987). Used as an independent variable, scale may provide a surrogate for constraints that modulate ecological processes at specific levels of organization (see Allen and Starr, 1982; Rykiel *et al.*, 1988). Thus, population level phenomena such as seedling establishment may be explained by the presence of $< 1\ m^2$ sites that are safe places for germination (Harper, 1977), while the composition of communities may require information about environments spanning kilometres (Milne and Forman, 1986).

Despite the recognition of a multi-scale paradigm in ecology (Delcourt *et al.*, 1983; Senft *et al.*, 1987; Wiens, 1989), there is little quantitative theory describing how qualitative changes occur in dynamic processes as consequences of landscape pattern. Critical phenomena are well known in condensed matter physics, where matter changes phase at particular points in time or at critical temperatures or densities (e.g., Orbach, 1986). Phase changes represent fundamental reorganizations of the system and have the conceptually attractive property of being characteristics of an entire ensemble of complexly behaving particles. Much as Van der Waal used critical points to interrelate the phase transitions of different materials (Rosen, 1978), ecologists should begin searching for critical points about which to relate apparently disparate landscapes or species to one another in common terms. One goal of this paper is to define critical points for simulated ecological processes and thereby reveal fundamental properties shared by numerically different results.

Animal species vary in home range area, metabolic rates, and movement rates, and therefore operate on different temporal and spatial scales. Mandelbrot's (1983) fractal geometry implies that animals may perceive different resource densities, patch perimeter lengths, and patch sizes within a given landscape due to inter-specific variation in home range area, dispersal rate, and other factors that constitute the scale at which organisms operate (Milne *et al.*, 1989; Milne, 1990). Here, we rely on fractal geometry to represent landscape patterns in ways that are directly related to inter-specific variation in the scales at which animals operate.

The central notion in fractal geometry is that measured quantities vary as a power of the resolution at which measurements are made (Stanley, 1986). Quantities that may be distributed fractally, such as density, patch perimeter length, mass, and patch area, behave according to the general scaling law:

$$Q = kL^{f(Dq)}, \tag{1}$$

where Q is a measured quantity (e.g., mass, density), L is the length scale used to perform the measurement, $f(D_q)$ is some function of the fractal dimension D_q of Q, and k is a constant (Stanley, 1986). In this paper, $f(D_q)$ is simply D_q itself, whereas other applications require a transformation of D_q. As in Euclidean geometry, the dimension describes the tendency of the quantity, or set, to fill the space within which it occurs. For example, smooth, differentiable, Euclidean 1-dimensional lines may reside in a plane of dimension 2. Fractal sets tend to be fragmented or rough (i.e., differentiable at no point on the set), and consequently have noninteger dimensions (Voss, 1988; Feder, 1988). For example, a fragmented plane, such as the distribution of barren soil in a grassland, occupies less than the 2-dimensional space of the plane, and consequently exhibits fractal dimensions of ~ 1.8 (Wiens and Milne, 1989).

Organisms that gather resources in differently sized home ranges (e.g., Brown, 1981) may perceive differences in resource abundance. In a landscape with sparsely distributed resources, a large home range may include a greater total amount of resources than a randomly located small home range.

We constructed a model to explore the interactions between scale-dependent foraging activity and fractal landscape patterns. Our major goal was to determine how animals that forage at different ecological scales interact with heterogeneous distributions of forage. To approximate biological reality for a wide range of species, simulated foraging was governed by known allometric relationships, resource distributions were represented by remotely sensed data, and patches of available forage were represented by fractal landscape patterns. We used the empirical foundation of Peters (1983) and others to investigate the ecological implications of spatially and temporally heterogeneous landscapes.

2. The Model

The model consisted of two major parts: a simulation of vegetative pattern over the landscape and a simulation of mammalian grazing during the winter, or non-growing season. The landscape model relied on remotely sensed imagery to represent green vegetative biomass produced during the growing season. The biomass was then used as a template to simulate the spatial distributions of feeding areas that changed spatially from one winter to the next. The non-feeding areas were barriers that restricted foragers' access to food. The foraging model was based on allometric relationships between body mass and several ecological, metabolic, and behavioral characteristics of animals.

Landscape Patterns and Simulation

Biomass distributions of forage were represented by remotely sensed data obtained from the Landsat Thematic Mapper (TM) sensor. Data were collected 10 September 1987 over the 100,000-ha Sevilleta National Wildlife Refuge (Long Term Ecological Research site), 110 km south of Albuquerque, New Mexico (Milne, 1990). The Sevilleta receives approximately half its total annual precipitation from July to September. Thus, biomass estimates from September imagery represent the standing crop biomass available during the winter foraging season.

An estimate of the energy available in green vegetative standing crop biomass (joules $g^{-1}m^{-2}$) was derived from the TM data as the ratio between radiance measured in the near-infrared (TM band 4) and the red parts of the spectrum (TM band 3; Goetz *et al.*, 1985). Limited direct measurements of standing crop biomass were available for two sites, so a linear regression was made between the standing crop of oven-dried green biomass and the TM 4/3 ratio. Biomass estimates were transformed into units of usable J/g, based on the percentages of carbohydrates, proteins, and fats in *Bouteloua gracilis* (Morrison, 1947), a dominant grass species in the Sevilleta. The J/g were weighted by the specific dynamic action (Peters, 1983, p. 105) for each type of molecule to yield the total net J/g obtained by foragers.

To investigate the implications of landscape change on forager activity, three winter seasons (180 days each) were simulated for one landscape. Biomass was renewed to the same initial distribution at the start of each winter. Thus, there was no annual variation in the initial distribution and total abundance of forage biomass. However, access to particular grams of forage varied between years.

Foraging was restricted by fragmented patches that served as barriers within the landscape. In nature, barriers occur when snow covers portions of the winter range, or when particular conditions of tree cover or slope aspect provide an inappropriate thermal regime for foraging.

The patterning of barriers and feeding areas changed over the three years of the simulation according to a simple scenario. The probability p that feeding areas occurred on the landscape during a given year followed a Gaussian distribution with a mean centred in the second year of a three-year time line. For the first year, p was used to divide the unit interval into two bins, from 0 to p (feeding area) and from p to 1 (barrier). Each TM 4/3 ratio representing biomass was divided by the maximum ratio observed to yield a number from 0 and 1, inclusive. Thus, each ratio was located in one of the two bins on the unit interval, and the corresponding state (i.e., feeding area or barrier) was mapped onto the landscape. A similar strategy was used for year 3 except that the bins were reversed, with the first bin (barrier) of width $1 - p$ and the second bin (feeding area) ranging from p to 1. During year 2, three bins were required, with the middle bin representing the barriers and the distal bins representing feeding areas. Spatial autocorrelation in the TM ratios produced realistic aggregation (e.g., Gardner *et al.*, 1987) and a temporally shifting mosaic pattern in the feeding areas.

Scale-Dependent Landscape Pattern

Spatial autocorrelation may produce consistent changes in resource density with changes in scale (Burrough, 1981; Mandelbrot, 1983; Stanley, 1986). The fractal patterns of the feeding areas created in the landscape simulation were characterized using a probability density function that described aggregation. Following Voss (1988), feeding areas were measured each winter by centering sampling windows of length L on each feeding pixel (Fig. 1), and then counting the number of feeding pixels m in the

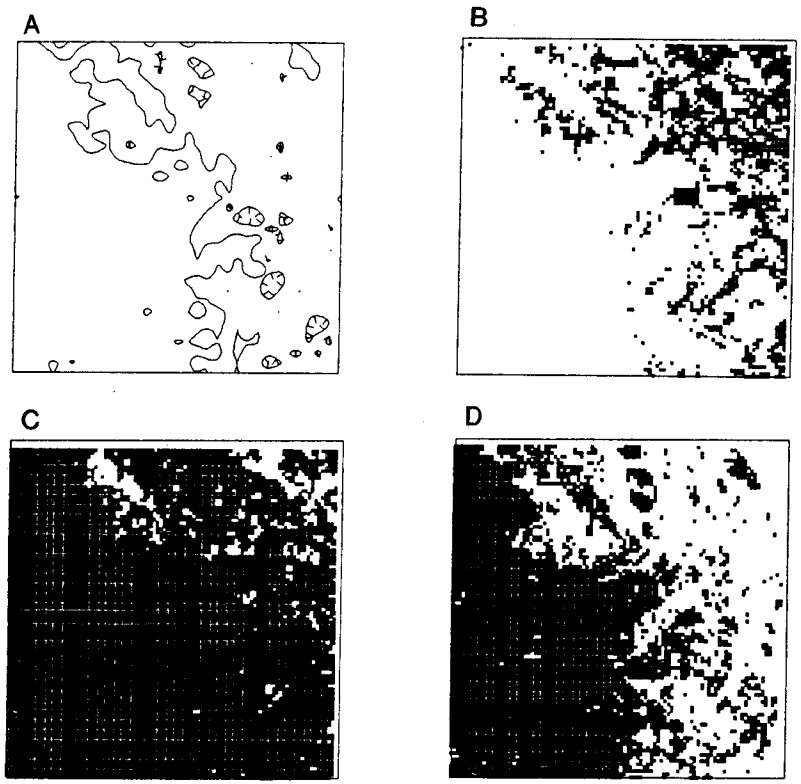

FIG. 1. Distributions of available joules and feeding areas; (A) isopleths represent locations containing the mean number of joules available during the first foraging bout of each winter. (B) Feeding areas (shaded cells) in year 1, (C) year 2, (D) year 3.

window. Thus, the probability density function, pdf, $P(m, L)$ gives the probability of finding m pixels in a window of length L (Voss, 1988). The pdf has moments generated by

$$M(L)^q = \sum_{m=1}^{N(L)} m^q P(m, L), \tag{2}$$

where $M(L)^q$ is the qth moment and $N(L)$ is the maximum value of m observed in windows of length L. Moments vary with L according to

$$[M(L)^q]^{1/q} = kL^{Dq}, \tag{3}$$

where the left hand side is analogous to Q in Eq. (1). Thus for $q=1$ the exponent of Eq. (3) is the so-called mass fractal dimension of the set (Voss, 1988, provides examples of other kinds of fractal dimensions as well). We used the mass dimension because it is sensitive to the spatial dependence of the feeding areas, whereas other fractal dimensions are less sensitive to spatial aggregation per se.

Moments for $q>1$ are sensitive to the preponderance of densely filled windows. Conversely, moments generated using $q \leqslant -1$ are sensitive to the preponderance of sparsely populated windows, and yield small exponents [Eq. 3] for fragmented patterns. Windows containing m pixels for which $m^q P(m, L)$ is large are places in the landscape where the geometry of the feeding areas contributes strongly to the qth moment [Eq. 2]. The spectrum of exponents for various values of q indicates the diversity of pixel configurations and the relative contribution of gaps and clusters to the statistical properties of the pattern.

Allometric Herbivory

Allometric relationships based on animal body mass were used to control animal density, home range size, metabolic rate, ingestion rate, speed, total cost of moving from one home range to another, the number of foraging bouts per winter (a bout is a unit of time during which ingestion occurs), and the number of visits to foraging locations within a home range during a bout (Fig. 2). First, the relationship between body mass and the density of mammals in the temperate zone (Peters, 1983, p. 294) was used to determine the number of foragers allocated to the 810-ha landscape. Then, the allometric relationship for home-range area (Harestad and Bunnell, 1979) was used to allocate an initial square foraging area to each animal. Animals were placed randomly on the landscape, contingent on the home ranges being contained within the landscape boundary.

The 180-day winter was divided by bout length (i.e., bout length was the

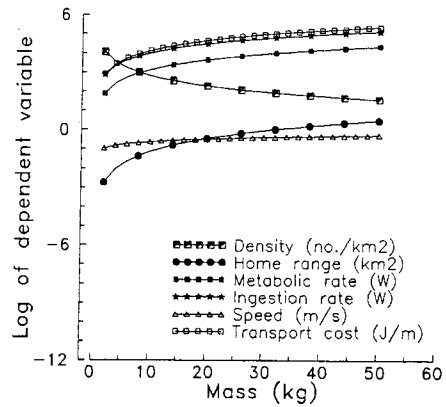

FIG. 2. Allometric relationships used to regulate herbivory. The ordinate represents each of the following: density (Peters 1983, p. 294), home range (from Harestad and Bunnel, 1979; cited in Peters 1983, p. 296), metabolic rate (Stahl, 1967), ingestion rate (Farlow, 1976), speed (Buddenbrock, 1934), and transport cost (Taylor, 1977).

allometric "minimum observation time" of Swihart *et al.*, 1988) to provide a mass-dependent number of bouts per winter, and thereby create a mass-dependent rate at which the foraging success of animals was evaluated. A preliminary simulation was conducted before the actual foraging simulation to determine the average number of visits each forager could make to random locations within the home range, given the length of the bout and the total travel distance possible by an animal of a certain mass (Buddenbrock, 1934; cited in Peters, 1983). Thus, even though random movements within the home range were simulated for convenience, the total distance traveled and the energy expended in moving were appropriate for the animal. The net energy gained by individuals was determined by metabolic costs (Stahl, 1967) and ingestion (Peters, 1983). Intraspecific competition was incorporated by allowing $\geqslant 2$ individuals to forage in the same pixel during a visit.

The home ranges of the animals were moved about the landscape when the metabolic and transport costs during a bout exceeded the energy gained by ingestion. Animals with energy deficits were moved in a random cardinal direction for distances $\leqslant 1.5$ times the width of the home range.

We expected that the allometric foraging rules would interact in complex ways with the landscape pattern. We further thought it possible to perform a transformation of time and of the energy available to the animals in order to relate the apparently disparate dynamics of the species directly to one another. We intended the transformation to reveal the commonalityof the allometric rules, despite the apparent differences in the numerical responses

of the species. A successful transformation would enable studies conducted in various landscapes to be interrelated, and thereby to reveal fundamentally similar rules used by many species.

Within-winter phase transitions in foraging during year 1 were examined relative to two state variables: total joules available in the feeding area and time. The temporal critical point t_{crit} was defined as the time when the percentage of animals moving in search of better home ranges reached the minimum for year 1, which was the only year with a unique minimum value for the percentage of animals moving, and therefore the only year for which phase transitions were examined. The criterion of minimum movement was used because it characterized a fundamental and discrete change in the foraging energetics of the populations, namely a switch from a phase of aggregation (i.e., decreasing percentage of animals moving) to one of population dispersal driven by the depletion of resources, i.e., increasing percentage of animals moving. The energy critical point J_{crit} was the total number of joules available in the feeding area at t_{crit}. By happenstance, t_{crit} and J_{crit} occurred at different times for each species. The critical values were used to normalize the energetics of animals of different body mass by dividing the total joules available at the start of each bout by J_{crit} and time by t_{crit}. Interested readers should see Zallen (1983) for a discussion of this normalization approach.

Three artificial characteristics enhanced the value of the simulations for understanding the interactions between landscape pattern and foraging. First, animals maintained a constant weight that was the same for all individuals on the landscape during a particular simulation. The allometric relations for the ecological behaviors and metabolic rates are robust over several orders of magnitude body mass, but have substantial variances over short ranges of mass. Thus, attempts to refine the mass-dependent behavior of individuals by allowing mass to fluctuate seemed unwarranted. Second, no mortality occurred over the duration of the simulations. By monitoring the activity of animals that reached starvation conditions, major transitions in the collective behavior of foragers appeared and revealed additional mass-dependent interactions between foragers and the landscape patterns. Finally, by focusing on winter range conditions, we eliminated potential complexity due to animal reproduction and plant growth.

3. Simulation Results

The simulations of landscape change and allometric herbivory revealed: (1) striking between-year changes in the geometry of the feeding areas, (2) between-year changes in the movement patterns of animals, (3) within-year phase transitions as the foragers shifted from a phase of increasing aggregation to one of dispersion in search of forage, and (4) forage "refugia" which persisted after the foragers shifted to the dispersal mode.

Changes in Landscape Geometry

The pattern of feeding areas changed annually (Fig. 1) with accompanying changes in the fractal geomtry of the patterns. The landscapes in years 1 and 3 exhibited greater fragmentation than the landscape in year 2, which essentially filled the plane at a fractal dimension of 1.99 (s.e. = 0.009). In years 1 and 3, feeding areas had fractal dimensions of 1.68 (s.e. = 0.001) and 1.93 (s.e. = 0.001), respectively, indicating relatively high fragmentation in year 1 and less fragmentation in year 3. Changes in the pattern of feeding areas obtained directly from the temporal change in the probabilities for the feeding areas and the distribution of biomass, and were not due to the foragers.

The scaling exponents for the moments of the $P(m, L)$ distributions provided a sensitive measure of the geometry of the feeding areas (Fig. 3). Feeding areas in year 2 had large exponents [Eq. 3] for negative values of q, indicating the relatively greater importance of gaps in the mosaic than in years 1 and 3. In the temporal progression from year 1 to 2 to 3, the landscape changed from fragmented, to nearly uniform, and back to fragmented.

Phase Transitions in Animal Movements

The movements and energetics of animals varied according to both the body mass of the animal and the pattern of forage the animals were

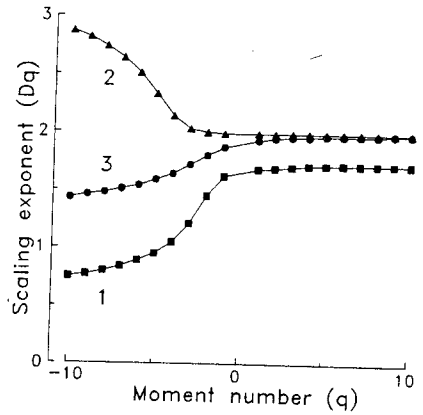

FIG. 3. Scaling exponents of the qth root of the qth moments of feeding areas during the three winter seasons. The exponents at $q = 1$ are the "mass" fractal dimensions of the patch mosaics.

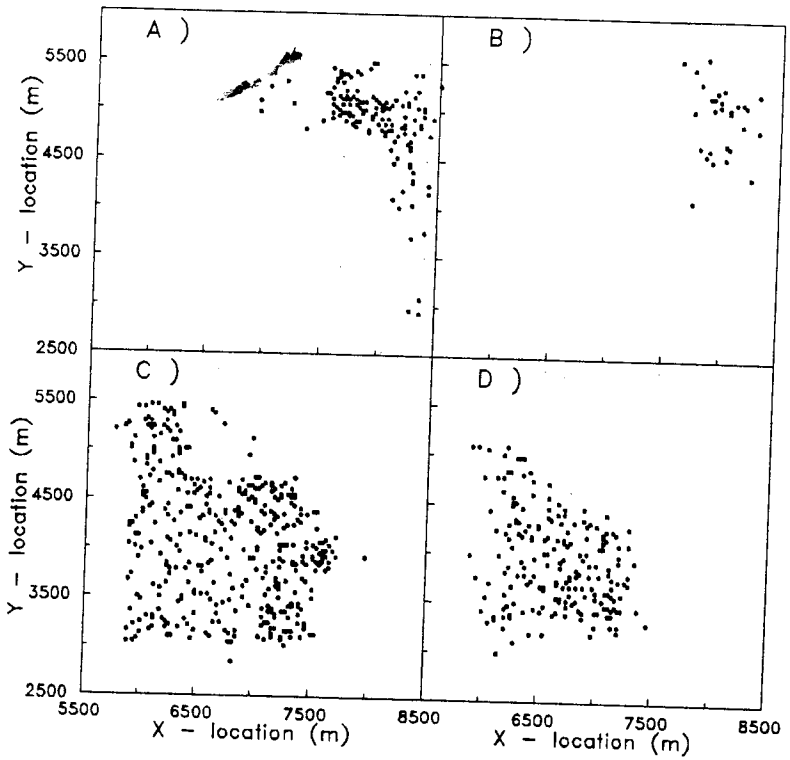

FIG. 4. Locations of animals with favorable energy balances (stationary home ranges) during the bout that yielded the maximum total gain in energy in years 1 and 2: (A) locations of 2-kg animals, year 1; (B) 6-kg animals, year 1; (C) 2-kg, year 3; (D) 6-kg, year 3.

allowed to consume. Beginning at random locations at the start of each winter, animals with net energy losses moved randomly until they lodged in locations that yielded positive energy balances. Eventually, successful foragers became aggregated (Fig. 4) in regions corresponding to the distribution of feeding areas (Fig. 1). The vagaries of the random walks toward the favorable feeding sites implied that: (1) food was consumed over the course of the walk, thereby altering the food available to other animals, and (2) some favorable feeding sites were not depleted while animals aggregated in, and depleted, other favorable sites.

During the first winter, 3 kg animals exhibited a period of relatively sedentary behavior followed by increasing dispersion and mobility (Fig. 5a). At first, the animals lodged within rich food patches until the resources within their home ranges were depleted. They then moved

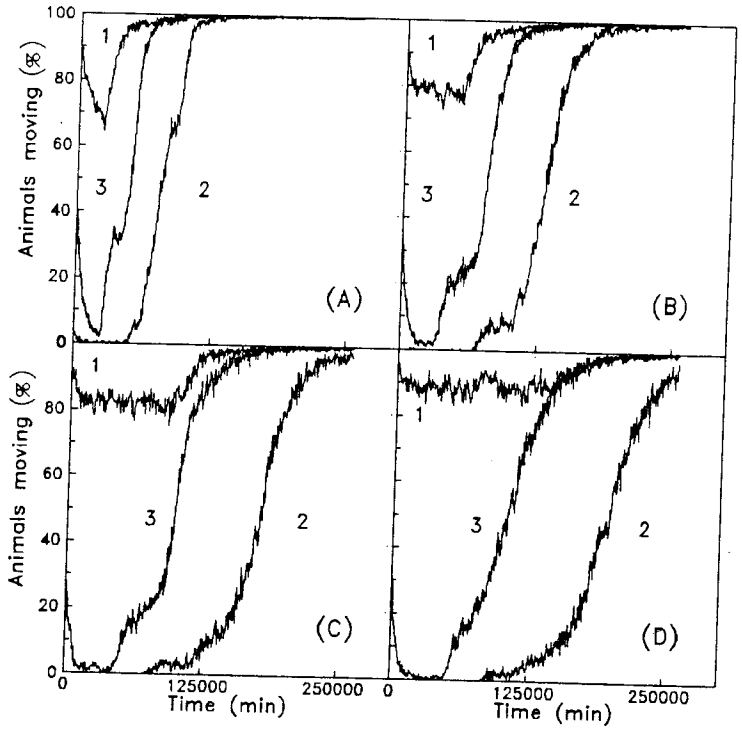

FIG. 5. Dynamics of the animals (% of total) moving in search of more favorable home range locations. Curves labelled according to year: (A) 3-kg animals; (B) 4.5-kg; (C) 5.5-kg; (D) 6-kg.

randomly until they encountered richer patches, if any. At the end of the winter, virtually 100% of the individuals were moving in search of food and consequently were no longer aggregated as in Fig. 4.

During the first winter, the more massive animals exhibited longer periods of relative immobility than the lighter animals (Fig. 5). The curves for the third year had prominent jagged regions in the ascending part of the curve, corresponding to a temporary slowing of the increase in mobility as animals encountered isolated patches of available forage in the more fragmented regions of the landscape (Fig. 1(d)). Once the forage was exhausted in these patches, the animals continued steadily to increase in mobility until reaching an asymptote at 100% mobility.

Species varied in the duration of the aggregation phase, the absolute percentage of animals moving at the end of the aggregation phase, and in the rate at which the population approached 100% mobility (Fig. 5). We

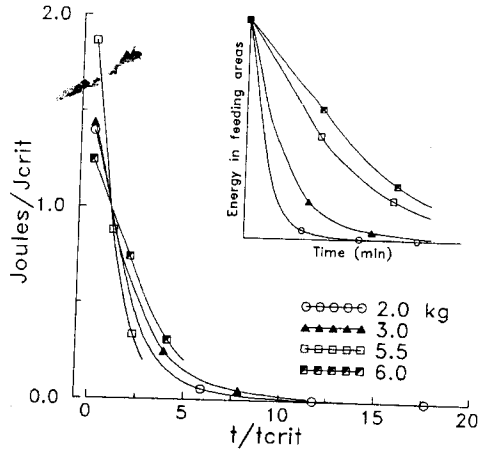

FIG. 6. Phase plane of the normalized energetics and time sequences for year 1. The ordinate shows the joules available in feeding areas divided by the joules available during the bout in which the % of animals moving their home ranges reached a minimum (i.e., the critical point). The abscissa is time divided by the time at which the critical point occurred. Symbols indicate every 200th bout. The inset shows the untransformed trajectories.

standardized the apparently disparate patterns of the species by dividing the number of joules present in the feeding areas at the start of each bout by the number of joules present at the critical point (i.e., joules/J_{crit}), and by a similar treatment of the time axis (Fig. 6). By definition, the standardization forced each curve through the point (1, 1) corresponding to the critical point, i.e., joules/$J_{crit} = 1$ and $t/t_{crit} = 1$. The curves approached the critical point from the upper left corner of the graph because the total joules available decreased monotonically from the first bout. By placing the symbols on the curves at every 200th bout, the lack of vertical alignment of the symbols revealed the extent of the temporal rescaling accomplished by the transformation (Fig. 6). Thus, the rescaled curves adjusted for the lack of temporal alignment between the critical points of the various species.

The intercepts of the rescaled curves varied with body mass, unlike the intercepts of the untransformed curves. Variation among intercepts represented either: (1) differences among species in the effective abundance of forage perceived by the populations at the beginning of the winter, or (2) an artifact due to the somewhat unsophisticated method of determining the critical point. Stochastic variation in the percent of animals moving may have made the absolute minimum percent of moving animals a poorer criterion for the critical point than some other criterion, e.g., the minimum of a running average. In short, the standardization "stretched" or

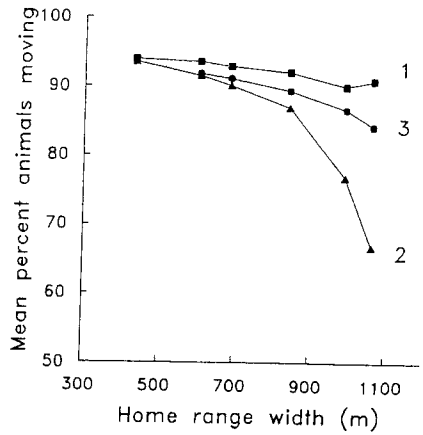

FIG. 7. Scaling of the mean percent of animals moving in search of favorable home range locations during the three years.

"contracted" the energy and time axes for each species relative to the species' critical point.

Some of the standing crop remained even after the animals switched from an aggregation phase to a mobile phase. From the standpoint of the forage, there remained forage "refugia" that escaped predation during part of the aggregation phase. Thus, even though negative energy balances prompted animals to become mobile, forage biomass remained temporarily unused on the landscapes.

There were inter-annual effects on the mass-dependent tendency of animals to move about the landscape in search of food (Fig. 7). Scale-dependent foraging success was represented by the average percent of animals moving as a function of the square root of the home range area, i.e., a length scale. After fitting power functions to the curves (Fig. 7), t-tests indicated that the slopes for years 1 and 3 were significantly different from the slope found for year 2 (1 vs. 2, $t = 5.9$, $p < 0.025$; 1 vs. 3, $t = 3.7$, $p < 0.025$). Animals with large home ranges moved less (found food more readily) than smaller animals, and this effect was most pronounced in year 2 (Fig. 7).

The shift from a fragmented to uniform landscape pattern essentially eliminated the aggregation phase of the within-year foraging movements (Fig. 5). Uniform distributions of feeding areas during year 2 enabled foragers to find resources immediately at the beginning of the winter. Foragers depleted resources until the mean number of joules per home range was less than the amount needed to ensure a positive energy balance. Then, as for years 1 and 3, the percent of mobile animals grew logistically

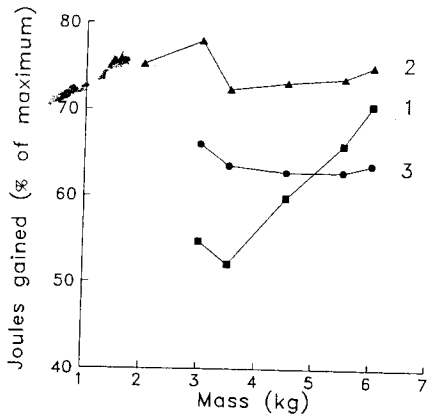

FIG. 8. Mean energetic gain in each of the three years.

(e.g., Fig. 5(d), year 1 vs. 2), indicating that animals remained stationary longer when initial resource levels were high.

Finally, the mean energy gains, as a function of animal mass (Fig. 8), indicated possible interactions between the distribution of the feeding areas and the underlying heterogeneous distribution of forage. If forage were distributed uniformly, Fig. 8 would have resembled Fig. 7, due to the strict correspondence between the locations animals were allowed to graze and the distribution of forage. However, the remotely sensed representation of forage biomass imparted heterogeneity to the resource within the feeding areas, thereby making the feeding areas an incomplete representation of forage spatial patterning.

In summary, the patterning of feeding areas changed from highly fragmented, to uniform, and back again to fragmented. The animals exhibited strong transitions from sedentary to mobile, and the transitions indicated changes in the energetics of the population. The average foraging success of individuals varied between species as a function of body mass.

4. Discussion

The simulations illustrated several novel characteristics of landscape pattern and interactions between foragers and the landscape. The transition from aggregated foraging to increased dispersion was modified by landscape pattern, and it was modified further by the scale at which the foragers operated (Fig. 5). By switching from stationary to mobile, foragers effectively increased the scale at which they searched, yielding greater gains per unit time than would be netted by stationary animals in an energetically poor landscape. The increase in movement rates represented a potentially adaptive rescaling of foraging, not unlike the nomadic movement exhibited by ungulates.

We found a relationship between the geometry of the feeding areas (Fig. 3) and the movement tendencies of the animals (Fig. 7). The curves in both cases were ranked similarly along the ordinate. Years 1 and 3 exhibited greater similarity to each other than to year 2. The dense feeding areas in year 2 and the ecological characteristics of large animals (Fig. 2) enabled large animals to maintain stationary home ranges (Fig. 5). The more fragmented geometries in years 1 and 3 tended to mobilize animals of all body sizes, because home ranges of all sizes contained relatively small foraging areas [Eq. 3]. Thus, the fractal characterization of the landscape (Fig. 3) may be a good predictor of a species' foraging success, and we expect to see greater differences among species as the range of body mass values increases.

Enhancement of the model may produce other behaviors found in natural populations. By adding allometric reproduction (Peters, 1983), we would expect to observe selection for species with high reproductive rates that compensate for the rapid depletion of resources by small, densely populated species. In contrast, given the exponentially greater energetic costs of reproduction in larger animals, we would expect to see selection for mobility and herding behavior, rather than high fecundity. Thus, interactions between sparse resources and physiological constraints could produce quite different selective pressures for organisms of different body mass.

Forage biomass refugia emerged due to an interaction between the movements of animals and the landscape pattern. For example, during the third winter, nearly 1.8×10^{12} J remained within the allowable foraging sites after the 3-kg species switched from the aggregation to mobile phase (Fig. 6). Seedlings of species that seldom reproduce sexually due to herbivory (e.g., *Populus tremuloides*) may escape predation by virtue of the fragmented distribution of the seedlings (e.g., Mueggler and Bartos, 1977). The probability that a plant occupies a refugium will vary inversely with the scale at which the predator operates (see Fahrig and Paloheimo, 1988).

We anticipate that by allowing many species to forage simultaneously, the model will reveal scale-dependent interspecific competitive effects in which the outcome of competition will be modified by the geometry of the landscape. If so, particular landscapes may be most suitable to species operating at some scales and not others. The challenge will be to predict the competitive dominants from knowledge of resource geometry. Adding allometric recruitment, mortality, and predation (e.g., Peters, 1983) to the model could make the richness of the interactions between landscape pattern, dynamics, and body mass very complex. The fractal geometry of

landscapes (Milne, 1988; O'Neill *et al.*, 1988) and scale-dependent variation in organismal perceptions of resource density could regulate demographics, foraging success, and the assembly of communities.

Models of this type are needed to understand the possible consequences of dynamic landscape mosaics that affect many ecological interactions (Milne, 1991). Similarly, studies of biotic diversity may benefit from a scale-sensitive characterization of ecological interactions that are modified by the fractal geometry of landscapes.

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