Movement rules for herbivores in spatially heterogeneous environments: responses to small scale pattern

John E. Gross[1], Colleen Zank[2,3], N. Thompson Hobbs[1,2] and Donald E. Spalinger[4]
[1]Natural Resource Ecology Laboratory, Colorado State University, Ft. Collins, CO 80523, U.S.A.;
[2]Mammals Research Section, Colorado Division of Wildlife, 316 West Prospect, Ft. Collins, CO 80526, U.S.A.; [3]Current address: POB 72478, Parkview 2122, Johannesburg, South Africa; [4]Texas Agricultural Experiment Station, Texas A&M University, 1619 Garner Field Road, Uvalde, TX 78801, U.S.A.

Foraging herbivores respond to the spatial pattern of resources at a variety of scales. At small scales of space and time, existing models capture the essence of the feeding process and successfully predict intake rates. Models that operate over larger scales have not exhibited a similar success, in part because we have a limited understanding of the rules used by animals to make decisions in spatially complex environments, or of the consequences of departing from these rules. To evaluate the rules that large herbivores use when navigating between forages, we examined movements of bighorn sheep foraging on apparent prey (alfalfa plants) in hand-constructed patches of plants. Observations of movements and path lengths were compared to simulations that used a variety of different rules-of-thumb to determine a search path. Rules used in simulations ranged from a random walk with various detection distances, to more complicated rules that solved a variant of the travelling salesman problem. Simulations of a random walk yielded movement lengths that exceeded observations by a factor of 3 for long detection distances, and by 30-fold for short detection distances. Observed move distances were most closely approximated by simulations based on a nearest-neighbor rule — over 75% of all moves by bighorn sheep were to the closest available plant. Movement rules based on random walks are clearly inappropriate for many herbivores that typically consume visually apparent plants, and we suggest the use of a nearest-neighbor rule for modelling foraging by large herbivores.

1. Introduction

Foraging by large herbivores influences the structure and function of ecosystems by altering the dynamics of plant communities (Ellison 1960, Norton-Griffiths 1979, Mack and Thompson 1982, Gessaman and MacMahon 1984, Milchunas and Lauenroth 1993, Dodd 1994), by modifying the distribution and turnover of nutrients (Hobbs and Schimel 1984, Schimel et al. 1986, Jaramillo and Detling 1988, McNaughton et al. 1988, Pastor et al. 1988, Ruess and McNaughton 1988, Hobbs et al. 1991, Pastor and Naiman 1992), and by affecting disturbance regimes, particularly the frequency and intensity of fires (Madany and West 1983, Mills 1983, Hobbs et al. 1991). In addition, the mobility of herbivores allows them to create and maintain spatial variation in these processes at a variety of scales (Laws 1970, Belsky 1984, McNaughton 1985, Hobbs et al. 1991, Jaramillo and Detling 1992). Thus, understanding herbivore movements emerges as an important component for understanding spatial heterogeneity in natural landscapes (McNaughton 1985, Detling 1988, Schlesinger et al. 1990, Pastor and Naiman 1992).

Landscape-level models of ecological processes portray the causes and consequences of spatial pattern. This portrayal often requires depicting the movements of large herbivores in some reasonable fashion (e.g., directed movement; Hyman et al.

1991, Turner *et al.* 1993). Abstractions of herbivore movement can be derived from understanding the rules that animals use to navigate among resources (Senft *et al.* 1987). However, empirical studies of movement rules of foragers have emphasized observations of predators searching for prey that are either cryptic (Holling 1959, Holling 1965, Smith 1974, Zach and Falls 1976, Speakman 1986) or predators searching for a food that cannot be evaluated prior to actual consumption (Pyke 1981, Wolf and Hainsworth 1991). This situation, common to animals that might be described as traditional predators, obviously does not apply to herbivores feeding on plants that are visually apparent. Here, we focus on evaluating rules-of-thumb that ungulates or other visually-oriented predators might use to travel between isolated, but apparent, plants or patches of food.

The time and cost of travelling between food items can be substantial, even when a forager can readily locate and move directly between foods. In this case benefits may be maximized primarily by reducing travel costs, rather than by careful selection for item size or quality. Thus, to maximize intake rate the foraging animal would need to solve a variant of the 'traveling salesman problem', identifying the shortest path that visits a number of discrete locations. This is an extremely difficult problem to solve when there are relatively few items, and it becomes logistically impossible to solve as the number of stops increases (see Anderson 1983 for a non-technical discussion such analytically intractable problems). Animals are typically confronted with a spatially complex environment containing many potential foods, and they are limited in their ability to collect, synthesize, and analyze information (Real 1991). Because cognitive processing abilities are limited, it is likely that foraging animals use parsimonious rules-of-thumb to navigate between foods.

We evaluated the consequences of using relatively simple rules-of-thumb for moving between foods. We did this by simulating the paths that animals would use to move between plants and comparing these model predictions to the paths taken by bighorn sheep (*Ovis canadensis*). Our analysis is restricted to patches where all food items are of equal quality (size, nutrient content, etc.) and are readily apparent when they fall within the visual range of the forager.

2. Methods

2.1. Animals and experimental apparatus

We evaluated the movement patters of bighorn sheep foraging on hand assembled patches of plants that differed in dispersion pattern. Feeding trials were conducted within a fenced field (approximately 50 m x 85 m) in which we placed 36 individual alfalfa (*Medicago sativa L.*) plants at specific coordinates within a central area of 40 m by 70 m. No plants were within 5 m of any fence. At each coordinate an individual plant was placed in a plastic pipe (18 mm diameter by 7.5 cm long) attached to a metal rod that was driven into the ground. Plants were held firmly by a rubber stopper pressed into the pipe from below. Each plant was numbered with a tag that could be seen from at least 15 m. All existing vegetation in the field was mowed to a very short height.

The alfalfa plants we presented to sheep were trimmed to a uniform size (30 cm tall; 1 g of dry matter) and visual appearance. The distance between plants in the hand-constructed patches we used in feeding trials were very close to those calculated from computer-generated plant coordinates (average difference between measured and calculated distance = 2.5 cm, [1.0% of the actual distance], $n = 32$).

The locations of individual plants in patches were determined by independently choosing x and y coordinates from a uniform random distribution. We created two patch types, a 'random' type that contained 36 independent plant locations, and a 'clumped' type that consisted of 12 randomly chosen points, around which we randomly distributed 3 plants within 5 m of the point. Seven different patterns of plant distribution (4 random and 3 clumped patterns) were created and each pattern was used for two consecutive days. Subsequent analyses of plant patches failed to detect significant differences in the distribution of plants, thus we

grouped all data together. Overall, the patches used in foraging trials are described by the equation:

$$E(n,L) = k_p(L)^{d_p}$$

where E(n,L) is the expected number of plants within an L x L (m) square, and is described by a density constant, k_p (plants/m²), and the fractal dimension, d_p (dimensionless), (Schroeder 1991:220). For our patches, k_p averaged −3.84 (se = 0.25), and d_p averaged 1.93 (se = 0.07), indicating that we achieved a nearly random distribution of plants in the foraging arena.

All foraging trials were conducted at the Colorado Division of Wildlife Foothills Wildlife Research Facility (Fort Collins, Colorado) during October and November, 1992. We used captive-reared bighorn sheep ewes (N = 7; body mass = 74−87 kg) fed a basal diet of dried alfalfa hay supplemented once weekly with concentrate pellets. To ensure an interest in feeding, we removed food from the animals overnight and conducted trials from 07:00−10:30 hrs each morning. Before data collection, all animals were habituated to the experimental apparatus and fresh alfalfa used in all feeding trials.

2.2 Behavioral measurements

We initiated feeding trials by introducing a single bighorn sheep into the foraging area from a holding pen located at one end of the arena. Data collection began when the animal took its first bite. We subsequently recorded the number of each plant visited, the time of arrival at the plant, and an index of the path taken to the plant (see below).

We recorded two measures of the distance travelled between plants. First, we simply calculated the straight-line distance between plants, based on their respective coordinates. To estimate the actual distance travelled by an animal, we assigned each move an index from 1 to 4 based on the curvature of the path. An index of 1 represented a straight line, and indices of 2, 3, and 4 represented arcs that substended 30, 50, or 180 degrees of a circle. Using these indices, we multiplied the direct-

line path distance by 1.00, 1.032, 1.252, or 1.571 to estimate the actual distance travelled. Trials were restarted at the animal's current location if an animal was temporarily distracted but then continued feeding. We ended trials when a sheep either lost interest in foraging on the alfalfa plants or when an animal had consumed most of the plants and clearly had difficulty locating an uneaten plant (e.g., all ungrazed plants were far away). We conducted 1 trial per animal each day.

2.3 Modelling approach

Our analyses apply to the relatively simple situation of an animal foraging in a patch populated by plants that are essentially identical in value and apparency. We assume that a plant is completely consumed when visited by an animal, and it does not regenerate over the period of a feeding bout. Thus, there is no reward associated with revisiting a plant, and an animal will achieve the greatest overall reward and the greatest reward rate by visiting all plants exactly once, using the shortest path between the plants. We assume that the cost of foraging is proportional to the distance moved, and that the reward of eating a plant is always greater than the cost of moving to that plant.

The spectrum of rules that could describe the movements of animals between foods is bounded at one extreme by a random walk (RW), and at the other by the shortest possible path to all available items, the travelling salesman (TS) solution. Our TS rule differs slightly from the classical travelling salesman problem because it does not require the animal to return to the point of origin. Between the RW and TS rules exist a myriad of strategies that include a correlated random walk, a spiral or systematic search, and what we call a 'moving window' rule (MW; similar to the 'L-step look-ahead'; Altmann 1974, Anderson 1983). The MW strategy is a variant of the TS rule, and is employed as follows. An animal looks ahead from its current location and evaluates all potential paths to n items (MW-n). It then chooses the shortest path, moves to the n plants and 'consumes' them, and continues by repeating the process. If there are fewer than n
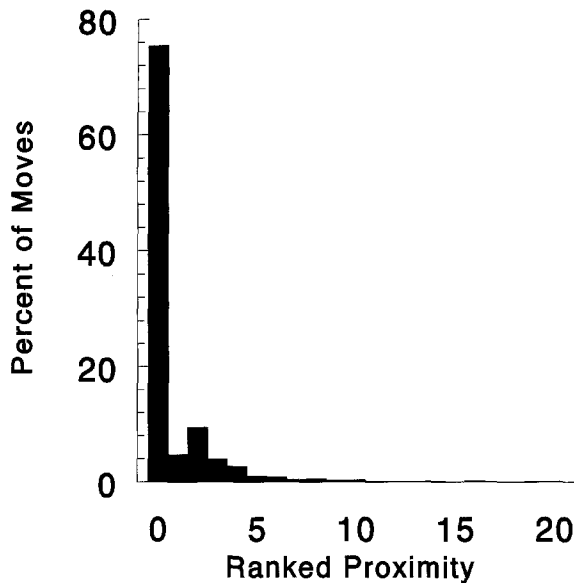
Fig. 1. The percentage of moves by bighorn sheep in feeding trials to plants ranked by their proximity to the animal. The nearest-neighbor plant was assigned a rank of 1, the second-closest plant was assigned a rank of 2, etc.

Fig. 2. Frequency distribution of move distances by bighorn sheep foraging on alfalfa plants. Sheep rarely moved to a plant more than 10 m away.

items left, the animal 'consumes' all remaining items using the shortest path between them. When n is equal to 1, the animal always moves to the nearest-neighbor (NN) plant and when n is equal to the total number of plants, the MW and TS solutions are the same.

Here, we examined the consequences of using different variants of the RW and MW strategies. First, we simulated a RW strategy in the same patches used for foraging trials. We varied the distance at which an animal could detect a plant (the *detection distance*, in m), and we assumed that once the animal was within the detection distance of a plant, it moved directly to it. If more than one plant fell within the detection distance, the animal used a nearest-neighbor rule and moved directly to the closest plant. We also simulated foraging paths using a MW rule, with window sizes from 1 (a NN rule) to 10. For each rule, we conducted simulations using 10 unique random starts in the 7 different patches used in our bighorn sheep trials (70 simulations for each rule).
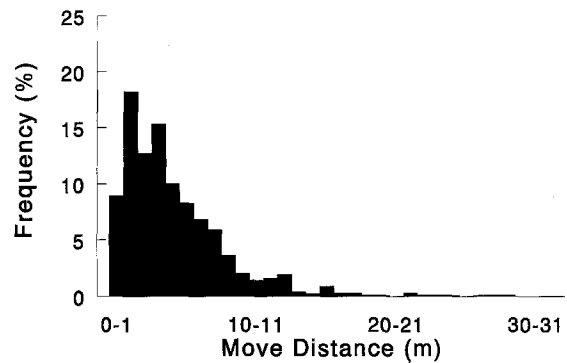
3. Results

3.1 Trials with bighorn sheep

After several days of habituation, sheep readily consumed the alfalfa we offered them in the feeding trials. Our analyses were based on 1376 moves between individual plants from the 71 trials that bighorn sheep completed. In each trial, bighorn sheep visited an average of 19.4 of the 36 plants we offered.

Bighorn sheep typically moved from one plant to the closest available plant (Fig. 1; 75% of all moves), and the frequency of moves to plants that were located farther away declined rapidly. Over 90% of all moves were to one of the three plants that were closest to the animal. For the 1376 individual movements recorded, the average distance moved between plants by the sheep was 5.33 m. By comparison, the average straight-line between the same plants was 5.18 m (Fig. 2). More than 75% of the time, bighorn sheep moved directly between plants, and an additional 19% of the travel paths deviated only slightly (an increase in travel distance of about 3%).

When sheep failed to move to the closest available plant, they usually travelled to a plant that was at nearly the same distance. For example, about 50% of moves to a plant that was not the nearest-neighbor resulted in additional travel of less than 2 m (Fig. 3), and over 95% of all non-NN moves
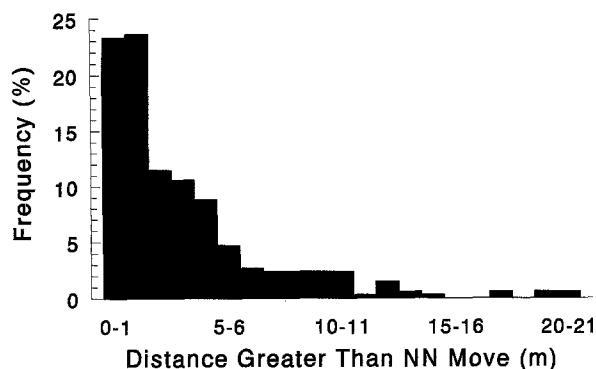
Fig. 3. Frequency distribution of the additional distance travelled by bighorn sheep when they choose to move to a plant that was not a nearest-neighbor (NN). When bighorn sheep chose to move to a plant that was not the nearest-neighboring plant, it nevertheless moved to a nearby plant, and incurred only small additional travel costs. The additional distances moved were categorized into 1 m classes (0–1 m, 1–2 m, etc.).
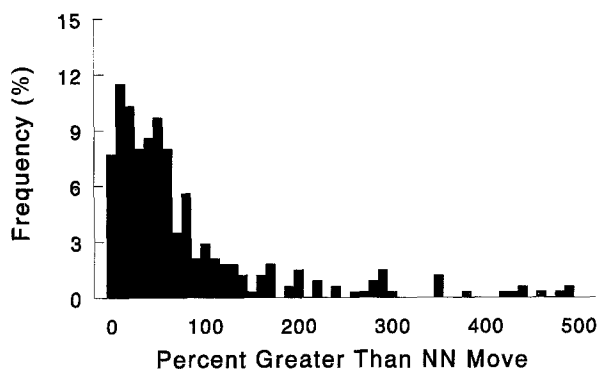

Fig. 4. Frequency distribution of the percentage increase in move distance for moves where sheep choose a plant that was not the nearest-neighbor.

were to plants that were less than 6 m farther than the closest available plant. Hence, movements between plants other than nearest-neighbors typically increased travel distances by less than 50% (Fig. 4).

3.2 Simulation modelling

The lengths of foraging paths generated from simulations using a random-walk (RW) rule were much greater than those we observed in foraging trials. For a randomly-walking herbivore with a detection distance of 2 m, the average simulated distance necessary to encounter 25 plants was 4022 m, about
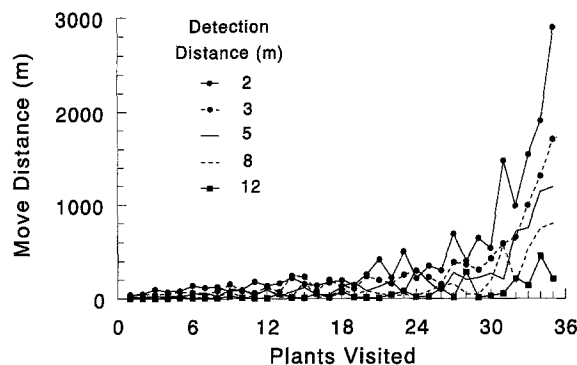

Fig. 5. Foraging path move distance as a function of the number of plants visited using a random walk rule with various detection distances. Animals moved directly to a plant that fell within the detection distance, or to the closest plant if more than one fell within the detection range. Simulations were run using the same distributions of plants that were employed in the bighorn sheep foraging trials.

30 times greater than the average of 134 m that we observed in our feeding trials. As the simulated detection distance increased, the length of the foraging path converged with that of a nearest-neighbor rule. However, even with a detection distance of 12 m, the average length of a path to 25 plants was 462 m, a 3-fold increase over observed foraging path lengths. As more plants within a patch were consumed, RW strategies performed increasingly poorly and the average distance travelled between plant captures increased dramatically (Fig. 5). We limited our analysis of RW detection distances to 12 m because bighorn sheep rarely moved directly to a plant more than 12 m away. Only 4 of the 46 moves longer than 12 m were to the closest plant, and only once did a bighorn move directly to the closest plant when it was more than 12 m away.

When compared to the RW strategy, moving-window (MW) and NN rules typically reduced the length of a foraging path by more than an order of magnitude. However, the use of MW rules resulted in only a slightly greater foraging efficiency (about 10%) over the more parsimonious NN rule (Fig. 6), and in fact resulted in a longer path lengths when foraging continued until all plants in a patch were consumed. This occurred because the use of a moving-window rule often resulted in 'leaving' a near-by plant uneaten. After almost all plants were consumed, the forager was forced to move long dis-
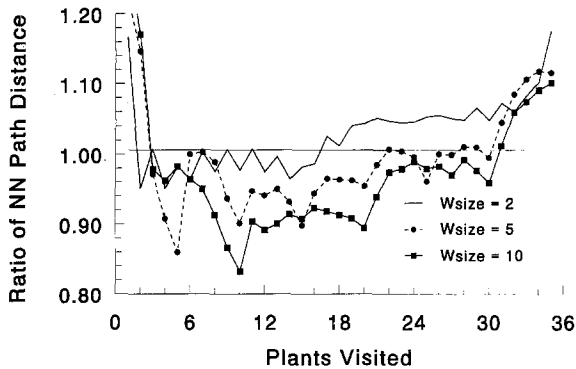
Fig. 6. The ratio of the foraging path length using various window-sizes (Wsize) to the length of foraging path using a nearest-neighbor rule. Means of 10 simulations conducted on the seven patch distributions used in the bighorn sheep foraging trials. Points below the horizontal reference line represent paths that were shorter than that resulting from a nearest-neighbor movement rule.
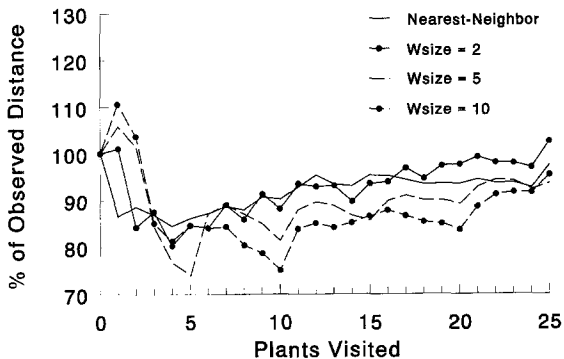

Fig. 7. A comparison of observed lengths of foraging paths of bighorn and simulation results. The dotted horizontal line at 100% is the observed distance, and the other lines depict path lengths generated by simulations that employ a nearest-neighbor rule, or a moving-window rule with a window size of 2, 5, or 10 plants. Points below the reference line represent strategies that are more efficient (shorter paths) than those observed, and points above the line represent paths longer than those observed.

tances to obtain the last few, widely scattered, plants.

Observed path lengths of foraging bighorn sheep were most closely approximated by simulations incorporating a NN or small window size rule (*i.e.*, 2–3 plants; Fig. 7). We obtained an insufficient number of observations to extend the comparison of observations to simulations beyond the consumption of 25 plants.

4. Discussion

4.1 Relevance to landscape models

Senft *et al.* (1987) characterized foraging by large herbivores as a nested hierarchy of responses to landscape features – plants, small patches, large patches, landscapes, and regions. An important, unresolved question emerged from their analysis: Are the responses of foragers to large scale patterns simply the aggregate of many small decisions? Alternatively, are those responses emergent – do animals respond directly to all levels in a foraging hierarchy? This question is vital for landscape ecologists, because answering it forces us to identify the scales at which spatial heterogeneity has the greatest impact on the way foragers function (Kolasa and Rollo 1991). Our work suggests that when plants are apparent to the herbivore and are embedded in a matrix producing a high contrast (*sensu* Kotliar and Wiens 1990) between sought after and rejected plants, then we should expect that the foraging movements of herbivores will be governed by local, small scale patterns.

Developing faithful models of many ecosystems depends in a fundamental way on understanding the mechanisms that account for foraging paths of large herbivores. However, studies of foraging paths have most often focussed on invertebrates (*e.g.*, Pyke 1978, Hoffmann 1983, Kareiva and Shigesada 1983, Turchin 1991, Winkelman and Vinyard 1991, Crist *et al.* 1992, Crist and Wiens 1994), and a few species of birds (Smith 1974, Zach 1976, Pyke 1981). Data from herbivorous mammals are exceedingly rare (but see Ward and Saltz 1994).

In the absence of data, models that incorporate foraging by large herbivores have employed several different rules to determine animal movements. For example, two recent models used directed movement at a larger scale and then assumed random searches within a smaller grid (Hyman *et al.* 1991, Turner *et al.* 1993), while another assumed a nearest-neighbor rule for plants within a detection distance, and a correlated random walk when there were no nearby plants (Roese *et al.* 1991). Observations of bighorn sheep clearly support the use of

nearest-neighbor rules for situations where plants are within view, but further experiments will be needed to determine search rules used over larger scales, such as between patches that are visually isolated.

It is essential to identify the rules that animals use while foraging to develop and test individual-based models that operate on large scales (Johnson *et al.* 1992, Turner *et al.* 1993, Judson 1994). Simulations of the boreal forest have shown that movement rules used by moose affect the spatial pattern of browse plants as well as the energetic status of the moose (Moen *et al.* 1993). As with our experiments, non-random patterns of foraging increased net feeding efficiency of animals. When forages are abundant, the search rule employed by a herbivore is probably unimportant, since encounter rate with foods does not limit foraging efficiency (Spalinger and Hobbs 1992, Gross *et al.* 1993a). However, as food abundance declines, an herbivore's ability to efficiently locate and move between forages can strongly affect the pattern of resource depletion and ultimately, survival of the animal (*e.g.*, Turner *et al.* 1993).

4.2 Relevance to studies of foraging by vertebrates

Previous studies of foraging by vertebrates identified strategies that increase searching efficiency for cryptic prey (*e.g.*, Smith 1974, Zach and Falls 1976, Speakman 1986). However, herbivores frequently consume prey that can be seen from a relatively long distance, thus rules that help reduce the length of travel between plants are likely to be more important than rules used to search for cryptic prey. When this situation prevails, our data show that the use of a random walk rule is inappropriate simply because it results in unrealistic estimates of travel distances (Fig. 5, Folse *et al.* 1989). The alternative rules we used in simulations yielded estimates of foraging path distances that were quite similar and were, in general, only slightly more efficient than those resulting from a nearest-neighbor rule.

The search paths of various invertebrates are relatively well documented (reviewed by Bell 1991), but spatial movements of large herbivores have

rarely been studied or analyzed. Ward and Saltz (1994) found that gazelles feeding on lilies followed a path that was far more systematic than a random walk. Gazelle foraging paths were characterized by a series of short moves, interspersed with occasional long, straight moves to other forage 'patches'. Gazelles increased foraging efficiency by concentrating feeding efforts in patches with higher densities of lilies, and by moving between patches using a direct path.

Our results demonstrate the value of evaluating a spectrum of strategies that animals might use to solve complex problems (Janetos and Cole 1981, Ward 1992). The use of simple rules-of-thumb is well established in economic theory, based primarily on the rationale that accurate and complete information is costly to acquire and time-consuming to analyze (Simon 1959, Janetos and Cole 1981). Foraging animals confront similar constraints (Dukas and Ellner 1993). It was possible to solve the travelling salesman problem with the number of plants used in our experiments, but the number of routes that would need to be evaluated using an optimized program would be $> 10^{10}$. Observations of bighorn sheep provide no indication that they can accomplish such an intellectual feat, and it seems unlikely that the slight increase in foraging efficiency from using a complex rule would offset the additional time required to obtain and process more complete information.

A central feature of our approach is that it allows one to link the spatial distribution of foods to the behavior of individuals. Ecologists have been reluctant to build foraging models that specifically respond to spatial heterogeneity despite the clear importance of spatial pattern to foraging processes (O'Neill *et al.* 1988, Kotliar and Wiens 1990, Milne *et al.* 1992, Wiens *et al.* 1993). Foraging models have traditionally started by observing, for example, the encounter rate of a feeding animal, rather than by predicting encounter rate from the spatial properties of the habitat. By building and testing mechanistic models that predict the intake rate of foraging herbivores over small times and distances (Spalinger and Hobbs 1992, Gross *et al.* 1993b) and linking these to processes that occur over larger scales, we gain insight to the response of foraging

behavior to environmental conditions that change over time and space.

Acknowledgements

References

Altmann, S.A. 1974. Baboons, space, time, and energy. Amer Zool 14: 221−248.

Anderson, D.J. 1983. Optimal foraging and the traveling salesman. Theor Pop Biol 24: 145−159.

Bell, W.J. 1991. Searching Behaviour. Chapman and Hall, London.

Belsky, A.J. 1984. Role of small browsing mammals in preventing woodland regeneration in the Serengeti National Park, Tanzania. Afr J Ecol 22: 271−279.

Crist, T.O., Guertin, D.S., Wiens, J.A. and Milne, B.T. 1992. Animal movement in heterogeneous landscapes: an experiment with Eleodes beetles in shortgrass prairie. Functional Ecology 6: 536−544.

Crist, T.O. and Wiens, J.A. 1994. Scale effects of vegetation on forager movement and seed harvesting by ants. Oikos 69: 37−46.

Detling, J.K. 1988. Grasslands and savannas: regulation of energy flow and nutrient cycling by herbivores. In Concepts of Ecosystem Ecology. pp. 131−148. Edited by L.R. Pomeroy and J.J. Alberts. Springer-Verlag, Berlin.

Dodd, J.L. 1994. Desertification and degradation in Sub-Saharan Africa. BioScience 44: 28−34.

Dukas, R. and Ellner, S. 1993. Information processing and prey detection. Ecology 74: 1337−1346.

Ellison, L. 1960. Influence of grazing on plant succession of rangelands. Bot Rev 26: 3−78.

Folse, L.J., Packard, J.M. and Grant, W.E. 1989. AI modelling of animal movements in a heterogeneous habitat. Ecol Modelling 46: 57−72.

Gessaman, J.A. and MacMahon, J.A. 1984. Mammals in ecosystems: their effects on the composition and production of vegetation. Acta Zool Fennica 172: 11−18.

Gross, J.E., Hobbs, N.T., and Wunder, B.A. 1993a. Independent variables for predicting intake rate of mammalian herbi-vores: biomass density, plant density, or bite size? Oikos 68: 75−81.

Gross, J.E., Shipley, L.A., Hobbs, N.T., Spalinger, D.E. and Wunder, B.A. 1993b. Functional response of herbivores in food-concentrated patches: tests of a mechanistic model. Ecology 74: 778−791.

Hobbs, N.T. and Schimel, D.S. 1984. Fire effects on nitrogen mineralization and fixation in mountain shrub and grassland communities. J Range Manage 37: 402−405.

Hobbs, N.T., Schimel, D.S., Owensby, C.E., and Ojima, D.S. 1991. Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. Ecology 72: 1374−1382.

Hoffmann, G. 1983. The search behavior of the desert isopod Hemilepistus reaumuri as compared with a systematic search. Beh Ecol Sociobiol 13: 93−106.

Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. Can Ent 41: 385−398.

Holling, C.S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem Ent Soc Can 45: 1−60.

Hyman, J.B., McAninch, J.B. and D.L. DeAngelis. 1991. An individual-based simulation model of herbivory in a heterogeneous landscape. In Quantitative Methods in Landscape Ecology. pp. 443−475. Edited by M.G. Turner and R.H. Gardner. Springer-Verlag Berlin.

Janetos, A.C. and Cole, B.J. 1981. Imperfectly optimal animals. Beh Ecol Sociobiol 9: 203−209.

Jaramillo, V.J. and Detling, J.K. 1988. Grazing history, defoliation, and competition: effects on shortgrass production and nitrogen accumulation. Ecology 69: 1599−1608.

Jaramillo, V.J. and Detling, J.K. 1992. Small-scale heterogeneity in a semi-arid North American grassland. I. Tillering, N uptake and retranslocation in simulated urine patches. J Appl Ecol 29: 1−8.

Johnson, A.R., Wiens, J.A., Milne, B.T. and Crist, T.O. 1992. Animal movements and population dynamics in heterogeneous landscapes. Landscape Ecology 7: 63−75.

Judson, O.P. 1994. The rise of the individual-based model in ecology. Trends Ecol Evol 9: 9−14.

Kareiva, P.M. and Shigesada, N. 1983. Analyzing insect movement as a correlated random walk. Oecologia 56: 234−238.

Kolasa, J. and Rollo, C.D. 1991. The heterogeneity of heterogeneity: a glossary. In Ecological Heterogeneity. pp. 1−23. Edited by J. Kolasa and S.T.A. Pickett. Springer-Verlag, New York.

Kotliar, N.B. and Wiens, J.A. 1990. Multiple scales of patchiness and patch structure: a hierarchial framework for the study of heterogeneity. Oikos 59: 253−260.

Laws, R.M. 1970. Elephants as agents of habitat and landscape change in East Africa. Oikos 21: 1−15.

Mack, R.N. and Thompson, J.N. 1982. Evolution in steppe with few large, hooved mammals. Amer Nat 119: 757−773.

Madany, M.H. and West, N.E. 1983. Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. Ecology 64: 661−667.

McNaughton, S.J. 1985. Ecology of a grazing ecosystem: the

Serengeti. Ecol Monogr 55: 259–294.

McNaughton, S.J. Ruess, R.W. and Seagle, S.W. 1988. Large mammals and process dynamics in african ecosystems. BioScience 38: 794–800.

Milchunas, D.G. and Lauenroth, W.K. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecol Monogr 63: 327–366.

Mills, J.N. 1983. Herbivory and seedling establishment in postfire southern California chaparral. Oecologia 60: 267–270.

Milne, B.T., Turner, M.G., Wiens, J.A. and Johnson, A.R. 1992. Interactions between the fractal geometry of landscapes and allometric herbivory. Theor Pop Biol 41: 337–353.

Moen, R.A., Pastor, J. and Cohen, Y. 1993. Effect of foraging strategy on energetics of moose (Alces alces) and spatial patterns of browse availability. Bull Ecol Soc Amer 74 (Supplement): 363.

Norton-Griffiths, M. 1979. The influence of grazing, browsing, and fire on the vegetation dynamics of the serengeti Tanzania, Kenya, In Serengeti: Dynamics of an Ecosystem. pp. 310–352. Edited by A.R.E. Sinclair and M. Norton-Griffiths. University of Chicago Press, Chicago.

O'Neill, R.V., Milne, B.T., Turner, M.G. and Gardner, R.H. 1988. Resource utilization scales and landscape pattern. Landscape Ecology 2: 63–69.

Pastor, J. and Naiman, R.J. 1992. Selective foraging and ecosystem processes in boreal forests. Amer Nat 139: 690–705.

Pastor, J., Naiman, R.J., Dewey, B. and McInnes, P. 1988. Moose, microbes, and the boreal forest. BioScience 38: 770–777.

Pyke, G.H. 1978. Optimal foraging: movement patterns of bumblebees between inflorescences. Theor Pop Biol 13: 72–98.

Pyke, G.H. 1981. Optimal foraging in hummingbirds: rule of movement between inflorescences. Anim Beh 29: 889–896.

Real, L.A. 1991. Animal choice behavior and the evolution of cognitive architecture. Science 253: 980–986.

Roese, J.H. Risenhoover, K.L. and Folse, L.J. 1991. Habitat heterogeneity and foraging efficiency – an individual-based model. Ecol. Modelling 57: 133–143.

Ruess, R.W. and McNaughton, S.J. 1988. Ammonia volatilization and the effects of large grazing mammals on nutrient loss from East African grasslands. Oecologia 77: 382–386.

Schimel, D.S., Parton, W.J., Ademsen, F.J., Woodmansee, R.G., Senft, R.L. and Stillwell, M.A. 1986. The role of cattle in the volatile loss of nitrogen from a shortgrass steppe. Bio-

geochemistry 2: 39–52.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L. Huenneke, L.F., Jarrell, W.M., Virginia, R.A. and Whitford, W.G. 1990. Biological feedbacks in global desertification. Science 247: 1043–1048.

Schroeder, M. 1991. Fractals, Chaos, Power Laws: Minutes from an Infinite Paradise. Freeman, New York.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. and Swift, D.M. 1987. Large herbivore foraging and ecological hierarchies. BioScience 37: 789–799.

Simon, H.A. 1959. Theories of decision-making in economics and behavioral science. Amer Econ Rev 49: 253–283.

Smith, J.N.M. 1974. The food searching behaviour of two European thrushes. II. The adaptiveness of the search patterns. Behaviour 49: 1–61.

Spalinger, D.E. and Hobbs, N.T. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. Amer Nat 140: 325–348.

Speakman, J.R. 1986. The optimal search speed of terrestrial predators when feeding on sedentary prey: a predicative model. J Theor Biol 122: 401–407.

Stephens, D.W. and Krebs, J.R. 1986. Foraging Theory. Princeton University Press, Princeton, NJ.

Turchin, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. Ecology 72: 1253–1266.

Turner, M.G., Wu, Y., Romme, W.H. and Wallace, L.L. 1993. A landscape simulation model of winter foraging by large ungulates. Ecol Modelling 69: 163–184.

Ward, D. 1992. The role of satisficing in foraging theory. Oikos 63: 312–317.

Ward, D. and Saltz, D. 1994. Foraging at different spatial scales: Dorcas gazelles foraging for lilies in the Negev Desert. Ecology 75: 48–58.

Wiens, J.A., Stenseth, N.C., Van Horne, B. and Ims, R.A. 1993. Ecological mechanisms and landscape ecology. Oikos 66: 369–380.

Winkelman, D.L. and Vinyard, G.L. 1991. Gyrinid searching tactics: empirical observations and a tactical model. Beh Ecol Sociobiol 28: 345–351.

Wolf, L.L. and Hainsworth, F.R. 1991. Hummingbird foraging patterns: visits to clumps of Ipomopsis aggregata inflorescences. Anim Beh 41: 803–812.

Zach, R. and Falls, J.B. 1976. Foraging behavior, learning, and exploration by captive ovenbirds (Aves: Parulidae). Can J Zool 54: 1880–1893.