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Energy, Fractal Movement Patterns, and Scale-Dependent Habitat Relationships of Urban and Rural Mule Deer

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ENERGY, FRACTAL MOVEMENT PATTERNS, AND SCALE-DEPENDENT HABITAT RELATIONSHIPS OF URBAN AND RURAL MULE DEER

by

Mark F. McClure

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

UTAH STATE UNIVERSITY
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ABSTRACT

Energy, Fractal Movement Patterns, and Scale-Dependent
Habitat Relationships of Urban and Rural Mule Deer

by

Mark F. McClure, Doctor of Philosophy

Utah State University, 2001

Major Professors: Dr. John A. Bissonette and Dr. Michael R. Conover
Department: Fisheries and Wildlife

I studied the behaviors, movement dynamics, habitat relationships, and population characteristics of Rocky Mountain mule deer (*Odocoileus hemionus*) using urban and rural winter ranges in Cache Valley, Utah, from January 1994 to February 1998. There were 2 goals to my research endeavors. The first was to assess how and why the behaviors and demographic characteristics of urban deer differed from those of rural deer. The second was to assess the scale-dependent responses to habitat and the scale-dependent patterns of habitat use by deer living in each area. To accomplish the first goal, I compared the prevalence of migration, the spatial and temporal patterns of migration, and the spatial patterns of home range use between urban and rural deer. I also compared deer reproduction and population density in each area. I then explain how behavioral and demographic dissimilarities between urban and rural deer may have corresponded to differences in their net energetic gains (NEG) on seasonal ranges. These explanations, when combined graphically, generated a time-specific hypothesis of lower NEG by urban deer on a year-round basis. To accomplish the second goal, I developed new methodologies for analyzing animal movement pathways (which represent signatures of how animals respond to habitat), and animal patterns of habitat use. These methodologies explicitly incorporated the effects of spatial scale by employing fractal geometry and information theory. The results of these analyses showed that urban and rural deer responded to their habitats in similar ways at coarse resolutions of analysis (100-600 m), but differently at fine resolutions of analysis (4-60 m). I argue that similarities in habitat response at coarse resolutions reflected a common movement process that allowed deer maximize use of their home ranges while minimizing energetic expenditures. With respect to patterns of habitat use, urban deer concentrated in areas with concealment vegetation, which was highly fragmented across all resolutions of analysis. Rural deer, on the other hand, dispersed throughout areas containing shrubby vegetation at fine resolutions, and south-facing slopes at coarse resolutions. Interpretation of these results is discussed in detail.

(146 pages)

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There are many individuals who helped me in some form or fashion during my Ph.D. program, and it is therefore impossible that I formally thank all of them in this brief tribute. In particular, however, I am very grateful to my five committee members: John Bissonette, Michael Conover, Mark Ritchie, Terry Sharik, and Michael Wolfe. Throughout my education as a Ph.D. student, these scientists and scholars have encouraged me to set high academic standards for myself, and offered competent assistance when I needed it. Especially helpful was John Bissonette, one of my major professors, who showed genuine interest in many of my ideas, regardless of how well I articulated them. His diplomacy and aplomb are personal attributes that I'll strive to emulate throughout my professional career. Michael Conover, my other major professor, was also instrumental in ensuring that my education adequately prepared me to make a significant contribution to the ecological sciences. Without fail, he helped me clarify questions of theoretical and practical importance, and insisted that I keep my research as defensible as possible. Mark Ritchie, although not one of my major professors, undoubtedly played the role of one. Several of the ideas in this dissertation may have never germinated if he had not spent many hours sharing his knowledge with me.

In addition to these scholars, David Peak illuminated my understanding of fractal geometry and information theory, both of which are integral components to my dissertation. David Roberts demonstrated a remarkable understanding of spatial ecology, and always welcomed me into his office to discuss my ideas and the interpretation of my

results. Gary Belovsky was also a wealth of knowledge and experience, and could be counted on to take a critical look at my research questions and the approaches I proposed to answer these questions. Daniel Watson helped synthesize some of the technicalities of analyzing spatial data, and wrote several computer programs that calculated the fractal dimensions of spatial patterns. Lisa Nordstrom, a Ph.D. student in my cohort, discussed many ideas with me and offered a clear mind when mine was muddled. I thank them all.

In the field, I was fortunate to work with several first-rate students, including Timothy Veenendal, Charles Shaw, Gary Tucker, and Gerald Wiscomb. Together, we captured 78 mule deer, 2 dogs, and 1 cow. It is worth noting that not one of these animals was harmed during the trapping and handling process. We also gathered thousands of deer locations during the day and night, and made hundreds of behavioral observations of deer. I commend these students for their dedicated work in the field.

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Mark F. McClure

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CHAPTER 1

THEMATIC CONTEXT AND PREVIEW OF RESEARCH

Continued increases in the human population and concomitant urban developments have resulted in significant alteration and reduction of wildlife habitats. Accordingly, one of the primary aspirations of many wildlife ecologists is to understand and predict how these developments affect animal behaviors and populations. The questions ecologists often wish to answer include: 1) how do habitat changes associated with development influence the way animals perceive and respond to their environments, 2) will these changes inhibit animals from using specific areas of the landscape, and 3) how will these changes influence population numbers and dynamics? My dissertation research was designed to provide a foundation upon which to answer these questions with respect to mule deer (*Odocoileus hemionus*) living in the foothill regions of the Rocky Mountain West. My study was conducted in Cache Valley, Utah.

My research protocol was simple: compare the behaviors, patterns of habitat use and response, and population characteristics of mule deer using urban versus rural winter ranges. This protocol allowed me to infer 1) how urban winter ranges differed fundamentally from adjacent rural winter ranges, and 2) how urban and rural deer responded to and used their respective habitats. The main chapters of my dissertation correspond to this organization. Chapter 2 examines the differences between urban and rural winter ranges as characterized by deer behavior and demography. Chapters 3 and 4 pertain to the habitat responses and patterns of habitat use by urban and rural deer.

In Chapter 2, I develop a graphical hypothesis of the year-round net energetic gains (NEG) of deer using urban and rural winter ranges. The qualitative properties of this hypothesis are generated by exploring the differences in the behavioral and demographic characteristics of deer using each area. Specifically, I compare the prevalence of migration, timings of migration, winter home range size, and patterns of home range use between urban and rural deer. I also compare deer densities and reproductive performance on each winter range. I then explain how behavioral and demographic differences between urban and rural deer might reveal discrepancies in their NEG on seasonal ranges. Because energy is likely to have a dominating influence on deer survival and reproduction, these discrepancies between urban and rural deer thus represent a time-specific hypothesis of the fundamental differences between urban and rural winter ranges. After developing this hypothesis, I use it to identify when factors associated with forage and risks may have differentially affected urban and rural deer.

In Chapter 3, I assess how urban and rural deer respond to habitat by measuring the fractal dimensions of their movement pathways. A movement pathway provides a record of how animals respond to habitat based on the degree to which it fills space. And a fractal dimension measures a pathway's space-filling attributes across multiple resolutions of analysis. Before I attempt to assess urban and rural deer responses to habitat, however, I first show that the existing methods used to assess the space-filling attributes of movement pathways are unreliable. Therefore, I develop a new technique (Slider-D) for determining the fractal dimensions of movement pathways. After Slider-D is explained, I use it to show that urban and rural deer respond to their respective habitats in fundamentally similar ways once pathways exceed a certain length (~ 80 m). Based on these findings, I then hypothesize that similarities in D result from a behavioral process that allows deer to maximize use of their home ranges while minimizing the energetic expenditures associated with movement. I also hypothesize that differences in resource patchiness or landscape complexity cause urban and rural deer to exhibit different responses to their habitats when path segments are short (4-60 m).

In Chapter 4, I develop a 2-staged methodology for analyzing scale-dependent patterns of habitat use. I then use this methodology to show 1) how the spatial patterns of urban and rural deer point locations change with resolution, and 2) how the degree of correspondence between point locations and different habitat types change across this same range of resolutions. The first stage characterizes the distribution of deer locations, and the second stage provides a starting point for understanding the underlying basis for these distributions. An important finding that arises from these analyses is that urban deer locations are relatively space-filling at fine resolutions of analysis, and relatively fragmented at coarse resolutions. Stage 2 shows that these patterns of space use by urban deer are influenced largely by habitat components that reduce risk exposure, whereas those of rural deer are influenced by components that increase energy or nutrient intake.

In Chapter 5, I integrate and synthesize the findings from Chapters 2 to 4. In doing so, I recapitulate how and why mule deer were affected by urban developments on their winter ranges of Cache Valley, Utah. I also suggest how the techniques that I develop to analyze animal movement pathways and scale-dependent patterns of habitat use open new avenues of research.

CHAPTER 2

BEHAVIOR AND DEMOGRAPHY OF URBAN VS. RURAL MULE DEER: THE RISK-ENERGY TRADE-OFF

Abstract: Continued urban development on mule deer (*Odocoileus hemionus*) winter ranges demands that wildlife managers learn how urban habitats differ from surrounding rural areas, and how these differences affect deer behavior and demography. To assess such potential differences, I compared the behavioral and demographic characteristics of mule deer using urban and rural winter ranges of Cache Valley, Utah. Key behavioral differences included the following: 1) migration to high-elevation summer range was more prevalent among urban deer than rural deer, 2) urban deer initiated spring migrations before rural deer, 3) urban deer returned to winter ranges before rural deer in the fall, 4) winter home ranges of urban deer were much smaller than those of rural deer, and 5) within home ranges, locations of urban deer were clustered around concealment vegetation, whereas those of rural deer were dispersed broadly throughout the landscape. Demographically, urban deer exhibited lower densities and lower fawn:doe ratios than rural deer. I explain how these behavioral and demographic dissimilarities may have corresponded to differences in urban and rural deer net energetic gains (NEG) on seasonal ranges. These explanations, when combined graphically, suggest a time-specific hypothesis of lower NEG by urban deer on a year-round basis. I use this hypothesis to argue that risk avoidance prevented deer from foraging broadly, and thus selectively, on urban winter range.

INTRODUCTION

Urban developments have usurped large tracts of mule deer winter range in the Rocky Mountain and Intermountain West. Presumably, developments are detrimental to mule deer populations because the overall availability of winter habitat is reduced, and migratory corridors are obstructed (Wallmo 1978, Rost and Bailey 1979, Reed 1981, Smith et al. 1989). Despite these large-scale effects, however, mule deer have adapted locally to many urban areas (Conover 1995). But, there is currently no indication that they thrive in urban settings as do white-tailed deer (*Odocoileus virginianus*; Swihart et al. 1995, McClure et al. 1997, Warren 1997). As a case in point, Vogel (1989) reported that mule deer declined while white-tailed deer increased as developments encroached the Gallatin Valley of Montana. Given the continued development on winter range, it behooves managers to learn how urban habitats differ from traditional (rural) winter ranges, and how these differences affect deer behavior and population performance.

One difference between urban and rural habitats may relate to risks, which obviously are important to consider because they cause the immediate deaths of individuals. Perhaps more importantly, however, is that risks induce stress and heighten vigilance, resulting in elevated metabolic rates and reduced foraging effort (Geist 1971, Freddy et al. 1986). Moreover, by avoiding risks, deer may limit their access to areas containing quality forage (Hornocker 1970, Sweeney et al. 1971, Nelson and Mech 1986). These behavioral or physiological changes brought on by risks will, in turn, manifest themselves as diminished nutritional or energetic gains (Lima and Dill 1990, Quenette 1990).

In urban areas, one might presume that the effects of risks on deer are minimal, as there is likely to be little predation or hunting. However, deer in urban areas face the risk of automobile collisions, and harassment by people and dogs. Although these risks are difficult to quantify, it is reasonable to conclude that they are more ubiquitous than the predation risks that rural deer encounter. Risk exposure in urban areas may therefore be higher than that in rural areas for a given amount of movement. Consequently, to reduce risk exposure, urban deer might be expected to limit their movements and foraging activities more so than rural deer. These behavioral changes would be evidenced as smaller home ranges, and patterns of habitat use that correspond to hiding cover. At a larger scale, urban deer might be expected to reduce risk exposure by migrating out of urban areas each spring, and by minimizing the time they spend on winter range between fall and spring migrations.

Forage characteristics may also differentiate urban and rural winter ranges. Urban areas contain both native and an assortment of exotic vegetation, which tends to be scattered broadly across the landscape in small patches. Forage in rural areas, on the other hand, is less diverse, consisting only of native and agricultural vegetation. Therefore, by increasing their mobility (i.e., expanding their home ranges), urban deer should be able to forage more selectively than rural deer, a behavior that may result in higher energetic and nutritional gains (Short 1981, Hobbs 1989, McCorquodale 1993). Alternatively, urban deer may have relatively small home ranges if they can satisfy their nutritional or energetic needs in a smaller area. On another note, much of the exotic vegetation in urban areas is irrigated and fertilized, thus providing green and succulent forage throughout summer and into the fall. Accordingly, it might be expected that urban deer would take advantage of this forage by remaining on winter range the year-round, or by returning to winter range in early fall.

Note that these behaviors are, for the most part, counter to those expected for deer attempting to minimize risk exposure in urban areas. Therefore, one might presume that behaviors directed toward avoiding risks or finding forage would have different consequences with respect to the physical condition of individuals, which, in turn, may have repercussions on population performance (Geist 1981, Anholt 1997).

To assess how urban environments change deer behavior and demography, and to gain insight into how these changes might be explained by risks and forage, I compared the behavioral and demographic characteristics of mule deer using adjacent urban and rural winter ranges of Cache Valley, Utah. The behavioral characteristics that I compared included: 1) the prevalence of migration, 2) the timings of spring and fall migration, 3) the size of winter home ranges, 4) the degree of aggregation within winter home ranges, and 5) the spatial associations between yearly home range locations. The demographic characteristics that I compared included 1) population density, and 2) reproductive performance, indexed via fawn:doe ratios.

STUDY AREAS

The urban and rural study areas were situated at the west-facing base of the Wasatch Mountains in Cache Valley, Utah, approximately 100 km north of Salt Lake City (Fig. 2-1). The 32-km^2 urban area encompassed the cities of Logan, River Heights, and

Providence. The 42-km^2 rural area was centered 15 km north of the urban area, and about 4 km east of Richmond, Utah. Elevations were similar in the 2 areas, averaging 1500 m. Climate also was similar, and was typical of the Intermountain West with dry, warm summers, and cold, snowy winters. Snow depths from November through March ranged from 0 to 40 cm in both areas, and averaged 8 cm in the rural area and 6 cm in the urban area (Utah State University, Climate Center). No snow remained on the ground from April to October.

The urban area consisted mostly of residential housing, with housing densities ranging from 0.15 to 8.0/ha. A few small farms were interspersed within the urban area. Vegetation was diverse, with exotic and native species (i.e., the same species found in the rural area), as well as fields of alfalfa, wheat, and corn. Hunting was prohibited in the urban area, as most of it was within city limits. The rural area, in contrast, contained only a few scattered farm houses. Vegetation consisted of alfalfa and wheat fields interspersed in a rangeland dominated by big sagebrush (*Artemisia tridentata*), antelope bitterbrush *(Purshia tridentata*), cheatgrass (*Bromus tectorum*), and crested wheatgrass *(Agropyron desertorum*). Bigtooth maple (*Acer grandidentatum*), serviceberry *(Amelanchier spp*.), and Utah juniper (*Juniperus osteosperma*) were also dispersed throughout the area. Coyotes (*Canis latrans*) and mountain lions (*Puma concolor*) lived in the rural area, and posed potential risks to deer.

Migratory urban and rural deer summered at elevations of 2100 to 2900 m in the Cache National Forest of northern Utah and southern Idaho (Fig 2-1). Douglas-fir (*Pseudotsuga menziesii*) and quaking aspen (*Populus tremuloides*) comprised the bulk of overstory vegetation. On average, there was no difference in the summer ranges of migratory urban and rural deer, as their summer home ranges were intermixed.

METHODS

Deer Capture and Sampling

I captured 54 deer in the urban area from 4 January to 13 February 1994, and from 10 to 14 February 1995. I attached radiocollars to 18 females (11 adults, 7 fawns), and marked the remaining 36 deer with numbered neckbands or ear tags. I captured 24 deer in the rural area from 18 December 1994 to 10 January 1995. I attached radiocollars to 16 females (12 adults, 4 fawns), and marked the remaining 8 deer with numbered ear tags. I refer to deer wearing ear tags or neckbands as marked deer, which distinguishes them from radio-telemetered deer. I captured all deer in Clover traps and restrained them manually. I dispersed traps widely throughout each area to obtain representative samples of animals in each area.

Deer Behavior

Prevalence pf Migration.--I considered deer to be migratory if they moved between seasonal ranges that did not overlap. I estimated the proportion of non-migratory deer using the urban area by combining data from summer and winter locations of radio-telemetered deer (see below) and sightings of marked deer on winter range during summer. To find marked deer during summer, I systematically searched the urban area 10 times between 1 July and 31 August, 1994 and 1995. Additionally, I asked urban residents to record sightings of all marked and unmarked deer throughout the summer. I estimated the proportion of nonmigratory deer using the rural area from summer and winter locations of radio-telemetered deer (see below); sightings of marked deer were not attempted in the rural area. I compared statistically the proportions of nonmigratory deer using urban and rural areas with chi-square contingency tables.

Timings of Migration.--To determine when deer migrated in the spring, I searched for radio-telemetered animals 2 times per week from April through June using ground surveillance and radio-telemetry. If a radio signal was received, I circled the area (radii of 100-500 m) from which it emanated, and recorded deer locations to the nearest 500 m on U.S. Geological Survey (USGS) 1:24,000 topographic maps. I considered a deer to have begun spring migration when: 1) it was first located ≥ 2 km outside its respective winter range in the spring, with no subsequent return until fall, or 2) when its radio signal could no longer be received within its winter range, and subsequent observations revealed that the deer was alive with a functional radio collar.

To determine when deer returned to winter range, I searched for radio-telemetered animals in and near winter ranges 2 times per week from September through December. I considered a deer to have completed its fall migration when it was first located ≤ 2 km from its winter range of the previous year. I compared statistically the timings of migration between urban and rural deer in 1995 and 1996 by recording departure or return dates on a Julian calendar, and performing Van der Waerden tests (SAS Institute, Inc., 1988). To assess whether the timings of migration corresponded to environmental or forage conditions, I also monitored qualitatively weather patterns (thermal conditions, snow cover) and forage conditions (degree of dessication), and obtained weekly summaries of precipitation and temperature from the Utah State University Climate Center.

Spatial Patterns of Migration.--I calculated migration distances as the distance between centroids of winter and summer locations of radio-telemetered deer. During summer (July and August), I located radio-telemetered animals ≥ 3 times. For approximately half of these locations, I followed radio signals until deer were seen. For the other half, I estimated deer locations by circling the areas from which their radio signals emanated (radii of 100 - 1000 m). I plotted summer locations of radio-telemetered deer on USGS 1:24,000 topographic maps to the nearest 1000 m.

Winter Home Range Size.--From 1 January to 31 March 1995 and 1996, I located radio-telemetered animals every 2 to 5 days during 1 of 3 time intervals: 1) dawn or dusk, which included the hour before and after sunrise, or the hour before and after sunset, 2) the day, 1000 to 1600, and 3) the night, 2200 to 0400. Approximately 40% of these locations were made during the dawn/dusk interval, 40% during the day, and 20% during the night. These intervals were designed to capture the full spectrum of deer activity patterns and thus provide an adequate description of home range size and patterns of home range use. I determined most locations (80%) by following radio signals in vehicles or on foot until animals were seen. When a deer was sighted, I used a hand-held global positioning system (GPS; mean error = 46 m, SE = 6.4 m) to estimate my location. I then added the directional distance from the GPS unit to the deer to estimate the deer's location. Direction was determined with a hand-held compass (± 2°) , and distance was estimated visually. Sighting distances were always < 100 m for urban deer and < 200 m for rural deer. When I could not see radio-telemetered deer (e.g., when it was too dark or when deer were in thick cover), I determined their locations by circling the areas from which their radio signals emanated (radii of 20-50 m for urban deer and 50-100 m for rural deer), and plotting their locations on USGS 1:24,000 topographic maps. I recorded all locations of radio-telemetered deer during winter as UTMs, which were rounded off at 10 m. I estimated winter home range size for urban and rural deer via the minimum convex polygon (MCP, 95%) method in the program CALHOME (Kie et al. 1994). I statistically compared MCPs of urban versus rural deer for 1995 and 1996 with t-tests.

Aggregation Within Winter Home Ranges.--To determine how deer distributed themselves within their home ranges, I developed the following metric to estimate the degree of aggregation of location coordinates:

$$S = \frac{\sum_{i=1}^{N} d_i}{N} \Big/ X$$

where S is an index of aggregation; d_i is the distance from a location to the nearest neighboring location; N is the number of locations; and X is the linear extent of an animal's home range, calculated as the distance between the outermost locations. The value of S can range between 0 and 1, with smaller values indicating a greater degree of aggregation, and larger values indicating a greater degree of dispersion. This index allows for standardized comparisons among spatial patterns of any extent. What this means is that small and large areas can be compared. Note that if X is removed, the equation reduces to the mean nearest neighbor value for all coordinate locations. Also note that in order to make meaningful comparisons among animals, the number of locations should be equal. My sample sizes for urban and rural deer all ranged between 28 and 32. I compared the values of S between urban and rural deer in 1995 and 1996 using t-tests.

Association Between Yearly Home Range Locations.-- I quantified the association between a deer's locations from consecutive winters, 1995 and 1996, in 2 ways. First, I calculated a centroid value from a deer's locations each winter (1 January-31 March), and quantified overlap between each set of locations by measuring the distance between centroids from consecutive years. I then used t-tests to determine whether distances between yearly centroids for urban and rural deer differed. Second, I used the multi-response permutation procedure (MRPP; Biondini et al. 1988) to test whether sample locations from the 2 consecutive years came from a common probability distribution. The null hypothesis of the MRPP is that the distribution of an animal's locations for each year are the same; a significant test, therefore, indicates a change in use of an area between years (White and Garrot 1990).

Demographic Characteristics

Reproductive Performance.--To index the reproductive performance of urban and rural deer, I recorded fawn-doe ratios while migratory and nonmigratory deer lived on winter ranges (December-April). Throughout this period, I searched for deer in each area and classified them as fawns (< 12 months), does (yearlings and adults), or bucks on 8-10, 2-hr occasions each winter. To ensure that ratios were representative of deer using each area, I selected a subset of these counts in which 1) deer were classified in $\geq$ 5 locations in each study area, and 2) sample size (fawns + does) was > 40. Because classification counts on different days were not independent (i.e., the same deer may have been counted on different days), formal statistics were not used to compare the ratios of urban and rural deer.

Densities.--I estimated population numbers of urban and rural deer using mark-resight methods. For urban deer, I estimated population size on 6 occasions from February to March, 1994, and on 3 occasions from February to March, 1995. Each estimate entailed a 3-hr visual search (telemetry was not used to locate deer) for radio-telemetered, marked, and unmarked deer throughout the study area. I input count data from each search into the immigration/emigration model of the program NOREMARK to generate Lincoln-Petersen estimates of population size (G. C. White, Colo. St. Univ., pers. comm., Neal et al. 1993). I demarcated the boundaries of the study area based on the outermost locations of marked and radio-telemetered deer during the winters of 1994 and 1995. Radio-telemetered and marked deer observed within this area from February to March each year were assumed to be available for NOREMARK estimates. Because each search was conducted by only 1 observer, I were confident that deer were not counted more than once during a search. Additionally, because the entire study area was searched, I assumed that all deer (radio-telemetered, marked, and unmarked) had an equal probability of being sighted.

For rural deer, I estimated population size on 3 occasions from February to March,

1995. Counting procedures for rural and urban deer were similar, with 1 exception: I considered only radio-telemetered deer known to be within the rural study area during counts to be available for population estimates (marked deer were also included in estimates in the urban area). Rural deer tended to range broadly across the landscape, and I were therefore unsure which marked deer were within the study area during the counts. In contrast, urban deer home ranges were very small, and I were confident that all marked deer were in the study area during counts. I verified which radio-telemetered rural deer were available for each count by scanning the study area with telemetry following the count.

RESULTS

Fates of Radio-Telemetered and Marked Deer

Of the 54 radio-telemetered or marked urban deer, 9 were killed by automobiles on winter range, 1 was illegally shot on winter range, 3 died from unknown causes on winter range, 3 were killed by hunters on high-elevation summer ranges, and 2 were killed by automobiles on high-elevation summer ranges from January 1994 to January 1997; 19 were alive, and 17 were unaccounted for when the study was terminated (January 1997). Of the 24 radio-telemetered or marked rural deer, 1 was killed by an automobile on winter range, 1 was killed by a mountain lion on winter range, 1 was ensnared in a barbed-wire fence and died on winter range, 1 died of an unknown cause on winter range, and 2 were killed by hunters on high-elevation summer range from January 1995 to January 1997; 11

were alive, and 7 were unaccounted for when the study was terminated. Deer that were unaccounted for may have been alive but 1) eluded detection, 2) lost their ear tags or neckbands, and thus could not be identified, or 3) moved out of their respective winter ranges. Or, they may have died unbeknownst to me.

Deer Behavior

Prevalence of Migration.--Of the 54 radio-telemetered or marked urban deer, 45 were migratory, 4 were nonmigratory with overlapping seasonal ranges, and 5 died before their migratory/nonmigratory behaviors could be determined (i.e., they died before deer migrated in the spring). Of the 4 nonmigratory deer, 2 were radio-telemetered and 2 were marked. I were confident that these were the only 2 marked, nonmigratory deer in the urban area because they were each sighted on > 5 occasions in July and August during meticulous searches for nonmigratory deer, and they were the only 2 marked deer to be observed by urban residents. Incidentally, urban residents also observed the 2 radio-telemetered nonmigratory deer during the summer on numerous occasions, suggesting that nonmigratory deer were readily observed. Of the 16 radio-collared rural deer, 8 were migratory, 6 were non-migratory, and 2 died before their migratory/nonmigratory behaviors could be determined. Based on these numbers, the proportion of migratory to nonmigratory deer using the urban area was significantly higher than that of deer using the rural area ($\chi^2 = 9.98$, df = 1, $P < 0.005$).

Overall, I frequently observed deer in the rural area during summer (July and August). On one occasion, I saw 18 deer (9 does and 9 fawns) in the rural area in a 1-hr period during late August. On the other hand, I rarely saw deer in the urban area; nor did residents who documented sightings of deer in their yards. Of the deer that I did see in the urban area during summer, not one was a fawn.

Timings of Migration.--Urban deer commenced spring migrations between 14 April and 1 June, 1994-1996, while rural deer did so between 14 May and 2 June, 1995-1996 (Fig. 2-2). Spring migrations occurred 2-3 weeks sooner for urban deer than rural deer in both 1995 ($P < 0.001$) and 1996 ($P < 0.001$). In general, onset of migrations for urban and rural deer appeared to follow spring green-up on winter ranges, which in turn, corresponded to average temperatures in April and May. Monthly mean temperatures in April were 10.0 C°, 7.9 C°, and 8.1 C° for 1994-1996, respectively. Monthly mean temperatures in May were 16.2 C°, 10.4 C°, and 12.5 C° for 1994-1996, respectively (Utah State University, Climate Center).

Migratory urban deer returned to winter range between 16 September and 15 November, 1994-1996 (Fig. 2-2), while rural deer returned to winter range between 3 October and 15 November, 1995-1996 (Fig. 2-2). Return dates of urban and rural deer to winter ranges were similar in 1995 ($P = 0.253$), but different in 1996 ($P = 0.029$). In general, the return of deer to winter range did not appear to coincide with shifts in weather or snow accumulations in the mountains. Moreover, there was no relationship between the timings of fall migration and the onset of hunting season (i.e., urban deer did not seek refuge from hunters in urban areas). Instead, median dates of return to winter range appeared to be correlated with the dessication of forage on high-elevation summer range, which was likely determined by precipitation levels from the previous year

(October-August). Precipitation was low in 1993/94 at 29.5 cm, high in 1994/95 at 59.5 cm, and moderate in 1995/96 at 41.2 cm (Utah State University, Climate Center).

Spatial Patterns of Migration.--Of the migratory deer, 14 of the radio-telemetered urban deer migrated east and northeast to summer ranges in the Cache National Forest of northern Utah and southern Idaho, and 1 migrated south to a summer range on the valley floor (Fig. 2-1). Mean distance between winter and summer ranges for migratory urban deer was 31.5 km (range = 3.5-52.1). Seven of the 16 radio-telemetered rural deer migrated east and north-east to summer ranges in Cache National Forest; 1of the migratory rural deer could not be located during summer. Mean distance between winter and summer ranges for migratory rural deer was 14.5 km (range = 8.0-24.1). Migratory urban and rural deer intermixed on summer range (Fig. 2-1). Winter ranges were discrete, however, as all radio-telemetered deer tracked for > 1 year exhibited fidelity to their winter ranges. These behaviors were evidenced by both migratory and non-migratory deer.

Winter Home Range Size.--Urban deer home ranges were approximately 0.25 the size of rural deer home ranges (Table 2-1), representing a statistical difference in 1995 ($P = 0.005$), and in 1996 ($P = 0.001$).

Aggregation Within Winter Home Ranges.--Clearly, the relatively small winter home ranges of urban deer contributed to the shorter distances between home range locations (i.e., nearest neighbor values; Table 2-1, Fig. 2-3). However, after standardizing for the linear extent over which locations could be distributed, urban deer still clustered their movements more so than rural deer; dispersion indices (S) for urban deer were significantly smaller both in 1995 ($P < 0.001$) and in 1996 ($P = 0.029$). Based on observations of habitat use, it was clear that the clustering of urban deer locations corresponded to concealment cover (see Chapter IV).

Association Between Yearly Home Range Locations.--The mean distance between the center of winter relocations (centroids) for 1995 and 1996 changed by 513 m ($n = 8$, SD = 286) for urban deer and 755 m ($n = 9$, SD = 502) for rural deer (Table 2-2). These distances for urban and rural deer did not differ significantly from each other ($t = -1.24$, $P = 0.24$). Nevertheless, the MRPP revealed that urban deer were more likely than rural deer to shift the way they distributed themselves within their home ranges from winter to winter (Table 2-2). A visual inspection of deer relocations revealed why most urban deer spatial distributions changed (Fig. 2-3). Within home ranges, urban deer clustered their movements around several key areas that provided concealment and loafing cover. Although home ranges overlapped from year to year, many of these key areas did not. Instead, urban deer tended to use some areas during 1 year, but not the following year. Rural deer, on the other hand, dispersed their movements over the same areas each winter, and were not restricted to regions that provided concealment cover.

Demographic Characteristics

Fawn:Doe Ratios.--Fawn:doe ratios of urban deer (0.41-0.61) were conspicuously smaller than those of rural deer (0.62-0.84) in 1995 and 1996 (Fig. 2-4). Moreover, ratios of urban deer were 30-40% less than those of deer living in other rural areas throughout northern Utah from 1994 to 1996 (D. Austin, UTDWR, pers. comm.), suggesting that fawn:doe ratios were uncommonly low in the urban area. Although I did not separately quantify fawn:doe ratios of migratory and nonmigratory deer during winter, I did observe that only migratory does had fawns in the urban area, whereas migratory and nonmigratory rural appeared to have fawns in equal numbers.

Densities.--Lincoln-Petersen estimates of population size indicated there were 149 urban deer in 1994, 161 urban deer in 1995, and 336 rural deer in 1995 (Table 2-3). These estimates translated to densities of $\approx$ 4.8 urban deer/km^2 in 1994 and 1995, and 8.0 rural deer/km^2 in 1995.

DISCUSSION

Behavioral and demographic characteristics of urban and rural deer differed markedly during My study. Demographically, the relatively low fawn:doe ratios of urban deer indicated that natality or neonatal survival was substantially lower for deer using the urban area. In addition, the lower densities of urban deer during winter implies that fewer animals could exist in the urban area, and combined with fawn:doe data, suggest that density-dependent natality, if operating, occurred at a lower carrying capacity. Collectively, these data suggest that the urban area was an inferior winter habitat compared to the rural area. In addition, the relatively few nonmigratory urban deer, none of which appeared to reproduce, indicates that the urban area was also a relatively poor summer habitat.

These conclusions can be drawn because all deer exhibited fidelity to their summer and winter ranges, and migratory deer intermixed on a common summer range, where they were exposed to comparable forage, risk, and environmental conditions. As such, dissimilarities between urban and rural deer were likely caused by factors inherent to winter ranges. Moreover, because thermal and environmental conditions were equivalent on the 2 winter ranges, risks or forage probably caused these dissimilarities.

Overall, these conclusions conflict with those drawn for white-tailed deer in the north central U.S. Swihart et al. (1995) reported that urban deer in this region achieved reproductive rates equivalent to those of rural deer when deer densities were similar in the 2 habitats. The authors thus proposed that urban environments created ideal conditions for the rapid growth of white-tailed deer populations. When comparing sympatric populations of urban white-tailed and mule deer in Montana, however, Vogel (1983, 1989) found that white-tailed deer exhibited higher natality and lower fawn mortality than mule deer. He thus proposed that the demographic characteristics exhibited by white-tailed deer, combined with their increased nocturnal activity patterns, made them more capable of tolerating the disturbances, and utilizing the resources, in urban habitats than mule deer.

In this vein, the demographic differences between urban and rural deer in My study may have reflected the inability of deer to 1) utilize fully the resources, and 2) cope with the risks, in urban settings. If so, interpretations of the behavioral disparities between urban and rural deer should correspond to these demographic differences, as resource use and risk avoidance are both behaviorally driven. To ensure that behavioral interpretations are compatible with deer demography, however, it is necessary to couch them in terms of a common currency (Anholt 1997). Energy is likely to represent such a currency, as survival and reproduction of Rocky Mountain mule deer are generally limited by the year-round energy balances of individuals (Short 1981, Hobbs 1989, Bartmann et al. 1992), and both foraging behavior and risk avoidance affect the net energetic gains (NEG) of these individuals (Geist 1981, Beier and McCullough 1990, Schmitz 1991, Parker et al. 1996). Therefore, assuming energy has such a subsuming influence, I hypothesize that the behaviors of urban deer, relative to those of rural deer, corresponded to lower NEG on a year-round basis, which reflected inferior demographic characteristics, i.e., natality.

Below, I explain how the behavioral dissimilarities between urban and rural deer might have corresponded to the potential differences in deer NEG on seasonal ranges, under the assumption that both risks and forage affected these gains. I combine these explanations graphically, to construct a time-specific hypothesis of energy acquisition throughout the year (Fig. 2-5). I then use this hypothesis to propose how urban and rural habitats might differ from each other with respect to risks and forage.

Relating Behaviors to Energy

Prevalence of Migration.-- Migration is thought to have evolved so animals could take advantage of spatial and temporal variations in habitat quality (Taylor and Taylor 1977, Dingle 1980, Fryxell and Sinclair 1988). Therefore, given that habitat quality is reflected in deer NEG, the prevalence of migration should correlate with the deviation in the combined NEG of migratory versus nonmigratory animals on seasonal ranges (Fretwell 1972, Nicholson et al. 1997). If so, the proportion of migratory urban deer (92%) may have corresponded to a large difference in the combined NEG of migratory versus nonmigratory animals during summer (Fig 2-5). This difference would have been less distinct for rural deer, as only 60% of them were migratory (Fig. 2-5).

Timings of Migration.--The timings of mule deer migrations have been correlated with several proximate (i.e., environmental) cues (Garrot et al. 1987, Kucera 1992, Nicholson et al. 1997). These correlations generally indicate, however, that the onset of migration is geared ultimately towards maximizing NEG via more profitable foraging or reduced energetic losses (Parker and Stuart 1976, Nicholson et al. 1997, McCorquodale 1999). In spring, this temporal behavior ensures that deer will boost their energy plane prior to birthing, which is crucial for successful reproduction (Short 1981, Fryxell and Sinclair 1988). In fall, this temporal behavior enables deer to buildup fat reserves as much as possible prior to the critical winter period (Wallmo and Regelin 1981, Garrot et al. 1987).

In this study, urban deer migrated 2-3 weeks sooner than rural deer in spring, suggesting that NEG on high-elevation summer range exceeded those on urban winter range before they did on rural winter range (Fig. 2-5). In fall, migratory urban deer returned to winter range before migratory rural deer; but, this trend was somewhat inconclusive as there was considerable overlap in the dates urban and rural deer arrived on their winter ranges. Overall, however, this trend suggests that NEG on high-elevation summer range dropped below those on urban winter range before they did on rural winter range; albeit, these energy crossovers were probably near each other (Fig. 2-5).

Note that these interpretations regarding spring and fall migrations implicitly suggest that the NEG of nonmigratory urban deer were less than those of nonmigratory rural deer between spring and fall. Why? The availability of high quality forage on both winter ranges peaks in early summer, when vegetation is most succulent (Short 1981, Wallmo and Regelin 1981). Accordingly, maximum energy intake rates by nonmigratory urban and rural deer would have occurred at this time. Energetic interpretations of the temporal patterns of migration thus concur with those based on the prevalence of migration.

Home Range Size and Patterns of Use.--Home range size within a species is commonly thought to relate inversely with resource density (Mace et al. 1983). This explanation is logical because increased resource density allows animals to fulfill their energetic needs in a smaller area. Assuming animals are not territorial, a corollary to this explanation is that animal density should increase with resource density. And, if animal density is low in a resource rich habitat, reproduction should be high. In this study, home range sizes of urban deer were only 1/4 those of rural deer, but density and reproduction were also lower in the urban area. This explanation of home range size thus seems dubious, and is unlikely to reflect the differences in NEG of urban and rural deer during winter.

McCorquodale (1993) offers a more appropriate explanation for ungulates during winter: In the absence of disturbance, high energy intake rates are achieved by increased search effort for forage of the best quality, a behavior that manifests as larger home ranges and more dispersed patterns of habitat use. This hypothesis is rooted in optimal foraging theory (MacArthur and Pianka 1966), and implies that, within the constraints of minimum intake, maximum energy is obtained via selective foraging (Jarman 1974, Schmitz 1990).

In this study, the small home ranges and clustered patterns of habitat use of urban deer indicate that their search effort was less than that rural deer. One explanation for reduced effort by urban deer is that valuable forage was so sparse in the urban area that the energetic payoffs of pursuing it were not worthwhile; deer were better off limiting their movements, and conserving their energy reserves. This explanation is untenable for several reasons. First, most forage in urban and rural areas was desiccated and dormant during winter. Therefore, average forage quality should have been similarly poor in these 2 areas, as quality is determined largely by succulence (Short 1981). Second, the urban area contained the same plant species found in the rural area. Presumably, urban deer could have eaten these plants if they searched for them. Finally, exotic vegetation was diverse and ubiquitous in the urban area, and should have been valuable to deer if they availed themselves to it.

Rejection of this explanation suggests that reduced search effort by urban deer may have led to energy intake rates that were lower than those of rural deer during winter. If so, urban deer may have also had lower NEG during this period (Fig. 2-5), as processes affecting energy intake exert a greater effect on deer energy balances during winter than processes affecting energy expenditure (Hobbs 1989). This inference agrees with the observation that urban deer migrated earlier in the spring, as low NEG during winter should correspond to earlier energy crossovers between urban winter range and high-elevation summer range. This inference also agrees with the disparate fawn:doe ratios of urban and rural deer, which indicate that urban deer entered the birthing season in relatively poor condition.

Risks vs. Forage

Corroboration between behavioral and demographic characteristics imparts confidence in my hypothesis of deer NEG, and suggests that I interpreted accurately the dissimilar behaviors of urban and rural deer. As such, this hypothesis implicitly helps identify when factors associated with forage and risks may have differentially affected urban and rural deer. For instance, this hypothesis suggests that forage characteristics could not have explained the small home ranges of urban deer during winter. Therefore, it is likely that risks played a key role.

On many occasions, I observed deer fleeing from dogs and people in the urban area. I also observed people throwing rocks at deer, and once I saw a person shooting at deer with a pellet gun. In addition, one of the radio-telemetered urban deer was illegally shot and killed in the urban area, and more than 17% of the sampled urban deer were killed by automobiles while on winter range during my study. Clearly, the spatial behaviors of urban deer during winter were, in part, responses geared toward reducing exposure to these risks. By compressing their home ranges, urban deer crossed fewer streets, and exposed themselves to fewer people and dogs. By clustering their movements around areas with concealment vegetation, they also reduced their chances of detection and disturbance. And by shifting their year-to-year distributions to different patches of concealment vegetation, they adjusted their patterns of habitat use as certain areas became more or less risky.

The consequence of these behavioral modifications is that urban deer likely traded off access to potential forage, and thus selection opportunities, with risk avoidance. In addition, given that urban deer spent more time in hiding cover, their overall feeding effort may have been reduced, which would have exacerbated this trade-off. The outcome of this trade-off is that urban deer may have reduced risk exposure at a cost of lower energetic or nutritional gains, which, in turn, had repercussions at the population level.

My hypothesis of NEG also suggests that risks may have caused urban deer to migrate sooner than rural deer in spring. This inference can be drawn because many regions of the urban area contained the same type of high-quality vegetation (e.g, alfalfa, emerging forbs) that was found in the rural area during spring. And, as noted in other studies (Wallmo and Regelin 1981, Garrot et al. 1987, Kucera 1992), there appeared to be a correlation between the timings of migration and spring green-up, suggesting that urban deer were indeed responding to forage at this time. Therefore, it is plausible that the risks inherent to the urban area reduced the intake of quality forage during spring; urban deer could better increase their foraging gains by migrating early, thereby accessing the emerging vegetation on less risky transitional and summer ranges.

Unlike the timings of spring migration, the return of urban deer to winter range in fall appeared to be unaffected by risks. Instead, the temporal patterns of fall migration by both urban and rural deer were consistent with other recent findings, which suggest that deer time their migrations to make optimal use of quality forage on winter ranges (Garrot et al. 1987, Nicholson et al. 1997, McCorquodale 1999). For example, Garrot et al. (1987) suspected that deer in Colorado migrated from high-elevation summer range to agricultural winter range before snow accumulations or adverse thermal conditions forced them from the mountains. Early migrations allowed deer to take advantage of irrigated forage on agricultural winter range when nutritional quality of native vegetation on summer range was declining because of plant senescence. This is likely the scenario for both urban and rural deer in My study. Urban winter range contained an assortment of irrigated vegetation, and both urban and rural areas contained several late-season alfalfa fields. This vegetation remained green in the fall, contrasting sharply against the desiccated, native vegetation.

Given that risks were largely responsible for the small winter home ranges and early spring migrations of urban deer, it is plausible that they also discouraged deer from using the urban area during summer. Bowyer (1986) and Loft et al. (1987) noted that fawn mule deer required more hiding cover than adult deer. Therefore, the high potential for disturbance and harassment in the urban area should have forced deer to seek areas with greater security; migration may have been an obligatory response to avoid the adversity associated with urban habitats (Taylor and Taylor 1977).

MANAGEMENT IMPLICATIONS

Migratory urban and rural deer intermixed on a common summer range, but they both exhibited fidelity to their respective winter ranges. Fidelity to seasonal ranges is perpetuated through matrilineal associations (Geist 1981, Mathews and Porter 1993), and its occurrence has been documented extensively. A potential detriment of fidelity to seasonal ranges is that it may constrain dispersal (Garrot et al. 1987). Therefore, if urban deer migrate onto an inferior winter range, tradition may compel them to stay there.

My data do suggest that urban winter range was inferior to rural winter range for most of the year, except for perhaps a brief stint in the fall. However, this conclusion was drawn from a comparison between 1 urban and 1 rural study area over several years of moderate snowfall. Further studies are needed in different regions, and under different environmental conditions. During years of heavy snowfall, urban winter ranges may be superior to surrounding rural areas, as much of the shrubby vegetation in urban areas would stand above the snow, whereas that in rural areas would be buried. Regardless, the results of this study emphasize the need to conserve undeveloped regions of traditional mule deer winter ranges. If the goal is to boost mule deer populations in or near urban settings, I recommend enhancing the amount of concealment vegetation available to deer. On the other hand, if control is needed, it may be possible to regulate deer distribution by manipulating the arrangement or accessibility of hiding cover.

Because most urban deer were migratory, they can be harvested away from city limits where traditional hunting techniques are feasible. However, many deer returned to urban areas before the general hunting season. Therefore, hunting season dates may need to be changed if urban deer are to be targeted. Moreover, because urban and rural deer intermixed on a common summer range, the only option for selective management of urban deer may be to harvest them on transitional ranges during periods of fall migration.

LITERATURE CITED

Anholt, B. R. 1997. How should we test for the role of behaviour in population dynamics? Evolutionary Ecology 11:633-640.

Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a

Colorado mule deer population. Wildlife Monographs 121:1-39.

Beier, P., and D. R. McCullough. 1990. Factors influencing white-tailed deer activity patterns and patterns of habitat use. Wildlife Monographs 109:1-51.

Biondini, M. E., P. Mielke, and E. F. Redente. 1988. Permutation techniques based on euclidean analysis spaces: a new and powerful statistical method for ecological research. COENOSES 3:155-174.

Bowyer, R. T. 1986. Habitat selection by southern mule deer. California Fish and Game 72:153-179.

Conover, M. R. 1995. What is the urban deer problem and where did it come from? Pages 11-18 *in* J. B. McAninch, technical coordinator. Proceedings of the 1993 symposium of the north central section, The Wildlife Society.

Dingle, H. 1980. Ecology and evolution of migration. Pages 1-11 *in* S. A. Gauthreaux, Jr., editor. Animal migration, orientation, and navigation. Academic Press, New York, New York, USA.

Freddy, D. J., M. W. Bronaugh, and M. C. Fowler. 1986. Responses of mule deer to disturbances to persons afoot and snowmobiles. Wildlife Society Bulletin 14:63-68.

Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, New Jersey, USA.

Fryxell, J. M., and A. R. E. Sinclair. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology and Evolution 3:237-241.

Garrot, R. A., G. C. White, R. M. Bartmann, L. H. Carpenter, and A. W. Alldredge.

1987. Movements of female mule deer in northwest Colorado. Journal of Wildlife Management 51:634-643.

Geist, V. 1971. A behavioural approach to the management of wild ungulates. Pages 413-434 *in* E. Duffy and A. S. Watt, editors. The scientific management of plant and animal communities for conservation. Blackwell Scientific Publishers, Oxford, UK.

_____. 1981. Behavior: adaptive strategies in mule deer. Pages 157-225 *in* O. C. Wallmo, editor. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, Nebraska, USA.

Hobbs, N. T. 1989. Linking energy balance to survival in mule deer: development and test of a simulation model. Wildlife Monographs 101:1-39.

Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho primitive area. Wildlife Monographs 21:1-39.

Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. Behaviour 48:215-267.

Kie, J. G., J. A. Baldwin, and C. J. Evans. 1994. CALHOME: home range analysis program. U.S. Forest Service, Pacific Southeast Research Station, Fresno, California, USA.

Kucera, T. E. 1992. Influences of sex and weather on migration of mule deer in California. Great Basin Naturalist 52:122-130.

Lima, S. L., and L. M. Dill. 1990. Behavioral risks made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619-640.

Loft, E. R., J. W. Menke, J. G. Kie, and R. C. Bertram. 1987. Influence of cattle stocking rate on the structural profile of deer hiding cover. Journal of Wildlife Management 51:655-664.

MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of patchy environments. American Naturalist 100:603-609.

Mace, G. M., P. H. Harvey, and T. H. Clutton-Brock. 1983. Vertebrate home-range size and energetic requirements. Pages 32-53 *in* I. R. Swingland and P. J. Greenwood, editors. The ecology of animal movement. Clarendon Press, Oxford, UK.

Mathews, N. E., and W. F. Porter. 1993. Effect of social structure on genetic structure of free-ranging white-tailed deer in the Adirondack Mountains. Journal of Mammalogy 74:33-43.

McClure, M. F., J. A. Bissonette, M. R. Conover., and D. D. Austin. 1997. Range expansion of white-tailed deer (*Odocoileus virginianus*) into urban and agricultural areas of Utah. Great Basin Naturalist 57:278-280.

McCorquodale, S. M. 1993. Winter foraging behavior of elk in the shrub-steppe of Washington. Journal of Wildlife Management 57:881-890.

_____. 1999. Movements, survival, and mortality of black-tailed deer in the Klickitat Basin of Washington. Journal of Wildlife Management 63:861-871.

Neal, A. K., G. C. White., R. B. Gill, D. F. Reed, and J. H. Olterman. 1993. Evaluation of mark-resight model assumptions for estimating mountain sheep numbers. Journal of Wildlife Management 57:436-450.

Nelson, M. E., and L. D. Mech. 1986. Relationship between snow depth and grey wolf predation on white-tailed deer. Journal of Wildlife Management 50:471-474.

Nicholson, M. C., R. T. Bowyer, and J. G. Kie. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78:483-504.

Parker, G. A., and R. A. Stuart. 1976. Animal behavior as a strategy optimizer: evolution of resource assessment strategies and optimal emigration thresholds. American Naturalist 110:1055-1076.

Parker, K. L, M. P. Gillingham, T. H. Hanley, and C. T. Robbins. 1996. Foraging efficiency: energy expenditure versus energy gain in free-ranging black-tailed deer. Canadian Journal of Zoology 74:442-450.

Quenette. P. Y. 1990. Functions of vigilance behaviour in mammals: a review. Acta Oecologia 11:901-818.

Reed, D. F. 1981. Conflicts with civilization. Pages 509-535 *in* O.C. Wallmo, editor. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, Nebraska, USA.

Rost, G. R., and J. A. Bailey. 1979. Distribution of mule deer and elk in relation to roads. Journal of Wildlife Management 43:634-641.

SAS Institute, Inc. 1988. SAS/STAT user's guide, release 6.03 edition. SAS Institute, Cary, North Carolina, USA.

Schmitz, O. J. 1990. Management implications of foraging theory: evaluating deer supplemental feeding. Journal of Wildlife Management 54:522-532.

_____. 1991. Thermal constraints and optimization of winter feeding and habitat choice in white-tailed deer. Holarctic Ecology 14:104-111.

Short, H. L. 1981. Nutrition and metabolism. Pages 99-127 *in* O.C. Wallmo, editor. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, Nebraska, USA.

Smith, D. O., M. Conner, and E. R. Loft. 1989. The distribution of winter mule deer use around home sites. Transactions of the Western States Section of the Wildlife Society 25:77-80.

Sweeney, J. R., R. L. Marchinton, and J. M. Sweeney. 1971. Responses of radio-monitored white-tailed deer chased by hunting dogs. Journal of Wildlife Management 35:707-716.

Swihart, R. K., P. M. Picone, A. J. DeNicola, and L. Cornicelli. 1995. Ecology of urban and suburban white-tailed deer. Pages 35-44 *in* J. B. McAninch, technical coordinator. Urban deer: A manageable resource? Proceedings of the 1993 symposium of the north central section, The Wildlife Society.

Taylor, L. R., and R. A. J. Taylor. 1977. Aggregation, migration, and population mechanics. Nature 265:415-421.

Vogel, W. O. 1983. The effects of housing developments and agriculture on the ecology of white-tailed deer and mule deer in the Gallatin Valley, Montana. Thesis, Montana State University, Bozeman, Montana, USA.

_____. 1989. Response of deer to density and distribution of housing in Montana. Wildlife Society Bulletin 17:406-413.

Wallmo, O. C. 1978. Mule and black-tailed deer. Pages 31-41 *in* J. L. Schmidt, and D.

L. Gilbert, editors. Big game of North America, ecology and management. Stackpole Books, Harrisburg, Pennsylvania, USA.

_____, and W. L. Regelin. 1981. Rocky Mountain and intermountain habitats. Pages 387-421 *in* O. C. Wallmo, editor. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, Nebraska, USA.

Warren, R. J. 1997. The challenge of deer overabundance in the 21st century. Wildlife Society Bulletin 25:213-214.

White, G. C., and R. A. Garrot. 1990. Analysis of wildlife radio-tracking data. Academic Press, New York, New York, USA.

Table 2-1. Minimum convex polygon (MCP, 95%) home ranges and dispersion metrics for deer wintering in urban and rural areas of Cache Valley, Utah, 1995 and 1996.

	1995						1996					
	Urban			Rural			Urban			Rural		
Metric	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*
MCP (ha)	275	140	11	1095	365	11	299	179	10	1172	636	11
Nearest neighbor[a] (m)	106	33	11	359	74	11	104	40	10	335	95	11
Dispersion index[b]	0.033	0.006	11	0.053	0.007	11	0.036	0.016	10	0.050	0.007	11

[a] Denotes the distance from 1 location to its nearest neighboring location, averaged across all locations.

[b] Denotes the nearest neighbor value divided by the spatial extent of x- and y-coordinates; smaller values indicate a more clustered distribution.

Table 2-2. Metrics indicating the degree of overlap between mule deer home range locations during the winters (1 January-15 March) of 1995 and 1996 in Cache Valley, Utah.

Study area	Deer ID	Distance between yearly centroids (m)[a]	MRPP P-value[b]
Urban	1510	502	0.0033
	1531	548	0.0221
	1551	198	0.1184
	1980	243	0.1173
	2605	601	0.0002
	2625	496	0.0141
	2703	909	0.0005
	2760	810	0.0041
Rural	1165	786	0.0222
	1357	311	0.6797
	1455	1844	0.0040
	1525	353	0.4257
	1545	1286	0.0122
	1565	672	0.2821
	2717	472	0.2998
	2726	578	0.4043
	2736	496	0.1800

[a] Equals the mean UTM from 1995 locations minus the mean UTM from 1996 locatio

[b] A significant value ($P < 0.05$) indicates that UTMs from 1995 and 1996 are not from the same probability distribution.

Table 2-3. Mark-resight estimates of population size for mule deer living in a 32-km^2 urban area and a 42-km^2 rural area of Cache Valley, Utah.

Area	Year	Minimum number	Estimate (95% CI)	Sighting occasions
Urban	1994	116	149 (136-166)	6
Urban	1995	108	161 (136-200)	3
Rural	1995	229	336 (275-452)	3

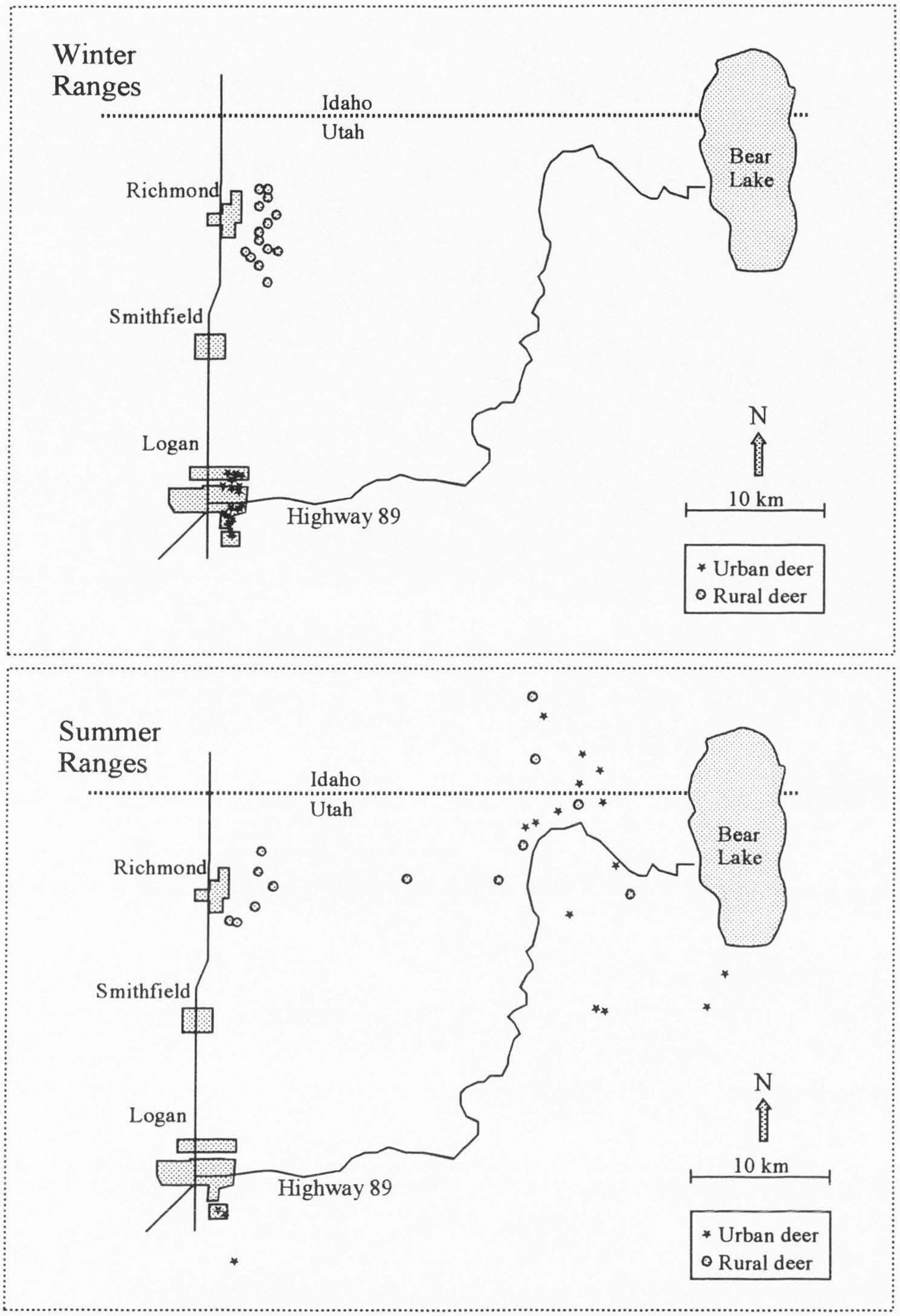


Figure 2-1. Seasonal ranges of 17 radio-telemetered mule deer wintering in an urban area and 14[1] radio-telemetered mule deer wintering in a rural area of Cache Valley Utah, 1994-1996. [1]One of the rural deer could not be located on summer range.

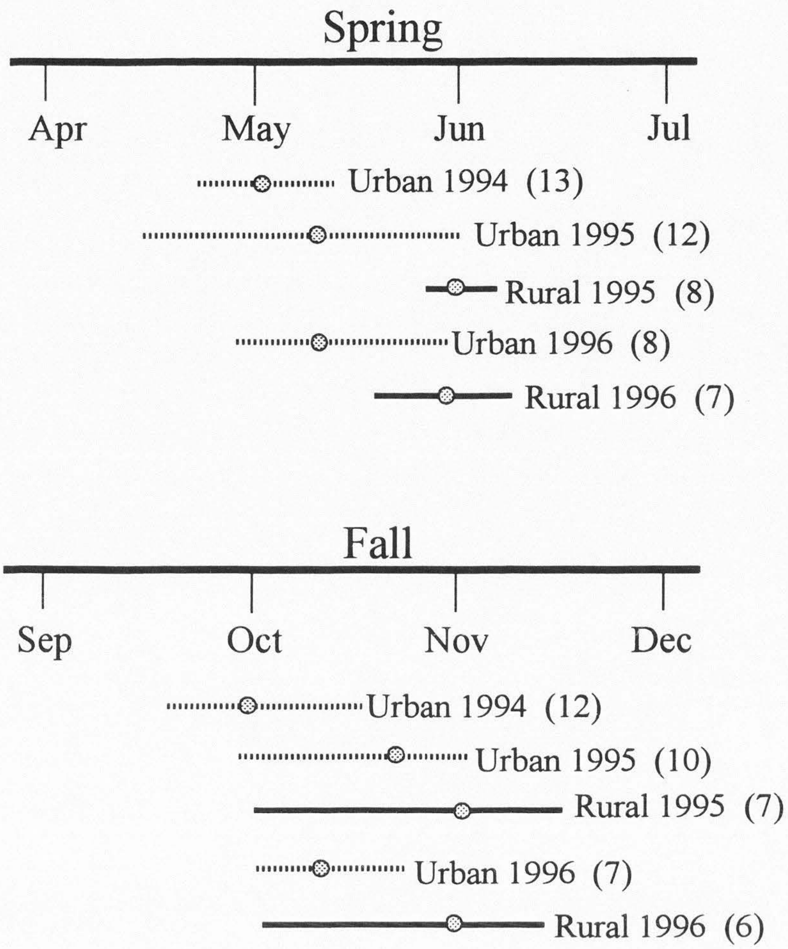


Figure 2-2. Timings of spring and fall migration for deer wintering in urban and rural areas of Cache Valley, Utah. Circles are median dates, and lines represent ranges. Sample sizes are in parentheses.

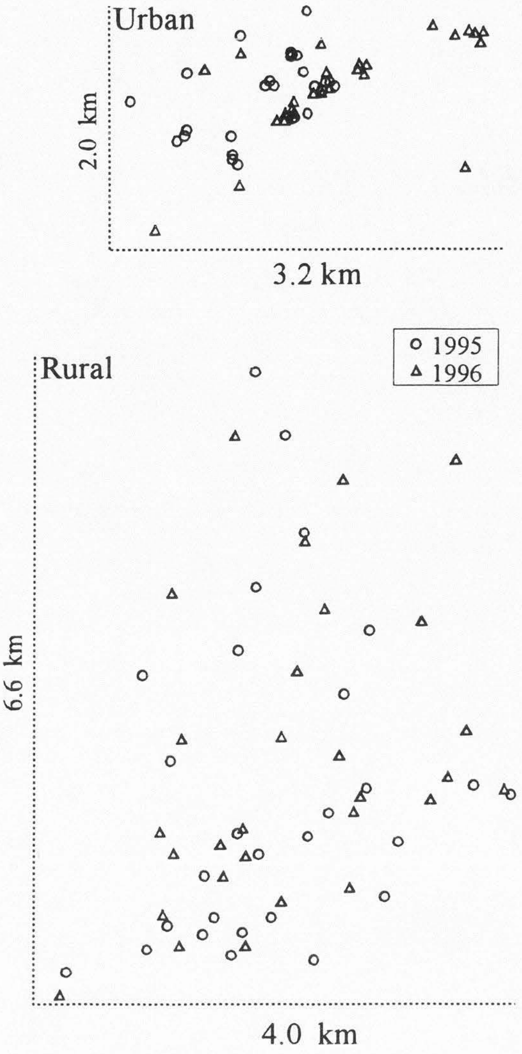


Figure 2-3. Representative examples of how radio-telemetered deer dispersed their movements on urban and rural winter ranges of Cache Valley, Utah, January-March 1995 and 1996. Note that the locations of the urban deer encompass a smaller area, and are more clustered relative to those of the rural deer.

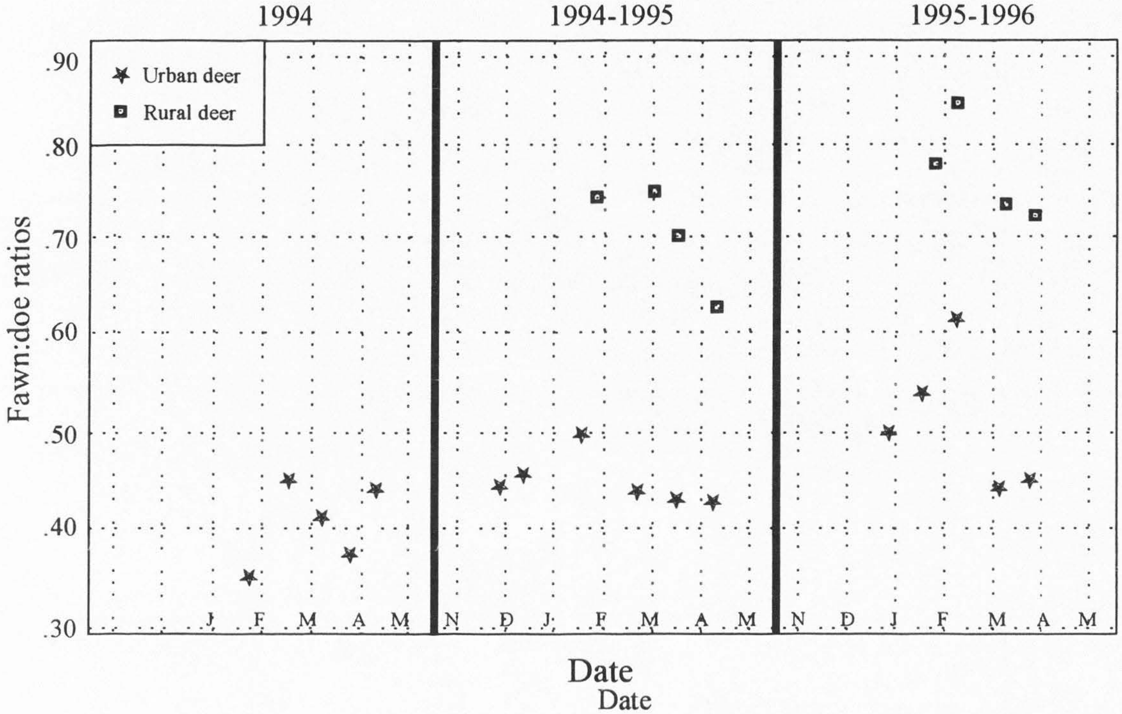


Figure 2-4. Fawn:doe ratios of mule deer wintering in a 32-km^2 urban area and a 42-km^2 rural area of Cache Valley, Utah.

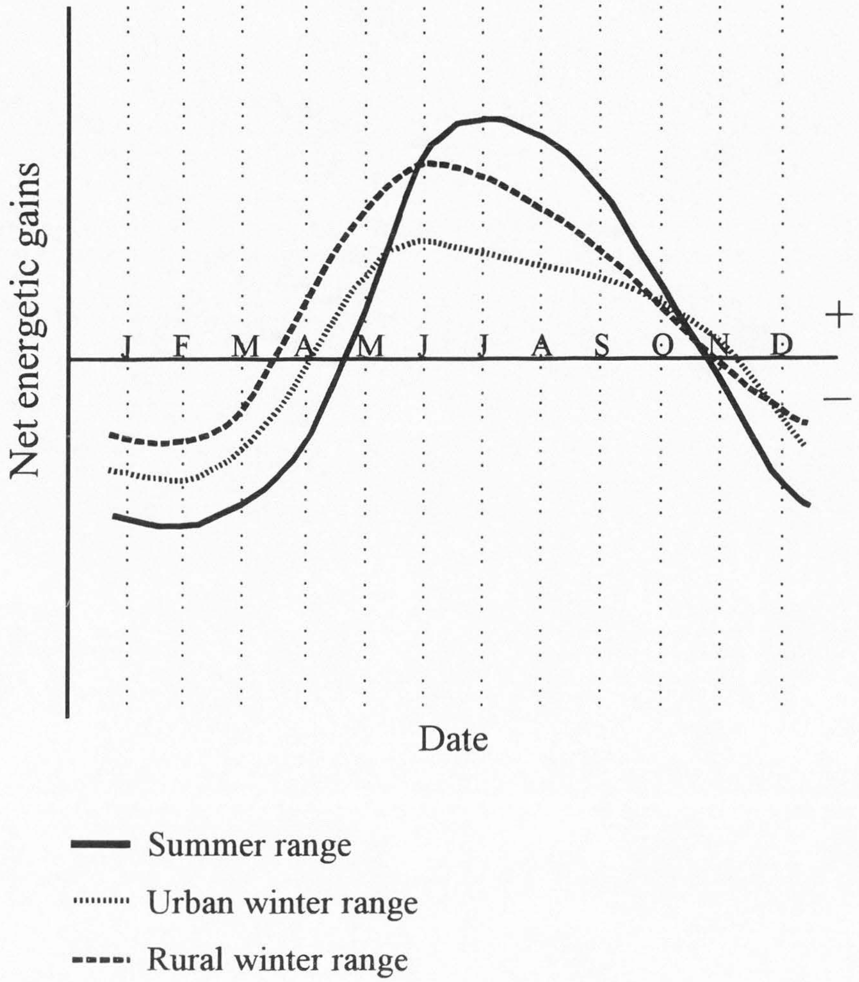


Figure 2-5. Time-specific hypothesis of the net energetic gains by migratory and non-migratory mule deer using urban and rural winter ranges, and high-elevation summer ranges of Cache Valley, Utah. Qualitative differences in energy curves correspond to dissimilar behaviors and demographics of deer in each area. These differences may be influenced by risks or forage, both of which manifest themselves as net energetic gains. Crossovers between energy curves (urban versus summer and rural versus summer) indicate when migrations should occur.

CHAPTER 3

FRACTAL ANALYSIS OF MOVEMENT PATHWAYS: A REVISED METHODOLOGY AND AN ENERGETIC INTERPRETATION

Abstract: Fractal analysis of animal movement pathways has become increasingly popular in the recent literature. By describing a pathway's space-filling attributes over multiple resolutions of analysis, a fractal dimension (D) indexes how animals respond to habitat as a function of scale. Accordingly, D has been used as a tool for assessing 1) how different species respond to habitat, and 2) how landscape heterogeneity influences an animal's "scale(s) of response." The use of fractal analysis has been criticized, however, because estimates of D may be based on fallacious interpretations of a pathway's scale-invariant properties. In this chapter, I show that the most common technique used to calculate D, the divider method, is likely to produce erroneous results, thereby invalidating inferences regarding how animals respond to habitat. After showing that other existing techniques are also problematic, I introduce a technique, the slider method, that solves some of the problems inherent to analyzing pathway data. I then use this technique to assess how D changes as a function of resolution (δ) for mule deer (*Odocoileus hemionus*) movements in urban and rural areas. This technique shows that the relationship of D versus δ increased monotonically for pathways of urban and rural deer, and that D at asymptote was nearly identical for urban and rural pathways. However, the δ at which asymptotic D was reached, referred to here as δ^*, was finer for rural pathways than urban pathways. Based on these findings, I hypothesize that the value of D at asymptote (~1.3) represents

an intrinsically driven movement pattern that allows animals to sample the resources in their home ranges while minimizing their energetic expenditures. At δs finer than δ^*, response to habitat is, in part, driven by animals cuing in on resources or landscape patterns, particularly in the animal's most immediate surroundings. Accordingly, it is at these fine δs that habitat heterogeneity must be measured.

INTRODUCTION

Movement is the means by which mobile animals find resources and avoid risks (e.g., predators, stressful thermal conditions). By moving, however, animals incur energetic expenditures. Movement patterns are thus likely to result from behavioral interactions with habitat in which animals attempt to balance several factors affecting their fitness. Clearly, the outcomes of these interactions will be manifested in the distributional and demographic composition of populations (Levin 1992, Wiens 1995, Turchin 1998). In the words of Taylor and Taylor (1983, p.181): "Without movement the individual has no behavior and the population has no cohesion so that distribution in space is isolated from distribution in time and there is no survival." Not surprisingly, studies of animal movement have an extensive history in the ecological sciences.

At the heart of these studies is the analysis of movement pathways, which, conceptually, represent the signatures to how animals interact and respond to habitat. That is, movement pathways reveal how resources are encountered or sampled, and how much energy is expended traversing across a given landscape.

To describe and analyze movement pathways, researchers have recently employed an approach based on fractal analysis (Dicke and Burrough 1988, Crist et al. 1992, With

1994, Wiens et al. 1995, Nams 1996, Etzenhouser et al. 1998, McIntyre and Wiens 1999). In its simplest interpretation, a fractal dimension (D) indexes the degree of space-fill or tortuosity of a movement pathway (Mandelbrot 1983, Dicke and Burrough 1988). Conceptualizing the surface upon which an animal travels as 2-dimensional, D can theoretically range from 1, which indicates the pathway is a straight line, to 2, which indicates the pathway is so convoluted that it visits all points in a portion of 2-dimensional space. The pathways of real organisms will lie between these theoretical possibilities.

Usually, the calculation of D for any pattern or object is accomplished by performing a multiple resolution (δ) analysis, where δ is the degree of refinement (e.g., ruler size, box size) at which the pattern or object is measured. As such, fractal analysis has been widely accepted as a solution for describing and comparing the properties of different-sized patterns or objects (Sugihara and May 1990, Johnson et al. 1995, Milne 1997). The analysis takes the general form:

$$P = k\delta\Phi(\delta) \qquad (1)$$

where P is some property (e.g., length, shape, distribution) of the object or pattern at a given δ, k is a prefactor to the power law, and the exponent $\Phi(\delta)$ is a simple function of δ. In most cases, k and $\Phi(\delta)$ are calculated empirically by linear regression of logarithmically transformed data (P and δ) in equation 1; k is the y-intercept, and $\Phi(\delta)$ is the slope of the line, such that $\Phi(\delta)$ = D. If there is a strong fit to the regression, the pattern or object is considered to be statistically self-similar across a specified range of δs, and in a generic way is dubbed as being “fractal” (Anvir et al. 1998). A true fractal, in a purely mathematical sense, would require the pattern or object to be self-similar over many orders of magnitude (Mandelbrot 1983). For ecological systems, however, the primary concern is that D is calculated over the orders of magnitude pertinent to the organisms or precesses in question (Milne 1997, Tsonis et al. 1998, Ritchie and Olff 1999).

Because fractal analysis explicitly incorporates multiple δs, several researchers have suggested that D of a movement pathway may identify an animal's "scale of response" to a landscape (Crist et al. 1992, With 1994, Wiens et al. 1995, McIntyre and Wiens 1999). That is, when a pathway appears "fractal" over a biologically relevant range of δs, D represents a scale-invariant index of how an animal perceives and responds to habitat. Smaller values of D imply that animals perceive and respond to habitat at a coarse grain, where grain is the scale (i.e., size of area) at which the animal views and measures the landscape. Larger values of D, conversely, imply that response occurs at a fine grain, e.g., animals perceive the landscape as if it consists of many small, proximal patches (Levin 1992, Ritchie 1998).

The scale of response concept has several touted applications. First, D can be used to assess similarities or differences in how various species respond to habitat heterogeneity (landscape structure and resource patchiness) in a way that is independent of body size, physiology, diet, life history, and vagility (Wiens et al. 1995). Similarities in D among species may indicate that movement patterns, and thus responses to habitat, are influenced by a common set of processes or constraints. Second, D can be used to assess how a species changes its scale of response when habitat heterogeneity changes (With 1994, Etzenhouser et al. 1998, McIntyre and Wiens 1999). As such, it provides a starting point for experimental and theoretical investigation into how animals will respond to different landscapes. Along these same lines, it has been proposed that shifts in D at different ranges of δ may indicate a concomitant shift in the processes responsible for the movement pattern (Crist et al. 1992, Johnson et al. 1992, With 1994). For instance, the various habitat components to which an animal responds (e.g., forage versus hiding cover) may exhibit different spatial patterns (distributions) at a given grain of perception. If so, an animal must adopt multiple scales of response to effectively use these components (Morrison et al. 1992, Nams 1996).

Essential to the scale of response concept is that estimates of D, and changes in D, must accurately portray a movement pathway's tortuosity or space-filling attributes over the biologically relevant range of δs. That is, the technique used to calculate D must correctly identify whether the pathway is "fractal" over this range, or whether D changes as a function of δ. In these regards, Turchin (1996) has questioned the use of fractal analysis because estimates of D in past studies appeared to be based on fallacious interpretations of a pathway's scale-invariant properties, i.e., D was not constant across all δs of analysis, but appeared to increase as a function of δ.

In this chapter, I argue that the most common technique used to calculate D, the divider method, tends to erroneously inflate the value of D for most movement pathways. Moreover, the inflation of D is exacerbated at large divider sizes, giving the false impression that D increases as a function of δ. This flaw thus suggests that any inferences regarding an animal's scale(s) of response may be dubious when the divider method is used. To determine if this flaw is rectified with other existing techniques, I also examine 2 additional methods that have been used to calculate D of movement pathways: the

Vfractal (Nams 1996) and the Katz-George method (Bascompte and Vilà 1997). Upon demonstrating that these techniques are also problematic, I then introduce a technique, the slider method, that solves some of the problems inherent to analyzing pathway data. This technique is essentially a modification of the box-counting procedure (Hastings and Sugihara 1993) of calculating D of spatial patterns.

For illustration, I use the slider and divider methods to analyze the movement pathways of mule deer living in urban and rural areas of Cache Valley, Utah. This example highlights the problems with the divider method, and shows that the 2 methods produce fundamentally different D versus δ relationships. Based on the D versus δ relationship obtained via the slider method, I propose that deer movements are a function of 1) habitat heterogeneity in the 2 areas at fine δs of analysis, and 2) a common process that allows deer to maximize use of their home ranges while minimizing energetic expenditures. This interpretation adds interesting and potentially valuable insight to the scale of response concept.

PROBLEMS WITH DIVIDER-D AND OTHER EXISTING METHODS

The Divider Method

Implementation of the divider method is accomplished by "stepping" dividers (δs; rulers, circles) of different lengths over the movement pathway (Dicke and Burrough 1988, Klinkenburg 1994). D is then calculated from the equation

$$P = k\delta^{1-D}. \tag{2}$$

To determine if the tortuosity of the pathway is constant or changes across δ, D can be estimated piecemeal from the regression of log (*P*) verus log (δ) over several narrow ranges of δ (Nams 1996), or the residuals for the entire regression (finest δ to coarsest δ) can be examined to identify trends across all δs of analysis (Milne 1997). Note, however, that D is based on characterization of the whole pathway at each range of δs; the pathway is not partitioned into pieces.

The divider method can overestimate D of movement pathways in 3 ways. The first, dubbed the "remainder effect," exaggerates D of nearly all linear data, and results from the fact that a non-integer number of steps (dividers) is generally required to cover a line (Aviles et al. 1987, Klinkenburg 1994). These fractional step lengths tend to get larger as a function of δ, but they need to be retained in the calculation of D to maintain consistency across different δs; rounding causes additional problems (Klinkenburg 1994). The second source of overestimation is an exacerbation of the remainder effect and results when movement pathways double-back on themselves, e.g., an animal walks along a trail, then turns around and walks the trail in the opposite direction. The divider method mistakes this behavior as increased tortuosity, when in actuality, the pathway has not changed. As the divider is "stepped" along a pathway, it searches for the nearest intersection point. If this intersection is 180° in the reverse direction, the remaining segment of the pathway in the forward direction is not added to the total path length. On average, remaining segments increase with divider size, leading to an artificially steep relationship between log *(P)* and log(δ), thus inflating D at larger divider lengths (Table 3-1). The third source of overestimation occurs when pathways consist of patchy movements in localized areas (i.e., the pathway circles around and crosses over the top of itself) followed by relatively linear movements between patches (Fig. 3-1). In this scenario, which is likely common for most movement pathways, small dividers detect tortuosity in localized patches, but larger dividers step over these patches, again leading to an artificially steep negative relationship between log (*P*) and log (δ). If movements inside these patches are extensive, the slope of the log-log plot can become so steep that D exceeds 2. This, of course, is theoretically impossible, as D of a spatial pattern cannot exceed its embedding dimension (Feder 1988). The embedding dimension, in this case, is the 2-dimensional plane upon which the animal travels.

The Vfractal Method

The Vfractal method (Nams 1996) is based on dividing a movement pathway into pairs of steps. Each step is a straight line of length δ. Because a pathway will normally have curvature, each pair of steps forms a V. Each V, in turn, describes how convoluted the pathway is by 1) the degree of the angle in the notch of the V, or 2) the distance between the outer points of the 2 steps. Nams (1996) derives 4 different estimators of D that can be obtained from these Vs.

The main advantage of these estimators is that each V gives a separate estimate of D for that part of the pathway (the divider method characterizes the whole path, not pieces of it). Therefore, by combining Vs, variance estimates of a pathway's tortuosity at different δs can be obtained. Unfortunately, it is easy to see that this method suffers from some of the same problems plaguing the divider method; Vs confuse pathways that double-back on themselves as increased tortuosity, and Vs at fine δs will recognize patchy movements while Vs and coarser δs will completely step over these patches. Our simulations showed that these problems were pervasive and real.

The Katz-George Method

Bascompte and Vilà (1997) used the fractal index of Katz and George (1985) to characterize movement pathways. The index is defined as:

$$D = \frac{\text{Log}\,(n)}{\text{Log}\,(n) + \text{Log}\,(d/L)}, \qquad (3)$$

where n is the number of steps, L is the total path length (sum of step segments), and d is the planar diameter (greatest distance between any 2 points). Although this index is computed easily, one of its main shortcomings is that it does not calculate D over different δ*s*. Instead, D is simply computed at the δ at which the steps (path segments) were measured, and the estimated D represents an average for the entire pathway. Consequently, it is impossible to determine if D is constant or changes as a function δ. Another drawback is that D can range from 1 to infinity, which makes interpreting the index in 2- or 3-dimensional landscapes perplexing.

A NEW METHOD: SLIDER-D

In attempt to overcome the problems associated with existing techniques, I modified the box-counting method (Mandelbrot 1983, Hastings and Sugihara 1993) of calculating D to handle pathway data. This method is implemented by covering a pathway with a set of square boxes of side length δ (Fig. 3-2). Within each box, there are 4 cells of side length δ/2. The number of boxes and cells containing a piece of the pathway are summed and D at a given δ is calculated as:

$$D = \frac{\text{Ln}\, N_{\delta/2} - \text{Ln}\, N_{\delta}}{\text{Ln}\, [1/(\delta/2)] - \text{Ln}\, [1/\delta]}, \tag{4}$$

where N_{δ} is the number of boxes in the grid containing a piece of the pathway, and $N_{\delta/2}$ is the number of cells in the grid containing a piece of the pathway, such that $N_{\delta/2} \geq 2N_{\delta}$. Like the divider method, this method calculates D based on characterization of the whole pathway, not pieces of it. To compute D at different δ, the box size of the grid is varied.

Note that with slight modification and rearrangement, equation 4 is a discrete version of the box-counting algorithm, which is given by:

$$P = k\delta^{-D}, \tag{5}$$

where P is path length measured by the number of boxes occupied by the pathway, and δ is box size. The objective of performing discrete analyses (i.e., at each δ) is to illuminate the shape of the D verus δ relationship.

To handle pathway data, the slider method makes 2 modifications to the classic box-counting procedure. The first modification consists of 2 steps. First, each box is positioned in such a way that the maximum length of the pathway is covered. Second, the box is slid vertically and horizontally until the fewest number of cells are occupied while simultaneously maintaining maximum path length coverage. For linear pathways, this will entail abutting box boundaries. But for convoluted pathways, this modification may entail overlapping box boundaries, i.e, moving boxes over the top of each other (Fig. 3-2). The purpose of this modification is to ensure that the pathway is covered by the fewest number of boxes, which is a fundamental prerequisite of fractal analysis (Mandelbrot 1983).

The second modification requires that the cells containing a piece of the pathway be counted only once while the pathway is contained within a box (Fig. 3-2). This means that the pathway can circle around in a box infinitely, passing through each cell many times; but, the maximum cell count for that box cannot exceed 4. This modification is intuitive because once a pathway occupies all space in a portion of 2-dimensional plane, further movements cannot drive the pathway into the next dimension. In essence, this modification cures the patchy movement problem that plagues the divider method. With these 2 modifications, the slider method can of effectively measure all types of pathways (Fig. 3-3).

Because the slider method only considers the number of boxes and cells occupied by a pathway, interpretation of D is restricted to the pathway's space-filling attributes. The divider method, on the other hand, attempts to measure the actual length of the pathway, and interpretation of D therefore relates to pathway tortuosity. Although this distinction may seem subtle, as the 2 measures are likely highly correlated, I propose that the slider method may be more useful because commensurate box-counting procedures can be used to measure landscape patterns or resource distributions to which movements may be associated (Loehle and Li 1996, Ritchie 1998). The divider method is only applicable with line data.

A CASE STUDY: ANALYSIS OF DEER MOVEMENTS USING THE SLIDER AND DIVIDER METHODS

To evaluate the results of the slider and divider methods for animals using free-ranging environments, and to examine the D versus δ relationship over 2-3 orders of magnitude, I analyzed the movement pathways of mule deer in urban and rural areas of Cache Valley, Utah. The habitat components to which deer used in each area exhibited markedly different spatial distributions (see Chapter 4). Moreover, housing, roads and fences in the urban area probably altered the complexity of the landscape relative to that in the rural area. Consequently, these 2 areas afforded a unique opportunity to test if landscape pattern influenced D of deer movements across a range of δs.

Study Areas

The urban and rural areas were situated along the west base of the Wasatch Mountains, approximately 100 km north of Salt Lake City, and were used primarily by migratory mule deer during winter (November-April). The urban area was contained within the City of Logan and surrounding residential communities. The rural area was centered 15 km north of the urban area. Elevation (~1500 m) and climate were similar in both areas. Snow depths ranged from 5 to 40 cm during periods of data collection (January-March, 1997 and 1998), and temperatures were also similar, ranging from -20 to 6 C°.

Residential housing (0.15-8.0 houses/ha) dominated the urban landscape, and vegetation was diverse, consisting of exotic and native species as well as plowed crop fields. The rural area, in contrast, was characterized by a more open landscape. Vegetation consisted of crop fields in a rangeland dominated by big sagebrush (*Artemesia tridentata*), bitterbrush (*Purshia tridentata*), cheatgrass (*Bromus tectorum*), and crested wheatgrass (*Agropyron desertortum*). Ravines and north-facing slopes contained patches of big-toothed maple (*Acer grandidentatum*).

Field Methods and Data Analyses

I collected mule deer pathway data from January to March, 1997 and 1998 by 1) following deer trails in the snow, and 2) plotting the movements of telemetered deer on aerial photographs (scale = 1:1000). These 2 techniques allowed us to capture the essence of deer movement pathways from fine (4 m) to coarse (600 m) δs. My objective was to collect snow trail data at a large enough extent, and telemetry data at high degree of accuracy, so the δs used to calculate D from these 2 collection procedures overlapped.

To collect snow trail data, I walked along tracks at 1-m step increments and recorded Cartesian coordinates at locations where the bearing of the pathway changed by $> 3^\circ$ from the previous bearing (Fig. 3-4). I measured bearings to the nearest 1° with a hand-held compass. I selected trails in multiple regions throughout each study area to provide representative samples of deer movements in these areas. I followed trails until 300 coordinates were recorded, or until trails could not be identified (e.g., they were lost in other tracks). To ensure trails adequately sampled the movements of deer in each area, I did not analyze trails with < 30 coordinate locations, or trails that were < 50 m in extent (distance between 2 outermost coordinates).

To collect telemetry data, I recorded the locations of telemetered deer as Universal Transverse Mercator coordinates (UTMs) every 2-60 min. (Fig. 3-4); shorter time intervals were used when deer were active (e.g., dawn and dusk), whereas longer intervals were used when deer were resting (e.g., middle of the day). I determined the locations of telemetered animals by either 1) observing them visually, and pinpointing their UTMs on aerial photographs, or 2) circling the areas from which their radio signals emanated (radii of search were 20-50 m for urban deer and 50-90 m for rural deer), and estimating their UTMs as the center of these areas. Circling radio-signals was required when deer were in thick cover, and could not be seen without disturbing them. During these times, and during visual observations, I was exceedingly careful not to alarm deer, thus allowing their movement behaviors to be as natural as possible. This was less of a problem in the urban area, as I could more readily approach deer in a vehicle. Consequently, the search radii for deer in thick cover were shorter in the urban area than the rural area.

The deer I followed did not associate with each other, and their home ranges did not overlap during winter. Their movements thus encompassed different regions of each study area. I recorded the locations of telemetered deer for up to 48 hr, or as long as they could be followed (i.e., deer occasionally traveled into areas that were inaccessible). To ensure telemetry pathways adequately sampled the movements of deer in each area, I did not analyze pathways with < 50 coordinate locations, or pathways that were < 1 km in extent.

I analyzed urban and rural movement pathways using the slider and divider methods. For snow trail data, I set the finest δ (minimum box size) of analysis at 3 m, which was 3 times the δ at which data were collected. For telemetry data, I set the finest δ of analysis equal to 3 times the coarsest δ at which data were collected. This value averaged 160 m for urban pathways and 260 m for rural pathways. The coarsest δ (maximum box size) of analysis for snow trail and telemetry analyses was set at 1/4 the extent of each pathway, where extent was defined as the distance between the 2 outermost coordinates of a pathway. After setting the coarsest δ for each pathway, D was then calculated at δs equal to 1/6, 1/8, 1/12 ... the extent of each pathway, until the finest δ was achieved. To ensure the results from the slider and divider methods were commensurate, I estimated D via the divider method as the slope of the line created by the 2 points of δ and δ/2, i.e., the same points used in the slider method.

Although one may think the difference in minimum δ for urban and rural telemetry pathways would inherently influence their D values, it does not. Because D of a pathway is calculated at a box size ≥ 3 times the distance between the farthest apart consecutive coordinate locations at its finest δ, boxes essentially ignore the "shape" of the pathway that would exist if viewed at an even finer δ. Therefore, if one measured (collected the Cartesian coordinates of) a pathway in which points were x and $2x$ distance apart, calculation of D at a box size of $6x$ would produce the same D for the pathway measured at x and $2x$.

For the slider method, I analyzed each pathway 2 times at each δ. Each analysis entailed placing the starting box at the beginning or ending of the pathway. The mean of these 2 analyses was used to represent D at each δ. For the divider method, I analyzed each pathway 100 times. Each analysis involved randomly shifting the starting point of the divider, before it was walked forwards and backwards across the pathway. The mean of these 100 replications was used to represent D at each δ. I used the computer program FRACTAL 3.0 (Nams, NSAC, pers. comm.) to perform the divider method calculations.

The results of the slider method show that D increased monotonically as a function of δ for both urban and rural pathways. To evaluate the shape of these curves, I used non-linear regression (DUD method, SAS Inc. 1988) to fit the equation:

$$D = \frac{(D_{max})(\delta)}{\delta_{1/2} + \delta} \tag{6}$$

to the observed patterns. D_{max} is the D value (y-axis) at saturation and $\delta_{1/2}$ is the δ (x-axis) at 0.5 saturation. To compare statistically the increase in D as a function of δ between urban or rural pathways, I used a sampling-with-replacement bootstrapping procedure. Ninety randomly selected estimates of D were used for each bootstrapping replicate, and 30 replications were preformed. I used t-tests to determine if the δ at which 50 and 95% of the asymptote was achieved differed between urban and rural pathways. I refer to 95% saturation as δ^*, or the δ at which D reached asymptote.

Because telemetry pathways of urban deer were measured at a greater precision than those of rural deer, the pattern of D versus δ contained many D estimates at δs of 160-260 m for urban telemetry pathways but none for rural telemetry pathways. To compensate for this discrepancy, and thus make comparisons between urban and rural movements valid, I removed all estimates of D within this range before fitting equation 6 to the D versus δ relationships.

Because several estimates of D were derived from each pathway, the bootstrapping comparisons between urban and rural pathways were not necessarily based on independent samples. Therefore, I used an additional test to determine whether urban or rural pathways were more space-filling at δs prior to asymptotic D. This test consisted of 2 parts. The first was to determine the mean linear distance between sequential coordinate locations for each snow trail pathway. Means for each pathway were then used as independent samples to compare whether urban or rural deer walked a greater straight-line distance before turning. The second part was to determine the mean turning angle between sequential coordinate locations for each snow trail pathway. Means for each pathway were then used as independent samples to compare whether urban or rural deer turned more sharply. I used t-tests to determine if distances between turns and angle of turns differed for urban and rural deer. These comparisons were useful because the asymptotic relationships of D versus δ were revealed largely by snow trail pathways.

Results

After discarding pathways that did not meet the criteria of minimum extent and minimum coordinate locations, I analyzed 12 urban snow trails (7 from 1997, and 5 from 1998), and 12 rural snow trails (6 from 1997, and 6 from 1998), as well as telemetry pathways of 11 urban deer (7 from 1997, and 4 from 1998), and 6 rural deer (4 from 1997, and 2 from 1998). Absolute length (summed distance between sequential coordinate locations) of pathways averaged 406 m (SD = 201) for urban snow trails, 704 m (SD = 290) for rural snow trails, 4717 m (SD = 1652) for telemetry pathways of urban deer, and 4532 m (SD = 1651) for telemetry pathways of rural deer. Pathway extents (distance between outermost coordinate locations) averaged 233 m (SD = 103) for urban snow trails, 425 m (SD = 264) for rural snow trails, 1401 m (SD = 601) for telemetry pathways of urban deer, and 1894 m (SD = 362) for telemetry pathways of rural deer. Combined, there were 147 estimates of D for urban pathways, and 130 estimates of D for rural pathways.

The divider method produced patterns of D versus δ that increased linearly for the pathways of urban and rural deer (Fig. 3-5). The slider method, in contrast, produced patterns of D versus δ that increased monotonically toward asymptote for pathways of both urban and rural deer (Fig. 3-6). Nonlinear regression revealed that the asymptote of D was 1.318 for urban pathways and 1.302 for rural pathways (Fig. 3-7). Bootstrapping indicated that the asymptote of D was approached at finer δs for rural pathways than urban pathways ($n = 30$, $p < 0.01$); 50% saturation occurred at a δ of 34 m for urban pathways and 17 m for rural pathways, and 95% saturation occurred at a δ of 110 m for urban pathways and 57 m for rural pathways (Fig. 3-7).

That rural pathways were more space-filling, and therefore should have approached asymptotic D, at finer δs was corroborated by the comparisons between turning frequencies and turning angles of snow trail pathways for urban and rural deer. Urban deer made turns > 3° every 7.25 m ($n = 12$, SE = 0.45), whereas rural deer did so every 3.62 m ($n = 12$, SE = 0.20). These distances differed statistically ($t = 7.96$, df = 22, $P < 0.0001$). The turning angles of snow trail pathways did not differ ($t = 0.95$, df = 22, $P = 0.36$), however, as the mean turning angle was 33.1 m ($n = 12$, $SE = 1.40$) for urban deer and 35.1 m ($n = 12$, $SE = 1.66$) for rural deer.

Discussion of Results

Comparison of Slider and Divider Methods.--The D versus δ relationships produced by the slider and divider methods exhibited some similarities, but differed in their overall appearance. Both methods showed that D was lowest at fine δs of analysis, thus indicating that movement pathways were most linear and least space-filling at δs approaching deer body size. Both methods also showed that D was not constant across all δ of analysis (4 - 600 m), but tended to increase over a range of δs. Specifically, the slider method showed that D increased over a finite range of δs (~ 4 - 100 m), but remained relatively constant at δs coarser than this range (~ 100 - 600 m). That is, D appeared to asymptote when movement pathways were analyzed via the slider method. The divider method, in contrast, showed that D increased across all δs.

A visual inspection of deer movement pathways reveals why D continued to increase at coarse δs (~100 - 600 m) when the divider method was used. As pathways increased in extent, they were more likely to double-back on themselves, and to exhibit concentrated movements in localized areas, i.e., they were characterized by patchy movements. Neither of these movement behaviors increases the amount of new space occupied by a pathway, but they do increase the number of times a space is reoccupied. It is these movement behaviors that cause the divider method to erroneously inflate the value of D. The slider method, on the other hand, does not consider these movement behaviors an increased source of space-fill, and therefore likely provides a more realistic portrayal of the D versus δ relationship.

Interpretation of the Slider Method Results.-- The nonlinear relationships of D versus δ indicate clearly that the space-filling attributes of deer movement pathways were not self-similar across all δs within an animal's home range. As such, interpretations of deer responses to habitat across these δs will be invalid if self-similarity is assumed. However, the shape of the D versus δ relationships does suggest that the space-filling attributes of deer movements became self-similar once δ coarseness reached a certain level (δ^*), i.e., once D achieved asymptote. Interestingly, the asymptotic values of D were nearly identical for the pathways of urban (1.318) and rural (1.308) deer, thus indicating that their space-filling attributes were equivalent from intermediate (100 m) to coarse (600 m) δs of analysis. Why would D of deer movement pathways asymptote, and why would the asymptotes of pathways for urban and rural deer converge to a common value?

One hypothesis that simultaneously addresses these questions is that habitat characteristics (e.g., resource distributions, landscape complexity) to which deer responded caused 1) movement pathways to become scale-invariant over the δs defining the asymptotic portion of the D versus δ relationships, and 2) the pathways of urban and rural deer to be equally space-filling. This hypothesis is untenable for several reasons. First, the different habitat types which deer selected and avoided in each area exhibited markedly different spatial patterns across the landscape (see Chapter 4). Moreover, the spatial patterns of these types were not fractal over the range of δs defining the asymptotic portion of the D versus δ relationships. Second, the home ranges of rural deer were approximately 4 times larger than those of urban deer (see Chapter 2). Therefore, rural deer likely integrated information regarding habitat characteristics over larger areas than urban deer. Third, man-built structures (houses, roads, fences) in urban settings likely altered the complexity of the landscape from the perspective of deer using these habitats.

Given that habitat characteristics inadequately address these questions, a logical deduction is that a behavioral process or mechanism explains why D of movement pathways was asymptotic, and why the pathways of urban and rural deer converged to a common value of D. That is, a D-value of ~1.3 may reflect the way deer respond to the world, regardless of habitat characteristics. Deer are "programmed" to traverse the landscape in such a way that the space-filling attributes of their movements will achieve this value.

Why would such an intrinsic process exist? I propose the answer to this question relates to the trade-off animals face between accessing resources and minimizing the energetic expenditures of traveling. Animals that are confined to a home range must meet their energetic and nutritional needs within a predefined space. While searching for the resources that satisfy these needs, however, it behooves animals to move in such a way that their energetic expenditures are minimized. A D-value of ~ 1.3 may represent the optimal movement geometry by which animals can sample different regions of space, and thus all resources, in their home ranges, while simultaneously minimizing energy consumption.

That a D-value of ~ 1.3 represents an optimal movement geometry is supported by the fractal transport models derived by West et al. (1997). These models demonstrate that shunting material throughout a surface or volume is optimally achieved by distribution networks that obey 1/4-power scaling. In 2-dimensional systems, this scaling relationship predicts that a network will have D-value of 1.33 (B. Enquist, pers. comm.). Therefore, when a vascular system in a plant or animal is viewed in 2 dimensions (i.e., a cross section), a fractal-like branching system with a D of 1.33 will require the least amount of energy (e.g., hydrodynamic resistance) to supply the entire organism with material (blood, water, nutrients). A branching system with a D > 1.33 will supply the entire organism with material, but resistance also increases. On the other hand, a branching system < 1.33 will not supply the entire organism with material. Not surprisingly, the models by West et al. (1997) conform well with observations of living systems when D of networks are measured via the box-counting procedure. For instance, Fitter and Stickland (1992) reported that D of plant roots grown between 2 plates of glass (which is effectively a 2-dimensional system) was indistinguishable from 1.33.

In this vein, I propose that movement pathways with a D of ~1.3 will allow animals to use the least energy to access resources within their home ranges. Movements with a $D < 1.3$ would prevent animals from sampling all regions of their home ranges, i.e., movements are too linear. Movements with a $D > 1.3$ would consume more energy than was necessary to sample these regions.

At δs finer than δ^* (the δ at which asymptotic D was effectively achieved), D increased as a function of δ coarseness for pathways of both urban and rural deer. A potential explanation for these patterns is that deer could more readily detect the immediate surroundings of their habitats at finer perceptual δs, i.e., localized areas of the landscape were within deer scales of detection and response. As such, deer walked more directly, as they could discern resources, or lack thereof, and respond to landscape structure (e.g., barriers to movement) within these localized areas. As the area of perception expanded, however, deer were less capable of differentiating their surroundings, and D of movement pathways approached the intrinsically driven value of 1.3.

Studies by Gross et al. (1995) bolster this argument by demonstrating that movement paths of foraging bighorn sheep (*Ovis canadensis*) most closely approximated simulations based on nearest neighbor rules-of-thumb when plants were within short detection distances, i.e., when plants were close to the animal. As detection distances increased, however, and plants were not within view, these simulations became less predictive. Conversely, simulations based on random walks predicted poorly the lengths of foraging paths, but predictions improved as a function of detection distance. At short detection distances, random walk simulations of path length were 30 times greater than observed path lengths. At long detection distances, simulated path lengths were only 3-4 times longer than observed path lengths. Interestingly, D of a random walk will approach a value of 2.0 at coarse δs of analysis. This value is 3-4 times larger than the optimal movement geometry characterized by a D-value of 1.3 (i.e., [2.0-1.0]/[1.3-1.0] = 3.33).

Given that movement decisions at δs finer than δ^* were affected by the ability of deer to differentiate their surroundings, it might be expected that habitat characteristics would have their greatest effect on movement pathways at these δs. Animals should respond to the distribution of resources and landscape complexity (e.g., barriers, topography) at these fine δs, and animals exposed to different characteristics should move differently. For example, movement barriers tend to reduce a landscape's dimensionality, i.e., they make a 2-dimensional environment more linear (Milne 1992, Ritchie 1998); pathways should become less space-filling as a result. Similarly, resources that comprise small, isolated patches should linearize movements (Bell 1991).

In my study, the pathways of rural deer were, on average, more space-filling than those of urban deer at fine δs (4 - 60 m) of analysis. Consequently, δ^* was achieved at a relatively finer δ for rural pathways. These differences in D at fine δs likely resulted from disparate habitat characteristics in the 2 study areas. Specifically, fencing and housing may have linearized the urban landscape, thereby constraining deer movements. In addition, within localized areas (e.g., areas < 60 x 60 m in extent), forage shrubs in the rural area were clumped within specific topographic regions, whereas shrubs in the urban area consisted largely of isolated patches in yards. Accordingly, the different movement patterns exhibited by urban and rural deer at fine δs may have, in part, arisen from animals attempting to sample the forage in their respective habitats.

SYNOPSIS AND HYPOTHESES

Understanding movement patterns is crucial for developing mechanistic explanations of how animals encounter and interact with resources on a landscape. These explanations, in turn, will contribute to the development of faithful models of population, community, and ecosystem dynamics (Johnson et al. 1992, Milchunas and Lauenroth 1993, Gross et al. 1995). A logical first step to understanding movement patterns is to describe them in a meaningful way. Clearly, to be meaningful, such descriptions must consider explicitly the effects of scale, i.e., the size of a pathway as defined by its grain and extent (With 1994). Fractal analysis accounts for the effects of scale by measuring movement pathways over multiple δs.

In this chapter, I used a modified methodology to estimate D of deer movement pathways. The results of this analysis suggest that movement patterns might be governed by a behavioral process that allows animals to "cover" the different regions of habitat space in the most energetically effective way. Assuming this hypothesis is tenable, it is conceivable that the movements of other species would also be governed by similar behavioral processes. If so, an ensuing question is under what landscape or resource conditions would movement pathways not exhibit average D values of ~ 1.3?

One such circumstance might occur when resource distributions are highly fragmented, i.e., resources are characterized by a D value < 1.3. In such a scenario, it would behoove animals to adopt more linear movement pathways, so they could walk directly to resource patches. Ward and Saltz (1994) showed that Dorcas gazelles (*Dorcas gazella*) foraging on lilies in the Negev Desert exhibited such a pattern. In their study area, lily patches were separated by large expanses of barren terrain. Gazelle foraging paths were correspondingly characterized by a series of short moves within patches, interspersed with long, straight moves between patches. In this scenario, between-patch movement pathways may have been guided by memory or olfaction.

Pathways may also deviate from a D value of 1.3 when the landscape is perceived as linear. For instance, pathways of animals using only corridors for travel will exhibit D values equaling that of the corridor. Alternatively, the landscape may be so structurally complex that animals must follow topographic contours, passages through dense vegetation, or trails. In the latter scenario, D of movement pathways may be greater or less than 1.3.

To test these hypotheses, D of movement pathways would need to be calculated for various resource distributions and landscape settings under free-ranging conditions. Most other studies that have calculated D of movement pathways were conducted in artificially bounded systems (Wiens et al. 1995, Etzenhouser et al. 1998, McIntyre and Wiens 1999), and it is therefore unknown whether animal movements were influenced by system boundaries. Consequently, the results from past studies cannot be used to support or reject these hypotheses. In addition, most previous studies have used the divider method to calculate D of movement pathways. This method will likely yield unreliable results. Finally, most studies have measured pathways that are short relative to an animal's daily movements. D has therefore been calculated over a narrow range of fine δs. Based on this study, D will not be constant at these fine δ of analysis, perhaps because habitat is within the animal's scale of detection and response, and movements represent a sensory-driven behavior toward resource distributions and landscape structure.

This latter conclusion is important because it suggests that the effects of habitat heterogeneity will only influence movements at fine δs. Accordingly, the δ at which movements patterns become intrinsically driven (i.e., δ^*) may represent the coarsest δ at which landscape heterogeneity and resource patchiness should be measured.

LITERATURE CITED

Anvir, D., O. Biham, D. Lidar, and O. Malcai. 1998. Is the geometry of nature fractal? Science 279:39-40.

Aviles, C. A., C. H. Sholtz, and J. Boatwright. 1987. Fractal analysis applied to characteristic segments of the San Andreas Fault. Journal of Geophysical Research 92:331-334.

Bascompte, J., and C. Vilà. 1997. Fractals and search paths in mammals. Landscape Ecology 12:213-221.

Bell, W. J. 1991. Searching behaviour. Chapman and Hall, London, UK.

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

Dicke, M., and P. A. Burrough. 1988. Using fractal dimensions for characterizing tortuosity of animal trails. Physiological Entomology 13:393-398.

Etzenhouser, M. J., M. K. Owens, D. E. Spalinger, and S. B. Murden. 1998. Foraging behavior of browsing ruminants in a heterogeneous landscape. Landscape Ecology 13:55-64.

Feder, J. 1988. Fractals. Plenum Press, New York, New York, USA.

Fitter, A. H., and T. R. Stickland. 1992. Fractal characterization of root system architecture. Functional Ecology 6:632-635.

Gross, J. E., C. Zank, N. T. Hobbs, and D. E. Spalinger. 1995. Movement rules for herbivores in spatially heterogenous environments. Landscape Ecology 10:209-217.

Hastings, H. M., and G. Sugihara. 1993. Fractals: a user's guide for natural sciences. Oxford University Press Inc., New York, New York, USA.

Johnson, A. R., B. T. Milne, and J. A. Wiens. 1992. Diffusion in fractal landscapes: simulations and experimental studies of tenebrionid beetle movements. Ecology 73:1968-1983.

Johnson, G. D., A. Templeman, and G. P. Patil. 1995. Fractal based methods in ecology: a review of analysis at multiple scales. COENOSES 10:123-131.

Katz, M. J., and E. B. George. 1985. Fractals and the analysis of growth paths. Bulletin of Mathematical Biology 47:273-286.

Klinkenburg, B. 1994. A review of methods used to determine the fractal dimension of linear features. Mathematical Geology 26:23-46.

Levin, S. 1992. The problem of pattern and scale in ecology. Ecology 73:1943-1967.

Loehle, C., and B.L. Li. 1996. Statistical properties of ecological and geological fractals. Ecological Modeling 85:271-284.

Mandelbrot, B. B. 1983. The fractal geometry of nature. W. H. Freeman, San Francisco, California, USA.

McIntyre, N. E., and J. A. Wiens. 1999. How does habitat patch size affect animal movement? An experiment with darkling beetles. Ecology 80:2261-2270.

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

Milne, B. T. 1992. Spatial aggregation and neutral models in fractal landscapes. American Naturalist 139:32-57.

_____. 1997. Applications of fractal geometry in wildlife biology. Pages 32-69 in J. A. Bissonette, ed. Wildlife and landscape ecology. Springer-Verlag Inc., New York, New York, USA.

Morrison, M. L., B. J. Marcot, and R. W. Mannan. 1992. Wildlife-habitat relationships: concepts and applications. University of Wisconsin Press, Madison, Wisconsin, USA.

Nams, V. O. 1996. The Vfractal: a new estimator for fractal dimension of animal movement paths. Landscape Ecology 11:289-297.

Ritchie, M. E. 1998. Scale-dependent foraging and patch choice in fractal environments. Evolutionary Ecology 12:309-330.

_____, and H. Olff. 1999. Spatial scaling laws yield a synthetic theory of biodiversity. Nature 400: 557-560.

SAS Institute, Inc. 1988. SAS/STAT user's guide, release 6.03 edition. SAS Institute, Cary, North Carolina, USA.

Sugihara, G., and R. M. May. 1990. Applications of fractals in ecology. Trends in Ecology and Evolution 5:79-86.

Taylor, L. R., and R. A. J. Taylor. 1983. Insect migration as a paradigm for survival by movement. Pages 181-214 *in* I. R. Swingland and P. J. Greenwood, eds. The ecology of animal movement. Clarendon Press, Oxford, UK.

Tsonis, A. A., O. Biham, and D. A. Lidax. 1998. Fractality of nature. Science 279:1614-1616.

Turchin, P. 1996. Fractal analysis of animal movement: a critique. Ecology 77:2086-2090.

_____. 1998. Quantitative analysis of movement. Sinauer Associates, Sunderland, Massachusetts, USA.

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

West, G. B., J. H. Brown, and B. J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. Science 276: 122-128.

Wiens, J. A. 1995. Landscape mosaics and ecological theory. Pages 1-26 *in* L. Hansson,

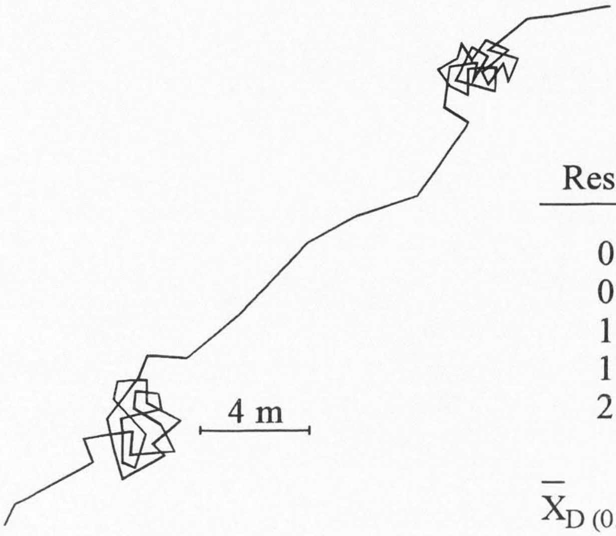
L. Fahrig, and G. Merriam, eds. Mosaic landscapes and ecological processes. Chapman and Hall, London, UK.

_____, T. O. Crist, K. A. With, and B. T. Milne. 1995. Fractal patterns of insect movement in microlandscape mosaics. Ecology 76:663-666.

With, K. A. 1994. Using fractal analysis to assess how species perceive landscape structure. Landscape Ecology 9:25-36.

Table 3-1. How the divider method overestimates the fractal dimension of straight-line movement pathways when pathways double-back on themselves.

Range of resolutions (as a fraction of path length extent)	Fractal dimension		
	1 Pass	1 Round-trip	3 Round-trips
0.01 to 0.32	1.0	1.039	1.081
0.01 to 0.02	1.0	1.007	1.011
0.02 to 0.04	1.0	1.011	1.023
0.04 to 0.08	1.0	1.032	1.059
0.08 to 0.16	1.0	1.061	1.082
0.16 to 0.32	1.0	1.164	1.261



Resolution (m)	Divider D
0.50 - 1.00	1.19
0.75 - 1.50	1.44
1.00 - 2.00	1.98
1.50 - 3.00	2.04
2.00 - 4.00	2.31

$$\bar{X}_{D\,(0.50\,-\,4.00)} = 1.78\ (r^2 = 0.91)$$

Figure 3-1. Simulated example of how the divider method can erroneously inflate the fractal dimension (D) of a patchy movement pathway. Note that the estimate of D tends to increase as a function of divider width (resolution). Note also that the method can actually force D beyond the 2-dimensional surface in which the pathway is embedded.

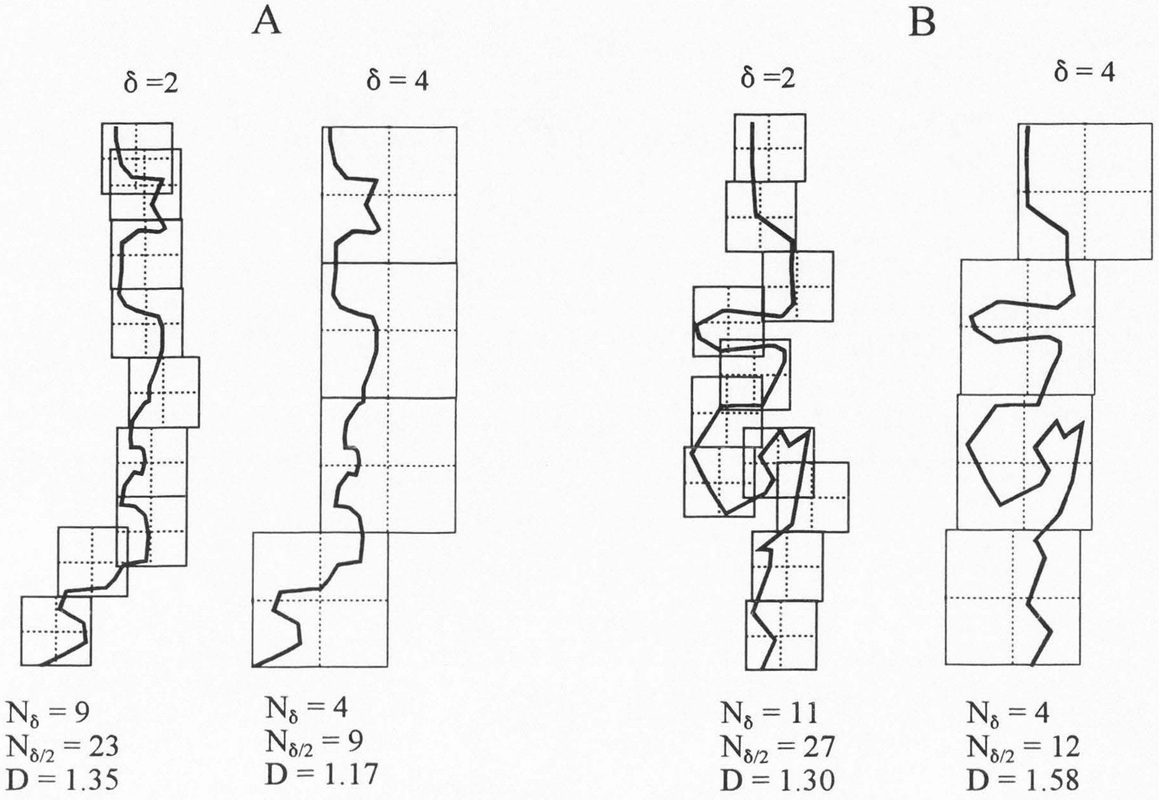
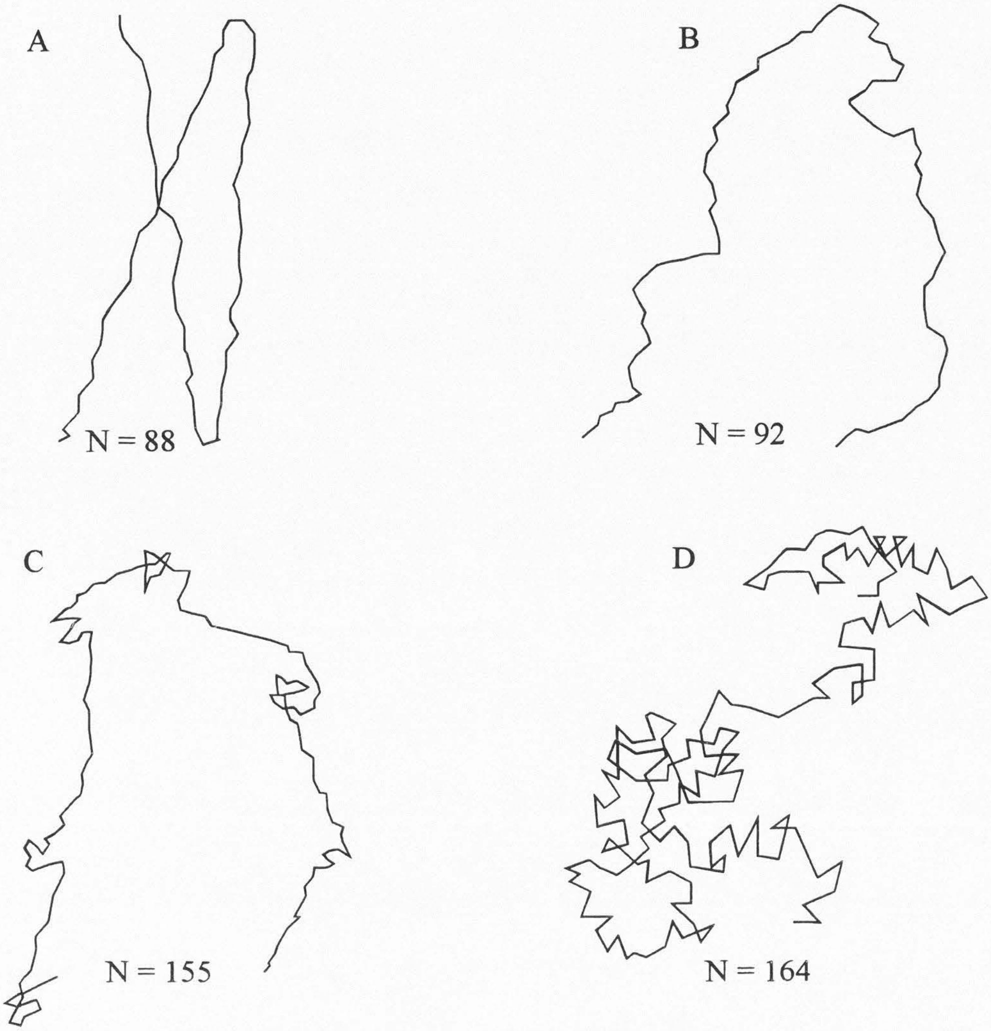


Figure 3-2. Slider method calculations of D at 2 resolutions for 2 hypothetical movement pathways. D is accurately determined by simultaneously counting the fewest number of boxes (N_δ) and cells ($N_{\delta/2}$) that can be occupied by the pathway. Each box is positioned in such a way that 1) the greatest length of the pathway is covered, and 2) the fewest number of cells are occupied. When the end of a pathway is approached, a box is counted in the reverse direction if the remaining path segment is too short to occupy ≥ 2 cells, e.g., $\delta = 2$ of A. If the pathway can pass through the intersection of the 4 cells in box, only 2 cells are counted, e.g., $\delta = 2$ of A.



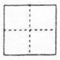
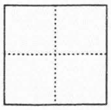
	Fractal Dimension			
δ	A	B	C	D
	1.03	1.20	1.36	1.76
	1.04	1.32	1.20	1.82

Figure 3-3. Slider method estimates of D for 4 hypothetical movement pathways at 2 resolutions (drawn to scale). N is the number of coordinates used to derive the pathway. Pathway D is a random walk.

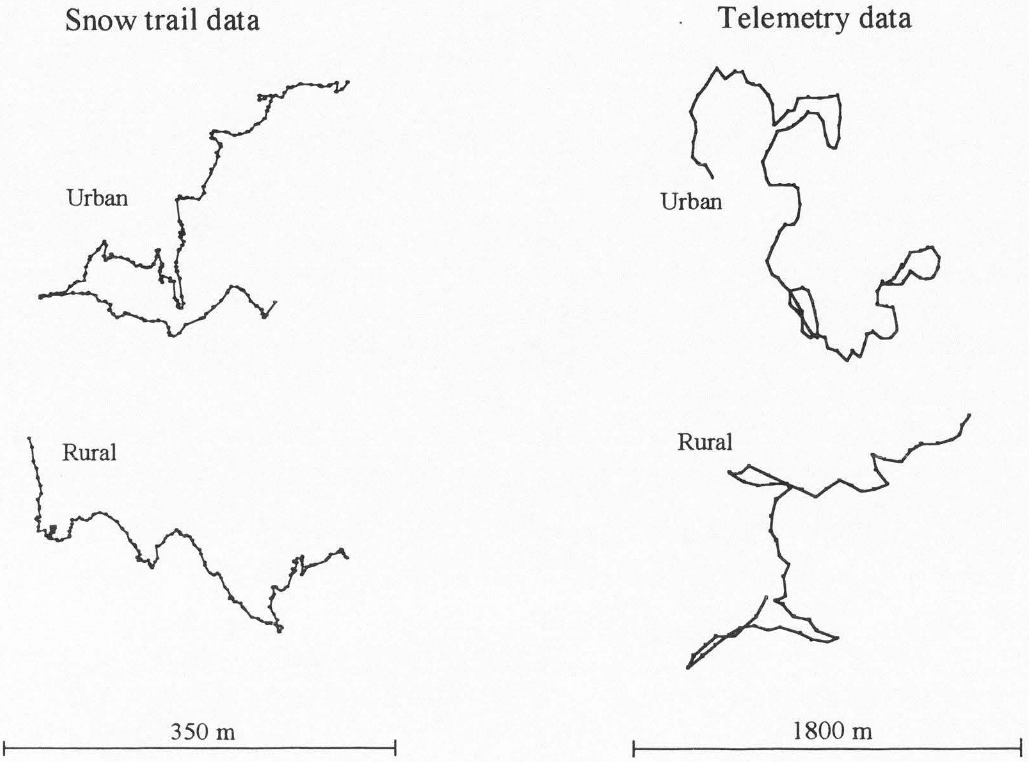


Figure 3-4. Mule deer movement pathways determined by following trails in the snow and by locating telemetered animals every 2-60 minutes in urban and rural areas of Cache Valley, Utah.

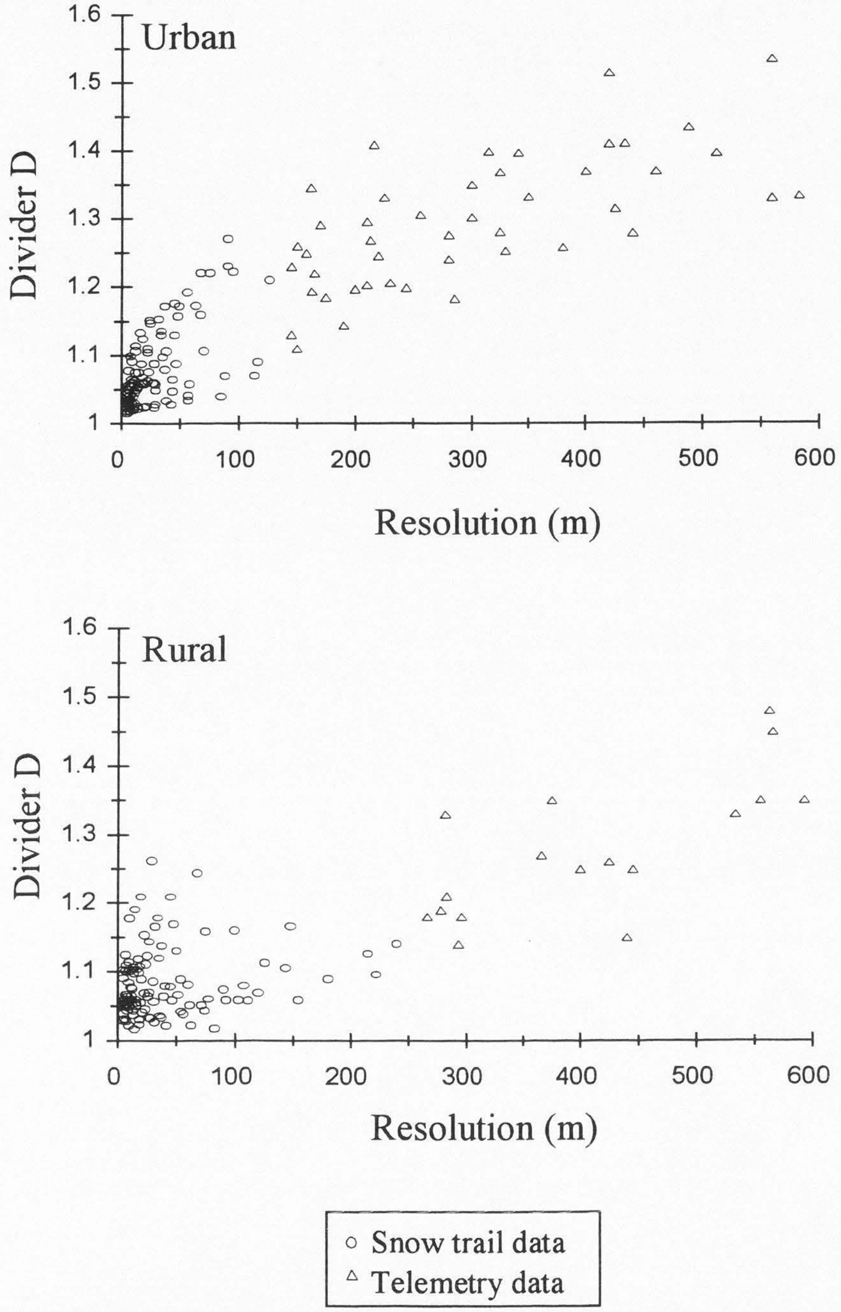


Figure 3-5. Fractal dimension (D), calculated via the divider method, versus resolution (δ) for mule deer movement pathways in urban and rural areas of Cache Valley, Utah. Each point represents an estimate of D at a given δ for a snow trail or a telemetry pathway.

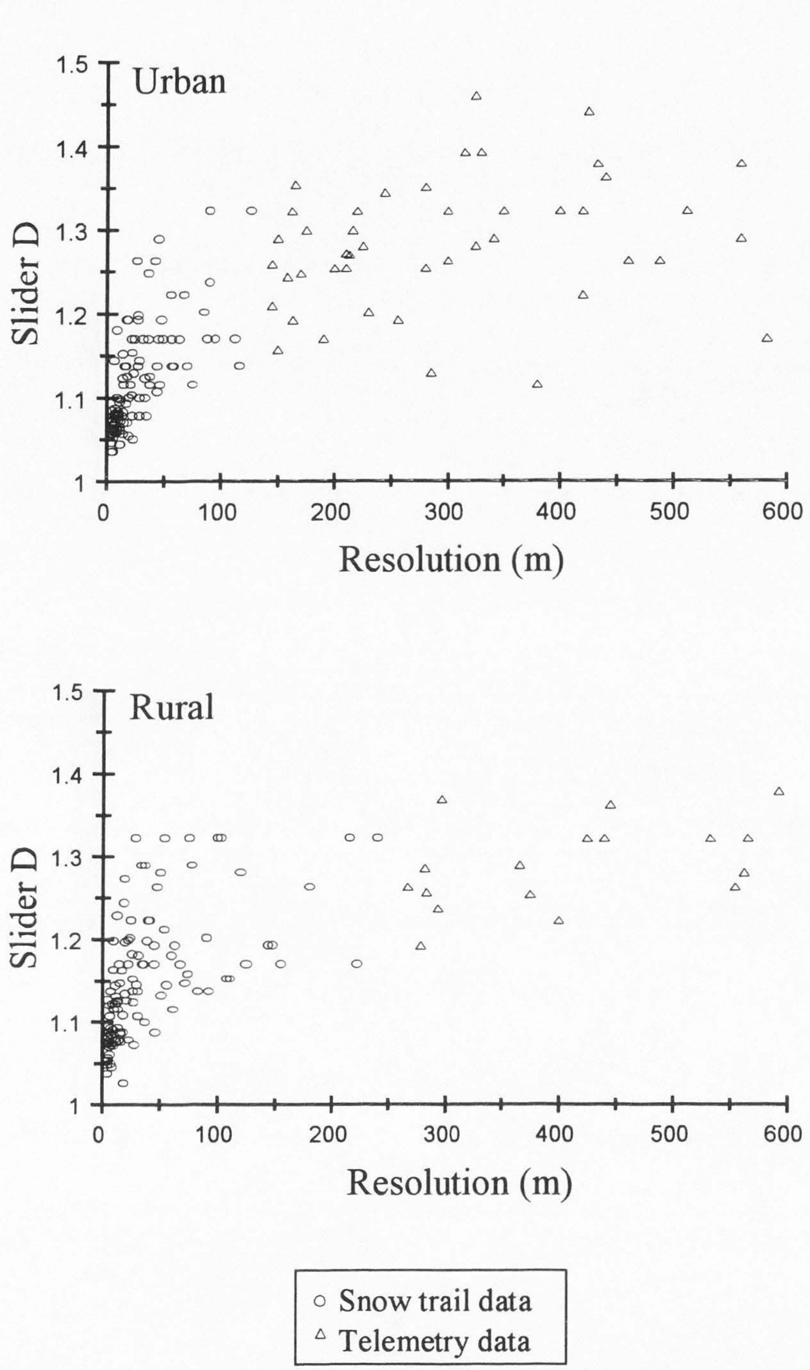


Figure 3-6. Fractal dimension (D), calculated via the sweeper method, versus resolution (δ) for mule deer movement pathways in urban and rural areas of Cache Valley, Utah. Each point represents an estimate of D at a given δ for a snow trail or a telemetry pathway.

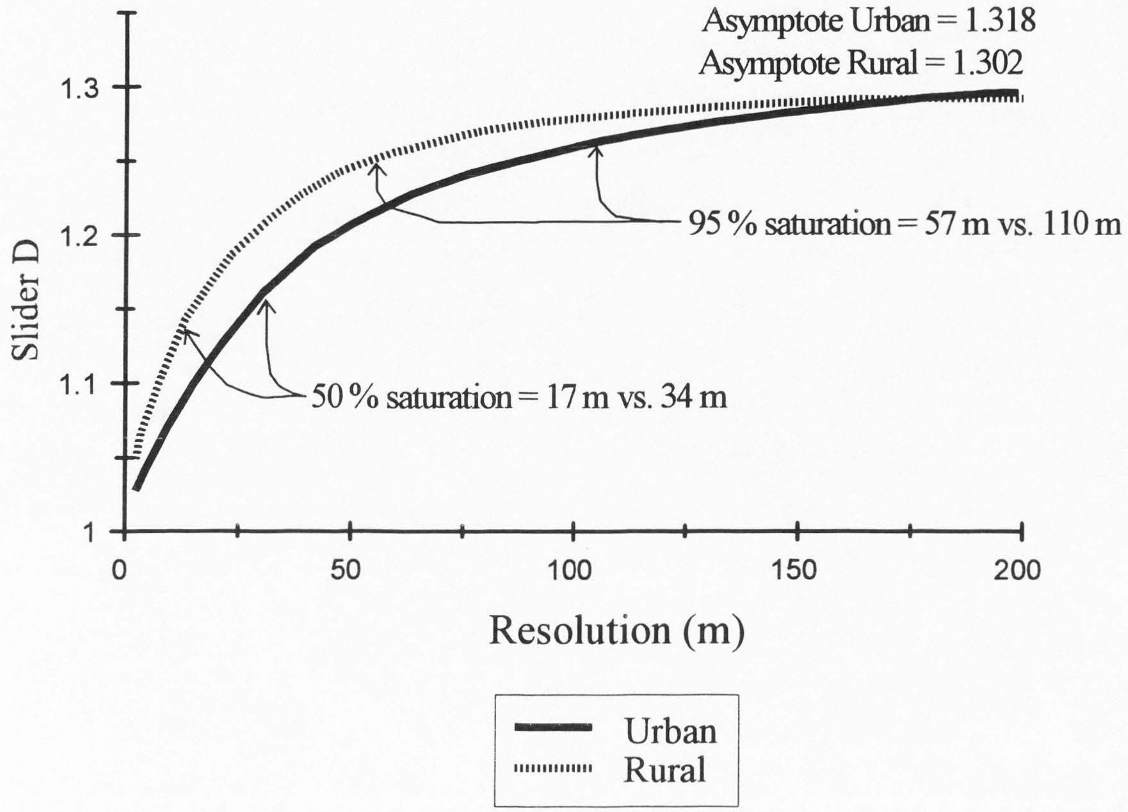


Figure 3-7. Nonlinear regression fit to the asymptotic relationships of D versus resolution (δ) for movement pathways of urban and rural deer in Cache Valley, Utah.

CHAPTER 4

SCALE-DEPENDENT PATTERNS OF HABITAT USE: AN EXAMPLE WITH URBAN AND RURAL MULE DEER

Abstract: Animals' patterns of habitat use are often scale-dependent. Therefore, the study of these patterns should consider explicitly how animals use habitat space, and how scale-dependent use relates to different habitat components. I address these scaling issues by developing a 2-staged methodology for analyzing patterns of habitat use. In stage 1, animal locations are compared to random locations using information fractal dimensions (IFDs). These comparisons reveal the degree to which animal locations uniformly fill space across a range of resolutions (δs) on a landscape. In stage 2, the classic index of "use vs. availability" is combined with a ratio of IFDs for animal locations vs. random locations that characterizes the spatial associations between animal locations and habitat types. This procedure thus reveals how correspondence between animal locations and habitat types changes with δ. I used this methodology to examine patterns of habitat use by mule deer (*Odocoileus hemionus*) living in urban and rural areas of Cache Valley, Utah. Urban deer locations were highly space-filling at fine δs of analysis, but highly fragmented and aggregated at coarse δs. Conversely, rural deer locations were less space-filling at fine δs, and less fragmented and aggregated at coarse δs. Relationships between animal locations and different habitat types revealed why these patterns occurred. Urban deer locations were strongly associated with concealment vegetation, which was highly fragmented (i.e., a low IFD), across all δs of analysis. Thus, highly aggregated patterns of space use corresponded to fragments of escape cover. Rural deer locations, on the other

hand, were most strongly associated with shrubby vegetation at fine δs, and south-facing slopes at coarse δs. Both of these habitat types exhibited a relatively higher IFD than urban concealment vegetation, and both indexed habitat components associated with forage. This methodology thus enabled me to link patterns of space use with patterns of habitat type use while explicitly incorporating the effects of spatial pattern and scale.

INTRODUCTION

The analysis of animal-habitat relationships is a pervasive theme in ecology, and understanding these relationships is central to wildlife management and conservation. Conceptually, animal-habitat relationships represent an interface between the behavior of individuals and population-level phenomena. In other words, how animals interact with habitat influences their probability of finding food and mates or avoiding risks and stressful thermal conditions. These interactions, in turn, affect the demographic variables of birth and death. Accordingly, wildlife-relationships form the underpinnings to the mechanistic explanations of many ecological processes, including population and community dynamics (Holt 1987, Levin 1992, Block and Brennan 1993, Wiens et al. 1993).

In general, animal-habitat relationships are studied from 2 perspectives: habitat selection and habitat use. Selection refers to the behavioral processes by which individuals choose habitat components, and is often considered to be based on hierarchical decisions made by the animal (Johnson 1980, Senft et al. 1987, Morrison et al. 1992). Use is the manifestation of these processes, and represents the pattern of habitat exploitation and avoidance on a landscape at either an individual or population level (Hall et al. 1997). For clarity, I refer to habitat components as specific resources or areas of a landscape that allow animals to achieve some goal, e.g., to obtain energy or nutrients, to warm or cool themselves, or to avoid risks. This term differs from habitat type, which I use later to mean a human-imposed description of an area containing particular vegetative or physical attributes. Habitat types may contain one or several habitat components, and are often used as indices to these components.

Like many ecological disciplines, the study of animal-habitat relationships is complicated by the effects of scale (Morris 1987, Wiens 1989, Orians and Wittenberger 1991, Milne 1997). Here, scale refers to size of some landscape feature as determined by 1) the grain (finest δ) at which it is measured by a researcher or perceived by an organism, and 2) its extent (see definitions in Turner and Gardner 1991).

The effects of scale on animal-habitat relationships are important to consider for 3 reasons. First, morphology, sensory capabilities, and memory dictate the perceptual realm (finest to largest δs of perception) over which an animal can respond to habitat (Kotliar and Wiens 1990, Morrison et al. 1992, Havelka 1995, Ritchie 1998). As such, habitat selection can only occur within this realm. Second, a habitat component to which an animal responds may not be distributed fractally. Accordingly, patterns of use are likely to change across δ in correspondence with the distribution of this component. Third, the various habitat components that are important to animals (e.g., food vs. hiding cover) may exhibit different distributions. Therefore, patterns of use may change at different δs as exploitation is directed toward these various subsets of habitat.

To comprehend the effects of scale on patterns of habitat use, researchers have commonly employed 1 of 2 approaches. The first is to vary the unit of measurement (e.g., box size) at which habitat use and habitat type availability are computed, whereby box size is supposed to index the δ at which animals perceive and respond to habitat. A fundamental problem with this approach, however, is that the number of habitat types contained within a box tends to increase as a function of box size. Therefore, it becomes increasingly difficult to determine the types to which animals are using at coarse δs of analysis; many types may occur in boxes where animal locations are present or absent, regardless of whether animals are actually exploiting or avoiding these types.

The other approach is to partition patterns of habitat use into a predefined hierarchy, e.g., home ranges within a landscape, activity areas within a home range, and sites for specific behaviors within an activity area. This approach is appealing because several studies have indicated that animals may select areas containing habitat components sequentially, from large to small extents (Hutto 1985, Senft et al. 1987, Morrison et al. 1992). However, this approach assumes that the researcher knows a priori the components to which animals respond at each hierarchical level, and the organismically defined δs at which to measure these components.

In this chapter, I develop a 2-staged methodology for assessing animal patterns of habitat use that explicitly incorporates the effects of scale. The aim of the first stage is to determine how the spatial patterns of animal locations change across a range of δs, thereby indexing scale-dependent use of habitat space. The aim of the second stage is to assess the degree of correspondence between animal locations and different habitat types as a function of δ. These 2 stages are interrelated because patterns of space use should, in part, be explained by the correspondence between animal locations and habitat types.

Both stages of this methodology use IFDs (Scheuring and Riedi 1994, Johnson et al. 1995, Loehle and Li 1996) to incorporate the effects of scale. In doing so, this methodology preserves the grain at which animal locations and habitat types are measured throughout all δs of analysis. As such, this methodology ensures that no information is lost, and that use of different habitat types is based on whether animal locations are actually inside or outside these types, as δ coarseness increases.

THE INFORMATION FRACTAL DIMENSION

The IFD is related to the fractal dimension (Mandelbrot 1983) calculated via the box-counting method (Hastings and Sugihara 1993) in that it indexes the degree of space filled by a spatial pattern. It differs from the box-count fractal dimension by accounting for the intensity (density or frequency) at which a pattern occurs in different regions of space (i.e., its degree of aggregation); a box-count fractal dimension only considers whether the pattern is present or absent in space. As such, the IFD can deal with non-binary maps containing multiple observations per cell or pixel. Specifically, the IFD quantifies the deviation from spatial uniformity of the probabilities of occurrence of a spatial function (Loehle and Li 1996).

To calculate an IFD at discrete δs, a spatial pattern is covered with a grid of square boxes of side length δ_L. Within each box, there are 4 cells of side length $\delta_{L/2}$. The number of points (pixels, x-y coordinates) that fall within each cell and box are summed and the IFD is computed as:

$$\mathrm{IFD} = \frac{\sum_{\delta/2=1}^{K_{\delta/2}} P_{i(\delta/2)} \,\mathrm{Ln}\, P_{i(\delta/2)} - \sum_{\delta=1}^{K_{\delta}} P_{i(\delta)} \,\mathrm{Ln}\, P_{i(\delta)}}{\mathrm{Ln}\,[1/(\delta/2)] - \mathrm{Ln}\,[1/\delta\,]} \qquad (1)$$

where K_δ *and* $K_{\delta/2}$ are, respectively, the number of boxes or cells containing ≥ 1 point. P_i is the relative frequency of points contained within a given cell or box, and is given by:

$$P_i = \frac{N_i}{\sum_{i=1}^{M} N_i} \qquad (2)$$

Here, N_i is the number of points or pixels (e.g., habitat measured at δ grain) in a given cell or box, and M is the total number of points or pixels in the spatial pattern. Note that only non-empty boxes are used to calculate P_i. Also note that M remains constant across all δs. To compute IFDs at different δs, the box size of the grid is varied (Loehle and Li 1996).

For 2-dimensional maps, the IFD ranges from 0 to 2, representing a gradient of spatial patterns from sparsely distributed (i.e., highly fragmented) to uniform plane-filling, in which every cell of a box contains an equal number of points (Fig. $4\text{-}1_{\text{A-D}}$). In general, at any given δ, the IFD behaves like the box-count fractal dimension and increases with the proportion of space occupied, but, for a given proportion, larger values tend to reflect space-filling dispersion within boxes (Fig. $4\text{-}1_{\text{I-J}}$). IFD departs from the classic box-count dimension when patterns deviate from uniformity (compare Fig. $4\text{-}1_{\text{E}}$ to $4\text{-}1_{\text{G}}$ and Fig. $4\text{-}1_{\text{F}}$ to $4\text{-}1_{\text{H}}$). That is, for patterns that are more aggregated in some cells than others, the IFD will be less than that derived from a binary map characterized by presence/absence data.

METHODOLOGY FOR ANALYZING PATTERNS OF HABITAT USE

Stage 1--Patterns of Space Use

In the first stage of analysis, IFDs computed from animal point locations are compared to those computed from an equal number of random locations across a range of δs of interest. These comparisons index the degree to which animal locations uniformly fill space, thereby revealing the δs at which they are most fragmented and aggregated, and most dispersed and evenly distributed (i.e., uniformly space-filling). A relatively fragmented spatial pattern (low IFD) indicates that only isolated patches of the landscape are used at a given δ, or much of the space at that δ is avoided. And an aggregated spatial pattern means that use is clustered in some areas more than others. Conversely, a uniformly space-filling pattern (high IFD) indicates that areas of the landscape are utilized fully at a given δ, and use is evenly concentrated in these areas.

These comparisons are relative because the quantitative differences between IFDs computed from animal and random locations will change with sample size. However, determining the δs at which animal locations are relatively fragmented or uniformly space-filling will generally be unaffected by sample size, given that animal locations are drawn from a common distribution (Fig. 4-2). This is so because the function of IFD vs. δ for a truly random pattern is based solely on the number of points in the pattern (Fig. 4-3); hence, IFDs should be equal across δ if boxes of different sizes were standardized by the number of points they could potentially contain. As such, this function represents a "sample-specific" reference for indexing the space-filling uniformity of point locations.

The random function of IFD vs. δ also provides conservative guidelines for establishing the number of locations needed to identify the δs at which animal locations are most fragmented and aggregated or uniformly space-filling. First, the random function should be near 2 (e.g., 1.9) at coarse δs of analysis, thus ensuring that animal locations could occupy most portions of a 2-dimensional space if their distribution was determined by chance alone. Second, there should be enough locations to guarantee that the IFD at δ grain exceeds 0, as values of 0 indicate that the space-filling attributes of a random pattern could not be detected. Note that these guidelines should be met while safeguarding against spatial autocorrelation among animal locations. This safeguard is necessary because the objective of the analysis is to determine how animal locations are distributed in a given habitat space over a finite interval of time. Autocorrelation among locations may bias space use patterns towards specific regions of the study area (White and Garrot 1990).

Stage 2--Correspondence Between Animal Locations and Habitat Types

The second stage of analysis is to assess the degree of correspondence between animal locations and habitat types at the δs of interest. This assessment consists of 2 steps. The first step relates the proportion of animal locations contained within a habitat type (Q_z) to the proportion of the study area occupied by that type (Z). This relationship takes the form Q_z/Z, which, in itself, represents the underlying basis upon which classic "use vs. availability" indices are calculated (see Alldredge and Ratti 1986, 1992; White and Garrot 1990; McClean et al. 1998 for reviews). That is, Q_z/Z represents proportional habitat type use vs. habitat type availability, and only accounts for the relative abundances of animal locations and investigator-defined habitat types. When this ratio equals 1, animals are considered to exhibit a neutral response to a given habitat type. When Q_z/Z is greater than 1, habitat type use is considered to exceed that expected by chance alone, whereas the opposite is deemed true when Q_z/Z is less than 1.

If the distribution of habitat types and animal locations do not change with δ or if animal locations are random, this ratio is sufficient to assess use vs. availability. These scenarios are unlikely to exist in heterogeneous habitats, however. Therefore, the second step needed to assess correspondence is to determine the degree to which animal locations associate spatially with a given habitat type. It is these spatial associations that will likely change with δ.

Assessment of these spatial associations can be accomplished by calculating 2 ratios. The first is based on the IFD of animal locations contained within a habitat type ($I_{c|z}$) vs. the IFD of all animal locations (I_t). This ratio ($I_{c|z}/I_t$) reveals the degree to which animal locations uniformly disperse (fill the space) in a habitat type relative to the degree to which they disperse throughout the entire landscape. The second ratio is based on the IFD of random locations that fall inside a habitat type ($I_{r|z}$) vs. the IFD of all random locations (I_{rt}). This ratio ($I_{r|z}/I_{rt}$) reveals the expected dispersion within a habitat type relative to that on the entire landscape, given that the spatial patterns of habitat use are explained by chance alone.

The difference between these 2 ratios ($I_{c|z}/I_t - I_{r|z}/I_{rt}$) indexes the degree to which animal locations associate spatially to a given habitat type. A positive association (a value greater than 0) occurs when deviations from space-filling uniformity of animal locations are explained more by habitat type distribution than that expected by chance.

These 2 steps are combined, and an index of correspondence, R, is defined as:

$$R = \frac{Q_z}{Z} + \left[\left(\frac{I_{c|z}}{\mathrm{I}_t} - \frac{I_{r|z}}{I_{rt}} \right) \frac{Q_z}{Z} \right], \tag{3}$$

which, in effect, weights the classic use vs. availability index by the spatial associations between animal locations and a given habitat type. Specifically, when there is a positive spatial association between animal locations and a habitat type, R will exceed Q_z/Z. When there is a negative association, R will be less than Q_z/Z (Fig. 4-4).

By explicitly incorporating these spatial associations, R reveals how correspondence between animal locations and habitat types changes with δ. As such, R is useful for detecting the δs at which correspondence to a single habitat type is highest or lowest (Fig 4-5), e.g., R will be highest at the δ in which animal locations most closely match habitat type distribution. When more than 1 habitat type is considered, R also provides insight into how use might be directed toward these different types at different δs. This latter application is particularly valuable because habitat types are likely to overlap each other, or one type might be nested within the other (Fig. 4-6).

It is important to note that R is always based on observations made at δ grain, and that changes in R across δ result from changes in the density and dispersion of animal locations inside a habitat type relative to all animal locations. Consequently, ascertaining the accuracy at which animal locations should be measured, and the δ at which habitat types should be classified is not a trivial task. A fundamental requirement of this analysis is that δ grain and the accuracy of animal locations are fine enough to coincide with a species' immediate perceptual realm (e.g., visual range), thus ensuring that *R* reflects what animals can actually detect from any point location.

AN EXAMPLE WITH DEER IN URBAN AND RURAL HABITATS

I employed this 2-staged methodology to examine the patterns of habitat use of mule deer living on urban and rural winter ranges in northern Utah. The objectives of the study were to determine how deer in each area used habitat space, and how correspondence between animal locations and various habitat types changed as a function of δ. Embedded within the latter objective, I wanted to answer 2 questions: 1) how does *R* differ from the classic index of use vs. availability, and 2) do different habitat types become more or less important relative to each other as δ changes?

Study Areas

The urban and rural areas were situated along the west base of the Wasatch Mountains in the Cache Valley, approximately 100 km north of Salt Lake City, and were used primarily by migratory mule deer during winter (November-April). The urban area was contained within the City of Logan and surrounding suburban communities. The rural area was centered 15 km north of the urban area. Elevation (~ 1500 m) and climate were similar in both areas. Snow depths ranged from 5 to 40 cm during periods of data collection (January-March, 1995 and 1996), and temperatures were also similar, ranging from -20 to 6 C°.

Residential housing (0.15-8.0 houses/ha) dominated the urban landscape, and vegetation was diverse, consisting of exotic and native shrubs as well as cultivated fields. The rural area, in contrast, was characterized by a more open landscape. Vegetation consisted of grain and alfalfa fields in a rangeland dominated by big sagebrush (*Artemesia tridentata*), bitterbrush (*Purshia tridentata*), cheatgrass (*Bromus tectorum*), and crested wheatgrass (*Agropyron desertortum*). Ravines and north-facing slopes contained patches of big-toothed maple (*Acer grandidentatum*). The rural area exhibited a slightly more diverse topography than the urban area, containing several hilly areas with north- and south-facing slopes of < 30°.

Methods

Deer Locations.--I recorded the locations of 10 radio-telemetered urban deer and 10 radio-telemetered rural deer (all adult does) from 1 January to 15 March, 1995 and 1996. These deer were part of a larger sample of tagged deer in each area (see chapter II), and were selected because they were rarely observed together. As such, I assumed their movements were unrelated. Their home ranges were dispersed, but relatively contiguous and overlapping throughout each area. By combining the locations from these animals, I was able to increase the range of δs over which patterns of habitat use were measured on each winter range.

I located each deer every 3 days (resulting in 25 locations/deer/winter) during 1 of 3 time intervals: 1) dawn or dusk, which included the hour before and after sunrise, or the hour before and after sunset, 2) the day, 1000-1600, and 3) the night, 2200-0400. Approximately 50% of these locations were during the dawn/dusk interval, 25% from the day, and 25% from the night. These intervals were designed to capture the full spectrum of deer activity patterns and thus provide an adequate description of habitat use. I determined most locations (80%) by following radio signals in vehicles or on foot until animals were seen. When a deer was sighted, I used a hand-held global positioning system (GPS; mean error = 46 m, SE = 6.4 m) to estimate my location, and added the directional distance from the GPS unit to the deer to estimate the deer's location. Direction was determined with a hand-held compass (± 2°), and distance was estimated visually. Sighting distances were always < 200 m for urban and rural deer. When I could not see a radio-telemetered deer (e.g., when it was too dark or when deer were in thick cover), I determined its location by circling the areas from which its radio signals emanated (radii of 20-50 m for urban deer and 50-100 m for rural deer), and plotted its position on a USGS 1:24,000 topographic map. I recorded all deer locations as Universal Transverse Mercator coordinates (UTM), which were rounded off at 10 m.

Stage 1 Analyses.--I calculated the IFDs across δ for the combined 1995 and 1996 locations of the 10 radio-telemetered deer in each study area ($\underline{n} = 500$). I compared deer IFDs to random IFDs by scattering 500 random points within each study area. The rectangular boundaries of each study area were demarcated by the outermost x- and y-coordinates of all deer locations. These 2 areas were of similar extent, thus allowing useful comparisons between patterns of space use for urban and rural deer. Not all regions in each study area were accessible to deer (e.g., fenced areas, or areas preempted by large buildings). Therefore, I excluded random points that fell in these regions, and added other random points until sample size reached 500. Because slightly different patterns may arise from different sets of random points, I calculated IFDs for 30 different sets of 500 random points, and averaged the results at each δ.

For both deer and random locations, the coarsest δ of analysis equaled 1/3 the extent of each study area. This meant that IFDs were calculated with 9 boxes and 36 cells at the coarsest δ. IFDs at δs of 1/4, 1/6, 1/8... the extent of each study area were then calculated until box size approached 100 m. For each calculation, I rotated the grid of boxes surrounding the study area 18 times (5° per rotation) and computed separate estimates of the IFD for each rotation. I then used the estimate that covered the spatial pattern with the fewest boxes to represent the "true" IFD at each δ (Mandelbrot 1983).

It is worth noting that the measurement precision of urban and rural deer locations differed approximately 20% of the time. Specifically, there was a greater error associated with rural deer locations when deer positions were determined by circling the areas from which radio signals emanated. This difference in precision may have potentially caused the IFDs of rural deer locations to be lower than those of urban deer at fine δs of analysis, thereby invalidating any comparisons. To determine if this was the case, I added 50-100 m of random error to the affected locations of urban deer. By doing so, the error for urban and rural deer locations was equal. This increase in error had no effect on the IFDs of urban deer locations.

Stage 2 Analyses.--I determined the degree of correspondence between deer locations and 4 habitat types in the urban area and 6 habitat types in the rural area. Types in the urban area included: 1) cultivated fields, which during winter could be described as large areas devoid of vegetation, 2) regions of high housing density (> 4 houses/ha), 3) concealment vegetation, and 4) shrubby vegetation. Types in the rural area included: 1) cultivated fields, 2) south-facing slopes (150-210° from magnetic north, with an angle of slope > 15°), 3) north-facing slopes (330-30° from magnetic north, with an angle of slope > 15°), 4) concealment vegetation, 5) shrubby vegetation, and 6) stands of grass, i.e., open grassy areas with no shrubs or trees. I defined concealment vegetation as areas of vegetation that could hide the location of a standing deer from an observer situated 20 m or more away in any direction. I defined shrubby vegetation as areas containing shrubs or small trees (at densities > 10/ha) that could be browsed by deer. Overall, these different habitat types were easily measured, and were believed to differ with respect to foraging opportunities, thermal conditions, and risk potential during winter.

I demarcated the boundaries of different habitat types on aerial photographs (scale: 1:660) while ground-truthing each study area. I then recorded the presence of each habitat type at a box size (δ grain) of 1-ha, whereby boxes centered on UTM coordinates 100 m apart. At least 25% of a box needed to be filled by a type for the box to be considered "occupied." A box could contain none to several habitat types. I determined the proportions of habitat occupied by each type (Z) by summing all 1-ha boxes containing a type. I then computed the δ-by-δ IFDs for 1) animal locations inside each type ($I_{c|z}$) , 2) all animal locations (I_t), 3) random locations that fell in each type each type ($I_{r|z}$), and 4) all random locations (I_{rt}). As in stage 1, IFDs were based on estimates that covered the spatial pattern with the fewest number of boxes. Finally, the degree of correspondence, R, between animal locations and different habitat types was computed via equation 3.

Results

Stage1.--Visually, the distributions of urban and rural deer locations differed markedly (Fig. 4-7). Urban deer locations appeared relatively clustered, as many regions of the study area received heavy use while other regions received little or no use. Conversely, rural deer locations were more spread out, occupying most regions of the study area. The δ-by-δ comparisons between deer IFDs and random IFDs quantified these patterns of space use, revealing the δs at which deer locations were most fragmented and aggregated, and most uniformly space-filling (Fig. 4-8).

Notably, urban deer locations were most uniformly space-filling from 100 to 400 m. At this range of δs, the IFDs of deer locations exceeded those of random locations by approximately 0.5 of a dimension, indicating that certain patches of the landscape were utilized fully by deer at this range of δs, and that use was evenly concentrated in these patches. At the other extreme, urban deer locations were most fragmented and aggregated from 2000 to 3000 m, indicating that patterns of habitat use corresponded most closely to isolated patches of the landscape at this range of δs. Rural deer locations, on the other hand, were most uniformly space-filling from 400 to 600 m, and most fragmented and aggregated at 3300 m.

Because the urban and rural study areas were of similar size, the functions of IFD vs. δ for random locations in the 2 study areas were nearly identical (Fig. 4-8). As such, meaningful comparisons between patterns of space use for urban and rural deer could be drawn. For instance, urban deer locations were far more space-filling than rural deer locations at fine δs of analysis (100-300 m). At coarse δs (800-3000), however, urban deer locations were markedly more fragmented and aggregated than those of rural deer.

Stage 2.--The 4 urban and 6 rural habitat types occupied from 5 to 32 % of the available habitat space (Figs. 4-9 and 4-10), and exhibited a variety of spatial patterns, which overall, were not self-similar across all δs of analysis (Tables 4-1 and 4-2). Deer locations occurred within all of the habitat types in each area, but Q_z/Z varied considerably among types (Tables 4-3 and 4-4). The index of correspondence, *R*, calculated via equation 3, revealed 1) how the δ-by-δ spatial associations between deer locations and each habitat type affected the classic index of use vs. availability, and 2) the δs at which patterns of habitat use corresponded most positively and negatively with the different habitat types (Tables 4-3 and 4-4).

In particular, the distribution of urban deer locations corresponded most positively to concealment vegetation at all δs of analysis (Table 4-3). Moreover, the degree of correspondence between deer locations and concealment vegetation was far greater than that estimated by the classic index of use vs. availability (Q_z/Z) throughout this range of δs. Correspondence between deer locations and areas containing shrubby vegetation was also greater than that expected by chance at all δs of analysis. And interestingly, R was noticeably larger than Q_z/Z only at an intermediate range of δs (300-1200 m). Also of interest is that correspondence between deer locations and regions of high-housing density was less than that expected by chance at fine (200-600 m) and coarse (1500-3000 m) δs of analysis, but greater than that expected by chance from 600 to 1200 m. Correspondence between deer locations and cultivated crop fields was far less than that expected by chance at all δs of analysis, and this result was most evident at fine δs.

In the rural area, deer locations corresponded most positively to areas containing shrubby vegetation at relatively fine δs of analysis (200-625 m), and south-facing slopes at intermediate to coarse δs of analysis (625-3300 m; Table 4-4). In concordance with these patterns, *R* for shrubby vegetation was noticeably greater than Q_z/Z at fine δs, whereas *R* for south-facing slopes was noticeably greater than Q_z/Z at coarse δs and less than Q_z/Z at fine δs. As in the urban area, correspondence between rural deer locations and cultivated crop fields was far less than that expected by chance at all δs of analysis, and negative correspondence was most evident at fine δs. Finally, deer locations corresponded positively, albeit weakly, to concealment vegetation, grass stands, and north-facing slopes in the rural area. *R* for these 3 habitat types differed negligibly from Q_z/Z.

Interpretation and Discussion of Results

Stage 1.--A fundamental finding of the comparisons between deer and random IFDs was that both urban and rural deer locations were most uniformly space-filling at relatively fine δs, and most fragmented and aggregated at relatively coarse δs. The first part of this finding has a simple explanation. Most landscapes are heterogeneous, whereby some areas differ structurally or functionally from other areas (Kolasa and Rollo 1991). Consequently, at fine δs, the relatively high space-filling nature of deer locations likely reflected high internal utilization of certain areas of the landscape (e.g., patches containing habitat components) that differed from other areas.

The second part of this finding has 2 potential explanations. The first is that the same patches utilized fully by deer at fine δs may have exhibited a fragmented distribution at coarse δs. Therefore, if these same patches largely influenced patterns of habitat use at all δs, the distribution of deer locations would have coincided with the fragmented distribution of these patches at coarse δs. An alternative explanation is that patterns of habitat use may have been largely influenced by a different set of patches at coarse δs, and these patches exhibited a distribution more fragmented than that expected by chance at these δs. In either case, the distribution of deer locations appeared to be explained by the internal availability of certain landscape patches at relatively fine δs, and the degree to which these or other patches were fragmented at relatively coarse δs.

Although these patterns of space use were qualitatively similar for deer in urban and rural areas, they differed quantitatively. Specifically, differences between the IFDs computed from deer and random locations indicated that the internal utilization of landscape patches in the urban area was highest from 100 to 400 m. In contrast, the internal utilization of landscape patches in the rural area was highest from 400 to 600 m. These findings thus suggest that the landscape patches most utilized by urban deer at fine δs were considerably smaller and more isolated than those most utilized by rural deer. That the IFDs of urban deer locations were only greater than those of rural deer from 100 to 400 m supports this inference.

At intermediate to coarse δs (600-3000 m), the IFDs of urban deer locations were much lower than those of rural deer locations. Therefore, a plausible hypothesis is that the landscape patches most utilized by urban deer at coarse δs were also more fragmented than those most utilized by rural deer. Moreover, it might be expected that the landscape patches most utilized by urban deer at coarse δs would be most fragmented (i.e., characterized by a relatively low IFD) at 2250 m as this is the δ at which the IFD of urban deer locations was lowest. For this same reason, it might be expected that the patches most utilized by rural deer at coarse δs would be most fragmented at 3300 m.

Stage2.--The δ-by-δ relationships between animal locations and various habitat types helped illuminate the patterns of space use observed in stage 1. That is, the index of correspondence, *R*, revealed why urban deer used relatively small landscape patches at fine δs, and why their patterns of space use were relatively fragmented and aggregated at coarse δs.

In the urban area, deer locations corresponded most positively with concealment vegetation at all δs of analysis, suggesting that patterns of habitat use were influenced primarily by habitat components that reduced risk exposure (see Chapter 2). Moreover, *R* for concealment vegetation was greater than the classic index of use vs. availability (Q_z/Z) across this range of δs. This result indicated that there was a positive spatial association between animal locations and concealment vegetation from δs finer than a deer's immediate perceptual realm to δs encompassing the home ranges of several individuals. In other words, the distribution of concealment vegetation appeared to have as much of an effect on the location of specific activity areas as it did on the areas demarcating home ranges.

It is not surprising, therefore, that urban deer locations were most uniformly space-filling from 100 to 400 m, as it was throughout this range of δs that the IFDs of concealment vegetation were lowest. In particular, at a δ of approximately 200 m, the IFD of concealment vegetation was only 0.89, which meant that patches of it were, on average, so small and isolated that they occupied areas less than 100 m across. At intermediate to coarse δs, patches of concealment vegetation were also highly fragmented. Accordingly, these same patches of concealment vegetation that largely influenced patterns of habitat use at fine δs, also caused patterns of habitat use to be fragmented and aggregated at coarse δs. Notably, it is easy to see that like deer locations, the IFD of concealment vegetation was most fragmented at 2250 m (Table 4-2).

Also in the urban area, regions containing shrubby vegetation were used more than that expected by chance at all δs. This result was expected because shrubs generally comprise the bulk of forage biomass eaten by Rocky Mountain mule deer during winter (Wallmo and Regelin 1981). What *R* revealed, however, was that there was a positive spatial association between deer locations and the distribution of shrubby vegetation only at δs ranging from 300 to 1200 m, and this association increased with δ coarseness throughout this range. A likely explanation for this pattern is that at δs coarser than the size of patches fully occupied by concealment vegetation (i.e., 200 m), deer roamed their home ranges in search of forage. The farther they roamed, the more their point locations corresponded to the distribution of forage. However, as δ approached the size of deer home ranges, which in the urban area averaged 275 ha (see Chapter II), observed patterns of habitat use were no longer affected by the foraging movements of individuals. Accordingly, the spatial associations between deer locations and shrubby vegetation diminished at these coarse δs.

The degree of correspondence between deer locations and high-density housing across δ also appeared to coincide with deer movements within home ranges, as *R* increased from 200 to 1200 m. In this case, however, *R* indicated that areas containing high-density housing were used less than that expected by chance across most δs. Given that patterns of habitat use were largely influenced by risk avoidance, this result was anticipated because the potential risks to urban deer (e.g., harassment by people and dogs, collisions with automobiles) were likely most prevalent in areas of dense housing. However, these areas also possessed valuable forage, and they overlapped considerably with areas containing shrubby vegetation. Therefore, as deer increased their movements in search of forage and away from concealment vegetation, more and more point locations occurred within areas of high-density housing. Accordingly, the spatial associations between deer locations and high-density housing increased until δ approached the extent of movements within home ranges. At the coarsest of these δs (i.e., 700-1200 m), R actually indicated that areas of high-density housing were used more than that expected by chance.

Finally, the minimal use of crop fields by urban deer was also expected because these areas consisted of bare ground during winter, and thus provided no forage or cover. Again, however, R tended to increase with δ coarseness until δ approached the size of deer home ranges. As argued above, this result probably reflected the movements of individuals within their home ranges. That is, the farther deer moved beyond areas containing concealment vegetation, the more likely they were to travel across barren crop fields in search of forage.

In the rural area, the high degree of correspondence between deer locations and shrubby vegetation at all δs suggests that patterns of habitat use were influenced strongly by habitat components that increased energy or nutrient intake, i.e., forage availability. However, it was only at fine δs (200 - 625 m) that the distribution of shrubby vegetation appeared to affect these patterns, as the spatial associations between deer locations and this habitat type were negligible at coarser δs. What this means is that the distribution of shrubby vegetation likely affected the location of specific feeding areas within home ranges, but not home range areas themselves, which averaged 1100 ha for rural deer (see Chapter 2).

The high degree of correspondence between rural deer locations and south-facing slopes across all δs also infers that forage availability largely influenced patterns of habitat use in the rural area. This inference is logical because emerging forbs and grass, which constitute important winter foods of Rocky Mountain mule deer (Wallmo and Regelin 1981), as well as shrubs are often most accessible on south-facing slopes during winter. Interestingly, the spatial associations between rural deer locations and south-facing slopes were positive only at an intermediate to coarse range of δs (625-3300 m), and *R* increased throughout this range. This result thus suggests that the distribution of south-facing slopes had its greatest effect on patterns of habitat use at δs corresponding to foraging areas the size of deer home ranges.

This result is also the mirror image of that pertaining to the spatial associations between rural deer locations and shrubby vegetation. As such, it suggests that rural deer patterns of use were directed toward 2 different, yet partially overlapping features of the landscape, each at different range of δs. The values of *R* for shrubby vegetation and south-facing slopes corresponded to this switch in deer patterns of habitat use.

These patterns of habitat use directed toward shrubby vegetation at fine δs and south-facing slopes at coarse δs accounted for the space-filling uniformity of rural deer locations. That is, deer locations were most uniformly space-filling at about 600 m, which coincided with the coarsest δ at which there was a strong spatial association between locations and shrubby vegetation. Not surprisingly, the IFD of shrubby vegetation in the rural area at 600 m was much greater than that of concealment vegetation in the urban area. This explains why rural deer locations were dispersed (highly space-filling) within larger landscape patches than urban deer locations, i.e., 600 vs. 300 m. At coarse δs, the IFD of south-facing slopes was lowest at 3300 m, thus coinciding with the δ at which rural deer locations were most fragmented. Note, however, that the IFDs of south-facing slopes were higher that the IFDs of concealment vegetation in the urban area at coarse δs. This difference illuminates why rural deer locations were less fragmented than urban deer locations at these coarse δs.

SUMMARY

A fundamental goal of wildlife-habitat studies is to determine how and why animals distribute themselves the way they do on a landscape. By pursuing this goal, researchers hope to improve their grasp of the relationships between habitat characteristics, the behavior of individuals, their survival and reproduction, and ultimately population dynamics across space and time. In this chapter, I proposed a 2-staged methodology for analyzing wildlife-habitat relationships. The first stage describes the distribution of animal locations on a landscape, and the second stage provides a starting point for gaining insight into the underlying basis for these distributions. Unlike previous approaches, this methodology explicitly incorporates the effects of spatial pattern and scale. In the example given, this methodology showed that the effects of pattern and scale did indeed influence deer-habitat relationships in both urban and rural areas.

As proposed, this methodology does not achieve its full potential. In particular, assessing the degree of correspondence between animal locations and habitat types was based on presence/absence data for each type. This procedure is the crudest way to classify habitat, as in all likelihood, each habitat type will vary quantitatively with respect to the characteristics used to define it. To overcome this shortcoming, these characteristics within each type can be ranked at the δ at which habitat types are measured, i.e., δ grain or pixel size. Ranked pixels can then be used to weight the expected probabilities of animal locations occurring in each type.

LITERATURE CITED

Alldredge, J. R., and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management 50:157-165.

_____, and _____. 1992. Further comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management 56:1-9.

Block, W. M., and L. A. Brennan. 1993. The habitat concept in ornithology: theory and applications. Pages 35-91 *in* D. M. Power, editor. Current ornithology. Volume 11. Plenum Press, New York, New York, USA.

Hall, L. S., P. R. Krausman, and M. L. Morrison. 1997. The habitat concept and a plea for standard terminology. Wildlife Society Bulletin 25:173-182.

Hastings, H. M., and G. Sugihara. 1993. Fractals: a user's guide for natural sciences. Oxford University Press, New York, New York, USA.

Havelka, M. 1995. A question of scale: the effects of environmental heterogeneity on populations. COENSOSES 12:83-87.

Holt, R. D. 1987. Population dynamics and evolutionary processes: the manifold roles of habitat selection. Evolutionary Ecology 1:331-347.

Hutto, R. L. 1985. Habitat selection by nonbreeding, migratory land birds. Pages 455-476 *in* M. L. Cody, editor. Habitat selection in birds. Academic Press, New York, New York, USA.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Johnson, G. D., A. Templeman, and G. P. Patil. 1995. Fractal based methods in ecology: a review of analysis at multiple scales. COENOSES 10:123-131.

Kolasa, J., and C. D. Rollo. 1991. The heterogeneity of heterogeneity: a glossary. Pages 1-23 *in* J. Kolasa and S. T. A. Pickett, editors. Ecological heterogeneity. Springer-Verlag, New York, New York, USA.

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

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943-1967.

Loehle, C., and B. L. Li. 1996. Statistical properties of ecological and geological fractals. Ecological Modeling 85:271-284.

Mandelbrot, B. B. 1983. The fractal geometry of nature. Freeman Press, San Francisco, California, USA.

McClean, S. A., M. A. Rumble, R. M. King, and W. L. Baker. 1998. Evaluation of resource selection methods with different definitions of availability. Journal of

Wildlife Management 62:793-801.

Milne, B.T. 1997. Applications of fractal geometry in wildlife biology. Pages 32-69 *in* J. A. Bissonette, ed. Wildlife and landscape ecology. Springer-Verlag, Inc., New York, New York, USA.

Morris, D. W. 1987. Ecological scale and habitat use. Ecology 68:362-369.

Morrison, M. L., B. J. Marcot, and R. W. Mannan. 1992. Wildlife-habitat relationships: concepts and applications. University of Wisconsin Press, Madison, Wisconsin, USA.

Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137: S29-S49.

Ritchie, M. E. 1998. Scale-dependent foraging and patch choice in fractal environments. Evolutionary Ecology 12:309-330.

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

Scheuring, A, and R. H. Riedi. 1994. Applications of multifractals to the analysis of vegetation pattern. Journal of Vegetation Science 5:489-496.

Turner, M. G., and R. H. Gardner. 1991. Quantitative methods in landscape ecology: an introduction. Pages 3- 14 *in* M. G. Turner, and R. H. Gardner, editors. Quantitative methods in landscape ecology. Springer-Verlag New York, New York, USA.

Wallmo, O. C., and W. L. Regelin. 1981. Rocky Mountain and Intermountain habitats.

Pages 387-421 *in* O.C. Wallmo, editor. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, Nebraska, USA.

White, G. C., and R. A. Garrot. 1990. Analysis of wildlife radio-tracking data. Academic Press, New York, New York, USA.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.

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

Table 4-1. Information fractal dimensions of 4 habitat types on an urban mule deer winter range of Cache Valley, Utah.

	IFD			
Resol. (m)	Crop field	High-density housing	Concealment vegetation	Shrubby vegetation
187	1.54	1.44	0.89	1.30
281	1.62	1.55	1.03	1.44
375	1.65	1.70	1.05	1.56
562	1.69	1.68	1.26	1.60
750	1.65	1.70	1.30	1.67
1125	1.65	1.71	1.29	1.67
1500	1.52	1.58	1.28	1.60
2250	1.51	1.75	1.23	1.59
3000	1.59	1.50	1.29	1.48

Table 4-2. Information fractal dimensions of 6 habitat types on a rural mule deer winter range of Cache Valley, Utah.

	IFD					
Resol. (m)	Crop field	South slope	North slope	Concealment vegetation	Shrubby vegetation	Grass stand
208	1.65	1.46	1.45	1.15	1.50	1.42
312	1.70	1.35	1.42	1.28	1.50	1.45
417	1.74	1.56	1.48	1.35	1.59	1.45
625	1.71	1.49	1.50	1.37	1.59	1.54
833	1.66	1.48	1.30	1.37	1.59	1.51
1250	1.72	1.54	1.26	1.40	1.65	1.59
1660	1.68	1.48	1.28	1.39	1.70	1.55
2500	1.75	1.54	1.33	1.48	1.72	1.59
3333	1.75	1.31	1.30	1.42	1.65	1.48

Table 4-3. Degree of correspondence (*R*, calculated via eqn. 3) between mule deer locations and 4 habitat types on an urban winter range of Cache Valley, Utah, 1995-1996. Numbers in parentheses represent proportional habitat type use vs. habitat type availability, which, unlike *R* do not account for the spatial associations between animal locations and habitat types at each resolution of analysis.

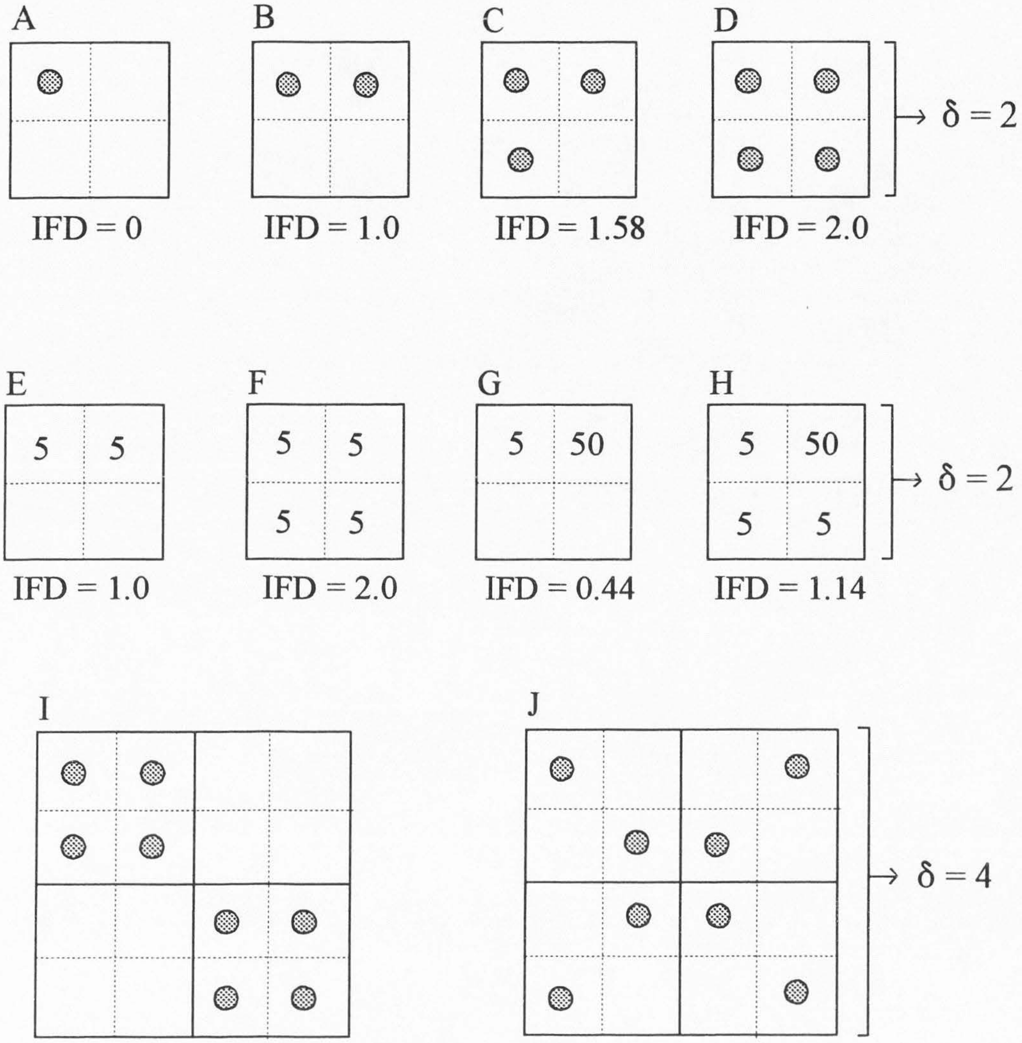
	R^1			
Resol. (m)	Crop field (0.16)	High-density housing (0.97)	Concealment vegetation (7.98)	Shrubby vegetation (2.65)
187	0.01	0.58	11.80	2.58
281	0.02	0.68	10.71	3.36
375	0.03	0.74	11.04	3.78
562	0.04	0.88	10.71	3.82
750	0.06	1.14	11.10	3.83
1125	0.07	1.20	11.25	3.87
1500	0.11	0.88	10.81	2.80
2250	0.09	0.87	10.45	2.70
3000	0.07	0.82	10.38	2.55

[1] A value > 1 indicates that the habitat type was used more than that expected by chance, whereas the opposite is true if a value is < 1.

Table 4-4. Degree of correspondence (*R*, calculated via eqn. 3) between mule deer locations and 6 habitat types on a rural winter range of Cache Valley, Utah, 1995-1996. Numbers in parentheses represent proportional habitat type use vs. habitat type availability, which, unlike *R* do not account for the spatial associations between animal locations and habitat types at each resolution of analysis.

	R^1					
Resol. (m)	Crop field (0.53)	South slope (2.61)	North slope (1.22)	Concealment vegetation (1.36)	Shrubby vegetation (2.27)	Grass stand (1.63)
208	0.11	2.08	1.30	1.53	3.06	1.16
312	0.24	2.07	1.23	1.55	2.93	1.36
417	0.41	2.32	1.22	1.31	2.86	1.85
625	0.42	2.80	1.25	1.23	2.80	1.85
833	0.41	2.87	1.14	1.39	2.30	1.86
1250	0.41	3.08	1.21	1.50	2.30	1.91
1660	0.48	3.20	1.23	1.50	2.37	1.92
2500	0.55	3.35	1.28	1.49	2.36	1.70
3333	0.55	3.45	1.30	1.50	2.29	1.65

[1] A value > 1 indicates the habitat type was used more than that expected by chance, whereas the opposite is true if a value is < 1.



δ	IFD
2	2.0
4	1.0

δ	IFD
2	1.0
4	2.0

Figure 4-1. Information fractal dimensions of various spatial patterns. A-H are for a resolution (δ) of 2 units, and I and J are for δs of 2 and 4 units. A-B and I-J are based on presence/absence data, and E-H are based on intensity data, i.e., ≥ 1 point per cell.

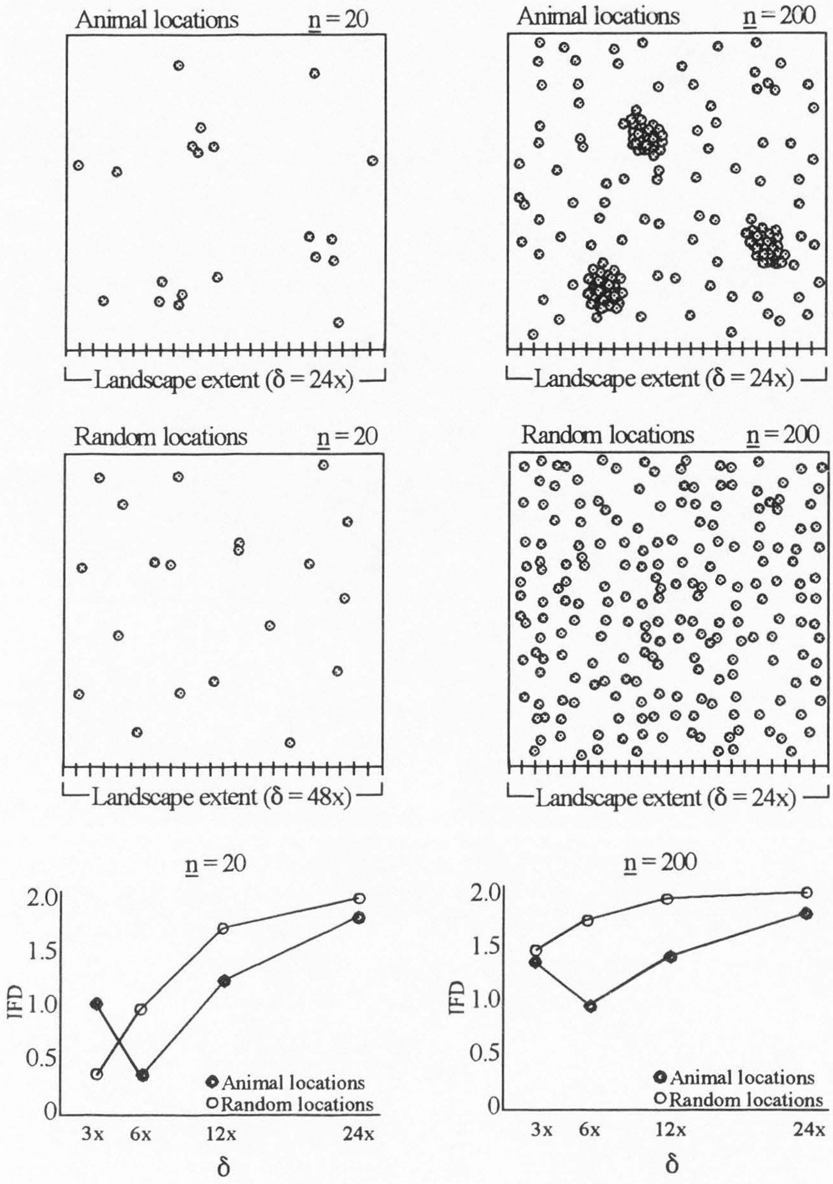


Figure 4-2. Simulation showing that changes in sample size do not affect the qualitative interpretation of the relative differences between IFDs computed from animal and random locations. In this simulation, 60% of animal locations cluster in 3 patches and 40% are distributed randomly around these patches. Note that the function of IFD vs. δ for animal and random locations changes quantitatively with sample size, but animal locations remain most uniform space-filling at a δ of 3x, and most fragmented and aggregated at a δ of 6x.

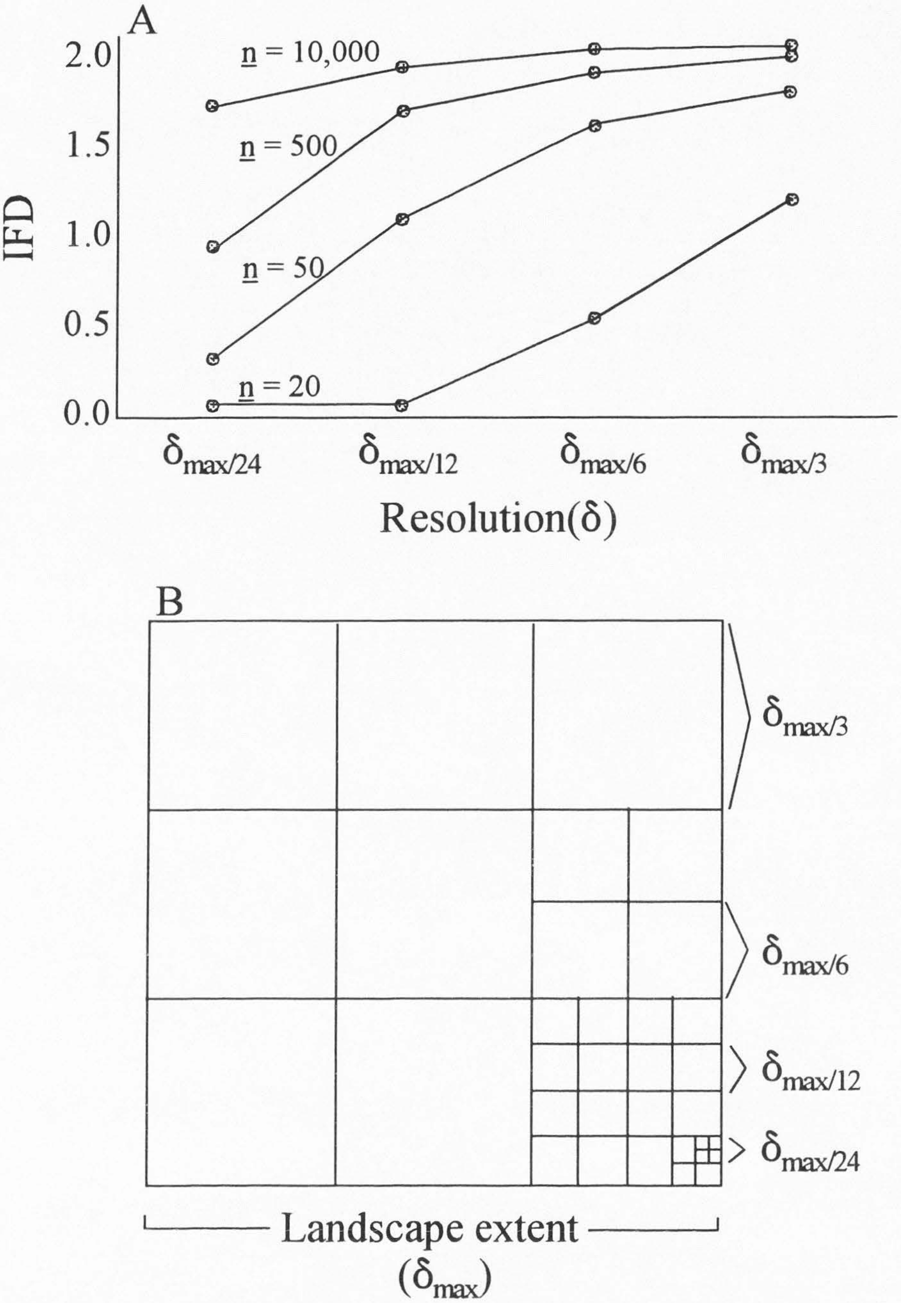
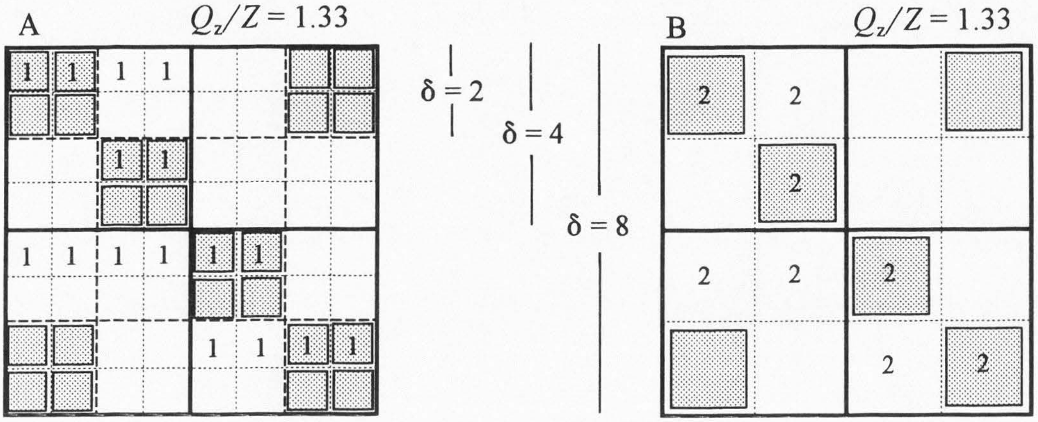


Figure 4-3. IFD vs. δ for a various number (N) of random locations (A) distributed within a landscape space (B). Note that the function of IFD vs. δ changes predictably with the number of locations. Also note that IFDs approach, but do not achieve, a value of 2 because random points are not stacked evenly in space.

Dist.	Q_z	Z	$I_{c\|z}$	I_t	$I_{r\|z}$	I_{rt}	R
A	0.5	0.5	1.0	1.9	0.9	1.9	1.05
B	0.5	0.5	0.8	1.9	0.9	1.9	0.95

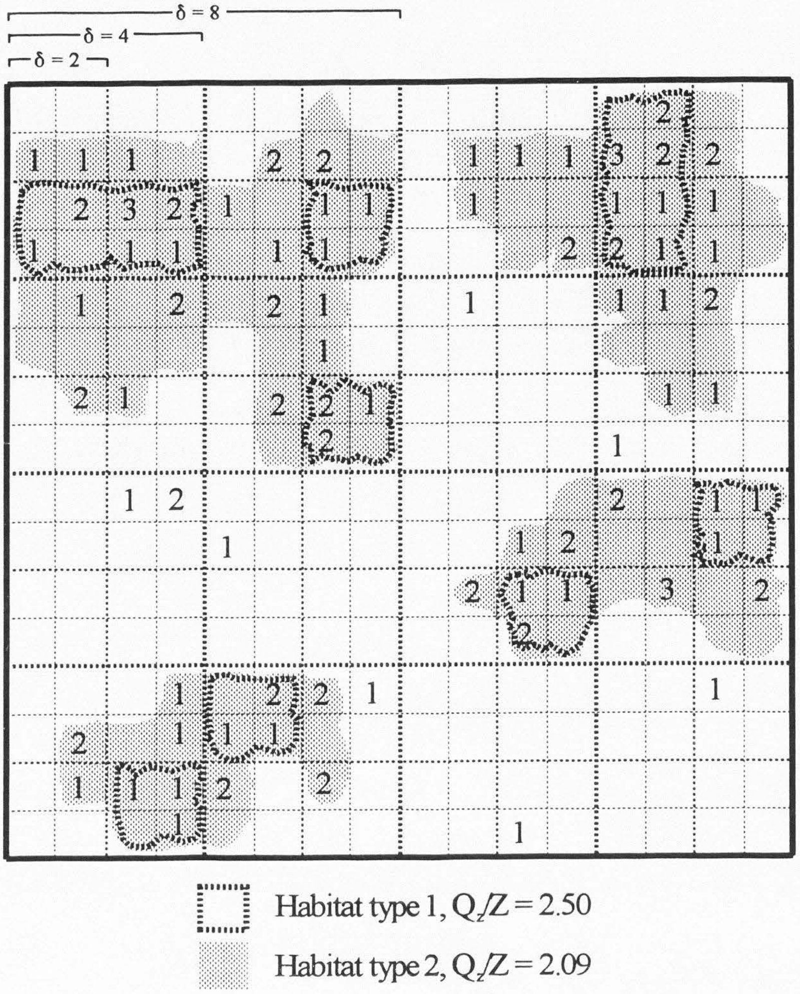
Figure 4-4. Demonstration of how the spatial associations between animal locations and a single habitat type affect the classic index of use vs. availability (Q_z/Z). Shaded areas are the grains of habitat space occupied by the habitat type, and numbers are the number of times animal locations occur in each grain of habitat space. Note that Q_z/Z suggests that use of the habitat type by both distribution A and B equals that expected by chance alone. Clearly, however, animal locations in A match the distribution of the habitat type, whereas those in B do not. The value of R (eqn. 3) accounts for these spatial associations.



δ	R
2	1.33
4	1.97
8	1.08

δ	R
4	1.97
8	1.08

Figure 4-5. Demonstration of how the degree of correspondence (R) between simulated animal locations and a habitat type changes with δ. In A, δ grain of habitat and accuracy of animal locations are measured at 1 unit. In B, they are measured at 2 units. Note that R equals the classic index of use vs. availability (Q_z/Z) at a δ of 2, and is highest at a δ of 4; these patterns can be detected visually. Note also that changing δ grain does not affect R.



δ	*R* Type 1	*R* Type 2
2	5.05	2.65
4	2.85	2.95
8	2.55	2.45

Figure 4-6. Simulation that shows how *R* detects changes in use of 2 habitat types, 1 of which is nested within the other, at 3 δs of analysis. At a δ of 2, use is most strongly directed toward habitat type 1, and at a δ of 4 use switches to habitat type 2.

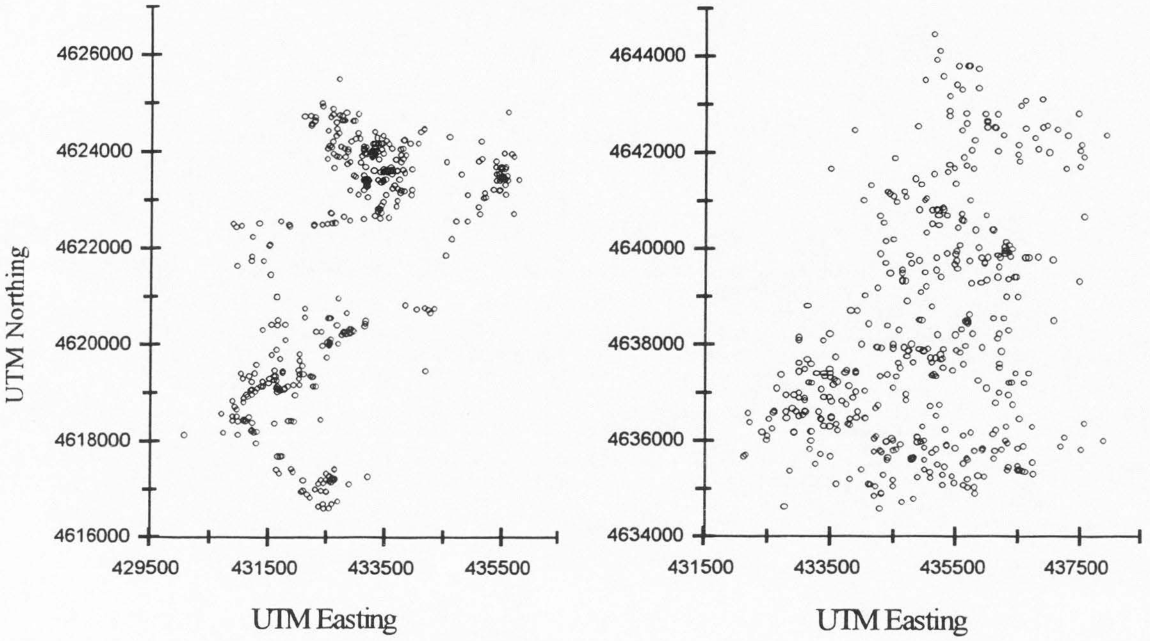


Figure 4-7. Distribution of 500 point locations from 10 mule deer (50 locations/deer) with overlapping home ranges in an urban (A) and a rural (B) area of Cache Valley, Utah.

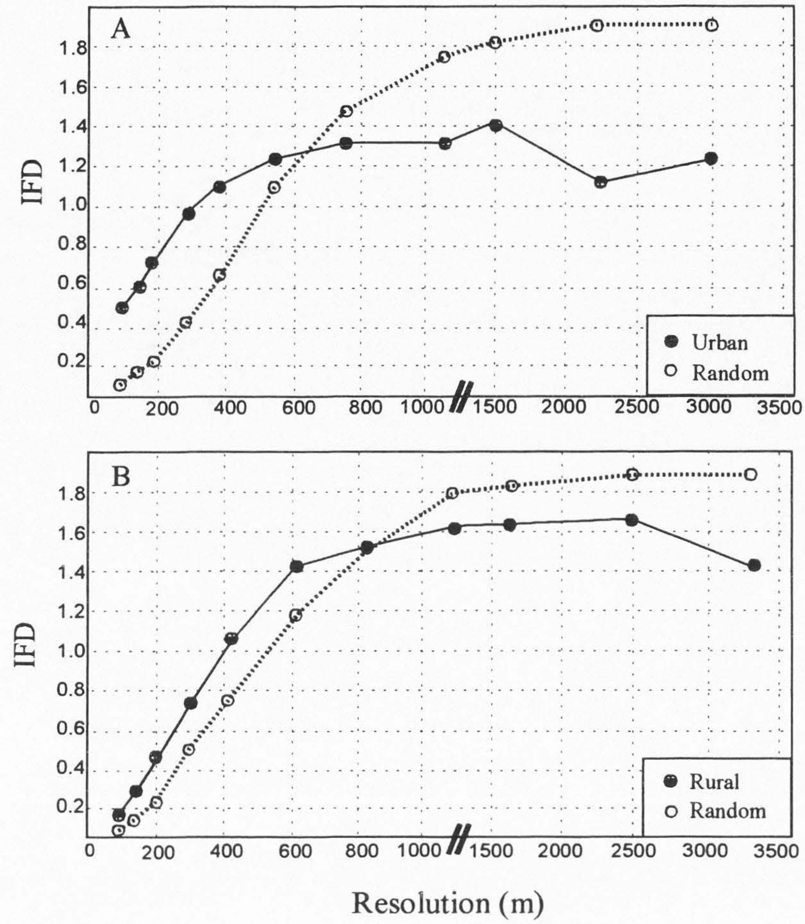


Figure 4-8. IFDs computed from 500 deer locations (10 deer, 50 locations/deer) and 500 random locations on an urban winter range (A), and a rural winter range (B) in Cache Valley, Utah. The analyses show that both urban and rural deer locations are most uniformly space-filling at fine δs of analysis, and most fragmented and aggregated at coarse δs of analysis. Comparisons between the 2 analyses reveal that urban deer locations are far more uniformly space-filling at fine δs (100 - 400 m), and more fragmented at coarse δs (800 - 3000 m).

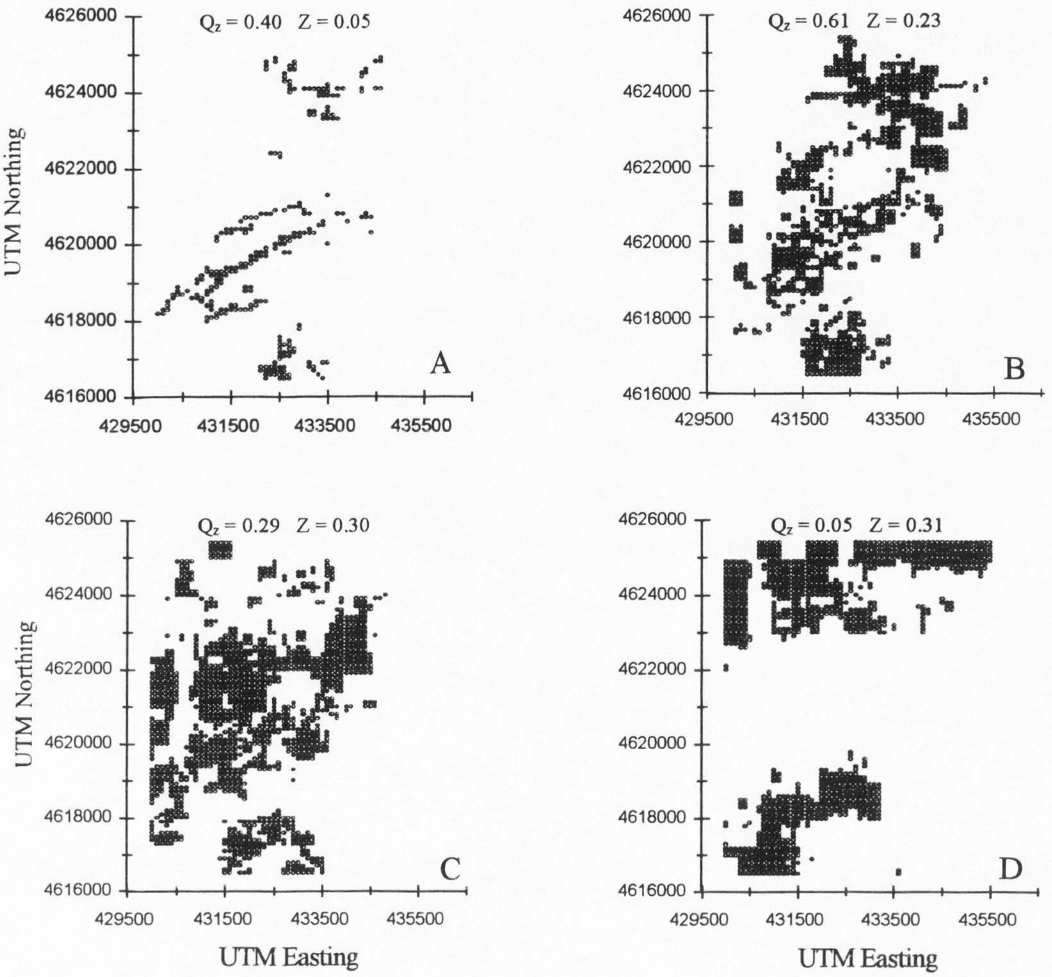


Figure 4-9. Distribution of (A) concealment vegetation, (B) shrubby vegetation, (C) high-density housing, and (D) crop fields on an urban mule deer winter range of Cache Valley, Utah. Q_z = the proportion of animal locations (see Fig. 4-7) in each habitat type, and Z = the proportion of the study area occupied by that type.

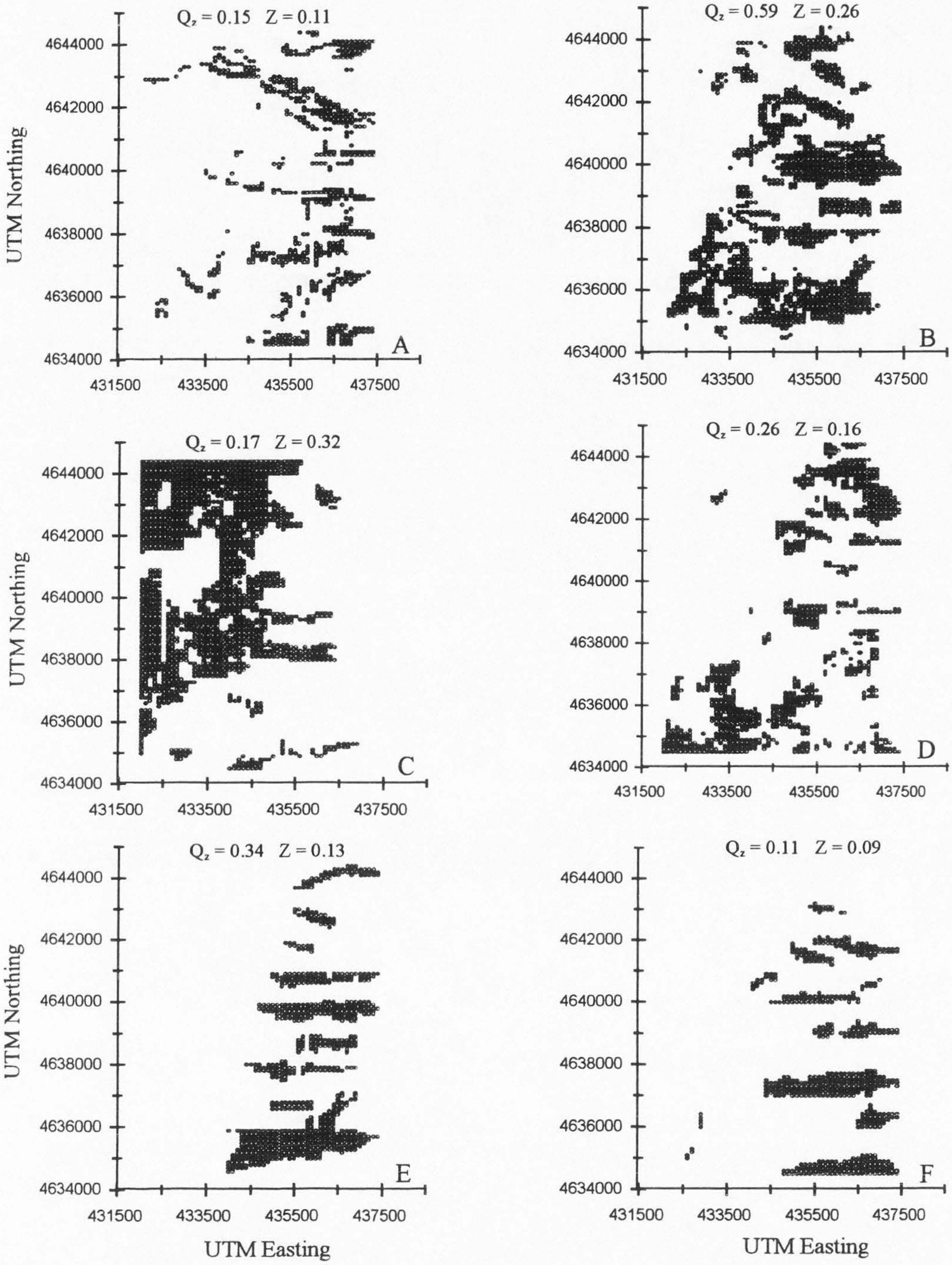


Figure 4-10. Distribution of (A) concealment vegetation, (B) shrubby vegetation, (C) crop field, (D) grass stand, (E) south-facing slope, and (F) north-facing slope on a rural mule deer winter range of Cache Valley, Utah. Q_z = the proportion of animal locations in each habitat type (see Fig. 4-7), and Z = the proportion of the study area occupied by that type.

CHAPTER 5

SYNTHESIS AND INTEGRATION OF RESEARCH FINDINGS

The time-specific hypothesis of deer net energetic gains developed in Chapter 2 suggests strongly that the urban habitat was inferior to the rural habitat during my study. That is, this hypothesis implies that migratory and nonmigratory deer using the urban winter range were energetically deprived relative to their rural counterparts. Moreover, the potential disparities in forage conditions on urban and rural winter ranges could not comprehensively explain the different behavioral and demographic characteristics of urban and rural deer. Therefore, it is likely that risks played a large role in reducing the relative quality of the urban habitat. Specifically, risks in the urban area appeared to have a large impact on deer spatial and temporal behaviors. Changes in behavior, in turn, acted as a self-imposed constraint on the ability of deer to access forage and perhaps the amount of time they spent foraging. This constraint manifested itself as inferior demographic characteristics of urban deer.

The scale-dependent patterns of habitat use identified in Chapter 4 corroborate the hypothesis that risks played a dominate role in the behaviors of urban deer. Patterns of space use by urban deer were explained largely by the distribution of concealment vegetation, which consisted of relatively small patches that were highly fragmented throughout the urban area. Consequently, the distribution of hiding cover had as much of an effect of the locations of specific activity areas as it did on the location of home ranges. Therefore, by restricting their patterns of habitat use to areas that provided refuge from risks, urban deer did not fully utilize the resources in the urban habitat. Patterns of habitat use by rural deer, on the other hand, appeared to be unaffected by risks. Instead, rural deer made full use of the rural landscape.

Although the spatial and temporal behaviors and patterns of habitat use differed between urban and rural deer, the results of Chapter 3 indicated that the fractal dimensions of their movement pathways converged to a common value of approximately 1.3. For both urban and rural deer this value was achieved once pathways exceeded 80 m. This finding thus suggests that risk avoidance by urban deer did not influence how they responded to habitat, i.e., the way they moved when searching for resources. For instance, urban deer did not walk in a straight line when traveling between areas of concealment vegetation. Instead, it appears that perceived risks in the urban area forced deer to minimize 1) the extent of their movements (i.e., home range size), and 2) the amount of time each day was spent in areas not containing concealment vegetation. The latter conclusion can be inferred because the sampling regimes used to estimate patterns of habitat use were similar for urban and rural deer (Chapter 4).

On a more conceptual note, the fractal dimensions of deer movement pathways observed in Chapter 3 have potentially profound implications for the study of animal spatial ecology. First, it is quite remarkable that the fractal dimensions of movement pathways for both urban and rural deer converged to a common value of ~1.3. This value is remarkable because urban and rural deer patterns of habitat use were influenced largely by different habitat components, and these components exhibited markedly different distributions on the landscape (Chapter 4). Therefore, given that habitat heterogeneity could not explain the similarities in urban and rural deer movements, I surmised that the observed patterns reflected an intrinsically driven mechanism that allows animals to sample the resources in their home ranges while minimizing energetic expenditure. Although this hypothesis seems like a stretch, it is easy to conceptualize how such an optimal movement geometry could have evolved through natural selection. Clearly, this hypothesis warrants further investigation.

Also, a question of theoretical and practical importance to the field of spatial ecology is: Can observations of movements at fine resolutions be used to explain animal patterns of habitat use on a landscape? Although I did not set out to specifically address this question, cursory interpretation of my results might lead one to conclude that movement pathways and observed patterns of habitat use on a landscape are unrelated. This conclusion is easily drawn because patterns of habitat use by urban and rural deer were clearly different from each other, but their movement pathways appeared similar. Upon contemplating this question, however, I believe that correspondence between movements and patterns of habitat use could not have been determined with the methods I used. Measurement of deer movement pathways was purely a function of space. On the other hand, measurement of deer patterns of habitat use incorporated both space and time, i.e., the likelihood that a deer would be located in a specific area was influenced by how much time the animal spent in that area. Therefore, before these 2 concepts can be linked, measurements of deer movements will need to incorporate a temporal element.

Overall, my research provides a preliminary assessment of 1) how and why urban winter ranges differ from rural winter ranges, and 2) how urban and rural deer respond to and use their respective habitats. As such, my research findings can be used to make informed decisions regarding the management of urban mule deer (Chapter 2). In addition, my research endeavors involved developing new techniques for assessing how animals respond to habitat across scale (Chapter 3), and how patterns of habitat use change as a function of scale (Chapter 4). These techniques, and the results that they produce, open several new avenues of research that should help ecologists start thinking about how the behaviors of individuals influence population-level phenomena. Specifically, these techniques provide the means of incorporating scale into how animals search for and detect resources, and how resource and landscape patterns influence animal distributions.

CURRICULUM VITAE

MARK F. McCLURE

February 2001

OBJECTIVE: To obtain a career in teaching and research in the ecological and wildlife sciences.

EDUCATION:

High School Diploma: 1985. Catalina High School, Tucson, AZ

B.S. Wildlife Science: 1991, GPA: 3.65/4.0 Cum Laude, University of Arizona

M.S. Wildlife Science: 1993, GPA: 4.0/4.0 University of Arizona

Ph.D. Wildlife Science: 2001, GPA: 3.85/4.0 Utah State University

RESEARCH EXPERIENCE:

Graduate Research Assistant (Ph.D.)

Department of Wildlife Sciences, Utah State University. January 1994 -February 2001.

I developed new methodologies to assess scale-dependent wildlife-habitat relationships, and used these methodologies to relate the effects of urban development on mule deer behaviors and population dynamics in Cache Valley, UT. Specifically, I developed new approaches for analyzing and modeling movement and distributional patterns of animals. These approaches combined elements of fractal geometry, information theory, body-size allometry, bioenergetics, and optimality theory. I linked scale-dependent patterns of habitat use to landscape characteristics using a new index of 'use versus availability' that explicitly incorporated the effects of scale. Additionally, I organized and conducted meetings with metropolitan residents and landowners to assess human attitudes towards migratory and non-migratory deer using urban and rural settings. I collaborated with biologists and managers from the Utah Division of Wildlife Resources to integrate research efforts and human desires into management objectives and long-range ecosystem planning. **Contact** and supervisor: John A. Bissonette, Utah Cooperative Fish and Wildlife Research Unit, USGS-BRD, Utah State University, (435) 797-2511.

Graduate Research Assistant (M.S.)

Department of Wildlife Sciences, University of Arizona. July 1991 - August 1993.

I investigated population structure, patterns of habitat use, social behaviors, and foraging patterns of coyotes living at the interface of Saguaro National Park and Tucson, AZ. I collaborated with Park Service personnel to incorporate research findings into management plans designed to reduce conflicts between coyotes and residents living near the park boundary, while simultaneously adhering to the objectives of the Park Service. **Contact** and supervisor: William W. Shaw, Department of Wildlife and Fisheries, University of Arizona, (520) 621-7255.

Research Consultant

San Pedro Riparian National Conservation Area. July - August 1993.

I surveyed small mammal diversity and abundance in various vegetative communities to help establish a conservation and management database. I documented geographic variations exhibited by small mammals in this region. Information was used to develop a comprehensive strategy for protecting all species in this unique ecosystem. **Contact**: William W. Shaw, Department of Fisheries and Wildlife, University of Arizona, (520) 621-7255.

Research Project

University of Arizona. August - December 1991.

I investigated the occurrence of heavy metals (e.g., cadmium, copper, lead) in food chains at the base of copper mine tailings. Specifically, I measured the concentrations of heavy metals in soils, plants, and an herbivore (cottontail rabbits) near Arizona copper mines to determine if metals were transferred and concentrated in plants and rabbits. **Contact** and supervisor: Paul R. Krausman, Department of Wildlife and Fisheries, University of Arizona, (520) 621-7255.

Field and Lab Research Technician

USDA, Agriculture Research Service, Tucson, AZ. 1986 - 1988, 1990 - 1991.

I conducted field experiments designed to illuminate the competitive interactions between grasses and legumes (*Acacia spp.)* in desert and semi-arid ecosystems. I performed laboratory experiments designed to understand relationships between seed germination and soil water-holding-capacity. Also, I assisted with field research in South Africa and Botswana to improve grass establishment in rangeland restoration projects. Supervisors: Stuart Hardegree and Jerry Cox, USDA-ARS.

Research Technician

Lake Nakuru National Park, Kenya. October 1989 - March 1990.

I studied the social, spatial, and temporal behaviors of baboons and suggested non-lethal management strategies that could be implemented to prevent baboons from crossing park boundaries and damaging nearby maize fields. I coordinated meetings with subsistence farmers and Kenya Park Service personnel to foster communication regarding Park Service objectives and the needs of farmers. This study was coordinated by Egerton University and World Wildlife Fund. Also, I assisted Rhino Rescue and Park Service personnel develop techniques to study movements and habitat relationships of 17 black rhinoceroses and 1 white rhinoceros in the park by analyzing distinguishing footprint characteristics. I collected field data and helped establish the database used to assess patterns of habitat use versus habitat availability. Supervisor: David Ndumbu, Department of Biology, Egerton University, Njoro, Kenya.

TEACHING EXPERIENCE:

Provisional Lecturer

Graduate Landscape Ecology, Utah State University. Fall 1998, Spring 1999, Spring 2000.

I lectured on applications of fractal geometry in ecological studies, concepts of body-size allometry and biological scale-dependence, the use of landscape metrics to measure environmental complexity, animal-habitat relationships, and evaluation of resource availability based on organismal perception of scale and habitat. This latter topic dealt directly with linking animal sensory capabilities and modes of locomotion to behaviors, e.g., optimality theory.

Substitute Lecturer

Undergraduate Habitat Relations, Utah State University. February 1996.

I lectured on techniques used to measure habitat and landscape characteristics at multiple spatial scales, and introduced the software program Fragstats, and the interpretation of its output. I also lectured on general concepts pertaining to behavioral ecology, and specifically how animal form and function related to foraging behavior and patterns of habitat selection.

Lecturer

Sinaloa and Chihuahua, Mexico. October 1992.

I discussed concepts of biological diversity, conservation biology, and natural resource management to University of Arizona alumni participating in field study programs throughout the Copper Canyon region.

Lecturer

Introductory Wildlife Management, Egerton University, Kenya. January 1990 - March 1990.

I taught an undergraduate wildlife management class. I lectured on concepts of wildlife-habitat relationships, density-dependence, population exploitation theory, population projection matrices, and life tables. I assisted with animal identification and led discussions regarding competition, predation, animal anatomy and physiology, and animal behavior during field courses in Kenya's national parks.

Undergraduate Teaching Assistant

Introductory Marine Biology, University of Arizona. August - December, 1987.

I discussed food web dynamics, community structure, and taxonomy of tidal pool ecological systems during field courses in Puerto Peñasco, Mexico. I also designed and proctored field examinations.

PUBLICATIONS:

McClure, M. F., J. A., Bissonette, M. R. Conover, and D. D. Austin. 1997. Range expansion of white-tailed deer (*Odocoileus virginianus*) into urban and agricultural areas of Utah. The Great Basin Naturalist. 57:278-280.

McClure, M. F., N. S. Smith, and W. W. Shaw. 1996. Densities of coyotes at the interface of Saguaro National Monument and Tucson, Arizona. The Southwestern Naturalist. 41:83-86.

McClure, M. F., N. S. Smith, and W. W. Shaw. 1995. Diets of coyotes near the boundary of Saguaro National Monument and Tucson, Arizona. The Southwestern Naturalist. 40:101-104.

SUBMITTED MANUSCRIPTS:

McClure, M. F., J. A. Bissonette, M. R. Conover, and M. E. Ritchie. Behavior and demography of urban versus rural mule deer: the risk-energy tradeoff. *The Journal of Wildlife Management.*

McClure, M. F., M. E. Ritchie, J. A. Bissonette, and M. R. Conover. Fractal analysis of animal movement: a new method and an energetic interpretation. *Ecology.*

McClure, M. F., J. A. Bissonette, M. E. Ritchie, and M. R. Conover. Scale-dependent patterns of habitat use: An example with urban and rural mule deer. To be submitted to *Landscape Ecology* by October 2000.

MANUSCRIPTS IN PREPARATION:

McClure, M. F. Scale-dependent relationships between animal movement and patterns of habitat use: An example with mule deer. To be submitted to *The Journal of Applied Ecology* or *Landscape Ecology* by summer 2001.

TECHNICAL REPORTS:

McClure, M. F., M. R. Conover, and J. A. Bissonette. 1999. Impacts of urbanization on mule deer. Fair Chase - The Boone and Crockett Club. Spring Issue.

McClure, M. F., J. A. Bissonette, M. R. Conover. 2001. Cache Valley deer investigations: a search for management solutions. Utah Division of Wildlife - Management Report.

GRANTS:

McClure, M. F. 1999. Fractal analysis of animal movements: a revised methodology and new insights. National Aeronautics and Space Administration (NASA). $250.

McClure, M. F. 1997. Habitat relationships of migratory mule deer on urban winter ranges. The Boone and Crockett Club. $6,000.

McClure, M. F., M. R. Conover, and J. A. Bissonette. 1996. The suitability of urban areas as migratory mule deer winter ranges. The Boone and Crockett Club. $6,000.

McClure, M. F. 1995. How scale affects the management of urban versus rural mule deer: knowledge needed to drive management decisions. The Jack Berryman Institute. $5,000.

PROFESSIONAL PRESENTATIONS:

McClure, M. F. 2000. Wildlife-habitat relationships and the effects of scale. Invited speaker for the Department of Zoology seminar series at the University of Guelph, Ontario, Canada.

McClure, M. F., M. R. Conover, and J. A. Bissonette. 1999. Behavioral adaptations of urban mule deer: consequences at the population level. The Wildlife Society 6th Annual Conference. Austin, Texas.

McClure, M. F., J. A. Bissonette, M. E. Ritchie, and M. R. Conover. 1999. Fractal analysis of animal movements: a revised methodology and new insights. International Association of Landscape Ecologists - Annual Conference. Snowmass Village, CO.

McClure, M. F., J. A. Bissonette. 1999. A multifractal approach for studying scale-dependent wildlife-habitat relationships. 2nd International Wildlife Management Congress. Gödöllő, Hungary.

McClure, M. F., J. A. Bissonette, and M. R. Conover. 1999. Behaviors and population characteristics of mule deer using urban winter ranges of northern Utah: are urban habitats ecological traps? The Western States and Provinces 1999 Joint Deer and Elk Workshop. Salt Lake City, UT.

McClure, M. F., J. A. Bissonette, and M. R. Conover. 1998. Movement dynamics and site fidelity patterns of urban mule deer in Utah. The Wildlife Society 5th Annual Conference. Buffalo, NY.

McClure, M. F., J. A. Bissonette, and M. R. Conover. 1998. Behavioral adaptations and population characteristics of mule deer using urban winter ranges in Cache Valley, Utah. The Utah Chapter of the Wildlife Society Annual Conference. Cedar City, UT.

McClure, M. F., J. A. Bissonette, M. E. Ritchie, and M. R. Conover. 1997. A scale-dependent approach for studying wildlife-habitat relationships. The Wildlife Society 4th Annual Conference. Snowmass Village, CO.

McClure, M. F. 1993. Population characteristics and foraging habits of coyotes living at the interface of Saguaro National Monument and Tucson, Arizona. The Western States Wildlife Society Conference. Farmington, NM.

AWARDS AND HONORS:

NASA-MSU Professional Enhancement Award, 1999
Safari Club International Scholarship Recipient, 1992
Phi Kappa Phi Honor Society, 1989
Dean's List, 1989. Honor Roll 1985-1988.

ORGANIZATIONS:

The Wildlife Society
The Jack Berryman Institute
East African Wildlife Society

OTHER SKILLS:

Fragstats, SAS, SPSS, C
Telemetry, GPS, Spectrophotometry
Spanish

PEER-REVIEWER FOR:

Southwestern Naturalist
Great Basin Naturalist