ABSTRACT

FAVREAU, JORIE M. The effects of food abundance, foraging rules and cognitive abilities on local animal movements. (Under the direction of Roger A. Powell.)

Movement is nearly universal in the animal kingdom. Movements of animals influence not only themselves but also plant communities through processes such as seed dispersal, pollination, and herbivory. Understanding movement ecology is important for conserving biodiversity and predicting the spread of diseases and invasive species.

Three factors influence nearly all movement. First, most animals move to find food. Thus, foraging dictates, in part, when and where to move. Second, animals must move by some rule even if the rule is “move at random.” Third, animals’ cognitive capabilities affect movement; even bees incorporate past experience into foraging. Although other factors such as competition and predation may affect movement, these three factors are the most basic to all movement. I simulated animal movement on landscapes with variable patch richness (amounts of food per food patch), patch density (number of patches), and variable spatial distributions of food patches. From the results of my simulations, I formulated hypotheses about the effects of food abundance on animal movement in nature. I also resolved the apparent paradox of real animals’ movements sometimes correlating positively and sometimes negatively with food abundance. I simulated variable foraging rules belonging to 3 different classes of rules (when to move, where to move, and the scale at which to assess the landscape). Simulating foraging rules demonstrated that variations in richness and density tend to have the same effects on movements, regardless of foraging rules. Still, foraging rules affect the absolute distance and frequency of movements. In my third set of simulations, I simulated a range of spatial and temporal cognitive constraints and demonstrated that omniscience is not necessarily the optimal cognitive state from an energetic standpoint.

I tested my hypotheses on the effects of food abundance with data from free ranging female black bears (*Ursus americanus*) in Pisgah Bear Sanctuary (North Carolina, USA) and female kinkajous (*Potos flavus*) in Parque Nacional Soberanía (Panama), two species with low predation risk. Depending on the season, black bear movements can be explained, by food patch richness, density or both richness and density. Female kinkajou move length correlated positively with patch richness and density. The number of moves of female kinkajous correlated negatively with patch richness of all foods that kinkajous eat and selectivity. In contrast, food patch richness and density did not affect male kinkajous' moves (length and number). Instead, male kinkajous increased foraging time on all foods that they eat as patch density decreased. Male kinkajous also decreased their selectivity on subsets of foods that they eat as patch richness increased.

My results are broadly interesting because they demonstrate that the success of the habitat productivity hypotheses depends on how food is measured (patch richness or density), sex, species, and foraging and non-foraging behaviors (foraging selectivity, responses to moonlight).

THE EFFECTS OF FOOD ABUNDANCE, FORAGING RULES AND COGNITIVE ABILITIES ON LOCAL ANIMAL MOVEMENTS

by

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BIOGRAPHY

I chose Illinois Wesleyan University (Bloomington, Illinois) for undergraduate study because I was interested in veterinary medicine and Wesleyan has an excellent biology program. At Wesleyan I volunteered at a small zoo and realized that zoology and conservation interested me, not the medical aspect of animal biology. Despite changing my focus, I finished a Bachelor's degree in biology at Wesleyan because a solid biology background is important to understanding zoology.

After graduating from Wesleyan in 1991, I monitored bald eagle nests as a temporary biologist for the Arizona Game and Fish Department. Next, I landed a job as a keeper at Brookfield Zoo in Chicago because I had interned in the hoofed stock department after my sophomore year and worked as a summer seasonal in the Children's Zoo after my junior year. I spent most of the next five years in the carnivore department. Working at Brookfield Zoo, an excellent institution with a solid commitment to the animals' well being and to conservation, was a wonderful experience because I witnessed a variety of animal behavior and became familiar with conservation efforts. Nonetheless, during my fourth year at the zoo, I desired to begin graduate school to gain skills necessary for working with conservation organizations and to return to field work.

Conservation requires understanding animals’ relations to their habitats and the socioeconomic and cultural factors of the people who share that habitat. I wanted to develop those skills and management skills. DePaul University's (Chicago, Illinois) program requires students to tailor their courses to reflect their profession, thereby providing management knowledge directly applicable to their profession. I began classes in 1994 while working full time at the zoo. Class work centered on real projects at the zoo and other conservation organizations. In 1997, I completed my M.A. with an emphasis on wildlife conservation management.

Meanwhile, I pursued a series of seasonal field jobs to learn field research techniques. In 1996, I tracked and monitored reintroduced California condors for the United States Fish and Wildlife (USFWS) California Condor Program. Then, I searched for the Po-o-uli, an endangered Hawaiian honeycreeper for the United States Geological Survey, Biological Resources Division (USGS-BRD). I ran a Monitoring Avian Productivity and Survivorship (MAPS) station in Indiana, censused hawks in the Florida Keys, and surveyed flying squirrels, voles, and *Peromyscus* for the United States Department of Forestry (USFS) in Alaska.

In fall 1999, my husband and I moved to Albany New York where I worked for The Adirondack Council, a non-profit, non-governmental organization that is dedicated to protecting the Adirondack Park through advocacy, education, and legal action. Working for the Adirondack Council was a piece of my experiential education that I would not have sought; however, I now view that experience as an important component of my pre-PhD experience.

While at the Adirondack Council, I realized it was time to continue my formal education. I was interested especially in applied wildlife management (particularly nongame species) and conservation of threatened species/ecosystems. I chose North Carolina State University (Raleigh, NC) to earn a PhD in zoology because NCSU fit the parameters that I sought. In addition, Roger Powell and his research intrigued me.

I TA'd a variety of courses at NCSU such as Mammalogy and Molecular Biology, which was a good experience because it introduced me to teaching, refreshed my undergraduate biology knowledge, and introduced me to techniques such as polymerase chain reactions (PCR) that had not existed while I was an undergraduate. The dedication and commitment of some of the professors for whom I taught, especially Dr. Harold Heatwole and Dr. Sam Mozley, also inspired me and taught me how to teach. While a TA, I realized that an ideal career for me was to teach at a small school where learning was a primary objective. I also wanted a school that would be near my research site and places where I could frequently take students into the field.

Due to family obligations, I moved to New York after finishing my coursework. I planned to not work and, instead, finish writing my dissertation during the next year. Fate intervened in the form of an offer to teach General Biology at Siena College in Loudonville NY. My teaching schedule was demanding but I was not worried as a position as a visiting instructor was a great way to get teaching experience and I figured I would finish my dissertation the next year. As it turned out, Siena College asked me to teach a second year and I didn't finish my dissertation that year either.

In fall 2005, I began teaching in a tenure track position in the Fish and Wildlife Science Program at Paul Smith's College (Paul Smith's, New York), the only baccalaureate granting college in the Adirondacks. At Paul Smith's, I teach courses such as Conservation Biology and Wildlife Management. In June 2006, I defended my dissertation.

ACKNOWLEDGEMENTS

I am grateful to Nathan for making personal and professional sacrifices to support me while I was in graduate school. I am grateful to Siena College for giving me the opportunity to gain teaching experience as a visiting instructor. I am immensely grateful to interim Provost Helena Sturnick, the faculty, and students at Paul Smith's College for their faith and support as I finished my dissertation. I am grateful to the Matlab community for allowing me to lurk on their website to learn how to program!

I learned quite a bit about modeling in this process, including in ways that I never expected. So, I thank Roger Powell for being a model of academic purity, Roland Kays of the New York State Museum for being a model of realism and practicality, and fate for giving me Yin and Yang as my co-chairs.

I thank Richard Lancia for being a model of the wildlife biologist that I hope to become. I thank Mike Mitchell for modeling (or at least trying to model) me into an upstanding NCSU student. I thank Nick Haddad for adopting me into his lab and allowing me to be part of his working laboratory model. I thank George Hess for introducing me to biological models . . . and for being a model teacher.

I thank other models of teaching: Sam Mozley, Harold Heatwole, and Jennifer Thompson. I thank Allan Weatherwax at Siena College for modeling how to balance vital research and effective teaching at a small, undergraduate institution. I learned much from each of you. And, importantly, I thank Jennifer Sevin for being a model of fun and productivity.

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CHAPTER 1: INTRODUCTION TO MOVEMENT ECOLOGY

"Make everything as simple as possible, but not simpler."

-- Albert Einstein

I've radio-tracked California condors (*Gymnogyps californianus*) across valleys, a rattlesnake (*Crotalus horridus*) across her home range in the Catskill Mountains, and black bears (*Ursus americanus*) in North Carolina. I've monitored peregrine falcons (*Falco peregrinus*) along the Hudson River in New York, documented raptor (Families Accipitridae, Falconidae, and Cathartidae) migration through Florida, searched for a critically endangered honeycreeper (po'o-uli, *Melamprosops phaeosoma*) in Hawaii, mist-netted passerines (Order Passeriformes) in Indiana, and live-trapped northern flying squirrels (*Glaucomys sabrinus*) and other small mammals in Alaska. Even though the experiences are diverse, they have something in common, namely, animal movement. During each of these experiences, I wondered what forces shaped the animals movements. I wondered "Why move there?", "Why move then?" and "How have past experiences shaped today's movement?" These questions drive my research.

IMPORTANCE AND APPLICATION OF MOVEMENT ECOLOGY

Movement ecology underlies or interlocks with most biological and ecological processes. Movements are a basic component of an individual's life and a species' natural history as movements are influenced by foraging and affect habitat use (Frair et al. 2005, Kie et al. 2005) and home ranges (Burt 1943). Movements may shape the availability of food resources (Janson 2000). Movements influence spread of disease (Andrews and Ferris 1966, Caraco et al. 2002, Rosatte 2002) and are influenced by disease (Bradley and Altizer 2005). For example, public health scientists are concerned about the effects of bird migration on the spread of West Nile virus (Ostfeld et al. 2005). Likewise, the spread of H5N1 bird flu is attributed to bird movement (Simonite 2005). Movements of white tailed deer (*Odocoileus virginianus*) are of particular interest now with respect to the spread of chronic wasting disease (Conner and Miller 2004, Farnsworth et al. 2005).

Movement patterns provide insight into population distributions (Turchin 1991) and affect population dynamics through predation (Austin et al. 2004). Humans affect animals' movements (e.g., Maier et al. 1998, Hodges et al. 2000, Bhattacharya et al. 2003) which can affect animals' survival. Competition influences movement (Giraldeau et al. 1994, Duvall and Schuett 1997) as evidenced by animals reaching an ideal free distribution (Sutherland 1983). Food abundance and distribution affect movements and movements affect population and community processes that ultimately influence food distribution and abundance (Fig. 1.1). Movements affect habitat and community structure through seed dispersal (Pratt and Stiles 1983, Holbrook and Smith 2000) and herbivory (Moen et al. 1997). Conversely, habitat structure shapes animal movement via corridors (Tewksbury et al. 2002) and barriers (McDonald and St Clair 2004). Understanding the effects of movement on communities and populations enables ecologists to predict movements.

Moving animals provide ecological services such as pollination (Bhattacharya et al. 2003, Townsend and Levey 2005) and seed dispersal (Darwin 1859, Westcott and

Graham 2000). Agricultural entomologists can apply movement principles when controlling agricultural pests. Specifically, understanding distances and path shape (sinuosity) could help agricultural entomologists choose release locations for insects that prey on agricultural pests. Movements of insects and terrestrial vertebrates also have the potential to spread genetically modified plants (Darvill et al. 2004, Kreyer et al. 2004).

Managing movements can have an economic benefit by minimizing damage to agriculture (e.g., herbivores, from insects to elephants). Wildlife managers should understand the effects of animal damage control on movements (Mosillo et al. 1999) and apply knowledge about movements to hunting and trapping regulations (Powell 1993). Knowledge of movements can be applied to the human dimensions of wildlife management, including education. For instance, wildlife biologists can concentrate education efforts in the areas where California condors travel.

Conservation biologists apply knowledge of animal movements when restoring habitats and species to those habitats (Cramer and Portier 2001), controlling the spread of invasive species (Vellend 2002), assessing reintroduced species (Tear et al. 1997), designing reserves (Holland et al. 1996), and managing habitat such as creating corridors (Tewksbury et al. 2002, Gehring and Swihart 2004).

Movement behavior, such as local movements in response to fruit patchiness, can be selected for and lead to new movement behaviors, such as migration (Levey and Stiles 1992). Evolution of movement behavior in one species affects and is affected by other species (Stiles 1975, Chapman and Chapman 2002).

Because movements are a foundation for all of these processes and applications, my research into the fundamental determinants of movements has far reaching ramifications and applications.

OVERVIEW OF DISSERTATION

No standard source defines movement metrics, people use terms differently, and some good measurements are not used because researchers do not know them. Because defining terms is a logical place to start, chapter 2 reviews and encourages standardization of movement terms.

Movement is nearly universal in the animal kingdom. Three factors influence nearly all movement and each of the 3 factors acts as a leg in a tripod. First, most animals move to find food. Thus, foraging dictates, in part, when and where to move. Second, animals must move by some rule even if the rule is “move at random.” Many animals probably do not move at random but instead by more complex rules such as the Marginal Value Theorem, foraging in the patch that they occupy until the patch value falls below the mean patch value on the landscape (Charnov 1976). Third, animals have some degree of information that influences movement. Even spiders make movement decisions (Wilcox and Jackson 1998), bees incorporate past experience into foraging (Dukas 2001), and ants process spatial information (Beugnon et al. 1995). Long lived vertebrates with more complex brains are likely to have even more complex cognitive abilities. Other factors such as predation, breeding, and competition, also influence movement; yet, it makes sense to start an investigation with the most basic things that affect movement. Therefore, my dissertation focuses on the effects of food, movement rules, and information on movement.

Chapters 3 to 5 address each of the 3 fundamental influences on movement. Food is often cited as affecting travel distance, yet no theoretical work explores thoroughly the effects of food on movement. Just as importantly, a paradox appears to exist from empirical studies in which food abundance sometimes correlated positively and sometimes negatively with movement. In chapter 3, I explore the effects of 3 characteristics of food (patch richness, density, and distribution) on movements (path length, number of moves, and move length). In addition, I seek to determine if the mechanisms for movement (responses to patch richness and density) can account for seemingly paradoxical movements.

Chapter 4 explores the effects of three types of movement rules: rules that affect when to leave a patch, how to chose a patch, and on which scale to assess patches. Movement rules affect path length through move length, and number of moves.

Chapter 5 investigates the effects of cognitive constraints, the amount of information known by an animal, on movement. When I started my research, other researchers commented that animals should be knowledgeable about the locations and amounts of food in their home ranges because animals that know the most would be selected for. I challenge this assumption by exploring if cognitively constrained animals can perform as well as animals that know the amounts and locations of all food on the landscape.

In each of these 3 chapters, I simulate movement and observe the responses when food, rules, or information change. In each case I sought the most parsimonious model by making the most parsimonious assumptions about the factors that were not being tested. These models seek to explain a system by building from the ground-up (sensu, Dunbar 2002). Another benefit of my approach is that I generated hypotheses *a priori* that can be tested in natural systems.

Previous work showed that home range size of black bears in Pisgah Bear Sanctuary in North Carolina correlated positively with food abundance in spring, correlated negatively with food abundance in fall, and did not correlate with food abundance in summer (Powell et al. 1997). In chapter 6, I test the movement hypotheses generated by my simulations to see if seasonal movement trends of black bears in Pisgah Bear Sanctuary can be explained by the hypotheses generated in chapter 3.

Although black bears in Pisgah provided a good system to test my predictions because the population was monitored over 20 years, analysis was limited because most individual bears were radio-tracked for no more than 2 years. Also, food abundance was calculated per season and bears may have responded to food abundance on finer time scale (days or weeks). In chapter 7, I test the food abundance hypotheses that I generated in chapter 3 by examining kinkajou (*Potos flavus*) movements in Parque Nacional Soberania over a year in response to variation in yearly fruit abundance. Because the same kinkajous were followed throughout the study period and fruit abundance was calculated twice a month, I avoided some of the analytical problems that occurred with the bear data.

I did not test hypotheses about rules (chapter 4) and information (chapter 5) because the objective for my dissertation was to investigate theoretical effects of rules and information. The effects of rules and information on movement are difficult to test because the experimenter needs to manipulate the rules that guide animal movement and the information that animals know. With creative experimental design, behavioral ecologists can determine what rules animals use (Krebs et al. 1977, Brown et al. 1997), but they cannot change the rules animals use and also hold constant other aspects of experimental design. The effects of information can be tested by manipulating the information available to an animal either by manipulating the animal's environment or the animal's cognitive abilities (realm of experimental psychologists). Alternatively, the effects of information could be studied through interspecific studies where experimenters know the information available to different species. For instance, birds that cache food have good spatial memories (Kamil and Balda 1985, Shettleworth 1990).

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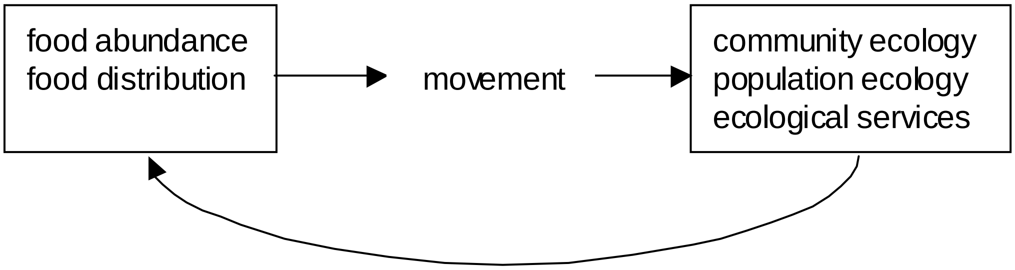

FIG. 1.1. A brief overview of movement ecology. Food abundance and distribution affect movements, which, in turn, affect landscape level ecological processes. Landscape level ecological processes affect food abundance and distribution.

CHAPTER 2: STANDARD MOVE MENT TERMS AND DEFINITIONS

THE NEED TO STANDARDIZE MOVEMENT TERMS

During the past 2 decades, satellite and GPS (global positioning system) transmitters have increased the number of animal locations that can be collected. Geographic information system (GIS) and GPS technology has greatly enhanced researchers' abilities to analyze movement.

Despite the prevalence of movement studies and recent progress in techniques to measure and analyze movements, movement metrics are not used or defined universally. In part, this is because movement metrics have not been compiled in any one place. Animal behavior textbooks address movement such as migration but do not define or discuss movement metrics such as path sinuosity or moves (example, Grier and Burk 1992, Alcock 2005). Biology and ecology dictionaries define home range, migration, dispersal and nomadism, but do not define path or move (e.g., Collin 1998, Thain and Hickman 2000). Even telemetry texts do not quantitatively define local movements such as path sinuosity; instead, they focus on estimating home range size, and other biological factors such as survival rate and population size (e.g., Kenward 2001; Priede and Swift 1992, but see Kernohan et al. 2001; White and Garrott 1990 for some discussion).

Ambiguity has several causes. First, some types of movements have several names. McKey and Waterman's "meander ratio" (1982) is the same as "ratio of actual distance traveled to straight line distance" (Powell 1978), index of straightness (Batschelet 1981), tortuosity (Dicke and Burrough 1988), sinuosity (Benhamou 2004), and ADT/SLD (actual distance traveled to straight line distance) (Musiani et al. 1998).

Second, some terms have been used to denote multiple movement behaviors. "Movement pattern" can refer to any type of movement, such as activity (Meyer et al. 2000), distance moved and number of paths (Beier et al. 1995), path shape and displacement (Bowne and White 2004), home range size and core areas (e.g., Anstee et al. 1997), fidelity (Ciucci et al. 1997), and kinds of movement (Gentile and Cerqueira 1995). Third, some terms describing movement are vague, relative, or qualitative. Words or phrases such as "more circuitous routing" (Caro 1976), "more vigorous" (Caro 1976) and "irregular" (Strong and Johnson 2001) make it difficult to compare results across studies or to insure that a term is applied appropriately across studies.

Finally, despite a plethora of terms to describe movement, terms might be used only by the authors that coined them or just within the discipline where they originated. For example "c-value", the number of new quadrats entered on second day divided by the total number of quadrats entered on the second day, (Strier 1987, Kaplin 2001) is used only by primatologists. Infrequent use of a term may result from a lack of consistency in meaning or measurement, from duplication of an existing definition, or because researchers lack awareness of the term.

Lack of standardization is evident when searching the literature. I searched for terms used to describe animal movement in major animal ecology journals (Table 2.2) with ISI Web of Science (The Thomson Corporation, Philadelphia, PA). For terms that returned >200 records, I sampled randomly 50 records and estimated the accuracy for all records. The results were mixed. Some well standardized terms, such as "dispersal", had many records (>2500) and most of the records accurately identified papers that were about dispersal (Table 2.2). The less standard terms such as "consistency" returned 196 records of which only 3 meant consistency as generally defined by Rasmussen (1980) and only Rasmussen used his definition. The remaining 193 records did not use the term consistency to describe movement. Movement bout returned 0 records, perhaps because movement bouts are rarely measured. Sinuosity and tortuousity returned 11 records for movement studies suggesting that other terms are used. Even path length had only 22 records that were appropriate to animal movement.

Lack of standardization makes discerning trends or doing a metanalysis difficult. Turchin (1991) noted that lack of conformity among movement study methods makes comparisons among studies difficult; therefore, Turchin suggested a set of basic movement terms and their definitions. Nonetheless, Turchin (1991) did not suggest terms to describe path sinuosity, intensity of space use, fidelity or other patterns of space use or re-use. Lack of standard terms makes it difficult to locate appropriate studies. To integrate studies on path “tortuosity” one must search for papers that use the word “sinuosity”, “tortuosity”, “meander ratio”, “straightness index”, or “ADT/SLD”. Even so, such a search will fail to locate studies in which an author created a novel term or used a phrase such as “ratio of actual travel distance to straight line distance.” Because terms are used variably, a search of terms finds irrelevant papers. Standard terms for frequently studied movement characteristics are needed. Existing words and definitions should be critiqued and a set of universal terms that are standard, descriptive, concise, and precise should be created. Standard, unambiguous terms will allow researchers to find published research to compare movements among different species, systems or life stages; and test ecological and ethological hypotheses. Ecologists must review terms and definitions and “calibrate” them (Weckerly 1992, Hall et al. 1997, Moffett 2000).

Because the study of movement ecology is developing and ambiguity exists, now is a good time to review movement terms and definitions.

Thus, the purposes of this paper are three-fold. The first purpose is to summarize movement terms and definitions and to be a reference for design of movement studies. The second purpose is to suggest unambiguous, standard terms where ambiguous terms are used currently. The third purpose is to identify movement definitions that are weak and need further investigation. I hope to provide a set of universal movement metrics that are directly comparable across multiple movement studies.

MOVEMENT TERMS

I compiled and categorized a list of most major movement terms in the animal behavior and ecology literature (Table 2.3). The terms are biologically meaningful, quantitatively robust, and quantify movements. I include basic movement terms describing direction, distance, and duration as well as more complex vocabulary that describes paths and movements in home ranges. Throughout, I made suggestions for a more consistent and clear terminology.

Basic movement terms

Path, move and step describe an animal's movements. A **path** is a "complete spatio-temporal record of a followed organism from the beginning to the end point of observations" (Turchin 1998). Turchin's definition is consistent with the common meaning of path in the English language (Simpson and Weiner 1989). Paths reflect animal behavior such as foraging, avoiding predation, and defending territories. The biological scale at which paths are described depends on the questions being addressed. A study of dispersal distance may look at a path length over the entire dispersal time while a study on breeding behavior might measure paths on a scale of hours. A **move** is a “segment of a path between two consecutive stopping points” (Turchin 1998). A move is differentiated from a **step** by defining a step as the change in location that occurs over a fixed time (Kareiva and Shigesada 1983, Turchin 1998). Move and step are not differentiated the same way in the Oxford English Dictionary (Simpson and Weiner 1989), yet Turchin’s definitions make sense and have been adopted in movement studies. Moves represent animal behavior as animals move among stopping places, for example a hummingbird foraging among flowers. Steps are determined by a researcher and may not represent directly the biology of an animal. In some cases, movement analyses benefit from measurements on a temporal scale finer than animal stops. For instance, documenting the winding characteristic of an insect’s path to understand dispersal or searching strategies, benefits from sampling locations at fixed time intervals. Path, move and step are the basic building blocks to describe animal movement and should be applied with the precise definitions by Turchin (1998).

Turchin (1998) defined **movement** as “the process by which individual organisms are displaced in space over time.” Defined as such, movement does not differentiate between self-propulsion and movement caused by chance events outside of an animal’s control (for example being blown to a new island by a hurricane). I suggest that Turchin’s definition be applied only to animals (or plant seeds) that are not capable of directed movement. For animals that are capable of directed movement, movement would be defined better as the act or behavior of an animal changing its location.

Because path, move and step are precise, it is more effective to use those terms when they apply and to use the general term movement to discuss a suite of movement characteristics.

Turchin did not discuss **movement bouts**, which are delineated by an animal's behavior as a period of movement. Movement bouts usually correspond to a biologically complete behavior, all the steps or moves that occur during a behavior from beginning to end. Movement bouts can be recognized as "a period when the pauses between consecutive movements are equal to, or shorter than, the time of the previous movement" (Westcott and Graham 2000) or by a break in a log survivor function (Fagan and Young 1978) or log frequency (Sibly et al. 1990), although neither of these methods have stood up to scrutiny (Sibly et al. 1990, Nams 2006).

Movement pattern does not have a specific meaning. As with movement, replacing movement pattern with more specific words is often more appropriate. For instance, "daily movement patterns were observed" illustrates little. "Daily variation in elevational migration", for example, describes a specific movement pattern.

In common use, **mobility** is the property of being able to move. In the ecological literature, mobility has been used at least 3 ways. Mobility has been used as a general term that does not describe particular movements, replacing a suite of other movement terms, such as daily travel distance and distance between extreme diel locations (Labisky and Fritzen 1998). It should not be used to describe properties of path length or other movements. Doncaster and Macdonald (1991) and Lent and Fike (2003) used mobility to mean a change in location of a home range, specifically the amount of time for a complete home range relocation (Doncaster and Macdonald 1991). I suggest that *home* *range shift* is more clear. Finally, mobility has been used as a measure of the ability of an animal to move. This measure has been termed a **mobility index** and is best applied to invertebrates when home range measures are not effective (Berger et al. 1999) or to animals that do not have home ranges (as in Norbury et al. 1994). A mobility index can be measured by daily distance traveled (Berger et al. 1999) or distances traveled over shorter time periods (Norbury et al. 1994). Mobility should be reserved to mean the ability to move.

Motility is sometimes used to mean mobility or movement. Turchin (1998) defined motility as "the parameter in the Fokker-Planck diffusion equation that quantifies the rate of population spread." The Oxford English Dictionary defines motility as "capable or power of moving (as quality of organism)" (Simpson and Weiner 1989). Thus animals that move are motile and motility does not describe movement.

Terms describing movement duration, direction and distance

Duration, direction and distance are basic quantitative measures that describe movement (Turchin et al. 1991). **Duration** is simply the length of time over which a path, move, step or movement bout occurs. Duration can be an important metric when describing biological processes such as dispersal.

Direction or "the relative point towards which one moves" (Simpson and Weiner 1989) can be described simply as relative turns such as toward and away, or overall direction or a net direction (Bowne et al. 1999). Direction can also be quantified as left or right turns (McIntyre and Vaughn 1997) and analyzed by categorizing pairs of turns (right, right; right, left; left, right; and left, left) with a chi-squared test (Turchin 1998).

Turning angle, another measure of direction, can be calculated from successive directions (Turchin et al. 1991). Direction can also be calculated as a probability of movement by summing probabilities of moving in different directions (0 indicates random movement and 1 indicates completely directed movement) (Pyke 1978, Powell 1993, Mauritzen et al. 1999). **Absolute direction**, “direction measured with respect to north” (Turchin 1998) or that measured with compass bearings must be analyzed with circular statistics (Zar 1999). Depending on the research goals, direction can be measured effectively in any one of these ways. Direction is important to determining if movements are random, what stimuli affect movements, and how those stimuli affect movements. For instance, analyzing direction can elucidate the effects of corridors on movement (Haddad 1999). **Directional bias** is nonrandom movement towards or away from a direction (Turchin 1998). **Directional persistence** is when moves are successively aimed in the same direction (Turchin 1998).

Distance, the length between two points, is commonly used to describe movement. Distance has been reported as day journey length (Andelt and Gipson 1979, Fuller and Kat 1990, Watts 1991, Patterson et al. 1999) and daily mean distance (DMD) (Jedrzejewski et al. 2001). Some researchers recognize that animals do not travel in straight lines and, therefore, label movement distances as minimum daily movement (MDM) (Delibes and Beltran 1985, Ross and Anderson 1990), net displacement (Wiens et al. 1993, With 1994), net distance (Bowne et al. 1999), total distance (Mauritzen et al. 1999) and straight line distance (Musiani et al. 1998). Other specialized distances have been reported: distance between hourly locations (Andelt and Gipson 1979), between consecutive feeding spots (Watts 1991), between the two most distant fixes [“great axis”

(Spitz and Janeau 1990)], distance between extreme diel locations (DBE) (Doebel and McGinnes 1974)] and between the most distant location to a den (Walton et al. 2001). Distance can be used to predict population spread or probability of interactions, such as between social groups.

I suggest that this plethora of distance terms be distilled to travel distance and straight line distance. *Travel distance (TD)* refers to the actual distance traveled. In their methods, authors can report if they calculated the mean travel distance, so the term does not have to include the word mean as in "mean travel distance." *Straight-line distance* (SLD) is the distance between two locations, not necessarily the actual distance traveled (Andelt and Gipson 1979, Walton et al. 2001). Travel distance is a gross distance while straight-line distance is a net distance. Both travel and straight-line distance are important biologically. For instance, gross distance is more meaningful for energetic studies while net distance is more applicable to creating conservation reserves. Whether reporting travel or straight-line distance, authors should report what distance was measured, for example, diel, hourly or between sites of biological importance (feeding, resting, etc). Distances should be quantified by their central tendencies. Often, however, extremes, such as minimum and maximum distances traveled, have important associations on predicting biological processes such as dispersal distance (Gaines and Denny 1993).

Travel speed can be calculated from travel distance (TD) and duration. Speed, the travel distance divided by duration during which speed was constant, can be reported per minute or hour or other appropriate time period. Speed can be applied to calculating predation efficiency. Speed may be an indication of habitat selection (Dickson et al. 2005).

Travel rate (Labisky and Fritzen 1998) can be reported when speed is not constant, for instance, when locations are separated by a large unit of time such as daily telemetry locations. For example, authors may report the number of kilometers traveled per 24 hour period (Reynolds 1984, Patterson et al. 1999). Travel rate may provide an estimate of the length of time to cross a home range or complete migration.

Terms describing path shape

Qualitative descriptions of path shape, such as small zone, loop, ranging, zigzag (Spitz and Janeau 1990); north-south (Jewell 1972); and other class types (Laundre and Keller 1981) are applied less frequently than quantitative measures, which are generally termed sinuosity.

Sinuosity, or how winding a path is, has also been called tortuosity (Dicke and Burrough 1988), a linearity index (Spencer et al. 1990), an index of straightness (Batschelet), a straightness index (Bovet and Benhamou 1988), circuity (Garshelis et al. 1983), and meander ratio (McKey and Waterman 1982). To avoid redundancy of terms, I suggest that the plethora of terms describing the turns and curves of a path be condensed to only one word. Sinuosity and tortuosity are defined in the Oxford English Dictionary (unlike linearity index) and both refer to the curviness of a path (Simpson and Weiner 1989). Because no clear reason exists for choosing sinuosity or tortuosity, I suggest arbitrarily that sinuosity should be used.

Circuitous paths refers to a class of sinuous paths in which the path forms returns to where it started (Caro 1976).

Quantifying the number of turns on a path indicates the degree to which a path winds. One method of quantifying turns is to score turns in 45-135° in each direction as 1 point and turns 225-315° as 2 points (Goss-Custard 1970, Caro 1976). Frequency of direction reversals (Turchin et al. 1991), the ratio of number of turns to total distance (Caro 1976) can also describe path shape. Each of these measures can be good measures when appropriately applied.

Sinuosity has been defined as the ratio path length to straight line travel distance (PL/SLD) (Powell 1978). Sinuosity has also been defined as the inverse, straight-line (bee-line) distance divided by path length (SLD/PL) and termed a linearity index (Bell and Kramer 1979, Spencer et al. 1990). When sinuosity is measured as the ratio of straight-line distance to travel distance (SLD/PL), a range of values is created from 0 to 1 where 1 is a straight travel path and as sinuosity approaches 0, the path is very curvy. The property of ranging from 0 to 1 makes SLD/PL preferable to PL/SLD. In general, SLD/PL is a good measurement as long as the path is not a random walk (Benhamou 2004). When the final destination is not known, sinuosity can be calculated by a similar index, G/PL, where G is calculated from the global projection after n steps [for more details see (Benhamou 2004)]. Because the accuracy of SLD/PL decreases with step length, Benhamou (2004) offered ΔD/PL, which corrects for the inadequacies of SLD/PL and works whether or not the final destination is known (Benhamou 2004). Because the SLD/PL (or G/PL) increases as the path becomes straighter, I propose that SLD/ PL (or G/PL) be termed a straightness index.

Sinuosity can also be measured in degrees/distance$^{1/2}$ from the standard deviation of relative turn angles after rediscretization where R is the rediscretization step length (RTA_R). That is, $S = 1.18\ (\sigma\ (RTA_R))\ /\ R^{1/2}$ (Bovet and Benhamou 1988, Socha and Zemek 2003). In contrast to SLD/PL, higher values of *S* indicate a more sinuous path. *S* should be termed a sinuosity index (as in Benhamou 2004) because as paths become more sinuous, *S* increases. This measure does not perform well for all turning angles and step lengths (Benhamou 2004). Appropriateness of a method for measuring sinuosity depends on whether the movement is directed or random (Benhamou 2004).

Fractals, patterns that exist across different scales, measure curvilinear phenomena such as coastlines. Fractals have also been calculated to describe path shape (Dicke and Burrough 1988, Crist et al. 1992, Wiens et al. 1995, Bascompte and Vila 1997, Edwards et al. 2001, Atkinson et al. 2002). Although fractals can be appropriate to describe animal movement (Hagen et al. 2001), especially if the fractal measurement (D) is particular to a certain scale (Nams and Bourgeois 2004), measuring path sinuousity with fractals is not appropriate because fractals do not account for move length (Benhamou 2004).

Terms describing home range shape and size

Just like accumulated steps or moves result in paths, accumulated paths result in home ranges. Burt's (1943) definition of a home range, " . . . that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range.", is applied most frequently. In fact, a home range represents an accumulation of movements that may include a temporal component. That accumulation of movements can be described by home range size, shape, and differential use, including amount and patterns of reuse and fidelity.

Few researchers quantify **home range shape** (but see Covich 1976, Eason 1992, Blackwell and Macdonald 2000, Adams 2001, Collinge and Palmer 2002). A hexagon (Barlow 1974) or circle requires less energy to visit the same amount of area compared to a long rectangle. Still, landscape features, such as mountains and rivers, often influence home range shape (Garshelis and Pelton 1981, Eason 1992, Powell and Mitchell 1998). Shape description can be as simple as the ratio of length to width (Garshelis and Pelton 1981). Another shape descriptor is eccentricity (ECC) where ECC approaches 1 as the range becomes more symmetric (Swihart and Slade 1985, Spencer et al. 1990). A shape descriptor based on eigenvalues for three dimensional space (Koeppl et al. 1977) has been employed little, although it was used to look for a correlation between home range shape and squirrel species (Armitage and Harris 1982) and has been used for two dimensional movements to judge home range linearity (Garshelis and Pelton 1981).

Home range size provides basic information about animal movements. Size can be measured on different time scales, for instance, daily, seasonal, annual or lifetime ranges. Primatologists who have continuous visual observations of their subjects often calculate home range size with a grid (Haugen 1942, Mohr 1947). Fifty-two percent of the 18 studies published from January 2000 to May 2006 in the International Journal of Primatology calculated home range size with the grid method. Home range size is quantified frequently as a minimum convex polygon (MCP) (Mohr 1947) or with kernel density estimators (Worton 1989, Seaman and Powell 1996). Brownian bridges incorporate time spent at a location into estimating home range size (Bullard 1999), but are used infrequently. At present, kernel density estimators provide the best readily available estimate of home ranges for a small number of locations for most animals (Powell 2000). Still, the best estimator of a home range size depends on the research question and the data (Powell 2000). Each estimator can be compared across studies when established standards are followed.

Movements within a home range are helpful in elucidating home range mechanisms or understanding biologically important events or processes. Depending on the question, one or more of the following measures of spatial use may be appropriate.

Terms describing differential use of home ranges

Movements in a home range result in disproportionate use of areas in that home range, sometimes resulting in patterns of use. **Use, utility or utilization distributions (UD)** (VanWinkle 1975), the distribution of probabilities of animals' positions in space, can be calculated by kernel density (Worton 1989, Seaman et al. 1998), nearest neighbor (Getz and Wilmers 2004), Brownian bridge (Powell 2000), grid cells (Mohr 1947) and other estimators that index the proportional use of a home range. Typically, 50% and 95% UDs represent the area that an animal has a 50% and 95% chance of occupying. Although a UD of 50% or 95% is arbitrary biologically, it is often the best representation of a core area (50%) and actual home range that excludes exploratory movements (95%). The areas of their home ranges that animals appear to consider most important (core areas) can be delineated more precisely by constructing a log survivor curve and identifying the break point (Powell 2000). For further discussion of defining core areas see Wray et. al. (1992). For a review of different ways to measure core areas, see Samuel (1985) and Samuel and Green (1988). Other measures of differential use are centers of activity (Hayne 1949, Casimir and Butenandt 1973, Stouffer and Caccamise 1991), diurnal activity centers (Hudgins et al. 1985), biological attraction points (Don and Rennolls 1983), and describing differential use of quadrats (Laundre and Keller 1981).

A variety of methods quantify the proportion of quadrat use, for instance, the proportion of quadrats that were entered more than once (McKey and Waterman 1982), the percent of the quadrats that were visited (Marsh 1981), and the number of quadrats used more than 10% of the time (Baba et al. 1982). Proportion of quadrat use can also be calculated as the number of times or percent of time that an area is used. Quadrat use diversity can be measured with Shannon-Wiener and evenness (McKey and Waterman 1982). One of the major criticisms of quadrat-based methods is that no clear strategy exists for choosing the grid size. Quadrat size is likely to vary among species and researchers, making cross study comparisons difficult. R.A. Powell (pers. comm..) suggested defining quadrat size with a method similar to defining the bandwidth in kernel density estimators might be appropriate, especially if spatiotemporal factors are considered (sensu Katajisto and Moilanen 2006). Differential use should be quantified with UDs.

An animal's distribution of use across its home range ranges from even to clumped. A variety of clumping indices have been used, including the Shannon Diversity Index (McKey and Waterman 1982), a coefficient of dispersion ("standard deviation of the number of sightings per cell divided by the mean") (Chapman 1988), ratio of the variance to mean for a Poisson distribution (Pielou 1969, Hurlbert 1990), Morisita's

Index I_δ (Morisita 1971), Lloyd's index of mean crowding (Lloyd 1967, Payne et al. 2005), and Rasmussen's index for clumping (RU). Morisita's, Lloyd's and Rasmussen's have held up to scrutiny and are appropriate to calculate animals' use of space .

Another measure of differential use is **intensity of use (IU)**, which is the intensity of movements. IU has also been termed "intensity of movement (penetration)" or IP (Goszczynski 1986). I suggest the concept should be consistently termed intensity of use. Animals that move quickly through their ranges saturate their ranges faster than animals that move slowly or have a higher intensity of use. Intensity of use has been calculated as the ratio of the distance traveled in a day to the home range area for that day (Goszczynski 1986, Schmidt et al. 2003) and as the total path length divided by the square root of the area used (Loretto and Vieira 2005). Lagarde et al (2003) quantified the number of fixes that it took to estimate 25%, 50%, and 75% of an individual animal's home range and called the measure home range saturation. Intensity of use has been defined also as a ratio of 50% to 95% of adaptive kernel home ranges (Lent and Fike 2003). Because it is dimensionless, Loretto and Vieira's intensity of use is a more logical method than Goszczynski's for characterizing how thoroughly an area is traversed. To my knowledge, no one has critiqued either of these measures, nor Lagarde's or Lent and Fike's measures. Statistical robustness of each measurement should be tested.

Fidelity has been used to describe a consistent location of a home range or an area within a home range [such as a core (Jolly and Pride 1999) or feature within a range such as a road (Reimchen 1998)]. Utility distributions (as discussed earlier) measure fidelity to locations within a home range. The measures of utilty distributions described earlier are robust estimators of fidelity within a home range and should be used for describing fidelity in a home range. The term fidelity should be reserved for describing the probability that an animal's home range stays in the same place over time. Fidelity of home range location can be measured by comparing the difference in centers of home ranges among periods of time (Labisky et al. 1999, Lent and Fike 2003). Home range fidelity has also been quantified as probability of pairs of locations separated by a period of time "to be closer together than random pairs of locations from the radio-tracked population, bounded by its distribution over a specified time" (Schaefer et al. 2000). Connolly (1979) introduced a method for calculating home range fidelity by quantifying deviations from expected quadrat use. Multiple range permutation procedures (MRPP) also used to calculate fidelity (Van Dyke et al. 1998). Volume of intersection has been used to determine overlap among home ranges (Millspaugh et al. 2004) and could be applied to calculating fidelity. Similarly, Pianka's niche overlap (Pianka 1974) has been applied to determining overlap of home ranges (Powell 1987) and could be applied to calculating fidelity. For further discussion of fidelity measures, read White and Garrott (1990). The methods for measuring fidelity are disparate and no single method has been applied in a way that it could be considered a standard. Furthermore, I do not know of any critical comparison of the different methods to calculate fidelity. The concept and methods of measuring fidelity need further investigation.

The opposite of fidelity has been termed plasticity (Gordon 2000), drifting (Doncaster and Macdonald 1991), and seasonal shifts (Silvius and Fragoso 2003). I suggest *home range shift* be used exclusively when describing lack of fidelity of a home range.

Temporally autocorrelated fidelity, such as seasonal or daily reuse of a particular area within a home range, is **consistency**. Consistency describes the proportion of time in a location that is constant in different time periods ("If the amount of time spent by an individual or group in each portion of its range during a given time period is perfectly and linearly related to the amount of time spent in those portions during another time period, then the two patterns of range use are perfectly consistent.") (Rasmussen 1980). Rasmussen (1980) suggested that, although the Pearson product-moment correlation coefficient and the Kendall and Spearman rank correlation coefficients are fairly robust measures of consistency, they are not ideal for when ranges overlap only slightly. Doncaster (1990) disagreed, showing that the Spearman rank correlation coefficient is robust even when overlap is small. Schoener's ratio is a "relative entity that uses mean squared distances to represent the distances between consecutive pairs of observations relative to distances from the observations to the arithmetic mean centre" (Mauritzen et al. 2001). Site fidelity can also be detected when just the denominator from Schoener's ratio is less than that of random paths (Spencer et al. 1990). Each of these methods should be investigated to determine if one method is most robust or if different situations require different estimators.

Consecutive use and systematic use are two specific cases of consistency. Chapman (1988) calculated **consecutive use** by calculating the proportion of quadrats from one sample period that were occupied in the next sample period. Strier (1987) created a c-value where c equals b/a where b is the number of new quadrats entered on the second day and a is the total number of quadrats entered on that second day. c-values range from 0 to 1, where 0 indicates that no new quadrats were entered while 1 indicates that all quadrats were new. Neither Chapman's or Strier's methods should be constrained to their original definitions with sample periods and days, respectively, as the units. Instead, the time units should vary with the objective of the study to be suitable biologically (e.g., sampling period, hour, day, season). Chapman's and Strier's methods are not entirely satisfactory because quadrat size is biologically arbitrary. Scaling quadrat size to be biologically meaningful or standardized would increase the value of both Chapman's and Strier's calculations of consecutive use. For instance, the quadrats of a consecutive use value could be standardized to represent 10% of total home range size. Chapman's or Strier's methods may each be appropriate depending on study objectives. Alternatively, quadrats could be defined by using a technique similar to the method suggested by Katajisto and Moilanen (2006) for defining bandwidth for kernel density estimators.

Systematic use of a home range can be determined by examining a series of short term home ranges (e.g., daily) within a long term home range (e.g., multiday). Vectors extending from the arithmetic center of the animal's long term home range to each center of the short term home ranges can be ranked and Spearman's rank correlation coefficient applied to determine if short term home ranges are randomly or systematically placed within the long term home range (Cameron 1995).

Types of movement

I have discussed paths, components of paths (e.g., move length) and conglomerations of paths (e.g., home range). On a larger scale, one can discuss different categories of movement as intermittent or continuous because the pauses in intermittent location can be as ecologically important as active movement (Kramer and McLaughlin 2001). Other types of movement include: dispersal, migration, nomadism, and local movement within a home range. Dispersal and migration describe specific types of movement. Dispersal is "movement of organisms away from the place of birth or from centers of population density" (Ricklefs 1990). Migration is movement from one seasonal range to another seasonal range (Ricklefs 1990). Nomadic individuals "move widely in search for food, and to settle and breed where it is locally abundant" (Andersson 1980). Movement within a home range is not widely known by a single term, although sometimes it is termed local movement (e.g., Piper et al. 1997, Kernohan et al. 2001). A search of 42 natural history, animal behavior and ecology journals (Table 2.1) on Web of Science (26 June 2005) for local move* returned only 18 papers. This sharply contrasts with 2153 results for migrat* and 3160 results for dispersal. Although it could be that fewer studies have been done on movements within a home range, it is unlikely. Alternatively, the term local movement is not widely used. Local movements should be listed as a key word.

CONCLUSIONS

Consensus on the definition and use of movement terms as well as complete and standardized ways to describe movements will advance the study of animal movement. All movement terms must be biologically meaningful, precise and reusable. Some words, such as sinuosity, are clear and do not need further definition. Other words, such as "exploratory" (Burt's (1943) "occasional sally") need to be defined precisely. I suggest standardized terms and definitions to be applied to animal movement studies.

The statistical robustness of some of these terms needs to be investigated. Surely, the need for new terms and definitions will arise. When those terms can be defined independently of dimension or scale [such as Intensity of Use (IU) and fractals], they will be more useful to compare movement patterns across taxonomic groups and systems.

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Table 2.1. Journals searched for movement terms

American Midland Naturalist
American Naturalist
Annales Zoologici Fennici
Animal Behaviour
Behavioral Ecology
Behavioral Ecology and Sociobiology
Behaviour
Biotropica
Canadian Field-Naturalist
Canadian Journal of Zoology
Ecological Modelling
Ecological Monographs
Ecological Research
Ecology Letters
Ethology and Sociobiology
Ethology
Ecology and Evolution
Folia Primatologica
International Journal of Primatology
Japanese Journal of Ecology
Journal of Animal Ecology
Journal of Ecology
Journal of Field Ornithology
Journal of Mammalogy
Journal of Wildlife Management
Journal of Zoology
Mammal Review
Mammalia
Northeastern Naturalist
Northwestern Naturalist
Oecologia
Oikos
Primates
Quarterly Review of Biology
Southeastern Naturalist
Southwestern Naturalist
Tropical Ecology
South African Journal of Wildlife Research
South African Zoology
Trends in Ecology & Evolution
Wildlife Monographs
Wildlife Society Bulletin
Zoo Biology
Zoologica

TABLE 2.2. Numbers of published papers that contained the listed movement terms. Results are from an ISI Web of Science search in July 2005 that searched the journals in Table 2.1 for all years available on the Science Citation Index (1945 to June 2005). The first column lists each search term exactly how I searched for it. Web of Science uses an asterisk (*) to search for any permutation of the search term and Boolean search. The second column is the total number of citations returned. The third column is the number of citations from column 2 that were defined as in this paper. If < 200 citations were returned, all papers were examined. If >200 total citations were returned by the search, 50 citations were randomly chosen and categorized.

Movement terms	**total citations returned by search**	**% using term as defined in this paper**
clumping and home range	1	0
clumping and move*	6	0
clumping and range use	1	100
clumping and space use	0	0
consecutive and move*	51	0
consecutiveness	0	n/a
consistency	196	1
consistency and range use	2	100
dispersal NOT(plant or seed)	2537	~90
distance, travel	30	100
distance, straight-line	9	89
evenness and home range	2	100
fidelity	410	<10
fidelity and home range	51	100
fidelity and range use	8	100
home range	1253	~100
home range shape	3	100
home range size	385	~100
kernel	95	93
MCP	21	100
minimum convex polygon	64	100
migration	2162	~100
mobility	282	>90
motility	58	~0
move	511	>90
movement	1647	>90
movement bout	0	n/a
move length	3	100
movement pattern	28	75
nomad*	71	~100
path	290	~ 80
path length	26	85
intensity of use	4	75
saturation and movement	14	0
saturation and range use	0	n/a
saturation and space use	0	n/a
sinuosity, path	0	n/a
sinuosity	8	75
speed	630	~ 15
speed and move*	126	~ 95

TABLE 2.2 (CONTINUED).

Movement terms	**total citations returned by search**	**% using term as defined in this paper**
step	412	<10
step and move*	41	<10
step length	9	78
straight-line distance	See distance, straight-line	
systematic	8	13
tortuosity	7	71
travel distance	See distance, travel	
travel rate	2	100
rate of travel	3	100
turning angle	8	100
use distribution	5	20
utility distribution	0	n/a
utilization distribution	18	100

TABLE 2.3. Set of suggested movement terms in alphabetical order, their abbreviations (if an abbreviation exists), definitions, and methods to measure. Most metrics are standard while others need further investigation to determine strengths, weaknesses, validity of assumptions, or if alternative measures would be more accurate or effective. Those terms are denoted by †.

Movement terms	**Definition**	**Measured by**
consistency†	"If the amount of time . . . is perfectly and linearly related to the amount of time spent in those portions during another time period, then the two patterns of range use are perfectly consistent" (Rasmussen 1980)	1. Pearson product moment correlation coefficient (Rasmussen 1980) 2. Kendall rank correlation coefficient coefficient (Rasmussen 1980) 3. Spearman rank correlation coefficient coefficient (Rasmussen 1980, Doncaster 1990)
direction	"the relative point towards which one moves" (Simpson and Weiner 1989c). Direction is a general term that can refer to either absolute or relative direction.	See absolute and relative direction.
direction, absolute	"direction measured with respect to North" (Turchin 1998)	compass bearings
direction, relative	Direction of one move, step or path measured with respect to directions of other moves, steps or paths.	1. right/left (e.g., McIntyre and Vaughn 1997) 2. turning angle (the angle between successive path directions) (Turchin et al. 1991) 3. sum probabilities (Pyke 1978) 4. net direction (e.g., Bowne et al. 1999)
directional, bias	"tendency of individuals to move in a nonrandom direction" (Turchin 1998)	
directional, persistence	"autocorrelation between directions of subsequent moves" (Turchin 1998)	
distance	A measure of the spatial extent between two locations of times of interest, for example, distance between extreme diel locations. Also see straight line and travel distance.	Euclidean distance

TABLE 2.3 (CONTINUED)

Movement terms	Definition	Measured by
distance, travel (TD)	The distance actually traveled that incorporates path sinuosity and is often longer than straight line distance	Euclidean distance that is measured on a short enough spatial scale to capture the actual distance traveled (e.g., Shimooka 2005)
distance, straight-line (SLD)	The distance between two locations occupied by an animal, not the actual distance traveled	distance from starting point to ending point (Musiani et al. 1998)
duration	The length of time over which a path, move step or movement bout occurs	time
evenness †	A measure of how homogeneity of spatial distribution of space use	1. Rasmussen's Index (RU) (Rasmussen 1980) 2. Shannon Diversity Index (McKey and Waterman 1982) 3. coeffecient of dispersion (Chapman 1988) 4. Lloyd's mean crowding (Lloyd 1967, Payne et al. 2005)
fidelity†	The probability of occupying the same site.	1. Schoener's ratio (Mauritzen et al. 2001) 2. time tables (Connolly 1979) 3. volume of intersection (Millspaugh et al. 2004) 4. multiple range permutations procedures (Van Dyke et al. 1998) 5. difference in center locations (Labisky and Fritzen 1998)
home range shape	The contour of a home range.	1. eccentricity (Swihart and Slade 1985, Spencer et al. 1990) 2. eigenvalues (Koeppl et al. 1977) 3. ratio of length to width (Garshelis and Pelton 1981, Garshelis and Garshelis 1984)
home range size	" . . . that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of the home range." (Burt 1943)	1. grids 2. minimum convex polygon (MCP) (Mohr 1947) 3. UD a. kernel density estimator (Worton 1989, Seaman and Powell 1996) b. local nearest neighbor (Getz and Wilmers 2004)

TABLE 2.3 (CONTINUED)

Movement terms	Definition	Measured by
intensity of use (IU)	The concentration of movements in an area.	1. distance traveled divided by the square root of the area used . (Loretto and Vieira 2005) 2. number of fixes to estimate total area used (Lagarde et al. 2003) 3. ratio of 50% hr area to 95% hr area (Lent and Fike 2003)
mobility	"ability to move" (Simpson and Weiner 1989d)	n/a
mobility index	A measure of an animal's ability to move, especially animals that do not have home ranges.	Can be measured a variety of ways such as interfix distance or daily travel distance (Norbury et al. 1994, Berger et al. 1999)
motility	1. "the parameter in the Fokker-Planck diffusion equation that quantifies the rate of population spread." (Turchin 1998)	n/a
	2. capable or power of moving (general quality of organism) (Simpson and Weiner 1989d)	n/a
move	"segment of the path between two consecutive stopping points" (Turchin 1998)	Euclidean distance
movement	1. "the process by which individual organisms are displaced in space over time." (Turchin 1998) 2. act or behavior of an animal changing its location as a result of its actions (could include spiders moving to a point that allows the wind to move them)	n/a
movement bout	A distinct movement behavior from beginning to end.	1. "a period when the pauses between consecutive movements are equal to, or shorter than, the time of the previous movement (Westcott and Graham 2000) 2. a break in a log survivor function (Fagan and Young 1978)
path	"the complete spatio-temporal record of a followed organism from the beginning to end of observations" (Turchin 1998)	Euclidean distance
saturation	see intensity of use	

TABLE 2.3 (CONTINUED)

Movement terms	Definition	Measured by
sinuosity	A measure of a path's curviness or winding.	1. straightness index (SLD/PL) (Bell and Kramer 1979, Spencer et al. 1990) 2. sinuosity [$S = 1.18 (\sigma (RTA_R)) / R^{1/2}$] (Bovet and Benhamou 1988, Socha and Zemek 2003) 3. fractal dimension (*D*) (Bascompte and Vila 1997)
step	"a displacement between two successive coordinate fixes" (Turchin 1998)	Euclidean distance
travel rate	The ratio of distance to duration for a period of time where the ratio is variable.	1. Σ (travel speeds)/total observation time (e.g., Labisky and Fritzen 1998). 2. Σ (travel distance)/total observation time
travel speed	The ratio of distance to duration for a period of time where the ratio is constant	distance traveled/observation time (e.g., Shimooka 2005)
use, utility or utilization distribution (UD)	a probability distribution of an animal's position in space	kernel density estimators (Worton 1989, Seaman and Powell 1996)
use, consecutive[†]	A pattern of space use that is ordered temporally.	c-value (b/a where b is the number of new quadrats entered on second time unit and a is the total number of quadrats entered in the first time unit) (Strier 1987)
use, systematic[†]	A pattern of space use that is ordered spatially.	Orderly procession of vectors drawn from the center of a home range to centers of each of the daily (or other time unit) home ranges (Cameron 1995)

CHAPTER 3: EFFECTS OF PATCH RICHNESS, DENSITY AND DISTRIBUTION ON FORAGING MOVEMENTS

ABSTRACT.

I simulated animal movements with a spatially explicit, individual-based model to predict the effects of food availability on animal movement. Specifically, I determined potential effects of patch richness (amount of food per site), density (number of food sites), and food site distribution on path length (total distance traveled), move length (distance traveled between stopping places), and number of moves. Simulated animals assessed single food patches and moved to the patches with the highest net value.

My model makes the following predictions, which should be tested with field data. Generally, when resources are limited, path and move lengths correlate positively with patch richness. As the richness of food patches increases, path length, move length and number of moves are not affected by increases in food patch richness beyond a certain level. When richness and density are very low, path and move lengths correlate positively with the density of food patches. At higher levels of food abundance, path and move lengths correlate negatively with patch density. Number of moves correlates positively with patch density until it asymptotes at the maximum number of moves possible. Uniformly distributed food patches cause paths to be longer than other food patches that are distributed randomly or aggregated.

These results are broadly interesting because they suggest that path length responds differently to changes in food abundance caused by patch richness than by patch density as well as relative abundance of food and patch distribution. This provides a mechanistic explanation for the apparent paradox in field data where some movements correlate positively and other movements correlate negatively with food abundance.

Key words: abundance; density; distribution; food; movement; moves; patch; path; richness; step.

INTRODUCTION

Most animals move to find food. Thus, food often drives animal movement. Animals may move in response to amount, location, or type of food. For example, move lengths may correlate to distances between resources. Number of moves may be influenced by food preference (spend less time at less preferable foods and move more often) or the speed with which animals consume resources. Some factors that affect movement have been tested rigorously (e.g., predation risk, Gilliam and Fraser 1987). Although, the effects of food abundance and distribution have not been examined frequently in natural systems, field ecologists make assumptions about the effects of food on movement and attribute changes in movements to changes in food abundance (Isbell et al. 1998) and distribution (Boyd 1996). In this chapter, "movements" refer to path length, move length and number of moves in a path where a path is the actual distance that an animal travels. Moves are fragments of a path delineated by where an animal stops (Turchin 1998).

Effects of food abundance on movement

Home range size should increase with increased food requirements such as those that arise from increased body size (McNab 1963, Harestad and Bunnnell 1979) and metabolic rates (Gittleman and Harvey 1982). As expected, a negative correlation between home range size and food abundance has been found for a variety of mammals, including carnivores (Fuller and Kat 1990, Joshi et al. 1995, Valenzuela and Ceballos 2000, Herfindal et al. 2005, McCarthy et al. 2005), rodents (Taitt 1981, Sullivan et al. 1983, Ostfeld 1986, Ims 1987), lagomorphs (Hulbert et al. 1996), primates (Albernaz and Magnusson 1999), and ungulates (Mysterud 1999). Harestad and Bunnell's (1979) habitat-productivity hypothesis does not differentiate between amount of food per food patch (patch richness) or the number of food patches on the landscape (patch density).

The habitat-productivity hypothesis refers to home range size but not to move length, number of moves or path length. Increased travel distances can lead to an increase in home range size depending on the intensity [degree of concentration of movements in an area, (Chapter 2, Loretto and Vieira 2005)] with which a range is used. Therefore, path length should be scrutinized separately from home range size. Similar to home range size, path length may correlate negatively with food abundance for a variety of primates (Henzi et al. 1992), ungulates (Tufto et al. 1996), and carnivores (Jedrzejewski et al. 2001). In each of these situations, when more food is available, animals travel less distance to maintain energetic needs.

Surprisingly, significant positive correlations between food and movement have been reported for several species of primates (Nunes 1995, Doran 1997). This seemingly paradoxical response (both positive and negative correlations between food abundance and movement) is apparent even within a species or among related species (Julien-Laferriere 1995, Hulbert et al. 1996, Fortier and Tamarin 1998, Fashing 2001, Bravo and Sallenave 2003).

Paradoxical responses might be explained by energetics. Animals might move less when less food is available because it is not energetically efficient to forage. That is, the energy content of food is so low that more energy is required to forage for the food than would be gained by consuming it. Or, paradoxical responses might be explained if an animal's aversion to risk is determined by its energetic state (Wunderle and Coto-Navarro 1988, Abrams 1994).

Home range size might vary positively with food abundance if animals use the additional resources to increase their own growth rate (Powell et al. 1997) or increase their mass (which would be an important before hibernation or season with scarce food). Alternatively, when food decreases in abundance, animals could reduce their diet selectivity and maintain the same size home range (Clutton-Brock 1977, Leighton and Leighton 1983). Responses could be shaped by food availability in a previous season. For instance, the first flush of food in spring may produce a different response than the same amount of food after a summer of plenty.

I hypothesize that paradoxical responses can be a mechanistic response to two different aspects in food abundance. That is, when food abundance varies due to fluctuations in patch richness (amount of food per food site), animals may adjust movement distance. When food abundance varies due to changes in patch density (the number of food sites) animals may adjust the frequency of their movements. Because length and frequency of moves could be affected by different components of abundance, the source of changes in food abundance could explain the paradoxical response. This explanation is more parsimonious than the risk averse explanation in that animals are not required to have the complex cognitive capabilities required to calculate risk.

Effects of food distribution on movement

In most natural systems, food is not distributed evenly across the environment but is patchy, with food presence and abundance varying spatially and temporally. Examples of food patches in nature include groups of prey and groves of masting trees. The habitat-productivity hypothesis does not predict the effects of food patch distribution on home range size. The resource dispersion hypothesis predicts that territory size depends on distribution of resources because patchy resources reduce the correlation between increased food richness and the area that contains a given amount of resources (Johnson et al. 2002). Patchy food distribution appeared to influence movements of black bears in the southern Appalachians, resulting in smaller home range than predicted by productivity alone (Powell and Seaman 1990). Food distribution does not result in significant differences for path length for darkling beetles (*Eleodes extricata*); still, when food is patchy, hungry beetles have significantly shorter step lengths and net displacement distances than do fed beetles (McIntyre and Wiens 1999). Patchy food distributions results in larger home ranges for palm civets (*Paradoxurus hermpahoroditus*) than when food is distributed uniformly (Joshi et al. 1995). Models of red squirrel (*Sciurus vulgaris*) movements show that high patch density results in small home range size and less overlap (South 1999). Distances among resources influences home range sizes of white-nosed coatis (*Nasua narica*) while food abundance does not (Valenzuela and Macdonald 2002). I hypothesized that changes in food distribution, like abundance, can affect frequency and length of moves and affect movements.

Advantages of modeling movement

Factors besides food (e.g., competition, predation, weather) also affect movement. In addition, animals may modify their behaviors (selectivity, foraging tactics) as food or other factors change. These confounding factors make it difficult for field ecologists to isolate and determine the factors that affect movement. Furthermore, fieldwork shows a correlation but not a cause and effect. Modeling can simplify natural systems and control confounding variables to isolate the hypothesized effects of food abundance and distribution on movement. Modeling has been applied successfully to animal movement, such as providing insight into understanding how movements are affected by anthropogenic artifacts (Cramer and Portier 2001), movements affect species distribution (With and Crist 1996, Macdonald and Rushton 2003) and to determine what search tactics shaped movements (Higgins and Strauss 2004).

Spatially explicit, individual-based models are appropriate for investigating how the environment can affect movement because individually based models allow a ‘bottom-up’ investigation (Lorek and Sonnenschein 1999). Bottom-up exploration provides insight into mechanisms. Spatially explicit, individual-based models are particularly effective for investigating movement including the effects of corridor width on movement (Baur and Baur 1992), patches on dispersal distance (Hein et al. 2004), and the mechanisms responsible for home range formation and placement (Mitchell and

Powell 2004). Spatially explicit, individual-based models have increased our understanding of spatial distribution of foragers (Fryxell et al. 2004), foraging strategies (Lewison and Carter 2004), and efficiency in foraging (Ohashi and Thomson 2005). I created individual based models and simulated landscapes with varying food patch richnesses and densities to determine the effects of food abundance and distribution on animal movement.

Objectives

Because paths comprise moves, path lengths change by changing move length, the number of moves, or both move length and number of moves so that their product increases. My first objective was to determine the mechanism (move length, number of moves or both) for changes in path length. My second objective was to create testable hypotheses about the effects of food abundance and distribution on path length, move length and number of moves of a foraging animal. My third objective was to investigate causes of paradoxical movement: Can an increase in food abundance sometimes result in a decrease in path length and sometimes result in an increase in path length? If so, what is the mechanism of paradoxical movement? My objective was not to determine optimality; I did not assess the foraging efficiency of animals.

METHODS

Landscape

I simulated animal movement on a landscape of 100 x 100 cells with impermeable edges. Cells containing food were food patches. For a landscape of 100 x 100 cells, food patches spaced uniformly with 10, 3, 2 and 1 empty rows and columns of cells between food patches resulted in 100, 625, 1156 and 2500 food patches respectively (Fig. 3.1a). To create a landscape of resources distributed randomly, 100, 625, 1156 and 2500 food patches were placed randomly without replacement (Fig. 3.1b). Landscapes with aggregated food patches consisted of 25, 156, 289 and 625 clusters of 4 cells containing food. Patches were aggregated moderately where the 4 food cells in a cluster did not necessarily occupy contiguous cells (Fig. 3.1c). Alternatively, patches were highly aggregated where 4 cells containing food occurred in a contiguous square patch creating a super-patch (Fig. 3.1d).

Each cell *x* had a net value (V_x) that was the food value (F_x) of that cell discounted by the travel cost to cell *x* from the cell occupied by the animal (cell *i*). Travel cost was the product of the distance between cells *x* and *i* (d_{ix}) and a travel constant (T). That is,

$$V_x = F_x - (d_{ix} \bullet T).$$

Net value of a cell depended on the current location of the animal and was recalculated at each time step. All values can be considered to be in energy gain or loss.

Effects of food abundance and distribution on movement

Food abundance in my model was a simple function of patch richness (amount of food per cell with food) and patch density (number of cells with food on the landscape). I simulated a range of food values (F_i) for each of the patch densities (table 3.1), ranging from 1 to a value where further increases did not affect movements. One food value was used in each simulation.

The same four densities of total food patches (Table 3.1) were simulated in each distribution. To determine if movements responded to the density of the super-patches or patch size, I simulated patchy landscapes where the total number of super-patches (each consisting of 4 food patches) equaled the number of patches (each consisting of 1 food cell). I also simulated patchy landscapes where the total number of super-patches (each comprised 2-, 3- or 4-patches) equaled the total number of patches (each comprised a single cell).

To determine the effects of food distribution, I compared movements on landscapes with even, random, and moderately and highly aggregated distributions of food patches.

Animal movement

Each simulation was run for 25 time steps and represented a set of animal movements that might be obtained from field observations. Animals knew the richness and locations of all food patches. For each simulation, the animal started in the center of the landscape and moved to the cell with the highest value (V_x) (which could result in the animal staying in the same location) and consumed c amount of food, thereby decreasing the value of the occupied cell. Food abundance was not replenished and could decrease to 0.

I determined values for c and T between the limiting conditions of when travel cost was too high (an animal could not move) and consumption was too low (an animal might sit in a cell consuming food and not move). I determined travel cost and consumption amounts that allowed movement when patch richness was 10 energy units per cell containing food, for 100 patches that were moderately aggregated. From the results of these simulations, I chose travel costs and consumption amounts that resulted in movement.

Variability in food types, nutrients and preferences contributing to food value do not need to be modeled explicitly because the animals are modeled to forage for the total patch value (sensu Lewis 1980). Searching is included in travel costs while handling is costs are incorporated into the value of the food.

Foraging movements of simulated animals were summarized as path length, move length and number of moves (Table 3.2). Movements were recorded after the initial move to the cell with the highest food value until 25 time units had elapsed. Path length was the total distance traveled during the simulation. Move length was the distance traveled in each time increment. Because patches were distributed randomly for some simulations and animals chose randomly among cells when cell values were equal in those cells, the mean values for 200 iterations are reported. All simulations were coded in Matlab.

Assessing, traveling, and foraging occurred within the same time unit. Animals did not engage in any other behaviors. Larger landscapes would not affect the results because the animals moved for a short period of time and did not consume all the food on the landscape. Resources did not renew, but the simulation is run for such a short time span that renewal for a comparable time in a natural system would not occur.

RESULTS AND DISCUSSION

Travel cost and consumption amount

The value for the travel constant (T) correlated negatively with move length, number of moves, and path length for nearly all patch densities (Fig. 3.2a-c). This makes sense because as the value for the travel constant (T) increased, the values of other cells on the landscape (V_x) decreased. When V_x was depressed, the value of the occupied cell (V_i) was greater than the values of other cells (V_x). When $V_i > V_x$, animals do not move. Output from the simulations conformed to the expectations for changes in movements resulting from the value of the travel constant, providing some validation for the model. For further simulations, I chose a travel constant of 0.2, insuring that the value of the travel constant was not so high that it constrained simulated animals from moving, yet the travel constant still affected movement.

When animals consumed little, consumption amount per time unit (c) correlated positively with move length, number of moves, and path lengths (Fig. 3.2a-c). Move length was affected by consumption amount because as c increased, the food value of occupied cells on the landscape (F_i) decreased more quickly, ensuring that the value of cells that had been visited could not be greater than the value of cells that had not been visited. This meant that animals traveled farther to find food. Number of moves increased with consumption amount (c) because as an animal consumed more per time, the value of the occupied cell (V_i) decreased faster, V_i became less than V_x sooner, and the animal had to leave the occupied cell sooner. Number of moves plateaued at the maximum number of moves possible in 25 time steps. Output from the simulations conformed to the expectations for changes in movements due to consumption amount, providing some validation for the model. For further simulations, I chose a consumption amount of 0.9, insuring that consumption amount (c) did not prohibit movement, yet still affected movement.

Patch richness when food patches were distributed uniformly and randomly

For food distributed uniformly, at low richness and density, move length correlated positively with richness (Fig. 3.3a). At high richness and densities, move length did not respond to changes in food richness (Fig. 3.3a). It makes sense for animals to move farther as patch richness increases because the value of rich patches on the landscape (F_x) offsets the cost to travel to a new patch. That is, if richness is low, animals cannot move very far because travel cost ($d_{ix} \cdot T$) is relatively high. Once richness (F) reaches a level where travel cost ($d_{ix} \cdot T$) has relatively little effect on the value of a patch to an animal, path length stabilizes and further increases in richness (F) does not increase path length.

Number of moves correlated positively with richness at low richness and then leveled off at higher richness (Fig. 3.3b). I expected animals to move less when patches had low richness (F) than high richness. Number of moves plateaued at the maximum number of movement opportunities (t). Food patches can have low values when food value (F) is low due to low food richness or when travel costs ($d_{ix} \cdot T$) are high relative to food richness.

In the simulations, for food distributed uniformly, path length (Fig. 3c) correlated positively with move length (Fig. 3a) and number of moves (Fig. 3b). An increase in move length could have resulted in paths lengthening, not changing (decreased in number of moves cancels increased in move length), or shortening (decreases in the number of moves overrides increased move length). Number of moves could also have caused any of the three responses. For landscapes with food patches distributed randomly, patterns of movement were similar qualitatively to movements on landscapes with food distributed uniformly (Fig. 3.3d-f).

Patch richness when food patches were aggregated

When food was moderately aggregated, patch richness had a similar effect on movements as when food sites were distributed uniformly and randomly although density had a gradual effect (Fig. 3.4a-c). Richness had the same effect for this distribution as described for the other distributions for the same reasons. In contrast to the other distributions, the changes in movements are not as sharp because the values vary less. Move length varies less because most moves were among patches that were clumped. Mean move length did not exceed 2.5 cells whereas mean move length when food patches were distributed uniformly and randomly were approximately 10 and 6 respectively. Similarly, when food patches were aggregated, number of moves remained high (between 20 and 25 cells) while number of moves for other distributions dropped as low as 9 cells.

At most densities when food patches were aggregated tightly, move length (Fig. 4d), number of moves (Fig. 4e), and path length (Fig. 4f) displayed unimodal responses to patch richness before plateauing. A unimodal response was displayed because, as richness increased initially, animals could afford to travel farther. Once richness reached a threshold value, moves shortened because animals moved among the cells in a super-patch and not among super-patches. Distance among cells in a super-patch is shorter than distance among super-patches. Initially, number of moves correlated positively with richness because animals could remain in a cell without depleting the value of the cell below the value of other cells on the landscape. Number of moves reached a low point and then began to increase with richness because patch richness was great enough to allow animals to travel more often. Like the other distributions, number of moves reached a plateau at the number of moves allowed by the length of time in the simulations. Animals moved similarly in landscapes where the total number of patches was constant at 100, 625, 1156 and 2500 patches but the number of cells (2, 3 and 4) in a patch was variable (Fig. 3.5a-c). Therefore, the unimodal movement response was caused by the landscape characteristic that patches were aggregated, not by the total number of patches.

When food patches were aggregated tightly, movements plateaued later (when richness was > 20) than when food patches were aggregated loosely (when richness was ~ 4). In the simulations where the density of super-patches (consisting of 2-, 3- and 4-cell food patches) equaled the density of 1-cell food patches from the random simulations (Fig. 3.5a-c), movements also plateaued when richness was > 20. Therefore, the late plateau was caused by interpatch distance among super-patches, not by the number of patches or by amount of food per patch.

Furthermore, when I simulated 2-, 3-, and 4-cell food super-patches and kept constant the total density of patches, the number of food patches in a super-patch correlated negatively with move length until densities were high (Fig. 3.5d). Move length correlated negatively with number of patches in a super-patch because distance among patches decreased as the number of patches in a super-patch increased. When distance among patches is short, travel cost ($d \cdot T$) is small relative to when distance among patches is far. When travel cost is low, the value of neighboring cells is likely to be greater than the value of the occupied cell after food has been consumed ($V_i < V_x$). This makes it energetically efficient to move more when the number of patches is greater. When the number of patches in a super-patch increased from 2 to 4, move length decreased (Fig. 3.5e) because distance to the closest cell with food (d_{ix}) decreased. Therefore, animals did not have to move as far to find a food as when fewer patches were on the landscape. Thus, both number of patches and the number of cells constituting a super-patch affected movements, including path length (Fig. 3.5f), in patchy landscapes.

Despite the more complex response of movements when food patches were aggregated tightly than when food patches were distributed uniformly, randomly or loosely aggregated, movements plateaued at similar values when patches were aggregated tightly as when patches were aggregated loosely.

Patch density when food patches were distributed randomly and uniformly

Move length correlated negatively with patch density (Fig. 3.3a) because increased food locations decreased interpatch distance. In contrast, patch density correlated negatively with number of moves (Fig. 3.3b) because, when patch density was low, distance (d_{ij}) between patches was large and travel costs ($d_{ij} \cdot T$) were high relative to potential gain (F) at a patch. This prohibited moving and constrained the number of moves.

When food was distributed uniformly and richness was very low, path length correlated positively with patch density (Fig. 3.3c). Yet, for higher food abundance, path length correlated negatively with patch density except for the landscape with the least food patches. When animals moved on the landscape with the least patches they moved the farthest, which should make them have the longest paths (Fig. 3.3a). Still, animals moved the least number of times when patch density was low (Fig. 3.3b). Because animals moved much less frequently when patch density was low, their paths were not the longest.

Movements had similar qualitative responses to patch density when patches were distributed randomly (Fig. 3.3d-f) as when they were distributed uniformly, except patch density correlated entirely with path length.

The highest density that was simulated (2500 patches on the landscape) may be unnaturally high but it represents a range of possibilities. It appears the effects of density had no upper limit on move length, although number of moves reached a threshold.

Patch density when food patches were aggregated

Patch density had a similar effect when patches were moderately aggregated as it did when patches were distributed randomly or uniformly (Fig. 3.4a-c). Density also had the same general effect when patches were tightly aggregated, although the response was opposite and more complex at low richness (Fig. 3.4d-f). This response was different than the responses observed for the rest of the distributions because interpatch distance was much less for cells in a patch and much greater for patches than for any other distribution. This translated to fewer but longer moves.

Number of moves correlated negatively with patch density at low richness. As richness increased, number of moves became correlated positively with patch density for the same reasons that they were correlated positively for other distributions (interpatch distance decreased as density increased, thereby making it feasible to move more often).

Effects of food distribution

The relationship of movements in response to each of the distributions for each density was similar. Food sites distributed uniformly generally resulted in the longest path and move lengths. Tightly aggregated patches resulted in longer paths and moves than the paths and moves of uniformly distributed food only where the unimodal response peaked. Yet, after the peak, uniformly distributed food had longer paths and moves. When food sites were distributed randomly path and move lengths were second in length to those produced by uniformly distributed food sites. Food patches that were moderately aggregated had the shortest paths and moves.

Animals moved most frequently when food was distributed uniformly followed by movements in response to landscapes where food was distributed randomly and aggregated moderately. Generally, when food was tightly aggregated in distribution, number of moves, animals moved the least. Again, fewer moves can be attributed to the increased interpatch distance, making it less effective energetically for animals to move.

The results from the simulations (path lengths are shortest when resources are aggregated) corroborate field data from black bears (Powell and Seaman 1990) but do not corroborate field data from civets (Joshi et al. 1995). This indicates that the effect of distribution may also be a product of the number of patches in a super-patch, the distance among patches and super-patches, and the scale on which the distribution is determined.

Summary: factors affecting move length and number of moves

To make it energetically worthwhile to move, $V_i < F_x + (d_{ix} \cdot T)$. Therefore, whether or not to move and where to move depends on both patch richness and density.

Because move length depends on the amount of food per food patch (F_x), F_x must reach a critical threshold for moves to occur. As the amount of food per food patch (F_x) increases, move length can increase. Move length can be affected by the value of food patch (F_x), the travel constant (T) or consumption amount (c).

Maximum number of moves is capped by time, not value of food patch (F_x), the travel constant (T) or consumption amount (c). Minimum number of moves can be zero when distance among food patches (d_{ij}) is large, the travel constant (T) is high, or consumption amount (c) is very small.

Hypotheses

My simulations led to the following hypotheses:

1) Move and path lengths correlate positively with patch richness whether the food is randomly, uniformly or patchily distributed until path and move lengths reach a threshold.

2) Number of moves correlates positively with patch richness whether the food is randomly, uniformly or patchily distributed until number of moves reaches a threshold.

3) When food richness and density are very low, path and move lengths correlate positively with the density of food patches. When food patch richness and density are high, path and move lengths correlate negatively with patch density.

4) Number of moves correlates positively with patch density at low levels until a threshold is reached.

5) Paths are longest when food patches are distributed uniformly, followed by paths when food patches are distributed randomly and moderately aggregated.

To my knowledge, these are the first predictions offered *a priori* that explain the theoretical effects of resource abundance and distribution on path length, move length and number of moves. Simulating animal movement under variable food abundance and distribution isolated the effects of food abundance and distribution. These effects would have been difficult to expose in a field study.

Resolution of seemingly paradoxical field data

Empirical studies report seemingly paradoxical responses to increased food abundance: sometimes movement correlates positively and sometimes movement correlates negatively with food abundance. My simulations demonstrated that these movements can be explained by at least 4 mechanisms. First, overall food abundance varies through changes in patch density or patch richness, which had opposite effects on movements. That is, an increase in patch richness caused path and move length to increase while an increase in the density of food sites caused a decrease in path length. Second, at low patch densities the number of moves depressed path length so that patch density correlated positively with path length. This pattern was seen in the simulations when food was distributed uniformly. Third, an interaction between patch richness and density affected the response of path and move length to density. For tightly aggregated resources, when richness was low, density correlated positively with path and move length, but when richness was high, density correlated negatively with path and move length. Fourth, food distribution influenced how changes in food richness affected path length. That is, if the distribution of food patches changed from a random distribution to a uniform distribution as patch richness increased, move length would correlate positively with patch richness. In contrast, if the distribution of food patches changed from being distributed uniformly to being distributed randomly as patch richness increased, move length would correlate negatively with patch richness. Thus, the paradox disappeared when food abundance is split into patch density and patch richness. Even simple, general behavior rules like the ones in these simulations could cause movement distances and frequencies to vary in response to changes in food abundance.

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TABLE 3.1. Summary of the parameter values used in the simulations.

Parameter	**Range of values**
food values	1-10 food units (for all distributions) 10 - 40 food units (for highly aggregated only)
patch density	100, 625, 1156, 2500 food patches on the landscape
amount consumed (c)	0.9 food units/time unit
travel cost (T)	0.2 food units/cell width
time steps	25
iterations	200

TABLE 3.2. Definitions of each movement metric calculated from the foraging movement output.

Movement	**Definition**
path length	total distance traveled during simulation
move length	distance traveled during one time step
number of moves	number of changes in location during the simulation

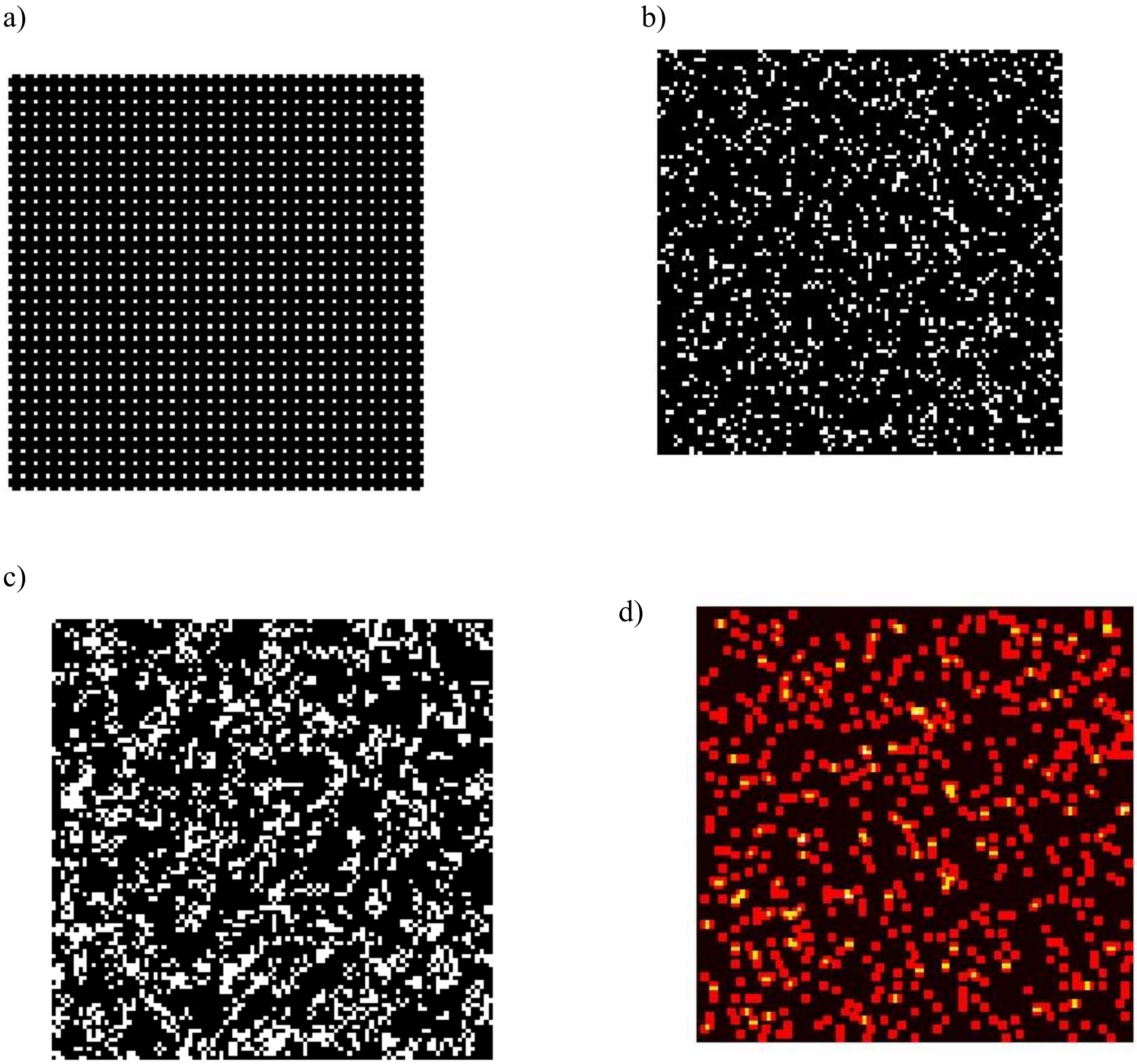

FIG. 3.1. Distribution of 1156 food patches. Patches were distributed (a) uniformly, (b) randomly, (c) moderately aggregated, and (d) tightly aggregated. The black matrix represents no food. For a - c, white cells represent 10 food units. For d, red cells represent 10 food units, yellow units represent 20 food units (where 2 patches overlap), a few white cells represent 30 food units (where 3 patches overlapped).

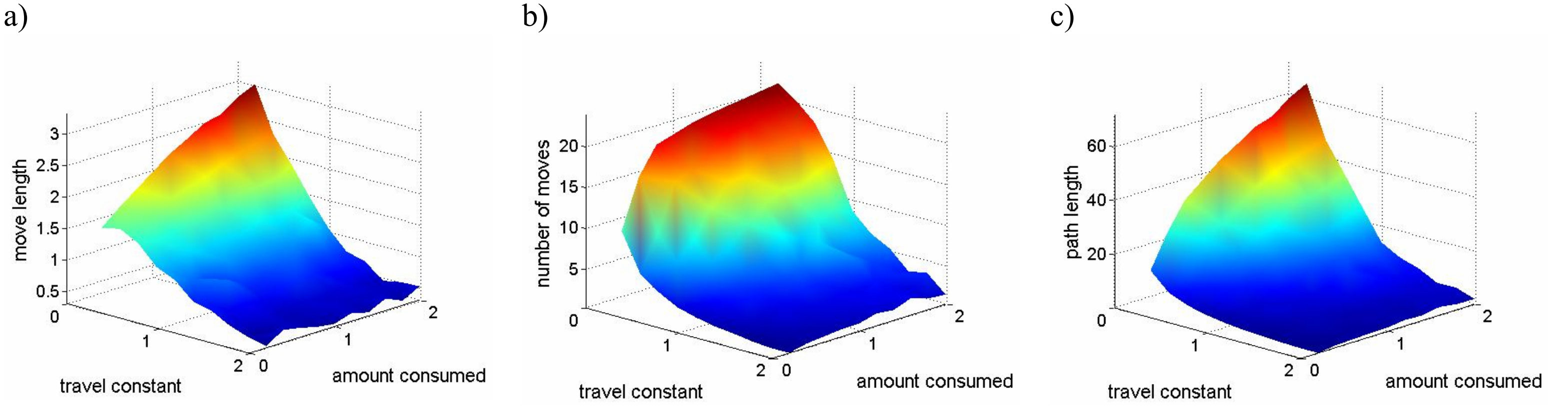

FIG. 3.2. The response of (a) move length, (b) number of moves, and (c) path length to travel constant (x-axis) and consumption amount (y-axis). One hundred food patches were moderately aggregated. Food patch value was 10.

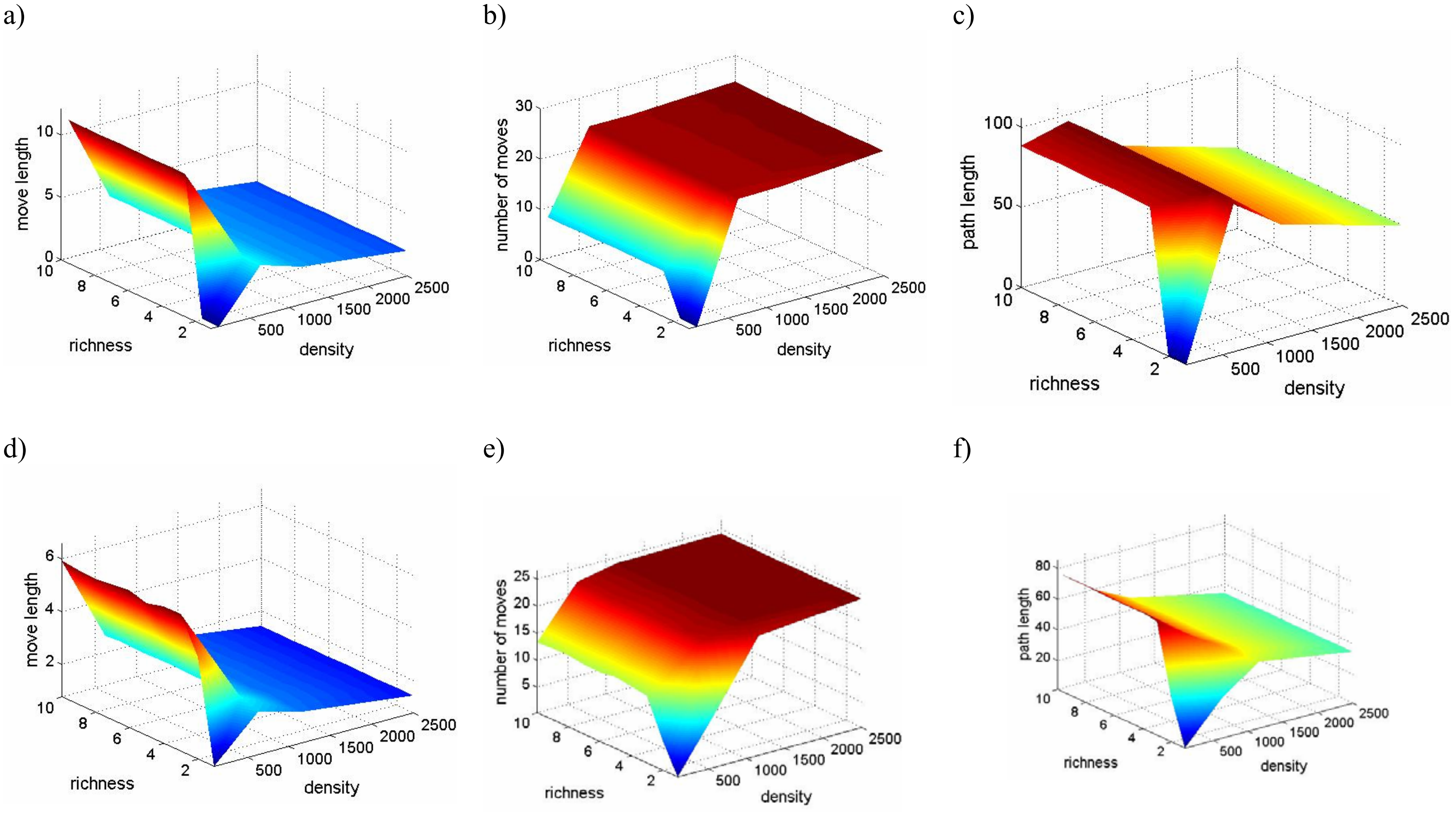

FIG. 3.3. The effects of patch richness (x-axis) and density (y-axis) on (a) move length, (b) number of moves, and (c) path length for resources distributed uniformly and on (d) move length, (e) number of moves, and (f) path length for resources distributed randomly. Path length is a product of move length and number of moves. Consumption was 0.9/time unit and travel cost was 0.2/cell width.

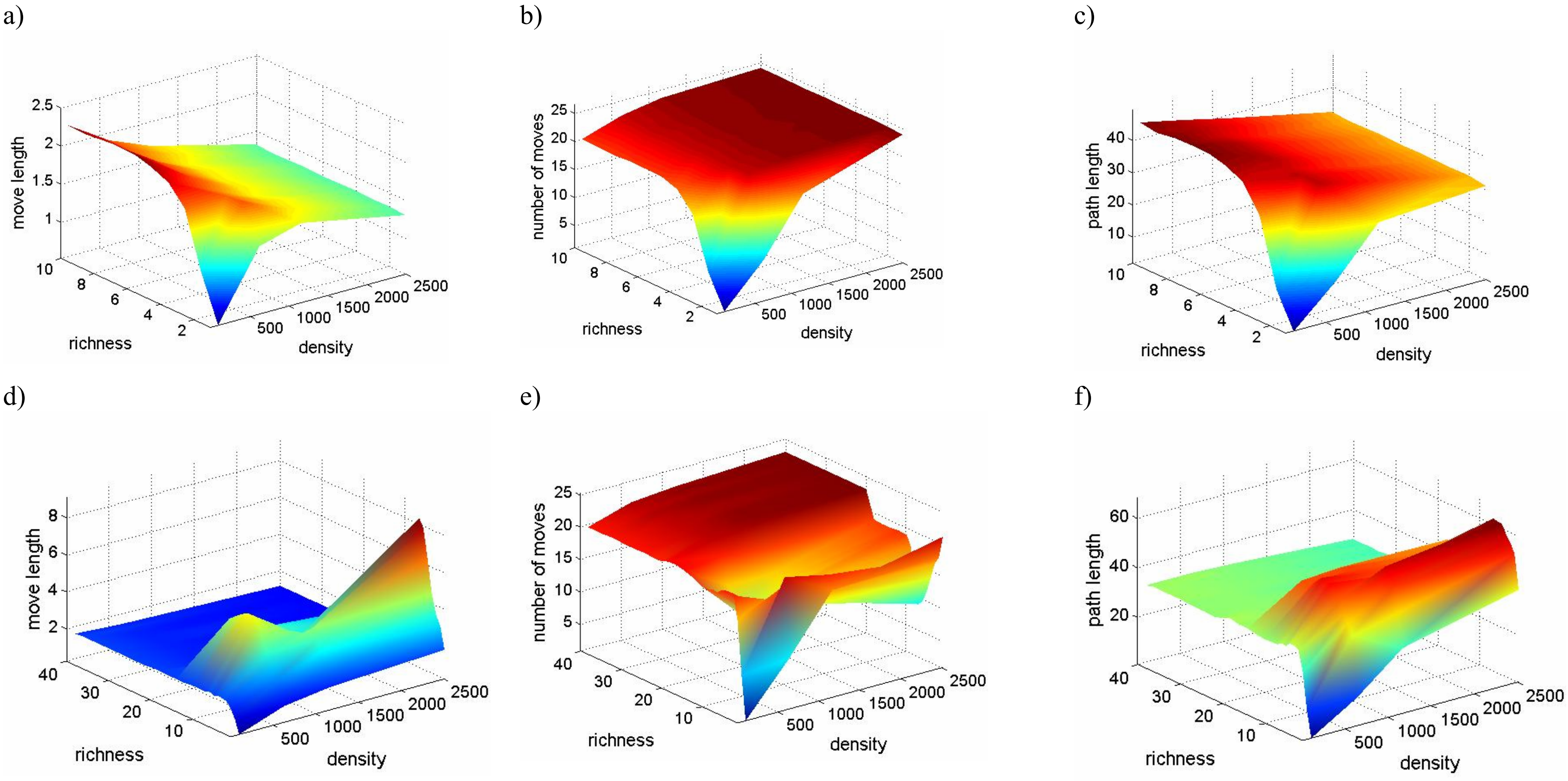

FIG. 3.4. The effects of patch richness (x-axis) and density (y-axis) on (a) move length, (b) number of moves, and (c) path length for moderately aggregated resources and on (d) move length, (e) number of moves, and (f) path length for tightly aggregated resources. For tightly aggregated resources, larger values for richness were simulated than for the other distributions because path length did not stabilize until resource values were greater than 10. Path length is a product of move length and number of moves. Consumption was 0.9/time unit and travel cost was 0.2/cell width.

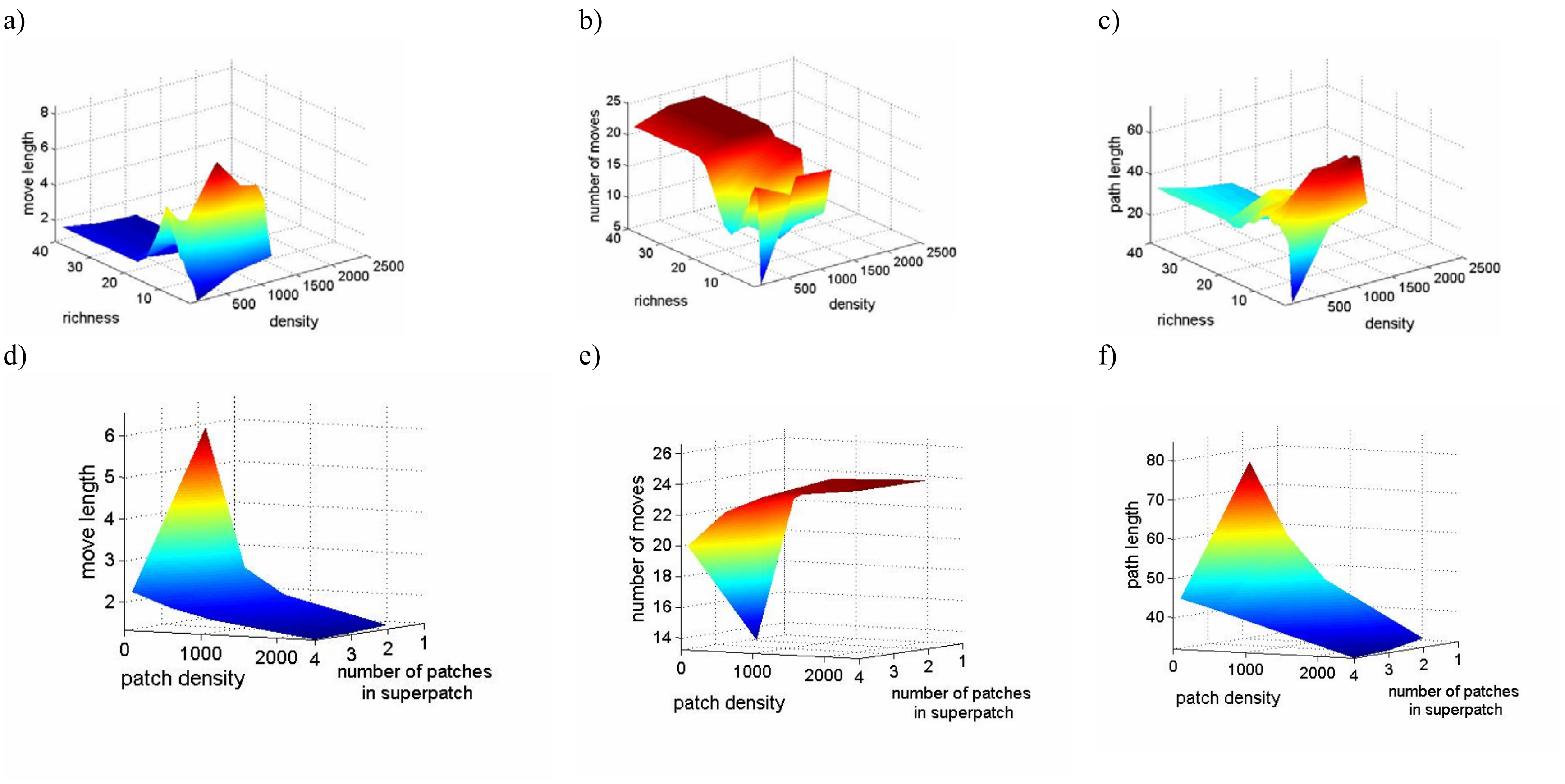

FIG. 3.5. Effects of patch richness (x-axis) and patch density (y-axis) on (a) move length, (b) number of moves, and (c) path length where the number of super-patches (comprised of 4 food patches) equals the number of food patches in random simulations (as in Fig. 3.3d-f). Effects of size of super-patches where 2, 3, and 4-food patches constituted a super-patch on (d) move length, (e) number of moves, and (f) path length. Consumption was 0.9/time unit and travel cost was 0.2/cell width.

CHAPTER 4: EFFECTS OF FORAGING RULES ON MOVE LENGTH AND NUMBER OF MOVES

ABSTRACT.

Applicability and optimality of foraging rules have been investigated for several decades, yet the effects of the foraging rules on animal movement are not understood well. I simulated animals moving according to departure, cell selection, and assessment rules. Departure rules were move: (1) when the occupied cell no longer had the highest net value, (2) at a fixed time, (3) according to Charnov's Marginal Value Theorem, (4) when food at the occupied site reached a giving up density, and (5) at random times. Cell selection rules were move to (1) the cell with the maximum net value, (2) the closest cell with food, and (3) random locations. Two assessment rules were examined: a fine and coarse scale assessment of the landscape. The results demonstrated that departure rules shaped path length through number of moves. Cell choice rules affected number and length of moves. Assessing the landscape on a coarse scale resulted in longer paths at a greater energetic cost.

Paradoxical movements, a negative or positive correlation with food abundance, can also be explained by these results. Using a giving up density as a departure rule can result in a seemingly paradoxical movement response depending on the relative value of food on the landscape. Switching foraging rules can also elicit a seemingly paradoxical response.

Key words: foraging rule; fixed time; giving up density; model; move; marginal value theorem; paradoxical; path.

INTRODUCTION

Animals may not consciously calculate the potential net gain in energy or probability of finding food. Nonetheless, animals typically forage in ways that maximize energy gain (Davies 1977, Zach 1979, Lewis 1982), minimize competition (Tamura et al. 1999) and balance their diets (Belovsky 1978). Much theoretical and experimental effort has gone into proposing the foraging rules that animals follow (e.g., Brown et al. 1997, Nishimura 1999, Nonacs 2001). Yet, the effects of foraging rules on local movements have not been investigated well theoretically or empirically, although Higgins and Strauss (2004) examined the effects of search rules on paths. A better understanding of how foraging rules affect movement will help ecologists to infer likely foraging rules from observed movements patterns and understand and predict ecological processes.

Food occurs frequently in patches in natural systems (e.g., Taylor et al. 1978, Condit et al. 2000) and animals forage in response to patch characteristics such as amount of food per patch and distance among patches (Chapter 3). Movement patterns may be shaped by foraging rules, such as rules governing departure time from a food patch, selection of a new food patch, and the scale on which the landscape is assessed. Foraging rules might be dictated by whether an animal should move to be most energetically efficient, to diminish predation risk (by minimizing move length or number of moves), to maximize covering a territory (maximize path length), or other behaviors.

Departure rules

Departure rules dictate when an animal should leave a food patch. One departure rule is to move when the occupied patch does not have the highest net value (WallisDeVries et al. 1999) (Table 4.1). If the occupied patch offers the highest net value, the animal remains in the occupied patch. By being adaptable enough to move whenever the value of the occupied patch falls to a point where it no longer has the highest value, an animal ensures that it is always in the best patch on the landscape.

Another rule is to leave a patch after a fixed time, regardless of the amount of food remaining at the occupied patch or other patches (Hayslette and Mirarchi 2002). Under this strategy, animals do not always occupy the patch with the most food and may leave a patch that still has the most food on the landscape. Theoretically, fixed time is a good strategy when the variance of patch richness is low (Valone and Brown 1989). Leaving after eating a fixed number of items is a related strategy (WallisDeVries et al. 1999). For uniformly distributed food, leaving after eating a fixed number of items or after a fixed time is optimal (Iwasa et al. 1981).

A third departure rule is to use amount of food in a patch (a giving up density) as an indication of when to move from an occupied food patch (Brown 1988). Animals may forage most efficiently by using a giving up density if foraging success depends on the density of food. For instance, searching for seeds can be more time consuming when only a few seeds remain in the leaf litter than when many seeds are in the same amount of leaf litter. This strategy may vary among different species that prey on different items, even in the same system (Brown et al. 1997). Application of this strategy even varies between captive and wild individuals of the same species (Focardi et al. 1996) and animals may fail to leave a patch when it falls to a minimum value (Nonacs 2001, Price and Correll 2001). Failure to implement such a rule could be due to the inability to perceive food densities (Hayslette and Mirarchi 2002) or application of another rule.

A fourth departure rule is for animals to leave a patch when the food value of the occupied patch falls below the mean value of all food patches, this behavior follows the Marginal Value Theorem (Charnov 1976). In Charnov's Marginal Value Theorem model, animals evaluate the net energetic return of patches on the landscape, accounting for travel cost to each patch. Animals should stay in rich patches longer than in less rich patches and animals should stay in patches longer when the number of food patches is low. The Marginal Value Theorem has empirical support in some systems (Cowie 1977) yet not in other systems (Nonacs 2001). Animals may not forage as predicted by the marginal value theorem if they need to sample patches or respond to other factors such as predation risk.

A fifth departure rule is to leave a patch after a random time spent foraging in the patch. This strategy might be as efficient as other strategies when food is very abundant. Some animals appear to move randomly (Kareiva and Shigesada 1983). Random movement has been modeled by determining the probabilities of movement from empirical data (Baur and Baur 1992, With and Crist 1996, Berger et al. 1999).

Patch selection rules

Patch selection rules determine where an animal goes when it leaves a patch. One patch selection rule is to move to the location that offers the highest net gain in energy. Maximizing energy has been a classic component of optimal foraging theory (Pyke

1984), empirically supported in movement studies (WallisDeVries et al. 1999), and modeled frequently (Railsback et al. 1999, Fryxell et al. 2004). Maximizing resources might be the optimal foraging strategy for some animals.

Alternatively, animals could move to the closest patch that has a minimum amount of food. Animals subject to predation may minimize predation risk by minimizing travel distance as long as a minimum amount of food is obtained. This strategy has also been modeled (Turner et al. 1993, Moen et al. 1997, Carter and Finn 1999, South 1999, Fryxell et al. 2004), yet animals do not always choose the closest patch (Janson 2000).

A third patch selection rule, moving to a random place, also has a theoretical and empirical history (e.g., Baur and Baur 1992, Focardi et al. 1996, Hein et al. 2004). Moving randomly can be nearly as productive as other strategies when resources are unknown (Adler and Kotar 1999).

Scale of assessment

A third class of foraging rules addresses the scale at which animals assess their habitat. Animals might assess patches on scales ranging from a fine (single small patches) to coarse (groups of patches). Scale can have profound effects on movements, including home range size (Anderson et al. 2005) and habitat selectivity (WallisDeVries et al. 1999, Frair et al. 2005). The scale on which an animal assesses patches has the potential to affect movement; yet the effect of assessment scale on movements has not been investigated. Most theoretical and empirical foraging studies assume that animals assess patches on a fine scale.

Absolute and relative effects of rules on movements

Different foraging rules might or might not produce different movement patterns by affecting move lengths, the number of moves, or path length (the product of move lengths and number of moves). For instance, when the departure rule dictates leaving when the patch falls below a given amount of food and the amount of food is less than the threshold amount to leave, path length should be the same as when animals assess whether or not to leave in every time step. Also, when animals use a minimum threshold as a cue to leave a patch and the amount of food at the patch is greater or equal to that threshold, path length should be the same as when animals leave after a fixed amount of time.

A constant relationship among foraging rules might exist. For instance, one foraging rule may always result in paths longer than paths resulting from another foraging rule. Alternatively, the relationship among foraging rules might depend on the values that animals use in the foraging rules.

Objectives

My first objective was to understand how departure, patch selection, and assessment rules affect movements (move length, number of moves, and path length). My second objective was to elucidate the mechanism for changes in path length by examining the effects of move length and frequency on path length.

METHODS

Simulations: landscape and animal movement

The landscape and animal movement were simulated in the same way as described in the methods in chapter 3. Food patches were moderately clumped and initially contained 10 food units. Except for the preliminary simulations, 1156 food patches were on the landscape. Animals left an occupied cell based on departure rules and chose a cell to which to move based on cell selection and assessment rules. I evaluate the effect of varying rules on movement.

Departure rules

I ran preliminary simulations for a range of times (1-10 time units) and amount of remaining food (1-10 food units) used as cues to leave a cell. The results determined the values for the rest of the simulations. I simulated 3 densities to ensure that density did not affect how animals responded to changes in the times and amount of food as departure cues. Path length decreased as animals used a longer fixed time (Fig. 4.1a) as a cue to leave an occupied cell. Path length increased as animals used larger food values as cues to leave an occupied cell (Fig. 4.1b). If the fixed time before leaving the cell was large, an animal would not leave the occupied cell. Likewise, if animals used a minimum threshold to determine when to leave the cell and the value of the cell was low, animals would not leave the occupied cell. From these simulations, I determined that, for the rest of the simulations, animals would leave after 2 time units and when the amount of food remaining in the cell was 8. The values allowed animals to move at approximately the same rates as when animals assessed the landscape in every time step.

I examined the effects of 5 departure rules on movement (Table 4.2). When animals moved according to the Marginal Value Theorem and cell values depend on travel costs, movement depended on the radius of neighboring cells that are assessed. In these simulations, animals used a radius of 10 neighboring cells to calculate mean cell value on the landscape. Two permutations of a random rule were simulated, frequent random, with a 80% chance of moving each time step, and less frequent random movement, with a 50% chance of moving per time step. For examining departure rules, all animals used the selection rule of moving to the cell with the maximum net value. Animals assessed single cells rather than groups of cells.

Cell selection rules

I simulated 3 selection rules. For the rule to go to the closest cell with a value above the minimum value, I set the minimum value at 0.02 (essentially any cell containing food). For the rule to go to a random cell, I set a small radius (5 cells) and large radius (15 cells) from the occupied cell. Animals assessed single cells rather than groups of cells in every time step.

Assessment scale

Although animals knew the locations and amounts of all the food on the entire landscape, they could assess the landscape at one of two scales: a fine scale (the value of single cells) or coarse scale (the value of groups of 4 cells). The value of each single cell was the food value of the cell discounted by travel cost. The value of each group of 4 cells was the summed food value of all 4 cells discounted by the travel cost to the center of the group of cells. Animals assessed every cell or group of cells in every time step and moved to the cell or groups of cells with the highest net value.

Output

I quantified movement responses to departure, cell selection and scale assessment rules as mean path length, move length and number of moves from 200 iterations. Net energy at the end of 25 time steps was calculated as the total amount of food consumed discounted by total travel costs.

RESULTS

Effects of departure rules on movements

Departure rules did not influence move length much except when the food was low (Fig. 4.2a). Departure rules did dictate the number of moves (Fig. 4.2b). For increasing amounts of food patch richness, number of moves increased and then plateaued for all of the departure rules except when animals used the amount of food in the occupied cell as a cue to leave the occupied cell (giving up density). When the animal used a giving up density, increased cell richness initially increased the number of moves. Once the amount of food in the cell equaled the cue to leave the cell (in this case, 8), the number of moves decreased. When richness was low, most departure rules produced similar numbers of moves. When richness was intermediate, animals moved the most when they assessed whether or not to leave in every time step or based on the amount of food in the occupied cell. Once richness was greater than the amount of food that cues animals to leave the cell, animals moved the least number of times when they assessed whether or not to leave in every time step. Because move length was not influenced much by different rules, the pattern seen for the relationship between patch richness, rules and path length is very similar to that seen for richness, rules and number of moves (Fig. 4.2b and Fig. 4.2c).

Effects of cell selection rules on movements

When animals moved to the cell with the highest net value, move length increased initially and then no longer responded to increased amount of food per food cell (Fig. 4.3a). When animals moved to the closest food cell, move length increased initially and then decreased in response to amount of food per food cell (Fig. 4.3a). When animals moved to random locations, amount of food per food cell had no effect on move length (Fig. 4.3a).

Number of moves increased and then plateaued in response to amount of food per food cell, whether animals chose cells with the highest net value or the closest cells (Fig. 4.3b). When cells were chosen at random, the number of moves was not affected by cell richness (Fig. 4.3b). Moving randomly resulted in the most moves while moving to the closest cells resulted in the least moves.

When animals chose cells by moving to the cell with the highest net value, path length initially increased as food increased but then plateaued (Fig. 4.3c). When animals chose the closest cell, path length increased and then decreased slightly in response to amount of food per food cell (Fig. 4.3c). When animals moved to random locations, path length did not change in response to amount of food per food cell (Fig. 4.3c). Random movements resulted in the longest paths, followed by moving to the cells with the highest net value, then the closest cells.

Effects of assessment scale on movements

When animals assessed the landscape on a fine scale, move lengths, number of moves, and path lengths increased and then plateaued in response to amount of food per food cell (Fig. 4.4a-c). In contrast, when animals assessed the landscape on a coarse scale, changes in the amount of food per food cell did not change the number of moves or move length.

Optimal foraging rules

When patch richness was low (≤ 3), leaving cells after a fixed time netted the most energy (Fig. 4.5a). When amount of food per food cell was intermediate (3 - 9), leaving cells when the cell fell below the mean value of food cells (marginal value) was the most energetically efficient foraging strategy. For high food richness, moving at random infrequent times was the most efficient. Among the cell selection rules, moving to the closest cell that contained food was most energetically efficient for all values of food per cell (Fig. 4.5b). Assessing single cells was more efficient energetically than assessing multiple cells (Fig. 4.5c).

DISCUSSION

Effects of departure rules

Departure rules did not affect move length because departure rules dictated when, not where, to move. Departure rules affected number of moves. Thus, number of moves, not move length, determined path lengths.

Using the amount of food in a cell as a cue to leave generated a different response than the other departure rules. In my simulations, animals used a value of 8 to determine when to leave a cell. When amount of food per food cell was below 8, movements were similar to movements generated from other departure rules. When the amount of food per food cell ≥ 8, number of moves decreased with increasing food abundance because the net value of most of the occupied cells was above the threshold and the animals did not move in each time unit. Move length did not affect path length because of departure rules. Thus, the number of moves shaped path length.

Although the responses to amount of food per food cell were similar qualitatively among the departure rules, animals foraging in the same environmental conditions can have different path lengths depending on the departure rule that is used. Assessing whether or not to leave at every time step cannot change; therefore, path length resulting from that departure rule would not change. Still, a change in the value for another movement rule, such as the distance for a random move, could change which rule produced the longest path. Therefore, the relationship of movements stemming from the departure rules depended on the values for each rule.

When animals used the marginal value theorem as a rule and cell net values were calculated from the entire landscape, movement did not occur when the amount of food per food cell was low because the mean net value of food on the landscape was negative (most cells are beyond a reasonable travel distance). Only when food per cell was high did the food on the landscape become large enough to allow the animal to leave the occupied cell. Calculating mean cell value from surrounding smaller "neighborhoods" translated to a higher mean cell value (as travel cost had a relatively smaller effect) and decreased the threshold for which animals begin to move. Similarly, for smaller landscapes, the threshold for movement would be lower. Because the net value is a product of the neighborhood size, the relationship between using the Marginal Value Theorem and other rules is relative. Furthermore, Charnov did not analyze explicitly the effect of landscape size or travel cost on optimal foraging, so it is worth noting that path length is affected by travel cost and landscape size when animals move according to the marginal value theorem.

For these simulations, the path lengths of animals assessing movements in every time step and animals using the remaining food in the occupied cell were approximately equal. Quantifying path length, move length or number of moves would not provide enough information to determine the foraging rules of an animal. Generally, the amount of remaining food or foraging time would be calculated to determine what rules animals use to forage. Still, animals using different departure rules can move with similar frequencies and distances, so caution should be used when trying to infer foraging rules from move length, number of moves, or path length.

Effects of cell selection rules

By definition, moving to the cells with the highest values, the closest cells with food, or a random distance, affected move length and, thus, path length; therefore, move length was controlled by cell selection rules. Although the random distance that an animal moved did not affect the number of moves, the other cell selection rules influenced the number of moves. Therefore, path length is largely a product of move length.

Moving to the cell with the highest net value resulted in longer moves than moving to the closest cell. In contrast, animals that moved to the closest cells had a minimum food value threshold that had to be met to move. Random movements could produce path lengths that are longer or shorter than any other cell selection rules depending on the random distance.

Effects of assessment rules

For reasons already described in the departure rules results, assessing on a fine scale resulted in initial increases in frequencies and distances of moves and increased path lengths. Assessing the landscape on a coarse scale did not result in a positive relationship between path lengths and food abundance because assessing a group of cells allowed movements at low abundance (unlike when single cells were assessed).

Assessing the landscape on a coarse scale, such as in clumps of 4 cells, allowed animals to move farther and more often than assessing on a fine scale (single cells) because travel cost had relatively less effect on a patch of 4 cells than a single cell.

Because animals can afford to travel farther and more often when assessing groups of cells, assessment on a coarse scale results in longer paths.

Although the results are unambiguous, these are results for the simulations described here. Animals may change foraging rules when they change the scale at which they assess the landscape. For instance, if animals assess the landscape at larger scales (consisting of several foraging subsites), they may incorporate a spatial rule into their foraging such as “visit each of the subsites within a patch before leaving the patch.” Further work should be done to determine the foraging rules, how foraging rules depend on other foraging rules, and the effects of changing foraging rules.

Local movement predictions

Departure rules influence path length by affecting the number of moves. Cell selection rules affect move length and number of moves. Assessing on a coarse scale allows animals to travel farther by increasing both move length and number of moves. Qualitative predictions about the relationships of movements within each class of rules suggest some general relationships (Table 4.3). Some rules result in movements that are always longer or shorter than movements that result from other rules. Still, an absolute ranking of path length, move length and number of moves based on foraging rules cannot be established because movements depend on amount of food per food cell, the number of food patches, travel cost, consumption amount, and rule value. For particular systems, ecologists could determine the relationship of movements given foraging rules and biological values for those rules.

Optimal foraging rules

For departure rules, net energy could be maximized at different food abundances by choosing appropriate departure rules. For instance, at very low amounts of food per food cell, leaving at fixed times resulted in a shorter path than when food was more abundant and animals left at infrequent, random times. In this case, switching rules would be an optimal strategy. Changing foraging strategies resulted in path length becoming correlated negatively with food abundance. No energetic reasons existed for animals to switch among cell selection rules and assessment scales tested here.

Although it might seem that assessing a group of cells could result in the most energetically efficient way to assess the landscape, it was not. A related but different problem is to assess cells sequentially (i.e., the traveling salesman problem). Assessing several steps ahead does not always result in more optimal foraging than assessing single steps (Anderson 1983). Rules that rely on more information are not necessarily the most adaptive from an energetic standpoint.

Foraging rules as mechanisms for "paradoxical" movements in response to changes in food abundance

Movements are predicted frequently to correlate negatively with food abundance (McNab 1963), although sometimes positive correlations are predicted (Chapter 3) and occur (Hulbert et al. 1996, Fortier and Tamarin 1998, Fashing 2001, Bravo and Sallenave 2003). Modeling animal movement suggested that this apparent paradox can be resolved by differentiating between components of food abundance with animal movements correlating negatively with the number of food locations and positively with amount of food at each food location (Chapter 3). If foraging rules affect movements, they also could be a mechanism for this apparent paradox. Foraging rules might act in one of two ways. First, although some foraging rules catalyze movements to correlate positively with food, other foraging rules might cause movements to correlate negatively with food. Second, if animals change foraging rules in response to changes in food abundance, the rules may account for the apparent paradox. That is, as the amount of food per food patch increases, animals may travel farther until a point where the animal switches foraging rules. Then, despite further increases in food, travel distance may decrease.

Animals may switch rules to maximize energy. A rule that is most efficient energetically when food patches have little food may not be the most efficient when food patches have more food. Alternatively, animals might change foraging rules to meet other biological demands such as mating. McNamara (1990) hypothesized that animals do not maximize foraging intake during the summer because substantial weight gain would be energetically counterproductive due to the increased travel costs incurred by extra weight. Powell (in review) rejected the hypothesis that bears should minimize food intake in spring and maximize food intake in fall to optimize weight gain over an annual foraging cycle.

For most foraging rules, increases in amount of food per food cell resulted in a unidirectional response for path length (Fig. 4.2a, 4.3a and 4.4a). Using a giving up density, however, resulted in a bidirectional response. Therefore, seemingly paradoxical responses could be caused by an animal using giving up density to decide when to leave an occupied cell.

My results provide no evidence that, if the cell selection rules or scale changed, a change in foraging rules as the amount of food per food patch increased would create a paradoxical response. In contrast, changing departure rules could result in a response that appears paradoxical. For instance, animals may assess whether or not to move in every time step when food is scarce. As food becomes more plentiful, animals could switch to using a fixed time as way to judge when to move. In this case, path length would correlate negatively with food per food location.

Application of results

Foraging rules are not always considered explicitly in movement models. For example, models that examine correlated random walks may not consider explicitly when to leave a patch or the scale on which patches should be assessed. When foraging rules do not affect local movements, then it does not matter to ecologists what rules animals use to forage. In that case, ecologists could concentrate on determining the factors that affect local movement patterns (such as resource abundance and distribution, and predation) instead of trying to determine what rules animals use to forage. If foraging rules do not affect movement, modelers would not have to include foraging rules in models.

Where foraging rules affect local movements, such as path length, foraging rules need to be explicitly included in movement models. Incorporation of foraging rules in movement models will allow ecologists to predict ecological processes better such as seed dispersal and pollination as well as spread of diseases or invasive species.

Furthermore, understanding the effects of foraging rules may help interpret local movements of real animals. Change in food abundance is cited frequently as a cause for change in movements. Although the number of food patches and amount of food per food patch affects movement (Chapter 3, Powell et al. 1997, Jedrzejewski et al. 2001), departure, cell selection and assessment rules also influence movement. Care should be used when ascribing change in movement to change in food abundance, as change in movement may have resulted from switching foraging rules.

Nonetheless, foraging rules are not the only factors that affect paths. Complex movement behaviors acting in concert with foraging rules also affect path length. For instance, some animals are central place foragers, periodically returning to a nest. Animals may employ mixed rules (Valone and Brown 1989, Nishimura 1999) or switch among foraging strategies (Helfman 1990). In addition, suboptimal behaviors based on simple rules might occur (Janetos and Cole 1981). Therefore, local movement studies should consider foraging rules and other movement behavior.

Although resulting movements (i.e., path length) might affect selection of foraging rules (i.e., if animals are best adapted when they maximize path length), resulting movements may not always influence rule selection. That is, animals may not maximize path length. Instead, they may behave in a way to minimize or maximize other parameters, for instance, travel cost, amount consumed or net energy might influence selection of foraging rules. Applying knowledge of how foraging rules affect movements to how those movements affect survivorship and productivity will provide insight into the adaptiveness of foraging rules.

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TABLE 4.1. Definitions of foraging rules used in simulations. Real animals move among food patches instead of cells.

RULES	DEFINITION OF RULES
Departure Rule	
every time	At every time step, decide whether or not to move to a new cell
fixed time	At a fixed time, move to a new cell
giving up density	When the occupied cell depreciates to a given value, consider moving to a new cell
Marginal Value Theorem	When the occupied cell's value falls below the average net value on the landscape, move to a new cell
random	At a random time, move to a new cell
Cell selection rules	
highest value	Move to the cell with the highest net value
closest cell	Move to the closest cell containing some minimum amount of food
random cell	Move to a random cell within a given radius
Assessment scale	
fine scale	Assess the net value of single cells
coarse scale	Assess the net value of groups of 4 cells

TABLE 4.2. Values that were used to compare rules within each class of foraging rules: departure rules (every time step, fixed time, at a giving up density, net energetic gain of occupied cell is less than mean value of all cells in 10 cell radius, frequent and infrequent random times); cell selection rules (cell with highest net value, closest cell with a value above a minimum value, near and far random locations); and assessment scale (fine and coarse). Density of food cells was 624 for all simulations.

Foraging rules	**DEPARTURE RULES (DEFINED IN TABLE 4.1)**	**Departure rule value**	**CELL SELECTION RULE**	**Cell selection values**	**Assessment scale**
departure	assess at every time step	n/a	highest net value	n/a	fine
	fixed time	2 time units	highest net value	n/a	fine
	when cell reaches a minimum value	8 food units	highest net value	n/a	fine
	net energetic gain of occupied cell is less than mean value of all cells in 10 cell radius	n/a	highest net value	n/a	fine
	random, - infrequently - frequently	- 0.5 probability of moving per time step - 0.8 probability of moving per time step	highest net value	n/a	fine
cell selection	every time step	n/a	highest net value	n/a	fine
	every time step	n/a	closest cell greater than a minimum value	0.02 food units	fine

TABLE 4.2 (CONTINUED)

Foraging rules	DEPARTURE RULES (DEFINED IN TABLE1)	Departure rule value	CELL SELECTION RULE	Cell selection values	Assessment scale
	every time step	n/a	random cell in a radius - near - far	radius of - 5 cells - 15 cells	fine
assessment scale	every time step	n/a	maximum net value	n/a	fine
	every time step	n/a	maximum net value	n/a	coarse

TABLE 4.3. General relationships among rules observed in simulations within each class of foraging rules (departure, cell selection and assessment rules).

Leave the occupied cell	**Relationship to other rules in the same class of rules**
when it does not have the highest net gain	Move more often and have longer paths than animals that move after a fixed time or when a giving up density is reached.
after a fixed amount of time	Depending on the amount of time, animals could move more or less frequently than other rules.
when food depletes to a given value	Depending on the giving up density, animals could move more or less frequently than other rules
according to the Marginal value theorem	Depending on the radius of knowledge that an animal has, animals may move less often and shorter distances than when move at every time, fixed time or at a giving up density (as in these results).
at a random time	Depending on the probability of moving, animals could move more or less frequently than other rules.
Move to a cell that	
has the highest net value	move farther and more often than moving to the closest cells
is closest to the occupied cell	the shortest and least number of moves
is at a random place	the most moves; depending on the distance could have the shortest or longest moves
Assessment	
fine	shorter and fewer moves than at a coarse scale
coarse	farther and more moves than at a fine scale

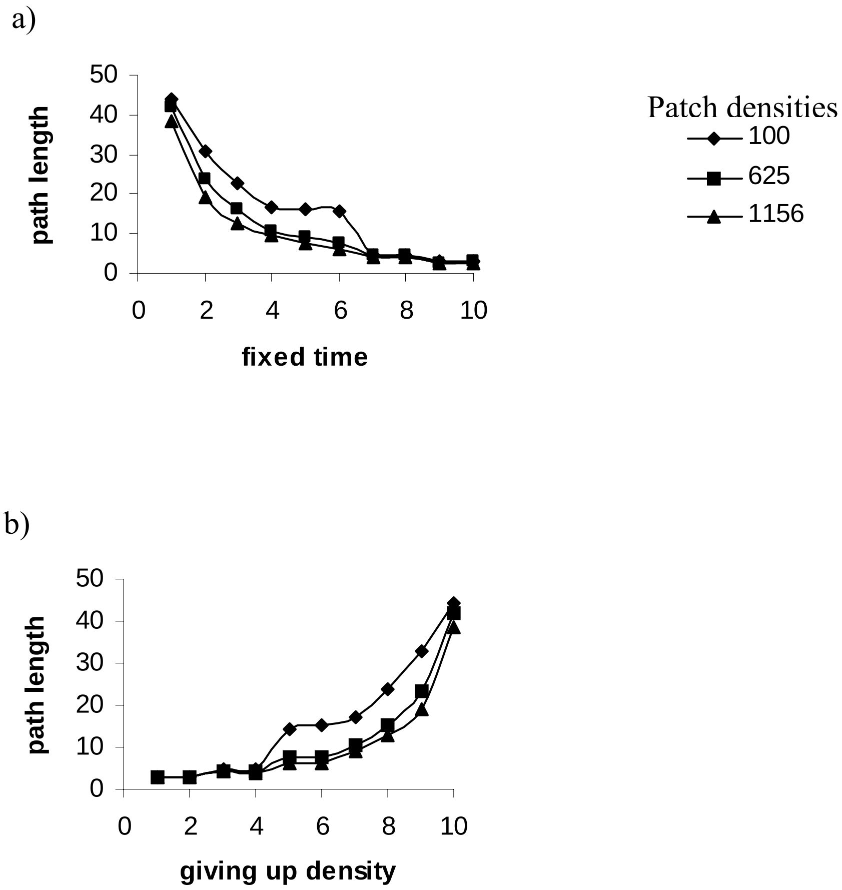

FIG. 4.1. Path lengths from investigating effects of values of departure rules a) leaving at a fixed time and b) leaving when a giving up density is reached. The cell selection rule was “move to the cell with the highest net value” and the assessment scale was 1 cell.

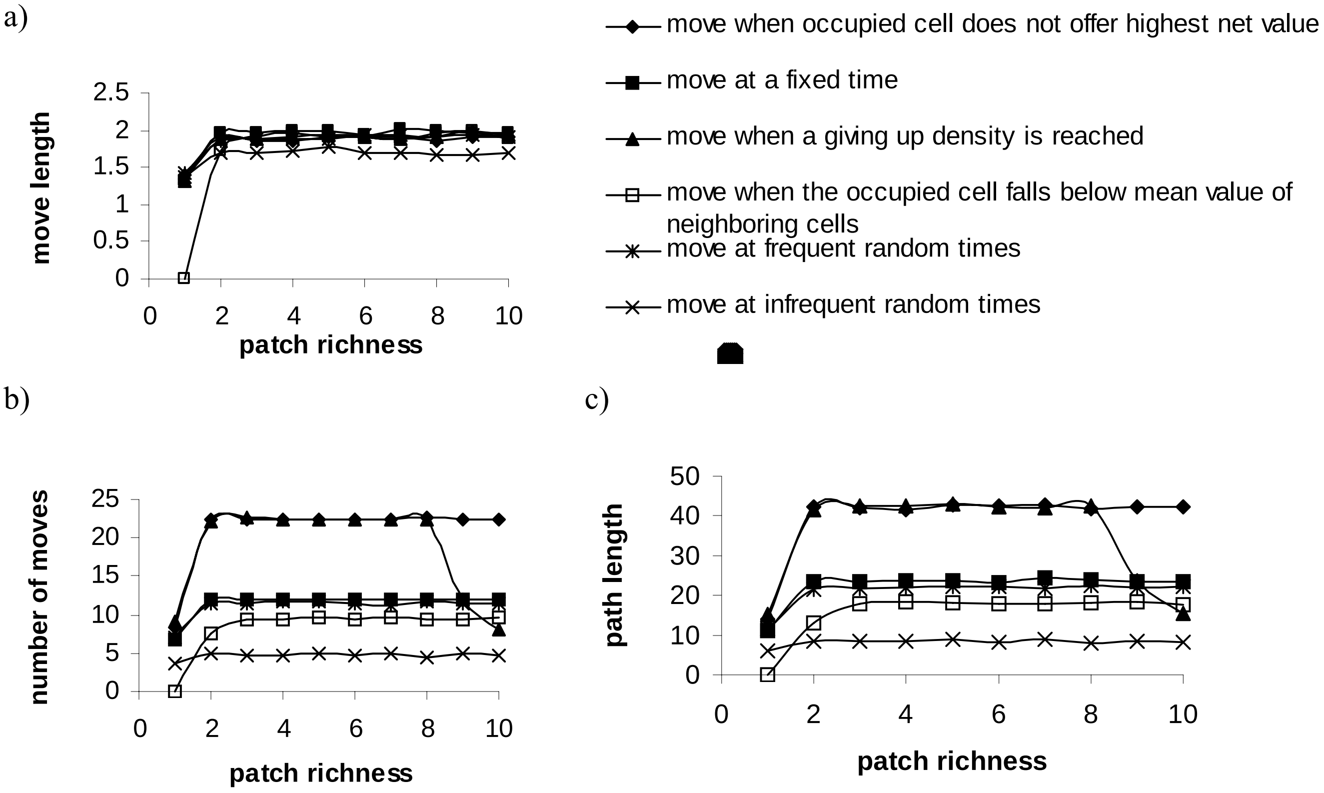

FIG. 4.2. A comparison of the effects of departure rules (see legend) on a) move length, b) number of moves, and c) path length. Animals selected new cells by going to the cell with the highest net value. Assessment was on a scale of 1 cell. Amount of food per food cell (patch richness) is on the x-axis. 624 food cells were clumped on the landscape.

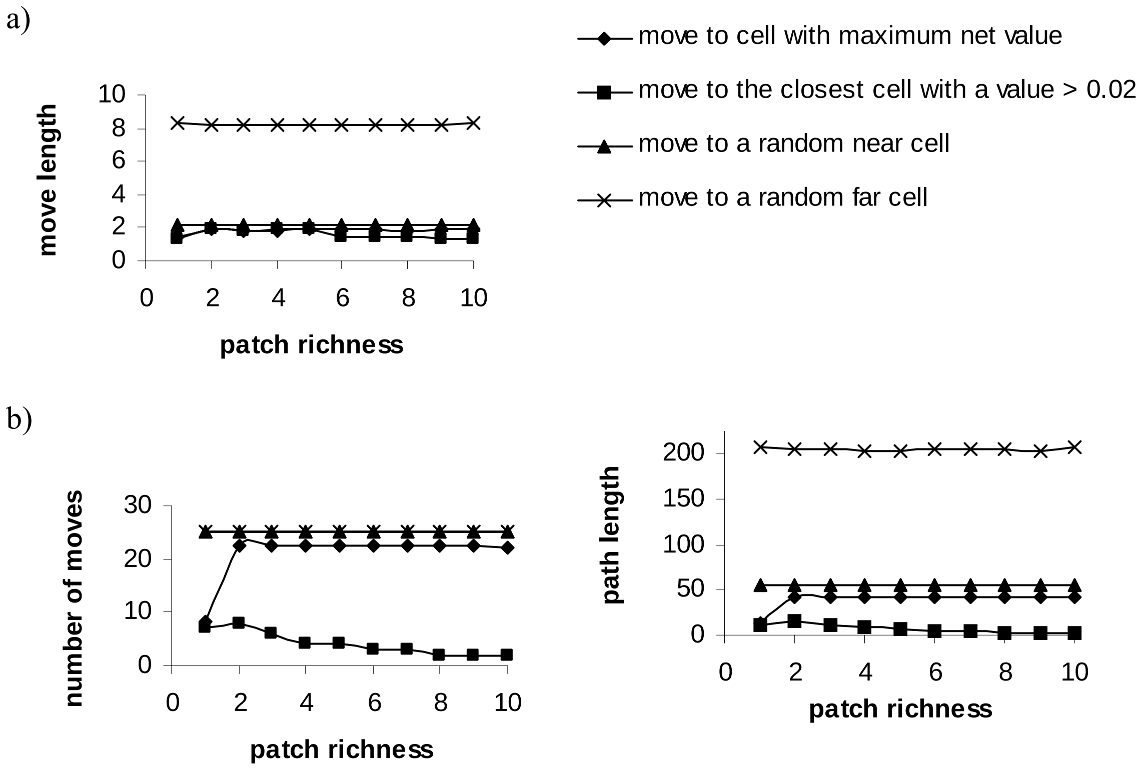

FIG. 4.3. A comparison of cell selection rules (see legend) on a) move length, b) num,ber of moves, and c) path length. In every time step, animals assessed whether or not to leave an occupied cell. Animals assessed single cells. Amount of food per food cell (patch richness) is on the x-axis. 624 food cells were clumped on the landscape.

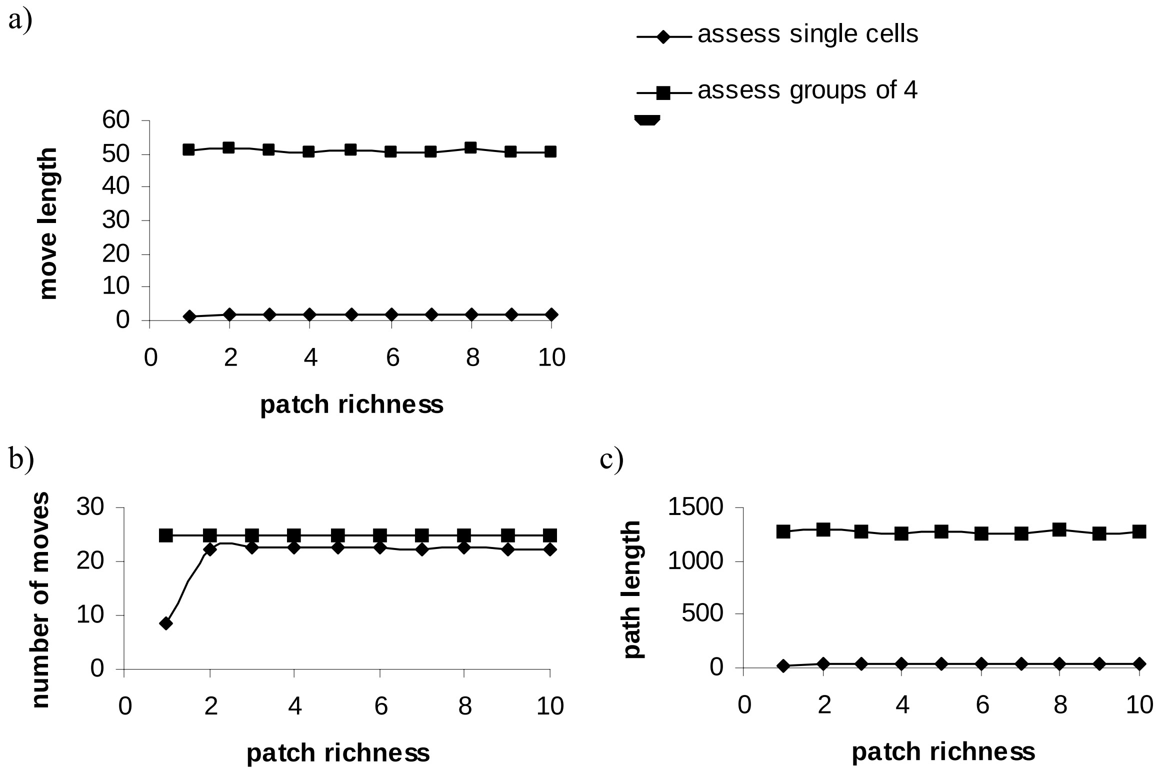

FIG. 4.4. The effects of assessing cells on a fine scale (single cells) and a coarse scale (4 cells) on a) path length, b) move length and c) number of moves. In every time step, animals assessed whether or not to leave an occupied cell. Animals moved to the cell with the highest net value. Amount of food per food cell (patch richness) is on the x-axis. 624 food cells were clumped on the landscape.

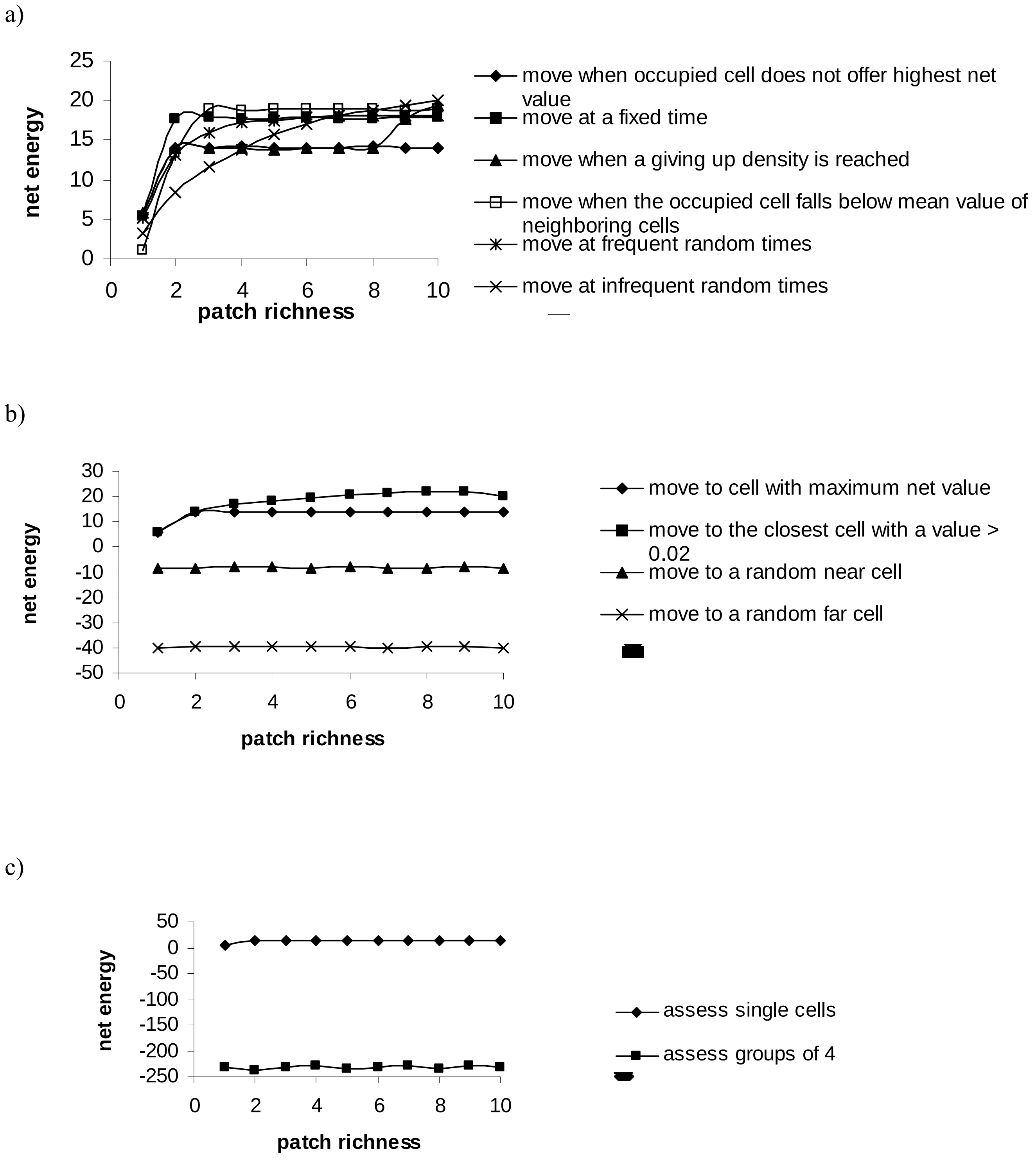

FIG. 4.5. The effects of a) departure rules, b) cell selection rules, and c) assessment scale on net energy gain. Animals assessed the value of single cells and selected cells with the highest net value of food. 624 food cells were clumped on the landscape.

CHAPTER 5: COGNITIVELY CONSTRAINED ANIMALS CAN BE AS FIT AS OMNISCIENT ANIMALS

ABSTRACT.

The information or knowledge that an animal has about its environment should affect its movement patterns and fitness. My objectives were to determine (1) how spatially and temporally variable information affect animal movement and (2) the types of cognition that might be selected based on the consequences for movements and energetics. I simulated animals foraging under variable cognitive states: (1) omniscience (animals knew all food values and travel costs), (2) limited spatial information (animals knew food values for only neighboring cells), (3) limited temporal information (memory of food value decayed exponentially with time), (4) spatial ignorance (food values were unknown, so animals move to a random place), and (5) temporal ignorance (the best time to move is unknown, so animals move at a random time). Omniscience did not result in extreme (shortest, longest, least, or most) or unique values for move length, number of moves, number of cells foraged in, or intensity of use. Furthermore, omniscience did not result in the least travel costs, highest consumption or highest net energy gain. Therefore, omniscience is not necessarily the best adapted cognitive state and it should not be assumed that omniscience confers a greater fitness than limited or ignorant cognitive states.

Key words: cognition; ignorant; intensity of use; memory; model; move; omniscient; home range.

INTRODUCTION

How does temporally and spatially variable information affect movement?

Food abundance and distribution (Chapter 3, Henzi et al. 1992, Tufto et al. 1996, Jedrzejewski et al. 2001) and foraging rules (Chapter 4, Higgins and Strauss 2004) affect animals' movements, including how often and how far an animal moves between locations. Information, or that which an animal perceives and remembers, should also affect movement. For instance, animals with no knowledge of resource distributions may be most successful at finding resources by moving in a random walk (Bovet and Benhamou 1988) or Lévy flight (Viswanathan et al. 1996, Viswanathan et al. 1999). As cognitive ability increases, non-random movement patterns should develop if such movements increase foraging success. Lab and field experiments (e.g., Krebs et al. 1977, Shettleworth 2001) have demonstrated complex and variable cognitive capabilities of animals. Likewise, much has been learned about the effects of information on foraging (Clark and Mangel 1984, Mitchell 1989, Stephens 1989, Garber 2000, Janson 2000, Sandlin 2000), but the effects of information on other movements are not well studied.

Information stems from perception. Perceptual range varies among species (Zollner 2000), may be affected by environmental factors (Yeomans 1995, Zollner and Lima 1999, Schooley and Wiens 2003), may be correlated to body size (Mech and Zollner 2002), and is not necessarily isotropic (Olden et al. 2004). Spatial perceptions can be stored cognitively (Menzel 1978, Gould 1986, Manser and Bell 2004).

Birds rank values of food resources (Woodrey 1990, Cristol 2001). Birds (Sherry et al. 1981, Shettleworth and Krebs 1982, Kamil and Balda 1985) and mammals (Jacobs and Liman 1991, Jacobs 1992, Macdonald 1997, Devenport et al. 2000) remember food cache locations. Least chipmunks (*Tamias minimus)* remember which resources renew; they revisit renewable resources but not non-renewable resources (Devenport et al. 1998). Honeybees (*Apis mellifera*) avoid visiting flowers that held potential predators on previous visits (Dukas 2001). Animals also forget over time (Gleitman 1971, White 2001) resulting in spatial knowledge that is temporally dependent (Olton 1985).

Information influences a variety of behaviors such as thermoregulation (Chelazzi and Calzolai 1986) and prey capture (Lomascolo and Farji-Brener 2001). Movement decisions based on information can increase fitness of individuals by contributing to successful predator avoidance or increased foraging success. For instance, eastern chipmunks (*Tamias striatus)* in their home ranges travel a shorter distance to escape predators than when they are translocated outside their home ranges (Clarke et al. 1993). Similarly, prairie voles (*Microtus ochragaster*) that are familiar with an area travel shorter distances to reach cover than prairie voles unfamiliar with an area (Jacquot and Solomon 1997). Information about a habitat may also stem from the ability to predict habitat characteristics accurately for a habitat that has not been sampled. For example, primates know that when fruit is ripe at an occupied tree, fruit will be available at other trees of the same species (Menzel 1991).

Animals might be omniscient for all practical purposes, knowing the environmental characteristics that are important to their fitness. In this chapter, I define omniscience as knowing all the food locations and amounts of food at those locations. Alternatively, animals might be ignorant of food locations, travel costs and the times to move that will maximize occupation of food patches with the most food. Either extreme is unlikely (Clark and Mangel 1984, Spencer 1992, Hirvonen et al. 1999) and a more biologically realistic scenario is that animals have limited information.

Information may be distributed normally over a group of patches: high in an occupied patch and decreasing with distance from the occupied patch. Such a distribution of information may be a function of animals' perceptual ranges or it could result from rapidly changing landscapes. Limited spatial information can be illustrated by a black bears on the south side of a 400 m^2 berry patch. Without going to the north side of that patch, the bear may know that the berries on the north side are at approximately the same density as the south side. The bear may not know the berry densities in other patches because other bears may have depleted those patches. Piscivorous marine birds, such as penguins, may know, at one time, the location of a school of fish in which the penguins are foraging, even though the location of the school changes. Therefore, penguins know the food value for the location they occupy but not for neighboring locations. American bison (*Bos bison*) know local information better than regional information about food (Fortin 2003). Limited spatial information has been modeled for non species specific models (Beecham and Farnsworth 1998), for Florida panthers (*Puma concolor coryi*) (Cramer and Portier 2001) and moose (*Alces alces)* (Roese et al. 1991). A variable environment resulting from ephemeral resources and competition may make it difficult to predict food accurately. In these cases, animals may not make assumptions about patches that they visited in the past, but can no longer perceive.

In contrast, in a spatially stable environment, information may not decrease with distance from animals' current locations (spatially), but may decrease exponentially with time as a result of memory decay (Ebbinghaus 1964, Gleitman 1971, Mayes 1983) or because food was eaten by competitors. In this case, information will be highest for the patches last visited and decrease with elapsed time. Animals might not assume anything about places they have not visited, even if the patches are a short distance from the animals' current locations. Furthermore, animals remember characteristics about places they have visited, but those memories decay with time. For example, in a field experiment, foraging decisions of least chipmunks and golden-mantled ground squirrels (*Spermophilus lateralis*) demonstrated that they understood that their ability to predict food availability decreased with time (Devenport and Devenport 1994). Limited temporal information has been modeled (Folse et al. 1989). Some models have included a period of acclimation for the virtual animals to learn the locations of resources (South 1999).

Another possibility is that animals are ignorant and have no relevant foraging information about their environment. Although it seems that most vertebrates and even many invertebrates have the cognitive capability to know their environments, it is possible that some animals are effectively ignorant about food resources. For instance, if food is ephemeral, either due to its short-life (e.g., flowers that bloom for a short time) or high competition for the food source (e.g., antelope carcass that is eaten quickly by vultures), animals would not know when or where to find the food until they find it by chance. Alternatively, food could be so abundant [e.g., periodical cicadas (*Magicicada spp.*)] that an animals' success in locating food is not dependent on cognitive ability. Food can be abundant enough that animals find food when moving randomly (Ricklefs 2004) and do not need to know food locations. Alternatively, a forager may not have the experience to know the location of food because the forager just dispersed to a new place or the area with which it was familiar had catastrophic change such as a forest fire. Another explanation for ignorance is that ignorant animals are the most fit (greatest fecundity or survival). For example, a lack of post natal spatial knowledge could catalyze male mouflon (*Ovis musimon*) to return to natal grounds for breeding, thereby reducing inbreeding (Dubois et al. 1995).

I hypothesized that spatial and temporal knowledge affect movements. Therefore, my first objective was to determine how spatially and temporally variable information affect animal movement. Boinski asked a similar question, “How can we distinguish between complex, multivariate decision-making algorithms from ‘rules of thumb’ solutions?” (Boinski 2005: 680). She suggested that an answer could be found with long term studies of individuals beginning at birth so that researchers know what animals know (Boinski 2005). As Boinski stated, this approach is “onerous.” I posit that insight into her question can be gained by modeling various cognitive states and movement. Modeling permits underlying cognitive states to be known accurately and complex situations to be manipulated so that causality can be isolated. Modeling can determine adaptiveness of cognitive states (Shettleworth 1998).

Should natural selection favor omniscient animals?

Ability to perceive, interpret and remember information is correlated with brain size. For example, the size of the hippocampus is larger in birds that remember food storage (Krebs et al. 1989) and nest (Clayton et al. 1997) locations than those that do not remember these locations. The hippocampus is smaller in birds that lack experience (Clayton and Krebs 1994) than individuals that have experience. Large brain size of frugivorous rodents, bats and primates is hypothesized to be a function of the complexity of storing and remembering information (Harvey and Krebs 1990). Although cognitive abilities evolved early in vertebrates (Broglio et al. 2003), brains are expensive metabolically, resulting in selection against large brains (Aiello and Wheeler 1995). In addition, information can be expensive to gather (Gould 1974, Koops and Abrahams 1998). Even if information was not costly, a variable environment might negate the value of the information (Koops and Abrahams 1998). Although natural selection might favor omniscience over limited information or ignorance, stronger selective forces might counteract the forces selecting cognitive abilities. For example, volant birds are selected to be light in weight. Brains capable of complex cognitive processes increase in morphological complexity and weight. These 2 selection forces are at odds; an upper limit to bird brain size may by constrained by weight. Similarly, an evolutionary trade off exists for bats between brain size and gonad size (Pitnick et al. 2006).

Although behavior, such as foraging under predation risk, (Bouskila and Blumstein 1992, Abrams 1994) has been predicted for animals with limited information, these predictions still do not explain the effects of information on adaptive fitness. Are omniscient animals the most fit? If not, what cognitive abilities might be selected and under what circumstances? How does the amount or kind of information affect fitness?

The foraging goals of species and individuals vary with life history needs, making it difficult to assess fitness in a general model. Species that experience high predation risk alter foraging strategies (Werner et al. 1983, Nonacs and Dill 1990) and might minimize travel distance or frequency of moves. Species that need to gain weight to survive winter might maximize energy intake. For instance, black bears move to maximize net energy gain during fall (Powell et al. 1997). Individuals may maximize reproductive success by maximizing path lengths (Croft et al. 2003), home range sizes (Fisher and Lara 1999, Jedrzejewski et al. 2002) or intensity of use of their ranges. Therefore, maximizing total consumption (often assumed in optimal foraging), minimizing travel distance, or maximizing home range size might confer fitness. Consequently, for a general model, fitness can be assessed by examining a suite of foraging movements and energetics (consumption amount, travel costs and net energy gain) to compare the effects of omniscience to other cognitive states.

My second objective was to examine the effects of variable cognitive states on fitness by comparing movements and energetics among cognitive states to determine if omniscient states result in extreme or unique values. Omniscience has the potential to be the optimal cognitive state if omniscient animals have movements or energetics to one extreme compared to other cognitive states. For instance, if omniscient animals have the shortest or longest moves, omniscience could confer the greatest fitness. If omniscient animals have the highest net energy gain, omniscience has the potential to be the most optimal cognitive state. If movements or energetics of omniscient animals are indistinguishable from other cognitive states, it is doubtful that omniscience confers an adaptive advantage.

METHODS

I simulated local movements as described in chapter 3. In addition, in every time step, resources renewed for every food patch as $F_{t+1} = F_t + (F_t * r)$ where F_t is the food value at time t and r is a renewal rate of 0.0001. This renewal rate created a slow renewal relative to the patch consumption rate, as in natural systems; yet allowed food to renew enough during the 550 time steps of each simulation that animals would revisit the cells (because food was not depleted to low values). Food patches could not be depleted below 0.01 food units nor could they renew above 20 food units/cell.

I simulated 5 cognitive states: omniscience, limited spatial information, limited temporal information, spatial ignorance, and temporal ignorance. When omniscient, the virtual animal knew the foraging costs and benefits on the landscape, such as travel cost to every cell and the exact amount of food in every cell.

Limited spatial information constricted animals to knowing only cells within a radius of the occupied cell. Animals had no knowledge about the cells outside their range of information and ascribed a food value of the global mean to those cells. The global mean was the mean for all cells on the landscape, including those cells with no food.

Limited temporal information constrained the animals to knowing food values for recently visited cells only. The animals assumed a global mean for the food value of all other cells. The animals knew the travel cost to all cells on the landscape. With time, memory of food value decayed exponentially as $F_t = F_a \cdot \exp^{-\delta T}$ where F_t is the food value (in food units) at time t, F_a is the actual food value (in food units), T is time elapsed and δ is the memory decay rate. Decay rates were 0.0001 to 0.0009 (increments of 0.0001), 0.001 to 0.009 (increments of 0.001), and 0.01 to 0.05 (increments of 0.01). Because animals had to visit patches to have knowledge, decay began after 50 time steps. See Table 5.1 for parameter values.

In the spatial ignorance model, the animals were ignorant of all food values so they moved in random directions and distances for up to the length of the entire landscape. I simulated distances ranging from 0 – 100 in increments of 1.

In the temporal ignorance model, the animals were ignorant of when to move so they moved at random times to the cell with the highest net value. I simulated a range of probabilities of movement from 0 to 1.0 in increments of 0.1.

I quantified movements as the number of moves and move length. Moves were defined as travel between 2 consecutive locations (Chapter 2, Turchin 1998). Home range size was measured as the number of cells in which an animal foraged and as a minimum convex polygon (Powell 2000). Intensity of use was calculated as the ratio of the path length to the square root of the area used (Chapter 2, Loretto and Vieira 2005). Large values represented high intensity of use while small values represent low intensity of use.

Amount of food consumed, travel costs, and net energy (food consumed discounted by travel costs) were calculated, each in food units. Because memory decay started after 50 time steps, movements and movement energetics were calculated using only the last 500 time steps for all simulations. Because the simulations were stochastic, mean movement and energetic values were calculated from 200 simulations.

The relative advantage of cognitive states was determined by comparing movements and energetics of omniscient animals to those with cognitive constraints to determine if extreme or unique responses resulted from omniscience. Extreme movements and energetics were defined as longest, shortest, least, or most. Movements and energetics were deemed unique if the movements or energetics for omniscient animals were < or > 10% of the values for animals with constrained cognition.

RESULTS

Effects of cognitive states on move lengths

As the radius of knowledge increased from 0, move length increased then decreased, then increased to a plateau (Fig. 5.1a) Omniscient animals (animals whose radius of knowledge was 100) did not move any farther than animals that had a radius of knowledge of at least 10. An increase in decay rate caused move length to decrease exponentially until a point at which further increases in decay rate did not affect move length (Fig. 5.1b). Omniscient animals (with a memory decay rate of 0) moved the farthest. When animals were ignorant spatially and moved by choosing travel distance from a random distribution, as the upper limit of the random distribution increased, move length was nearly constant (Fig. 5.1c). When animals were ignorant temporally and assessed whether or not to move based on a probability of 0 to 1, move length increased monotonically as probability of moving decreased (Fig. 5.1d).

Moves were shortest when animals had rapid memory decay (e.g., $\delta = 0.001$). Moves were longest when animals were spatially ignorant and moved large distances (e.g., >2). Limited cognitive states such as limited spatial knowledge (~>10) and temporal ignorance (for all ranges of temporal ignorance ~>0.01) and spatial ignorance (probability of moving ~2), resulted in move lengths that were comparable to move lengths of omniscient animals.

Effects of cognitive states on number of moves

When knowledge was limited spatially, number of moves decreased initially as knowledge increased, then increased and stabilized (Fig. 5.2a). Animals that knew the values of cells in at least a radius of 10 cells, did not move any farther than omniscient animals. When knowledge was limited temporally, number of moves decreased initially as knowledge increased, then increased and stabilized (Fig. 5.2b). Omniscient animals (with a memory decay rate of 0) moved the most number of times. When animals were ignorant spatially, number of moves decreased slightly as random distance increased (Fig. 5.2c).

When animals were ignorant temporally, number of moves increased monotonically with probability of moving (Fig. 5.2d).

A low chance of moving (e.g., $p = 0.1$) and limited spatial information (radius of knowledge = 3 or 4) constrained the number of moves the most. Moving random distances >10 caused the most number of moves. Omniscient animals moved approximately the same number of times as animals foraging by other strategies (radius > 10 and $p > 1.0$). Therefore, omniscient animals did not move the most or least, nor a unique number of times.

Effects of cognitive states on home range size and use

Home range size, as measured by a minimum convex polygon, increased as spatial knowledge increased until around a radius of 20 cell widths (Fig. 5.3a). From a radius of knowledge of 20 cells to omniscience (a radius of knowledge of 100 cells), home range size did not increase any further. Home range size dropped rapidly as memory decay increased, increased slightly, and then stabilized (Fig. 5.3b). Home range size correlated positively with distance of random movements (Fig. 5.3c). Home range size increased monotonically as probability of moving increased (Fig. 5.3d).

Animals that had limited spatial knowledge, memory decay (e.g., $\delta = 0.003$ - 0.005), a low chance of moving, and that moved short random distances (e.g., 2 or 3 cell widths) had the smallest home ranges. Moving to random, distant locations was the only cognitive condition that resulted in home range sizes larger than omniscient animals. All degrees of memory decay resulted in home ranges smaller than the home ranges of omniscient animals. Home range size was similar for animals that were omniscient, knew their neighboring cells in radius >20, moved at random times (~1), and moved to random locations (> 20 cell widths).

As animals became less spatially ignorant, the number of cells in which they foraged decreased initially, then increased and stabilized (Fig. 5.3a). As animals' memories decayed, the number of cells in which they foraged decreased initially, then increased and stabilized (Fig. 5.3b). As the random distance of moves increased, number of foraging cells increased initially, then decreased slightly (Fig. 5.3c). As the probability of moving increased, the number of cells in which animals foraged increased slightly (Fig. 5.3d).

Animals that had limited radii of knowledge (~ 4 - 5 cells), those that experienced memory decay (δ = 0.002 - 0.004), and had a low chance of moving (0.01) foraged in the fewest cells while animals that foraged by moving to random locations foraged in the most cells. Omniscient animals foraged in a number of cells similar to animals that were limited spatially (>10 neighboring cell widths), had a memory decay rate > 0.2, had ~ 1.0 chance of moving, and animals that moved a large random radius (~100).

When animals had limited radii of knowledge, they used their home ranges more intensely than animals that had a greater radius of knowledge, including omniscient animals (Fig. 5.4a). Animals with a very low memory and omniscient animals with no memory decay used their home ranges the least intensely (Fig. 5.4b). As memory decay increased, intensity of use increased, then decreased before stabilizing at a value approximately equal to that of omniscient animals. Intensity of use correlated positively with random distance of moving (Fig. 5.4c). Intensity of use increased as probability of moving increased (Fig. 5.4d). Intensity of use was not calculated for $p = 0$ because it is meaningless to discuss intensity of use when an animal does not move.

Animals that moved at random times used space least intensely. Animals that had no spatial information used their home ranges most intensely. When probability of moving was 1, intensity of use reached the intensity of use displayed by omniscient animals. When animals moved to a random distance of approximately 20 cells, their intensity of use was similar to that of omniscient animals.

Effects of cognitive states on energetics

As the radius of knowledge increased towards omniscience, consumption amount initially increased, decreased, then increased and stabilized (Fig. 5.5a). As memory decayed from omniscience, consumption amount decreased and then stabilized (Fig. 5.5b). The distance of random movements had no effect on consumption amount (Fig. 5.5c). As the probability of moving increased, consumption amount increased and then stabilized (Fig. 5.5d).

As the radius of knowledge increased towards omniscience, travel cost initially increased, decreased, then increased and stabilized (Fig. 5.5a). As memory decayed from omniscience, travel cost decreased and then stabilized (Fig. 5.5b). Distance of random movements correlated positively with travel cost (Fig. 5.5c). Travel cost increased monotonically with probability of moving (Fig. 5.5d).

As the radius of knowledge increased towards omniscience, net energy initially increased, decreased, then increased and stabilized (Fig. 5.5a). As memory decayed from omniscience, net energy increased slightly, decreased and then stabilized (Fig. 5.5b). Distance of random movements correlated negatively with net energy (Fig. 5.5c). As the probability of moving increased, net energy increased, peaked at 0.2 and then slowly decreased (Fig. 5.5d).

No animals were able to consume more food than omniscient animals, although limited temporal knowledge could result in consuming at least as much as an omniscient animal. Animals with limited or no temporal knowledge consumed at least the same amount of food as did omniscient animals. All four cognitive constraints could result in less food consumption than when animals were omniscient.

Animals with memory decay experienced the lowest travel costs while animals that moved random distances experienced the greatest travel costs. Animals that had a limited spatial cognition (radius of knowledge > 10) and animals that had a high probability of moving at random times (p = 1.0) had travel costs similar to the travel costs of omniscient animals.

Animals that moved random distances had the lowest gain in net energy, and it was negative. Animals that experienced rapid memory decay also had a negative net energy gain. Animals with limited spatial knowledge (radius > 20) could gain the same net energy during foraging as omniscient animals. Animals that were temporally ignorant and had a low chance of moving (e.g., 0.2) could gain more energy than omniscient animals.

The same general results occurred when food was distributed randomly and at different densities.

DISCUSSION

Two general classes of predictions can be made, predictions among values for a single cognitive state and predictions among multiple cognitive states. An example of a prediction from the 1st class is: “Move lengths are longer when memory decays rapidly than when memory decays slowly.” An example of a prediction from the 2nd class is: “Animals that experience memory decay have shorter moves than omniscient animals.” Both types of predictions are included in the following discussion.

Effects of cognitive states on move lengths

After a point, despite increases in the radius of knowledge, animals cannot afford to travel further because travel costs constrain movements. Therefore, animals with limited radii of knowledge travel the same distance as omniscient animals, but spatially limited animals never move farther or have more moves than omniscient animals.

High rates of memory decay result in shorter moves than when decay rates were low because high decay rates depressed the perceived food value of patches and constricted animals to patches that were more recently visited even if other patches had greater net values. Thus, animals move fewer times and less distance when their memory decayed. When memory decays and animals choose locations based on their memories, move lengths and number of moves are shorter and fewer than for omniscient animals.

Temporal ignorance (moving at random times) does not affect move length because the time of moving does not affect where animals move. Temporal ignorance affected the number of moves because, as probability of moving increased, animals moved more often, increasing the number of moves. Real omniscient animals have less than 100% chance of moving when travel costs are relatively high or food abundance is relatively low. Therefore, temporally ignorant animals can move more often than omniscient animals.

Animals that moved to distant random locations (spatially ignorant) moved farther than animals constrained to moving to close random locations and, thus, had longer moves. The rate of change in move length decreased as random distance increased because move length was bounded by landscape size. Because moving to random locations was not dependent on cell values, spatial ignorance resulted in the longest moves. Therefore, real ignorant animals could move farther than omniscient animals. Omniscience does not result in the shortest or longest move lengths and the relationship among moves from different cognitive states is also dynamic. Number of moves is not affected by the location to which animals move, therefore number of moves was not affected by spatial ignorance.

Effects of cognitive states on home range size and use

When home range was measured as a minimum convex polygon, random movements did not produce the largest home ranges because random movements had equal opportunity to move in any direction. Animals that did not move randomly were less likely to move back in the direction from which they came because they had depleted the food. Home range size was small for animals with memory decay because they were constrained to a smaller area by their short moves. Home range size was small for temporally ignorant animals that had a low chance of moving because they seldom moved.

When measured by the number of cells in which animals foraged, animals that moved random distances had the largest home ranges because the animals could move anywhere. Home range size was the smallest when memory decayed because the animals were limited by past experiences and could not move to new home range. Home range size was also small when animals had a low chance of moving because they seldom moved.

Because animals that move to random places are more likely to move back and forth over the same area, random movers have a higher intensity of use of their home ranges than non-random movers. Memory decay constrained animals to an area, which increased their intensity of use of their home range. Likewise, animals with limited spatial knowledge were constrained to a smaller area than omniscient animals, thereby increasing their intensity of use. When animals were temporally ignorant and had a low probability of moving, intensity of use decreased because the animals were not moving.

Effects of cognitive states on energetics

Amount consumed, travel cost and net energy were direct results of numbers of moves and move lengths as well as the amount of food remaining in an occupied cell. Animals that moved very little consumed all available food and in subsequent time steps had no food left to consume, so not moving is a poor strategy when food intake should be maximized. Moving to random cells was the poorest strategy for maximizing food consumption and minimizing travel costs. Knowing where food is located would be selected for more strongly than when to move.

The value of omniscience

Partial spatial information was as good as full spatial information when travel costs prohibit traveling farther than the range of spatial information. When animals were temporally ignorant and the probability of movement was high, model animal movements were as efficient as when animals were omniscient. Therefore, movements under cognitive constraints with the values just outlined were the same as movements by omniscient animals.

Animals under cognitive constraints can function as well as omniscient animals because the cognitive constraints are not more constraining than other constraints on omniscient animals. If maximizing or minimizing movement distance or frequency allows an animal to be the most fit, omniscient animals are not the most fit under this model.

Some animals might be most fit if they maximize food consumption. This life history trait could be due to poor forage quality, variable forage, quick gut passage or needing a variety of food types. Animals do not have to be omniscient to maximize consumption. Whether animals were omniscient, had limited temporal information, had limited spatial information or were temporally ignorant they consumed the same amount of food.

Some animals might need to minimize travel costs, especially where cost is a surrogate for predation or other risk associated with travel. In this case, omniscience about food is not the best cognitive state. Limited temporal knowledge incurred by memory decay, limited spatial knowledge of neighboring cells, and random temporal movements all incurred less travel cost than omniscience.

If maximizing net energy is the most important correlate with fitness, as is assumed in many foraging models, omniscience is still not the optimal cognitive state. Movements arising from moving at random times, from limited temporal knowledge, and from limited spatial knowledge can do better than omniscience. In fact, if some resource minimum were all that is required, even rapid memory decay would suffice. Thus, obtaining a minimum can be achieved without omniscience.

Therefore, animals do not have to be omniscient to have optimal behaviors (whether extreme or unique). Omniscience would not necessarily be selected for based on its effects on movement behaviors and energetics. Furthermore, given that natural selection might select against large or complex brains, it is reasonable to assume that animals may not be omniscient. Similarly, limited attention, another cognitive constraint, can be optimal for foraging animals (Clark and Dukas 2003). Granted, these assessments are only for the model described in this paper. Animals with even more complex cognitive abilities, like the ability to solve the traveling salesman problem, might benefit from omniscience. The field of cognitive ecology would benefit from future research exploring the degree of cognitive ability that is selected.

Interestingly, cognitive constraints might increase the complexity of biological processes. For instance, lack of omniscience has been postulated to account for biological diversity through the creation of cognitive niches (Beecham 2001). Lack of necessity for omniscience might free energetically expensive brain tissue to be applied towards other cognitive tasks such as avoiding predation, competing successfully and finding mates. If animals do have cognitive constraints on their movements, these constraints might also affect distribution and population density on the landscape. In this case, cognitive constraints should be considered when predicting population dynamics.

The relationship among or within movements due to cognitive state might change if animals change foraging rules. A significant change in memory decay rate may result in animals switching to random movements. Similarly, when information diminishes from being complete to limited to non-existent, animals might change foraging rules. Further investigation, including testing these predictions, should be conducted. Also, continued work in modeling will elucidate how foraging rules should change in response to changes in information.

Application of results

In field studies, movements are ascribed often to food abundance or foraging rules. For instance, a negative correlation has been postulated (McNab 1963) and supported between home range size and food abundance (Sullivan et al. 1983, Joshi et al. 1995, Albernaz and Magnusson 1999, Valenzuela and Ceballos 2000). Cognitive state is credited rarely with changes in movements. An individual animal's cognitive capabilities are variable and develop as an animal develops. Juveniles of long-lived animals that are slow to reach sexual maturation do not have the same cognitive abilities as adults. Even adult animals' cognitive abilities change seasonally as evidenced by seasonal atrophy of the hippocampus in birds (Clayton et al. 1997). Even if an individual's cognitive abilities are constant, the changing environment may have the same functional effect on an animal's cognitive abilities. My results show that cognitive state can affect movements and should be considered when explaining movements.

Finally, cognitive state should be considered when modeling movements. Movement models tend to either assume that animals are ignorant (e.g., Austin et al. 2004) or omniscient (e.g., Russell et al. 2003). The results from simulations are affected by the degree of information that an animal possesses. In some cases, excluding or including accurate information known by an animal in a simulation may alter the outcomes of movement models.

CONCLUSIONS

Each of the movements measured here have real biological implications for the animals that are moving. Move lengths are results of distances between resources, the rate at which animals consume resources, predation risk, dispersal success, and other aspects of animals' natural history. Likewise, home range size is a product of resource distribution (Johnson et al. 2002) and mating structure (polygamous or monogamous) while intensity of use is shaped by resource renewal rates and other aspects of an animal's natural history.

Understanding cognitive limitations should be the first step towards understanding behavior (Yoerg 1991, Curio 1994). In this paper, cognitive limitations are invoked to explain variation in movements given constant food abundance, food distribution and foraging rules. I demonstrated several important implications with these simulations: 1) cognitive states affect movements, 2) cognitive states affect energetics through movements, 3) cognitive state is an important consideration when modeling animal movement, and 4) omniscience might not be the cognitive state for which animals are most strongly selected due to the lack of behavioral and energetic advantage it confers and the tendency to select against brains which are metabolically expensive.

My hypothesis that cognitively constrained animals can be as fit as omniscient animals should be tested with laboratory and field data. My hypothesis encourages incorporation of cognitive constraints into ethology and behavioral ecology.

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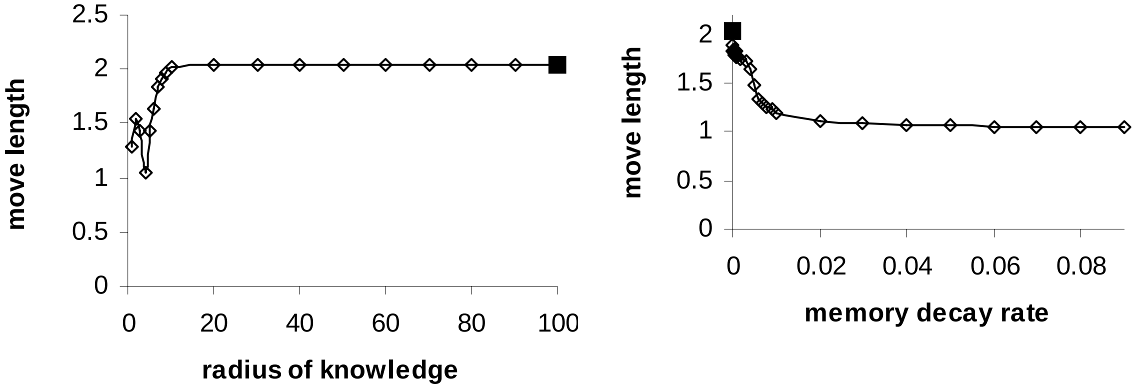
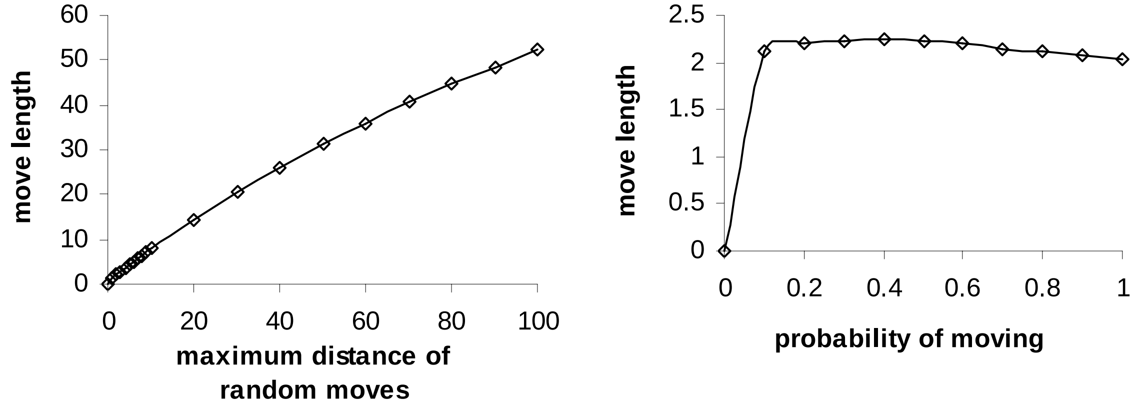
TABLE 5.1. Basic parameters and values underlying the simulations in which the effects of cognitive states and the effects of omniscience were examined.

Parameter	**value**
number of food patches	624
time steps (t)	550 time steps
mean food value (F)	10
consumed	0.9 food units/time step
min food/patch	0.1 food units
max food/patch	20 food units
travel cost	0.2 food units/cell
renewal rate (r)	0.0001
decay began	after 50 time steps
movements calculated	after 50 time steps
limited spatial information	knew neighboring cells only (1-10, 20-100, in increments of 10)
limited temporal information	memory decayed (δ = 0.0001-0.0009, 0.001-0.009, 0.01-0.09)
ignorant spatially	moved random distances (0-100 in increments of 1)
ignorant temporally	random chance of moving (0-1 in increments of 0.1)



a) limited spatially

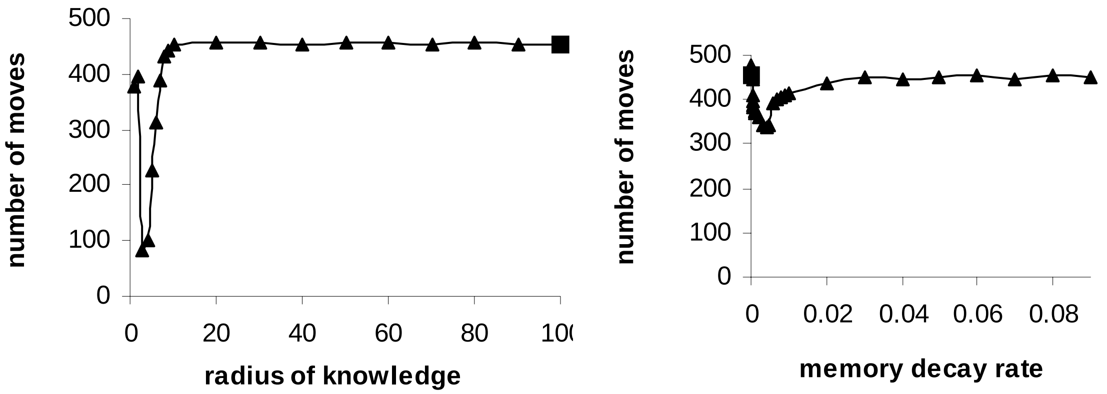
b) limited temporally



c) spatially ignorant

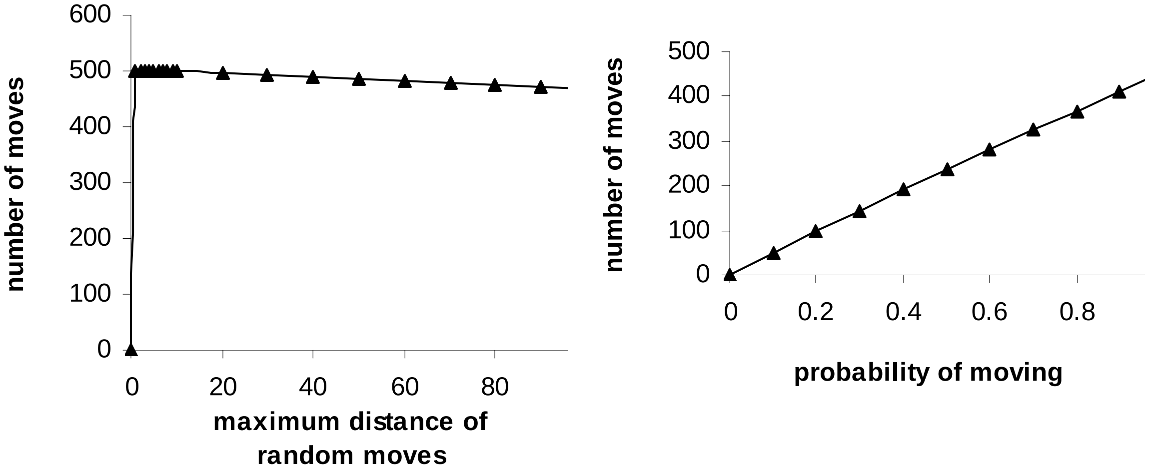
d) temporally ignorant

FIG. 5.1. Move length when information is (a) limited spatially, (b) limited temporally, (c) unknown spatially (movement distances are from a random distribution), and (d) unknown temporally (movement times are chosen from a probability). Animals were omniscient (marked by a solid square) when (a) the radius of knowledge was 100, and (b) decay was 0.



a) limited spatially

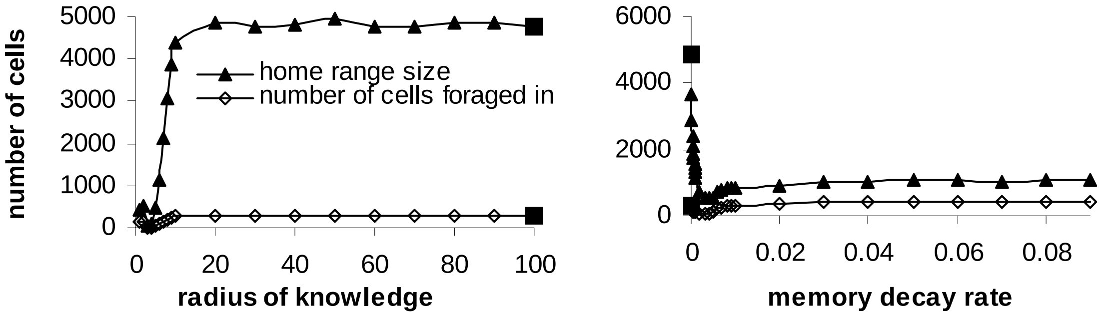
b) limited temporally



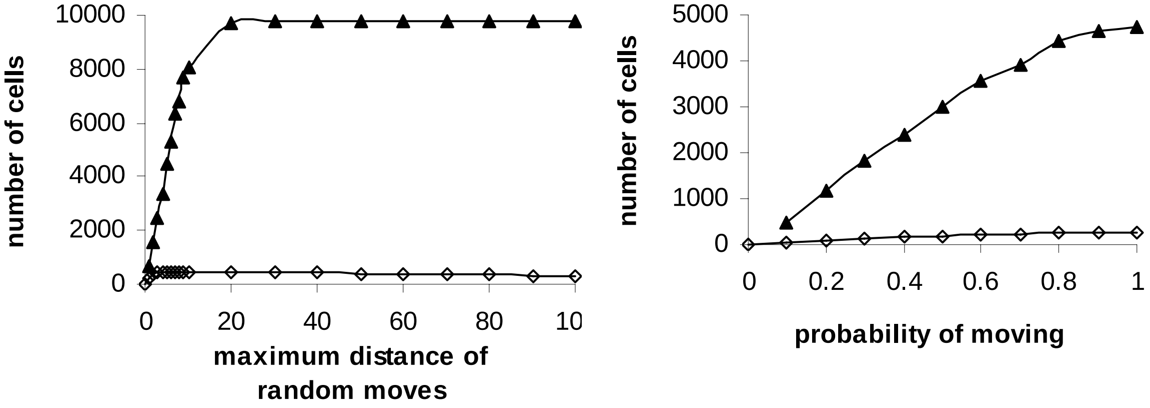
c) spatially ignorant

d) temporally ignorant

FIG. 5.2. Number of moves when information is (a) limited spatially, (b) limited temporally, (c) unknown spatially (movement distances are from a random distribution), and (d) unknown temporally (movement times are chosen from a probability). Animals were omniscient (marked by a solid square) when (a) the radius of knowledge was 100, and (b) decay was 0.

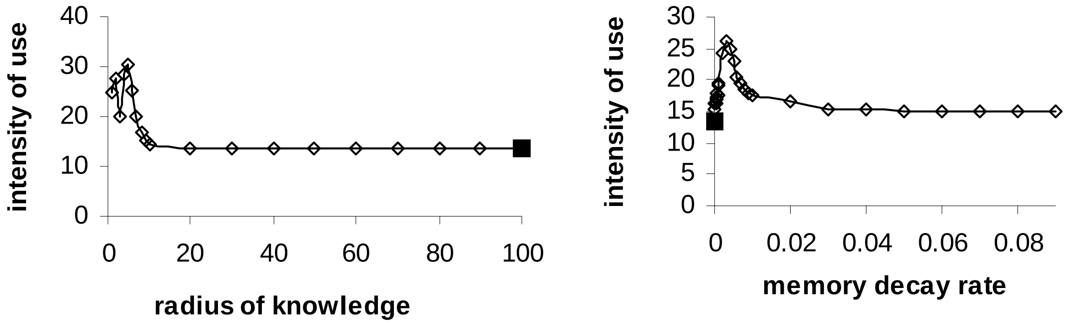

a) limited spatially

b) limited temporally

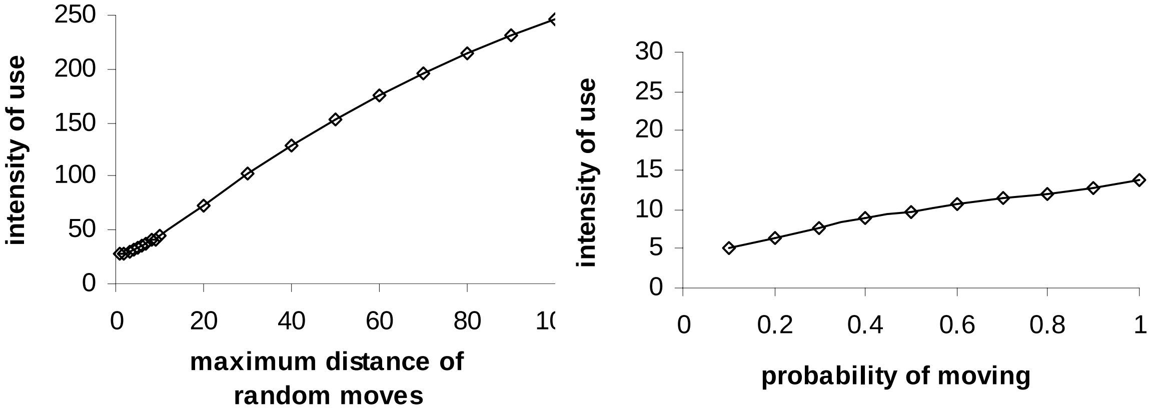

c) spatially ignorant

d) temporally ignorant

FIG. 5.3. Home range size as measured by the number of cells in which animals foraged and a minimum convex polygon. Information is (a) limited spatially, (b) limited temporally, (c) unknown spatially (movement distances are from a random distribution, and (d) unknown temporally (movement times are chosen from a probability). Animals were omniscient (marked by a solid square) when (a) the radius of knowledge was 100, and (b) decay was 0.


a) limited spatially

b) limited temporally

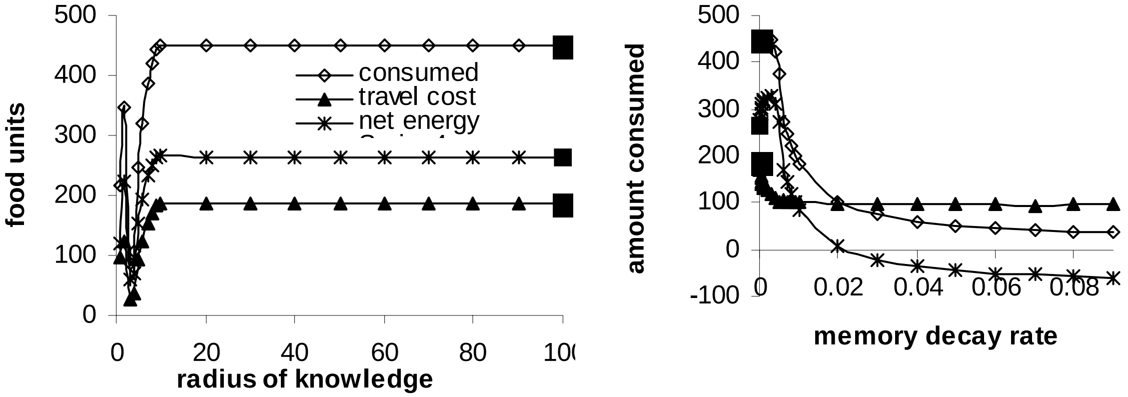

c) spatially ignorant

d) temporally ignorant

FIG. 5.4. Intensity of use calculated as path length/(area used$^{1/2}$). High intensity of use indicates intense use of an area. Information is (a) limited spatially, (b) limited temporally, (c) unknown spatially (movement distances are from a random distribution), and (d) unknown temporally (movement times are chosen from a probability). Animals were omniscient (marked by a solid square) when (a) the radius of knowledge was 100, and (b) decay was 0.

a) limited spatially

b) limited temporally



c) spatially ignorant

d) temporally ignorant

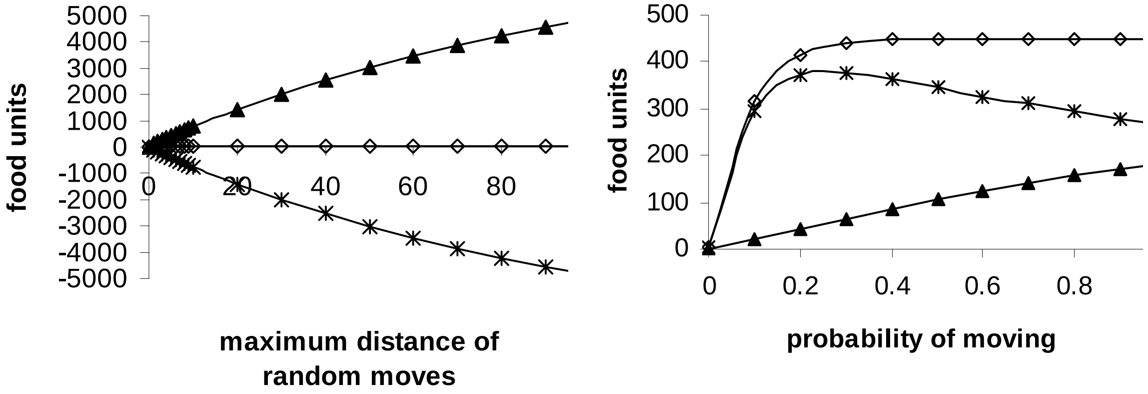


FIG. 5.5. Amount consumed, travel cost and net energy when information is (a) limited spatially, (b) limited temporally, (c) unknown spatially (movement distances are from a random distribution), and (d) unknown temporally (movement times are chosen from a probability). Amount consumed, travel cost, and net energy are measured in food units or energy. Consumption and travel cost of omniscient animals (marked by a solid square) occurred when (a) the radius of knowledge was 100, and (b) decay was 0.

CHAPTER 6: FOOD PATCH RICHNESS AND DENSITY PARTIALLY EXPLAIN TRAVEL RATE OF BLACK BEARS (*URSUS AMERICANUS*)

ABSTRACT.

Field data on black bear travel rates show complex relationships with food abundance, correlating positively with abundance (total biomass per area) in spring, correlating negatively in autumn, and not correlating in summer. My work in chapter 3 suggests that this complexity might be explained by separating the causes of food abundance into food patch richness (biomass per food patch) and density (number of food patches per area) of the primary food item. My model predicted generally that animals' travel rates should correlate positively with food patch richness and negatively with food patch density. In spring, travel rate of black bears did not respond to patch richness, but did respond to food patch density as predicted. In summer, travel rates responded only to patch richness and responded as predicted. In autumn, travel rates responded to patch richness and density but only patch density as predicted. These results are broadly interesting because they demonstrate that animals may respond to only patch richness, only patch density or both patch richness and density.

Key words: acorns; berries; black bear; food abundance; hard mast; movement; path length; squawroot; travel rate; Ursus americanus.

INTRODUCTION

Generally, bear (*Ursidae*) movement is affected by energetics stemming from body size (Smith and Pelton 1990) and foraging (Clevenger et al. 1990, Wong et al. 2004). As a result, bear home range size correlates negatively with food diversity (Smith and Pelton 1990) availability (Garshelis et al. 1983, McLoughlin et al. 2000), and habitat quality (McLoughlin et al. 2003). In particular, bears travel farther when hard mast crops are poor (Garshelis and Pelton 1981, Rogers 1987, Smith and Pelton 1990). Yet bears do not always move as predicted by the habitat-productivity hypothesis. Movements of a brown bear correlated positively and negatively with food abundance (Clevenger et al. 1990). Home range and travel rates of black bears in Pisgah Bear Sanctuary in western North Carolina (USA) correlated positively with spring food, did not correlate with summer food, and correlated negatively with autumn food (Powell et al. 1997, Sorensen 1997).

Bear food in Pisgah Bear Sanctuary

The primary spring food for bears in Pisgah Bear Sanctuary is squawroot (*Conopholis americana*), a perennial plant that parasitizes red oaks (*Quercus spp.*) (Percival 1931, Haynes 1971). Although squawroot is high in carbohydrates (Seibert and Pelton 1994, Kimball et al. 1998, Inman and Pelton 2002), it is a poor source of nutrition (Seibert and Pelton 1994). Few fruits are produced per plant relative to bears' energetic needs, bears do not readily digest the protective coat around the fruit (Seibert and Pelton 1994), and bears lose weight during spring and early summer foraging (Jonkel and Cowan 1971, Eagle and Pelton 1983). As the amount of squawroot fruit per plant is fairly constant, squawroot abundance on a landscape varies by changes in the number of plants (i.e., food sites). Still, squawroot plants are small (average shoot height = 12.58 cm, (Percival 1931)), so bears probably do not respond to the scale of squawroot plants. Bears may respond to squawroot on the scale of patches of squawroot under the red oak trees they parasitize. Squawroot production in Pisgah was patchy (Powell and Seaman 1990) and fairly common.

During the summer, blueberries (*Vaccinium spp.*), huckleberries (*Gaylusacchia spp.*), blackberries (*Rubus spp.*) and service berries (*Amelanchier spp.*) are primary foods for black bears in Pisgah. The number of berry patches is fairly constant throughout a season; few new berry patches grow and die during berry season. Instead, food abundance changes when biomass of berries on each bush changes. Berry production in Pisgah was also patchy (Powell and Seaman 1990, Reynolds 2006).

During autumn, bears depend on hard mast from red and white oak (*Quercus sp.*), beech (*Fagus grandifolia*) and hickory (*Carya sp.*) trees as the primary component of their diet. Oak tree stands occur more frequently in Pisgah than the rest of the stands combined (Reynolds 2006).

Bears' knowledge about food locations

Cognitive constraints and changing environments can limit what animals know about food patches. Bears are long-lived, faithful to their annual home ranges (Amstrup and Beecham 1976, Powell et al. 1997), shift their home ranges among seasons in response to changes in seasonal food locations (Garshelis and Pelton 1981), travel long distances (14 - 83 km) to find food when food is scarce (Rogers 1987), and female offspring occupy the same home range or feed in the same locations as did their mothers (Garshelis and Pelton 1981, Rogers 1987). Therefore, I assume that bears have few cognitive constraints in regards to food locations and substantial knowledge about food locations in their home ranges [e.g., cognitive maps, (Gallistel 1989)]. Bears' food sites tends to be spatially stable during a season and across a couple years. Although clearcuts in the Pisgah Bear Sanctuary age, food productivity changes gradually from year to year (Reynolds 2006) allowing bears time to learn the changes. Therefore, bears can rely on the environment remaining fairly stable and food occupying the same locations and offering similar amounts of nutrition from day to day and even from year to year.

Foraging rules and bear foraging behavior

No field data tests the rules by which bears forage. Still, bears respond to topography (Powell and Mitchell 1998), macrohabitats (Mitchell et al. 2002, Mitchell and Powell 2003), and microsites (Mattson 1997). Bears choose food types (Kimball et al. 1998, Gende et al. 2004), engage in 3rd order habitat selection (Costello and Sage 1994, Samson and Huot 1998, McLoughlin et al. 2002, Reynolds 2006), and forage at locations that offer optimal energetic return (Mattson 1997). Therefore, bears do not move to random locations in their home ranges. Animals may move to food patches that are the closest or food patches that offer the highest net energy. Black bears in the Pisgah National Forest do not share their range with interspecific competitors such as brown bears (*Ursus horribilis*), so they can afford to adopt the strategy of moving among high yield food patches, which are easy to harvest. Furthermore, bears are limited by bite intake (Welch et al. 1997) and it is expensive energetically for them to move, so bears may forage more efficiently by moving to food patches that offer the highest net value.

Foraging efficiency is increased by remembering food patch locations and contents, therefore bears probably do not leave food patches at random times. Leaving at a fixed time is an optimal foraging strategy when food abundance is not known (Iwasa et al. 1981). Because food patches are spatiotemporally predictable and bears appear to remember food locations, bears probably do not leave after a fixed time. Bears do not forage until they deplete berry patches (Pearson 1975, Rogers 1987), because they are limited by bite intake (Welch et al. 1997). Because of these limitations, bears may forage in a food patch until a giving up density when food is not abundant. For these reasons, bears probably do not leave after consuming a fixed number of items. Alternatively, bears may leave a patch when that patch no longer offers the highest energetic return. I modeled bears to go to patches with the highest net energy and remain there until the patch no longer offered the highest net energy.

Animals' foraging behavior depends on the spatial scale at which they forage (Ward and Saltz 1994, Morgan et al. 1997, Frair et al. 2005). The spatial scale at which bears assess the landscape is not well known, although it is known that bears use different criteria for 2nd and 3rd order selection (Johnson 1980, Reynolds 2006). A reasonable assumption is that bears assess the landscape on the scale of the size of berry patches. That is each patch is valued for itself and not averaged with neighboring habitat.

Hypotheses to explain the "paradoxical" movement of black bears in Pisgah

Sorensen (1997) hypothesized that, in Pisgah, bear movement could sometimes correlate positively and sometimes correlate negatively if seasonal food availability created conditions where, in some seasons, bears foraged on a negative energy budget and, in other seasons, bears foraged on a positive energy budget. Alternatively, it may be energetically optimal to gain the most weight at the end of their foraging cycle (McNamara et al. 1990) because it is energetically expensive to carry extra body weight (Witter and Cuthill 1993). Powell (in review) hypothesized and rejected that the cost of carrying body mass through annual foraging could cause home range sizes to be small in spring and large in autumn. Other empirical evidence also has not supported the hypothesis that animals should avoid gaining weight too early in a foraging cycle. (Lilliendahl 2002). Although Sorenson found some support for her hypotheses, scientific inquiry benefits from multiple hypotheses (Chamberlin 1890).

I hypothesize that bear movements may respond differently to food abundance arising from food patch richness (the amount of food per food patch) than food patch density (the number of food patches on a landscape). Whether bears respond to patch richness or density could account for bear movements correlating positively with food abundance in some seasons and negatively in other seasons. Here, I test hypotheses generated from my model (described in chapter 3) with bear movement and food abundance measured by patch density and richness.

METHODS

Study site

The 235 km^2 Pisgah Bear Sanctuary is located in the Pisgah National Forest in the southern Appalachian Mountains of western North Carolina, USA (Fig. 6.1). The sanctuary is closed to bear hunting and serves as a source to neighboring bear populations in the Pisgah National Forest (Powell et al. 1996). The Sanctuary is bordered by the Blue Ridge Parkway and other secondary roads and has several hiking trails and dirt roads running through it. Much of the sanctuary consists of uneven terrain, ranging from 650 m to nearly 1800 m in elevation. Often, fog shrouds the mountains in early morning and water runs through the rocky streams because of the 120 cm/year of rainfall (NOAA 2000). Temperatures range from 8.7°C in January to 25.4°C in July (NOAA 2000). Oak (*Quercus sp.),* tulip (*Liriodendron tulipifera*) and hemlock (*Tsuga sp.*) trees predominate. The understory comprises rhododendron (*Rhododendron sp.*) and mountain laurel (*Kalmia latifolia*) as well as the berry producing shrubs mentioned in the introduction.

Bear food

Sixty potential squawroot sampling sites were systematically identified across the Pisgah Bear Sanctuary in 1986. Of these, squawroot sampling sites were chosen due to proximity to roads and trails (usually < 1.0 km). Ten to 17 sites were surveyed annually in most successive years, depending on available time and not on squawroot abundance. At each site, 4 subsites were located 100 m in each cardinal direction from a central subsite. Squawroot was measured in May and June by collecting and weighing all parts of the squawroot plant that were above ground in a 10 m radius around the center of each subsite. Annual squawroot patch richness was calculated as the mean mass of squawroot per site with squawroot. Annual squawroot patch density was calculated as the percent of the sites that contained squawroot.

Berry sampling sites were identified systematically across the Pisgah Bear Sanctuary in 1986. Of these, potential berry sampling sites were identified as those that had at least one subsite with > 25% berry plant cover. Like the squawroot sites, each site consisted of a central subsite and 4 lateral subsites. Fourteen to 28 sites were visited each year. Again the number of sites that were sampled and the years of sampling depended on time available, not abundance. All berries were collected at each subsite with berries every 10 days from the beginning of berry production (end of June) to the end of berry production (end of August). Powell and Seaman (1990) provided more details on squawroot and berry sampling. Annual berry patch richness was calculated as the mean mass of berries for each site with berries. An index of berry patch density was calculated as the percent of subsites that produced berries.

Hard mast, the primary autumn food for black bears in Pisgah Bear Sanctuary, was indexed by the North Carolina Game Commission with Whitehead's (1969) method (M. D. Jones, North Carolina Game Commission, pers. comm.), which correlates with other hard mast indices (Perry 1999). Whitehead's index is based on the percent of the crown with acorns, the percent of the productive area of the crown that produced acorns, and the number of acorns on acorn producing twigs (Perry 1999) resulting in values from 0 to 10. Whitehead interpreted 0 - 2 as poor, 2 - 4 as fair, 4 -6 as good, and 6 to 8 as excellent production. The mean value for Whitehead's method for 1977 - 1988 in the Blue Ridge province of Georgia was 2.68 (Wentworth et al. 1992). Wentworth interpreted values ≤ 2 as poor, 2.01 – 3.0 as fair, and > 3.0 as good because index values rarely reach 10. Whitehead's index was calculated annually from at least 10 routes in western North Carolina for white oak, red oaks, hickory and beech. The mean index for all hard mast producing species was calculated annually from 1983 to 2001. The index value was interpreted as an index of hard mast patch richness. An index of the density of food patches was calculated as the number of sites that contained hard mast per the number of sites that were surveyed.

Bear travel rate

Between 1983 and 2001, black bears in Pisgah Bear Sanctuary were trapped with Aldrich foot snares modified for safety (Johnson and Pelton 1980), radio collared and tracked by triangulating usually 3 or more locations. Powell et al (1997) provided more details on trapping and radio tracking. I calculated path length as the distance between 2 consecutive triangulated locations. Because the time between locations was intermittent, I standardized path length as the path length per time, or travel rate (Chapter 2). Travel rates calculated from locations ≤ 8 hours apart correlated positively with the time elapsed between the 2 locations. Therefore, I used travel rates calculated from locations less than 8 hours apart.

Because the travel rates of bears in Pisgah Bear Sanctuary are affected by time of day (Sorensen 1997), I categorized 24 hour periods into 4 observation periods. The first observation period started at approximately 2300. Therefore the observation periods approximately represented night, dawn, day, and evening. Bear age class (Amstrup and Beecham 1976, Smith and Pelton 1990, Powell et al. 1997, Dobey et al. 2005) and sex

(Garshelis and Pelton 1981, Powell et al. 1997) can affect movement, so I analyzed just adult female bears.

Hypotheses

Hypotheses to explain bears' response to food patch richness and density were generated from the results of my model (Chapter 3). My model is general, not predicting exactly where patch richness or density changes from low to fair to high values. Acorn production and energy per ha in the study area was much higher than in northeastern Minnesota (United States of America) and the year of worst hard mast production was similar to mean energy/ha of hard mast in Minnesota (Powell and Seaman 1990). Still, it should not be assumed that bears in Pisgah have more mast available to them than bears in Minnesota because Pisgah presumably supports more wildlife biomass than is being supported by acorns in Minnesota. As the seasonal food data spans nearly 20 years, I assumed that bears perceived years of low and high richness and density as low and high. Because each year offered only one richness and density data point, I did not have enough data to test for observed thresholds and nonlinear responses, instead I only tested for linear changes in response to changes in food abundance.

I used a regression model with fixed and random effects (PROC MIXED in SAS V.8, SAS Institute, Cary NC) for each season to determine if individual bears, observation period, seasonal food patch richness and density, and an interaction between seasonal food patch richness and density significantly affected travel rate. I log transformed travel rate to normalize data. The categorical class of individual bear was treated as a random effect and I analyzed only seasons that had at least 20 travel rates.

RESULTS

Bear path lengths and travel rates

Mean sample size of path lengths per spring that had corresponding squawroot data was 114 (n=6, SD = 89.6) (Fig. 6.2a). Mean sample size of path lengths per summer that had corresponding berry data was 139.7 (n=11, SD = 62.1) (Fig. 6.2b). Mean sample size of path lengths per autumn that had corresponding hard mast data was 208.5 (n=10, SD = 190.5) (Fig. 6.2c).

When path lengths were standardized as travel rates (path length per elapsed time), mean spring travel rate for all spring seasons (x = 5.5 m/min, SE = 2.98, n=801) was not significantly different than summer travel rate for all summer seasons (x = 5.86 m/min, SE = 0.32, n = 1267) (2 tailed t-test, p = 0.466) (Fig. 6.3). Spring travel rate for all spring seasons was faster significantly than autumn travel rate for all autumn seasons (x = 4.95 m/min, SE = 0.115, n = 2086) (2 tailed t-test, p = 0.0017) and summer travel rate for all summer seasons was faster significantly than autumn travel rate for all autumn seasons (2 tailed t-test, p = 0.0296).

Bear food

Mean squawroot patch richness was 29.2 kg/ha (SD = 12.5, n = 9) (Fig. 6.3a). Mean squawroot patch density was 0.75 (SD = .15, n = 10) (Fig. 6.4a). Mean berry patch richness was 5.65 g/m^2 (SD = 3.1, n = 12) (Fig. 6.4b). Mean berry patch density was 0.91 (SD = 0.10, n = 12) (Fig. 6.4b). Mean hard mast patch richness index was 0.66 (SD

= 2.21, n=19) (Fig. 6.4c). Mean density of hard mast patches was 0.80 (SD = 0.07, n = 16, due to missing data for 1991, 1992 and 1996) (Fig. 6.4c).

Testing hypotheses

I tested my predictions for the effects of seasonal patch richness and density on movements for 6 spring seasons, 11 summer seasons, and 10 autumn seasons (Table 6.1). Movements for all adult female bears (Fig. 6.5) do not show predicted movements because individual status affected movements.

In spring, travel rate correlated positively with squawroot patch richness (0.01667, p = 0.45, PROC MIXED, SAS), squawroot density (1.2845, p = 0.06, PROC MIXED, SAS), and negatively with the interaction between squawroot richness and density (-0.01804, p = 0.46, PROC MIXED, SAS) (n = 728), but was only significant for density (Table 6.2).

In summer, travel rate correlated positively with berry patch richness (0.1180, p = 0.0082, PROC MIXED, SAS), berry patch density (0.2718, p < 0.33, PROC MIXED, SAS) and negatively with the interaction between berry patch richness and patch density (-0.1980, p = 0.0062, PROC MIXED, SAS) (n = 1267), but was only significant for richness and the interaction between density and richness (Table 6.2).

In autumn, travel rate correlated negatively and significantly with hard mast patch richness (-1.4980, p < 0.0001, PROC MIXED, SAS), hard mast patch density (-3.5021, p = 0.0030, PROC MIXED, SAS), and positively and significantly with the interaction between patch richness and density (1.6552, p = 0.0007, PROC MIXED, SAS) (n = 2083) (Table 6.2).

DISCUSSION

Travel rate

Spring and summer travel rate were the fastest while autumn travel rate was the slowest. These findings corroborate some studies of other black bear populations (Garshelis and Pelton 1981, Smith and Pelton 1990, Dobey et al. 2005), but conflict with other studies (Garshelis et al. 1983).

Travel rates can increase either due to bears traveling faster or spending more time traveling. If differences in seasonal travel rates are attributed to the time spent traveling, spring travel rates were probably the fastest because squawroot patches have less food per area than do berry or hard mast patches. Bears depleted squawroot patches and spent more time moving among food patches than when they fed on berries or mast. Autumn travel rates were probably the slowest because hard mast is more scattered spatially than berries and it takes bears longer to forage for loose acorns than a bunch of berries that where the berries are close to each other.

Effects of seasonal food patch richness and density on travel rate

Spring travel rate did not correlate significantly with squawroot patch richness. As Pisgah bears lost weight while foraging in spring (Powell et al. 1997) it is reasonable to assume that they forage on a negative energy budget. Squawroot patches contain relatively little squawroot compared to berry patches. Bears probably strip squawroot fruit from squawroot plants efficiently and spend little time in squawroot patches. So, it seems plausible that bears might not respond to squawroot patch richness. Alternatively, bears may not respond to squawroot patch richness because they also feed on colonial insects (Jonkel and Cowan 1971, Kasbohm et al. 1995) and other sources of animal protein during spring. Because density correlated positively with spring travel rate, travel rate was affected by squawroot density as predicted.

Berry patch richness correlated positively with summer travel rate while density did not correlate significantly with summer travel rate, it seems that berry patch richness is more important than berry patch density to bear movements. Bears probably could move fairly quickly and efficiently among berry patches because they distance among patches was smaller than the daily travel distance of bears. Foraging in a patch might require a relatively larger time investment. As bears spend more time in a patch and acquire more information, they probably forage more efficiently than when they first arrived in the patch. As a result, it would be disadvantageous for bears to move to new patches. Thus it is logical that bears respond to patch richness instead of patch density when foraging on berries.

Hard mast richness correlated negatively with autumn travel rate even though a positive correlation was predicted. Although no data exists for fall weight changes for bears in Pisgah (Powell et al. 1997), it is highly unlikely that the Pisgah bears would not try to maximize weight gain because low hard mast production affects negatively bear reproduction (Eiler et al. 1989, Elowe and Dodge 1989) and bears must gain enough weight during autumn to survive winter. Failure of bears to forage in response to patch richness as predicted by my model is evidence that bears did not forage according to the foraging rules that I modeled. As predicted, hard mast density correlated negatively with travel rate. Thus, bears responded to richness and density in autumn unlike spring or summer when they only respond to richness or density. Because acorn abundance from red and white oak trees (*Quercus spp.*) correlates to both density of masting oak trees and the abundance of acorns per tree (Healy et al. 1999, Greenberg and Parresol 2000), separating density and richness when analyzing the effects of acorn abundance is appropriate.

It is simplistic to think only one food affects movement in a season. The primary food may interact with other foods to affect movement (Garshelis and Pelton 1981). Furthermore, bears are opportunistic feeders and, when a primary food is low, they may replace it with other foods (Kasbohm et al. 1995). An assessment of other bear foods may help determine if bears respond to just their primary foods or are supplementing primary foods with alternative foods in times of food shortage.

Another complicating factor is that bears may respond to the current patch richness and density and probably the richness and density of a preceding period of time, for example, the previous week. Early in berry season bears might respond to the newly emerged rich food as if the patch richness was low, which it would be in the beginning. In addition, bears would have just been foraging on a negative energy budget, which may cause them to respond to abundant berries as if they were low. The response to early season berries could override the response to late season berries. Determining food abundance throughout the season (instead of once for the whole season) would help determine the temporal scale on which bears respond to food abundance. For example, do bears respond to food abundance for the previous day, week, or the entire season to that point in time? As bears adjust seasonal foraging in response to food abundance of previous seasons (Powell et al. 1997), it seems that bears probably adjust foraging within seasons. Also, bears move in response to a heterogeneous landscape, something that I did not model. Finally, individual bears were only observed for a couple of years and results could have been confounded by individual variation. Further testing of the hypotheses could be improved by following the same individuals over the course of the study.

Because richness and density was only calculated once each season, limited sample size for each season (6 spring, 11 summer, 10 fall) made it difficult to isolate the relationship of food abundance on travel rate. A small range of values for patch richness and density also complicated statistical analysis. By sampling food abundance throughout the season, sample size and range of values could be increased. Covariance between richness and density also made statistical analysis difficult. Unfortunately, in field settings, the covariance cannot be avoided.

As I hypothesized, patch richness and density both contributed to travel rate. Because only patch density contributed to spring movement, only patch richness contributed to summer movement, both richness and density contributed to fall movement, and richness and density have theoretically opposite effects on movement, it is possible that a mechanism for movements that sometimes correlate positively and sometimes negatively with food abundance can be found by breaking food abundance into richness and density. My data does not provide support for or refute either Sorensen's or Powell's hypotheses.

Foraging rules and cognitive constraints as explanations for observed bear travel rates

In chapter 4, my model demonstrated that departure rules such as deciding whether or not to leave at every time step, leaving at a fixed time, when the patch fell below the mean value of patches (according to Charnov's Marginal Value Theorem, Charnov 1976), and leaving at random times do not affect the general response of path length to patch richness. Using a giving up density as a departure rule, however, caused path length to correlate negatively with patch richness when patch richness is higher than the giving up density. It is possible that bears used a giving up density to decide when to leave a patch. My model also demonstrated when animals choose nearby food patches instead of patches with the highest net value, path length may correlate negatively with patch richness. Future research should investigate foraging rules as possible mechanism for affecting travel rate.

In chapter 5, my model showed that a small degree of spatial or temporal ignorance can result in movements that respond similarly to patch richness as movements by animals that know all food locations and how much food is at those locations. Even if bears do not know all food locations and the amount of food at each location, spatial and cognitive constraints may not have affected bear travel rate in Pisgah.

Wildlife Management

Berry abundance alone does not explain bear movement (summer, Powell et al. 1997). If only one measure of berry patch abundance can be obtained, berry patch density does the best at explaining travel rate of bears. Separating berry abundance into patch richness and density and using both does a better at explaining travel rate of bears than just patch richness. Bear biologists should measure berry patch density when seeking to explain the effects of food abundance on bear movement. Food abundance plays an integral role in not just movement, but also in growth and development of individuals, territorial behavior within populations, population dynamics, and community structure. Understanding the individual effects of food patch richness and density as well as their interactions is fundamental to understanding behavior and population dynamics, and can be applied to managing wildlife populations.

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Table 6.1. Seasons for which food data were calculated are denoted by SR (squawroot), B (berries), HM (hard mast). An asterisk (*) denotes that only richness could be calculated. **Bold** font indicates that at least 20 path lengths could also be calculated for that season. Therefore, bold food abbreviations denote the seasons for which both food and path length could be calculated.

1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
-	-	-	**SR**	**SR**	SR	-	-	-	-	SR	**SR**	**SR**	**SR**	-	-	-	**SR**	SR
-	-	-	**B**	**B**	**B**	**B**	**B**	-	-	**B**	**B**	**B**	**B**	-	-	**B**	**B**	B
HM	**HM**	**HM**	**HM**	HM	HM	**HM**	**HM**	HM*	HM*	**HM**	**HM**	**HM**	HM*	HM	HM	HM	**HM**	HM

TABLE 6.2. Coefficients from generalized linear models (PROC MIXED, SAS) testing the effects of seasonal food richness and density on travel rate of female black bears in Pisgah Bear Sanctuary from 1983 to 2000. Primarily, spring food was squawroot, summer food was berries, and autumn food was hard mast. Seasonal food patch richness and density were fixed effects while individual bear was treated as a random effect. All coefficients for seasonal foods were significant. Asterisks (*) indicate statistically significant results. **Bold** indicates that the direction of the observed effect corresponded to the direction of the predicted effect.

	Seasonal food patch richness	Seasonal food patch density	Interaction between patch richness and density
Spring	0.01667	**1.2845***	-0.01804
(n = 728)	(p = 0.45)	**(p = 0.06)**	(p = 0.46)
Summer	**0.1180***	0.2718	-0.1980*
(n = 1267)	**(p = 0.0082)**	(p = 0.33)	(p = 0.0062)
Autumn	-1.4980*	**-3.5021***	1.6552*
(n = 2083)	(p < 0.0001)	**(p = 0.0030)**	(p = 0.0007)

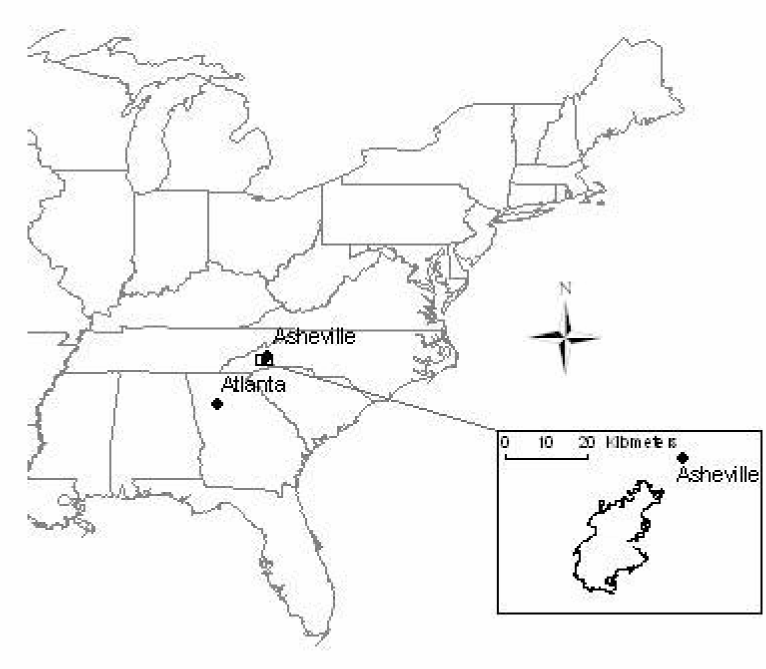

FIG. 6.1. Pisgah Bear Sanctuary is in western North Carolina, 8 km southwest of Asheville NC and 240 km northeast from Atlanta GA.

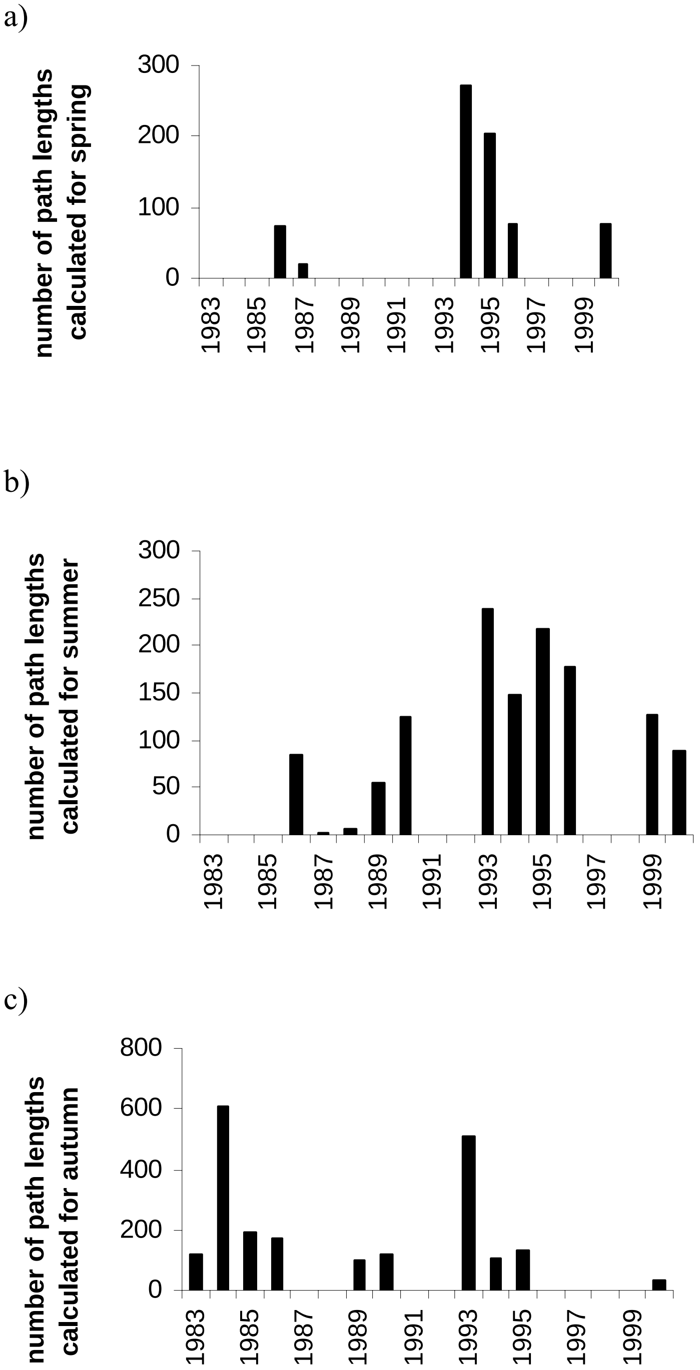

FIG. 6.2. Path length sample size for seasons that also had data on seasonal foods a) spring, b) summer, and c) autumn. Path lengths are for adult female black bears in Pisgah Bear Sanctuary (NC, USA).

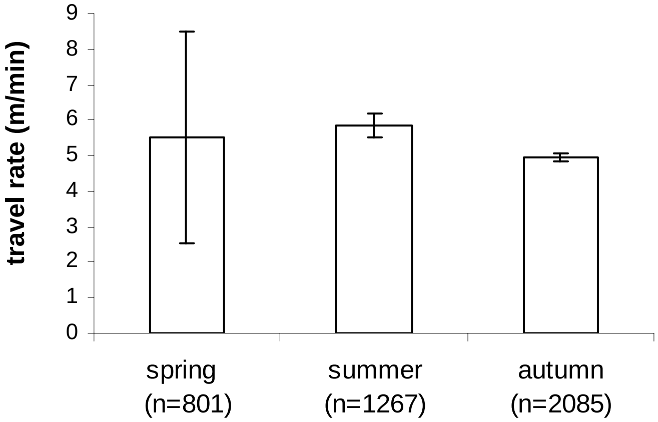

FIG. 6.3. Mean travel rate (m/min) with standard error bars of female black bears in Pisgah Bear Sanctuary 1981 - 2000 for spring, summer and autumn when at least 20 travel rates could be calculated for each season. Sample size for each season is under the season title. Mean spring and summer travel rates were not significantly different from each other (2 tailed t-test, p = 0.466), but both were significantly larger than mean autumn travel rate 2 tailed t-test, p = 0.0017, p = 0.0296).

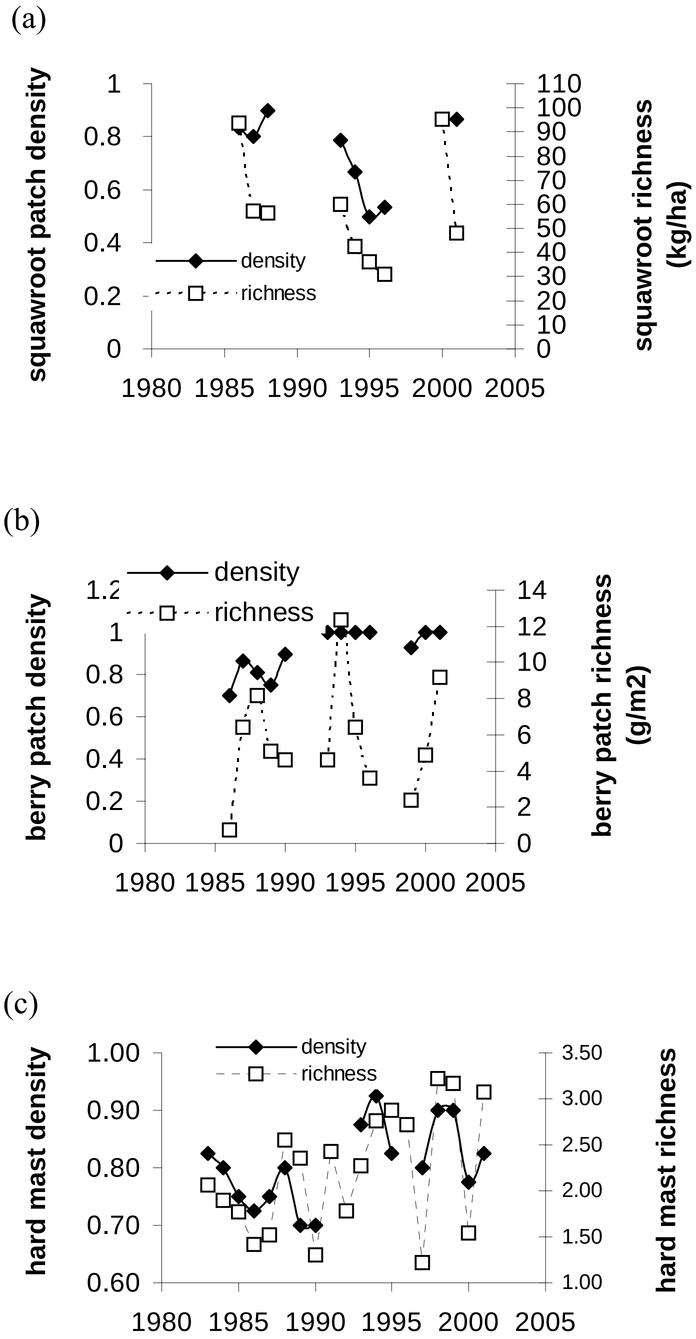

FIG. 6.4. Indices of food patch richness and density of each of the seasonal bear foods: (a) squawroot, a main spring food, (b) berries, a main summer food, and (c) hard mast, a main autumn food. Squawroot and berry richness indices were calculated as biomass/sampling site. Hard mast richness index was determined by estimating numbers of fruits per area on the trees. Density indices were calculated as the number of sites containing seasonal food per number of sampling sites. Food data was not calculated for all years due to time constraints. Data to calculate hard mast density for 1991, 1992 and 1996 was not available from the North Carolina Game Commission.

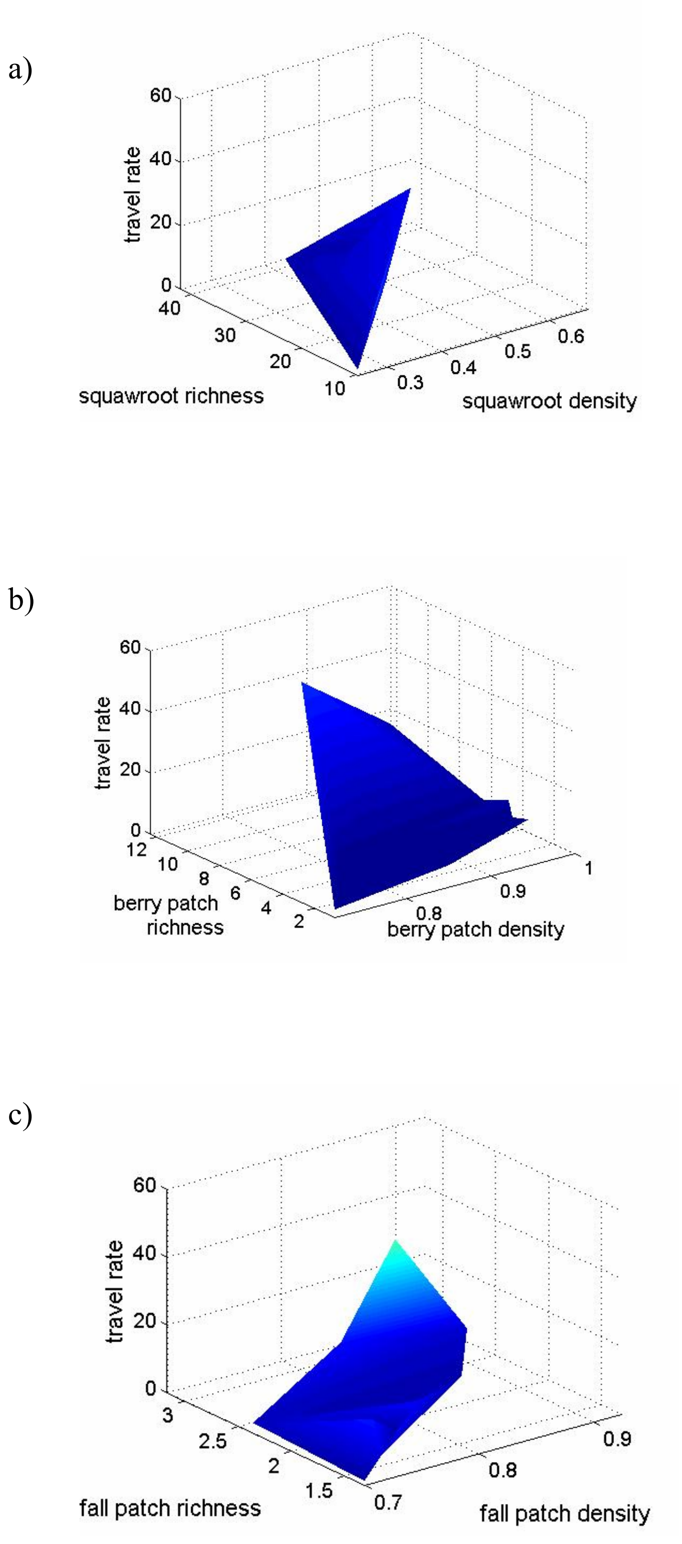

FIG. 6.5. Observed travel rates (m/min) of adult female black bears in Pisgah Bear Sanctuary (NC, USA) in response to their primary food in (a) spring (squawroot), (b) summer (berries) and (c) fall (hard mast). Darker shading represents slower travel rates while lighter shading represents faster travel rates.

CHAPTER 7: FOOD ABUNDANCE AND MOON ILLUMINATION AFFECT KINKAJOU (*POTOS FLAVUS*) MOVES

ABSTRACT.

I tested the food abundance hypotheses from chapter 3 with observations from free-ranging kinkajous (*Potos flavus*) in Panama. In addition, I tried to determine whether kinkajous responded to all fruit species they eat, fruit species they select, or the most important fruits in their diet. For females, patch richness and density for all diet categories correlated positively with move length, but generally not number of moves. Instead, their number of moves correlated positively with moon brightness. When food abundance decreased, females did not increase the amount of time that they foraged, but they spent more time foraging on foods that they select against. Males did not adjust their length or number of moves in response to changes in food abundance or moonlight. Instead, males increased their foraging time and the time they spent foraging on foods that they selected against.

Key words: abundance; density; food; kinkajous; model; move; patches; path; Parque Nacional Soberania.

INTRODUCTION

Kinkajous as a model system

My first objective was to test the food hypotheses formulated in chapter 3 with field data on kinkajou (*Potos flavus*) movements. Kinkajous are arboreal, medium-sized frugivores weighing 1.4 to 4.6 kg (Nowak 1991) that live in rainforests of Central America and northern South America (Ford and Huffman 1988). Kinkajous provide a good model organism for exploring local movements for several reasons. First, kinkajous are frugivores and need large amounts of fruit because their digestive tracts are not well adapted to frugivory (Julien-Laferriere 1999). Therefore, their foraging behaviors can be observed and quantified. Second, although tropical rainforests have high fruit productivity, fruit is a limiting factor for kinkajous as evidenced by a weight loss of approximately 20% in adults following times of low fruit production (Kays and Gittleman 2001, Kays 2003). Third, kinkajous experience low predation risk because they are nocturnal and avoid diurnal raptors, are too big for owls, and are small enough to stay out of reach of jaguars (*Panthera onca*). Intraspecific competition among kinkajous is relatively low as kinkajous travel alone 97% of the time and forage alone 80% of the time, yet still groom and sleep in groups (Kays 2003) and have overlapping home ranges within a group (Kays and Gittleman 2001). Furthermore, interspecific competition is minimized as kinkajous displace olingos (*Bassaricyon gabbii*) (Kays 2000), and spider monkeys (*Ateles geoffroyi*) were extirpated from the site in which kinkajous were observed for this study (Kays and Gittleman 2001). Because predation risk and competition are low, kinkajous' movements are not confounded with predator avoidance and competitive behaviors. Fourth, kinkajous habituate to human observers. Therefore, precise locations and movements can be recorded. Finally, captive kinkajous live 20 years (Ford and Huffman 1988), have large braincases (Ford and Huffman 1988), and learn spatial tasks (Braveman and Katz 1971). Other members of the Procyonidae, such as raccoons (*Procyon lotor*), are also considered intelligent. Therefore, it is likely that kinkajous are capable of remembering food locations and predicting food availability.

Tropical forests are a good system to test hypotheses on food abundance and movements because indices of fruit abundance in tropical rainforests can be measured, estimated, or indexed. Furthermore, fruit production in tropical forests exhibits periods of high and low fruit abundance (Foster 1982), leading to seasons where fruit limits reproductive behavior (Glanz and Thorington 1982, Worthington 1982) and populations (Leigh and Windsor 1982, Smythe et al. 1982). Although precipitation rates vary over a year, temperature is more constant annually than in temperate systems, reducing the confounding factors of seasonal temperatures and associated extreme phenological changes.

What dietary categories affect movement?

My second objective was to determine to what dietary category kinkajous respond. Foragers respond to fruit abundance on different spatial scales (Saracco et al. 2004) and could respond to fruit abundance within different dietary categories.

Through foraging observations and fecal analysis, Kays (1999a) concluded that kinkajous ate 78 species of fruit on his study plot. A fruit selectivity index revealed 20 fruit species that were selected by kinkajous (Kays 1999a). For each fruit, the fruit selectivity index was a ratio of the relative abundance of that fruit species in the diet to its occurrence. Based on the number of feeding bouts, amount of time spent eating, feces and fecal volume of fruit, fruits from 6 species (*Cordia panamensis, Inga sp, Astrocaryum standleyanum, Scheelea zonensis, Coccoloba parimensis, Chrysophyllum cainito*) and one genus (*Ficus spp.*) accounted for 48.6 to 58.7% of the fruit in a kinkajou's diet (Kays 1999a). This group of fruits was designated as important fruit species in a kinkajou's diet because these fruits constituted the majority of fruit in kinkajous' diets.

Because selected fruits and important fruits are subsets of all kinkajou fruit, it is more likely that kinkajous respond to changes in abundance in selected and important fruit than all fruits that kinkajous eat. Still, important fruits could be important because they are common, so kinkajous' movements may not be affected by the locations of important fruits. I hypothesized that kinkajous are most likely to respond to selected fruits because, by definition, kinkajous eat those fruits out of proportion to their availability.

What other factors that affect kinkajou movement?

My third objective was to determine what other factors affect kinkajous movement. I hypothesized that kinkajous adjust foraging time or selectivity in response to changes in patch richness or density. In addition, I hypothesized that kinkajous might move more pre-midnight than post-midnight because hunger was a stronger stimulus pre-midnight (when they first began foraging for that 24 hour period). My alternative hypothesis was that kinkajous might forage more post-midnight than pre-midnight because it was more energetically efficient to postpone weight gain until it was almost time to sleep again (*sensu* McNamara et al. 1990, Powell in review). Predation risk might affect movement. Predation risk might be correlated positively with moonlight as has been observed in small rodent studies (Brown et al. 1988, Kotler et al. 1991, Daly et al. 1992). Yet, because predation risk is generally low for kinkajous, I hypothesized that moonlight would not increase predation risk and reduce movements. In fact, I expected the opposite. Arboreal travel is risky for medium to large animals because a fall can result in serious injuries (e.g., broken bones in porcupines and primates). Therefore, I hypothesized that lack of moonlight might hinder kinkajou movements.

METHODS

Study site

Roland Kays monitored kinkajous and fruit availability (Kays 1999a) on the Limbo research plot in Parque National Soberanía in Panama (Fig. 7.1). The 104 ha lowland rainforest was predominantly second growth with some remnant old growth close to 400 years old (Robinson et al. 2000). During the wet season (April to December) mean daily temperatures ranged from a low of 23 to a high of 29º C and during the dry season from a low of 23 to a high of 32º C (Robinson et al. 2000). Annual rainfall is about 2600 mm (Karr 1971).

Fruit patch abundance

Twice a month, from February 1996 to January 1997, fruit was censused on 13 parallel transects spaced 25 m apart throughout the study plot. Each transect (existing field trails) was 0.5 m wide. Total transect length was 11.4 km. Fruit patches were defined as any group of fruit that contained at least two fruits less than 2 weeks old. Fruit patches were identified to species and the number of fruits was estimated as 10, 50, 100, 500, or 1000 fruits (Kays 1999a). Location of fruit patches was also recorded. For this study, I analyzed only data for fruit species kinkajous are known to eat. I multiplied the number of fruits at each location by the average wet biomass for each species of fruit (obtained from Korine et al. 2000, J. Wright, pers comm., Wendeln et al. 2000), yielding wet biomass of available kinkajou fruits for each semimonthly estimate. Trends in abundance of food on ground correlate with food in the canopy (van Schaik 1986), thus quantifying food on the ground can index of canopy food. Fruit on the ground represented fruit that was available to kinkajous in the trees 2 to 4 weeks earlier.

Patch richness was calculated as the sum of available wet biomass at each patch. An index of patch density was calculated as the number of trees with fruit that were counted during each census. Total fruit abundance on the study plot was calculated as the product of patch richness and density. Richness, density and total abundance were calculated for each dietary category (all fruit species eaten by kinkajous, fruit species selected by kinkajous and the most important fruit species in the kinkajou diet) and interpolated for dates between survey dates. Nearest neighbor distance among fruiting trees on the transect was calculated.

Kinkajou movements

Kays trapped, aged (<1 year were classified as juveniles, 1-2 years old were classified as subadults, and >2 years old were classified as adults), sexed and marked individually 25 kinkajous (Kays 1999b). Kays followed and monitored kinkajous with binoculars from February 1996 to January 1997. A red light facilitated nocturnal observations. Focal animals were rotated. Generally, Kays observed 1 kinkajou per night. Observation periods were from 1800 to 2400 or 2400 to 0600. Observations per individual were alternated between pre and post midnight periods.

Kays recorded the time and location when he first located a kinkajou and every subsequent move to a new location. I did not use the initial location in my analysis because it was not known how long the kinkajou had been at that location. I identified observation periods as those consecutive periods where at least one complete move was observed. Within observation periods, I calculated move length as the distance between stopping locations. Because the number of moves depended on the duration of observations, I standardized numbers of moves as the number of moves per hour calculated from the number of times that an animal moved divided by the length of time of the observation period. Kays also recorded behaviors and tree species in which kinkajous foraged, so I calculated foraging time and categorized foraging into diet selectivity categories.

Data analysis

I conducted regression analyses (PROC MIXED in SAS V.8, SAS Institute, Cary NC) to test the patch richness and density hypotheses formulated in chapter 3, to determine if kinkajous increased foraging time or decreased selectivity in response to decreased food availability. In each analysis, I included an interaction between patch richness and patch density and treated individuals as random effects.

I determined the amount of moonlight illumination from the daily moonrise and set times and the hourly moon brightness with MICA (Multiyear Interactive Computer Almanac) (Willmen-Bell Inc, Richmond Virginia USA). To determine if movements correlated positively or negatively with illumination, I conducted a regression analysis as described previously, but only included illumination as an explanatory variable.

RESULTS

Fruit abundance

Thirty-seven of the 78 fruit species eaten by kinkajous, 17 of the 20 species of selected fruits and all of the species of important fruits were indexed (Table 7.1). Total biomass for all fruits eaten by kinkajous peaked sharply in May/June and in September (Fig. 7.2a). Patch richness mirrored the May and September peaks and had an additional peak in March (Fig. 7.2b). Patch density peaked in early May and gradually declined to December (Fig. 7.2c).

Total biomass correlated with patch richness for selected fruit species (Fig. 7.2a). Patch richness had an additional peak in October (Fig. 7.2b). Patch density for selected species peaked sharply in May and gradually declined until the beginning of August (Fig. 7.2c). A minor peak in density occurred in September.

For important kinkajou fruits, the peaks in total biomass and patch richness were slightly correlated in May/June and August (Fig. 7.2a). Patch richness for important fruits peaked again in October (Fig. 7.2b). Patch density peaked in May and gradually declined until December 1996 resulting in densities similar to January 1996 (Fig. 7.2c).

All fruits eaten by kinkajous, fruits selected by kinkajous and the most important kinkajou fruits exhibited the similar qualitative changes in total abundance (Fig. 7.2a), richness (Fig. 7.2 b) and density (Fig. 7.2c).

Mean nearest neighbor distance among trees for each month ranged from 80 m to 400 m for all fruits eaten by kinkajous, 113 m to 4320 m for selected fruits, and 162 to 1445 m for important fruits (Fig. 7.3).

Kinkajou movements

I identified 86 observation periods for 11 individual kinkajous (6 male, 5 females; 7 adults, 3 subadults and 1 juvenile) (Table 7.2). Mean observation period length was 261 min (SD = 258). Observations modestly emphasized adults (73.9%) males (66.3%) and pre-midnight observation periods (60.2%). Observation periods occurred in every month (Fig. 7.4). The mean number of observation periods per month was 7.8 (SD = 5.0). The mean number of observation periods per individual was 7.8 (SD = 5.5) (Fig. 7.5). Number of observation periods per individual and total observation time per individual were highly correlated ($R^2 = 0.995$). Because number of moves was calculated from moves within observation periods, the sample size for move length (n = 503) was larger than the sample size of number of moves.

Male kinkajous moved a mean distance of 119 m (n = 315), which was not significantly different than the mean move length of females, which was 132 m (n = 188) (two tailed t-test, p = 0.778). Individual kinkajous had different average move lengths (ANOVA, p < 0.0001). Adults moved, on average, farther than subadults (two tailed t-test, $p < 0.0001$). Move lengths did not differ significantly if the observation periods were pre- or post-midnight (two tailed t-test, $p = 0.822$).

On average, males moved 1.24 times per hour ($n = 49$) while females moved 1.29 times per hour ($n = 27$), which was not significantly different (t-test, $p= 0.13$). Individual kinkajous moved significantly different number of times per hour (ANOVA, $p < 0.0001$). Adult and subadult kinkajous (t-test, $p = 0.284$) did not move a different number of times per hour. Observation period did not affect the move rate (two tailed t-test, $p = 0.50$).

Effects of fruit abundance on moves and behavior

For females, all diet categories (all fruits, selected fruits, important fruits) correlated positively with move length (Table 7.3). No diet categories correlated significantly with number of moves with the exception of all fruit richness (-0.00026, $p = 0.0338$) (Table 7.4). Fruit patch richness and density did not correlate significantly with foraging time (table 7.5). Fruit patch density in the all fruit category correlated positively with time spent foraging on species that kinkajous select against (4.502×10^{-6}, $p = 0.0694$). Female kinkajous did not change significantly the amount of time that they foraged on fruits they selected against in response to changes in fruit patch richness or density for the other diet categories (Table 7.6). Distance moved by female kinkajous did not correlate significantly with moon illumination but number of moves correlated positively and significantly with moon illumination (0.6638, $p = 0.0219$, Table 7.7).

Move length and number of moves of males did not correlate significantly with patch richness and density for any diet category (Table 7.3 and Table 7.4). Instead, males increased the amount of time that they foraged in response to decreased food patch density for all fruits (-0.00253, $p = 0.0193$) (Table 7.5) and for selected fruits (0.00518, $p = 0.0567$). Males also decreased their selectivity for selected fruits (1.949×10^{-6}, $p = 0.0129$) (Table 7.6) and important fruits (2.377×10^{-6}, $p = 0.0024$). Males did not change their movements in response to moonlight (Table 7.7).

DISCUSSION

Effects of food on moves and behaviors

Because kinkajous' mass decreased during times of low food abundance and fruit production peaked at an amount more than triple the mean yearly biomass, I interpreted fruit abundance to range from limited to plenty. Therefore, if food abundance influenced kinkajou movement, kinkajous at the Limbo study plot should respond to the changes in patch richness as did the virtual animals.

Fruiting phenology in 1996 was probably typical for the Limbo study plot because the phenology of fruit abundance at the Limbo study plot was similar to Barro Colorado Island in other years (Foster 1982). So, kinkajou movements for the study period were not affected by unusual temporal patterns in annual fruit production. Fruit patch distribution at Limbo was probably aggregated as has been documented for other tropical forests (Hubbell 1979, Condit et al. 2000, Valencia et al. 2004), even across spatial scales (Bunyavejchewin et al. 2003). So, it was logical to use model simulations where fruit was aggregated.

Kinkajous probably use fruit biomass rather than canopy size for selecting foraging trees for two reasons. First, fruit biomass is a direct measure of food and, in at least one primate species, biomass is a better indicator of foraging time than tree diameter or crown size (Miller and Dietz 2004). Second, kinkajous forage solitarily; therefore, it is not important for kinkajous to choose canopies that could support multiple individuals.

Kinkajous might be opportunistic foragers (not choosing patches based on type of fruit) (Julien-Laferriere 1999), but they do appear to move among patches. The distance that females move depends on fruit patch richness and density because the primary factor that affects female kinkajou movement is location and amount of fruit on the trees. Whether or not females chose to leave a tree does not depend on the amount of food in the tree or the number of fruiting trees, instead it depends on moonlight. Female kinkajous can probably move more safely and efficiently as moonlight increases. As richness and density increase, female kinkajous travel farther. This response is not what is predicted by the habitat-productivity hypotheses. Although the response to richness was predicted, the response to density was not predicted by my model in chapter 3. The response to density appears to have been overrode by the benefits of traveling in moonlight.

Males do not respond to changes in fruit patch richness or density in the same way as females. Because males do not alter their movements in response to changes in food abundance, they increase their foraging efficiency by increasing foraging time or decreasing selectivity. The response of males was not predicted by the habitat-productivity hypotheses or the hypotheses that I generated in chapter 3. Because the social system of kinkajous straddles both solitary and group-living strategies (Kays and Gittleman 2001), females might move as solitary animals and respond to fruit abundance while the movements of males are more group-like and did not respond to just food abundance. Male kinkajous defend territories (Kays 2003); and males might respond to females as a resource and not responded to food. Future work should determine if males are following females, avoiding females (females may be dominant), or neither. Perhaps the dominant male of the group (Kays and Gittleman 2001) responded differently to food abundance than did the subordinate male.

Move length of female kinkajous responded to each of the dietary categories (all, selected, and important foods). Number of moves of female kinkajous did not respond to any of the diet categories. Female kinkajous did not alter their moves solely to any diet category. Because the diet categories themselves were correlated, it may not have been possible to determine to which category the kinkajous responded. If the fruit in the category “all fruits eaten by kinkajous” was so abundant that kinkajous did not have to adjust their moves to get to food, it would be understandable that kinkajous do not respond to the diet category “all fruits”. Yet, fruit trees in the abundant category were at least 36 m apart on the transect (May) and up to 402 meters apart (November). Thus, fruit trees were spaced far enough apart that move length would be influenced if kinkajous respond to the fruit trees at the selection level of “all fruits eaten by kinkajous.”

If selected and important fruits were so rare that that they were too costly to travel to, kinkajous may not respond to the abundance of selected or important fruit patches. In most months, nearest neighbor distances among all fruit trees was significantly less than nearest neighbor distances of selected and important fruits. Selected fruit trees were at least 113 m and up to over 4000 m apart. Therefore, for some months, selected and important trees could have been too rare to which to travel. Because selected fruits are preferentially selected, kinkajous could move to maximize visits to selected fruit patches. Alternatively, kinkajous could have eaten selected fruits (passing non-selected fruits) as they moved, not choosing a path to maximize visits to fruit patches but maximizing the time they spent at those trees.

Effects of other factors on moves

Weather could affect movements. Yet, temperature was fairly constant over a year, kinkajous maintain core body temperatures between the ambient temperatures of 20º and 30º C (Muller and Kulzer 1978), and fluctuations of less than 10º C at the study plot should not greatly affect kinkajou movements. Furthermore, observations were conducted only in no to slight rain and not under windy conditions.

Juvenile mammals may move less because they weigh less (Cederlund and Sand 1994). Alternatively, juveniles may move more to learn about habitats (Holzman et al. 1992). Age related movement has been observed in raccoons (Fritzell 1978), another species in the kinkajou family. Furthermore, age class is tied to individual experience. It is not surprising that age class affected movement.

For animals to respond to food, they must know where it is and how much is present. Experience and knowledge of individual animals could affect movements. Because move length varied significantly among individuals, it is possible that individual experience shaped the distance traveled by kinkajous. Kinkajous are probably capable of complex cognition because they are procyonids and long-lived. Nonetheless, the cognitive capabilities of kinkajous have not been studied, with the exception of work by Braveman and Katz over 30 years ago (1971). Further investigation into the cognitive ecology of kinkajous could help determine if experience and individual ability to problem-solve affects kinkajou movements.

As move length and number of moves were not affected by whether the observation period was before or after midnight, it seems that hunger did not affect movement and kinkajous may not have been attempting to optimize travel distance in regards to daily weight gain. Still, it is possible that kinkajous optimize daily weight gain through selection of food types.

No predation or predation attempts were observed during the study. Because the kinkajous did not depress distance or number of moves in response to bright moonlight, nocturnal predation risk is probably low. Kinkajous move slowly and deliberately compared to some primates, have a prehensile tail that can also act as a balance, and can turn their hind feet to facilitate arboreal movements (including hanging by their hind feet), so movement risk might be low. At least one nocturnal primate [spectral tarsiers, (*Tarsius spectrum*)] increased move length in response to moonlight (Gursky 2003). Kinkajous might move more safely or efficiently when the moon illuminates the canopy.

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TABLE 7.1. All species of fruits that eaten by kinkajous that were censused on the Limbo study plot in Panama are listed. X denotes fruit eaten by kinkajous, fruits selected by kinkajous, and fruit important to kinkajous' diet. Fruits were considered to be selected if the ratio of the relative amount of a fruit species in the diet to the relative abundance of the species was greater than 1 (Kays 1999a). The 5 fruits that made the greatest percentage of feeding bouts, feeding time, number feces, and fecal volume were classified as important fruits (Kays 1999a).

	All	Selected	Important
Annona spraguei	X	X	
Astrocaryum standleyanum	X		X
Cayaponia granatensis	X	X	
Cecropia sp.	X	X	
Chrysophyllum cainito	X	X	X
Clusia odorata	X		
Coccoloba parimensis	X		X
Cordia panamensis	X	X	X
Cupania rufescens	X	X	
Diospyros artanthifolia	X	X	
Dipteryx panamensis	X		
Doliocarpus sp.	X		
Doliocarpus olivaceus	X		
Ficus bullenei	X		X
Ficus colubrinae	X		
Ficus dugandi	X	X	
Ficus insipida	X	X	X
Ficus obtusifolia	X	X	X
Ficus parensis	X	X	X
Ficus popenoei	X		X
Ficus trigonata	X		X
Ficus yoponensis	X	X	X
Guettarda foliacea	X		
Hyeronima laxiflora	X	X	X
Inga sp.	X	X	X
Lindackeria laurina	X		
Miconia impetiolaris	X	X	
Poulsenia armata	X		
Pourouma guianensis	X		
Protium panamense	X		
Quararibea asterolepis	X	X	
Scheelea zonensis	X	X	X
Socratea durissima	X		
Spondias mombin	X		
Spondias radlkoferi	X		
Unknown species 1	X		
Unknown species 2	X		

TABLE 7.1 (continued)

Tetragastris panamensis	X		
Tovomitopsis nicaraguensis	X		
Virola surinamensis	X		
Vismia billbergiana	X		
Zuelania guidonia	X		
Total	42	17	14

TABLE 7.2. Number of kinkajou observation periods according to maturity and sex.

	female	**male**	**total**
adult	28	37	65
subadult	0	20	20
juvenile	1	0	1
total	29	57	86

TABLE 7.3. Coefficients and statistical probability from a general linear model (PROC MIXED, SAS) testing the effects of fruit richness (amount of fruit per fruit tree), fruit density (an index of the number of fruit trees on the study area) and an interaction between fruit richness and density on move length for all fruit that kinkajous eat, fruits that kinkajous select, and important fruits in kinkajous diets. In the model, individual was a random effect. Fruit measured on the ground was assumed to index fruit available on the trees to kinkajous 2 weeks earlier. Asterisks (*) indicate significance. **Bold** font indicates predicted direction for coefficients that were significant.

(a)

	Fruit patch richness	Fruit patch density	Richness*density
Female kinkajous (n = 188)			
All fruit	**0.000114***	0.02677*	-8.07x 10^{-6}*
	(p = 0.0109)	(p < 0.0001)	(p < 0.0001)
Selected fruit	**0.000022***	0.07370*	-8.97 x10^{-6}*
	(p = 0.0429)	(p < 0.0001)	(p < 0.0001)
Important fruit	**0.000035***	0.03484*	-7.09E^{-6}*
	(p = 0.0054)	(p = 0.0004)	(p < 0.0001)
Male kinkajous (n = 315)			
All fruit	0.000026	-0.00615	1.733 x 10^{-7}
	(p = 0.6317)	(p = 0.2511)	(p = 0.9286)
Selected fruit	-3.69 x10^{-6}	-0.01281	1.531 x10^{-6}
	(p = 0.7341)	(p = 0.3709)	(p = 0.3626)
Important fruit	-9.86 x 10^{-6}	-0.00809	1.542 x10 $^{-6}$
	(p = 0.3821)	(p = 0.1716)	(p = 0.1885)

TABLE 7.4. Coefficients and statistical probability from a general linear model (PROC MIXED, SAS) testing the effects of fruit richness (amount of fruit per fruit tree), fruit density (an index of the number of fruit trees on the study area) and an interaction between fruit richness and density on the number of moves for all fruit that kinkajous eat, fruits that kinkajous select, and important fruits in kinkajous diets. In the model, individual was a random effect. Fruit measured on the ground was assumed to index fruit available on the trees to kinkajous 2 weeks earlier. Asterisks (*) indicate significance. **Bold** font indicates predicted direction for coefficients that were significant.

(a)

	Fruit patch richness	Fruit patch density	Interaction between richness and density
Female kinkajous (n = 27)			
All fruit	-0.00026* (p = 0.0338)	-0.01985 (p = 0.2854)	9.757×10^{-6} (p = 0.1126)
Selected fruit	-0.0003 (p = 0.514)	-0.09941 (p = 0.1255)	-0.00011 (p = 0.1097)
Important fruit	-0.00002 (p = 0.6621)	-0.05317 (p = 0.1097)	8.87×10^{-6} (p = 0.1224)
Male kinkajous (n = 49)			
All fruit	0.000105 (p = 0.6149)	0.01089 (p = 0.5877)	-2.95×10^{-6} (p = 0.6896)
Selected fruit	-0.00002 (p = 0.5666)	0.007170 (p = 0.8892)	1.46E-6 (p = 0.8071)
Important fruit	-0.00002 (p = 0.6104)	-0.00552 (p = 0.7977)	2.004E-6 (p = 0.6321)

TABLE 7.5. Coefficients from a linear regression between foraging time and richness and density of all fruits eaten by kinkajous, fruits selected by kinkajous, and fruits most important to kinkajous' diets. Asterisks (*) indicate statistical significance.

		females	males
All fruits	richness	4.807×10^{-6} (p = 0.2709)	-0.00001 (p = 0.2688)
	density	-0.00051 (p = 0.3492)	-0.00253* (p = 0.0193)
Selected fruits	richness	1.58×10^{-8} (p =0.9901)	-1.04×10^{-6} (p =0.5129)
	density	-0.00090 (p = 0.5993)	-0.00518* (p = 0.0567)
Important fruits	richness	1.184×10^{-6} (p = 0.3850)	-5.59×10^{-7} (p = 0.7251)
	density	-0.00058 (p = 0.3345	-0.00101 (p = 0.3057)

TABLE 7.6. Coefficients from a linear regression between time feeding on fruits selected against and richness and density of all fruits eaten by kinkajous, fruits selected by kinkajous, and fruits most important to kinkajous' diets. Asterisks (*) indicate statistical significance.

		females	males
All fruits	richness	4.502×10^{-6}* (p = 0.0694)	-2.1×10^{-6} (p = 0.6765)
	density	0.000037 (p = 0.9041)	-0.00034 (p = 0.5510)
Selected fruits	richness	-2.32×10^{-7} (p =0.7481)	1.949×10^{-6}* (p =0.0129)
	density	0.000315 (p= 0.7589)	0.000099 (p = 0.9419)
Important fruits	richness	2.776×10^{-8} (p = 0.9719)	2.377×10^{-6}* (p = 0.0024)
	density	-0.00020 (p = 0.5861)	0.000863 (p = 0.1087)

TABLE 7.7. Coefficients from regression (PROC MIXED, SAS) where move length of females and males is a function of moon illumination. Asterisks (*) indicate statistical significance.

	Coefficient
Females	
Move length (n = 188)	-0.1074 (p = 0.1797)
Number of moves (n = 27)	0.6638* (p = 0.0219)
Males	
Move length (n = 315)	0.05249 (p = 0.3947)
Number of moves (n = 49)	0.3467 (p = 0.1575)

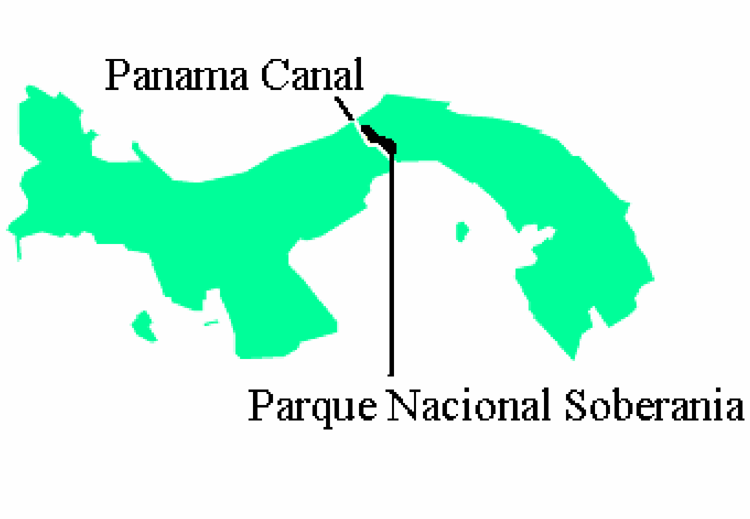

FIG. 7.1. Parque National Soberanía is located along the east side of the Panama Canal in Panama.

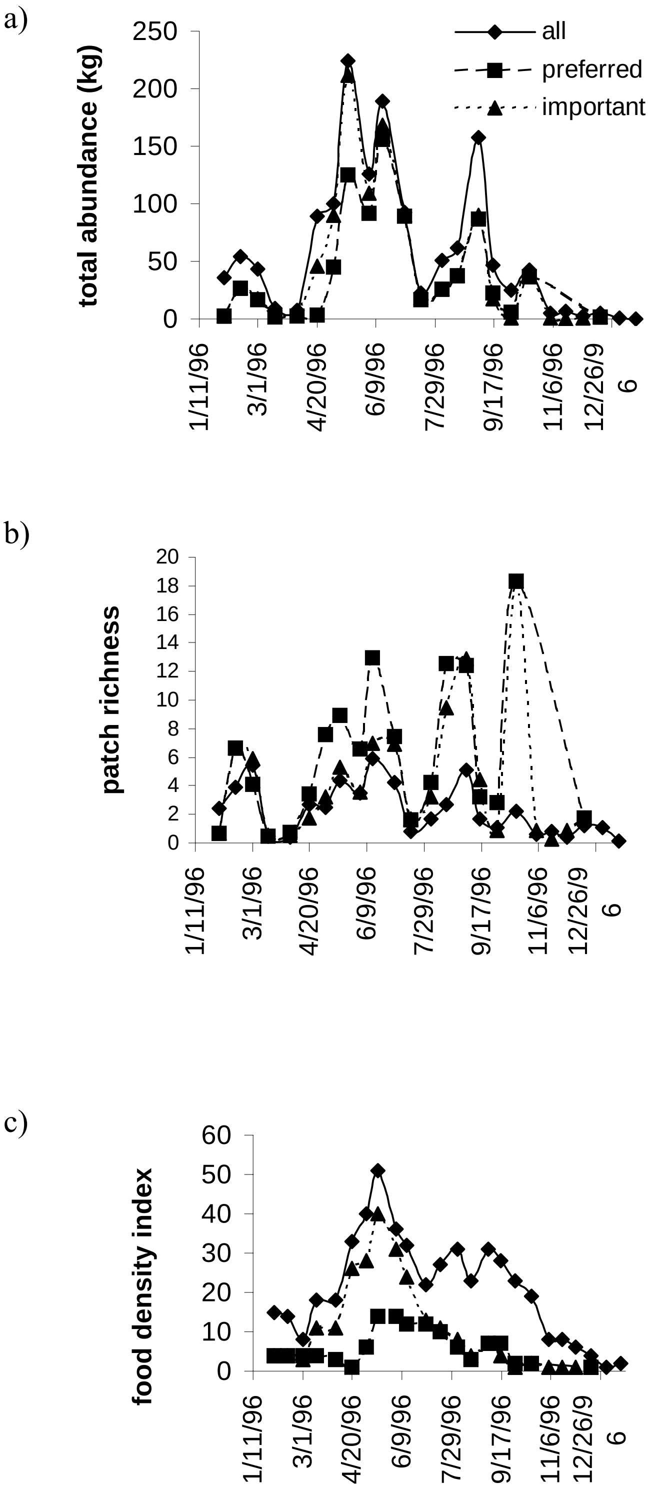

FIG. 7.2. (a) Total abundance, (b) patch richness, and (c) patch density for all fruits eaten by kinkajous, fruits selected by kinkajous, and fruits important to kinkajous at the Limbo study plot.

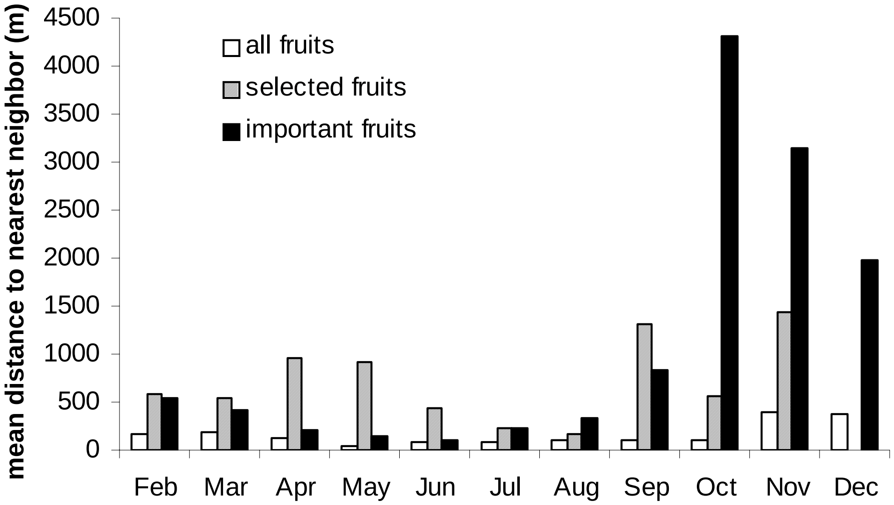

FIG. 7.3. Mean distance to nearest neighboring fruit patch along the transect by month for each of the fruit selection levels.

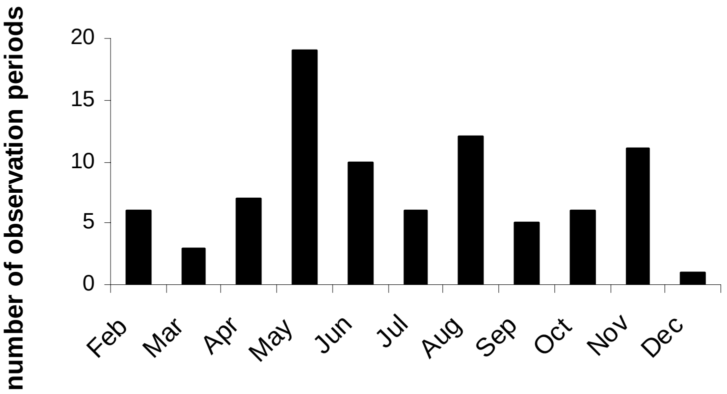

FIG. 7.4. Number of observation periods per month.

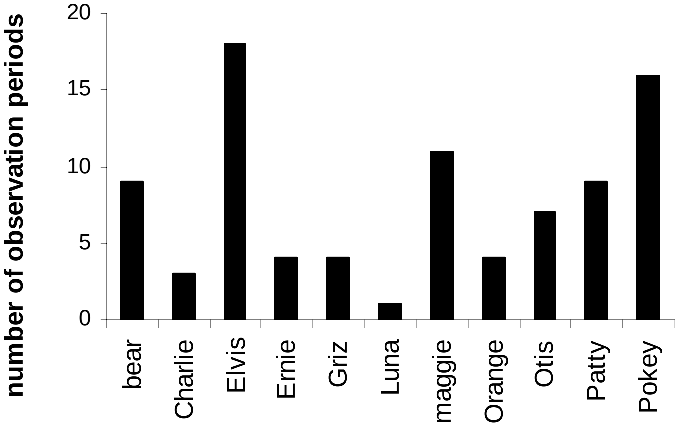

FIG. 7.5. Number of observation periods per focal animal.

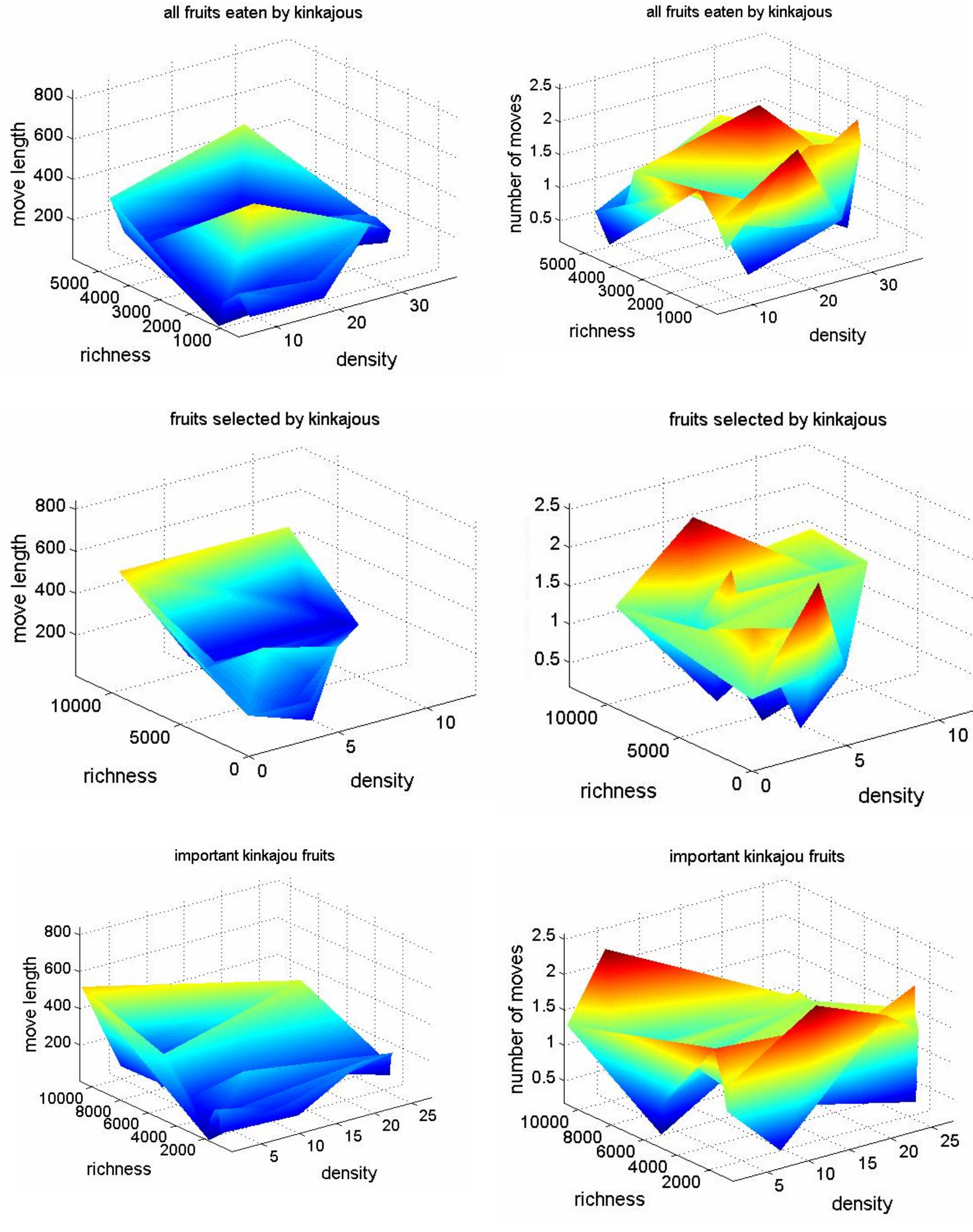

Fig. 7.6. Length and number of moves exhibited by female kinkajous in Parque National Soberanía (Panama) in response to indices of fruit patch richness and density for (a) all

fruits eaten by kinkajous, (b) fruits selected by kinkajous, and (c) fruits important to kinkajous.

CHAPTER 8: CONCLUSIONS: COMPLEXITY AND FUTURE DIRECTIONS OF MOVEMENT ECOLOGY

Movement is basic component of an individual's life history and a species's natural history, yet much work remains to be done to understand animals' movement within their home ranges. In chapter 2, I showed that movement terms and their definitions need to be standardized. In addition, some concepts and methods of measuring movement need additional scrutiny. In chapter 3, I demonstrated that, according to my model, whether animals should move according to the habitat-productivity hypothesis depends on how food abundance is defined (e.g., patch richness or density) and how movement is defined (number of moves or move length). In chapters 4 and 5, I demonstrated that basic components of movement models (e.g., foraging rules and cognitive constraints) can contribute to movement patterns and should be identified when modeling or making predictions about animal movement.

In chapters 6 and 7 (examining the results of the bear and kinkajou data), I showed that movement responses to food abundance can be complex because individuals of a species (e.g., bears) may respond to patch richness, patch density, or both, depending on the season. Individuals of a species may respond by altering their move lengths but not frequency (e.g., kinkajou females). Females of a species (e.g., kinkajous) may respond to both richness and density while males may not respond to either. Animals may adjust their movements in response to changes in food abundance, but they may also adjust other behaviors such as time spent foraging or selectivity (chapter 7, kinkajous).

And, of course, animal movement responds to factors besides food abundance, such as kinkajou females altering the number of times they moved in response to moonlight.

Field studies can be difficult to interpret because of confounding factors. As a model system, the kinkajou-tropical forest had few confounding factors and still the males did not appear to respond to changes in fruit abundance. Nonetheless, it is possible that the predicted movement response could have occurred and been overridden by confounding factors. If predicted correlations cannot be isolated in this study system (minimal predation, etc), it may be difficult to observe the effects of food abundance (if any) in more complex systems.

Even when correlations exist between fruit patch richness and density and movements, changes in food abundance may not <u>cause</u> changes in movement. Therefore, caution should be invoked when inferring that changes in food abundance cause changes in movements. Additional studies, in other systems and with other vertebrate species, is necessary before discounting or accepting the perception that animals' change their movements in response to food abundance. And, importantly, we need to determine when (under what ecological circumstances) changes in food abundance should affect movement.

Future work should continue to investigate the effects of foraging rules on movement and if changes in food abundance facilitate changes in movement rules. Future work should also determine how other behaviors, such as competition, predation, reproduction, and exploration affect movements. In particular, the effects of exploratory behaviors on movements need attention as very little research has been done in this area. Individual experience is another area that could benefit from future research (Bekoff

1995). Movement studies tend to focus on the level of species or populations, yet the data on bears and kinkajous demonstrate that movements vary among individuals. As researchers call for the incorporation of cognition into behavioral studies (Yoerg 1991, Lima and Zollner 1996, Shettleworth 2001) and the field of cognitive ecology continues to grow, cognition should be incorporated into the study of movement ecology. Certainly, the experiences and information accumulated by individuals will help answer Tinbergen's 4 why questions (Tinbergen 1963). These and other complexities of movement ecology need to be addressed so that movement, a basic behavior, can be better understood and applied to protecting and managing species.

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