

Linking Fitness Landscapes with the Behavior and Distribution of Animals

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Since its beginnings in the 1980s, the discipline of landscape ecology has grown rapidly, concurrent with advances in geographic information system (GIS) technology and increasing availability of georeferenced data. Ecologists and land managers are able to analyze patterns on multiple scales in ways not possible in the past. Indeed, ideas, approaches, and techniques emerge faster than they can be assimilated, resulting in a complex framework of concepts that lacks a unifying structure well supported by empirical data (Wiens 1999). This situation represents a double-edged sword for landscape ecologists. On one hand, the prospects for true paradigm shifts are exciting as we understand better the role of spatial phenomena in the function and management of populations and landscapes. On the other hand, these paradigm shifts will be particularly problematic for resource managers who must deal with promising new concepts of landscape ecology that provide little empirical support or direction for management actions. The risk of failure is high when a management strategy is based on concepts that keep changing.

In a discipline undergoing rapid change and progress, one should reassess regularly the assumptions that underlie dominant concepts so that conceptual

grasp does not exceed empirical reach. In this chapter, we evaluate some concepts and assumptions related to interactions across spatial scales between animals and their habitat. We focus on how habitat should be defined in landscape ecology. The ability to portray the distribution and characteristics of habitat in space, and therefore the ability to understand and manage animals that rely on that habitat, is fundamental to what many landscape ecologists do. Whether we want to understand metapopulation dynamics or patch use by individual animals, researchers and managers implicitly or explicitly define habitat as an integral part of their work. Seldom, however, do researchers and managers understand how well these models and maps actually portray the biological meaning of habitat to animals. We contend that models and maps based on rigorous evaluation of biological first principles are the only ones with the potential to provide robust insight into landscape ecology and lead to management actions that will yield desired results. Models adopted because they are convenient to our methods and technology, on the other hand, are very unlikely to do either. In the explosive growth of landscape ecology and in the use of GISs, important biological first principles have been dismissed too easily as fully justified assumptions or ignored completely. Specifically, we consider here how to define habitat biologically, how this definition has and has not been extended to landscape concepts and applications, and how definitions of habitat frequently used in landscape ecology are limiting. We also propose a definition of habitat based on fitness that should be more robust in landscape applications than traditional definitions. We conclude with an example of our concept applied to black bears and their use of habitat on a forested landscape in the southern Appalachians.

Habitat and Fitness

Like many words frequently used within a profession, the term *habitat* has become so widely used in animal and landscape ecology under so many circumstances that its meaning is confused at best. *Habitat* has become jargon, a vague concept that is widely and uncritically used. At the most basic level, the word *habitat* implies that some relationship between animals and their environment is being discussed. The nature of that relationship is rarely defined, however, resulting in ambiguities (at best) or inaccuracies (at worst; Hall et al. 1997).

Garshelis (2000, p. 112) outlined two distinct definitions of *habitat*. The first is "the type of place where an animal normally lives or, more specifically, the collection of resources and conditions necessary for its occupancy."

The second is “a set of specific environmental features that, for terrestrial animals, is often equated to a plant community, vegetative association, or cover type.” Garshelis maintained that the prevalence of the second usage confers legitimacy and is consistent with the normally accepted concept of “habitat use.” Morrison et al. (1992) acknowledged the frequent use of *habitat* to describe an area with a particular vegetative cover but maintained that a better definition is an area with the resources, environmental conditions, and presence or absence of predators that allows the occupancy, survival, and reproduction of a particular species. Hall et al. (1997) cogently discussed the use and abuse of the term *habitat* in the literature and issued a plea for standardization consistent with Morrison et al.’s (1992) definition. Corsi et al. (2000) added more complexity to the common uses of the term *habitat* by aligning them according to whether they had to do with Cartesian space (where a species is found) or environmental space (under what conditions a species is found), and whether they referred to biota (e.g., deer habitat) or land (e.g., riparian habitat). Corsi et al. (2000) showed that habitat originally was a species-specific property, but with the development of technologies for mapping habitat, land-based definitions became more prevalent because general habitat types easily distinguished by people are easy to map. However, the habitat needs of animals vary across species ranges and with the presence of predators, specific foods, and other resources and therefore cannot be identified as precisely as technologies can map them.

For a habitat model to be useful, it must explain or predict how animals will be associated with the vegetation and physical structure of a particular area. To do this, a model must relate habitat to an animal’s fitness or to its correlates. This may not be as obvious as it sounds and is certainly not as simple. Fisher (1930) described fitness for an animal as a relative measure that increases with increasing survival and number of offspring. Stearns (1992) defined fitness more precisely as the expected contribution of an individual to future generations, homologous to the definition of the intrinsic rate of increase, r , for a population. Like habitat, however, *fitness* has also become jargon in animal ecology, and the term is used widely without explicit definition. Although Fisher’s and Stearns’s definitions of *fitness* are straightforward, fitness is very difficult to measure empirically. Garshelis (2000) provided a detailed presentation of studies that have and have not addressed links between habitat and components of fitness, and he outlined challenges associated with discerning fitness in field studies. Essentially, two approaches exist for discerning the fitness of animals through observation. The most direct approach is to measure vital rates such as survival or reproductive success and infer

fitness from them. This approach has appeal because it deals directly with two major components of fitness. Nonetheless, we must emphasize that these are only components of fitness (Caswell 2001, p. 295). Juvenile survival, density dependency, environmental stochasticity, social status, and other factors can also affect fitness. An analysis of survival only will overestimate fitness for long-lived individuals that fail to reproduce, an analysis of reproductive success can misinterpret fitness for fecund individuals that die young, and an analysis of both survival and reproduction can misestimate fitness for individuals whose vital rates are influenced by population density or social status.

A second approach is to infer fitness indirectly from the behavior of animals based on the logic that animals show preferences for environmental characteristics that enhance their fitness. This approach has its theoretical foundations in foraging ecology (optimality) and in research that shows that natural selection has molded foraging decisions, patch selection, and time of patch occupation to maximize fitness or indices of fitness (Stephens and Krebs 1986). This approach has been used extensively in empirical studies of habitat use by animals largely because behavioral data, usually in the form of telemetry locations, are easier to collect than data on vital rates. This approach suffers from significant drawbacks because key assumptions must be made both about the behavior of animals and about what animals select. Behavior is highly plastic for members of most wildlife species, and intraspecific and interspecific interactions affect behaviors (e.g., use of space). Perhaps most problematic in this approach is that it entails a reasonable understanding of what animals select. Most habitat studies that use this approach rely on a posteriori correlations between measures of use by animals and arbitrary classifications of habitat. Not only is this poor science, but it assumes, usually without testing, that the classification schemes developed by the researchers accurately represent the ecological currency used by animals to make decisions. We know of no habitat classification schemes based directly and entirely on factors contributing to reproduction and survival of animals. Some schemes incorporate, to some extent, foods or escape cover potentially available from a particular cover type. However, two patches of the same cover type may have different value to an animal, depending on their sizes and juxtaposition with other resources. The extent to which habitat selection by animals matches human definitions of habitat should be extremely sensitive to the extent to which these definitions abstract important first principles that contribute to the fitness of the animals. Therefore, the ability of a posteriori correlation analyses to reveal relationships between animal behavior and arbitrary habitat definitions becomes more a function of good fortune than of good biology.

Fitness, like the intrinsic rate of increase for a population (r), can almost never be measured directly and therefore must be assessed indirectly with indices. No single index is universally satisfactory or practical for all species. Methods for discerning fitness in the field depend on research techniques available to study a species, its unique life history, and logistic constraints. At least as important, the ability to discern a relationship between fitness and habitat entails not only a reasonable index of an animal's fitness but also a reasonable model of how habitat contributes to that fitness. To fail to do both is to make one of two lamentably common mistakes. A habitat definition based on good estimates of fitness correlated to arbitrary habitat classes is based on inductive, not deductive, reasoning and amounts only to an untested hypothesis. A habitat model with a theoretical basis in fitness that is not tested against actual indices of fitness is also nothing more than an untested hypothesis. In either case, the link between fitness and habitat has not been rigorously established. A manager proposing to manage habitat using either approach has no confidence that management actions will yield desired results.

Calls to understand better the relationship between fitness and habitat are increasing but focus largely on better ways to discern fitness and not on identifying the properties of habitat that contribute to fitness. We suggest that the only definition of habitat with a functional biological basis is one that in some way ties resources contained within an area to the fitness of animals occupying (or potentially occupying) it. Arguments of prevalence aside, the first usage outlined by Garshelis (2000) and the preferred definition of Morrison et al. (1992) are the only definitions that explicitly satisfy this requirement. However, *any* definition of habitat portrays a fitness relationship between an environment and an animal, whether intended or not. Typological approaches to modeling this relationship are simply more abstract and less direct than explicit approaches. Conceivably, either approach has its time and place in landscape ecology and should be a function of where research questions or management objectives fall on two continua: spatial scale (fine scale, such as individual forest stands, to broad scale, such as a forested landscape) and ecological resolution (simple, such as presence of a single species, to complex, such as community structure). However, we see little evidence that managers and landscape ecologists select definitions of habitat based on these continua. Mismatches between the level of abstraction in habitat definitions, spatial scales, and ecological resolution lead not only to poor or misleading insights but also to the propagation of erroneous or vague biological concepts.

Habitat and Landscapes

Biological meaning, scientific predictions, and management utility for any habitat maps depend very much on the definitions used to generate the maps. We are very concerned that definitions of habitat among landscape ecologists are increasingly structured by artifacts of image classification, by an uncritical use of the ubiquitous concept of the habitat patch, and by an excessive reliance on inductive analyses to define habitat.

Classification

Organisms are distributed in a complex manner with respect to the resources that affect fitness. The need to simplify is clear, yet the means for simplifying that are consistent with biology are not always so clear. Distilling ecological patterns into identifiable types has a distinguished history in ecology. Among the earliest debates in ecological literature was whether associations between individual organisms inhabiting a common area were the product of tight interdependence between those organisms, forming an integrated community type distinguishable from others (Clements 1936), or merely a happenstance of the independent distributions of the organisms whereby no typological separation of communities is possible (Gleason 1926). Most ecologists agree now that these two ideas anchor the ends of a continuum. Some typological definitions of communities are justified, many are not, depending largely on scale and spatial heterogeneity. On a continental scale, for example, a community called "boreal forest" includes all species and ecological associations associated with boreal forests. On the scale of 1 m², however, numerous community components are absent because they are not uniformly distributed within boreal forests at all scales. The importance of scale in interpreting landscape patterns is well understood in landscape ecology (Wiens 1999), but the use of scale in defining habitat on a landscape is not.

Landscape ecology has an interesting history of its own with regard to defining ecological communities. In one of the earliest textbooks for landscape ecology, Forman and Godron (1986, p. 62) stated that "plant and animal communities are often mapped, and to do this they are named and classified. . . . The primary criteria used in classifications are appearance (physiognomy), species composition, dominant species, and habitat . . . at finer divisions, species composition is almost always used as the classification criterion." Interestingly, we could find no definition of the term *habitat* in the book, yet it is listed as a classification criterion for community

types. The vague use of *habitat* and a reliance on typological definitions of communities based on species composition are well rooted within the discipline. Some recent publications acknowledge more explicit definitions of *habitat* based on fitness but continue to rely on the use of habitat types (Kozakiewicz 1995; Morris 1995; Harris and Sanderson 2000). However, the clear majority of publications within landscape ecology either do not define habitat or treat it as a commonly understood entity that need not be discussed. Because the link between animals and where they live is the root of understanding metapopulation dynamics, habitat selection, and the distributions of animals on landscapes, a discipline that addresses these issues must understand what habitat is.

Much of the way landscape ecologists consider (or fail to consider) habitat definitions results from empirical and theoretical stumbling blocks: technological constraints that define the format of the data used in empirical studies and the dominant paradigm of the habitat patch. The first issue is an obvious one. Landscape ecologists and managers often use data derived from remotely sensed satellite imagery, where biological meaning must be inferred from variations in spectral data. Approaches to classifying ecological communities from such images abound and have been widely applied in models of habitat for animals (Scott et al. 1993). Although the confidence with which such definitions may be viewed is questionable (Williams 1996; Morgan and Savitsky 1998), few alternatives exist for converting truly large-scale landscape information into ecologically meaningful data. Nonetheless, landscape classification can generate only typological community definitions. Landscape ecologists who use these data to portray animal habitats must be critical of the assumptions used to define ecological communities from such an extreme, Clementsian perspective. These assumptions may be justified for certain communities or certain scales but by no means for all cases.

Patches

Despite the productive history of research related to habitat patches, we suggest that habitat definitions suffer from the seemingly universal faith landscape ecology has placed on the concept of the patch. Patch theory has its origins in optimal foraging (Charnov 1976) and has been an invaluable tool to pioneers in spatial patterns in ecology. Wiens (1995) explained the predominance in landscape ecology of patch theory over that dealing with spatial heterogeneity by noting that patch theory was familiar and easily adapted and that the concept of heterogeneity is diffuse and does not lend

itself well to rigorous theoretical development. Accordingly, patch theory has been integral to developing critical concepts in landscape ecology, particularly for models of metapopulations, biogeography, and ecological flow (Wiens 1995), and has become the analytical foundation for landscape analysis (Turner et al. 1991; McGarigal and Marks 1995). Consequently, the notion of habitat as a spatial array of internally homogeneous patches imbedded in an inert matrix has become fixed in landscape ecology, despite the fact that little empirical evidence exists to suggest that this model is as universal as it is used (Kareiva 1990).

Resources, and therefore individuals, populations, and communities, are patchily distributed in space. However, such patchiness does not mean that organisms are arranged in clearly defined polygons. Patchy distributions are those in which organisms of the same species are clumped in space rather than randomly or evenly distributed. At any scale, clumps of organisms have diffuse edges and heterogeneous densities within those diffuse edges.

Patches, patch characteristics, fragmentation of habitat into patches, and corridors connecting patches are reigning paradigms in landscape ecology that enjoy modest empirical support at best yet are widely and often uncritically applied. Although a powerful conceptual tool, a patch is nothing more than a habitat model, and its application suffers the same limitations as any definition of habitat. At broad spatial scales and coarse ecological resolutions, habitat expressed as homogeneous patches may have explanatory power for understanding the behavior or distribution of animals on a landscape. On fine scales, abstract definitions of habitat explain less and less. Thus, patches may help to explain metapopulation dynamics or behavior of individuals on one scale but not on another.

Inductive Analysis

Inductive reasoning comprises the essential first steps of the scientific method. When researchers collect data, analyze them statistically, and interpret the results without having a priori hypotheses, they use inductive logic to generate hypotheses (i.e., the interpretation of the results) suitable for testing. Only when these hypotheses are tested deductively (the remainder of the scientific method) can strong inferences be made and cause-and-effect relationships be established (Platt 1964). Clearly, robust insights such as these should form the basis for resource management. By contrast, inductively derived insights provide a risky foundation for management of natural systems because such insights are untested and therefore tenuous.

Nonetheless, studies that use a posteriori correlation analysis to associate presence of animals with habitat classifications are very common. Burnham and Anderson (1998) described this method as "data dredging" and argued that inferences drawn from such analyses do not have strong biological, statistical, or logical foundations. Nonetheless, most studies using this approach misrepresent their findings as conclusions rather than identifying them appropriately as hypotheses in need of testing with independent data sets. Granted, one cannot test hypotheses that have not been generated, and inductive analysis is the necessary starting point where no a priori hypotheses can be derived. For most questions relating animals to habitat, however, starting from scratch in this fashion should be uncommon because extensive theory and empirical literature are available to construct hypotheses for nearly all wildlife species. Therefore, the prevalence of habitat definitions based on a posteriori, correlational analysis suggests that landscape ecologists are more often than not in the business of continually generating but not testing new hypotheses of habitat relations. Without identifying which hypotheses are robust and which are not, insights into habitat associations will continue to be ambiguous, to have poor explanatory power, or to lack generality.

Problems with Polygons

Factors that may contribute to the plethora of post hoc analyses of animal habitat relationships include the ready availability of habitat data digitized as polygons and the widespread use of GIS software that depicts landscapes as polygons. Whereas habitat components that contribute to the fitness of animals are commonly modeled on very fine scales (e.g., food-producing plants, extent of escape cover), landscape-scale data simply do not exist for such fine-scale habitat components. Landscape researchers commonly assume a correlation between fine-scale components of habitat and the much coarser landscape data that are available on vegetation associations. When scales differ greatly, such assumptions become dubious.

In fact, reliance on typological definitions of community types for defining habitat, notions of habitat as patches, and the prevalence of inductively derived habitat definitions have created a normative model of habitat among practitioners of landscape ecology that is usually false. The model is simplistic and assumes homogeneity within habitat patches, assumes the existence of distinct boundaries for patches, has no explicit, rigorously established ties (either theoretical or empirical) to the fitness of animals, and is

most commonly expressed in GIS applications as a polygon. In the field of landscape ecology, we suggest that the characteristics of polygons have come to shape notions of habitat as much as the biology of the animals being studied. To illustrate our point, we extend the analogy of a human house as habitat that Garshelis (2000) described to illustrate difficulties in evaluating habitat selection. Before doing so we acknowledge that modern human behavior and habitations are limited analogs for wild animals and their habitats, and the parallels we draw here are very general.

Garshelis (2000) presented an imaginary house comprising three areas defined by their uses: the kitchen (meal preparation and eating), the bedroom (sleeping), and other rooms (all other activities, Fig. 5.1A). Note that each of these rooms represents a typological representation of its usefulness, without defining the details within each room that contribute to its use (a table in the kitchen, a bed in the bedroom), and therefore each room can be portrayed as a homogeneous "habitat" patch. Garshelis assigned a percentage of use to each of these rooms and calculated a habitat selection index based on the availability (area) of each room. By making the kitchen larger and the other rooms smaller without changing their percentage of use, he noted that the selectivity index changes, with the presumably improved kitchen counterintuitively becoming less important and the other rooms becoming more important despite being made smaller (Table 5.1). Based on this observation, he concluded that the sensitivity of the selection index to availability of habitat makes use-availability studies fatally flawed. Yet how much of his conclusion is based on use-availability methods and how much on the way he defined habitat?

A graduate student with a small kitchen once noted that increasing the size of her kitchen would do little to increase her use of it until her refrigerator was fixed. Her observation illustrates the point nicely that even though a kitchen contains all the components necessary for eating, more kitchen does not necessarily equate to more opportunities to eat. Therefore, a kitchen is an abstraction of the activities that occur within it. What would change if the value of areas within a house to human activities were portrayed, without regard for the type of the room? In this case we could depict the relative contribution of key resources (e.g., refrigerator, kitchen table, bed, sofa) to the well-being of the house's occupant. To avoid making assumptions of how the resident of this house will use the kitchen in general to maintain her well-being, we can predict how she will use the refrigerator, the stove, the kitchen table, and travel areas, based on what we know about human behavior. From these predictions of the occupant's behavior, we can deduce how the resources

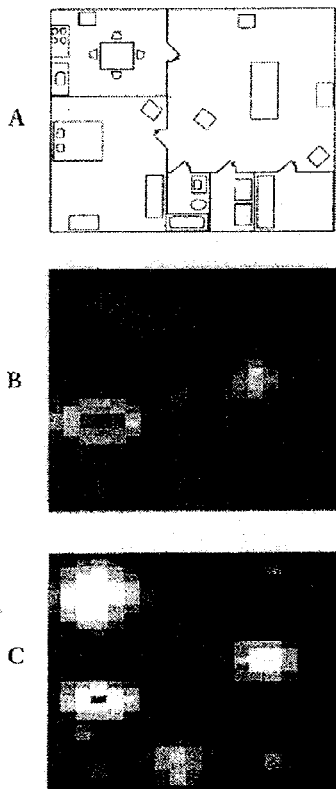


Figure 5.1 Schematic of a house including (A) rooms and objects in rooms that are used by the occupant of the house, (B) a continuous fitness surface depicting what we might guess the value (ranging from dark hues, low value, to light hues, high value) of each portion of the house is to the occupant based on the objects contained in each room and our knowledge of human behavior, and (C) use (ranging from dark hues, low use, to light hues, high use) of the house by the occupant over time, depicted as a utility distribution.

affect the occupant's well-being. These deductions about well-being must be context specific (i.e., the kitchen table will contribute more to the occupant's well-being if the refrigerator works than if it does not, and all resources in the kitchen will have less value if the house has no bed). Where a single location offers more than one resource (say, where standing in front of the stove and sitting at the table coincide in the cramped kitchen), the well-being value reflects the additive effects of multiple resources. The result can be presented

Table 5.1 Changes in how habitat selection is perceived based on whether habitat is modeled as a homogeneous type or as the value of resources to the fitness of the occupant. The analogy of a house and a human occupant is used to differentiate use of rooms defined by their function (kitchen, bedroom, other) based on available area of each room or the availability of resource values (refrigerator, bed, TV, etc.) important to the well-being (loosely analogous to fitness) of the house's occupant. Three different scenarios are presented: an unrenovated house, a renovated house where the kitchen is enlarged but the value of the resources is not increased by the enlargement, and a renovated house with an enlarged kitchen and resource values that are increased 50 percent by the enlargement (adapted from Garshelis 2000).

Rooms	Area		Resources ^a		
	% Used	% Available	Manly-Chesson Standardized Index ^b	% Available	Manly-Chesson Standardized Index
Before renovation					
Kitchen	20	10	.40	30	.20
Bedroom	50	20	.51	25	.60
Others	30	70	.09	45	.20
After renovation (no change in kitchen resources)					
Kitchen	20	20	.25	30	.20
Bedroom	50	20	.63	25	.60
Others	30	60	.12	45	.20
After renovation (kitchen resources increased by 50%)					
Kitchen	20	20	.25	39	.14
Bedroom	50	20	.63	22	.64
Others	30	60	.12	39	.21

^a Values of room components to the occupant's well-being were assigned on a 0 (no value) to 5 (high value) scale.

^b Percentage used/percentage available, standardized across rooms to sum to 1.

as a continuous surface representing the potential contribution of each place in the house to the occupant's well-being (Fig. 5.1B).

To construct such a surface, one must know (or be able to hypothesize) in advance how a given resource contributes to the subject's well-being (or fitness) and which resources are ultimately limiting. This approach changes the definition of the "habitat" within the house substantially because rooms are no longer depicted as homogeneous polygons with hard boundaries. The contribution of resources within each room to well-being is no longer

abstracted but modeled explicitly based on what is known or hypothesized about the occupant and her needs. In addition, we also no longer have difficulty with artificial polygon boundaries or with the permeability of polygons to movement between rooms. Now, the physical environment (walls) defines the hard boundaries to movement, and the value of explicit travel corridors (via doors) connecting resources can be depicted.

This depiction of habitat changes what we can learn from studying the occupant of the house in at least two ways. First, if we remain interested in the use of specific rooms (habitat types) but define the rooms according to the value of their resources, we can use relative availability of resources between rooms to evaluate use of the rooms by the house's occupant. This approach differs substantially from a typological approach because it does not assume that a given type has uniformly distributed resources or that all patches of a given type are equal. Habitat availability is no longer a simplistic function of the area of the type. Rather, the availability of the resources that contribute to well-being within one room are considered relative to the resources contained in the others. Obviously, when this is done, simply changing the size of the room does not affect an assessment of the value of the room (Table 5.1). The essential resources available within the kitchen (e.g., refrigerator, stove) that contribute to well-being are not changed when the kitchen is enlarged. By eliminating the tenuous assumption that resources are proportional to area that is implicit in a typological definition, we also eliminate the cause for the counterintuitive results of the use-availability analysis performed by Garshelis (2000). The problem was with the way habitat was defined, not the analytical technique used to understand its use. We are not arguing here for the validity of use-availability designs but that a sound biological foundation improves the rigor and performance of any analysis of animal behavior.

Use-availability data can be used to test the accuracy of a fitness surface model. Suppose increasing the size of a really cramped kitchen can make it better able to serve its purpose, as Garshelis (2000) suggested. If our model incorporates comfort for eating areas and multiple uses of comfortable areas (the table can now be used for studying), the area around the kitchen table will gain in value when the kitchen is enlarged. Suppose the remodeling increases the value of resources in the kitchen by 50 percent, but the occupant does not use the larger kitchen more, as was presented by Garshelis. The resulting use-availability analysis indicates a decline in selection for the enlarged kitchen and a counterintuitive increase in preference for the unchanged or smaller other rooms (Table 5.1). What are we to make of this situation, where a predicted increase in resource benefit did not increase its

use? Two possible conclusions exist. The value of a resource may be unrelated to the amount of time the occupant uses it. However, people generally do increase use of space when comfort and functionality increase. Alternatively, we modeled the value of the resources incorrectly, and the behavior of the occupant has allowed us to test and reject at least this part of our model. Clearly, this is the value of a priori modeling of fitness value in habitat; we can test our models as hypotheses, modify them accordingly, and then retest the new model with new data. When we predict the values of resources in a house based on what we know of the occupant, we can test our predictions using the occupant's behavior. This important step in modeling habitat is logically impossible and absolutely absent using a posteriori, correlational analyses. The failure of such analyses tells us nothing about why a model failed or how it might be modified or improved.

The second way to understand how habitat as a fitness surface changes our understanding of the house's occupant is to do away with the notion of rooms (habitat types) entirely. Obviously, people characterize rooms by types, but how much these characterizations structure our daily behaviors is not always obvious. Do we go to the kitchen when we are hungry, or do we go to the refrigerator? The answer to both is "yes" as long as we do not also have a refrigerator in the basement where we also keep food. In this latter case, a scientist interested in understanding the foraging behavior of people would be wrong to assume it occurred only in the kitchen (and would be mystified by the unexpected amount of time spent by the occupant in a certain corner of the basement). If a fitness surface can be estimated (Fig. 5.1B) and known locations or a utility distribution derived from known locations of the occupant exist (Fig. 5.1C), by far the most rigorous analysis of predicted habitat associations for an individual is to compare use by the occupant and the distribution of resources directly. In this approach, we can evaluate directly our biological understanding of the critical resources important to the occupant, dispensing with artificial typological abstractions. Because fitness relationships have been modeled a priori, we can have more confidence that behavior consistent with our models reflects true cause-and-effect fitness relationships than if we relied on inductive correlations.

Scaling Up

The biological merits of typological, patch-based definitions of habitats vary with spatial scale and ecological resolution because the assumptions of internal homogeneity and hard boundaries are not universally appropriate. By

contrast, habitat defined as a fitness surface has the same biological meaning across all spatial scales and ecological resolutions. Let's extend the house analogy to include houses (habitats) occupied by other people, say, the immediate neighborhood. Assuming all homes are of equal value, we can see the emergence of a more homogeneous resource distribution that begins to approach a polygon depiction (Fig. 5.2). Typological definitions still remain problematic at this spatial resolution, however, because they are limited in what they can tell us about the behaviors or distribution of the people in the neighborhood. They tell us nothing about how people travel between houses, which travel routes are used more often, or whether all living rooms are of equal value within the neighborhood. The simple designation of "living room" fails to explain the distribution of men within the neighborhood on Sunday afternoons during football season when one living room in the neighborhood has a big-screen TV, lots of chairs, a cooler of beer, and a coffee table full of munchies and others do not. Modeling fitness (or well-being) directly allows one to incorporate important differences in the distribution of resources for the entire neighborhood. Approximating this level of information with discrete habitat classes in a way that can explain accurately the behavior and distribution of people within the neighborhood would be very difficult indeed.

Scaling up further, let us consider the neighborhood in the context of the city that contains it. Now we can see a convergence between the city depicted as a homogeneous patch and as a fitness surface (Fig. 5.2), and indeed the patch depiction may be sufficient for modeling some important habitat relationships at this resolution. Some choices for residents at this level are reduced essentially to city or noncity, and the average habitat characteristics within the city may be enough to explain very general population trends for its occupants. Nonetheless, for occupants of the city, it would tell us nothing about good places to live, where shopping is convenient, and so on. The patch model would work best if this were a lone city that filled an isolated island, and distinctions between habitat within (dry land) and without (water) the city are starkest, and justifications for the hard boundary (the shoreline) are strongest. In a more complex environment, questions of clines connecting the city to adjacent rural or suburban habitats, connectivity to other cities, and so on again necessitate simplifying assumptions about how inherently continuous distributions of resources can be modeled as discrete classes. One may argue that at broad scales and coarse ecological resolutions such assumptions are justifiable, but we suggest that this is not always so, and such justifications should be addressed explicitly by those who make

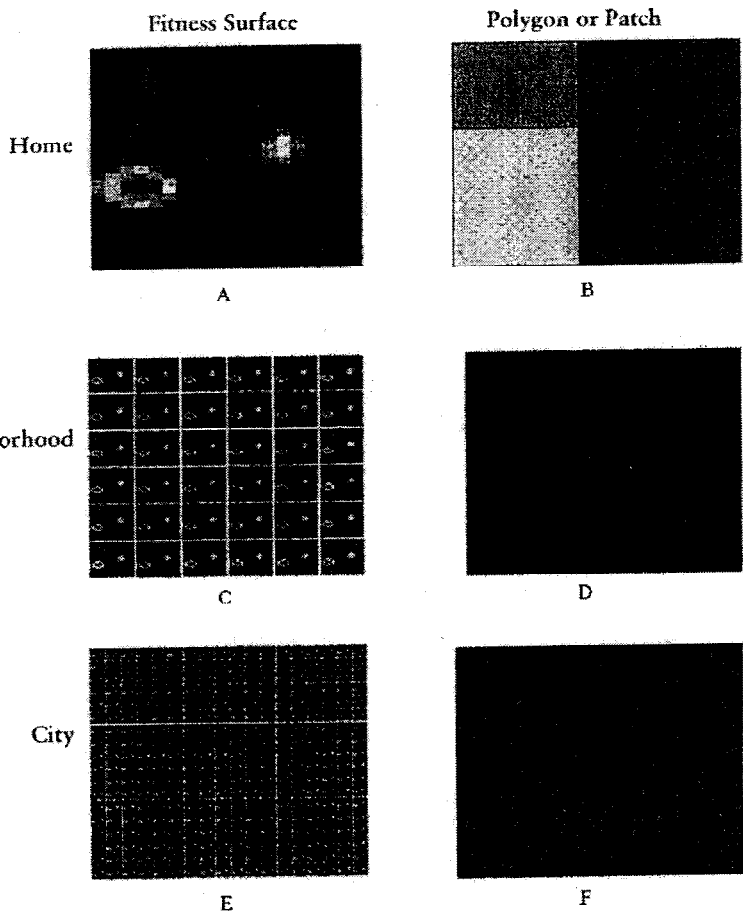


Figure 5.2 Comparison of hypothetical depictions of habitat for humans based on a fitness surface and on habitat types across scales, from house, through neighborhood (a collection of houses), to city (a collection of neighborhoods). A fitness surface depicts the distribution of resources that contribute to the well-being of human occupants within a habitat, whereas a habitat type is portrayed as a homogeneous patch or polygon based on a classification scheme (e.g., room types within a house, a neighborhood, or a city).

them and not established by the form of the data used. As an alternative, scaling up a fitness surface to a broad scale contains in essence the same biological information as a patch depiction but has the added capability of dealing with habitat heterogeneity within the large patch or with complex relationships between the patch, its surroundings, and other patches.

We have stretched the house analogy for definitions of habitat based on fitness quite far. Nonetheless, this analogy has illustrated that any definition of habitat models is, to one degree or another, the relationship between resources within that habitat and the fitness of an animal that occupies it. To whatever extent a definition abstracts or generalizes this relationship, it makes simplifying assumptions. Any habitat model simplifies, but we have shown that traditional depictions in landscape ecology of habitat as homogeneous patches of specific types have biological validity only at certain spatial scales and only for certain ecological questions. In contrast, we have presented a conceptual model of habitat as a fitness surface that retains its biological information across all scales and questions. By modeling fitness relationships directly, this approach makes fewer assumptions because it abstracts less. Because of this, and because fitness relationships can be modeled a priori as part of a hypothetico-deductive study design, robust insights can be expected from using this approach to study relationships between animals and their habitats. Although we have focused on behavior (habitat use) as our indicator of fitness in our examples, nothing prevents this approach from being applied to more direct measures of fitness such as reproduction and survival. In the next section, we present a brief overview of insights derived from an application of the fitness surface concept.

Fitness Surfaces and Black Bears

We have modeled habitat as a fitness surface and used it to infer much about the ecology of black bears living in the Pisgah Bear Sanctuary (35°17' N, 82°47' W) in the mountains of western North Carolina. Before proceeding further, we wish to acknowledge that when it comes to studying fitness relationships between wild animals and where they live, black bears do not rank high on the list of possible candidate species for study. Bears occur in low densities, they are elusive and live in difficult terrain, and they are long-lived and reproduce slowly. Consequently, detailed information on survival, reproduction, energetics, and behavior is extremely difficult to obtain. However, our understanding of habitat as a fitness surface developed mostly through serendipity as part of our work with bears. One works with the tools one has at hand.

Mitigating the difficulty of obtaining information from bears is the fact that intensive research on bears living in Pisgah has been ongoing since 1981. Over 20 years, approximately 225 bears have been captured nearly 400 times. Many of these bears were fitted with radio collars and tracked under

an intensive telemetry protocol that resulted in up to 400 location estimates for individual bears in a given year. Both the frequency and accuracy of locations in the sanctuary were facilitated by the Blue Ridge Parkway, which allowed rapid travel between conveniently located listening points and, because of its elevated location in the sanctuary, minimized the effects of the mountainous terrain on signal bias. Large numbers of accurate locations allow us to estimate the home ranges of bears with a high degree of detail and confidence. Another advantage to studying bears and their habitat is that black bears are predominantly vegetarian, and their diet varies predictably across seasons in the southern Appalachians, with predictable foods making up the bulk of the diet during each season. All food sources can be modeled with reasonable accuracy as fixed in space.

Modeling a Fitness Surface for Pisgah Bears

Zimmerman (1992) and Powell et al. (1997) developed a habitat suitability index (HSI) for black bears living in the southern Appalachians. They developed the index directly from the literature, without using any data collected on bears in the Pisgah Bear Sanctuary, and thus their index represented an a priori hypothesis for the relationship between bears and their habitat. This index was also explicit about how habitat components should contribute to the fitness of bears. The HSI comprises three life requisite variables essential to the fitness of bears: food, den sites, and resources that facilitate escape. Each of these, in turn, is constructed of habitat components (Table 5.2), whose relationship to habitat suitability for black bears is explicitly modeled. The index is spatially explicit, so that relative proximity to food sources and roads and the area of roadless forest are important. Much of the HSI can be modeled using GIS interpretation of U.S. Forest Service inventory data, digital elevation models of terrain, and digital line graphs of linear features such as roads and hydrology. Approximately one third of the HSI components must be estimated from field sampling (Table 5.2). Thus, the HSI consists of layered spatial depictions of the potential contributions of individual habitat components to the fitness of bears, and in its final form it is a continuous map of values that range from 0 (low quality and little potential contribution to fitness) to 1 (high quality and much potential contribution to fitness).

Between 1984 and 1994, we sampled 122 field sites systematically located throughout the sanctuary and used these data, along with data collected from 46 clear-cuts, aerial photographs, and topographic maps, to develop

Table 5.2 Habitat components used to calculate a habitat suitability index for black bears living in the southern Appalachians.

<i>Habitat Component</i>	<i>Relationship to Fitness of Bears</i>	<i>Method of Sampling</i>
Number of fallen logs/ha	Abundance of colonial insects	Field sampling
Anthropogenic food source	Availability of food from human point sources	Aerial or ground survey
Distance to anthropogenic food source	Costs of traveling to human food source	GIS
Distance between anthropogenic food source and escape cover	Risk of acquiring food from human sources	Topographic maps
Distance to perennial water	Abundance of grasses and forbs in spring	GIS
Percentage cover of <i>Smilax</i> spp.	Availability of fruit in fall	Field sampling
Percentage cover in berry species	Availability of fruit in summer	Field sampling
Presence of red oak species	Availability of squaw root in summer	Forest inventory data or GIS
Forest cover type	Availability of hard mast in fall	Forest inventory data or GIS
Age of stand	Productivity of hard mast	Forest inventory data or GIS
Number of grape vines/ha	Availability of fruit in fall	Field sampling
Distance to nearest road	Risk of encountering humans	GIS
Area of conterminous forest not bisected by roads	Risk of encountering humans	GIS
Percentage closure of understory	Escape cover	Field sampling
Slope of terrain	Escape cover, availability of caves for denning	GIS
Area in <i>Rhododendron</i> spp. or <i>Kalmia</i> spp.	Availability of thickets for denning	Aerial photo
Number of trees ≥ 90 cm DBH ^a /ha	Availability of large trees for denning	Field sampling

^a Diameter breast height (DBH)

an HSI map for the sanctuary. The map shows the predicted quality of habitat (potential contributions to fitness) for each 30- × 30-m pixel in the sanctuary (Fig. 5.3A). We reemphasize that this surface represents an a priori prediction of how each point in space may contribute to the fitness of a bear. It was not derived inductively from correlations between bear locations and arbitrary habitat types, it models first principle relationships between bears and components of their habitat that should be directly related to fitness, and its basis in typological habitat definitions is both minimal and biological (e.g., the use of forest cover type for fall foods reflects the importance of oaks to hard mast production in different forest types and assumes nothing else about contributions of forest types to the fitness of bears). Furthermore, the HSI map for the sanctuary represents a continuous surface that would be difficult to portray as polygons without losing information and even more difficult to develop strictly from polygon-based representations of habitat types such as forest cover (Fig. 5.3B).

Fitness Surfaces and Insights into Bear Biology

The HSI, expressed as a fitness surface, represents a hypothesized relationship between habitat and bears that can be tested as part of a hypothetico-deductive study design. Because the biological meaning of fitness surfaces should be independent of scale, we hypothesized that the HSI should be able to predict behavior of bears on multiple scales, comparable to Johnson's (1980) three orders of habitat selection. This proceeds from a logical extension: If bears prefer habitat that confers high fitness, then on the finest scale they should use areas within their home ranges proportional to the fitness value of those areas (third-order selection), on an intermediate scale they should choose from these landscapes only the best available sites to include within their home ranges (second-order selection), and on a broad scale they ought to choose portions of the landscape that contain high-quality habitat for the general location of their home ranges (first-order selection).

To assess third-order selection of habitat by bears, we evaluated the ability of HSI values to predict habitat preferences of 127 bears (38 adult males, 32 juvenile males, 55 adult females, and 2 juvenile females) within their home ranges and found that preference (estimated as $[\text{use} - \text{availability}] / [\text{use} + \text{availability}]$; Powell et al. 1997) was strongly related to HSI values ($p < .0001$, $r^2 = .45$; Fig. 5.3B). We have not compared values of the HSI with data on survival or reproductive success for individual bears because even after 20 years of work, we do not have enough data to do so.

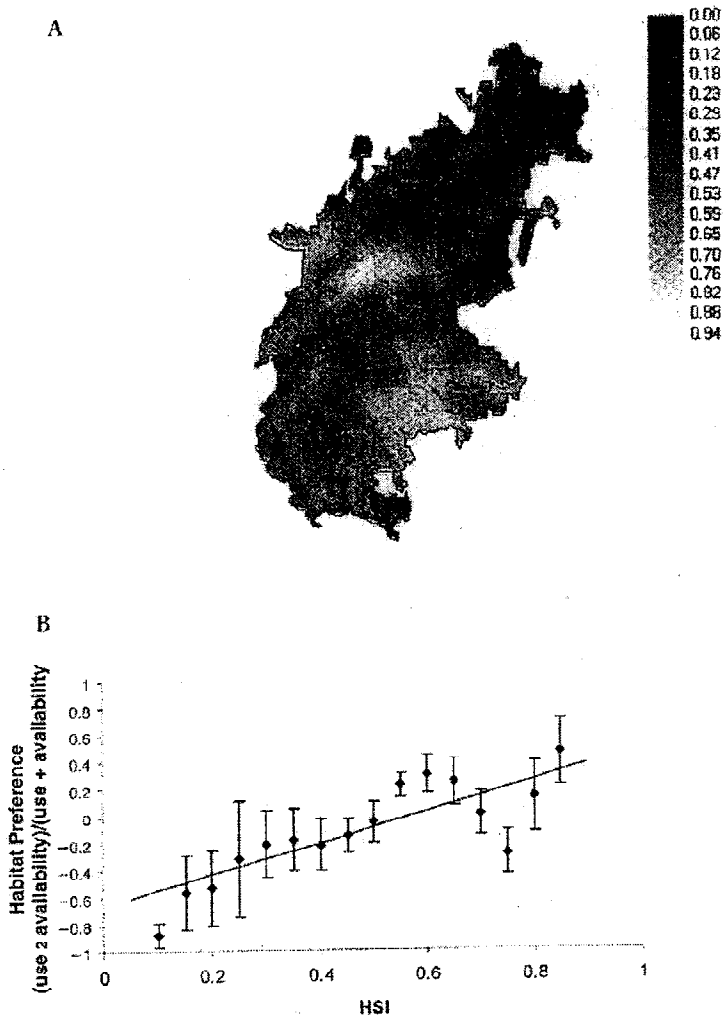


Figure 5.3 A habitat suitability index (HSI) for black bears in the southern Appalachians depicted as (A) a fitness surface for the Pisgah Bear Sanctuary in western North Carolina (HSI values range from 0, poor quality, to 1, high quality), and (B) the relationship between the HSI and habitat preferences of black bears living in the

Nonetheless, because we modeled the fitness relationship a priori, assumed (with justification) that bears would spend more time in areas that contribute more to their fitness, and found that bears use areas in direct proportion to their HSI value, we have good indirect evidence that the HSI is related to fitness.

Bears respond differently to the distribution of resources on the landscape depending on their age and sex. Adult males range widely (mean home range size of about 45 km²), and the size of their home ranges appears to be affected primarily by access to females during the breeding season and secondarily by food resources (Powell et al. 1997). Adult females have smaller home ranges (about 16 km²) whose sizes are affected most by the availability, location, and productivity of food (Powell et al. 1997). Because of this strong tie to food resources, we wanted to test whether the entire HSI or just the food component, F , of the HSI better predicted behavior of adult females. Therefore, we evaluated F against habitat preferences of adult females and found that it had an even stronger relationship ($p < 0.0001$, $r^2 = 0.78$; Mitchell 1997). We can deductively infer from this test that food resources are more important to the fitness of adult females living in the Pisgah Bear Sanctuary than a combination of food, denning, and escape resources. Our tests not only showed that our fitness surface can predict third-order habitat selection by bears, but also gave us biological insights that would be impossible to derive with the same level of rigor from inductive analysis.

To assess second-order habitat selection of bears, we developed a model of optimal selection of sites within that area for inclusion in the home range, based on habitat portrayed as a fitness surface (Mitchell 1997). Because of the particularly strong relationship between the home ranges of adult females and food resources, we depicted the fitness surface for Pisgah as a grid of 250 × 250-m cells (approximating our telemetry error of ±260 m), each cell was assigned its own value of F , and we modeled only the home ranges of adult females. For our home range model, we assumed that energy expended for travel diminishes the net value of resources distant from the center point. Because bears have home range cores (Powell et al. 1997), we modeled the fitness value of any given cell as the F value assigned to it (potential contribution of the cell to a bear's fitness) divided by the distance of that cell from the center point or core of the bear's home range (yielding an estimate of the average net contribution of that cell to the bear if it included it in its home range, F). Discounting the value of a distant resource by its distance has a long history in optimal foraging research (Stephens and Krebs 1986). The notion that travel distance should affect whether an animal selects an area

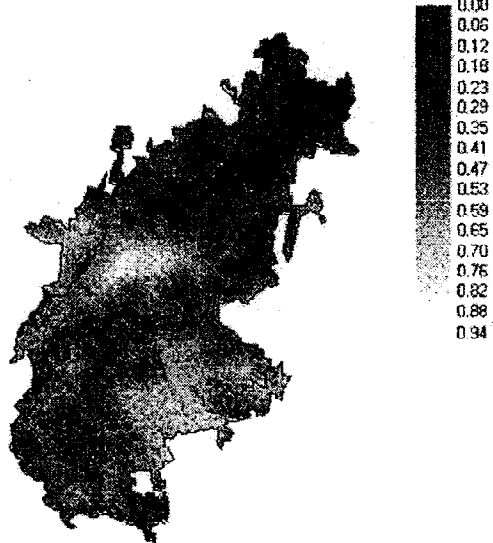
for inclusion in its home range strongly argues for a depiction of habitat as a continuous surface, where resource values can be discounted easily by distance between any two points in space. Such an approach would be difficult for landscapes comprising large polygons. For example, in discounting for distance, does one measure distance to the center of the polygon or to the edge? How would the high value of habitat on the near side of a large polygon be distinguished from the lower value on the far side? These are all problematic questions.

Dividing all cells by their distances from the center cell yields a highly kurtotic distribution where F is high near the center but declines exponentially with distance from the center. We modeled second-order habitat selection as the selection of cells in descending order of F until the home range contains fitness resources sufficient to satisfy a hypothesized minimum threshold for survival and reproduction. If all bears used these criteria only to choose home ranges, all would choose the same home range at the single best spot on the landscape. Clearly, bears do not do this. Therefore, we depleted the resources available to other bears after an initial bear selected its home range. Thus, resources on a landscape available to support a bear's home range change as more home ranges are added. Areas with high fitness values can support a high density of bears, but as these areas become depleted, bears will incorporate areas of lesser value into their home ranges, tending toward an ideal free distribution (Fretwell and Lucas 1970).

We used this home range model to generate simulated home ranges based on F for each of 42 home ranges of adult females living in Pisgah from 1981 to 1994. For each home range of a bear, F values were generated by dividing F values by their distance from the center (core) of the bear's true home range. Cells were then selected based on their F values until hypothesized minimum thresholds of accumulated F were reached. We compared the similarity of each of the simulated home ranges with the true home range using an index of spatial similarity, S (Mitchell 1997) that ranges from 0 (no similarity) to 1 (complete similarity). Models predicted the home ranges of bears with reasonable accuracy (Fig. 5.4C). When we considered the simulated home ranges that best fit true home ranges, average S was .80. Our models were able to emulate closely second-order habitat selection by bears using a fitness surface, which would not have been possible had we defined habitat typologically (Fig. 5.4A versus 5.4B).

We did not directly evaluate first-order habitat selection. As an indirect way of assessing how bears placed their home ranges on the landscape, we evaluated the spatial dispersion of their home range centers. At broad scales

A



C

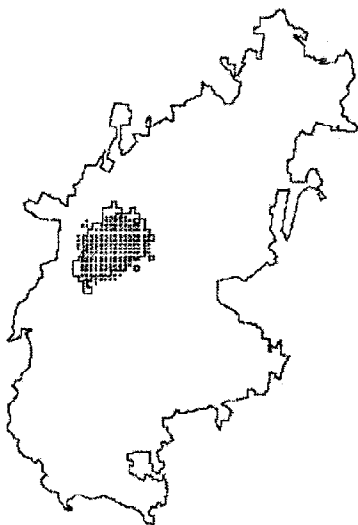
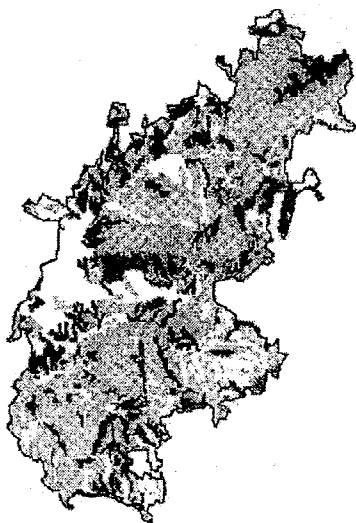
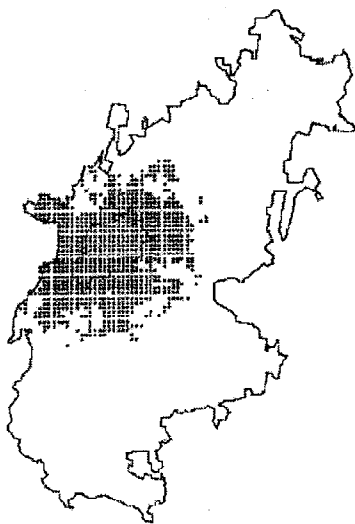


Figure 5.4 Habitat depicted as (A) a fitness surface for the Pisgah Bear Sanctuary and (B) a function of forest type, presented with the results of home range simulations for female bear 96 in 1984 generated from each of the depictions of habitat (C for the fitness surface, D for the definition based on forest type). Habitat values range from 0, poor quality, to 1, high quality. The solid outline within

B

0.00
0.06
0.13
0.19
0.25
0.31
0.38
0.44
0.50
0.56
0.63
0.69
0.75
0.81
0.88
0.94
1.00

D



the boundaries of the sanctuary in figures C and D depicts the true home range of bear 96; the dots depict the simulated home ranges estimated by an optimal home range model. The model selected patches for inclusion in simulated home ranges based on habitat quality and the distance of patches from the center of the home range.

one can expect home ranges of animals to cluster on areas that confer high fitness. We used our home range model to generate 100 simulated home ranges on the fitness surface of F for the sanctuary. Instead of using the center points of observed home ranges as starting points for our models as we did before, we used moving-windows analysis of the fitness surface (Isaaks and Srivastava 1989) to identify the best region of the sanctuary for establishing each home range center. Beginning with windows of large spatial extent, we identified the region within Pisgah with the highest average F value. Within this region we repeated the moving-windows analysis on increasingly finer spatial scales until the single point in space with the highest F value across all grains was identified. Each time a simulated home range was established, resources within that home range were depleted, changing the distribution of F for subsequent home ranges (Mitchell 1997). We then compared the spatial dispersion of simulated home range centers with observed home range centers of adult female bears that lived in Pisgah from 1981 to 1994. Spatial distributions for both simulated and true home ranges were clumped (mean/variance ratio was $.37 \pm .14$ for simulated home ranges and $.46 \pm .10$ for true home ranges) around areas of high F values. The similarity in spatial distribution between simulated and true home ranges suggested that our models mimicked first-order habitat selection by bears. Because of the broad scale of first-order selection, it would be interesting to see whether our results could be duplicated using typological definitions of habitat. The convergence of a fitness surface with a typological definition of habitat at broad scales (Fig. 5.2) suggests that this is a reasonable possibility.

We have demonstrated that a priori modeling of habitat as a fitness surface has allowed us to assess the behavior and distribution of bears across three spatial and behavioral scales: placement of home range locations on a landscape of cells, selection of individual cells for home ranges, and cell use within home ranges. To have such predictive capability, the relationship between our fitness surface and the behavior of bears must capture a biological pattern, a fitness relationship, beyond what a simple correlation between use and habitat types can portray. It is difficult to imagine a typological substitute that would accomplish the same objectives across all three orders of habitat selection. Few of the components of the HSI could be reasonably assigned to a broad habitat type and are for the most part distributed in space independently of each other. For instance, overstory vegetation is commonly used as a habitat class, but maps of the HSI and overstory types for our study area (Figs. 5.4A and 5.4B) are distinctly different. Although overstory may be a good predictor for some elements of bear habitat (e.g., production of

hard mast), it clearly captures little of the information that the entire HSI does. Given how closely our home range models were able to approximate the behavior of bears, we doubt that the same or better results could be achieved by defining habitat as polygons depicting overstory vegetation.

Making the Match

Our home range models approximate closely the behavior of bears on multiple scales for several important reasons that illustrate the points we have made in this chapter. First, our definition of habitat was biologically based and modeled directly components of habitat that contribute to the fitness of bears. This differs greatly from a typological definition, which assumes these largely independently distributed components of habitat can be abstracted into discrete habitat classes. Second, we portrayed habitat as a continuous fitness surface, thereby avoiding assumptions of homogeneity within habitat polygons and avoiding the problems of defining boundaries for patches or polygons. Third, our habitat model was developed and tested as an a priori hypothesis about the fitness relationship between bears and where they live. We have more confidence in our understanding of why bears behave in accordance with our predictions than we could were we relying on inductively derived, a posteriori correlations. Importantly, this depiction of habitat, without modification, yielded insights into the biology of bears on three different scales. Much has been written about the role of scale in understanding habitat relationships on landscapes (Wiens 1989), but little has been done to define that role. As long as we use a definition of *habitat* whose biological meaning is itself scale dependent, our conceptual and technical approaches will limit our understanding. Habitat depicted as a fitness surface offers in a single definition a biologically robust tool for understanding animal-habitat relationships across spatial scales and ecological resolutions.

Admittedly, using hypothetico-deductive research to develop a model of habitat as a fitness surface is an intensive, front-loaded process. Management agencies may find the time and effort needed to develop models, to estimate, and then to test fitness surfaces impractical or difficult to justify; inductive use of typological definitions is simpler and less time consuming. Nonetheless, the long-term trade-offs between the two approaches are worth considering. We have demonstrated that the efficacy of a typological definition of habitat as patches depends on a close match between the spatial scale and ecological resolution of the animal-habitat associations being modeled. We have also demonstrated the weaknesses of assuming that a posteriori

correlations between animals and abstract habitat classes reflect true fitness relationships. To achieve management objectives based on a single inductive, typological definition of habitat, a manager must be fortunate enough to model the right ecological relationship, at the right scale, using an untested habitat classification scheme that by chance reflects first-order fitness relationships. The likelihood of any of these fortuitous events occurring individually, much less in concert, can never be known under this approach; no assurance can be offered that management practices based on it will achieve their desired ends. Similarly, no assurance exists that they will not result in very unintended and undesirable consequences, either. A trial-and-error approach to evaluating different typological habitat definitions suitable for the scale and ecological relationships of interest, to arrive at one inspiring confidence as a basis for management actions, will easily be more exhaustive than simply modeling fitness and testing the model. Contrast the correlation approach with a fitness surface approach, in which habitat definitions are based on tested biological relationships and can yield robust predictions across spatial scales and ecological resolutions (achieving an economy of scales, so to speak). If one's objective is to obtain models of habitat that in the long term are cost-effective, are biologically robust, and provide sound foundations for successful management across multiple landscape scales, we suggest that adherence to traditional correlational approaches to modeling habitat is the riskier choice. At the very least, we recommend that both researchers and managers step back from the breathtaking pace of developments in landscape ecology and reassess the assumptions that underlie some of our commonly and uncritically accepted paradigms such as how habitat is defined and portrayed on landscape scales. We will have achieved our purpose if this chapter causes landscape ecologists to pause and think every time they see a polygon labeled as animal habitat.

Summary

A dominant paradigm in landscape ecology is depiction of habitat as a patch, with internal homogeneity and a distinct boundary. This definition is based on the ready availability of GIS data on vegetative communities classified from remote sensing, the role of patch theory in laying key foundations of landscape ecology, and the prevalence of a posteriori, correlative approaches to describing habitat of animals. Whereas each of these factors is appropriate or necessary for different management approaches, conceptual pursuits, or research questions, the combination of the three com-

monly seen for most depictions of habitat within landscape ecology has created a normative model of habitat among landscape ecologists that is usually false. Because any definition of habitat is, directly or indirectly, based on the fitness of animals, we advocate a definition of habitat that proceeds from biological first principles, where the distribution of resources critical to the survival and reproduction of animals is depicted in space, which we call a fitness surface. Habitat modeled and mapped in this way resembles a continuous (as opposed to a classified) surface. Assumptions about relationships between vegetation classes and key resources are minimized, as are the simplifying assumptions of depicting habitat as patches. Furthermore, unlike patch-based definitions of habitat, fitness surfaces are scale-independent and therefore should capture biological meaning at any spatial resolution. We suggest that such models must be developed a priori and tested with data on animals to maximize the scientific rigor of habitat definitions and thereby the confidence that researchers and managers can have in insights derived from them.

In this chapter, we demonstrated the weaknesses of depicting habitat as homogeneous patches that abstract biological reality in ways convenient to our methods and showed that depictions of habitat as a fitness surface are much less susceptible to these problems. We further demonstrated how a fitness surface, developed as an a priori hypothesis, can be used to derive insights on the ecology of black bears, at multiple spatial scales, that could not be achieved using traditional, patch-based definitions of habitat common in landscape ecology. The selection of the best definition to use in any research or management situation should be based on spatial scale and ecological resolution of interest. Because a fitness surface is generally more robust than patch-based definitions for both of these criteria, we recommend modeling habitat as a fitness surface.

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