Some Basic Principles of Habitat Use

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Abstract

The concept of habitat is a cornerstone in the management of wildlife. However, the understanding and management of habitat has been confused with loose terminology and flexible definitions that make communication difficult among biologists and with the public. My objective is to present some definitions related to habitat, summarize principles related to habitat use, and briefly discuss their implications to habitat management. I define habitat, habitat use, habitat selection, habitat preference, habitat availability, habitat quality, unused habitat, and critical habitat. Concepts related to habitat that biologists should be aware of include the concept that habitat has a specific meaning, habitat is species specific and scale dependent, and measurements matter. The management of habitat will be of little value unless biologists first determine an animal's habitat use patterns within a specific environment and then consider the evolutionary and human disturbances that influence it.

Introduction

In the simplest form, the habitat of an organism is the place where it lives (Odum 1971). This simple concept of habitat is informative, but one needs to go farther when discussing habitat in relation to wildlife management. Giles (1978) presents a wildlife-habitat-people triad that represents the three major aspects of wildlife management as equal and interactive. Thinking about any species is difficult without considering the species habitat or the human created influences, which so drastically influence them.

Most biologists would have a difficult time visualizing any organism without also visualizing its habitat. They go hand in hand. However, understanding habitats and managing them is not as simple even though there is an abundance of literature that addresses habitat (Verner et al. 1986, Hall et al. 1997). Leopold (1933) stated that "science had accumulated more knowledge of how to distinguish one species from another than of the habits, requirements, and inter-relationships of living populations." One of the earliest works examining the habitat of a species was Stoddards' (1931) study of bobwhite quail (*Colinus virginianus*). Since then, the field has advanced significantly. Leopold (1933) outlined the evolution of wildlife management as progressing through 5 stages: laws and regulations, predator control, reservation of land and refuges, artificial replenishment, and environmental controls. The last step could be expanded or a sixth step added: habitat management and control. However, as biologists' and land managers' understanding of habitat increases, the use of concepts and terms is not consistent. This distorts the communication among scientists in our disciplines, the lay person, and confuses the public because we give ambiguous, indefinite, and non-standardized responses to ecological inquiries in legal and public situations. All one has to do is quickly glance at the literature to see the different uses of terminology in relation to habitat (Hall et al. 1997). My objective is to summarize some of the basic definitions related to habitat, principles related to habitat, and briefly discuss the management of habitat.

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Habitat Terminology

Hall et al. (1997) examined how recent (i.e., 1980-1994) authors used habitat-related terms by reviewing 50 papers from peer-reviewed journals and books in the wildlife and ecology fields that discussed wildlife-habitat relationships. In their review of each paper, Hall et al. (1997) noted if habitat terms were defined and evaluated the definition(s) against standard definitions presented by Morrison et al. (1992) and Block and Brennan (1993), which were derived from Grinnel (1917), Leopold (1933), Hutchinson (1957), Daubenmire (1968), and Odum (1971). Of the 50 articles reviewed, only 9 (18%) correctly defined and used terms related to habitat. The following terms and definitions (Hall et al. 1997) are proposed as standard terminology.

Habitat

Habitats are the resources and conditions present in an area that produce occupancy, including survival and reproduction, by a given organism. Habitat implies more than vegetation or vegetation structure. It is the sum of the specific resources that are needed by organisms

(Thomas 1979). These resources include food, cover, water, and special factors needed by a species for survival and reproductive success (Leopold 1933). Wherever an organism is provided with resources that allow it to survive, that is habitat. Thus, migration and dispersal corridors and the land that animals occupy during breeding and nonbreeding seasons are habitat.

Habitat use

Habitat use is the way an animal uses the physical and biological resources in a habitat. Habitat may be used for foraging, cover, nesting, escape, denning, or other life history traits. These categories (e.g., foraging, escape) divide habitat but overlap occurs in some areas. One or more categories may exist within the same area, but not necessarily. An area used for foraging may be comprised of the same physical characteristics used for cover, denning, or both (Litvaitis et al. 1996).

The various activities of an animal require specific environmental components that may vary on a seasonal or yearly basis. A species may use one habitat in summer and another in winter. This same habitat may be used by another species in reverse order (Hutto 1985, Morrison et al. 1985).

Habitat selection

Habitat selection is a hierarchical process involving a series of innate and learned behavioral decisions made by an animal about what habitat it would use at different scales of the environment (Hutto 1985). Wecker's (1964) classical studies of habitat selection by deer mice (*Peromyscus maniculatus*) revealed that heredity and experience play a role in determining selection. Rosenwieg (1981) asserted that habitat selection was generated by foraging decisions. However, foraging is only one behavior driving habitat selection. Habitat may be selected for cover availability, forage quality and quantity, and resting or denning sites. Each of these may vary seasonally. If an individual or species demonstrates disproportional use for any factor, then selection is inferred for those criteria (Block and Breenan 1993). Hilden (1965) structured his ideas on habitat selection by categorizing the differences between proximate and ultimate factors. Proximate factors serve as cues an animal uses to determine the suitability of a site including the specific vegetation composition within a desired habitat. Reproductive success and survival of the species are the ultimate reasons that influence a species to select a habitat (Hilden 1965). The ability to persist is governed by ultimate factors such as forage availability, shelter, and avoiding predators (Litvaitis et al. 1996).

Several interacting factors have an influence on habitat selection for an individual (e.g., competition, cover, and predation). Competition is involved because each individual is involved in intraspecific and interspecific relationships that partition the available resources within an environment. Competition may result in a species failing to select a habitat suitable in all other resources (Block and Brennan 1993) or may determine spatial distribution within the habitat (Keen 1982).

Predation also complicates selection of habitat (Block and Brennan 1993). The existence of predators may prevent an individual from occupying an area. Survival of the species and its future reproductive success are the driving forces that presumably cause an individual to evaluate these biotic factors. With a high occurrence of competition and predators, an individual may choose a different site with less optimal resources. Once predators are removed, areas with necessary resources can then be inhabited (Rosenweig 1981).

Habitat selection is therefore an active behavioral process by an animal. Each species searches for features within an environment that are directly or indirectly associated with the resources that an animal would need to reproduce, survive, and persist. Habitat selection is a compilation of innate and learned behaviors that lie on a continuum of closed to open (i.e., learning) genetic programs (Wecker 1964). A genetic program gives an individual preadaptation to behave in a certain manner. Therefore, preadaptation to certain environmental cues plays an important role in habitat selection, but the potential for learning may exist in some species (Morrison et al. 1992).

Habitat preference

Habitat preference is the consequence of habitat selection, resulting in the disproportional use of some resources over others. Habitat preferences are most strikingly observed when animals spend a high proportion of time in habitats that are not very abundant on the landscape.

Habitat availability

Habitat availability is the accessibility and procurability of physical and biological components of a habitat by animals. Availability is in contrast to the abundance of resources, which refers only to their quantity in the habitat, irrespective of the organisms present (Wiens 1984). Theoretically, one should be able to measure the amounts and kinds of resources available to animals but in practice it is not always possible to assess resources availability from an animal's point of view (Litvaitis et al. 1994). For example, the abundance of a prey species for a particular predator could be measured, yet not all of the prey in the habitat is available to the predator because there may be factors, (e.g., ample cover) that restrict their accessibility. Similarly, Morrison et al. (1992) suggested that vegetation beyond the reach of an animal is not available as forage, even though the vegetation may be preferred. Measuring actual resource availability is important to understand wildlife habitat, but in practice it is seldom measured because of the difficulty of determining what is and what is not available (Wiens 1984). Consequently, quantification of availability usually consists of a priori or a posteriori measure of the abundance of resources in an area used by an animal, rather than true availability.

Habitat quality

Habitat quality refers to the ability of the environment to provide conditions appropriate for individual and population persistence. Hall et al. (1997) suggest that habitat quality is a continuous variable, ranging from low (i.e., based on resources only available for survival), to median (i.e., based on resources available for reproduction), to high (i.e., based on resources available for population persistence). Habitat quality should be linked with demographics, not vegetative features, if it is to be a useful measure. For example, Ables and Ables (1987) evaluated habitat quality by comparing two groups of Rocky Mountain elk in Yellowstone National Park. Unused or unoccupied habitat are useful when biologists and managers are discussing threatened, endangered, or rare species that are reduced in number to the point they cannot use some areas of habitat. However, if their numbers were greater they would use the “unused” habitat.

Critical habitat

Critical habitat is primarily used as a legal term describing the physical or biological features essential to the conservation of a species, which may require special management consideration or protection (U.S. Fish and Wildlife Service 1988). Because critical habitat can occur in areas within or outside the geographic range of a species (Shreiner 1976, U.S. Fish and Wildlife Service 1988) the definition is not ecologically specific enough to allow for easy and rapid delineation of critical areas for threatened and endangered organisms. Also, it is not definitive enough to satisfy many public interest groups concerned with U.S. Fish and Wildlife Service listing decisions. Critical habitat should be specifically linked with the concept of high quality hability; the ability of an area to provide resources for population persistence. This definition would make it an operational and ecological term and not political (Murphy and Noon 1991).

As exemplified by Hall et al. (1997) habitat terminology has been used in the literature vaguely and imprecisely. However, to be able to communicate effectively and obtain accurate information about habitats, land managers and biologists should be able to accurately measure all aspects of habitat.

General Concepts Related to Habitat Use

Definitions only help understand how organisms interact with their habitat. To be even more meaningful there are basic concepts that have evolved with the importance of habitat: habitat has a specific meaning, is species specific, is scale dependent, and measurements matter. Some of these concepts are implied in the definitions provided but additional emphasis is warranted.

Habitat Has A Specific Meaning

That biologists use the term habitat several ways is not useful, and is confusing to the public. Of course, habitats are variable but they all include the specific resources and conditions in an area that produce occupancy. This includes survival and reproduction. Habitat is frequently used to describe an area that supports a particular type of vegetation (Morrison et al. 1992). Vegetation is important but is only part of habitat that includes food, cover, water, temperature, precipitation, topography, other species (e.g., presence or absence of predators, prey, competitors), special factors (e.g., mineral licks, dusting areas), and other components in an area important to species that managers may not have identified. When habitat is viewed in this manner there are numerous components that are unique to the organism in question.

Habitat Is Species Specific

When I hear someone state “This is great wildlife habitat”, it is like walking into a brick wall and I can only guess what they mean. All the components necessary for reproduction and survival are not the same for all species and “great wildlife habitat” for one species may not even come close to serving as appropriate habitat for others. This has and will continue to be a problem because manipulations of the landscape will favor the habitats of some species but be detrimental to the habitats of others. A lot of effort has been placed on ecosystem management (Czech and Krausman 1997) in the 1990s, but when considering specific organisms the manager needs to consider their unique array of requirements for survival. With a knowledge of habitat requirements for the species of interest, the manager can make informed decisions as to how landscape alterations will influence plant and animal communities.

Habitat Is Scale Dependent

Macrohabitat and microhabitat are common terms but actually relate more to the landscape level at which a study is being conducted for a specific animal than to a type of habitat. Generally, macrohabitat refers to landscape-scale features such as seral stages or zones of specific vegetation associations (Block and Brennan 1993). Microhabitat usually refers to finer scaled habitat features. Johnson (1980) recognized this hierarchical nature of habitat use where a selection process will be of higher order than another if it is conditional upon the latter. He summarized four natural ordering habitat selection processes (Johnson 1980).

First-order selection. This is essentially the selection of the physical or geographical range of a species.

Second-order selection. The second-order selection is the home range of an individual or social group within their geographical range.

Third-order selection. This relates to how the habitat components within the home range are used (i.e., areas used for foraging).

Fourth-order selection. This order of habitat selection relates to how components of a habitat are used. If third-order selection determines a foraging site, the fourth-order would be the actual procurement of food items from those available at that site.

Based on these criteria, macrohabitat is first-order of habitat selection and microhabitat is similar to the second, third, and fourth levels in Johnson's (1980) hierarchy. Understanding these levels can have profound influences on the management of a species. For example, Etchberger and Krausman (in press) found that the desert bighorn sheep (*Ovis canadensis mexicana*) used most portions of the Little Harquahala Mountains in western Arizona (second-order selection) throughout the year but individual females used specific individual sites for lambing. In addition, site fidelity was strong for each site used by each female. Understanding the importance of these smaller areas at specific times to the population would influence the way the population is managed. This example also demonstrates that habitat use is temporal.

Measurements Matter

Habitat is not ambiguous and to understand how it interacts with a species one must ask the correct questions: What component is being measured? When is it being measured? And, how many samples are necessary for meaningful results? Obviously, to even pose these questions, one has to have knowledge of an animal's total life history strategy. Without it, measurements of habitat could be meaningless or erroneous. This is not always easy, even with well-studied species such as elk (*Cervus elaphus*). For example, for years many biologists accepted the concept that weather-sheltering effects of dense forest cover or thermal cover reduced energy expenditure and enhanced survival and reproduction. As a result, providing thermal cover for elk was a key habitat objective on elk ranges in the West. Cook et al. (1998), however, demonstrated that energetic status and reproductive success were not enhanced with thermal cover, and suggested that habitat management based on the perceived value of thermal cover should be reevaluated. The majority of the empirical support for the thermal cover hypothesis was derived from observational studies of habitat selection. Peek et al. (1982) and Cook et al. (1998) discussed and demonstrated the difficulty associated with determining habitat requirements from empirical observations of habitat use. They also demonstrated the need for scientific studies within a clear conceptual framework with adequate sampling rigor.

Implications to Habitat Management

Obviously, a discussion of managing habitat is not possible within the context of this manuscript. The reader should consult Morrison et al. (1992, 1998) or Pain and Bryant (1994) for a detailed treatment of contemporary management. However, much of what is addressed in this paper has implications to habitat management. Leopold (1933) developed the basic tenants of habitat management: that organisms require the essentials of food, water, cover, and special factors for survival. Giles (1978) and others built on this concept and developed the wildlife- habitat-human triad that is so critical to management today. The triad forces one to examine wildlife in the context of its evolutionary origin and see how wildlife is affected by human disturbances. There are numerous models and techniques biologists can use to manage habitats (that are readily available in the literature), but for them to directly benefit wildlife, biologists must first consider the animal and its habitat use within the environment (Morrison et al. 1998).

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