Chapter 2

Habitat

Habitat is considered one of the few unifying concepts in contemporary wildlife ecology. This conclusion is based on numerous studies that relate the presence, abundance, distribution, and diversity of animals to aspects of their environments—studies in which habitat is invoked to explain the evolutionary history and fitness of animals (Block and Brennan 1993). Others have likewise emphasized the importance of wildlife/habitat relationships. "Habitat use" by wildlife has been addressed by numerous researchers. (See the reviews in Verner et al. 1986; Bookhout 1994; and Morrison et al. 1998.) But as Hall et al. (1997) have pointed out, there are several problems with current studies and discussions of habitat use that lead to ambiguity and inaccuracy—a situation that bedevils communication among researchers and confuses land managers and restorationists who are attempting to implement research findings. Restorationists cannot be expected to incorporate the needs of wildlife into a project if the literature is confusing and contradictory.

Although many contend that studies of wildlife/habitat relationships have to be placed in the proper spatial and temporal context (Wiens 1989a; Morrison et al. 1992; Block and Brennan 1993; Litvaitis et al. 1994; Bissonette 1997), this has yet to happen to any great extent. Researchers must recognize that their perceptions of wildlife/habitat relationships depend on the different scales at which different animals operate—and at which we operate (Wiens 1989a; Huxel and Hastings 1999). Johnson (1980) and Hutto (1985), for example, have proposed that animals select habitat through a hierarchical spatial scaling process: selection occurs first at the scale of the geographic range; it occurs second at the scale where animals conduct their activities (that is, in their home ranges); it occurs third at the scale of specific sites or for specific components within their home ranges; and fourth, animals select how they will procure resources within these microsites. Hutto (1985) thinks that selection at the scale of the geographic range is probably genetically determined. Wecker (1964) and Wiens (1972) have demonstrated that selection at finer scales may be influenced by learning and experience and hence under the animal's control. Because wildlife/habitat relationships may be distinctly different at different scales, habitat researchers must be sure to state the scale at which their study is focused and be careful not to extrapolate their data beyond this scale. As Askins (2000) points out, restoration of animals demands an understanding of specific species, which depend on specific types of vegetation, breeding sites, and food.

In terms of temporal scale, researchers must specify when their study occurred and state the time period to which it applies. Morrison et al. (1998:168–172) point out that too many researchers ignore that temporal variation in resource use occurs—or if they do recognize this fact, they still sample only from narrow time periods where the resulting wildlife/habitat relationships apply minimally to other situations. Alternatively, researchers commonly sample from across broad time periods (years or summer or winter seasons) and then use averaged values for variables across the periods—a practice that may mask differences in resource use. Thus a restoration plan must consider the resources each species needs throughout the period of occupancy of the site, whether for a single season (say, winter) or throughout the year. If the species is resident, researchers must determine how its resource needs change with the seasons (for a bird that eats seeds in the winter, for instance, but insects in the summer).

If we want to advance wildlife ecology and thus wildlife restoration, we must be sure that our fundamental concepts are well defined and hence well understood. This not only improves discussion among ecologists by forcing us to use words scientifically and consistently. It also improves our discussions with managers, administrators, and the public, so that our answers are not confusing and ambiguous.

Peters (1991:76) has written about "operationalizing" ecological concepts if environmental scientists hope to further their science. By this, he means that concepts such as habitat should have operational definitions: practical, measurable specifications of the ranges of specific phenomena the terms represent. The definitions may change, of course, but if the concepts are to be scientifically useful, then the definitions must be sufficiently measurable that users can apply them consistently.

Block and Brennan (1993) and Hall et al. (1997) charge that definitions of the term *habitat* are often vague—ranging from how species are associated with broad, landscape-scaled vegetation to detailed descriptions of the immediate physical environment used by species. It is easy to recognize a similar tendency among studies in wildlife science. This vagueness and variability is nonproductive because it detracts from the ability to communicate effectively about habitat and related subjects.

A lack of explicit definition leads ecologists to a variety of approaches for measuring terms such as habitat use, selection, preference, and carrying capacity (Wiens 1984:398), making it extremely difficult for us to conduct comparisons within and between disciplines. Because standard definitions are rarely used, some writers have simply thrown up their hands at trying to provide them (Verner et al. 1986:xi). I think, however, that the prevalence of the word *habitat* in the wildlife, restoration ecology, and conservation biology literature, as well as prevalence of words related to habitat (such as community, ecosystem, and biodiversity), obliges us to develop standard definitions. If restorationists (and other resource managers) are to incorporate new ideas into their plans, it behooves all scientists to ensure their research results are clear and accessible to people from different backgrounds.

When Hall et al. (1997) reviewed papers from prominent journals and books in wildlife and ecology that discussed wildlife/habitat relationships, they examined *habitat* and related terms for use and consistency. Of the 50 articles they reviewed, 47 used the term *habitat*; of these articles, habitat was defined and used correctly (that is, in a species-specific context) in only 5 of the 47 papers (11 percent). The word was used weakly or poorly (without a definition, for example, or sometimes confused with a vegetation association) in 34 of the 47 papers (72 percent). It was used incorrectly (not defined, for example, and always confused with a vegetation association) in 8 of the 47 papers (17 percent). The term most often used incorrectly was *habitat type*; in only one instance was the word used as first defined by Daubenmire (1968).

Definitions

The definitions presented here are based on Block and Brennan (1993), Hall et al. (1997), and Morrison et al. (1998), who in turn based them on the original intent of such ecologists as Grinnell (1917), Leopold (1933), Hutchinson (1957), Daubenmire (1968), and Odum (1971). In addition to habitat—the focus of this chapter—I discuss the terms *niche*, *landscape*, and *resources.* I consider these definitions here because of their frequent use in wildlife and restoration ecology.

Habitat

I define *habitat* as the resources and conditions present in an area that affect occupancy by a species. Habitat is organism-specific: it relates the presence of a species, population, or individual (animal or plant) to an area's physical and biological characteristics. Habitat involves more than vegetation or vegetation structure; it is the sum of the specific resources needed by a species. Wherever an organism is provided with resources that affect its ability to survive, that is habitat. Migration corridors, dispersal corridors, and the land that animals occupy during breeding and nonbreeding seasons—all are habitat. Thus, habitat is not equivalent to *habitat type*, a term coined by Daubenmire (1968:27–32) that refers only to the type of vegetation association in an area or the potential of vegetation to reach a specified climax stage. Habitat is much more than an area's vegetation (such as pine-oak woodland). The term *habitat type* should not be used when discussing wildlife/habitat relationships. When we want to refer only to the vegetation that an animal uses, we should say *vegetation association* or *vegetation type* instead.

The confusion between habitat and habitat type has led to a general misconception about how to restore an area for wildlife. If habitat is species-specific, then any plot of land has numerous habitats; each habitat corresponds to a specific species. As you gaze across an area, therefore, you are viewing numerous habitats of likely different quality. Thus the definition of habitat as species-specific is an absolutely critical concept. It means that restoring vegetation, regardless of how well it matches some desired condition, can easily fail to restore the desired assemblage of wildlife. Failure to plan simultaneously for plant and animal restoration results in a hit-or-miss strategy for animals and clearly falls under the Field of Dreams hypothesis—"if you build it, they will come" (Palmer et al. 1997:295). Restoring vegetation restores wildlife habitat for *some* species, but not necessarily the species desired. Poor planning for wildlife may create an ecological trap in which an undesired species kills or harasses a desired species or its young.

I define the term *habitat use* as the way an animal uses (or "consumes," in a generic sense) a collection of physical and biological components (that is, resources) in a habitat. With respect to habitat selection, as mentioned previously, Hutto (1985:458) proposed that it is a hierarchical *process* involving a series of innate and learned behavioral decisions made by an animal about what habitat it will use at different scales of the environment. Likewise, Johnson (1980) refers to selection as the process by which an animal chooses which habitat components to use. Given the body of literature supporting the view of selection as a process, it is useful to define selection this way and hence to define *habitat preference* as the consequence of the process, resulting in the disproportional use of some resources over others.

Habitat availability refers to the accessibility of physical and biological components needed by animals—as opposed to the abundance of these resources, which refers only to their quantity in the habitat irrespective of the organisms present in the habitat (Wiens 1984:402). In theory, we should be able to measure the amounts and kinds of resources available to animals; in practice, however, it is often impossible to assess resource availability from an animal's point of view (Litvaitis et al. 1994). We can measure the abundance (by trapping) of a prey species for a particular predator, for example, but we cannot say that all of the prey present in the habitat are available to the predator because there may be constraints, such as presence of ample cover, that restrict their accessibility. Similarly, vegetation beyond the reach of an animal is unavailable for it to feed on, even though the vegetation may be its preferred forage. Although measuring actual resource availability is important for understanding wildlife/habitat relationships, in practice it is seldom measured because of the difficulty in determining exactly what is available and what is not (Wiens 1984:406). Consequently, quantifying availability usually consists of a priori or a posteriori measures of the abundance of resources in an area used by an animal, rather than actual availability. Thus in most instances the term *availability* should be avoided by biologists. The term *abundance* should be used instead because this is what is most commonly measured. Where the accessibility of a resource has in fact been determined for an animal, analyses to assess habitat preference by comparing use versus availability are valuable.

The term *habitat quality* refers to the ability of the environment to provide conditions appropriate for individual and population persistence. Quality is a continuous variable ranging from low- to medium- to high-quality habitats based on their ability to provide resources for survival, reproduction, and population persistence. Researchers commonly equate high-quality habitat with vegetative features that may contribute to the presence (or absence) of a species (as in Habitat Suitability Index models; see Laymon and Barrett 1986 and Morrison et al. 1991). Quality must be explicitly linked with demographic features, however, if it is to be a useful measure. Discussions of carrying capacity (Leopold 1933; Dasmann et al. 1973), for example, have equated a high-quality habitat with one that has a density of animals in balance with its resources. In the field, this often means giving a high rank to habitats with large densities of animals (Laymon and Barrett 1986). Van Horne (1983) has demonstrated that density is a misleading indicator of habitat quality, however, and the widespread occurrence of source and sink habitats in nature (Pulliam 1988; Wootton and Bell 1992) has persuaded many ecologists to deemphasize this ranking. Thus while carrying capacity may be equated with a certain level of habitat quality, the quality itself should be based not on the number of organisms but on the demographics of individual populations.

For a restorationist, the key concept is habitat quality. If your project's goal is to restore a viable population of breeding individuals, for example, the critical factors causing the species to survive and reproduce successfully must be present. And as we have seen, these factors go far beyond vegetation and include food (say, the specific arthropods in the vegetation), breeding sites of proper condition (say, shaded nest sites), and perhaps an absence of predators.

Terms such as *macrohabitat* and *microhabitat* are relative and refer to the scale at which a study is being conducted for the animal in question (Johnson 1980). Thus macrohabitat and microhabitat must be defined for each study on a species-specific basis. Generally, macrohabitat refers to broad-scaled features such as seral stages or zones of specific vegetation associations (Block and Brennan 1993)—which usually equate to Johnson's first level of habitat selection. Microhabitat usually refers to fine-scaled habitat features—which are important factors at levels 2 to 4 in Johnson's hierarchy. Thus it is appropriate to use the terms *microhabitat* and *macrohabitat* in a relative sense, and the scales to which they apply should be stated explicitly.

It should be evident, then, that quantifying habitat use can be very complicated—and this makes it hard to predict a species' distribution and its ability to colonize restored sites. Determination of key habitat factors, however, will identify the conditions where the species might occur. Such information leads to restoration actions (such as plant species composition and structure) and management actions (such as control of predators or competitors) that could allow for occupancy of a site not being used by the species.

Niche

Wiens (1989a:146) has called the *niche* one of the most variably defined terms in ecology. Two primary meanings have been given to the term. A species' *Grinnellian niche* is the range of environmental features that enable individuals to survive and reproduce. Grinnell's (1917) focus was on factors determining the distribution and abundance of species. The *Eltonian niche*, in contrast, describes the niche of a species as its functional role in the community, especially with regard to trophic interactions (Elton 1927). Hutchinson (1957) expanded this concept of the niche by mathematically describing a large number of environmental dimensions, each representing some resource or other important factor on which different species exhibit frequency distributions of performance, response, or resource utilization (Wiens 1989a:146). Each perspective results in a different emphasis of study: studies of individuals under the Grinnellian view and studies of communities under the Eltonian-Hutchinson view.

Arthur (1987) recommends that we follow MacArthur's (1968) quantification of the niche, which plots utilization against some quantifiable resource variable that he calls the *resource utilization function* (RUF). Arthur thinks it is better to build complexity as needed, as with RUFs, than to dissect it using some multidimensional concept. RUFs describe the choice of resources by animals; these choices may be constrained by predators, competitors, and other factors. I prefer this approach because it makes far fewer assumptions about organizational structure and can be tuned to fit specific questions.

Thus the habitat contains the resources that affect occupancy, survival, and reproduction, whereas the niche concerns access to these resources and use of them. These concepts raise critical issues in restoration planning, for we see that simply providing the resources might be inadequate to ensure that the restoration goal is met. For example, a restorationist must be concerned with the distribution and abundance of competitors for resources that are being planned for a target species. It does little good to provide food if the animal of interest will get killed trying to harvest it. Thus restoration might entail removing certain features that allow the competitor to occupy the site or even removing the competitor itself.

Landscape

Landscape can be defined as a spatially heterogeneous area used to describe features of interest (stand type, site, soil). King (1997:205–206) describes a landscape primarily by its spatial extent. A serious problem with application of the term *landscape* is that it is usually taken to mean a large area (1–100 km^2) (Forman and Gordon 1986; Davis and Stoms 1996). The perception of "landscape" to a small animal, however, is likely much different than that perceived by a large one. As King (1997:204) has noted, the fundamental themes of landscape ecology do not just apply to areas greater than a few square kilometers. The influence of spatial heterogeneity on biotic and abiotic processes can be addressed at virtually any spatial scale. Thus we should not place area limitations on the notion of landscape. Although describing landscape in terms of square kilometers is appropriate for certain applications (such as placing a restoration project in the context of a broad area), describing it in terms of a few square meters is appropriate for other uses (such as salamander/niche relationships).

Resources

Wiens (1989b:262) notes that although resources are involved in most explanations of community patterns, all too often they have been defined in ad hoc ways. Rarely are they measured directly or inferred to be limiting without any evidence. Thus to define a resource, the area of interest must be explicitly identified with respect to its spatial extent and broken down into its measurable elements.

Little attention has been given the identification and measurement of resources. As Wiens (1989a:321) has indicated, almost any environmental factor that correlates with the distribution, abundance, or reproductive performance of a species has been called a resource. But without a precise definition of the resources present, it is impossible to derive accurate patterns of resource use or niche relationships. I define a *resource* as any biotic or abiotic factor that is directly used by an organism. Resources that are limiting to an organism could then be referred to as *limiting resources.* Wiens (1989a:321–323) has also noted that the differences between resource abundance, availability, and use must be distinguished to be certain which one is actually being measured. *Resource abundance* is the item's absolute amount (or size or volume) in an explicitly defined area—for example, the number of food items in 1 ha. *Resource availability* is the amount of a resource actually available to the animal (that is, the amount exploitable)—for example, the number of food items in 1 ha that an ungulate can reach. *Resource use* is a measure of the amount of the resource directly taken (consumed, removed) from an explicitly defined area—for example, the number of food items in 1 ha that an animal consumes in a six-hour sampling period.

Determining the critical resources necessary for a target species—and identifying any constraints on the use of these resources—is a fundamental aspect of wildlife restoration. Here again, there are numerous natural history papers and general field guides that provide at least rudimentary information on these factors. The restorationist can list the species of interest to restoration and then identify the key resources—and constraints on their use—for each species. Many similarities among species will likely be evident. You can then use this list in your planning to maximize the opportunity for the species to actually use the restored site.

When to Measure

The behavior, location, and needs of animals change, often substantially, throughout the year. Many researchers ignore temporal variations in habitat use, however, which can undermine habitat assessments. Without knowledge of an animal's total requirements, restoration plans have limited and perhaps faulty implications.

The decision on when to measure is a study-specific problem determined by the natural history of the species of interest. Species that are permanent residents in the project area should be studied throughout the year. More and more studies are showing that animals often change their use of resources substantially between seasons (Schooley 1994; Morrison et al. 1998:168–172). The arthropod fauna available to birds, for example, shifts between species of trees as the seasons' change. Failure to provide the proper mixture of plant species could easily result in failure of a restoration project regardless of the vigor of the plants that are established. Intuitively we would expect that the fall and winter periods—when populations are at their greatest numbers (because of offspring), resources are declining (trees and arthropods are dying or going dormant), animals are physiologically stressed by dispersal or migration, and the weather is becoming more harsh—are the most difficult times for an animal.

What to Measure

Green (1979:10) has listed several criteria that should be considered when you are choosing variables to measure wildlife habitat:

- Spatial and temporal variability in biotic and environmental variables used to describe or predict impacts
- Feasibility of sampling with precision at a reasonable cost
- Relevance to the impacts and sensitivity of response to them

These criteria apply both in descriptive studies and in analyses of impacts (chemical spills, forest harvesting). Understanding the variability in the system of interest is critical in designing a restoration project. This variability includes natural, stochastic, or systematic change as well as measurement and sampling error. Researchers conduct a cost/benefit analysis either formally or informally when choosing variables for measurement: they must determine the precision necessary to reach the project's goals and then match all the sampling to this level of precision. Is the goal of the project to provide for simple presence or absence of a species, a specific density, or reproduction? These are questions the restorationist must answer before designing a project.

Spatial Scale

You must match the scale of analysis with the scale you wish to apply in restoration and management. In restoration, these decisions are driven by the size of the project area and the goals regarding wildlife. In general, the smaller the area, the more attention you must give to microhabitat parameters of the species of interest. This is because the probability that a specific habitat component will occur naturally increases as area size increases. For example, a large area is more likely than a small one to contain snags (standing dead trees), a rock outcrop, a pond, or a woodland stand.

The definition of "small" and "large" depends on the project. Many salamanders have home ranges of under 15 m^2 and are unlikely to move over 25 m (Grover 1998). Bratton and Meier (1998) note that salamanders in the southern Appalachians must be considered carefully during plant restoration: because salamanders move only short distances and will not cross even narrow dry areas, the scale of restoring salamanders is finer than that for most plants. The home ranges of other small to medium-sized terrestrial vertebrates, by contrast, can be 5 to 10 ha or more. Projects focused on one or just a few species must be guided by the natural history of these animals. Projects of larger scale that have more general goals (such as enhancing vertebrate diversity) must be guided by principles that relate general measures of the wildlife community (say, species richness) to general measures of the environment (say, vegetation structure).

The finer-scale (microhabitat) relationships almost always vary between locations and time periods and certainly between populations. The magnitude of these variations determines the generality of the model. (Generality refers to the model's applicability at other times and places.) Much of the wildlife/habitat literature has been criticized because of its time and place specificity (Irwin and Cook 1985). This criticism is misplaced, however, and shows a general lack of understanding of the relationship between the precision of the variables measured and the scale of application possible. The decision to develop broad-scale models versus fine-scale models should be based on the objectives of the study. The extensive approach cannot tell us how an animal reacts to changes in litter depth, or the local density of trees by species, or the occurrence of a predator in a specific patch of vegetation. Such details are necessary, however, for management of local populations of animals.

Wildlife managers get frustrated when models fail to work in their specific location. This frustration comes primarily from trying to apply a relationship based on broad measurements of vegetation to local situations. Likewise, models developed at a fine scale can seldom be generalized to other locations (Block et al. 1994). For the restorationist, this means you must give careful consideration to matching the type of information available to the specific size and characteristics of the project area.

Measurements: Conceptual Framework

Two basic aspects of vegetation must be distinguished: its structure (physiognomy) and the taxa of the plants (floristics). (See Figure 2.1.) Many ecologists initially concluded that vegetation structure and "habitat configuration" (size, shape, and distribution of vegetation in an area)—rather than plant taxonomic composition—were paramount in determining patterns of habitat occupancy by animals, especially birds. (See the review by Morrison et al. 1998:146–147.) But recent studies have shown that plant species com-

FIGURE 2.1.
The height and layering of vegetation, as well as the species composition of the plants, play central roles in determining an animal's use of habitat. Depicted here is remnant riparian vegetation along the lower Colorado River, Arizona. (Photo courtesy of Annalaura Averill-Murray and Suellen Lynn.)

position plays a greater role in determining patterns of habitat occupancy than previously thought. The relative usefulness of structural versus floristic measures is again primarily a function of the spatial scale of analysis.

A species that appears to respond to the physical configuration of the environment (its physiognomy) at the continental level may show little correlation with physiognomy at the regional or local level. Thus many animals may differentiate between gross vegetative types on the basis of physiognomy, with further refinement of the distribution (and thus abundance) within a local area based on plant taxonomic considerations.

MACROHABITAT AND MICROHABITAT. With the rise in studies of animal diversity, researchers began to develop various measures to relate the numbers and kinds of animals to the gross structure of the vegetation. Most famous is the relationship between foliage height diversity (FHD) and bird species diversity (BSD): as foliage layers are added, the number of bird species tends to increase (see Figure 2.2). In vertically simple vegetation, such as brushland and grassland, FHD would not be expected to provide a good indicator of animal diversity (at least for most vertebrates). Recognizing this problem, Roth (1976) developed a method by which the dispersion of clumps of vegetation such as shrubs forms the basis for a measure of habitat heterogeneity or "patchiness." In fact, Roth was able to relate BSD to this patchiness.

Returning to Figure 2.2, note that there is considerable scatter around the regression line. Thus the usefulness of this general principle as a site-specific predictor declines as the scale of application becomes increasingly fine—that is, as you go from macroscale to microscale, or from what are usually termed "landscape" projects to local projects. Measures of diversity sacrifice complexity for simplicity; this is why they are useful primarily at larger spatial scales. These indices collapse detailed information on plants—such as species composition, foliage condition (vigor), and arthropod abundance—into a single number.

Many of the current habitat models operate at the macrohabitat scale, including most statewide constructs of wildlife/habitat relationships (WHR) (Block et al. 1994), GAP models (Scott et al. 1993), and habitat suitability index (HSI) models (USFWS 1981). Most of these models use broad-scale categorizations of vegetation types (often mislabeled as "habitat types") as a predictor of animal presence or abundance. But many developers of these models substantially mismatch scales in the variables used to develop their models; this is especially evident in HSI and WHR models. Such mismatch-

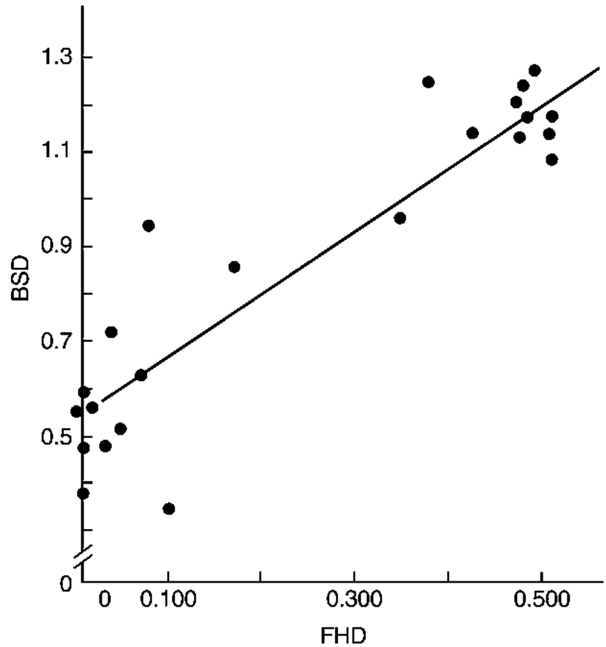

FIGURE 2.2.
Foliage height diversity (FHD) versus bird species diversity (BSD). Solid dots represent the study sites. (From M. F. Willson, "Avian Community Organization and Habitat Structure," Figure 1. *Ecology* 55:1017–1029. Copyright 1974.)

ing (entering microhabitat and macrohabitat variables into the same analysis, for example) ignores current theories concerning the hierarchic nature of habitat selection and makes it difficult to interpret a model's output. Models developed at the macrohabitat level help us to understand broad habitat relationships, but they should be limited to application at the broad scale.

Thus restoration projects that occur on relatively small areas (less than several km^2) usually concentrate on microhabitat relationships. And when the goal is to obtain successful survival and reproduction on the area, microhabitat factors and niche relationships (such as constraints on resource use) become the focus. Projects seeking to enhance biodiversity across large areas, in contrast, are likely to concentrate on gross measures of vegetation structure.

THE FOCAL-ANIMAL APPROACH. Most studies of microhabitat selection are variations of the *focal-animal approach.* These methods use the presence of an animal as an indication of the habitat being used by the species. No correlation between abundance and the environment is involved. Rather, the location of individual animals is used to demark an area from which environmental variables are measured. As detailed in the following section, an animal's specific location might serve as the center of a sampling plot. Or a series of observations of an individual might be used to delineate an area from which samples are then made. (See, for example, Wenny et al. 1993.) In either case, the major assumption is that measurements indicate the animal's habitat preferences. Many studies, for example, have used the location of a singing male bird or a foraging individual as the center of plots describing the habitat of the species (James 1971; Holmes 1981; Morrison 1984a, 1984b; VanderWerf 1993).

EXAMPLES. To what specific aspect of vegetation are animals responding? What are the stimuli causing the behavior that we call resource use? To answer these questions, we will consider a few examples of variables collected by researchers seeking to describe the habitat-use patterns of animals. This section is meant to give you a sense of the types of data you will need to design projects for the specific species.

James (1971) conducted one of the first and most-cited studies quantifying bird/habitat relationships. Using 15 measures of vegetation structure to describe the multidimensional "habitat space" of a bird community in Arkansas, she followed closely the methods that she and a colleague had developed (James and Shugart 1970). These methods are described in the next section. The conceptual framework and general analytic techniques (multivariate analysis of focal-bird observations) have led to a plethora of studies expanding upon her basic ideas. Indeed her strategy and methods are still in wide use. Murray and Stauffer (1995), for example, based their vegetation sampling on the James and Shugart methodology.

Dueser and Shugart (1978) had as their goal the description of microhabitat differences among the small-mammal species of an upland forest in eastern Tennessee. Their specific objectives were to characterize and compare microhabitats of species within the forest and to examine how species abundance and distribution relate to the availability of selected microhabitats. They gathered information for vertical strata at each capture site of a small mammal: overstory, understory, shrub level, forest floor, and litter-soil level. Table 2.1 lists the variables they collected. Note that they did not collect species-specific information on plants beyond designations of "woodiness," "evergreenness," and the like—an unfortunate omission for a microhabitat analysis, the ramifications of which are unknown. They paid special atten-

TABLE 2.1. Sampling Methods for Variables Measuring Forest Habitat Structure

Variable	*Sampling method*
1. Percentage of canopy closure	Percentage of points with overstory vegetation—from 21 vertical ocular tube sightings along the center lines of two perpendicular 20-m^2 transects centered on trap
2. Thickness of woody vegetation	Average number of shoulder-height contacts (trees and shrubs)—from two perpendicular 20-m^2 transects centered on trap
3. Shrub cover	Same as variable (1)—for presence of shrub-level vegetation
4. Overstory tree size	Average diameter (in cm) of nearest overstory tree—in quarters around trap
5. Overstory tree dispersion	Average distance (m) from trap to nearest understory tree—in quarters
6. Understory tree size	Average diameter (cm) of nearest understory tree—in quarters around trap
7. Understory tree dispersion	Average distance (m) from trap to nearest understory tree—in quarters
8. Woody stem density	Live woody stem count at ground level within a 1-m^2 ring centered on trap
9. Short woody stem density	Live woody stem count within a 1-m^2 ring centered on trap (stems $\leq$ 0.40 m in height)
10. Woody foliage profile density	Average number of live woody stem contacts with an 0.80-cm-diameter metal rod rotated 360° describing a 1-m^2 ring centered on the trap and parallel to the ground at heights of 0.05, 0.10, 0.20, 0.40, 0.60, . . . , 2 m above ground level
11. Number of woody species	Woody species count within a 1-m^2 ring centered on trap
12. Herbaceous stem density	Live herbaceous stem count at ground level within a 1-m^2 ring centered on trap
13. Short herbaceous stem density	Live herbaceous stem count within a 1-m^2 ring centered on trap (stems $\leq$ 0.40 m in height)
14. Herbaceous foliage profile density	Same as variable (10)—for live herbaceous stem contacts
15. Number of herbaceous species	Herbaceous species count within a 1-m^2 ring centered on trap
16. Evergreenness of overstory	Same as variable (1)—for presence of evergreen canopy vegetation
17. Evergreenness of shrubs	Same as variable (1)—for presence of evergreen shrub-level vegetation
18. Evergreenness of herb stratum	Percentage of points with evergreen herbaceous vegetation—from 21 step-point samples along the center lines of two perpendicular 20-m^2 transects centered on trap

(*continues*)

TABLE 2.1. *Continued*

Variable	*Sampling method*
19. Tree stump density	Average number of tree stumps ≥ 7.50 cm in diameter—per quarter
20. Tree stump size	Average diameter (cm) of nearest tree stump ≥ 7.50 cm in diameter—in quarters around trap
21. Tree stump dispersion	Average distance (m) to nearest tree stump ≥ 7.50 cm in diameter—in quarters around trap
22. Fallen log density	Average number of fallen logs ≥ 7.50 cm in diameter—per quarter
23. Fallen log size	Average diameter (cm) of nearest fallen log ≥ 7.50 cm in diameter—in quarters around trap
24. Fallen log dispersion	Average distance (m) from trap to nearest fallen log ≥ 7.50 cm in diameter—in quarters around trap
25. Fallen log abundance	Average total length (> 0.50 m) of fallen logs ≥ 7.50 cm in diameter—per quarter
26. Litter-soil depth	Depth of penetration (< 10 cm) into litter-soil material of a hand-held core sampler with 2-cm-diameter barrel
27. Litter-soil compactibility	Percentage of compaction of litter-soil core sample (variable 26)
28. Litter-soil density	Dry weight density (g/cm^2) of litter-soil core sample (variable 26) after oven drying at 45°C for 48 hr
29. Soil surface exposure	Same as variable (18)—for percentage of points with bare soil or rock

Source: R. D. Dueser and H. H. Shugart, Appendix. *Ecology* 59:89–98. Copyright 1978. Reproduced by permission of the Ecological Society of America.

tion to features of the forest floor—such as litter-soil compactability, fallen log density, and short herbaceous stem density—and found that certain of these soil variables played a significant role in describing the differences in microhabitats of the species studied.

Morrison et al. (1995) used time-constrained surveys to describe the microhabitats of amphibians and reptiles in the mountains of southeastern Arizona. Observers walked slowly, searching the ground and tree trunks and turning over movable rocks, logs, and litter to examine protected locations while a stopwatch ran. When the survey time stopped, a 5-m-diameter plot was then centered on the animals' location and served as the site where microhabitat conditions were measured: substrate temperature, various aspects of the vegetation, and other habitat characteristics.

Welsh and Lind (1995) analyzed the habitat affinities of the Del Norte salamander (*Plethodon elongates*) in relation to landscape, macrohabitat, and microhabitat scales. They presented a detailed rationale for the selection of methods, including choice of analytic techniques, data screening, and interpretation of output. The variables they measured, by spatial scale, are shown in Table 2.2.

These examples represent a useful starting point for designing a study of wildlife/habitat relationships. A note of caution: Do not try to duplicate the methods used in these studies exactly. Rather, select the variables that appear to predict something of interest about the species being studied. Gathering

TABLE 2.2. Hierarchic Arrangement of Ecological Components Represented by 43 Measurements of the Forest Environment Taken in Conjunction with Sampling for the Del Norte Salamander (*Plethodon elongates*)

HIERARCHIC SCALE
  Variable category
    Variables[a]

I. BIOGEOGRAPHIC SCALE[b]

II. Landscape scale
- A. Geographic relationships
  - Latitude (degrees)
  - Longitude (degrees)
  - Elevation (m)
  - Slope (%)
  - Aspect (degrees)

III. MACROHABITAT OR STAND SCALE
- A. Trees: density by size[c]
  - Small conifers (C)
  - Small hardwoods (C)
  - Large conifers (C)
  - Large hardwoods (C)
  - Forest age (in years)
- B. DEAD AND DOWN WOOD: SURFACE AREA AND COUNTS
  - Stumps (B)
  - All logs—decayed (C)
  - Small logs—sounds (C)
  - Sound log area (L)
  - Conifer log-decay area
  - Hardwood log-decay area (L)

(*continues*)

TABLE 2.2. *Continued*

C. SHRUB AND UNDERSTORY COMPOSITION (> 0.5 M)
- Understory conifer (L)
- Understory hardwoods (L)
- Large shrub (L)
- Small shrub (L)
- Bole (L)
- Height II—ground vegetation (B) (0–0.5 m)

D. GROUND-LEVEL VEGETATION (< 0.5 M)
- Fern (L)
- Herb (L)
- Grass (B)
- Height I—ground vegetation (B) (0–0.5 m)

E. Ground cover
- Moss (L)
- Lichen (B)
- Leaf (B)
- Exposed soil (B)
- Litter depth (cm)
- Dominant rock (B)
- Codominant rock (B)

F. Forest climate
- Air temperature (°C)
- Soil temperature (°C)
- Solar index
- % canopy closed
- Soil pH
- Soil relative humidity
- Relative humidity (%)

IV. MICROHABITAT SCALE

A. Substrate composition
- Pebble (P) (% of 32–64 mm diameter rock)
- Cobble (P) (% of 64–256 mm diameter rock)
- Cemented (P) (% of rock cover embedded in soil/litter matrix)

Source: H. H. Welsh and A. J. Lind, "Habitat Correlates of Del Norte Salamander, *Plethodon elongates,* in Northwestern California," Table 1. *Journal of Herpetology* 29:198–210. Copyright 1995. Reproduced by permission of the Department of Zoology, Ohio University

[a] Abbreviations used for the variables: C = count variables (number per hectare); B = Braun-Blanquet variables (percentage of cover in 0.10-ha circle); L = line transect variables (the percentage of 50-m line transects); P = percentage within 49-m^2 salamander search area.

[b] Level I relationships (the biogeographic scale) were not analyzed because all sampling occurred within the range. Spatial scales are arranged here in descending order from coarse to fine resolution.

[c] Small trees = 12–53 cm DBH (diameter at breast height); large trees = > 53 cm DBH.

data is time consuming, and careful planning during the process of variable selection will help you to focus the study.

How to Measure

In this section I review some common methods used to measure wildlife habitat. I cannot survey all the literature available for all taxa here; for a thorough review of basic sampling techniques for all the major taxa of wildlife see Cooperrider et al. (1986) and Bookhout (1994). My intent here is to enhance the restorationist's ability to gather and interpret the information necessary to guide projects aimed at specific wildlife species.

Sampling Principles

As we have seen, vegetation forms the traditional template for how we view wildlife/habitat selection. A cursory review of the methods in wildlife publications shows a reliance on standard techniques of quantifying the structure and floristics of vegetation: point quarter, circular plots and nested circular plots, sampling squares, line intercepts, and so on. These methods are used because they have been tested by plant ecologists in a multitude of environmental situations. Standard methods provide an established starting point from which biologists can adapt specific methods as needed. Standard methods also provide comparability between studies. There are many fine books that review sampling methods in vegetation ecology (Daubenmire 1968; Mueller-Dombois and Ellenberg 1974; Greig-Smith 1983; Cook and Stubbendieck 1986; Bonham 1989; Schreuder et al. 1993).

Sampling Methods

The most popular methods of measuring microhabitat originated with a protocol developed by James and Shugart (1970), who developed a quantitative method of obtaining vegetation data in a simple and standardized manner. Their original intent was to discover a method that could augment the data on bird populations being gathered in the National Audubon Society's "Breeding-Bird Censuses" and "Winter Bird-Population Studies" throughout the United States. But as noted earlier, their strategy has found wide applicability throughout the ecological community. Essentially they gathered data on the density, basal area, and frequency of trees as well as canopy height, shrub density, percent ground cover, and percent canopy cover. They established 0.1-acre (0.04-ha) plots to estimate tree density and frequency. To estimate shrub density they made two transects at right angles to one another across the 0.1-acre plots, counting the number of woody stems intercepted by their outstretched arms. An ocular (sighting) tube was used to estimate vegetation cover. They also provided details on how the sampling equipment could be constructed and offered examples of data sheets.

Earlier we discussed the importance of James's (1971) paper to our conceptualization of how animals perceive their environment. The methods used by James have had a pronounced influence on analyses of wildlife habitat. Circular plots are easy to establish, mark, measure, and relocate, and estimates of animal numbers within such plots can be statistically related to vegetation data in a straightforward manner. Plots provide for the sampling of vegetation and animals at specific locations in space and time. Thus plots are easy to pinpoint using geographic positioning systems (GPS), and their data can then be entered into geographic information systems (GIS). If plots can be considered independent data points (a function of the sampling design and behavior of the animals), then your sample size is equal to the number of plots you sampled. Or if you use the plots to sample from a single study area, they can be averaged and you can calculate associated measures of variance. Noon (1981) has presented a useful description of both the transect and the areal plot sampling systems. The problem with transects is that they cover relatively large areas and thus make it hard to relate specific animal observations (or abundances) to specific sections of the transect. Nevertheless, transects are widely used to provide an overall description of the vegetation of entire study areas.

In sum, then, fixed-area plots and transects can be used for site-specific, detailed analysis of wildlife/habitat relationships. The majority of sampling methods used since the 1970s to develop wildlife/habitat relationships—for subsequent multivariate analyses—have used fixed-area plots (usually circular) as the basis for developing of a sampling scheme that may then incorporate subplots, sampling squares, and transects. Now let us consider some of the more widely used methods.

Dueser and Shugart (1978) developed a detailed sampling scheme that combined plots of various sizes and shapes, as well as short transects (see Figure 2.3). Although designed for analysis of small-mammal habitat, the techniques can easily be adapted for most terrestrial vertebrates. Dueser and Shugart established three independent sampling units centered on each trap: a 1-m^2 ring; two perpendicular 20-m^2 arm-length transects; and a 10-m-radius circular plot. The 1-m^2 circular plot provided a measure of vertical

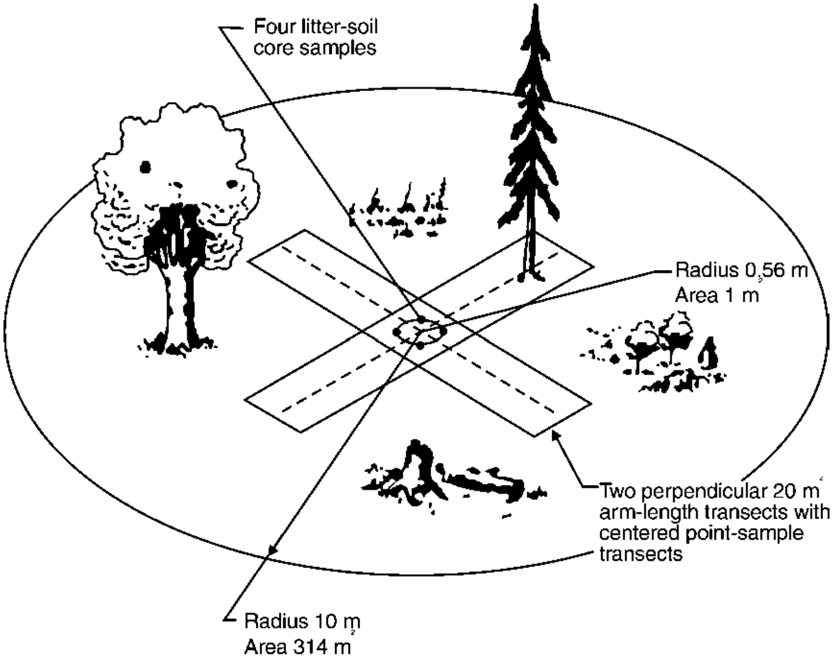

FIGURE 2.3.
Habitat variable sampling configuration used by Dueser and Shugart in their study of small-mammal habitat use. (From R. D. Dueser and H. H. Shugart, "Microhabitats in Forest-Floor Small Mammal Fauna," Figure 1. *Ecology* 59:89–98. Copyright 1978.)

foliage profile from the ground through 2-m height for both herbaceous and woody vegetation. Four replicate core-sample estimates of litter-soil depth, compactability, and dry weight density were made on the perimeter of this central ring. The two arm-length transects provided measures of cover type, surface characteristics, and density and evergreenness of the four strata of vegetation. Data recorded for each quarter of the 10-m-radius plot included the species, diameter at breast height, distance from the trap to the nearest understory and overstory trees, numbers of stumps and fallen logs, basal diameter and distance of nearest stump and fallen log, and total length of fallen logs.

In his analysis of snake populations, Reinert (1984) adopted techniques similar to those used in the bird study by James (1971) and the small-mammal study by Dueser and Shugart (1978). In fact, Reinert applied the basic conceptual framework used by the earlier authors in developing the rationale for his methods. Reinert made several modifications of their sampling methods, however. Notably he used a 35-mm camera equipped with a

28-mm wide-angle lens to photograph 1-m^2 plots from directly above the location of a snake. He then determined the various surface cover percentages by superimposing each slide onto a 10 × 10 square grid. Reinert, then, quantified his measure of cover values more rigorously than most workers, who usually use ocular estimates. His sampling scheme is summarized in Figure 2.4; his variable list is presented in Table 2.3. Note the similarity between Reinert's design and that of Dueser and Shugart, including the minor mixing of spatial scales. Reinert added several environmental variables that measured air, surface, and soil temperature and humidity. The values of these variables obviously depend on the time of day and the general weather conditions at the time of measurement; such constraints do not influence (are not correlated with) the other variables measured. Several popular techniques for quantifying foliage cover are presented in Figure 2.5.

Bibby et al. (1992) have compiled a basic but useful summary of habitat assessment techniques, including a description of mapping techniques for studies of avian ecology and an explanation of how to relate bird counts to environmental characteristics. (See also Chapter 6.) Figure 2.6 shows how

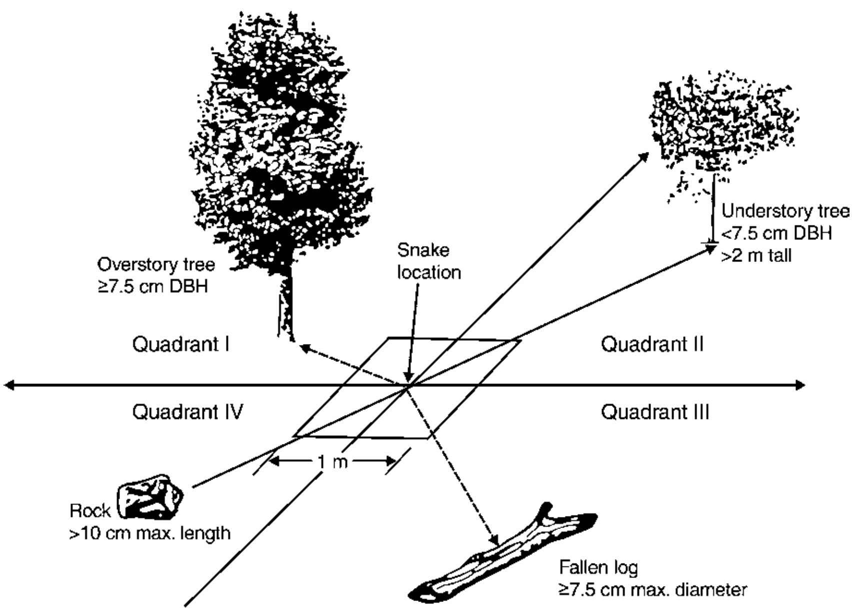

FIGURE 2.4.
Sampling arrangement for snake locations. (DBH = diameter at breast height) (From H. K. Reinert, "Habitat Separation between Sympatric Snake Populations," Figure 1. *Ecology* 65:478–486. Copyright 1984.)

TABLE 2.3. Structural and Climatic Variables Used by Reinert

Mnemonic	*Variable*	*Sampling method*
ROCK	Rock cover	Coverage (%) within 1-m^2 quadrant centered on snake location
LEAF	Leaf litter cover	Same as ROCK
VEG	Vegetation cover	Same as ROCK
LOG	Fallen log cover	Same as ROCK
WSD	Woody stem density	Total number of woody stems within 1-m^2 quadrant
WSH	Woody stem height	Height (cm) of tallest woody stem within 1-m^2 quadrant
MDR	Distance to rocks	Mean distance (m) to nearest rocks (>10 cm max. length) in each quarter
MLR	Length of rocks	Mean max. length (cm) of rocks used to calculate MDR
DNL	Distance to log	Distance (m) to nearest log (≥ 7.5 cm max. diameter)
DINL	Diameter of log	Max. diameter (cm) of nearest log
DNOV	Distance to overstory tree	Distance (m) to nearest tree (≥ 7.5 cm DBH)[a]
DBHOV	DBH of overstory tree	Mean DBH (cm) of nearest overstory tree within each quarter
DNUN	Distance to understory tree	Same as DNOV (trees < 7.5 cm, DBH > 2-m height)
CAN	Canopy closure	Canopy closure (%) within 45(cone with ocular tube)
SOILT	Soil temperature	Temperature (°C) at 5-cm depth within 10 cm of snake
SURFT	Surface temperature	Temperature (°C) of substrate within 10 cm of snake
IMT	Ambient temperature	Temperature (°C) of air 1 m above snake
SURFRH	Surface relative humidity	Relative humidity (%) at substrate within 10 cm of snake
IMRH	Ambient relative humidity	Relative humidity (%) 1 m above snake

Source: H. K. Reinert, "Habitat Restoration between Sympatric Snake Populations," Table 1. *Ecology* 65:478–486. Copyright 1984. Reproduced by permission of the Ecological Society of America.

[a] DBH = diameter at breast height.

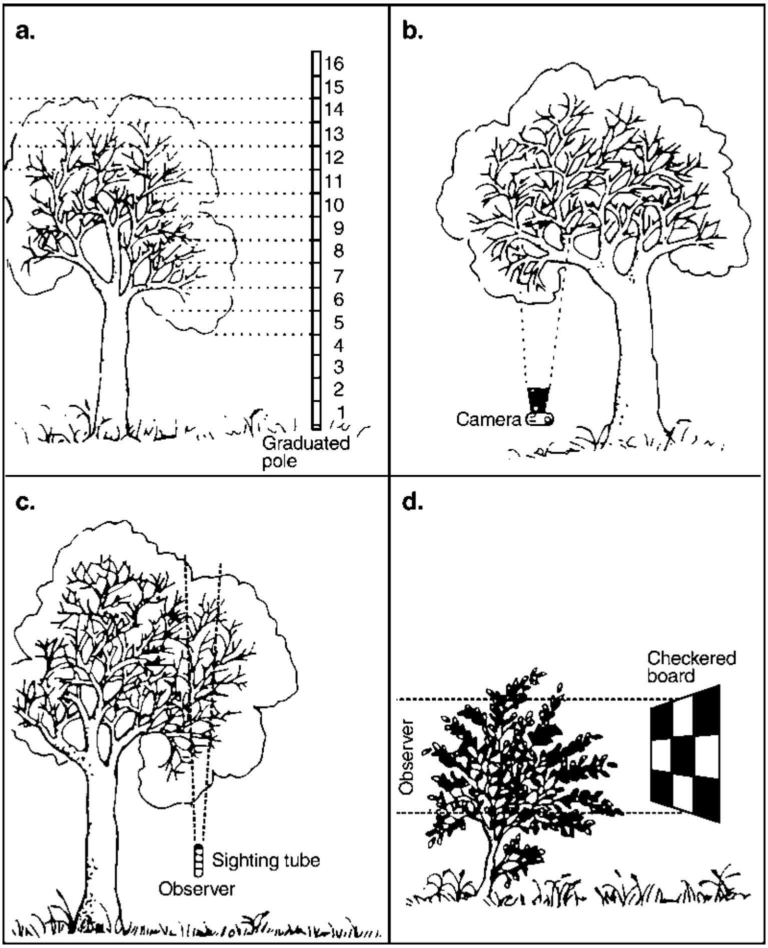

FIGURE 2.5.
Some commonly used devices to measure habitat variables in woodlands. (a) Graduated pole held upright—most useful to measure the features of the foliage in the shrub layer and low forests. (b) 35-mm camera with 135-mm or zoom lens—can be focused down through the forest profile (heights read off rangefinder) and used to assess foliage density through a vertical section of forest. (c) Sighting tube—observer looks directly up and assesses the canopy or shrub layer foliage density or divides the profile into height bands and assesses vegetation cover within each band. (d) Checkered board—used to assess vertical density of shrub layer. Observer walks away from the board until 50 percent of it is judged to be obscured by vegetation; this produces an index of the shrub density that can be repeated at a variety of heights. It is important to use the same observer, however, as people may differ in this ability. (From Bibby et al., *Bird Census Techniques,* Figure 10.10. Copyright 1992. Reprinted by permission of Academic Press.)

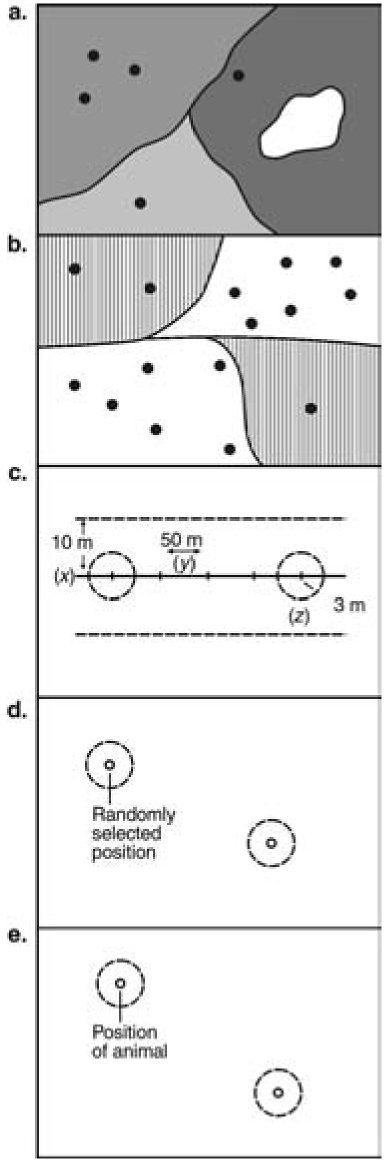

FIGURE 2.6.
Scale of habitat recording for wildlife studies. (a) All vegetation types are mapped without any habitat measurements and the locations of animals are marked on the map (solid dots). This method produces a broad understanding of habitat use, but it is difficult to test relationships statistically. (b) Habitat is subdivided into parcels on the basis of criteria such as vegetation age or plant species composition (white parcels represent recent clear-cutting; shaded parcels indicate old clear-cutting). Animal registrations (solid dots), derived from a mapping census, are allocated to each parcel and compared with quantitatively measured habitat variables. The habitat data from the parcels are produced independently of the mapping and a statistical comparison between the two to test any significant relationships is possible. (c) Habitat variables are recorded in standard sample plots at measured distances along the route of a transect count. This technique produces data on habitat variables in the same position as the transect count and allows the use of multivariate statistical methods to test relationships between animals and habitat variables. x = transect band width, y = measured transect segments, z = sample radius of habitat recording circle. (d) Habitat variables recorded in sample plots around the position of randomly located point counts. This technique produces detailed habitat data in the same position as the point count. Again this technique allows the use of multivariate statistical methods to test relationships between animals and habitat variables. (e) Habitat variables are recorded at the position of a territorial, feeding, or radio-located animal. This technique produces precise habitat data in an area selected by the animal. By recording habitat variables at a random selection of plots within the study area, it is possible to quantify an animal's habitat selection in terms of measured differences in the habitat variables it uses or avoids. (From Bibby et al., *Bird Census Techniques,* Figure 10.1. Copyright 1992. Reprinted by permission of Academic Press.)

these techniques—ranging from mapping of general bird locations to specific assessment of individual habitat use—can be applied in the field.

Lessons

To advance our understanding of habitat relationships will require increased cooperation among wildlife scientists, conservation biologists, and restorationists. Standardization of terminology would be a big step toward such cooperation by promoting use of a common language. The concept of habitat is well established in the scientific and popular literature, for example, yet the term is widely misunderstood and misused. Identifying critical resources that limit the distribution, abundance, survival, and reproductive performance of wildlife is a key factor in designing a restoration project. Moreover, the need to quantify constraints on the acquisition of resources—niche factors—has not been adequately recognized in studies of wildlife ecology and restoration.

Wildlife scientists have expended considerable effort studying efficient means of quantifying animal habitat. Restorationists will be able to accelerate the achievement of their project goals by studying the strengths and weaknesses of previous wildlife/habitat studies. That is: there is no reason to reinvent the wheel or repeat past mistakes. Oversampling or undersampling can be avoided through careful planning and the use of preliminary studies (see Chapter 4).

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