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WHAT IS HABITAT FRAGMENTATION?

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Abstract. Habitat fragmentation is an issue of primary concern in conservation biology. However, both the concepts of habitat and fragmentation are ill-defined and often misused. We review the habitat concept and examine differences between habitat fragmentation and habitat heterogeneity, and we suggest that habitat fragmentation is both a state (or outcome) and a process. In addition, we attempt to distinguish between and provide guidelines for situations where habitat loss occurs without fragmentation, habitat loss occurs with fragmentation, and fragmentation occurs with no habitat loss. We use two definitions for describing habitat fragmentation, a general definition and a situational definition (definitions related to specific studies or situations). Conceptually, we define the state of habitat fragmentation as the discontinuity, resulting from a given set of mechanisms, in the spatial distribution of resources and conditions present in an area at a given scale that affects occupancy, reproduction, or survival in a particular species. We define the process of habitat fragmentation as the set of mechanisms leading to that state of discontinuity. We identify four requisites that we believe should be described in situational definitions: what is being fragmented, what is the scale of fragmentation, what is the extent and pattern of fragmentation, and what is the mechanism causing fragmentation.

Key Words: forest fragmentation; habitat; habitat fragmentation; habitat heterogeneity.

Habitat fragmentation is considered a primary issue of concern in conservation biology (Meffe and Carroll 1997). This concern centers around the disruption of once large continuous blocks of habitat into less continuous habitat, primarily by human disturbances such as land clearing and conversion of vegetation from one type to another. The classic view of habitat fragmentation is the breaking up of a large intact area of a single vegetation type into smaller intact units (Lord and Norton 1990). Usually, the ecological effects are considered negative (Wiens 1994). In this paper, we propose that this classic view presents an incomplete view of habitat fragmentation and that fragmentation has been used as such a generic concept that its utility in ecology has become questionable (Bunnell 1999a).

In attempting to quantify the effects of habitat fragmentation on avian species, there is considerable confusion as to what habitat fragmentation is, how it relates to natural and anthropogenic disturbances, and how it is distinguished from terms such as habitat heterogeneity. Here, we attempt to provide sufficient background to define habitat fragmentation adequately and, as a byproduct, habitat heterogeneity. This paper was not intended as a complete review of the existing literature on habitat fragmentation but merely as a brief overview of concepts that allowed us to arrive at working definitions.

There are two ways to define habitat fragmentation. First, there is a conceptual definition that is sufficiently general to include all situations. We feel a conceptual definition is needed for theoretical discussions of habitat fragmentation. Second, there is a situational definition that relates to specific studies or situations. In this paper, we review current definitions and offer a revised conceptual definition of habitat fragmentation. In addition, we propose four requisites for building situational definitions of habitat fragmentation: (1) what is being fragmented, (2) what is the scale(s) of fragmentation, (3) what is the extent and pattern of fragmentation, and (4) what is the mechanism(s) causing fragmentation. To define habitat fragmentation, it is first necessary to review current understanding of how habitat is defined, and to contrast fragmentation and heterogeneity.

FRAGMENTATION—THE HABITAT CONCEPT

Prior to understanding fragmentation of habitat, the term *habitat* must be properly defined and understood. Habitat has been defined by many authors (Table 1) but has often been confused with the term *vegetation type* (Hall et al. 1997; see Table 1). As Hall et al. (1997) point out, habitat is a term that is widely misused in the published literature. The key features of the definitions of habitat in Table 1 are that habitat is specific to a particular species, can be more than a single vegetation type or vegetation structure, and is the sum of specific resources needed by a species. Habitat for some species can be a single vegetation type, such as a specific seral stage of forest in a region (e.g., old forest in Fig. 1a). This might be the case for an interior forest species where old forest interiors provide all the specific resources needed by this species. However, habitat can often be a combination and configuration of different vegetation types (e.g., meadow and old forest in Fig. 1b). In the example shown in Figure 1b, a combination of old forest and meadow are needed to provide the specific resources for a species. Old forest may

TABLE 1. TERMS AND DEFINITIONS FOR HABITAT FRAGMENTATION

Term	Definition	Source
Fragment	—noun: a part broken off or detached; an isolated, unfinished or incomplete part	Flexner and Hauck (1987)
	—verb: to collapse or break into fragments; to divide into fragments; disunify	
Fragmentation	—the act or process of fragmenting; the state of being fragmented	Flexner and Hauck (1987)
	—the disruption of continuity	Lord and Norton (1990)
	—the breaking up of a habitat, ecosystem, or land-use type into smaller parcels	Forman (1997:39)
Heterogenity	—the quality or state of being heterogeneous (composed of parts of different kinds; having dissimilar elements or constituents); composition from dissimilar parts; disparateness	Flexner and Hauck (1987)
	—uneven, non-random distribution of objects	Forman (1997:39)
Habitat	—the resources and conditions present in an area that produce occupancy—including survival and reproduction—by a given organism	Hall et al. (1997)
	—the subset of physical environmental factors that a species requires for its survival and reproduction	Block and Brennan (1993)
	—an area with the combination of resources (like food, cover, water) and environmental conditions (temperature, precipitation, presence or absence of predators and competitors) that promotes occupancy by individuals of a given species (or population) and allows those individuals to survive and reproduce	Morrison et al. (1992:11)
Vegetation type	—vegetation that an animal uses	Hall et al. (1997)
Habitat fragmentation	—the reduction and isolation of patches of natural environment	Morrison et al. (1992:12)
	—an alteration of the spatial configuration of habitats that involves external disturbance that alters the large patch so as to create isolated or tenuously connected patches of the original habitat that are not interspersed with an extensive mosaic of other habitat types	Wiens (1989:201)
	—landscape transformation that includes the breaking of large habitat into smaller pieces	Forman (1997)
	—when a large, fairly continuous tract of a vegetation type is converted to other vegetation types such that only scattered fragments of the original type remain	Faaborg et al. (1993)

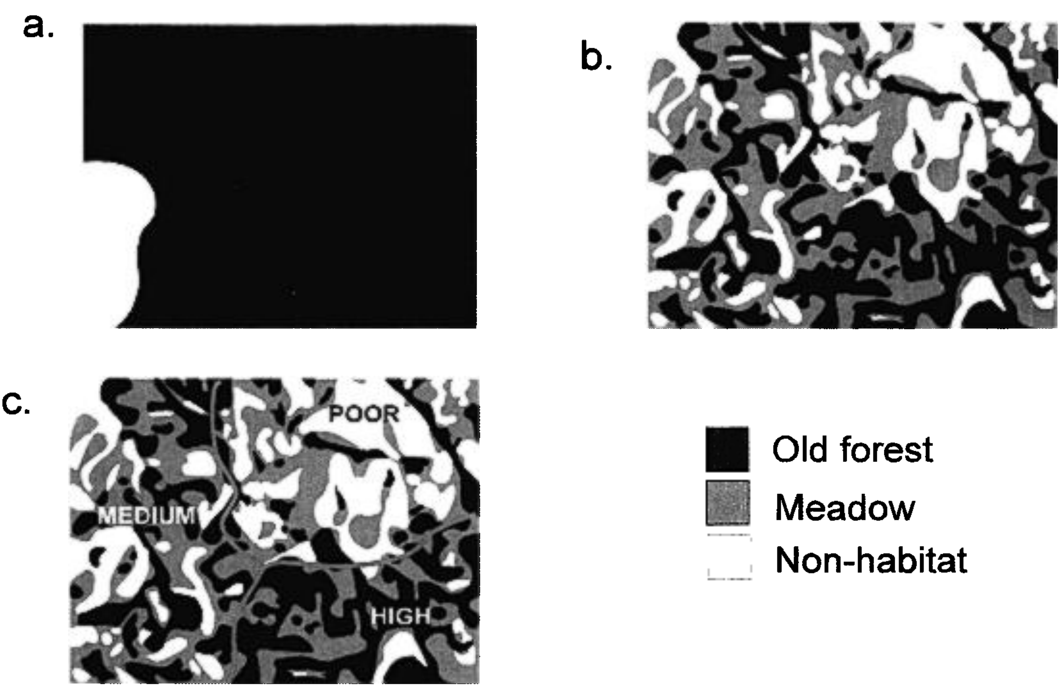

FIGURE 1. Example of habitat represented as (a) a single vegetation type, (b) a mosaic of different vegetation types, and (c) different mosaics of vegetation types representing different degrees of habitat quality.

provide some resources necessary for survival, whereas meadow might provide resources necessary for reproduction.

In addition to considering habitat versus non-habitat (the intervening matrix), habitat can have a gradient of differing qualities (Van Horne 1983) where *habitat quality* is defined as the ability of the environment to provide conditions appropriate for individual and population persistence (Hall et al. 1997). The idea that habitat can be a specific combination and configuration of vegetation types can be extended further to different combinations and configurations representing different levels of habitat quality (Fig. 1c). Poor habitat quality may result from too much of one vegetation type relative to another. Returning to the example from Figure 1b, too much meadow may provide sufficient resources for reproduction, but not enough for survival (Fig. 1c). Habitat quality is influenced by the mix and configuration of the two vegetation types (Fig. 1c).

An important consideration in both defining and understanding habitat fragmentation is that it ultimately applies only to the species level because habitat is defined with reference to a particular species. Habitat is proximately linked to communities and ecosystems only because these levels are composed of species. There is no concept of community or ecosystem habitat. For example, one cannot take a vegetation map and assess habitat fragmentation without reference to a particular species. Therefore, habitat fragmentation must be defined at the species level and those levels below (e.g., populations and individuals within species).

Fragmentation versus Heterogeneity

Based on existing definitions (Table 1), *fragmentation* can be viewed as both a process (that which causes fragmentation) and an outcome (the state of being fragmented; Wiens 1994). The definitions in Table 1 suggest that fragmentation represents a transition from being whole to being broken into two or more distinct pieces. The outcome of fragmentation is binary in the sense that the resulting landscape is assumed to be composed of fragments (e.g., forest) with something else (the non-forest matrix) between the fragments. In contrast, *heterogeneity* implies a multi-state outcome from some disturbance process. For example, contiguous old-growth forest can be transformed into a mosaic of different seral stages by some disturbance such as fire (e.g., Fig. 1b). If each seral stage, as viewed by a species, is a distinct habitat, then the result of the disturbance is an increase in habitat heterogeneity. In addition, if habitat is a combination of different vegetation types, then heterogeneity in vegetation types may influence habitat quality (e.g., Fig. 1c), but does not represent fragmentation.

Habitat fragmentation is heterogeneity in its simplest form: the mixture of habitat and non-habitat. However, the effects of habitat fragmentation is also dependent on the composition of non-habitat. The matrix of non-habitat may have a positive, negative, or neutral effect on adjacent habitat. For example, non-habitat consisting of agricultural fields may have a very different effect than non-habitat consisting of younger forest. The key point is whether intervening non-habitat affects the continuity of habitat with respect to the species. We argue that habitat fragmentation has not occurred when habitat has been separated by non-habitat but occupancy, reproduction or survival of the species has not been affected. Under this argument, key components in defining habitat fragmentation are scale, the mechanism causing separation of habitat from non-habitat (i.e., the degree to which connectivity is affected), and the spatial arrangement of habitat and non-habitat. For example, a narrow road dividing a large block of habitat may not affect occupancy, reproduction or survival for a wide-ranging species, such as a raptor. However, the road may affect a species with a narrower range, such as a salamander. Thus, fragmentation is from the species' viewpoint and not ours. We discuss these points in more detail further on.

The analogy of habitat fragmentation as equivalent to the breaking of a plate into many pieces (Forman 1997:408) is of limited utility. First, habitat fragmentation generally occurs through habitat loss; unlike the broken plate, the sum of the fragments is less than the whole. For example, in a uniform landscape composed entirely of a single habitat, fragmentation is only possible if accompanied by habitat loss. Thus, fragmentation usually involves both a *reduction* in area and a *breaking* into pieces (Bunnell 1999b). Second, the transition from being whole to being in pieces may lead to a change in quality of one or more of the fragments if habitat quality is a function of fragment size. For example, fragmentation of continuous forest (accompanied by an inescapable reduction in forest area) may change the quality of the fragments; habitat quality may increase for edge species and decrease for forest interior species (Bender et al. 1998).

When the effects of habitat loss and fragmentation are addressed independently, habitat loss has been suggested as having the greatest consequences to species viability (e.g., McGarigal and McComb 1995, Fahrig 1997). This observation led Fahrig (1999) to suggest the need to distinguish three cases: (1) habitat loss with no fragmentation; (2) fragmentation arising from the combined effects of habitat loss and breaking into pieces; and (3) fragmentation arising from the breaking apart but with no loss in habitat area. These three cases are illustrated in Figure 2. It is possible to illustrate these cases with reference to a common landscape only if the reference landscape is composed of at least one habitat and a surrounding matrix within the bounded landscape (Fig. 2). This occurs because case (3) requires the ability to shift the location of the focal habitat within the landscape boundaries. If there was no matrix within the landscape boundaries (e.g., the landscape was composed entirely of the single habitat), then only cases (1) and (2) in Fig. 2 would apply.

The possibilities illustrated in Fig. 2 are not artificial constructs. Conservation planning usually occurs in a context of habitat mosaics with a diversity of land uses and land ownerships. As such, case 3 is a common result of conservation tradeoffs. For example, wetland mitigation in the U.S. often requires no net loss in wetland area but allows a change in the spatial pattern and location of wetlands. Thus, it is possible to break one large wetland into two or more pieces, mitigate this loss somewhere else on the landscape by creating additional wetlands, and claim no net loss in area.

Fragmentation arising from habitat loss unavoidably leads to an increase in heterogeneity in habitat quality because the fragments may undergo a change in state either directly (through conversion) or indirectly through edge effects (see Bolger *this volume,* Sisk and Batten *this volume*). In light of the previous discussion, this possibility suggests that we need another case in addition to those discussed by Fahrig (1999). This case (case 4 in Fig. 2) includes changes in the spatial pattern of a habitat that are, or are not, accompanied by a change in the quality of the habitat. Case (4) would occur as a byproduct of case (2) depending on the habitat requirements of the species in question.

We attempt to capture these differences in outcome in a dichotomous flow diagram (Fig. 3). Following the diagram from top to bottom requires the investigator to answer a series of questions: "Has there been a reduction in area of the focal habitat?" "Has there been a change in spatial continuity of the habitat?" "Has there been a change in quality of the focal habitat?" Answering this progression of questions allows one to discriminate habitat loss from fragmentation, and to recognize cases where habitat quality has changed.

A final point is that fragmentation of vegeta-

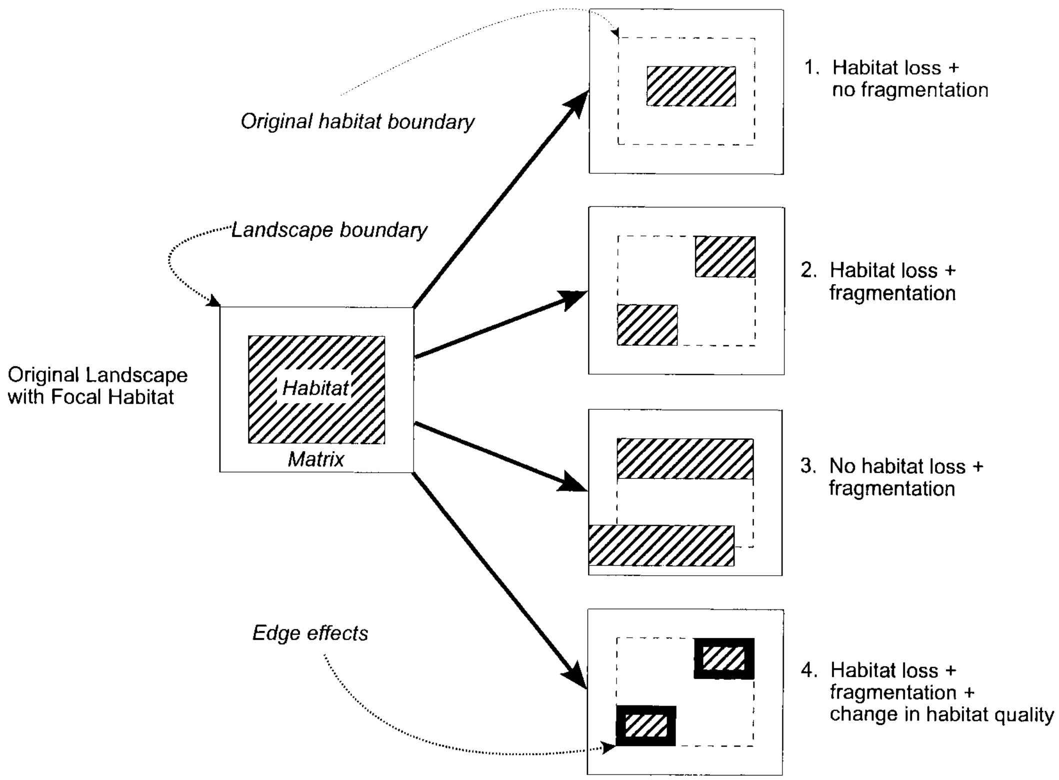

FIGURE 2. Four cases illustrating the relationship between habitat loss, habitat fragmentation, and change in habitat quality in a bounded landscape.

tion type and habitat fragmentation are often considered synonymous (e.g., the definition by Faaborg et al. (1993) in Table 1). However, the extent and effects of fragmentation can be very different when habitat is considered a single vegetation type or a combination of vegetation types (Fig. 4). Starting with the landscape in Figure 4, forest fragmentation would only be

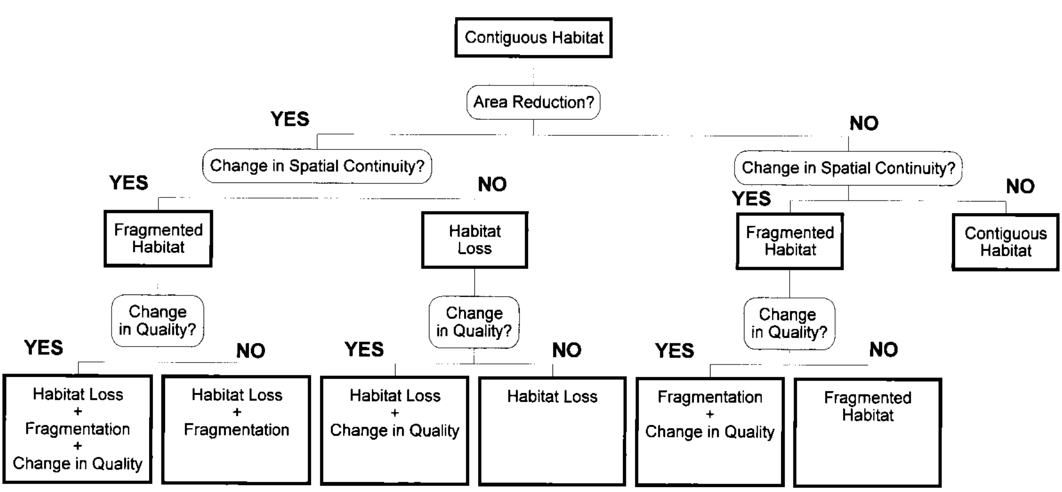

FIGURE 3. Flow diagram to differentiate between landscapes experiencing habitat loss, habitat fragmentation, and changes in habitat quality.

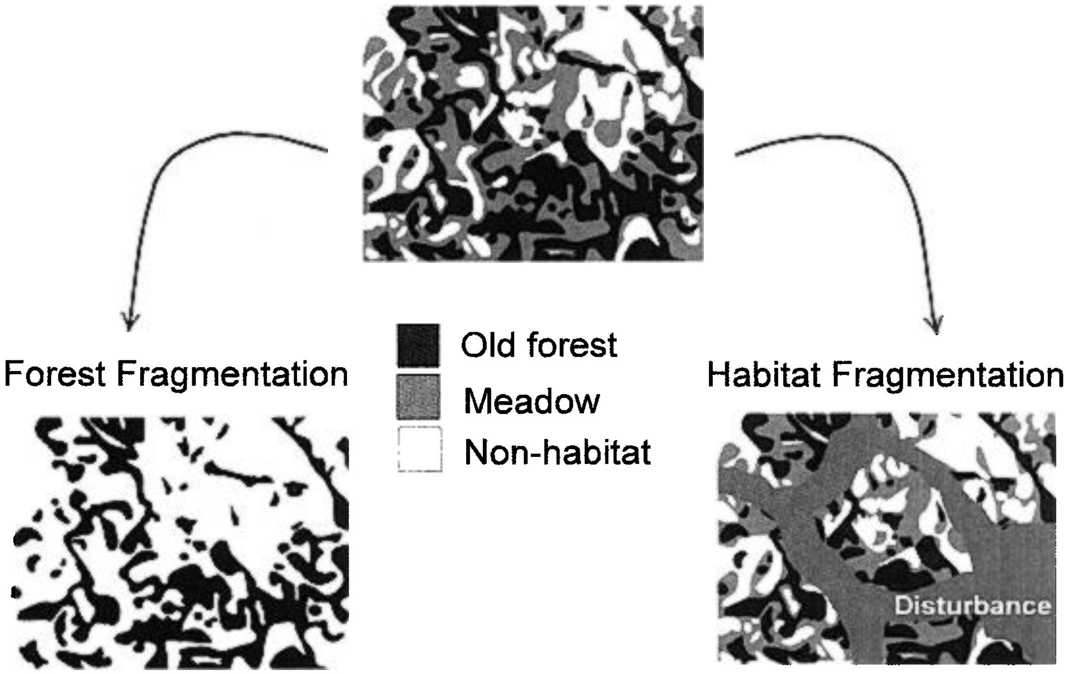

FIGURE 4. Schematic differences in forest fragmentation and habitat fragmentation in a landscape composed of a habitat consisting of two vegetation types (old forest and meadow).

considered as habitat fragmentation for a species whose habitat was solely defined as interior old forest (a single vegetation type). However, for the hypothetical example used previously where a species' habitat is composed of two vegetation types (meadow and old forest), habitat fragmentation would occur when some disturbance (such as a flood) disrupted the continuity in the configuration of these two vegetation types (Fig. 4). Thus, to define habitat fragmentation adequately, habitat must first be defined at a scale relevant to the species being examined.

What Is the Scale of Fragmentation?

The second requisite for defining habitat fragmentation is determining the scale at which fragmentation is occurring. Wiens (1973) and Johnson (1980) recognized different scales in understanding distributional patterns and habitat selection, respectively. For example, Johnson (1980) proposed first-order selection at the geographical range of a species, second-order at the home range of individuals or social groups, and third-order at specific sites within individual home ranges. A similar hierarchical scaling can be used in defining and understanding habitat fragmentation. For example, habitat fragmentation could be considered at a *range-wide scale* for fragmentation that occurs throughout a species geographic distribution, a *population scale* where fragmentation occurs within populations connected by varying degrees by animal movement, and a *home-range scale* for fragmentation that occurs within home ranges of individuals (Fig. 5). While this scaling can be subdivided into finer intermediate levels, the idea remains the same; habitat fragmentation is scale-dependent with different processes predominating at the different scales for a given species. For example, fragmentation at the range-wide scale can affect dispersal between populations, fragmentation at the population scale can alter local population dynamics, and fragmentation at the home range scale can affect individual performance measures, such as survival and reproduction. Clearly, the different scales are not mutually exclusive, but provide a unifying nested relationship that allows for understanding mechanisms and processes at different levels (Johnson 1980).

Rather than a hierarchical scale, Lord and Norton (1990) proposed a continuous gradient of scale. At one end of the gradient, they defined *geographical fragmentation* where fragments are large relative to the scale of the physiognomically dominant plants (Fig. 6a) and, at the opposite end, they defined *structural fragmentation* where fragments are individual plants or small

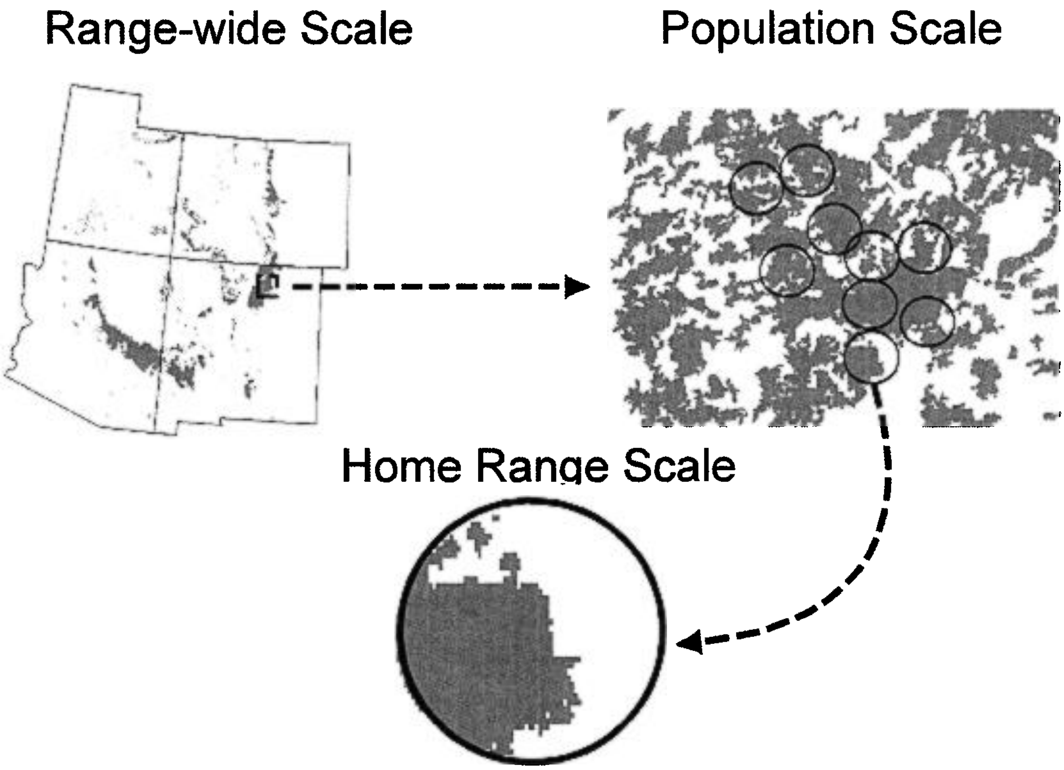

FIGURE 5. Example of three different scales at which habitat fragmentation can occur.

groups of plants (Fig. 6b). While this gradient puts fragmentation on a continuous scale, it lacks the biological connection of the species-centered, hierarchical approach advocated by Johnson (1980). The ideal would be a gradient that is continuous and that has a biological context. Regardless of how scale is measured, a situational definition should include scale because inferences to population and distributional processes for a given species are limited to whatever scale is being examined. Fragmentation that affects processes at the home range scale (i.e., individual survival and reproduction) do not necessarily affect processes at a population or range-wide scale (i.e., dispersal between populations of home ranges). For example, fragmentation that affects foraging sites within the home range of an individual may not impede the ability of the offspring of that individual to disperse across a wider area.

What Is the Extent and Pattern of Fragmentation?

Here, we refer to the *extent* of habitat fragmentation as the degree to which fragmentation has taken place within a specified spatial scale, whereas the *pattern* of fragmentation describes patch geometry, e.g., size, shape, distribution, and configuration. Extent describes how much fragmentation has taken place (Fig. 7) whereas geometry describes the pattern of habitat fragmentation. For example, the patterns of fragmentation in Figure 8 appear very different even though the total amounts of remaining habitat are the same. Various spatial parameters and statistics (e.g., Turner and Gardner 1991, McGarigal and Marks 1995) can be used to describe the different patterns in Figure 8. A considerable literature exists on how to describe the extent and pattern of habitat fragmentation and we will not review these quantitative methods here. However, a situational definition should include some measure of extent and pattern of fragmentation to place it in context.

What Is the Mechanism Causing Fragmentation?

Habitat fragmentation often occurs because of some disturbance mechanism. However, habitat fragmentation can be *static,* such as resulting from topographic differences (Forman 1997: 412). For example, habitat used by Mexican

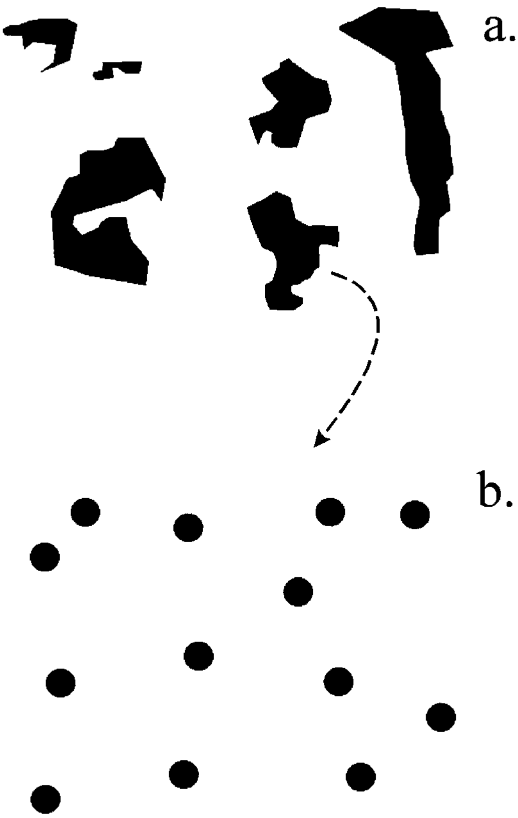

FIGURE 6. Example of (a) geographical fragmentation as illustrated by patches of sagebrush and (b) structural fragmentation as illustrated by the distribution of individual sagebrush plants on a plot within one of the patches (after Lord and Norton 1990).

Spotted Owls (*Strix occidentalis lucida*) is distributed on a range-wide scale in a highly fragmented manner across four states in the U.S. (Keitt et al. 1997; see Fig. 5). This distribution is essentially fixed over an ecological time frame.

Dynamic mechanisms occur with some frequency within a time frame that is applicable to the ecology of the species and the habitat they use. These mechanisms can be "natural" (fire, wind, etc.) or anthropogenic (logging, agriculture, urbanization, etc.; Forman 1997:413). In a given area at a given scale, these mechanisms can simultaneously fragment habitat for some species while creating habitat for others. In conservation issues, the mechanisms causing habitat fragmentation are often of primary concern, especially when these mechanisms are human-induced.

A complete description of fragmentation must include an understanding of how the matrix influences the ability of the habitat to support a species. If the matrix differs substantially from the original habitat, the impacts on the species may be more severe than if the matrix differs little. That is, fragmentation is also a function of the degree of contrast in quality between the focal habitat and its neighborhood. For example, both selective logging and building homes may cause fragmentation of unharvested forest but the consequences may be very different for the species that inhabit the landscape. Most measures of habitat fragmentation do not consider the effects of the matrix on the survival and reproduction of individuals or populations within the remaining patches.

Understanding what mechanisms are contributing to habitat fragmentation is important for placing habitat fragmentation into the context of either an acceptable ecological process (i.e., resulting from natural mechanisms) or a required conservation action (i.e., fragmentation resulting from anthropogenic mechanisms). Current dogma on habitat fragmentation is value-biased toward a negative connotation (Wiens 1994, Meffe and Carroll 1997); use of the term currently implies that the biological effects are negative. However, habitat fragmentation can be value-neutral or positive, depending on the species.

FRAGMENTATION—A CONCEPTUAL DEFINITION

We propose that the state (or outcome) of habitat fragmentation can be defined conceptually as *the discontinuity, resulting from a given set of mechanisms, in the spatial distribution of resources and conditions present in an area at a given scale that affects occupancy, reproduction, or survival in a particular species.* From this, the process of habitat fragmentation can be defined as *the set of mechanisms leading to the discontinuity in the spatial distribution of resources and conditions present in an area at a given scale that affects occupancy, reproduction, and survival in a particular species.* In developing these definitions, we incorporated definitions proposed by Lord and Norton (1990) and Hall et al. (1997; Table 1) and included three of the four requisites that we previously outlined. The fourth requisite, the extent and pattern of fragmentation, was not included because it hampers the ability of the definition to be general. However, scale and mechanism are included in the definition to avoid, even in general terms, misleading statements. The term habitat fragmentation has acquired a negative connotation over the years (Wiens 1994). Habitat fragmentation can occur naturally and the term should not be interpreted solely in terms of its potential negative impacts. Our definition re-

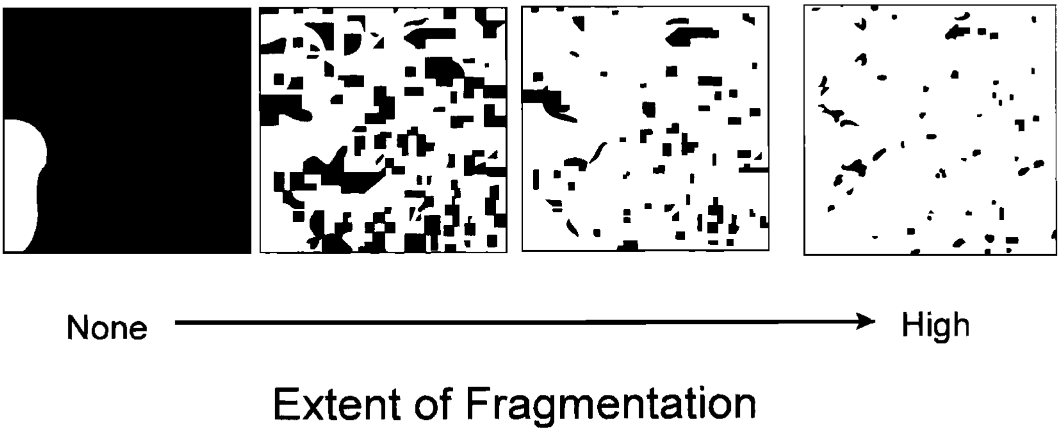

FIGURE 7. Schematic representation of changes in the extent of fragmentation (after Curtis 1956).

moves the value-bias that currently is attached to the phrase "habitat fragmentation."

How does our definition differ from previous definitions? We believe our definition is more specific than the definition proposed by Morrison et al. (1992) and explicitly incorporates the concept of continuity (Lord and Norton 1990) that is lacking in the definitions of Wiens (1989) and Forman (1997) (Table1). The definition by Faaborg et al. (1993) does not fit the definitions of habitat by Block and Brennan (1993) and Hall et al. (1997), and is more applicable to vegetation type fragmentation than to habitat fragmentation.

Situational Definitions

To state that "the habitat is fragmented" is insufficient for understanding the scope of a particular conservation problem or the potential effects on the status of a given species in a given area. When defining fragmentation for a given situation (say, within a particular study, conservation plan, or for a given species), statements about habitat fragmentation should include the four requisites discussed earlier. The first requisite, what is being fragmented, requires an understanding of a species' habitat. The second requisite, scale, is essentially a statement as to where inferences are being made and the level of habitat description being considered (e.g., stands of vegetation versus structure of vegetation within stands). The third requisite, extent and pattern of fragmentation, provides a description of the magnitude and type of habitat fragmentation. The fourth requisite, mechanisms, puts habitat fragmentation into a temporal scale (how rapidly changes occur over time) and also into an ecological and conservation context ("natural" versus anthropogenic, or situations in between).

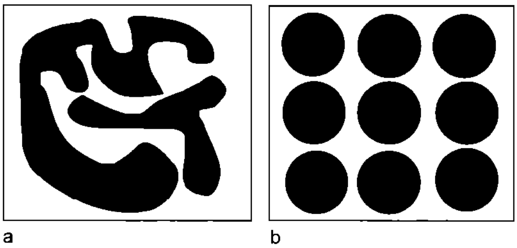

FIGURE 8. Examples of different patterns of habitat fragmentation for an area having equal habitat amounts but (a) fewer large patches with higher edge to interior ratio versus (b) greater number of small patches with lower edge to interior ratio.

A situational definition for habitat fragmentation will not necessarily be limited to a compact statement as is the conceptual definition. Rather, it should be considered as a series of paragraphs, or even an entire manuscript that includes the four requisites. However, the four requisites should be identified and stated clearly to put habitat fragmentation for a particular situation into its appropriate context.

CONCLUSIONS

By defining habitat fragmentation as we have proposed here, people will have to think more clearly about the characteristic attributes of fragmentation. While some may consider our attempts at defining habitat fragmentation as an over-emphasis on semantics, we agree with Peters (1991) and Hall et al. (1997) that vague and inconsistent terminology in the ecological sciences leads to ineffective and misleading communication, poor understanding of concepts, and generally sloppy science. Habitat is a unifying concept in ecology (Block and Brennan 1993) and central to many of the conservation problems that ecologists face. We believe that developing precise definitions for key concepts at the interface between ecology and conservation is paramount before these concepts become so muddled that ecologists become ineffective in their ability to deal with problems and to communicate those problems to others.

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