FRAGMENTATION OF TERRESTRIAL HABITAT: AN OVERVIEW FOR WILDLIFE BIOLOGISTS

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Abstract: Habitat fragmentation occurs when wildlife habitats change in area, configuration, or spatial relationships because of natural and anthropogenic mechanisms. Habitat fragmentation is arguably the greatest conservation challenge facing today's wildlife biologists, of which most biologists are keenly aware because habitat is a unifying resource for most wildlife conservation efforts. For the past few decades, wildlife biologists have assessed effects of habitat fragmentation on wildlife while billions of public and private dollars have been spent on habitat acquisition and wildlife conservation efforts to offset the effects of fragmentation. Recently, however, the conceptual basis of habitat fragmentation has been questioned along with how it is assessed. The primary reasons for questioning the concept are: (1) ambiguity of the definition of fragmentation; (2) using a variety of ambiguous metrics to quantify fragmentation and difficulty in linking these metrics and wildlife response measures; (3) classifying habitat loss and habitat fragmentation as negative outcomes has led to confusion between the 2 because they are both a process and an outcome; (4) habitat heterogeneity and dynamics confound effects from fragmentation; (5) inherent complexity of ecological systems has led to confounding effects and multicausal responses by wildlife; (6) species-specific responses to fragmentation has led to varied responses by wildlife; and (7) methodological problems exist with scientific assessments of the effects of fragmentation on wildlife. Fragmented habitats affect wildlife in negative, positive, and neutral ways depending on the mechanism, the magnitude, duration, frequency, and extent of the fragmentation, and habitat(s) and wildlife species affected. The interrelationship between loss and fragmentation also dictates wildlife responses. Assessments of fragmentation effects should focus on individual species because fragmentation occurs to habitats, and habitats are defined by individual species. Assessments involving multiple species should involve species that can represent the full range of impacts from fragmentation. Most research and conservation efforts have focused primarily on fragmentation as an outcome because fragmented landscapes of smaller habitat patches are obvious and immediate outcomes of fragmentation. The process of fragmentation must also be considered because attention is then focused on the spatial and temporal components of fragmentation.

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Wildlife habitats have been modified and changed by natural and anthropogenic causes throughout time since their initial occurrences on the landscape. Fragmentation occurs when the size of individual patches of desired habitats decreases along with concomitant increases in size of patches of otherwise presumably less-suitable and undesirable habitats. Fragmentation (1) causes changes in the amount of habitats; (2) isolates patches from other patches of the same or similar habitats; and (3) alters adjacency patterns of habitats by changing habitats and their spatial characteristics. The degree, extent, and pattern of fragmentation have changed through the millennia as natural and anthropogenic fragmentation mechanisms have also changed.

Biological entities, including wildlife, are affected by fragmentation, and fragmentation effects are highly variable for many reasons. There is a general consensus, however, that habitat fragmentation generally reduces biodiversity, and the greatest threat to wildlife is

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the conversion of habitats to other uses through the fragmentation process (Meffe and Carroll 1997, National Commission on Science for Sustainable Forestry 2005). This consensus rarely, however, recognizes the ambiguity in the concept as well as the difficulty in describing and measuring fragmentation. In addition, there are a few papers that provide an overview of the concept of habitat fragmentation and how wildlife are affected by fragmentation (Debinski and Holt 2000, Johnson 2001, Chalfoun et al. 2002, McGarigal and Cushman 2002, Fahrig 2003).

Assessment of fragmentation represents a formidable challenge to researchers and managers because it is a landscape-scale process (Walters and Holling 1990) that occurs at various spatial and temporal scales. Debinski and Holt (2000) found only 20 examples of published studies of habitat fragmentation experiments worldwide, which indicates how difficult it is to test hypotheses of habitat fragmentation through experimentation, yet many observational studies have been done where fragmentation is a research focus (McGarigal and Cushman 2002, Fahrig 2003). Fragmentation experiments are exceedingly costly, require very large study areas, and necessitate complicated experimental designs (Debinski and Holt 2000, Johnson 2001). When recommending and implementing management actions needed to conserve wildlife in the face of habitat fragmentation mechanisms, biologists are faced with the challenge of describing the nature of fragmentation, quantifying it, and assessing impacts on wildlife so that management recommendations are commensurate with the fragmentation impact. Biologists are faced with this challenge while working with limited budgets and resources so they must correctly focus their work on key fragmentation components.

Several seminal papers published 2–3 decades ago on habitat fragmentation (Forman et al. 1976, Whitcomb et al. 1981, Ambuel and Temple 1983, Harris 1984) framed the issue for many wildlife biologists who have since been working on the topic. Wildlife biologists and policy makers added habitat fragmentation concepts to their work, and an entire scientific discipline and set of conservation measures resulted. In typical fashion, recommendations to minimize fragmentation impacts preceded experimentation and analysis to critically evaluate the concept. Early on, however, the complexity of the concept and implications for researchers and wildlife managers were noted (Laudenslayer 1986, Verner 1986). As the concept matured, evaluation of the concept naturally followed. In turn, several recent papers questioned the concept of fragmentation along several lines, including how to define it, how to measure it, and how wildlife and other biological entities respond to fragmentation (e.g., Johnson 2001, Bissonette and Storch 2002, George and Dobkin 2002*a*, Haila 2002, Villard 2002, Bogaert 2003, Fahrig 2003). Haila (2002), in particular, critiqued the concept's 3 underlying assumptions, which he demonstrated to be unsupported by empirical evidence: (1) fragments are comparable to oceanic islands; (2) habitats surrounding fragments are non-habitat to a majority of organisms; and (3) natural pre-fragmentation conditions were uniform.

The concept of habitat fragmentation is currently so entrenched in the wildlife profession that it has become a rarely questioned axiom (Bissonette and Storch 2002, Haila 2002). Most published papers dealing with site-specific fragmentation studies conclude that habitat fragmentation overwhelmingly has negative consequences for wildlife despite some contrary evidence (Debinski and Holt 2000, Haila 2002, McGarigal and Cushman 2002). I do not claim that fragmentation lacks negative consequences for wildlife; negative consequences have been documented and are generally well accepted. However, because of the concept's ambiguity and complexity, we must question how the effects of fragmentation are evaluated by wildlife biologists, particularly because tremendous amounts of public and private financial and bureaucratic resources are used for expensive conservation actions undertaken to offset fragmentation effects.

Given these questions, it is timely to provide an overview of the concept of habitat fragmentation to improve our understanding of the concept and its application. My purpose is to outline what habitat fragmentation is from an operational perspective so that wildlife biologists can better address this important issue.

Specifically, I have 5 objectives: (1) clarify terminology on habitat fragmentation and distinguish it from related terms and concepts; (2) discuss challenges the concept represents for fragmentation assessments; (3) identify mechanisms that cause fragmentation; (4) discuss how biologists can better quantify the various components of habitat fragmentation; and (5) make recommendations for future work involving habitat fragmentation. Based on my review, no single paper that I found addressed these 5 objectives in a manner that focused on implications for wildlife biologists. To accomplish these objectives, I reviewed the published literature for appropriate topical papers that established the conceptual basis for habitat fragmentation and critiqued the concept. This paper is neither intended to be a thorough review of the concept of habitat fragmentation and how wildlife respond when habitats are fragmented, nor is it a review that entirely rejects or supports the concept, as many papers already have done this. Instead, I broadly review the concept and provide sanguine cautions to assist the work of wildlife biologists. This review should help us better understand and appreciate the complexity of the issue, learn about the strengths and weaknesses of the underlying concepts, understand where the data gaps are, and adopt some recommendations for applying and studying the concept. I focus here solely on fragmentation of terrestrial habitats because it is most germane to wildlife biologists. This is not meant to minimize the importance of aquatic habitats, but fragmentation of aquatic habitats is beyond the scope of this paper.

TERMINOLOGY

Habitat

The concept of "habitat" must be defined if we are to understand habitat fragmentation. The wildlife profession has struggled with a definition of habitat for decades, and it is only recently that a consensus on the term has developed (Hall et al. 1997). The recent definition by Hall et al. (1997:175) is particularly relevant to wildlifers: "*the resources and conditions present in an area that produce occupancy, including survival and reproduction by a given organism*." This definition implies that habitat is the sum of specific resources needed by a given species (Hall et al. 1997). In summary, habitats are specific to a particular species, can be more than a single vegetation type or vegetation structure, and are the sum of the species-specific required resources (Franklin et al. 2002:20). It logically follows, then, that fragmentation of habitat must be defined at the species level and below (e.g., subspecies, populations, and individuals) (Haila 2002). Assessing impacts of habitat fragmentation, therefore, must be quantified for individual species, and this approach is advocated in this and other papers (Franklin et al. 2002, Haila 2002, Fahrig 2003). A habitat classification system such as the California Wildlife Habitat Relationships System (CWHR) (Mayer and Laudenslayer 1988) is useful when classifying and describing habitat because it is a classification system with a habitat nomenclature. However, biologists must recognize that CWHR may sometimes fail when fully describing habitat used by a given species because: (1) it does not account for all possible resources and conditions that could be needed by a species to define its habitat, although CWHR has >60 habitats and >120 habitat elements that represent a wide array of possible resources and conditions; (2) CWHR is intended to classify habitat similarly for many species throughout California, hence it is not necessarily species specific; (3) CWHR generalizes habitat instead of making it more specific; and (4) CWHR generally lacks spatial parameters necessary for species-specific habitat definitions, although CWHR lends itself to use in spatial analyses.

Habitat Fragmentation

As previously stated, habitat fragmentation is considered an issue of substantial concern in conservation biology (Meffe and Carroll 1997) and scientific research (Haila 2002), and it has an important genealogy that affects how the concept is applied to wildlife studies and implemented for conservation purposes (Haila 2002, Villard 2002, Fahrig 2003). Several recent papers, however, have raised concerns about how the concept is studied and applied (Johnson 2001, Bissonette and Storch 2002, Franklin et al. 2002, Haila 2002, Villard 2002).

There are many definitions of fragmentation (Franklin et al. 2002) but all generally possess certain commonalities. Fragmentation is the process of breaking up a habitat, ecosystem, or land-use type into smaller parcels, and fragmentation is also an outcome where the fragmentation process changes habitat attributes and characteristics of a given landscape. Habitat fragmentation alters the spatial configuration of larger habitat patches and creates isolated or tenuously connected patches of the original habitat that are not interspersed with an extensive mosaic of other habitat types if these other habitats are unsuitable for a given species (Wiens 1990).

After a review of some of the most generally accepted definitions of habitat fragmentation, Franklin et al. (2002) developed definitions for the fragmentation outcome and fragmentation process that contained most of the requisites needed by wildlife biologists to fully understand the concept. For the purposes of this paper, the following definitions appear to be the best.

The outcome of habitat fragmentation is defined (Franklin et al. 2002:27) 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."* The process of habitat fragmentation is defined (Franklin et al. 2002:27) as the set of mechanisms that leads to the discontinuity in the spatial distribution of habitat. There are 4 key components of these 2 definitions: (1) discontinuity; (2) mechanism(s); (3) spatial distribution of resources in a given area; and (4) demographic attributes.

The concept of habitat fragmentation was derived from the theory of island biogeography (MacArthur and Wilson 1967), where the number of species increases with increasing size of islands (Haila 2002). Empirical studies of wildlife on islands of various sizes supported this theory, and the intellectual appeal and convenience of applying this theory to habitats on mainland continents led to its current favor by the wildlife profession (Harris 1984, Haila 2002). Villard (2002:319) and Haila (2002:327) used the term "intellectual attractor" to describe the concept because it was so rapidly adopted as a fundamental principle of our and other professions. It seems inconceivable to some wildlife biologists to question the concept, its background assumptions, and its implementation for conservation purposes because the concept fits nicely with our conservation goals. Along these lines, island biogeography theory has had "disciplinary promise" (Haila 2002:327) because it seemed poised to deliver strict adherence and analogous effects on mainland habitats. A strict analogy of this theory to mainland habitats, however, is somewhat misleading (Haila 1999, 2002; Bissonette and Storch 2002). A key point about the theory is that islands are surrounded by water, which is unsuitable habitat for island-dwelling terrestrial species. On the mainland, however, habitats are surrounded by other terrestrial habitats, many of which are suitable for wildlife before and after fragmentation. This discrepancy between islands and the mainland is a critical distinction that cannot be overlooked. In addition, there are substantial differences in ecosystems across wide geographic regions such that fragmentation must be viewed differently in these different regions (George and Dobkin 2002*a*, 2002*b*).

Wildlifers must be careful to avoid the temptation to focus inordinate attention on an intellectually appealing and seemingly intuitive concept like habitat fragmentation that gives them a convenient way to recommend conservation actions, particularly when fragmentation might play a minor role in wildlife conservation when considered in the broader context of habitat change (Haila 2002, Villard 2002, Fahrig 2003). Biologists should not overstate a conservation case on the grounds of habitat fragmentation when other more appropriate and defensible issues such as habitat loss (which causes habitat fragmentation; see below), invasive species, and failed and inappropriate land management policies may trump habitat fragmentation in terms of impacts on wildlife.

Fragmentation versus Heterogeneity

We must distinguish between fragmentation and heterogeneity because these interrelated concepts are not synonymous (Franklin et al. 2002, Fahrig 2003). Fragmentation is a process as well as an outcome, while heterogeneity is a multistate outcome of habitats from ≥1 disturbance processes (Haila 1999, Franklin et al. 2002). Habitat fragmentation as an outcome is the simplest form of heterogeneity—a mixture of habitat and non-habitat, which is a binary outcome (Franklin et al. 2002). This is the island analogy. Landscapes with their habitat mosaics, however, are typically multistate outcomes with a more complicated mosaic of habitats of varying levels of habitat suitability. This is the typical mainland analogy, and mainland mosaics are driven by disturbance and vegetation succession. A landscape with housing subdivisions scattered throughout coastal scrub habitats is an example of a fragmented landscape. The heterogeneous landscapes of California's foothill oak (*Quercus* spp.) woodlands are a classic example of the multistate outcome, and fire, geology, grazing, and browsing are some of the disturbances driving this dynamic mosaic in wildlands. In contrast, habitat homogeneity is an outcome where habitats do not occur in a multistate, and disturbances have either been limited or controlled to such an extent that a monoculture of habitats exists. Agricultural areas of California's Central Valley can be examples of homogeneity if one presumes that all agricultural types have equivalent value as habitat, a presumption that often ignores the known and varied habitat values of agricultural lands to many wildlife species.

Habitat for all species is heterogeneous on many scales because of both natural processes and human activities (Lord and Norton 1990). Heterogeneity occurs within and among habitats, which results in heterogeneous landscapes. In addition, heterogeneous landscapes result because most terrestrial wildlife will use many different habitats, and habitats form mosaics. A key point is that not all habitats have equal habitat suitabilities; in fact, some biodiversity measures, including species richness, which is a measure based on single-species habitat use, are greater in urban-dominated habitats than in wildland habitats (Ricketts and Imhoff 2003). Furthermore, heterogeneous landscapes result in heterogeneous distributions of populations at multiple spatial scales (Wiens 1989). Heterogeneous habitats coupled with multiple species, all occurring at multiple scales because of varying home ranges, body sizes, residency patterns, etc., should logically receive variable impacts from fragmentation. Heterogeneous habitats combined with heterogeneous population distributions means that fragmentation impacts will be variable and depend on the evaluation species and temporal and spatial scales used in the analysis of fragmentation.

Fragmentation and Loss

Habitat fragmentation and habitat loss are inextricably linked, and fragmentation generally occurs through loss (Franklin et al. 2002, Haila 2002). Habitat fragmentation ultimately rests on the loss of 1 habitat and its replacement by another that is ostensibly less suitable and tending toward unsuitable. When fragmentation and loss are addressed simultaneously, loss has the greatest consequences on species viability (McGarigal and McComb 1995, Fahrig 2003). Fahrig (2002) also points out that several modeling studies predicted large effects on biodiversity from both fragmentation and loss even though loss was found to be more important. Loss of habitat for 1 species, however, generally results in a habitat increase for another species, so loss is a species-specific determination.

CHALLENGES WITH THE CONCEPT OF HABITAT FRAGMENTATION

Species-Level Assessments in a Multispecies World

Habitat fragmentation must be defined at the species level, and many species occupy any given habitat patch and landscape, resulting in varied responses by different species when fragmentation occurs (Wiens 1990, Bissonette and Storch 2002, Fahrig 2003). This is the functional paradox of the fragmentation concept, particularly when fragmentation is analyzed using a biodiversity measure such as species richness. Many site-specific assessments of fragmentation use biodiversity measures and species turnover rates to demonstrate the negative effects of fragmentation (Debinski and Holt 2000, McGarigal and Cushman 2002, Fahrig 2003). There should be a trend for more species-specific assessments of fragmentation, and, although these are particularly helpful, they have limited inferential value beyond the species studied. Fragmentation assessments, however, should involve ≥2 species with differing habitat relationships if conservation and management actions are to be based on multiple species concerns. Wildlife are variously affected when their habitats are fragmented, and this conclusion is generally expected based on their ecological requirements (Wiens 1990). In addition, different aspects of fragmentation (e.g., perforation, attrition, etc.; see below) affect different species in different ways (Wiens 1990, Davidson 1998). For example, the productivity of 1 species may decline because of increased nest predation that results from perforation, while another species may increase immigration into the perforated habitat patches, resulting in an increasing population density not only in the patch but perhaps throughout the larger area.

The range of wildlife responses presents challenges for wildlife biologists when managing habitats for multiple species or assessing the impacts from habitat fragmentation because a full range of species and response variables must be considered. In addition, biologists face challenges because there are many opportunities to favor some species over others when undertaking conservation and management actions. While such favoritism is acceptable and driven by legal mandates (e.g., federal and state endangered species laws) and regulatory priorities (e.g., game species), there is the undeniable conundrum of preferring some species over others when developing management strategies or assessing impacts from habitat fragmentation.

Measuring Fragmentation

Measuring fragmentation is challenging, and there are many possible measures used to quantify habitat fragmentation. For example, there are 100 metrics of habitat fragmentation available in the program FRAGSTATS (McGarigal and Marks 1995). There is, however, little agreement on what metrics are the most appropriate, and it is difficult to translate metrics into conservation or management actions (Davidson 1998, Bogaert 2003). The fundamental issue with any metric is what the metric means from a biological standpoint. For example, how does patch shape index, 1 of 14 patch metrics in FRAGSTATS (McGarigal and Marks 1995) where a circle has a shape index = 1, relate to productivity, survivorship, or movements of a given species?

Patch size is a common fragmentation metric, yet it is an ambiguous measure because fragmentation and loss reduce patch sizes of some habitats while increasing patch sizes of other habitats. Contradictory results from the various metrics also present challenges because biologists must choose which metric yields the desired response measure. Furthermore, using patch size as a fragmentation measure assumes that patch size is independent of habitat (Fahrig 2003). Another fundamental issue regarding metrics is that, with so many possible, there are likely to be those that are positively and negatively correlated, and most researchers will not report all the metrics in their work. In addition, dozens of metrics combined with myriad possible population and ecosystem responses resulting from habitat fragmentation represent a statistical morass for researchers and managers alike (McGarigal and Cushman 2002). The complicated statistical analysis used by Franklin et al. (2000) to assess the effects of landscape characteristics on and population dynamics of the northern spotted owl (*Strix occidentalis caurina*) demonstrates how challenging it is to link fragmentation metrics with demographic measures, even for 1 species. There are many possible wildlife response measures, including those associated with behavior, demographics, movements, and health, that could be linked with fragmentation metrics.

Fragmentation must have a temporal reference so that metrics from a given area can be compared between ≥2 different time periods. The investigator can freely choose these time periods, but the time periods should be meaningful from the standpoint of habitat trajectories, species demographics, and disturbance regimes. To account fairly for habitat dynamics, future landscapes require modeling of landscape and habitat configurations and suitabilities with and without the effects of anthropogenic activities and/or regimes of natural disturbances and vegetation succession (Garrison 1992, Garrison and Standiford 1997, Boutin and Hebert 2002). Geo-referenced aerial photographs, satellite images, or other types of remotely sensing data are needed from $\geq$2 time periods to measure landscape changes so that the magnitude and extent of the fragmentation can be estimated. Furthermore, the reference periods, despite their intended comparisons, will certainly have equally likely ranges of positive, negative, and neutral impacts on species from landscape projects. In addition, projections of habitat conditions for the future-with and future-without scenarios double the assumptions and range of responses. Biologists must also determine the appropriate timeframes for the analysis based on combinations of biological and management considerations. Landscapes that could serve as controls, references, or replicates improve the scientific foundations of fragmentation assessments.

Habitat and Non-Habitat

Defining habitat and non-habitat is perhaps the most significant challenge in assessing fragmentation. Absent a land–water habitat dichotomy (MacArthur and Wilson 1967), such as, for example, terrestrial ecosystems with large water bodies or those dominated by intensive agriculture, the majority of wildland habitats landscapes do not sufficiently demonstrate this dichotomy. This is particularly true throughout North America where wildland habitat mosaics still dominate most of the region (George and Dobkin 2002*b*). Furthermore, habitat patches occur with varying degrees of suitabilities for the vast majority of species. Any query of a CWHR habitat suitability index model or similar statewide or regionwide system of wildlife habitat relationships models easily demonstrates the fact that there is a wide range of habitat suitabilities across habitat types. Furthermore, habitat suitability can change substantially with time; sometimes habitat suitability changes substantially for some species within a year or 2, potentially making fragmentation assessments quickly obsolete.

Making Inferences

Even if appropriate species, metrics, and habitat definitions are chosen for species-specific assessments, it is difficult to make strong inferences about the effects of habitat fragmentation on wildlife (Wiens 1990, Bissonette and Storch 2002, Haila 2002, McGarigal and Cushman 2002) for the following reasons:

1. Wildlife species respond in a multicausal manner to fragmentation. That is, the different life history patterns (e.g., generalists vs. specialists, species favoring early successional stages vs. species favoring late successional stages, etc.) result in different responses to fragmentation (Wiens 1990, Debinski and Holt 2000, Bissonette and Storch 2002, McGarigal and Cushman 2002). The "patch" is defined differently by each species so any anthropogenic definition of patches for multispecies assessments may yield inaccurate results depending on the species (Wiens 1990, Johnson 2001). Factors such as climate, predation, disease, and competition can drive population dynamics that might otherwise be linked to habitat change (Wiens 1990, Franklin et al. 2000, Garrison et al. 2003).
2. Time lags exist between the disturbance and the effect, and these lags vary at different spatial scales and for different species (Wiens 1990, Bissonette and Storch 2002, McGarigal and Cushman 2002). In general, most assessments of fragmentation are based on static area-only differences in populations and communities without accounting for temporal responses. Wiens (1990), however, shows that temporal responses are highly variable based on spatial scale and species ecology. That is, longer response periods occur for larger ecosystems and longer lived, more sedentary species, and vice versa. Time lags become particularly important when studies are done on habitat patches that have different histories of previous disturbances (Wiens

1990, McGarigal and Cushman 2002). Furthermore, turnover in local populations in fragmented systems is highly variable within and among habitat patches (Opdam 1991). The problem of time lags is particularly pronounced when studies are short term, as are most wildlife studies (Opdam 1991, Sallabanks et al. 2000, McGarigal and Cushman 2002). In addition, regrowth of vegetation after disturbances and other aspects of habitat change affect the time lags of responses by wildlife.

3. Biological and ecological thresholds of fragmentation are largely unknown (Johnson 2001, Boutin and Hebert 2002, Fahrig 2002). Patch size thresholds, for example, are largely unknown because little experimentation has been done (Debinsky and Holt 2000, McGarigal and Cushman 2002). Patch size thresholds are often inferred from life history attributes such as home range size, or from passive sampling, which has some scientific limitations (Johnson 2001). Thresholds are largely unknown for most of the fragmentation metrics even though software can generate these metrics. Because these thresholds are largely unknown, unexpected results could happen when fragmentation occurs. This goes for thresholds of responses to fragmentation, as well as definitions of the key thresholds of habitat and non-habitat. Knowledge of thresholds is absolutely critical for wildlife management purposes, where many recommendations for species conservation involve decisions about sizes of retained habitat patches. For this reason, wildlifers should be aware of the likelihood of errors of "commission", where area sensitivity thresholds are predicted but do not exist, and errors of "omission", where sensitivity thresholds exist but are not predicted. Basic ecological principles lead us to expect that there are thresholds where wildlife respond to some level of habitat loss or gain but these thresholds remain unclear for most species (Boutin and Hebert 2002, Fahrig 2003).
4. Differences in the ecology of various species result in nonrandom and nonlinear responses to fragmentation that are inherently species specific (Wiens 1990, McGarigal and Cushman 2002). Therefore, predictions of the effects of fragmentation are particularly difficult to make, especially when the underlying data are experimentally flawed, as is the case with many fragmentation studies (Debinski and Holt 2000, Johnson 2001, McGarigal and Cushman 2002, Fahrig 2003).
5. Effects are heavily influenced by the differences between the matrix (heterogeneity) surrounding the fragmented habitats and the fragmented patches themselves, especially if these patches resulted from disturbances or are remnant patches from previous landscapes that are more static and subject to natural disturbances (Johnson 2001, Franklin et al. 2002, McGarigal and Cushman 2002). The bottom line here is that not all habitat patches or landscapes are equal, and this heterogeneity results in confounding effects for any fragmentation assessment (McGarigal and Cushman 2002). Disturbances are major sources of change, and ecosystems and habitats do not exist in steady states. Therefore, structural differences occur in the matrix and patches at some level regardless of whether fragmentation is induced by wildland or anthropogenic disturbances.
6. The effects of fragmentation are heavily dependent on the temporal and spatial scales of observation (Johnson 2001, McGarigal and Cushman 2002). Studies that are of inadequate duration and study area size yield, at best, partial, incomplete, or spurious results. Study areas can be too small or too large, and study durations are often too short (Sallabanks et al. 2000). Spatial scale is very critical because inferences to populations and distributions for a given species are limited to the scale being examined (Wiens 1989, Johnson 2001, Franklin et al. 2002). In addition, fragmentation must be defined not only at the species level but also at the population and individual levels depending on the scale of concern (Franklin et al. 2002). The wide range of simultaneously operating ecological patterns and processes at different spatial

and temporal scales leads to difficulty in demonstrating the effects of fragmentation (Haila 2002, McGarigal and Cushman 2002). Managers and investigators must choose spatial and temporal scales that are most appropriate given various factors involving habitat and species ecology as well as logistical constraints.

7. Habitat and wildlife population dynamics are contingent on ecosystem history and trajectories and therefore subject to unpredictable stochastic events (Wiens 1990, Haila 2002). Although the future is unpredictable regarding climates, stochastic events, species changes, etc., we can safely assume that anthropogenic mechanisms will still operate in a deterministic manner where increasing amounts of wildland habitats are changed to human-altered habitats**,** but these also have trajectories, albeit often rather different from those of wildlands. In contrast, natural disturbance regimes may supersede any anthropogenic change on a landscape, rendering any conservation or management action occasionally meaningless. Severe wildfires in habitat reserves are a case in point. Both types of mechanisms must be accounted for in fragmentation assessments.
8. Passive sampling is one of the greatest methodological problems with fragmentation studies (Johnson 2001, Haila 2002). Passive sampling occurs when sampling effort increases as sample area size increases. Species richness and abundance estimates increase and/or have more stable variances with increasing sample effort, resulting in highly biased study results (Johnson 2001). Verner (1986) noted this problem and cautioned against potentially biased measures of populations and communities from habitat fragments. With most fragmentation studies, observers study habitat patches along a size gradient. When species richness increases as patches get larger, observers generally conclude that this supports the theory of island biogeography and then implicate habitat fragmentation as the source of this apparent negative impact (see Forman et al. 1976, Whitcomb et al. 1981, Ambuel and Temple 1983). In reality, however, there is a proportional increase in the sampling area and effort as patch size increases so more species and individuals are more likely to be found in larger areas. In addition, larger sites are more likely to contain at least 1 individual of a species, particularly uncommon or rare species (Johnson 2001, Haila 2002). Of course, this is a reason to favor conservation of larger patches, assuming that those patches possess all species expected within some geographic area. If sampling effort relative to sample area size is not accounted for, spurious results will be found (Verner 1986, Johnson 2001, McGarigal and Cushman 2002).
9. Fragmentation can occur only when the mosaic contains habitat and non-habitat (the binary mosaic), and the life history attributes of a given species (e.g., habitat relationships and demographics) greatly influence the definition of habitat and non-habitat (Franklin et al. 2002). There is a very low likelihood that any terrestrial habitat can be considered non-habitat because there is at least some value for at least 1 life requisite in most habitats for many species. Furthermore, the cause-and-effect outcome of fragmentation requires field studies of long timeframes and large study areas. Notable examples where this has been done include studies of avian nest success and predation (reviewed by Chalfoun et al. 2002), demographics and movements of the northern spotted owl (Franklin et al. 2000), and movements, population structure, and demographics of forest salamanders (reviewed by Welsh and Droege 2001). Most studies, however, demonstrating direct effects of fragmentation have experimental deficiencies, particularly with regard to avian nest success (see Debinski and Holt 2000, Johnson 2001, Chalfoun et al. 2002, McGarigal and Cushman 2002, Fahrig 2003).
10. When habitat loss is included with fragmentation assessments, there must be a zero-sum outcome of the habitat tally as habitat losses must be replaced by habitat gains (Davidson 1998, Fahrig 2003). It is tempting to subtract habitat losses from the landscape mosaic because lost habitats could

be viewed as unsuitable and are not replaced with suitable habitats. This is somewhat incorrect because all habitats have some value to wildlife and it doesn't account for the replacement of 1 habitat with another. This is especially important from the single-species context from which fragmentation assessments must be made. Habitat loses for 1 species may be compensated by habitat gains for other species. There might be a decline for the species experiencing loss, but another species might gain habitat under a fragmentation process

THE HABITAT FRAGMENTATION PROCESS

How Fragmentation Occurs

Fragmentation generally occurs through habitat loss such that loss must be viewed separately as a cause of fragmentation. Fragmentation can, however, involve habitat loss (reduction in amount) as well as breaking up or subdividing habitat patches that results in smaller and more isolated patches (Hunter 1997, Haila 1999, Franklin et al. 2002, Fahrig 2003). When habitat loss and fragmentation are addressed separately, habitat loss has the most significant consequences for species viability (Haila 2002, Fahrig 2003). Yet, fragmentation and loss go together, and it is very difficult to identify the relative significance of these causes of habitat change (Haila 1999). In reality, the distinction between them can be irrelevant for wildlife managers because we inevitably deal with both when attempting to conserve wildlife in fragmented habitats. For the sake of understanding, however, these causes must be distinguished because there are differing management implications for each.

Fragmentation operates in 4 different ways when loss and fragmentation are combined to describe and categorize the process (Franklin et al. 2002, Fahrig 2003): (1) habitat loss with no fragmentation; (2) the combined effects of habitat loss and breaking habitat into smaller patches; (3) breaking habitat into smaller patches without habitat loss; and (4) habitat loss and breaking habitat into smaller patches and also a reduction in habitat quality. These examples work for a common landscape that is composed of $\geq$1 habitat and a surrounding matrix within a bounded landscape. Cases (1) and (2) apply when the landscape is composed entirely of 1 habitat and there is no surrounding matrix. In reality, cases (2) and (4) are the most common ways that habitats are fragmented.

Habitat fragmentation is an aspect of a broader sequence of spatial and temporal processes that transform habitats and landscapes by natural or anthropogenic causes from 1 type to another (Forman 1995). Habitat change, however, is inevitable because no habitat or landscape is static. Vegetation succession is another common landscape-changing process that is ecologically significant and has various fragmentation outcomes (Forman 1995). For no fragmentation to occur with vegetation succession requires that all habitat patches retain their original spatial characteristics, something that is highly unlikely except for relatively brief time periods during the considerably longer succession sequence. Fragmentation must also be viewed in the context of the natural disturbance regimes and vegetation changes in the area (Haila 2002), and how disturbances fit into successional outcomes must also be recognized. In addition, habitat recovery or recruitment may ameliorate the initial and short-term impacts from fragmentation.

Landscapes change through 5 spatial processes that overlap to various degrees throughout the period of land transformation (Forman 1995), and fragmentation is just 1 outcome. These processes can occur under natural and anthropogenic circumstances. Perforation is the process of making holes in the habitat. Dissection is the carving up or subdividing the area with relatively equal-width ribbons of different habitats. Fragmentation is the breaking apart of the habitat into smaller pieces. Shrinkage occurs as the pieces continue to decrease in size. Attrition is the process whereby the remaining patches disappear through habitat degradation or vegetation succession. Hunter (1997) combined shrinkage with fragmentation and modified these processes such that 4 of the 5—dissection, perforation, fragmentation, and attrition—represent the stages of fragmentation. Dissection is the first stage, and it occurs when roads, transmission lines, rivers, and other linear features become barriers to movement. Perforation is the second stage, where small anthropogenically or naturally caused patches appear and edge effects start to become pronounced. Fragmentation is the third stage and occurs when the smaller patches increase in frequency and are reduced in size to the point at which the fragmented habitats begin to dominate the landscape. Attrition is the final stage where wildland or pre-fragmentation habitats remain as small, isolated patches amidst the landscape that is now dominated by a mosaic of fragmentation-changed habitats. These processes, regardless of sequence, are collectively lumped together into the single process of habitat fragmentation. An important distinction that must be made regarding these outlines of the fragmentation process is that habitats must be made unsuitable or of lowered suitability with a concomitant reduction in some measure of wildlife habitat quality. Conversely, if the disturbance process changes the habitat mosaic but there is no change in an appropriate measure of wildlife habitat quality, then it seems logical that fragmentation cannot occur. What occurs in the latter case is that habitat change has occurred but not fragmentation.

DETERMING IF FRAGMENTATION HAS OCCURRED

When determining whether fragmentation has occurred, at least 4 sources of information are necessary (Franklin et al. 2002). First, the type of habitat(s) being fragmented must be determined at the species level. Second, the spatial and temporal scales of the fragmentation must be determined. On a spatial scale, it should be questioned whether fragmentation is occurring within stands, between stands, among stands, and across the landscape. It is likely that fragmentation processes affect all 4 spatial scale levels, and stands themselves are essentially the fragments for analysis. Therefore, any change in size and configuration of stands works at all 4 spatial levels. On a temporal scale, habitat changes resulting from fragmentation must be accounted for with realistic timeframes that capture time lags and include the point at which some stasis or equilibrium is reached when habitat changes are stabilized after the disturbance occurred that initially caused the fragmentation. Third, the magnitude and type of fragmentation must be assessed. Fourth, the mechanisms causing the fragmentation must be identified and appropriate linkages must be made between the fragmentation mechanism and changes to the habitat and landscape. Knowledge about the mechanisms causing fragmentation is necessary so that the fragmentation can be placed into the context of a presumably natural and accepted ecological process or a presumably unacceptable anthropogenic process (Franklin et al. 2002, Haila 2002).

EFFECTS OF FRAGMENTATION ON WILDLIFE

The mechanisms and processes of fragmentation produce 3 types of effects: (1) patch-size effects; (2) edge effects; and (3) isolation effects (Fahrig 2003). Wildlife biologists must address all 3 because they generally occur with habitat fragmentation, and each effect requires different management actions (Franklin et al. 2002, Fahrig 2003). Patch-size effects require biologists to measure the size of habitat patches and make recommendations to retain or increase sizes of desirable patches and decrease sizes of undesirable patches. Edge effects require biologists to quantify habitat adjacency patterns and measure patch perimeters. Edge effect recommendations typically focus on softening habitat boundaries (e.g., retaining some habitat features and making patch boundaries more fluid and less dramatic) and putting habitats of more or less equivalent habitat suitabilities adjacent to each other. Finally, isolation effects have multiple requirements including patch size, inter-patch distances, locations of patches, and adjacency patterns. Recommendations for isolation effects typically involve minimizing inter-patch distances, providing corridors, and putting habitats of equivalent habitat suitabilities adjacent to each other. Retention and recruitment of desirable within-patch habitat attributes are common management recommendations for all 3 effects. If adjacent or nearby habitat patches are of equivalent habitat qualities, all effects are essentially non-existent.

Concerns about the effects of habitat fragmentation on wildlife have precipitated major wildlife conservation efforts throughout the United States. Notable examples of these efforts include habitat conservation and population inventory efforts for neotropical birds and forest raptors, such as the northern and Mexican (*S. o. lucida*) spotted owls. Yet, there is enough skepticism about the overall scientific validity of the fragmentation concept (Haila 2002, Villard 2002), as well as attempts to clarify the term and assess its conservation significance (Bissonette and Storch 2002, Franklin et al. 2002, Fahrig 2003), such that everyone interested in the issue should be skeptical when the term is uncritically invoked regarding the negative effects of habitat fragmentation on wildlife. There are several very good reviews of the various effects of habitat fragmentation on wildlife and other components of biodiversity that support this skepticism by demonstrating that varied impacts occur on wildlife (see Chalfoun et al. 2002, George and Dobkin 2002*a*, McGarigal and Cushman 2002, Fahrig 2003).

There are many reasons that wildlife are affected by habitat fragmentation which are elaborated by McGarigal and Cushman (2002) and Fahrig (2003). Negative effects are likely the result of 2 main causes. First, fragmentation implies that there is an increase in the number of smaller patches, and, at some point each patch becomes too small to sustain a local population. Second, a negative edge effect occurs when predation, competition, or parasitism increases with edges. With both effects, species in the fragmented patch have reduced survival, productivity, or occupancy resulting from increasing levels of predation, nest parasitism, and competition and/or worsened micro-climates.

Positive effects result from fragmentation for many reasons (Fahrig 2003). First, ecological relationships, particularly those involving predators and prey or competitive interactions, could be stabilized with fragmentation as greater numbers of smaller habitat patches provide increased refugia. Second, immigration rates can increase with fragmentation, and populations could then increase if immigration plays a particularly important role in population stability. If the amount of habitat is constant, increasing fragmentation actually implies shorter distances between patches as patches become smaller and more interspersed in the matrix. With decreasing distances between patches, the patches themselves become less isolated, thereby facilitating immigration into previously vacant patches. Third, populations may increase with fragmentation processes that increase the number of different habitats in a given area for those species requiring different habitats for different life requisites. Fourth, a fragmented landscape has the potential for greater degrees of complementary habitats and more interdigitation of different habitats; again, species favoring multiple but complementary habitats would benefit. Lastly, there can also be positive edge effects on some species, particularly those preferring habitat edges, which are often the cause of the negative effects on those species subjected to negative effects of fragmentation-induced edges (Fahrig 2003).

DISCUSSION

In summary, fragmentation is, at best, an ambiguous concept fraught with complexities that challenge its assessment (Franklin et al. 2000, Haila 2002, Fahrig 2003). Fragmentation is a concept that describes a landscape process that is ecologically complex and driven by unpredictable as well as deterministic mechanisms that produce predictable and unpredictable outcomes (Bissonette and Storch 2002). These mechanisms are anthropogenic and natural. In addition, the metrics used to quantify fragmentation are ambiguous (Davidson 1998, Bissonette and Storch 2002), and there are many ways that habitats can be fragmented (Franklin et al. 2002, Bogaert 2003**,** Fahrig 2003). Inferences from several empirical studies lead to the conclusion that any negative effects on wildlife from fragmentation are weak relative to habitat loss (Haila 2002, Fahrig 2003). In addition, inferences lead to the conclusion that the effects of fragmentation are at least as likely to be positive as negative (Fahrig 2003). Studies of habitat fragmentation effects were characterized by numerous problems with experimental design where sampling design, confounding effects, and fragmentation definitions compromised study results and led to uncertainty regarding the effects of habitat fragmentation (Johnson 2001, McGarigal and Cushman 2002, Fahrig 2003). Problems noted by these authors have undoubtedly been repeated with current studies of habitat fragmentation.

Conservation generalizations are often made regarding habitat fragmentation. There is a general consensus that fragmentation generally reduces biodiversity, and the greatest threat to biodiversity is conversion of habitats to other uses (Meffe and Carroll 1997, National Commission on Science for Sustainable Forestry 2005). In spite of the focus on fragmentation, Haila (1999) states that fragmentation resulting from habitat loss causes changes in wildlife for 2 reasons that are easily deduced from common ecological knowledge. First, any reduction in habitat means a reduction in the total amount of resources available for the wildlife species for which that habitat is defined. Second, because few wildland habitats are internally homogeneous, a reduction in habitat area also results in a decrease in the range of some of environments available in each habitat patch for some species. That said, it is possible to focus solely on habitat loss to justify conservation. Conversely, reductions in habitat areas are met with increases in area of other habitats, as well as increases in environments available in the increased habitat patches.

We must acknowledge that habitats are not in a steady state because habitat conditions continuously vary in time and space (Wiens 1990, Carey et al. 1999, Haila 2002), and that anthropogenic and natural fragmentation mechanisms are operating simultaneously. These 2 groups of mechanisms may or may not be linked. For example, active fire suppression by humans has increased densities of trees, which has led to increased tree mortality which, in turn, has increased fire risk for California's forests (U. S. Forest Service 2004). It is unrealistic and probably impossible to manage today's habitats toward a desired outcome that approximates their historical range of conditions (Carey et al. 1999, National Commission on Science for Sustainable Forestry 2005). Today's fragmentation mechanisms, such as increased human pressures, wildfire risk, and non-native species invasions, have increased their roles in causing habitat change and certainly loss over time, hence, wildlife biologists would be better served by directing management toward a future range of variation that will better sustain biodiversity with ongoing environmental change (Carey et al. 1999, Boutin and Hebert 2002, National Commission on Science for Sustainable Forestry 2005).

There is an inherent problem with making cases regarding negative impacts on wildlife when habitats are already essentially fragmented to various degrees, particularly habitats that are managed to promote plant growth and allow harvesting, as are commercial forests and agricultural lands. These are fragmented habitats by definition, particularly on private lands, which are managed artificially to create dynamic and fragmented habitats to achieve production and commodity goals. In these cases, biologists would be better served by working toward landscape conditions where fragmentation mechanisms are managed or controlled to retain maximum management flexibility. Boutin and Hebert (2002) suggested that landscape configuration, rather than habitat loss, be the priority for fragmentation assessments in forested habitats unless habitats of interest drop below some predetermined threshold. It seems that this recommendation could apply to other habitats as well, particularly those under similar management constraints such as agricultural lands. Wildlife managers working with these managed landscapes should identify a desired landscape configuration that is compatible with the resource management regime of the landscape. Fragmentation assessments might focus on habitat loss for habitats threatened mostly by loss, such as coastal scrub and oak woodland habitats, and appropriate thresholds should be used. Determining these thresholds, of course, remains problematic as others have noted (Bissonette and Storch 2002, Fahrig 2003).

A RECOMMENDED APPROACH

Wildlife biologists must use an empirically based and methodologically rigorous and consistent approach when assessing the effects of habitat fragmentation on wildlife (Johnson 2001, McGarigal and Cushman 2002). The following steps should be followed when designing research studies, conservation assessments, and management actions associated with habitat fragmentation, and these steps are based on approaches by Haila (2002) and McGarigal and Cushman (2002): (1) the anthropogenic and natural mechanism(s) causing habitat change must be identified (Franklin et al. 2002, Haila 2002); the spatial and temporal scales of the mechanisms and their relative contributions and roles in fragmentation on the landscape must also be identified; (2) appropriate wildlife species must be selected for the assessments, and these species must be numerous with a breadth of habitat relationship patterns so that a full range of effects will be detected (Garrison and Standiford 1997, McGarigal and Cushman 2002); there should be species that are positively and negatively affected by fragmentation, and their habitats must be adequately defined; (3) a landscape study area of appropriate size must be chosen because habitat fragmentation occurs at the landscape scale, and this landscape must be chosen based on the wildlife species chosen for the assessment, the fragmentation mechanisms, and land management considerations (Wiens 1990, McGarigal and Cushman 2002); (4) appropriate reference areas and reference periods must be selected for the assessment to allow for comparisons (Walters and Holling 1990, McGarigal and Cushman 2002), and the assessments should include future-with and future-without mechanism scenarios because habitats and landscapes are dynamic (Garrison 1992, Garrison and Standiford 1997); reference spatial and temporal scales must be commensurate with the fragmentation mechanisms and land management actions; (5) mechanisms resulting from natural disturbance regimes should be factored into assessments of anthropogenic mechanisms so that appropriate management actions can be implemented (Franklin et al. 2002, Haila 2002); (6) appropriate metrics must be chosen to measure fragmentation and loss (McGarigal and Marks 1995, Davidson 1998, Bogaert 2003); appropriate metrics are those that will be correlated with appropriate wildlife response variables including population and community attributes, demographics, and movements (Franklin et al. 2000, McGarigal and Cushman 2002), as well as yield correct measures of fragmentation; (7) for field research projects, problems associated with passive sampling, confounding effects, and data pooling must be avoided or, at worst, experimentally accounted for (Johnson 2001, Haila 2002) to strengthen results and conclusions; and (8) conservation actions must be commensurate with the magnitude and extent of the fragmentation and loss.

Habitat fragmentation will remain a pervasive and long-term threat to wildlife resources. That said, however, wildlife biologists must recognize that seemingly convenient and attractive scientific concepts like habitat fragmentation will not work if inappropriately applied. The additional work needed to gather sufficient data and build a solid case for habitat fragmentation will help ensure that conservation and management actions are appropriate and commensurate with the impacts on wildlife. After conducting these assessments and because of the ambiguity with the concept of habitat fragmentation, demonstrating that habitat loss has an impact on wildlife should be sufficient to undertake conservation and management actions. However, wildlife biologists must still make a rigorous and scientifically based case for habitat loss.

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