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Habitat Fragmentation in the Temperate Zone: A Perspective for Managers

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Abstract — Habitat fragmentation occurs when a large, fairly continuous tract of vegetation is converted to other vegetation types such that only scattered fragments of the original type remain. Problems associated with habitat fragmentation include overall habitat loss, increase in edge habitat and edge effects (particularly higher parasitism and nest predation rates), and isolation effects. Birds show variable responses to fragmentation, with the most conservation concern focused on so-called "area sensitive" species that remain only on large habitat fragments. Management responses to fragmentation include preservation of large tracts of habitat with minimal amounts of edge.

INTRODUCTION

The term "habitat fragmentation" has become a buzzword among conservationists and managers in recent years. Although new to some, researchers have been investigating this area extensively during the last 25 years. One can argue that modern approaches to habitat fragmentation began with the MacArthur-Wilson theory of island biogeography (1963, 1967). Since then, reviewers have noted over 700 publications dealing with some form of habitat fragmentation (Robinson, unpub.). Among these are several recent reviews of the role of fragmentation in declines of Neotropical migrant landbirds (Wilcove et al. 1986, Wilcove and Robinson 1990, Askins et al. 1990, Finch 1991, Robinson and Wilcove, in press). Here, we give a brief overview of what fragmentation is and why it can be detrimental, with a focus on Neotropical migrant landbirds. We suggest general management guidelines for fragmented regions, noting when further research is necessary for more quantitative guidelines for managers.

What Is Habitat Fragmentation?

Habitat fragmentation occurs 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. These remnants (also called isolates, habitat islands, fragments, patches, etc.) obviously occupy less area than the initial condition, are of variable size, shape, and location, and are separated by habitats different from the original condition. The classic example of fragmentation (fig. 1) shows how large, uniform tracts of forest and prairie were broken into small isolates through farm development; the analogy of conversion of a large "mainland" of habitat to an archipelago of habitat islands is certainly apparent.

In this paper, we are focusing on permanent fragmentation that has resulted in islands of habitat surrounded by dissimilar habitat types. Temporary fragmentation occurs through timber harvest practices which create holes of young forest within a matrix of mature forest. Although effects of this type of fragmentation are generally less severe than permanent

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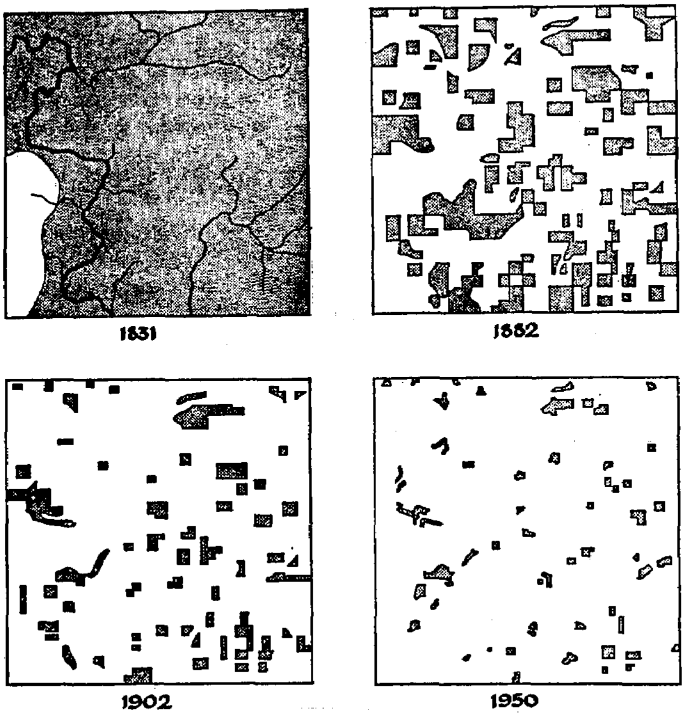

Figure 1. — Fragmentation of forest habitat in Cadiz Township, Wisconsin, over time. After Curtis 1956.

fragmentation, detrimental effects still exist. See the chapter on silviculture (Thompson et al., this volume) for information on temporary fragmentation.

PROBLEMS ASSOCIATED WITH HABITAT FRAGMENTATION

Habitat fragmentation results in both a quantititative and qualitative loss of habitat for species originally dependent on that habitat type (Temple and Wilcox 1986). As a consequence, the abundance and diversity of species originally present often declines, and losses are most noticeable in smallest fragments. Below we discuss mechanisms responsible for these changes, focusing on forest fragmentation because most work has been done in this habitat.

Habitat Loss

The most obvious effect of fragmentation is an outright quantitative loss of habitat for species dependent on the original habitat type in a region. Groups of species directly impacted by habitat loss through fragmentation include those with large home range requirements, very specific microhabitat requirements, and poor dispersal abilities (Wilcove et al. 1986, Wilcove 1988). For example, when home range or territory requirements of a species are greater than fragment size, the species often disappears. However, the factors listed above are usually not sufficient to explain why most Neotropical migrants decline in numbers or disappear from small fragments.

Increase in Edge Habitat and Edge Effects

Most Neotropical migrants utilize small territories (<2 ha), but may disappear from fragments tens or hundreds of times territory size. For these species, fragmentation results in qualitative changes in the remaining habitat (Temple and Wilcox 1986). As an area is fragmented, there is an increase in amount of edge relative to interior area and an increase in "edge effects" (Temple 1986). For our purposes, edge is defined as the junction between two dissimilar habitat types or successional stages. "Edge effects" are ecological characteristics associated with this junction that affect any number of biological traits (Harris 1988, Yahner 1988, Saunders et al. 1991) and which may extend great distances into a forest. These edge effects reduce quality of habitat for Neotropical migrant birds.

Why Is Edge Bad for Neotropical migrants? Traditionally, edge effect has been defined as an increase in abundance and diversity of wildlife found along the boundary between two habitat types (Leopold 1933). Because many game species are more abundant near edges, wildlife managers were generally taught that "edge" was good for wildlife and, in many cases, wildlife management was considered synonymous with creating edge habitat (Harris 1988).

Our concept of edge and edge effect has changed for a number of reasons. First, our definition of wildlife has expanded to include non-game species, many of which evolved within extensive areas of unfragmented habitat away from edges (Temple and Cary 1988). In addition, our way of defining edge effect has changed; instead of merely looking at number and abundance of species, we are using demographic parameters such as reproductive success. This is important because misleading conclusions can be reached by using only abundance as a measure of habitat quality (Van Horne 1983). For example, an apparent consequence of the increase in abundance and diversity of wildlife along edges is an increase in biotic interactions, such as predation, brood parasitism, and competition. Below, we discuss specifically how these changes often negatively affect Neotropical migrants.

1) **High Rates of Nest Predation.** Several species of mammalian and avian nest predators are more abundant along forest edge than in forest interior (Bider 1968, Forsyth and Smith 1973, Robbins 1979, Whitcomb et al. 1981). Studies using both artificial and natural nests have found that predation rates often are higher in small fragments than in larger ones and higher near edge in large forested areas than in the interior (e.g. Gates and Gysel 1978, Wilcove 1985, Small and Hunter 1988, Yahner and Scott 1988; fig. 2). A similar trend occurs on prairie fragments (Burger 1988, Johnson and Temple 1986).
2) **High Rates of Brood Parasitism.** The Brown-headed Cowbird (*Molothrus ater*) is also often more abundant along forest edges than in forest interior and

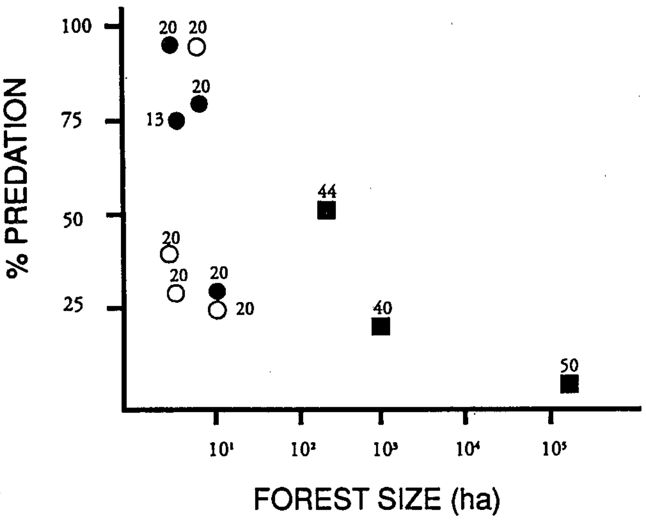

Figure 2. — Relationship between forest area and predation rates on artificial nests. Numbers above the points are sample sizes for each forest site. From Wilcove 1985.

parasitism rates are usually higher near forest edges (see Robinson et al., this volume). This is also true for prairie fragments (Johnson and Temple 1986).

3) **High Rates of Interspecific Competition.** Ambuel and Temple (1983) hypothesized that an increase in interspecific competition associated with increased abundance and diversity of potential competing edge species may adversely affect forest interior songbirds. However, no quantitative data exist to support this hypothesis at present.
4) **Reductions in Pairing Success.** Ovenbirds (*Seiurus aurocapillus*) living in forest fragments in Missouri were found to have lower chances of attracting a mate on smaller fragments (Gibbs and Faaborg 1990, Gentry 1989) and near edge of larger forests (Van Horn 1990). A similar pattern was found for this species in Ontario (Villard et al., 1992) and Minnesota (Donovan, unpub.). Lower pairing success was found in Wood Thrush (*Hylocichla mustelina*) and Red-eyed Vireo (*Vireo olivaceus*) where selective cutting had created clearings in a formerly continuous forest (Ziehmer, unpub.).
5) **Reductions in Nesting Success.** The above factors can have devastating demographic effects on Neotropical migrant birds. Temple and Cary (1988) found that only 18% of nests within 100 m of forest edge in Wisconsin were successful, while 70% of nests > 200 m from an edge were successful. Work by Hoover (1992) on Pennsylvania forest fragments ranging in size from 9.2 to > 500 ha found the probability of nest success correlated with forest area. Studies currently underway in the Shawnee Forest of southern Illinois and central Missouri also are finding that reproductive rates in many fragments are far below those needed to balance mortality.

How Far Do Edge Effects Extend? Unfortunately, we cannot give an exact distance for extent of edge effects. Vegetative changes may extend less than 30 m into a forest (Wilcove et al. 1986, Saunders et al. 1991), but edge-related predation rates have been suggested to extend 600 m into the forest (Wilcove et al. 1986), although other studies have suggested 50 to 100 m as a threshold (Gates and Gysel 1978, Burger 1988). Edge effects may vary with the regional landscape (see Freemark et al., this volume). In locations where cowbird densities are extremely high, parasitism rates may be high throughout the forest (Robinson et al., this volume), and in other areas where cowbird densities are low, parasitism rates may be low enough that no edge effects are apparent (Hoover 1992).

Isolation Effects With Habitat Fragmentation

To the extent that dispersal capabilities and the character of habitat separating fragments limit movement, relative isolation of a fragment may be detrimental to population survival. All other things being equal, theory suggests that isolated fragments might support fewer species or lower densities than less isolated fragments (MacArthur and Wilson 1967, Shafer 1990). Few data examining these patterns exist (Askins et al., 1990, Opdam 1991). Lynch and Whigham (1984) found that more isolated woodlots had fewer Neotropical migrant species than less isolated woodlots of comparable size and vegetation. On the other hand, Robinson (1992) found that extremely isolated woodlots in Illinois contained more forest-interior migrants than expected. Ongoing studies at the Connecticut Arboretum (Askins and Philbrick 1987, Askins et al. 1987) found recent increases in Neotropical migrant numbers, presumably because old fields that had isolated this site had grown into forests.

Neotropical migrants might be the vertebrate group least sensitive to isolation due to their long distance travel abilities. A recent study (Arguedes 1992) using DNA fingerprinting of Ovenbirds (*Seiurus aurocapillus*) found essentially no genetic differences between isolated populations as much as 150 km apart, suggesting high dispersal rates in mid-Missouri forest fragments. A better understanding of dispersal is needed to appreciate the role of isolation in fragmented regions. In particular, sexual variation in dispersal capabilities needs examination.

AVIAN RESPONSES TO HABITAT FRAGMENTATION

Although all of the above problems associated with habitat fragmentation do not paint a favorable picture for reproductive success of Neotropical migrants on fragments, it is not surprising that different species respond to fragmentation in different ways. Here, we briefly examine patterns by which different species respond to fragmentation to gain insight into how habitat management might minimize fragmentation effects.

Species-area Relationships. Recognizing the relationship between species-area patterns on oceanic islands and the equilibrium model, early researchers in habitat fragmentation censused birds on habitat fragments of varying size within a region (Bond 1957, Galli et al. 1976, Whitcomb et al. 1976, Robbins 1979, Hayden et al. 1985, and others). They found the number of species on a habitat island increased with increasing habitat size. A number of studies (reviewed by Askins et al. 1990) verified that area *per se* has the greatest influence on species number in a given area. Factors such as habitat heterogeneity, degree of isolation, and vegetation structure were relatively unimportant compared to habitat size. The slope of the species-area curve for a particular habitat may vary regionally, perhaps depending upon where the study was done in relation to the centers of ranges of species involved. This variation is considered in the landscape ecology chapter (Freemark et al., this volume).

Area Sensitive Species. A large number of studies in many areas, including Illinois (Blake and Karr 1984), Missouri (Hayden et al. 1985), Wisconsin (Ambuel and Temple 1983), Maryland (Robbins et al. 1989), New Jersey (Galli et al. 1976), and Ontario (Freemark and Merriam 1986), have shown that individual species are not randomly distributed with regard to habitat size.

By separating the component species found on fragments into several migration and habitat categories, it was shown that, as a group, long distance (Neotropical) migrants have steeper responses to fragment size than short distance migrants or permanent residents (fig. 3; Whitcomb et al. 1981 and others). Those species categorized as requiring forest interior habitat were also more area sensitive than edge or interior/edge species.

On a species-by-species basis, use of either an incidence function approach (Diamond 1975b) or analysis of "nested subsets" of species (Blake 1991) has shown very non-random distributions of species with respect to fragment size. Most importantly, these studies have noted "area sensitive" species, species which tend to occur in or achieve their highest densities only on large fragments. These patterns suggest the possibility of regional extinctions without preservation of large enough habitats.

Minimum Area Requirements and Source/sink Dynamics. With recognition that some species seemed to "require" large areas to exist, attempts were made to determine minimum area requirement (MAR) of each species within a region. MAR was defined in a variety of ways, ranging from "size class of habitat at which the frequency of occurrence undergoes a sharp decline" (Robbins 1979) to "the area in which young can be produced in sufficient numbers to replace adult attrition under the poorest conditions of weather, food availability, competition from other wildlife, and other disturbances" (Robbins et al. 1989).

Most early published estimates of minimum area requirements were based on presence-absence data from bird censusing. These did not anticipate the devastating effect of predation, parasitism, and other factors on nesting success of some species in habitat fragments. Biologists also did not appreciate the ability of species to continually colonize fragments where production was low or non-existent. To understand the regional dynamics of populations in fragments, a variety of source-sink models have been developed (Brown and Kodric-Brown 1977, Pulliam 1988). A sink population is one that does not produce enough young to replace adult mortality, and which exists because of continued colonization from elsewhere (the "rescue effect" of Brown and Kodric-Brown [1977]). A source produces enough young to replace breeding adults, and perhaps even enough to populate other fragments through dispersal.

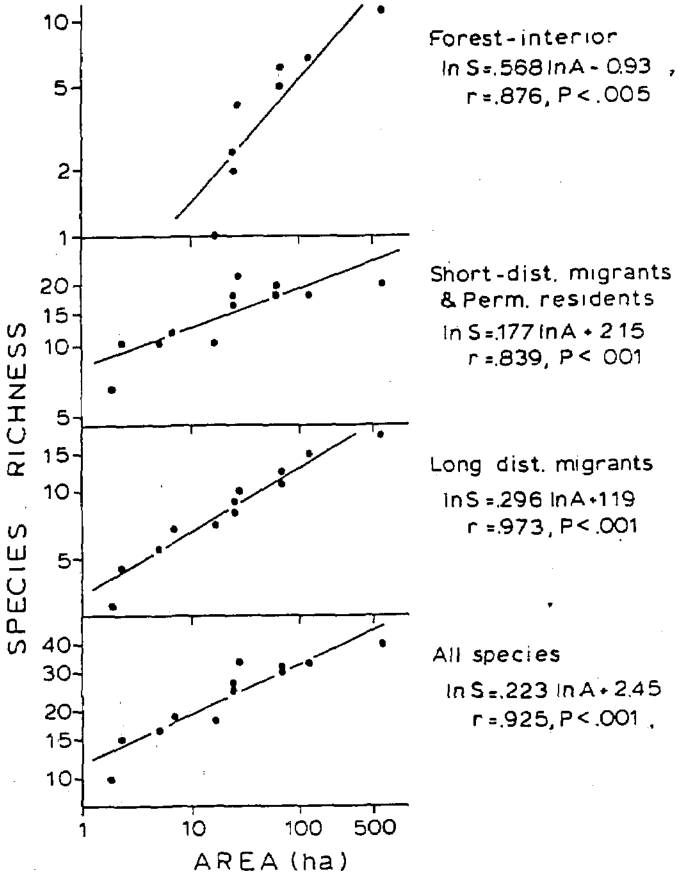

Figure 3. — Species richness (ln) within different ecological groups plotted as a function of area (ln) of forest tracts in east-central Illinois. From Blake and Karr 1984.

Unfortunately, the theory of source-sink dynamics is well ahead of our empirical knowledge; further insight requires both an understanding of population demography in a wide variety of habitats and knowledge of dispersal characteristics for each species. Suffice it to say that we are a long way from estimating true minimum area requirements for species in any region, let alone all regions.

HABITAT FRAGMENTATION: MANAGEMENT GUIDELINES

Selecting Fragments to Protect

Despite lack of knowledge about details of avian demography necessary to provide quantitative management strategies, we can provide general guidelines for assigning priorities when the goal is to provide quality breeding habitat for Neotropical migrant songbirds.

Single Large or Several Small (SLOSS). One of the first questions that arises and has been debated in the literature for over a decade (Simberloff and Abele 1976) is whether, given the choice, it is better to protect one large reserve or several small reserves whose total area equals the large reserve. The SLOSS debate initially focused on total number of species preserved and found, in theory, that more species might be preserved on several small reserves than one large one given certain assumptions about species distributions (Simberloff 1986). However, occurrence of area sensitive species only in habitats of large size makes most of these arguments invalid for Neotropical migrants. Rather, the general concensus when managing for breeding Neotropical migrants is that a single large reserve is better than several small reserves.

Reserve Size. Once a manager has decided to direct conservation efforts towards preserving large fragments that will provide quality breeding habitat, the next question is how large do fragments need to be. In a region that still contains large amounts of habitat, knowledge of fragment size that supports source populations would allow a manager to protect most important fragments. In a situation where few large fragments exist, that knowledge may be essential in choosing a fragment of proper size or, in the worst case, managing to make a fragment big enough to support source, or at least stable, populations.

Published minimum area requirements might serve as guidelines to determine fragment size required. As noted above, these are based on presence/absence data. In analyzing a set of 14 area sensitive species, Robbins et al. (1989) determined that 3,000 ha fragments were the minimum size that would retain all species of area sensitive forest birds in the Mid-Atlantic states. Fragments of 1,000 ha in mid-Missouri contain all expected species of Neotropical migrants found in that region (J. Faaborg, pers. obs.). To truly understand the minimum area required to support a stable or source population necessitates examining fitness components such as reproduction or survival in relation to habitat area (Martin et al., this volume; Maurer et al., this volume). Fragments of at least 3,000 ha may be needed in most regions to retain viable breeding populations of all species (Robbins et al. 1989). Perhaps even larger areas currently serve to maintain regional populations. In Missouri, the relatively vast Ozark forests support large Neotropical migrant breeding populations with low parasitism and nest predation rates; this area may be the source for many migrant populations occupying fragmented parts of Missouri. Once again, an understanding of details of demography and dispersal are needed to truly understand population dynamics.

It must be noted that, although large areas may be needed for maintenance of all species, smaller reserves are not without value. Some migrant species can successfully breed at least occasionally on small fragments, and edge and edge/interior species make extensive use of these fragments. If movement of individual birds between source and sink areas occurs between years, fragments may serve as important reservoirs for that part of the population that may not be able to find space to breed within source habitats in a given year. For the goals of many nature reserves, presence of particular Neotropical migrant species may be of value even if successful reproduction is not occurring. In these cases, areas equalling previously published values of minimum area requirements may serve to promote local biodiversity, even if the area is a population sink and not of value in long-term species preservation. It is possible that habitat fragments may be of critical importance to migrants moving through a heavily disturbed region.

Shape of Reserve. Fragment shape determines the ratio of edge to interior, with the ratio largest for long narrow fragments and smallest for circular or square fragments. Because reproductive success of Neotropical migrants is highest within forest interior away from edges, quality of habitat can be strongly influenced by fragment shape. Temple (1986) compared distribution of area sensitive migrants in forest fragments of different sizes and shapes. For each area, he recorded total area and core area (area 100 m from a forest edge) and compared species distribution as a function of these two variables. He found that core area was a better predictor of species occurrence than area alone. Hoover (1992), using Temple's definition of core area, found that core area was also a better predictor of Wood Thrush nest success than area alone. Consequently, compact shapes that maximize core area are favored over narrow shapes where edge habitat predominates, and management favoring too much edge may result in no acceptable core habitat within a fragment (fig. 4).

Location of Reserve. Birds on fragments are not isolated populations, but interact through dispersal with other populations. Therefore, it is also necessary to examine the question at a landscape level to determine how fragment location and isolation affect species distribution.

Our limited knowledge on influence of isolation on distributional patterns is hard to convert to conservation priorities. For example, fragments close to other fragments may support more species than isolated fragments, but in terms of maintaining local populations, isolated fragments may be extremely important because they are all that is left in the region. As is frequently the case when dealing with complex management issues, there is no cookbook solution, but by understanding the processes, a manager can better evaluate options.

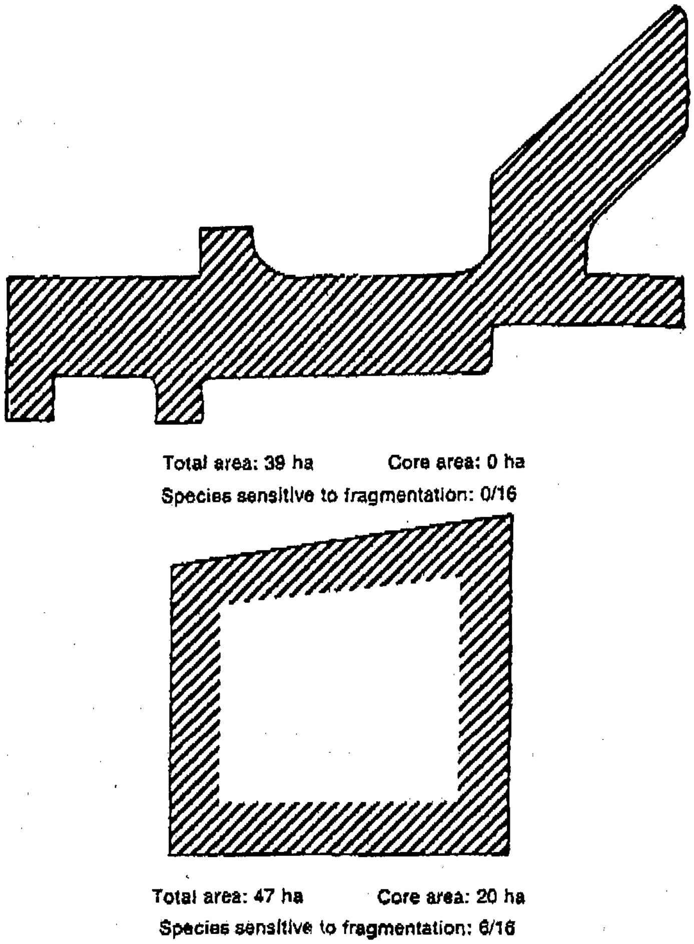

Figure 4. — Amount of edge and interior habitat on two forest patches of similar size but different shapes. From Temple 1986.

Corridors. One technique to minimize isolation of fragments is use of corridors-connecting strips of habitat that reduce fragment isolation. Although much theory about value of corridors exists (Simberloff and Cox 1987, Noss 1987), little data are available on actual value of corridors in the temperate zone (but see Saunders and Hobbs [1991]). Certainly, corridors are of more importance to small mammals or other organisms with limited dispersal capabilities than to Neotropical migrants. For breeding purposes, corridors are just long strips of edge, with associated problems. However, they may be important to migrants or to facilitate post-breeding dispersal, but more information is needed.

Managing Fragments

In many cases, managers will not be able to choose the size, shape, or location of fragments being managed. Instead, the concern may be how to best manage existing fragments. Guidelines for managing large fragments are similar to the guidelines used for managing contiguous forest (see Thompson et al., this volume). In general, a manager should minimize disturbance within forest interior. Openings, including roads and power lines, should be concentrated along existing habitat edges.

Small fragments, particularly those in suburban areas, will probably never provide quality breeding habitat for most area sensitive species. However, these small woodlots are frequently used as stop-over and foraging sites during migration, provide breeding habitat for short distance migrants and permanent residents, and may support non-breeding populations of Neotropical migrants. Although these fragments may not be important to long-term survival of Neotropical migrant bird populations, they may be of great importance in maintaining popular interest in Neotropical migrants, as most people see these migrants in small fragments or residential areas, not in major reserves.

We hope the above material helps managers understand why management guidelines that provide exact area requirements and such are not presently available. The general guidelines for nature reserve design provided by Diamond (1975a; fig. 5) still best summarize the qualitative approach managers should take in selecting and managing habitat remnants in fragmented environments. All other things being equal, bigger is better than smaller, compact shapes are better than narrow shapes, and reserves closer together or close to a source area are better than widely spaced reserves. As researchers discover details of Neotropical migrant demography and ecology, they will be able

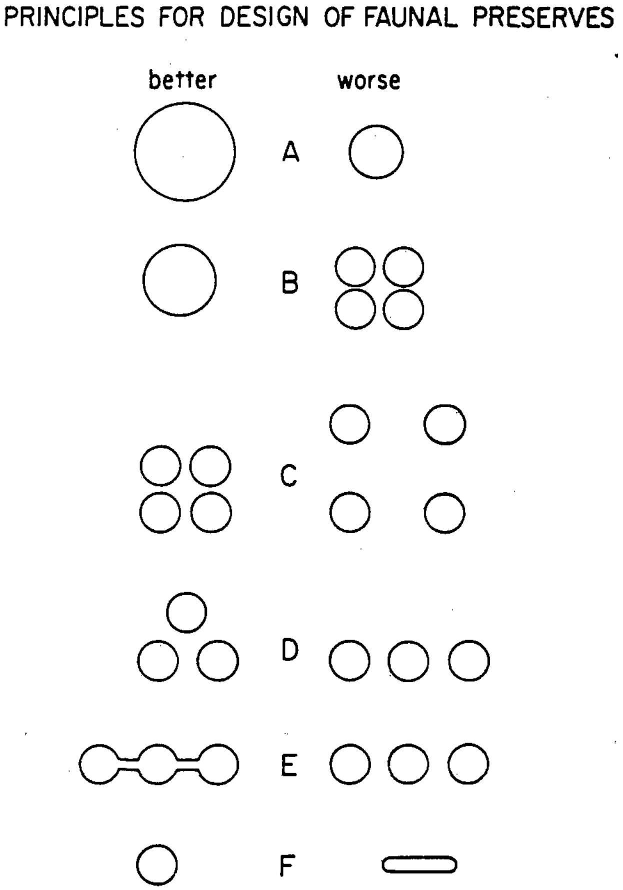

Figure 5. — Suggested qualitative principles for the selection and management of nature reserves, showing better and worse options with regard to extinction rates. From Diamond 1975a.

to provide more quantitative suggestions about details of minimum area requirements and extent of edge effects, but this will probably have to be done on a regional basis.

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