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Conceptualization and Measurement of Habitat Fragmentation from the Primates' Perspective

Víctor Arroyo-Rodríguez · Salvador Mandujano

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Abstract Habitat fragmentation is one of the principal threats to primates. Studies of primates in fragments usually conclude that fragmentation negatively affects some aspect of their biology or ecology. Nevertheless, the definition and quantification of fragmentation vary considerably among studies, resulting in contradictions and results that are difficult to interpret. We here 1) discuss the problems associated with the definition of habitat fragmentation and the ways of measuring it, 2) emphasize the importance of the concepts and methods from landscape ecology and metapopulation theory for the study of primates in fragmented landscapes, and 3) offer recommendations for more precise use of concepts associated with habitat fragmentation from the primates' perspective. When specific knowledge of the study species/population is available, we suggest that the definition of the variables to be measured should be functional from the primates' perspective, based, e.g., on their habitat requirements and dispersal capacity. The distance to the nearest fragment may not be the best way to measure the isolation between populations. Fragmentation *per se* is a landscape scale process and, hence, landscape scale studies are required to understand how species are distributed across heterogeneous landscapes. Finally, it is important to consider that what happens at the fragment scale could be the consequence of processes that interact at various spatial and temporal scales.

Keywords conservation · fragment · habitat loss · landscape ecology · metapopulations

V. Arroyo-Rodríguez (✉) · S. Mandujano
Departamento de Biodiversidad y Ecologia Animal, Instituto de Ecología A. C.,
Congregacion del Haya, Xalapa 91070 Veracruz, Mexico
e-mail: victorarroyo_rodriguez@hotmail.com

Present Address:
V. Arroyo-Rodríguez
Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México (UNAM),
Ex Hacienda de San José de la Huerta, 58190 Morelia, Michoacán, Mexico

Introduction

Hunting, habitat conversion, and habitat fragmentation have become the greatest threats to primate conservation (Cowlishaw and Dunbar 2000; Oates 1996). Evidence indicates that primate habitat countries are losing *ca.* 125,000 km^2 of forest annually (Chapman and Peres 2001), and that remnant populations are isolated in highly fragmented and low-quality habitats, which could lead to the extinction of populations and species in the coming decades (Cowlishaw 1999; Cowlishaw and Dunbar 2000). With this in mind, and given the ecological importance of primates in the maintenance of the structure and function of their ecosystems, e.g., seed dispersal (Chapman and Onderdonk 1998; Stoner *et al*. 2007), it is critical to identify the responses of primates to the loss and fragmentation of their habitat. It has become a priority concern in primate conservation biology (Cowlishaw and Dunbar 2000; Estrada *et al*. 2006a; Marsh 2003).

Studies of primates in fragments frequently conclude that fragmentation negatively affects some aspect of their biology or ecology (diet and home range size: Cristóbal-Azkarate and Arroyo-Rodríguez 2007; distribution: Arroyo-Rodríguez *et al*. 2008b; population size: Cristóbal-Azkarate *et al.* 2005; Wieczkowski 2004; social organization: Dias and Rodríguez-Luna 2006; Zunino *et al.* 2007; physiological stress: Chapman *et al.* 2006; Martínez-Mota *et al.* 2007). However, the way in which habitat fragmentation is defined and measured varies greatly among studies. Although some researchers compare landscapes with differing degrees of fragmentation (Arroyo-Rodríguez *et al*. 2008b; Mandujano and Estrada 2005), most studies are at the fragment scale, i.e., the fragment is the unit of analysis. Also, researchers have used different measures of fragmentation - usually fragment size and isolation- as well as different definitions of habitat fragment, matrix, isolation, connectivity, and habitat quality in describing the landscape. The differences in the conceptualization and measurement of fragmentation are frequently the origin of contradictions and results that are difficult to interpret (Lindenmayer and Fischer 2007).

We review literature that focuses on the effects of habitat fragmentation on primates to 1) discuss the problems associated with the definition of habitat fragmentation and the ways of measuring it, 2) evaluate the importance of the concepts and methods from landscape ecology and metapopulation theory for the study of primates in fragments, and 3) offer recommendations for more precise use of concepts associated with habitat fragmentation from the primates' perspective, i.e., based on the biology, ecology, or behavior of a given primate species. We first describe the process of habitat fragmentation and the theoretical approaches or paradigms usually used for its analysis. We then examine some of the problems associated with the definition of the variables to be measured, the experimental design, and the statistical analysis in studies with primates in fragments. Finally, we make some suggestions for the experimental design of studies with primates in fragments.

What Is Habitat Fragmentation?

Habitat fragmentation is a landscape scale process in which continuous unaltered habitat is reduced into smaller habitat remnants. This implies the loss of unaltered habitat and its subdivision into a variable number of remaining fragments scattered within a matrix of modified habitat (Andrén 1994). Besides the loss of unaltered habitat, the process of fragmentation results in 4 other effects: an increase in number of fragments, a decrease in fragment size, and an increase in both fragment isolation and total forest edge (Andrén 1994; Fahrig 2003).

Habitat fragmentation alters both the abiotic, e.g., radiation, temperature, humidity, wind speed, and biotic, e.g., population size, biodiversity, conditions near habitat edges: the so called edge effects (Saunders *et al.* 1991). In general, edge effects modify plant composition and vegetation structure in the fragments by increasing the mortality rate of large old-growth tree species, and decreasing the total basal area in smaller and more irregularly shaped fragments (Arroyo-Rodríguez and Mandujano 2006a). These vegetation changes can affect important plant species for primates, reducing the quantity and quality of food resources available to them (Arroyo-Rodríguez and Mandujano 2006b; Tutin 1999). Therefore, primates in habitat fragments are confronted with a modified environment of reduced area, increased isolation, and novel ecological boundaries.

Theoretical Approaches in Fragmentation Studies

Most theoretical models developed for fragmentation studies have focused on the spatial problem of fragmentation. These approaches usually analyze the impacts of size and spatial configuration of fragments on species richness, population size, and the long-term persistence of species. We consider =3 such models here: island biogeography theory, metapopulation theory, and landscape ecology.

The Island Biogeography Theory

Island biogeography theory (IBT), proposed by MacArthur and Wilson (1967), was the first theoretical approach developed for the study of the effects of fragmentation on natural communities (Haila 2002). The theory postulates that the number of species in isolated habitats is determined by the equilibrium between colonization, which depends on the degree of habitat isolation, and extinction, which depends on area, and predicts that the largest islands and those closest to the mainland will contain more species than smaller and more isolated habitats (MacArthur and Wilson 1967).

Several studies of primates have used IBT to analyze, e.g., species-area relationships in tropical rain forest fragments (Harcourt and Doherty 2005; Reed and Fleagle 1995), and to investigate the potential existence of extinction debts, i.e., time lag between initial habitat loss and eventual population collapse, among African forest primates (Cowlishaw 1999). Harcourt and Doherty (2005) reported a strong positive species-area relationship worldwide, and suggested that most forest fragments in which research is currently conducted are too small to save primate populations in the long term. Similarly, Cowlishaw (1999) suggested that in most African countries, >30% (*ca.* 4–8 species) of the forest primate species will become extinct in the coming decades. Further research with primates should incorporate this approach to provide a better understanding of species' susceptibility to changes in fragment area, particularly in the less studied continents, e.g., Africa and Asia (Harcourt and Doherty 2005).

Metapopulation Theory

Metapopulation theory (MT) was originally proposed by Levins (1970) and modified by Hanski (1999). The theory also evaluates processes of colonization and extinction of habitat remnants, but it focuses on single species. It postulates that the presence of a given species in an area depends on the balance between the rates at which local populations become extinct and those at which new populations of the same species are established by migrants from other populations in the landscape. Thus, a metapopulation exists as a set of several local populations, some isolated and some continuous within a fragmented landscape (Hanski 1999).

In general, few studies have addressed the problem of primate population conservation from a metapopulation perspective (Chapman *et al.* 2003; Escobedo-Morales and Mandujano 2007a, 2007b; Lawes 2002; Mandujano *et al.* 2006; Palacios-Silva and Mandujano 2007; Swart and Lawes 1996). For example, Lawes (2002) reported that small populations of *Cercopithecus mitis* in Afromontane forests of South Africa exist in metapopulations in which local extinctions are caused by the reduction in forest area and declining habitat quality. However, as shown by Swart and Lawes (1996) for *Cercopithecus mitis* in South Africa and Escobedo-Morales and Mandujano (2007b) for *Alouatta palliata*, in Los Tuxtlas, Mexico, the establishment of vegetation corridors can significantly improve metapopulation persistence.

Additional studies are needed to assess how habitat fragmentation and the placement, number, and connectivity of forest corridors affect the long-term distribution and population persistence of these and other primate species. They may be conducted via the long-term monitoring of primate populations in fragments, and the use of genetic markers to reliably track the gene flow between isolated subpopulations within a metapopulation. Studies focusing one or a few groups can provide some clues about the effects of fragmentation, but do not unravel the long-term trends in subpopulation dynamics.

Landscape Ecology

A landscape is an arbitrarily human-defined portion of land or territory that is delimited relative to the process or the organism of interest. Despite the availability of many alternative landscape models (Lindenmayer *et al.* 2008), most fragmentation studies use Forman's (1995) fragment-corridor-matrix model, which often portrays landscapes in a binary form composed of habitat and non-habitat.

Landscape ecologists study the effects of habitat spatial pattern on ecological processes. Although many ecological processes affecting populations and communities may operate at local scales, e.g., vegetation structure, resource availability, ecologists have highlighted the importance of examining ecological processes at the landscape scale (Dunning *et al.* 1992; Fahrig 2003; Lindenmayer *et al.* 2008). For example, Dunning *et al.* (1992) described 4 of such processes: 1) landscape complementation, 2) landscape supplementation, 3) the neighborhood effect, and 4) source-sink dynamics. The first 2 processes "occur when individuals move between fragments in the landscape to make use of non-substitutable and substitutable resources, respectively," such as foraging patches, breeding sites, and specific food sources. The third process "describes how a species' abundance in a particular fragment may be more strongly affected by characteristics of contiguous fragments than by those of more distant parts of the landscape" (Dunning *et al.* 1992, p. 169). Finally, the fourth process occurs when relatively productive fragments serve as sources of emigrants, which disperse to less productive fragments called sinks (Pulliam 1988). Subpopulations in sink habitat fragments depend on sources of immigrants for their persistence.

These processes could be occurring in primate populations living in highly fragmented landscapes (Arroyo-Rodríguez *et al.* 2008b; Chapman *et al.* 2003; Mandujano *et al.* 2004, 2006; Mbora and Meikle 2004). For example, Asensio *et al.* (2009) reported several cases of landscape supplementation by 2 groups of *Alouatta palliata* inhabiting two different forest fragments in Los Tuxtlas, Mexico. In this study, the groups used isolated trees, live fences, and neighboring forest patches to supplement their diets. Further, several primates live in fragments that do not exhibit characteristics required for these species' long term persistence, e.g., *Alouatta palliata* (Arroyo-Rodríguez *et al.* 2008b), *Cercopithecus mitis* (Lawes 2002), *Colobus guereza* (Chapman *et al.* 2003), and *Procolobus rufomitratus* (Mbora and Meikle 2004). These authors suggest that such fragments may function as sinks, while larger neighboring forest reserves may act as a source of individuals. Nevertheless, long-term studies monitoring primate population dynamics in landscapes with different deforestation levels are needed to assess to what extent the processes described above affect primate persistence in fragmented landscapes.

Although IBT, MT, and landscape ecology offer a robust foundation for tackling the conservation of biodiversity and target species in fragmented landscapes, many studies of primates attempt to explain biological and/or ecological problems based on processes that act mainly at a local scale, e.g., diet and activity pattern (Bicca-Marques 2003; Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Wong *et al.* 2006) and physiological stress and parasitism (Chapman *et al.* 2006; Cristóbal-Azkarate *et al.* 2006; Martínez-Mota *et al.* 2007). As populations in fragments are threatened by numerous processes working at different spatial and temporal scales (Fischer and Lindenmayer 2007), studies at local scales are also necessary to complement the understanding of species' responses to habitat fragmentation.

Problems Associated with the Definition of Variables

Despite all the theoretical efforts, important obstacles still exist in the experimental design of studies that analyze the effects of fragmentation on the biota (Ewers and Didham 2006; Harrison and Bruna 1999; Lindenmayer and Fischer 2007). In this section we discuss some problems associated with the definition of variables.

What Are Habitat and Non-Habitat?

Habitat may be broadly defined as the range of environments suitable for a given species (Hall *et al.* 1997). That is, it is a species-specific concept that generally refers to broad vegetation types, e.g., tropical rain forest, tropical dry forest, and cloud forest. Because native vegetation is important for many species, numerous researchers have equated habitat with native vegetation (Fischer and Lindenmayer 2007; Umapathy and Kumar 2003). Nevertheless, different primate species may have different habitat requirements, and most of them can use resources from many habitat suitability gradients (Bicca-Marques 2003; Michalski and Peres 2005), as well as from a number of agroecosystems (Estrada *et al*. 2006b). Therefore, the term habitat should be used carefully when several species are analyzed, e.g., in biodiversity research, because as Fischer and Lindenmayer (2007, p. 268) pointed out, "the broader use of the term habitat (i.e., equating it with native vegetation) can result in the under-appreciation of differences between the unique habitat requirements of different species, and the under-appreciation of the potential habitat value of modified environments for some species" (Fig. 1).

What Is a Fragment of Habitat?

Typically, fragmentation studies with primates have used definitions of fragment from the landscape's perspective, i.e., considering only structural characteristics of vegetation. For instance, some researchers use simple definitions based only on canopy continuity, e.g., "discrete forest masses separated by grasslands" (Zunino

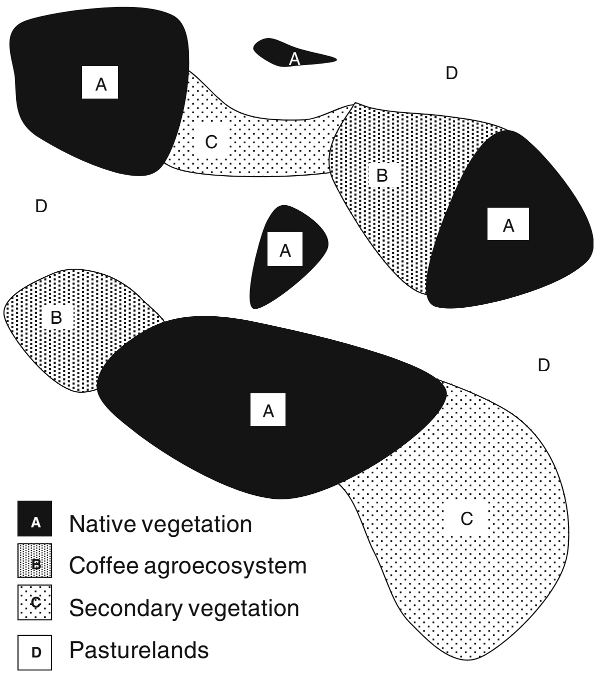

Fig. 1 Defining habitat and non-habitat based on vegetation types. Here, if the species of interest is a native vegetation specialist, it will have 5 fragments available (A), 2 of which are connected by forest cover. However, if the species also utilizes secondary vegetation, the habitat quantity available will be larger (A + C). If the species can also use coffee plantations, the habitat quantity available will be even larger (A + B + C).

et al. 2007, p. 968). Others consider the minimum fragment size and vegetation structure, e.g., "wooded area exceeding 1 ha that was composed mainly of trees greater than 10 m in height and with a canopy cover exceeding 50%" (Mbora and Meikle 2004, p. 69). Finally, other authors use definitions that include other fragment attributes such as isolation, e.g., "patches isolated … by at least 50 m" (Onderdonk and Chapman 2000, p. 590).

This structural approach to defining fragments may be parsimonious and valid, or even the only way, in many cases, but it can also be vague. The delimitation of habitat fragments may be relatively simple in landscapes dominated by few, highly contrasting vegetation types, e.g., tropical rain forest fragments vs. pasturelands (Mandujano *et al.* 2006). However, some fragmented landscapes are highly heterogeneous and the delimitation of habitat fragments can be more complicated (Figs. 1 and 2). Also, some fragment-dwelling species are able to compensate for habitat loss by making use of resources available in different vegetation types (Bicca-Marques and Calegaro-Marques 1994; Estrada *et al.* 2006b; Tutin *et al.* 1997), in a number of neighboring fragments (Asensio *et al.* 2009, Mandujano *et al.* 2004; Zunino *et al.* 2007) or even in the matrix (Asensio *et al.* 2009; Tutin *et al.* 1997): the process named landscape supplementation (*sensu* Dunning *et al.* 1992). Thus, the structural approach to defining fragment can underestimate habitat availability (Asensio *et al.* 2009; Bicca-Marques and Calegaro-Marques 1994), particularly when studying generalist primate species that can use resources from several vegetation types and different landscape elements.

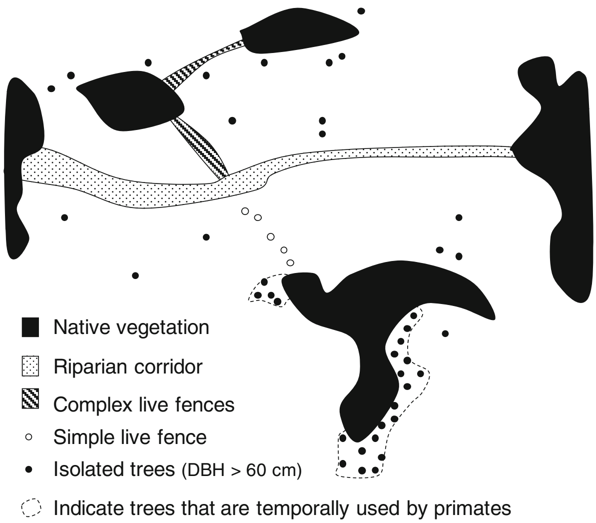

Fig. 2 Heterogeneous landscape composed of remnants of native vegetation; simple, i.e., single line of trees; and complex, i.e., vegetation corridor, live fences; a riparian corridor; and isolated trees. Some large isolated trees can temporarily be utilized by primates and, hence, they may be considered as part of the habitat fragment (dotted line). The riparian corridor may potentially be habitat for some species of primates, whereas for other species it may only serve as an element that allows them to move between fragments. Live fences may also allow the movement of primates between fragments, increasing the availability of habitat remnants for primates.

We propose that when specific knowledge of the study species/population is available, the definition of fragment should be species-specific, and a function of the species' habitat requirements and dispersal capacity. For arboreal primate species that rarely come down to the ground and that live in closed-canopy forests, habitat fragments can be defined as suitable forest remnants, isolated from each other by a matrix of inappropriate environment, e.g., human and agricultural settlement. If populations of the study species are exploiting various fragments of one kind of vegetation, or various vegetation types, it may be appropriate to consider all used vegetation/habitat fragments as a single fragment (Mandujano *et al.* 2004; Zunino *et al.* 2007; Fig. 1). Also, if primates are utilizing live fences, riparian corridors, among other landscape elements, as part of their home range, the used area of these elements should be considered as part of the study fragment, as these landscape elements are providing additional habitat (Asensio *et al.* 2009). Finally, if primates are exploiting resources from the matrix or from isolated trees close to the home fragment, it could be reasonable to consider a calculation, e.g., by using a geographic information system (GIS), of a buffer zone around the fragment to include these potential food sources as part of their home fragment (Fig. 2).

What are Fragment Isolation and Connectivity?

Fragment isolation and connectivity have become centrally important in both landscape ecology and conservation biology (Lindenmayer *et al.* 2008). Both may lead to changes in foraging and activity patterns, social organization, physiological conditions and diseases, and genetic variability. The variables are related, but are not synonyms. In general, isolation is an attribute at the fragment scale, while connectivity is usually defined at the landscape scale (Fischer and Lindenmayer 2007; Lindenmayer and Fischer 2007).

The most commonly used distance-based isolation metric in fragmentation studies is the Euclidian distance between habitat fragments (Bender *et al.* 2003; Tischendorf *et al.* 2003). Nearly all fragmentation studies with primates use distance-based isolation metrics such as the distance to the nearest fragment, and contrasting results have been found, even in the same region. For instance, Estrada and Coates-Estrada (1996) found that abundance of *Alouatta palliata* inhabiting a fragmented landscape in Los Tuxtlas, Mexico, correlates negatively with fragment isolation, while Cristóbal-Azkarate *et al.* (2005) did not find any significant relationship between the 2 variables in the same region. This could be due to the fact that distance between fragments is not a good measure of the effect of isolation on populations (Bender *et al.* 2003; Tischendorf *et al.* 2003). The isolation metric can underestimate the effects of isolation because it does not consider the presence of very small vegetation remnants (stepping stones), live fences, and other elements, e.g., isolated trees, in the matrix that can provide food and facilitate interfragment movements (Asensio *et al.* 2009; Bicca-Marques and Calegaro-Marques 1994).

Bender *et al.* (2003) and Tischendorf *et al.* (2003) demonstrated that area-based isolation metrics such as the amount of available habitat within a given radius of a fragment are the most reliable measure of fragment isolation (Fig. 3). From a biological perspective, these isolation metrics provide a direct measure of how much habitat, i.e., the potential source of food and individuals, is available in the vicinity of the home fragment (Fig. 3). These isolation metrics can be calculated manually or via GIS-based software packages such as FRAGSTATS (McGarigal and Marks 1995) and Patch Analyst (Elkie *et al.* 1999). Future studies should consider these constraints in the investigation of the effect of fragment isolation on primate populations.

Connectivity assesses the extent to which a landscape facilitates or impedes ecological flows or functionality. The flows include interfragment movements of animals such as primates. Different authors have used the concept in different ways (Fischer and Lindenmayer 2007; Lindenmayer and Fischer 2007), but 2 of the most commonly used types of connectivity in fragmentation studies are structural connectivity and functional connectivity (Moilanen and Nieminen 2002). The structural connectivity is defined by, e.g., the spatial pattern of the remaining habitat, the interfragment distance, and the presence of corridors, but does not incorporate the behavioral response of the individuals studied, while functional connectivity is an estimate of the relationship between the landscape spatial pattern and the capacity of the species of interest to move through the landscape (Fig. 4).

Because it is species-specific, the functional approach of connectivity is more accurate. However, it requires knowledge of the focal species' dispersal limitation. Various indices measure functional connectivity (several calculated via FRAGSTATS; McGarigal and Marks 1995). For instance, Palacios-Silva and Mandujano (2007) studied *Alouatta palliata* populations in Los Tuxtlas, Mexico, and used the ecological networks concept to assess changes in functional connectivity in a fragmented landscape under different scenarios of deforestation. The tolerance threshold values - interfragment distance over which the focal species cannot move between fragments- they used (200 m, 400 m, and 800 m) were far higher than those used by Alexander *et al.* (2006) in a study of *Alouatta pigra* in Belize (1000 m, 1600 m, and 2000 m). The studies demonstrate that functional connectivity can vary greatly depending on the tolerance thresholds used. More studies analyzing the ability of primates to move through the matrix are therefore necessary to have reliable measures of functional connectivity of a larger number of primate species, and will facilitate the development of efficient management strategies for primate conservation in fragmented landscapes (Lindenmayer *et al.* 2008).

Assessing the Composition and Structure of Vegetation

In general, tree canopy, vegetation type, and disturbance level are particularly important variables for arboreal primates that principally feed from leaves or fruits (Arroyo-Rodríguez and Mandujano 2006b; Skorupa 1988; Tutin 1999; Wong *et al.* 2006). Tree size is an indicator of food availability (Chapman *et al.* 1992), and can be measured using the diameter at breast height (DBH) of trees, their basal areas (Worman and Chapman 2006), or simply by quantifying the number of large trees (Arroyo-Rodríguez *et al.* 2007; Wieczkowski 2004). Plant diversity can be very important for primates (Cristóbal-Azkarate *et al.* 2005; Estrada and Coates-Estrada 1996). However, there are many ways to measure diversity, such as species richness, species density, and several diversity indexes (Shannon, Simpson; Halffter *et al.*

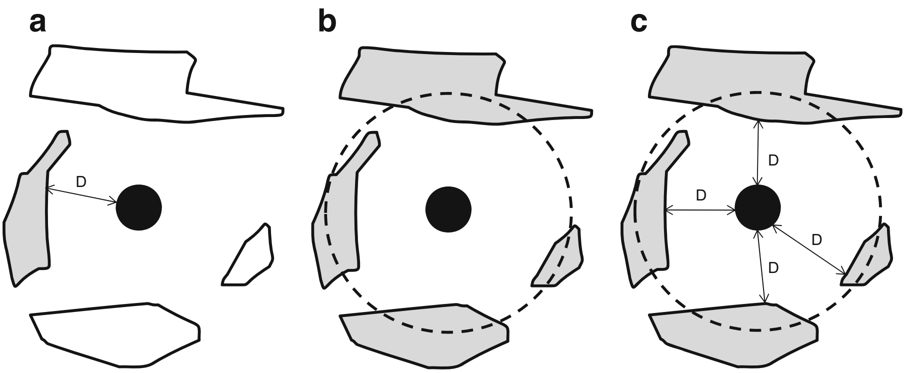

Fig. 3 Three different isolation metrics: (A) distance (D) to the nearest fragment (a distance-based isolation metric); (B) amount of available habitat (gray polygons) within a fixed radius (an area-based isolation metric); and (C) proximity index (a distance-weighted area-based isolation metric) that sums the ratios of fragment area/distance (A/D) for all habitat fragments that fall at least partially within a fixed radius. Area-based isolation metrics may be a better indicator of food availability and source of individuals in the vicinity of the study fragment.

2005). Each method calculates diversity in a different way and is therefore biased, so caution is advisable when comparing them and with the interpretation of the results (Halffter *et al.* 2005).

Estimating the availability of the top food plant species within the fragment can also be crucial. Methods include calculating their density, richness or basal area, as

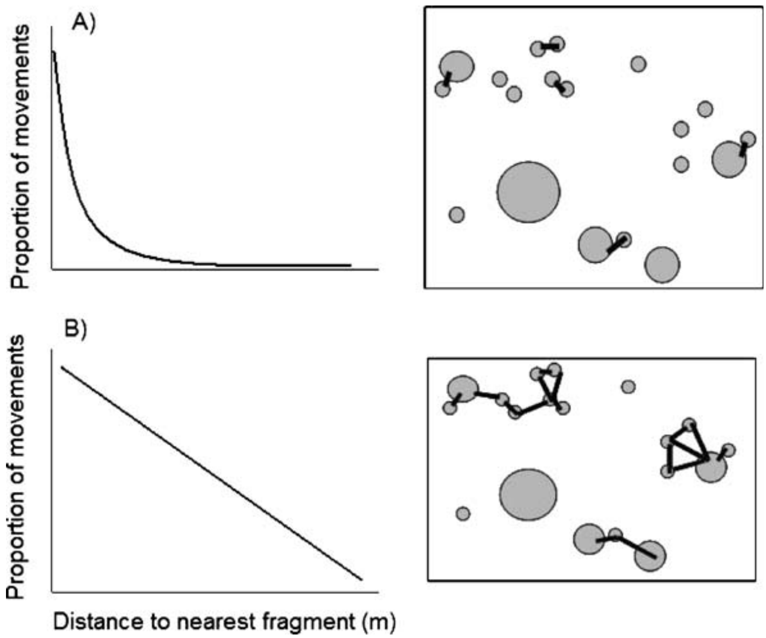

Fig. 4 Landscape connectivity (right) based on the displacement capacity of primates (left). When displacement capacity is low (A), landscape connectivity is low; when displacement capacity is high (B), landscape connectivity is high.

well as the importance value index (IVI) which combines frequency, density, and basal area (Arroyo-Rodríguez *et al.* 2007). Unfortunately, we still do not know which plant species are the most consumed by many primate species, and for others only a few studies are available. Also, many primate species, e.g., *Alouatta* spp., have highly variable diets that may change among study sites, so generalizations about the diet of primate species may not be possible in many cases. Without this information it is very difficult to estimate food availability in the fragments accurately and we cannot assess, for instance, how fragmentation may affect food availability, or how changes in food availability within the fragments may affect primate populations. This suggests that there is an urgent need for adequate studies of diet and activity patterns, particularly in the least-studied primate species, especially the ones facing habitat loss. Finally, once again it is important to remember that the vegetation attributes important for one primate species may not necessarily be the same for others, and therefore, if we manage a habitat to favor some species, we may harm others (Marsh and Loiselle 2003; Ojasti 2000).

Problems Associated with Experimental Design and Statistics

Once the variables to be considered and the way in which they will be measured are selected, the researcher should decide upon an experimental design, e.g., spatial and temporal scale of the analysis, and the most appropriate statistics to test the hypothesis of interest (Lindenmayer and Fischer 2007). In this section we describe the most common experimental designs and discuss some of the problems associated with them.

Sampling Designs

In general, one can classify fragmentation studies with primates into 6 categories: 1) those that study only one fragment of native or seminatural vegetation surrounded by a matrix of agricultural land (Arroyo-Rodríguez *et al*. 2008a; Bicca-Marques and Calegaro-Marques 1994; Tutin 1999), 2) those conducted in one or various fragments surrounded by water (Dias and Rodríguez-Luna 2006; Norconk and Grafton 2003), 3) those that compare one or various continuous habitats with one or various sites in a fragmented landscape (Gilbert 2003; Martínez-Mota *et al.* 2007), 4) those that consider various fragments occupied by primates within the same landscape (Chiarello and de Melo 2001; Cristóbal-Azkarate *et al.* 2006), 5) those that consider all of the fragments, occupied and unoccupied by primates, but exclusively within one landscape (Mandujano *et al.* 2006; Mbora and Meikle 2004; Onderdonk and Chapman 2000), and 6) those that consider all of the fragments, occupied or unoccupied by primates, in various landscapes with different degrees of fragmentation (Arroyo-Rodríguez *et al*. 2008b).

The first 2 approaches investigate the adaptations of the resident population(s) within a fragment [or island(s)], and, therefore, it is difficult to attribute these results to habitat fragmentation. Habitat fragmentation *per se* is a landscape scale process that leads to major physical, biological, and ecological changes within the remaining habitat (Saunders *et al.* 1991). The changes may vary in landscapes with different forest cover (Andrén 1998), which means that what happens in one or a few fragments may be different in landscapes with different proportion of remaining habitat (Arroyo-Rodríguez *et al.* 2009). Thus, as these two approaches are at the fragment scale, extrapolations to the landscape level are not possible (Fahrig 2003). Although the third approach conforms to the definition of fragmentation as a process, it has 2 inherent weaknesses per Fahrig (2003, pp. 490–491): "1) because habitat fragmentation is a landscape scale process, the sample size in such studies is typically only one (i.e., one continuous landscape and one fragmented landscape), and 2) this characterization of habitat fragmentation is strictly qualitative, that is, each landscape can be in only one of two states, continuous or fragmented, and we cannot analyze the relationship between the degree of habitat fragmentation and the magnitude of the species responses."

The results from the fourth approach allow us to relate the effects of fragment characteristics, e.g., size, isolation, habitat quality, to different attributes of primate populations within the fragments; however, given that the characteristics of the unoccupied fragments are not considered, the studies do not allow us to analyze the possible effects of fragmentation on the distribution and dispersion of animals in a fragmented landscape (fifth approach). Both the fourth and fifth approaches are at the fragment scale, and the sample size at the landscape scale is only one, meaning that landscape scale inferences are not possible (Fahrig 2003). Further, given that the majority of the spatial characteristics of fragments are strongly related to the quantity of remaining habitat in the landscape, the results of these kinds of studies do not allow us to identify the effects of fragmentation independent from the effects of habitat loss. Therefore, because fragmentation is a landscape scale process, fragmentation measurements are correctly made at the landscape scale (Fahrig 2003), and to answer specific questions, e.g., fragment occupation, population viability, the sixth approach could be considered the best way to study the effects of habitat fragmentation on primates.

What is More Important: Habitat Loss or Fragmentation?

Habitat loss and fragmentation are considered 2 of the principal threats to primates (Chapman and Peres 2001; Miller *et al*. 2004); however, most researchers measure both processes in ways that confuse their effects (Fahrig 2003). One of the advantages of an experimental design at the landscape scale is that it allows us to distinguish between the effects of fragmentation and the effects of habitat loss (Fahrig 2003). In general, landscape attributes such as number of fragments, mean distance to nearest fragment, or the total amount of edge, are strongly related in an nonlinear manner to the amount of habitat within a landscape, and, therefore, the effect of these attributes on the biota is not independent from the effect of habitat loss in the landscape (Fahrig 2003). Similarly, connectivity is also related in a nonlinear manner to the quantity of habitat remaining in the landscape (Andrén 1994; With *et al.* 1997), in such a way that below a certain threshold of habitat area, small changes in habitat quantity lead to big changes in connectivity (With *et al.* 1997). For this reason, it is recognized that the effects of fragmentation *per se* can be relatively more significant below certain thresholds of habitat amount remaining in the landscape (Andrén 1994; Fahrig 1997, 1998). Below this specific threshold of habitat amount, the probability of persistence of wild populations drops significantly. Researchers have not detailed the threshold values for primates, but in a preliminary study with *Alouatta palliata* in 3 fragmented landscapes in Los Tuxtlas (Mexico), Arroyo-Rodríguez *et al*. (2008b) demonstrated that both the proportion of occupied fragments and abundance of primates decreases suddenly in landscapes with <15% of remaining habitat. This suggests that the persistence of populations of *Alouatta palliata* could be compromised in the long term in landscapes with <15% of remaining habitat.

Given the importance of the management implications that these thresholds have for primate conservation, we urgently need to analyze the response of primates under different scenarios of habitat loss and fragmentation. To do this, we need to conduct studies at the landscape scale, i.e., with landscape as the level of analysis, considering landscapes with different habitat amount and different degrees of fragmentation. With such study designs, and appropriate statistical models, we can examine the effects of fragmentation while controlling for the effects of habitat quantity (Fahrig 2003).

As landscape area increases, so does the number of habitat fragments it potentially contains (Fahrig 2003) and, therefore, the sample size and reliability of fragment-scale studies. Increasing both sample size and reliability in landscape scale studies requires the study of as many landscapes as possible (n=3, at a minimum), which is why we recommend to consider smaller landscapes, e.g., 1000 ha. Larger landscapes are difficult and expensive, in both time and money, to sample. Thus, the larger the landscape size, the lower the number of landscapes the researcher can sample. To be considered as genuine replicas the landscapes must be independent, e.g., separated by geographical features, e.g., large rivers, lakes, coasts (Arroyo-Rodríguez *et al*. 2008b) that impede the exchange of individuals between landscapes. In this way, by increasing the sample size, i.e., number of landscapes, researchers can also study the effect of important synergies, such as the effect of post-fragmentation anthropogenic activities, e.g., logging and hunting, in parallel with the effect of fragmentation.

Conclusions

We summarized some problems related with the conceptualization and measurement of habitat fragmentation from the primates' perspective. Here we offer proposals to aid the investigation of the effects of habitat fragmentation on primates:

1) We should not forget that the concept habitat is species-specific, and keep in mind what is habitat and non-habitat for our focal species and focal populations.
2) Habitat is a gradient of quality, not a presence/absence variable. Evaluations of composition and vegetation structure within habitat fragments are therefore necessary to provide a complementary understanding of primates' responses to fragmentation.
3) The definition of fragment can be based only on the structural characteristics of the vegetation, i.e., structural approach. However, we propose that when specific knowledge of the study species/population is available, the definition of habitat

fragment should be functional from the primates' perspective, e.g., based on their habitat requirements, their dispersal ability between fragments, and their capacity to use different elements of the landscape.

4) The continuity of the tree canopy could be used as an important criterion to define different fragments, especially for those primate species that rarely come down to the ground and that are living in closed-canopy forests.
5) For species that can use various fragments within their home range, it may be appropriate to consider a collection of fragments as one fragment. Similarly, if the focal species is able to feed from other landscape elements, e.g., isolated trees, live fences, vegetation corridors, as part of its home range, the used area of these elements should be considered as part of the study fragment.
6) Care should be taken with the general use of distance to nearest fragment as a measure of isolation because this may not be the best way to measure the isolation between primate populations. The matrix may contain many elements invisible to GIS, e.g., isolated trees, live fences, that can reduce the isolation distance of fragments and mask its effects on primates.
7) Landscape scale studies are required to understand how species are distributed across heterogeneous landscapes. Fragmentation per se is a landscape scale process and, hence, its effect must be evaluated at this scale. For this reason, it is necessary to increase the number of study landscapes so that the effects of habitat fragmentation may be analyzed independently from the effects of habitat loss.

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