Chapter 2
Assessing Habitat Fragmentation Effects on Primates: The Importance of Evaluating Questions at the Correct Scale

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Abstract Forest-dwelling mammals such as primates could be particularly vulnerable to habitat fragmentation; however, the definition and quantification of fragmentation have varied considerably among studies. This has resulted in contradictions and thus results are difficult to interpret and compare. To encourage a consistent and more precise use of the term "habitat fragmentation," we reviewed 100 fragmentation studies on primates to quantify how fragmentation effects are assessed. We advocate that habitat fragmentation is a landscape-scale process that involves both loss and the breaking apart of habitat. Hence, independently analyzing both effects is necessary to assess the effects of the breaking apart of habitat while controlling for habitat loss (fragmentation per se). This needs to be done through landscape-scale studies (that is, using landscapes as the independent unit of observation); however, fragmentation studies on primates are typically at the single fragment scale, often with a single continuous forest used for comparison. We suggest that primate responses at the fragment scale can vary dramatically in landscapes with different habitat amounts

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and configurations. In this review we provide clear and consistent terminology to help future studies to accurately assess the effects of fragmentation on primates and to help to form a body of literature where comparisons among studies are possible?

Introduction

Habitat loss represents a significant threat to biodiversity and many ecological processes (Andrén 1994; Bender et al. 1998; Fahrig 1999, 2003). In contrast, habitat fragmentation per se, or the breaking apart of habitat while controlling for habitat area (sensu Fahrig 1999, 2003), has highly variable effects, which are sometimes positive and sometimes negative, depending on the species and the way in which fragmentation is measured (Henle et al. 2004; Ewers and Didham 2006; Fahrig 1999, 2003). The number of fragmentation studies has dramatically increased in past decades (Fig. 2.1); however, the term habitat fragmentation has been used in variable ways. This has resulted in contradictions and results that are difficult to interpret (Fahrig 2003; Lindenmayer and Fischer 2007).

Forest-dwelling mammals, such as primates, may be particularly vulnerable to habitat fragmentation (Chapman and Peres 2001; Arroyo-Rodríguez and Dias 2009). Despite the number of primate fragmentation studies (Fig. 2.1), the ways of conceptualizing and measuring fragmentation effects have been highly variable (Arroyo-Rodríguez and Mandujano 2009). This has led to conflicting conclusions from different studies about fragmentation effects on the same primate species (Arroyo-Rodríguez and Dias 2009). To encourage a consistent and more precise use of the term "habitat fragmentation," we first present what we view to be a useful description of what habitat fragmentation is and how it should be measured. Second, we present results from a search of the SCOPUS (©Elsevier, The Netherlands) database on 9 June 2010 for original papers containing "primate," plus "habitat fragmentation," "forest fragmentation," or "landscape fragmentation" in the title,

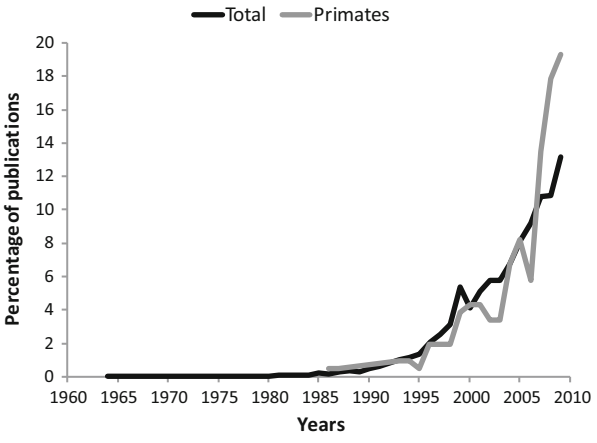

Fig. 2.1 Percentage of publications found in the SCOPUS database up to the end of 2009 containing "habitat fragmentation," "forest fragmentation," or "landscape fragmentation" in the title, abstract, and/or keywords (*black line*: total $n = 8{,}584$ papers). The same search was then conducted with the additional term "primate" (*grey line*: primates $n = 227$ papers)

abstract, and/or keywords. This search revealed a total of 227 papers. We randomly selected 100 of these papers and identified the ways in which habitat fragmentation effects are being assessed.

Evaluating and Measuring Habitat Fragmentation

Habitat may be broadly defined as "the range of environments suitable for a given species" (Hall et al. 1997). For primates this generally refers to broad vegetation types, such as tropical rain forest and tropical dry forest (Arroyo-Rodríguez and Mandujano 2009). Because native vegetation is important for many species, numerous researchers have equated "habitat" with native vegetation (Fischer and Lindenmayer 2007; Arroyo-Rodríguez and Mandujano 2009).

Habitat fragmentation is a landscape-scale process in which continuous habitat is broken apart into smaller pieces (fragments) scattered within a matrix of non-habitat. This implies the loss of habitat and its subdivision (fragmentation) into a variable number of fragments (Fahrig 1999; McGarigal and Cushman 2002; Fahrig 2003). However, habitat loss can occur without the subdivision of habitat (Fig. 2.2), and therefore, we advocate that it will be valuable for researchers to consider analyzing the independent effects of habitat loss and fragmentation to determine whether it is the overall loss of habitat or the separation of habitat into smaller pieces (hereafter termed "habitat fragmentation per se"; sensu Fahrig 1999, 2003) that actually causes negative effects on primates. This can only be done through landscape-scale studies, that is, by using landscapes as the independent units of observation (McGarigal and Cushman 2002; Fahrig 2003; Arroyo-Rodríguez and Mandujano 2009). By using fragments as the unit of analysis (hereafter named "fragment-scale studies"), researchers cannot differentiate between the effects of the habitat loss and the breaking apart of habitat, as both processes can result in smaller and more isolated fragments (Fahrig 2003; Fig. 2.2).

Most fragmentation measures (e.g., mean fragment isolation, total amount of edge, number of fragments) are strongly related in a nonlinear manner to the amount of habitat within a landscape, in such a way that below a certain threshold of habitat area, small changes in the extent of the habitat lead to big changes in these measures (Neel et al. 2004). For this reason, it is often difficult to determine the separate effects of habitat loss and fragmentation. For instance, studies with plants (Arroyo-Rodríguez et al. 2009) and animals (Andrén 1994; Pardini et al. 2010) suggest that species diversity in a fragment of a given size may vary in landscapes with different habitat amount. Actually, the effects of fragmentation per se are thought to be relatively more important below certain thresholds of habitat amount remaining in the landscape (Andrén 1994; Fahrig 1997, 1998; With and King 2001). Below this threshold of habitat amount, the probability of persistence of populations drops significantly. Given the crucial 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. This cannot be done through fragment-scale studies; it requires studies at the landscape scale.

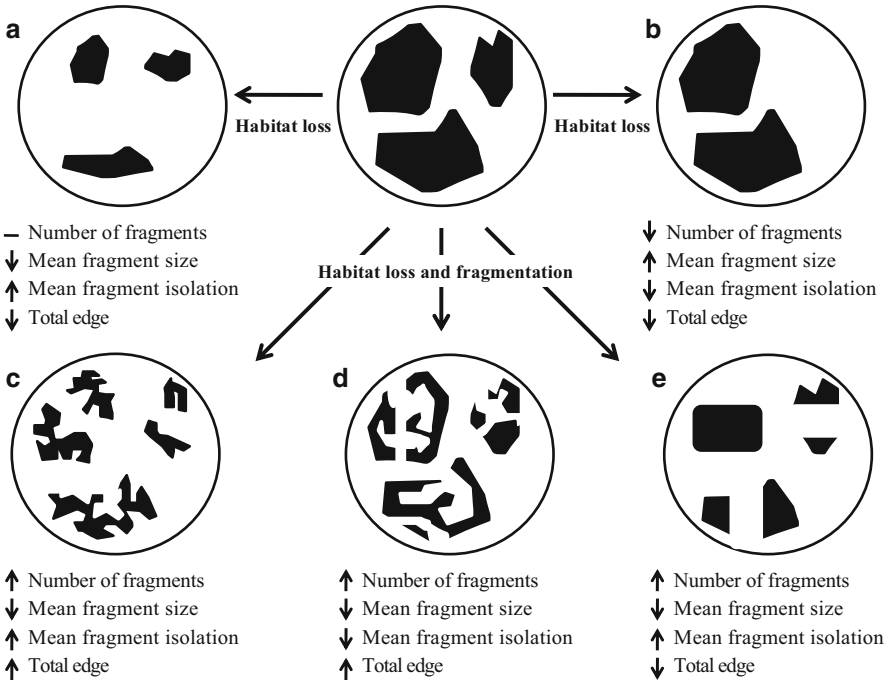

Fig. 2.2 Some (not all) of the effects of habitat loss on landscape spatial pattern. Habitat loss alone (A and B) can result in higher or lower mean fragment size and either higher or lower mean fragment isolation. The increase of the number of fragments with habitat loss and habitat fragmentation (C, D, and E) can lead to contrasting landscape spatial patterns (for instance, higher or lower mean fragment isolation and total habitat edge), but in all cases mean fragment size decreases. Other potential changes in landscape spatial pattern expected from habitat loss and fragmentation can be found in Fahrig (1999, 2003)

Additionally, the relationship between fragmentation and habitat configuration is very intricate (Fahrig 2003). The fragmentation process results in the reduction in habitat amount, increase in the number of habitat fragments, and decrease in sizes of habitat fragments (Fig. 2.2). However, other spatial attributes, such as total habitat edge and mean fragment isolation, can either increase or decrease with fragmentation (Fig. 2.2). Although the number of measures of fragmentation is huge (>40 measures: e.g., number of fragments, fragment density, total edge, edge density, landscape shape index, largest patch index; see McGarigal et al. 2002), researchers commonly measure only one effect (fragment size is the most frequent), whereas others assess two or three effects, but not more (Fahrig 2003), and rarely recognize the interrelationships among measures of fragmentation. As stated by Fahrig (2003, p. 492): "this leads to ambiguous conclusions regarding the effects of habitat configuration on biodiversity … and … makes results difficult to interpret." Also, as each aspect of fragmentation could potentially affect primates in different ways (Arroyo-Rodríguez and Dias 2009; Arroyo-Rodríguez and Mandujano 2009), using

one or few of these effects results in biased assessments of the general effects of habitat fragmentation on primates. For example, both abiotic conditions, such as temperature, humidity, and wind speed, and biotic conditions, such as population density, and species richness, can be altered near habitat edges: the so-called edge effects (Saunders et al. 1991). Edge effects can lead to vegetation changes, particularly in smaller and more irregularly shaped fragments (Laurance et al. 2000; Hill and Curran 2003; Arroyo-Rodríguez and Mandujano 2006), which can affect the abundance of the most frequently eaten food plant species for primates, reducing the quantity and quality of food sources available to them (Arroyo-Rodríguez and Mandujano 2006; Tutin 1999). Although these vegetation changes can significantly impact primates (population distribution: Arroyo-Rodríguez et al. 2007; population density: Worman and Chapman 2006; feeding behavior: Dunn et al. 2009), studies reporting edge and/or vegetation effects as synonymous of "fragmentation effects" are misusing the term "fragmentation," as total forest edge is strongly related to the amount of remaining forest in the landscape (Fahrig 2003). Furthermore, all of these processes have only been evaluated at the fragment scale, and it is unclear (i.e., not tested) whether they can be extrapolated to the landscape scale (McGarigal and McComb 1995).

Assessing Habitat Fragmentation Effects on Primates

Database

The 100 reviewed papers were published in 24 journals, but 84 % of these papers were found in 11 journals, almost half (47 %) in *American Journal of Primatology*, *International Journal of Primatology*, and *Primates* (Fig. 2.3a). These studies were conducted in 22 countries, but 89 % were from 11 countries, with Mexico, Brazil, and Madagascar being the best represented (Fig. 2.3b). They include 85 species from 35 genera, with 9 species (11 %) in ≥ 5 papers, *Alouatta palliata* being the most studied (Fig. 2.3c). In contrast, 44 species (52 %) were studied in only one paper. Primate genera followed a similar pattern: few (11 genera, 29 %) appeared in ≥5 papers, with *Alouatta* being the most studied, appearing in 38 papers (Fig. 2.3d). In contrast, 19 genera (50 %) were present in ≤2 papers, with *Galago*, *Lagothrix*, *Lemur*, *Leontopithecus*, *Lophocebus*, *Nomascus*, and *Nycticebus* studied in only one paper each.

Goals in Fragmentation Studies with Primates

Despite the fact that we limited our literature search to original papers containing the word "fragmentation" in the title, the abstract, and/or keywords of the paper, we found that approximately one-third (34 papers) of the 100 reviewed papers did not aim to explicitly or implicitly assess the effects of habitat fragmentation on primates.

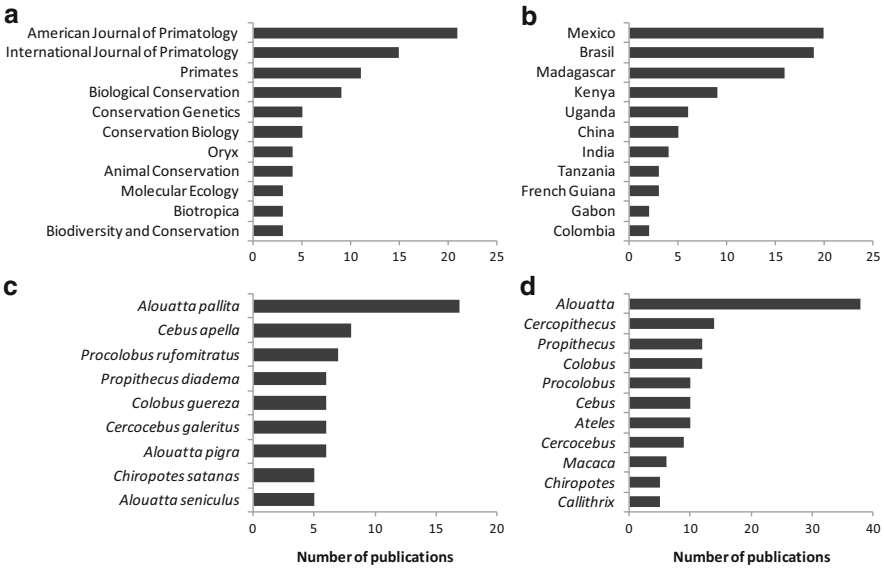

Fig. 2.3 Best represented journals (**a**), study countries (**b**), study species (**c**), and genera (**d**) in a review of 100 randomly selected papers from a SCOPUS search of papers containing the word "primate" and "habitat fragmentation," "forest fragmentation," or "landscape fragmentation" in the title, abstract, and/or keywords. The search resulted in a total of 227 papers from 1986 to 9 June 2010

Although most of these studies (28 of 34 papers) were performed in fragmented landscapes, their objectives were highly variable, from "investigating the effects of anthropogenic habitat degradation on group size, ranging, fecundity, and parasite dynamics" (Mbora et al. 2009) to "assessing habitat use of the monkeys in a series of succession habitats following clear-cutting" (Li 2004). In other words, they were not actually aimed at studying fragmentation effects directly. Hereafter, we focus our analyses and discussion on the remaining 66 papers which aimed to explicitly or implicitly evaluate the effects of habitat fragmentation on primates.

Experimental Designs

Three of the 66 studies (4 %) analyzed groups or populations in different geographical localities, without specifying the habitat configuration of the landscapes (for example, forest cover in the landscape, number of fragments, fragment size, fragment isolation, total forest edge) in which monkeys were studied (Morin et al. 1993; Bergl et al. 2008; Parker et al. 2008). However, the remaining 63 papers specified the habitat configuration of the landscapes in which monkeys were studied, and used forest fragments, islands, and/or continuous forests as the units of observation,

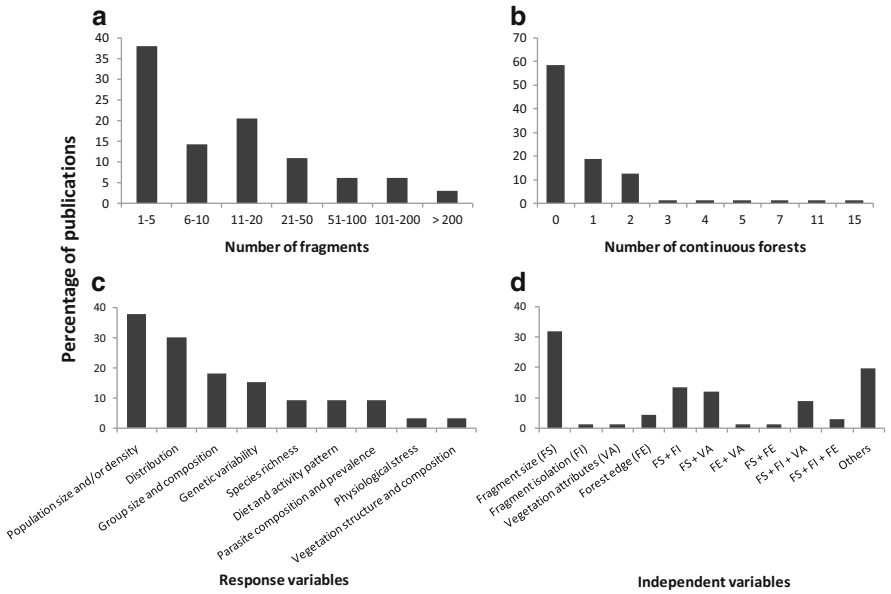

Fig. 2.4 Number of fragments (**a**) and continuous forests (**b**), response variables (**c**), and factors (**d**) measured in a review of 66 papers which aimed to assess the effects of habitat fragmentation on primates. The percentage of papers per category is indicated; however, as three studies analyzed primates in different geographical localities without specifying the habitat configuration of the landscapes in which monkeys were studied, the percentages in cases (**a**) and (**b**) are based on 63 papers (not 66)

that is, all were fragment-scale studies (Fig. 2.4a, b). From these studies, 13 (21 %) only described the study fragment(s)/island(s)/continuous forest(s), and did not give information on the habitat configuration surrounding the study sites, that is, they did not specify the habitat configuration of the landscape in which the study sites were imbedded (Lehman et al. 2006; Rangel-Negrín et al. 2009). Most of the studies that specified the habitat configuration of the landscape in which the sites were imbedded (50 papers) were performed in only one landscape (48 papers, 96 %; for example, Chapman et al. 2007; Silva and Ferrari 2009); one paper investigated two landscapes (Pope 1998); and another analyzed three landscapes (Arroyo-Rodríguez et al. 2008).

The average (± SD) number of study fragments/islands in fragment-scale studies (63 papers) was 48.8 ± 190 (median = 6 fragments), ranging from one fragment (5 papers; for instance, González-Solís et al. 2001; Lehman et al. 2006) to 1,502 fragments (Zhang et al. 2010; Fig. 2.4a). Thirty-six (57 %) papers focused their study on forest fragments/islands, whereas 27 papers (43 %) compared forest fragments with 1 (12 papers; for example, Chapman et al. 2007; Dausmann et al. 2008) to 15 (Michalski and Peres 2005) continuous forests (Fig. 2.4b).

Response Variables and Factors Assessed

The response variables were highly variable (Fig. 2.4c), including population size and/or density (Wahungu et al. 2005), distribution (Arroyo-Rodríguez et al. 2008), group size and composition (Umapathy and Kumar 2000), genetic variability (Mbora and McPeek 2010), species richness (Harcourt and Doherty 2005), diet and activity pattern (Dunn et al. 2009), parasite composition and prevalence (Gillespie and Chapman 2008), physiological stress (Martínez-Mota et al. 2007), and vegetation structure and composition (Stevenson and Aldana 2008). Some papers assessed more than one of these response variables. For example, Michalski and Peres (2005) examined the species richness and distribution of primate and carnivore assemblages in a Brazilian fragmented forest. Onderdonk and Chapman (2001) assessed variation in species richness, population size, and group composition and structure in Uganda.

The factors measured (predictor variables) were also highly diverse, but the most common were fragment size (47 papers, 71 %; for example, Harcourt and Doherty 2005), fragment isolation (18 papers, 27 %; Estrada and Coates-Estrada 1996), vegetation attributes (16 papers, 24 %; Asensio et al. 2007), and forest edge (5 papers, 8 %; Lehman et al. 2006) (Fig. 2.4d). Twenty-six papers (39 %) measured only one of these effects, with fragment size the most frequent (Fig. 2.4d). Nineteen papers (29 %) included two factors: fragment size and isolation (Estrada et al. 1999), fragment size and vegetation attributes (Singh et al. 2002), fragment size and forest edge (Quemere et al. 2010), or forest edge and vegetation attributes (Mbora and Meikle 2004). Finally, eight papers (12 %) included three factors: fragment size, fragment isolation, and vegetation attributes (Cristóbal-Azkarate et al. 2005) or fragment size, fragment isolation, and forest edge (Arroyo-Rodríguez et al. 2008; Fig. 2.4d).

Conceptual and Methodological Problems

The conceptual and methodological problems in papers aimed to evaluate the effects of habitat fragmentation on primates are that the studies (1) lack consideration of landscape context, (2) are conducted only at the fragment scale, (3) use small sample sizes, and (4) consider only one or a few measures of habitat fragmentation.

Lack of Consideration of Landscape Context

To fully assess habitat fragmentation effects on primates it is necessary to quantify (e.g., using a geographical information system) the habitat configuration in the landscape(s), but as stated above, there is a lack of this type of information in 25 % of the studies we reviewed. Studies in fragmented landscapes should consider that what happens at the fragment scale may vary in landscapes with different habitat

configurations and that it can be affected by processes that interact at various spatial and temporal scales (Andrén 1994; Fahrig 2003; Arroyo-Rodríguez et al. 2008, 2009). Information on the habitat configuration in the landscape, such as forest cover, connectivity, number of fragments, fragment size, and/or total forest edge surrounding the study sites, is necessary to assess processes operating at the landscape scale (neighboring effects, source–sink dynamics, landscape supplementation, landscape complementation: Dunning et al. 1992; metapopulation dynamics: Hanski 1999). For example, the neighboring effect predicts that species abundance in a particular fragment should be more strongly affected by characteristics of contiguous fragments than by those of more distant parts of the landscape. Source–sink dynamics also predicts that there can be individual movements from relatively productive fragments (sources) to less productive fragments (sinks) (Pulliam 1988). Thus, to understand which factors explain primates' responses to the characteristics imposed by particular forest remnants, and to test the effect of habitat loss and/or fragmentation on primates, it is necessary to describe the landscape spatial context surrounding the sites.

Conducting Studies Only at the Fragment Scale

All reviewed papers were at the fragment scale (i.e., they used fragments, islands, and/or continuous forests as the units of observation), and hence, they cannot evaluate the effects of the breaking apart of habitat while controlling for habitat area (Fahrig 2003). Although 27 out of 63 papers (47 %) analyzed ≥5 fragments, and related (e.g., using regression analyses) the effects of fragment characteristics, such as size, isolation, and habitat quality, to different attributes of primate populations, the effects of habitat loss and fragmentation are confounded in these kinds of studies (Fahrig 1999, 2003; Arroyo-Rodríguez and Mandujano 2009). Papers comparing primates inhabiting continuous forests and forest fragments/islands (47 %, see above) also have several weaknesses (Fahrig 2003). For example, as fragmentation is a landscape-scale process, the sample size for comparisons in such studies is in reality only two: one continuous landscape and one fragmented landscape. Furthermore, as stated in Fahrig (2003), this categorization of fragmentation is strictly qualitative (that is, each landscape can be in only one of the two states, continuous or fragmented, and it is not possible to analyze the relationship between the degree of habitat fragmentation and the magnitude of the species responses).

Using a Small Sample Size

Using larger sample sizes allows the researcher to achieve narrower inferential error bars, and more precise estimates of true population values, and hence, a larger sample size leads to increased precision in estimates of population properties

(Cumming et al. 2007). Of the 63 papers that used fragments, islands, and/or continuous forests as the unit of observation, a third (20 papers, 32 %) analyzed ≤4 study sites, and from these papers 5 (8 %) used only 1 fragment/island. As argued by Arroyo-Rodríguez and Mandujano (2009), with such a study design researchers can investigate the population(s) within 1 or few fragments/islands, but it is not possible to attribute these results to habitat fragmentation. These studies cannot establish the relationship between the spatial attributes (e.g., fragment size, isolation, and total edge) of the study sites and the response variable(s), nor can they identify which spatial attributes have the biggest influence on primates. To do so, there are different statistical approaches, such as multiple regression analysis, and path analysis, which need larger sample sizes (see below).

Similarly, we found that most studies analyzed islands, fragments, and/or continuous forests in only one landscape, and therefore, the sample size at the landscape level is only one (Fahrig 2003). With such a study design researchers cannot quantify the relationship between the degree of habitat fragmentation and the magnitude of the species responses. They also cannot assess the effect of fragmentation per se (that is, controlling for the effect of habitat loss) on primates, and cannot determine the threshold values of habitat amount below which the probability of persistence of populations drops significantly (Fahrig 2003; Arroyo-Rodríguez and Mandujano 2009).

Considering Only One or Few Measures of Habitat Fragmentation

Our review indicates that fragmentation studies on primates have only included four measures of fragmentation (Fig. 2.4d): fragment size, fragment isolation, vegetation attributes, and forest edge. Most of the papers measured only one of these effects (fragment size is the most frequent), and very few include two or more effects (see above). Surprisingly, none of the papers we reviewed evaluated the effects of the number of fragments remaining in the landscape on primates. This is perhaps one of the most obvious changes in habitat configuration caused by fragmentation, but we know virtually nothing about its effects on primates. Thus, further studies including a larger number of fragmentation measures will improve our understanding of the effects of habitat configuration on primates.

Each of these spatial attributes can have different effects on primates (Arroyo-Rodríguez and Dias 2009), and these effects depend on the habitat amount remaining in the landscape. For example, recent investigations analyzing tree species richness in three fragmented landscapes at Los Tuxtlas, Mexico, have demonstrated that species–area relationships may differ in landscapes with different forest cover (Arroyo-Rodríguez et al. 2009). These findings could have important implication for frugivorous–folivorous species such as primates, which can be affected by plant species richness availability in the home fragments (Estrada and Coates-Estrada 1996; Cristóbal-Azkarate et al. 2005). Actually, Arroyo-Rodríguez et al. (2008)

demonstrated that the spatial attributes affecting the probability of fragment occupancy by howler monkeys (*Alouatta palliata*) in Los Tuxtlas differed among landscapes with different forest cover. Thus, although many studies have demonstrated fragment size effects, fragment isolation effects, edge effects, and/or vegetation effects on primates, they are probably highly site dependent (see conflicting results among studies of these measures in Arroyo-Rodríguez and Dias (2009)), and do not allow assessment of the effects of fragmentation per se on primates. While extremely logistically difficult, studies comparing the effects of these spatial attributes in landscapes with different forest cover are necessary to have a better understanding of their impacts on primates.

Problems Related to the Interpretation of the Results in Primate Literature

Currently it is difficult to interpret the findings of many investigations in the primate literature. For example, we found that all the papers reviewed assessed habitat fragmentation without controlling for the effect of habitat loss, but most of them (49 out of 66, 74 %) suggested that observed patterns were a result of fragmentation, while they may not be, and 35 papers (53 %) even concluded that fragmentation was the cause of the observed pattern(s). For example, Gómez-Posada et al. (2009) assessed the density and population status of *Alouatta seniculus* in an isolated bamboo forest fragment in La Tebaida, Colombia, and concluded that their results demonstrate the tolerance of this species to fragmentation. Asensio et al. (2007) investigated the foraging habits of *A. palliata* in three forest fragments in Los Tuxtlas, Mexico, and concluded that monkeys cope well with the restrictions imposed by habitat fragmentation. Similarly, but comparing population density and species diversity between one large peninsula and nine small islands in French Guiana, Granjon et al. (1996) concluded that the results illustrated short-term effects of fragmentation at the community level for forest-dwelling mammals. All these conclusions are difficult to evaluate because, while fragmentation is a landscape-scale process, all these studies were conducted at the fragment scale. In particular, it is not possible to tell whether the observed effects are due to the overall loss of forest in the area, or something about the pattern of forest that remains following forest removal (for example, its degree of fragmentation per se), or some other human impact, such as hunting, that is correlated with forest loss. We suggest that the discussions in fragmentation studies should be limited to the spatial and temporal scales of analysis. If a study assesses monkeys in a number of fragments and finds that, for instance, the density and/or species richness of monkeys is positively associated with fragment area (Harcourt and Doherty 2005; Mbora and McPeek 2009), researchers should conclude just this, and not attribute the observed pattern to fragmentation, as it is highly probable that the results are difficult to extrapolate to the landscape scale (McGarigal and McComb 1995).

Conclusions and Recommendation for Future Research

Despite the growing number of publications evaluating primates in fragmented landscapes, we found that approximately 25 % of them do not describe the habitat configuration in the landscapes in which the monkeys were studied. We advocate that assessing habitat fragmentation effects requires adopting a landscape perspective, which includes quantifying the habitat configuration (forest cover, connectivity, number of fragments, fragment size, total forest edge, etc.) in the landscape(s). We also found that all primate studies are at the fragment scale, and thus, no study has evaluated the impact of habitat fragmentation controlling the effect of habitat loss, that is, they do not assess the effects of habitat fragmentation per se on primates.

To accurately quantify the relationship between the degree of habitat fragmentation and the magnitude of the species responses, researchers need to assess primate responses in a range of landscapes with different levels of habitat loss and fragmentation. By increasing the sample size (number of landscapes) researchers not only can assess the effect of fragmentation per se, but may also be able to assess the threshold values of habitat amount below which the probability of persistence of wild populations drops significantly. With such a study design, researchers can also study the effect of important synergies, such as the effect of post-fragmentation anthropogenic activities (logging and hunting) in parallel with the effect of fragmentation (see Ewers and Didham 2006; Arroyo-Rodríguez and Mandujano 2009). Although it is probable that, as demonstrated by Fahrig (1999, 2003) and Arroyo-Rodríguez and Días (2009), habitat loss has larger consistent negative effects on primates than habitat fragmentation per se, this hypothesis needs to be more thoroughly tested through landscape-scale studies.

This being said, it is important to acknowledge that primate researchers face a particular difficulty in assessing the effects of fragmentation per se. Given the spatial scale that is relevant for primate research, it will often be difficult or impossible to sample a sufficient number of landscapes with a wide enough range of value of habitat amount and fragmentation to conduct powerful statistical tests. Such constraints should be explicitly recognized by researchers and, in particular, extreme caution should be taken when interpreting the effect of landscape features on primates, whenever the analysis is only based on one landscape.

We highlight the importance of measuring and testing the effects of a larger number of fragmentation metrics, including the number of fragments remaining in the landscapes. The impact this landscape metric has on primates has not been tested, despite the fact that fragmentation consistently results in an increase in the number of forest fragments in the landscape.

In general, studies at the fragment scale should limit their conclusions to this scale, avoiding speculations about the impact of landscape-scale processes. This is particularly important in studies that test the effects of spatial characteristics, such as fragment size and isolation, of the study site(s) on primates, but not of the habitat configuration surrounding the study sites. These studies cannot test the impact of processes operating at the landscape scale.

To perform reliable and accurate landscape-scale studies we recommend investigating as many landscapes as possible, which is why we suggest considering smaller landscapes (e.g., 500–1,000 ha), adequately separated to impede the exchange of individuals among them and increase its independency (Arroyo-Rodríguez and Mandujano 2009). However, different biological attributes (e.g., distribution, population size, group composition, diet) are likely affected by different spatial scales (Theobald and Hobbs 2002), and therefore, researchers should evaluate questions at the correct scale.

References

Andrén H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366

Arroyo-Rodríguez V, Dias PAD (2009) Effects of habitat fragmentation and disturbance on howler monkeys: a review. Am J Primatol 71:1–16

Arroyo-Rodríguez V, Mandujano S (2006) Forest fragmentation modifies habitat quality for *Alouatta palliata*. Int J Primatol 27:1079–1096

Arroyo-Rodríguez V, Mandujano S (2009) Conceptualization and measurement of rainforest fragmentation from the primates' perspective. Int J Primatol 30:497–514

Arroyo-Rodríguez V, Mandujano S, Benítez-Malvido J, Cuende-Fantón C (2007) The influence of large tree density on howler monkey (*Alouatta palliata mexicana*) presence in very small rainforest fragments. Biotropica 39:760–766

Arroyo-Rodríguez V, Mandujano S, Benítez-Malvido J (2008) Landscape attributes affecting patch occupancy by howler monkeys (*Alouatta palliata mexicana*) at Los Tuxtlas, Mexico. Am J Primatol 70:69–77

Arroyo-Rodríguez V, Pineda E, Escobar F, Benítez-Malvido J (2009) Value of small patches in the conservation of plant-species diversity in highly fragmented rainforest. Conserv Biol 23: 729–739

Asensio N, Cristóbal-Azkarate J, Dias P, Vea JJ, Rodríguez-Luna R (2007) Foraging habits of *Alouatta palliata mexicana* in three forest fragments. Folia Primatol 78:141–153

Bender DJ, Contreras T, Fahrig L (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology 79:517–533

Bergl R, Bradley BJ, Nsubuga A, Vigilant L (2008) Effects of habitat fragmentation, population size and demographic history on genetic diversity: the cross river gorilla in a comparative context. Am J Primatol 70:848–859

Chapman CA, Peres CA (2001) Primate conservation in the new millennium: the role of scientists. Evol Anthropol 10:16–33

Chapman CA, Naughton-Treves L, Lawes MJ, Wasserman MD, Gillespie TR (2007) Population declines of *Colobus* in Western Uganda and conservation value of forest fragments. Int J Primatol 28:513–528

Cristóbal-Azkarate J, Veá JJ, Asensio N, Rodríguez-Luna E (2005) Biogeographical and floristic predictors of the presence and abundance of mantled howlers (*Alouatta palliata mexicana*) in rain forest fragments at Los Tuxtlas, Mexico. Am J Primatol 67:209–222

Cumming G, Fidler F, Vaux DL (2007) Error bars in experimental biology. J Cell Biol 177:7–11

Dausmann KH, Glos J, Linsenmair KE, Ganzhorn JU (2008) Improved recruitment of a lemur-dispersed tree in Malagasy dry forests after the demise of vertebrates in forest fragments. Oecologia 157:307–316

Dunn JC, Cristóbal-Azkarate J, Vea JJ (2009) Differences in diet and activity pattern between two groups of *Alouatta palliata* associated with the availability of big trees and fruit of top food taxa. Am J Primatol 71:654–662

Dunning JB, Danielson BJ, Pulliam R (1992) Ecological processes that affect populations in complex landscapes. Oikos 65:169–175
Estrada A, Coates-Estrada R (1996) Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. Int J Primatol 17:759–783
Estrada A, Anzures AD, Coates-Estrada R (1999) Tropical rain forest fragmentation, howler monkeys (*Alouatta palliata*), and dung beetles at Los Tuxtlas, Mexico. Am J Primatol 48:253–262
Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev 81:117–142
Fahrig L (1997) Relative effects of habitat loss and fragmentation on population extinction. J Wild Manage 61:603–610
Fahrig L (1998) When does fragmentation of breeding habitat affect population survival? Ecol Model 105:273–292
Fahrig L (1999) Forest loss and fragmentation: which has the greater effect on persistence of forest-dwelling animals? In: Rochelle JA, Lehmann LA, Wisniewski J (eds) Forest fragmentation; wildlife and management implications. Leiden, The Netherlands, pp 87–95
Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515
Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. Global Ecol Biogeogr 16:265–280
Gillespie TR, Chapman CA (2008) Forest fragmentation, the decline of an endangered primate, and changes in host-parasite interactions relative to an unfragmented forest. Am J Primatol 70:222–230
Gómez-Posada C, Álvarez Z, Giraldo-Chavarriaga P (2009) Densidad y estatus poblacional de monos aulladores rojos en un guadual, fragmento aislado, La Tebaida, Quindío, Colombia. Univ Scient 14:8–15
González-Solís J, Guix JC, Mateos E, Llorens L (2001) Population density of primates in large fragment of the Brazilian Atlantic Forest. Biodivers Conserv 10:1267–1282
Granjon L, Cosson JF, Judas J, Ringuet S (1996) Influence of tropical rainforest fragmentation on mammal communities in French Guiana: short-term effects. Acta Oecol 17:673–684
Hall LS, Krausman PR, Morrison ML (1997) The habitat concept and a plea for standard terminology. Wildl Soc Bull 25:173–182
Hanski I (1999) Metapopulation ecology. Oxford University Press, New York
Harcourt AH, Doherty DA (2005) Species-area relationships of primates in tropical forest fragments: a global analysis. J Appl Ecol 42:630–637
Henle K, Davies KF, Kleyer M, Margules C, Settele J (2004) Predictors of species sensitivity to fragmentation. Biodivers Conserv 13:207–251
Hill JL, Curran PJ (2003) Area, shape and isolation of tropical forest fragments: effects on tree species diversity and implications for conservation. J Biogeogr 30:1391–1403
Laurance WF, Delamonica P, Laurance SG, Vasconcelos HL, Lovejoy TE (2000) Rainforest fragmentation kills big trees. Nature 404:836
Lehman SM, Rajaonson A, Day S (2006) Lemur responses to edge effects in the Vohibola III classified forest, Madagascar. Am J Primatol 68:293–299
Li Y (2004) The effect of forest clear-cutting on habitat use in Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in Shennongjia Nature Reserve, China. Primates 45:69–72
Lindenmayer DB, Fischer J (2007) Tackling the habitat fragmentation panchreston. Trends Ecol Evol 22:127–132
Martínez-Mota R, Valdespino C, Sánchez-Ramos MA, Serio-Silva JC (2007) Effects of forest fragmentation on the physiological stress response of black howler monkeys. Anim Conserv 10:374–379
Mbora DNM, McPeek MA (2009) Host density and human activities mediate increased parasite prevalence and richness in primates threatened by habitat loss and fragmentation. J Anim Ecol 78:210–218

Mbora DNM, McPeek MA (2010) Endangered species in small habitat patches can possess high genetic diversity: the case of the Tana River red colobus and mangabey. Conserv Genet 11: 1725–1735
Mbora DNM, Meikle DB (2004) Forest fragmentation and the distribution, abundance and conservation of the Tana River red colobus (*Procolobus rufomitratus*). Biol Conserv 118: 67–77
Mbora DNM, Wieczkowski J, Munene E (2009) Links between habitat degradation, and social group size, ranging, fecundity, and parasite prevalence in the Tana River Mangabey (*Cercocebus galeritus*). Am J Phys Anthropol 140:562–571
McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecol Appl 12:335–345
McGarigal K, McComb WC (1995) Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecol Monogr 65:235–260
McGarigal K, Cushman SA, Neel MC, Ene E (2002) FRAGSTATS: spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: http://www.umass.edu/landeco/research/fragstats/fragstats.html
Michalski F, Peres CA (2005) Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. Biol Conserv 124:383–396
Morin PA, Wallis J, Moore JJ, Chakraborty R, Woodruff DS (1993) Non-invasive sampling and DNA amplification for paternity exclusion, community structure, and phylogeography in wild chimpanzees. Primates 34:347–356
Neel MC, McGarigal K, Cushman SA (2004) Behavior of class-level landscape metrics across gradients of class aggregation and area. Landscape Ecol 19:435–455
Onderdonk DA, Chapman CA (2000) Coping with forest fragmentation: the primates of Kibale National Park, Uganda. Int J Primatol 21:587–611
Pardini R, Bueno AA, Gardner TA, Prado PI, Metzger JP (2010) Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. PLoS One 5:e13666
Parker L, Nijman V, Nekaris KAI (2008) When there is no forest left: fragmentation, local extinction, and small population sizes in the Sri Lankan western purple faced-langur. Endang Species Res 5:29–36
Pope TR (1998) Genetic variation in remnant populations of the woolly spider monkey (*Brachyteles arachnoides*). Int J Primatol 19:95–109
Pulliam HR (1998) Sources, sinks, and population regulation. Am Nat 132:652–661
Quemere E, Champeau J, Besolo A, Rasolondraibe E, Rabarivola C, Crouau-Roy B, Chikhi L (2010) Spatial variation in density and total size estimates in fragmented primate populations: the golden-crowned sifaka (*Propithecus tattersalli*). Am J Primatol 72:72–80
Rangel-Negrín A, Alfaro JL, Valdez RA, Romano MC, Serio-Silva JC (2009) Stress in Yucatan spider monkeys: effects of enviromental conditions on fecal cortisol levels in wild captive populations. Anim Conserv 12:496–502
Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. Conserv Biol 5:18–32
Silva SSB, Ferrari SF (2009) Behavior patterns of Southern Bearded Sakis (*Chiropotes satanas*) in the fragmented landscape of eastern Brazilian Amazonia. Am J Primatol 70:1–7
Singh M, Singh M, Kumar MA, Kumara HN, Sharma AK, Kaumanns W (2002) Distribution, population structure, and conservation of lion-tailed macaques (*Macaca silenus*) in the Animalai Hills, Western Ghats, India. Am J Primatol 57:91–102
Stevenson PR, Aldana AM (2008) Potencial effects of Ateline extinction and forest fragmentation on plant diversity and composition in the Western Orinoco Basin, Colombia. Int J Primatol 29:365–377
Theobald DM, Hobbs NT (2002) Functional definition of landscape structure using a gradient-based approach. In: Scott JM, Heglund PJ, Morrison ML, Haufler JB, Raphael MG, Wall WA, Samson FB (eds) Predicting species occurrences: issues of accuracy and scale. Island, Washington, DC, pp 667–672

Tutin CEG (1999) Fragmented living: behavioral ecology of primates in a forest fragment in the Lopé Reserve, Gabon. Primates 40:249–265

Umapathy G, Kumar A (2000) The demography of the lion-tailed macaque (*Macaca silenus*) in rain forest fragments in the Animalai Hills, South India. Primates 41:119–126

Wahungu GM, Muoria PK, Moinde NN, Oguge NO, Kirathe JN (2005) Changes in forest fragment sizes and primate population trends along the River Tana floodplain, Kenya. Afr J Ecol 43:81–90

With KA, King AW (2001) Analysis of landscape sources and sinks: the effect of spatial pattern on avian demography. Biol Conserv 100:75–88

Worman COD, Chapman CA (2006) Densities of two frugivorous primates with respect to forest and fragment tree species composition and fruit availability. Int J Primatol 27:203–225

Zhang M, Fellowes JR, Jiang X, Wang W, Chan BPL, Ren G, Zhu J (2010) Degradation of tropical forest in Hainan China, 1991-2008: conservation implications for Hainan Gibbon (*Nomascus hainanus*). Biol Conserv 143:1397–1404

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