REVIEW ARTICLE

Effects of Habitat Fragmentation and Disturbance on Howler Monkeys: A Review

VÍCTOR ARROYO-RODRÍGUEZ[1]* AND PEDRO AMÉRICO D. DIAS[2]
[1]Centro de Investigaciones en Ecosistemas (CIECo), Universidad Nacional Autónoma de México, Morelia, Michoacán, México
[2]Instituto de Neuroetología, Universidad Veracruzana, Xalapa, México

We examined the literature on the effects of habitat fragmentation and disturbance on howler monkeys (genus *Alouatta*) to (1) identify different threats that may affect howlers in fragmented landscapes; (2) review specific predictions developed in fragmentation theory and (3) identify the empirical evidence supporting these predictions. Although howlers are known for their ability to persist in both conserved and disturbed conditions, we found evidence that they are negatively affected by high levels of habitat loss, fragmentation and degradation. Patch size appears to be the main factor constraining populations in fragmented habitats, probably because patch size is positively related to food availability, and negatively related to anthropogenic pressures, physiological stress and parasite loads. Patch isolation is not a strong predictor of either patch occupancy or population size in howlers, a result that may be related to the ability of howlers to move among forest patches. Thus, we propose that it is probable that habitat loss has larger consistent negative effects on howler populations than habitat fragmentation per se. In general, food availability decreases with patch size, not only due to habitat loss, but also because the density of big trees, plant species richness and howlers' home range size are lower in smaller patches, where howlers' population densities are commonly higher. However, it is unclear which vegetation attributes have the biggest influence on howler populations. Similarly, our knowledge is still limited concerning the effects of postfragmentation threats (e.g. hunting and logging) on howlers living in forest patches, and how several endogenous threats (e.g. genetic diversity, physiological stress, and parasitism) affect the distribution, population structure and persistence of howlers. More long-term studies with comparable methods are necessary to quantify some of the patterns discussed in this review, and determine through meta-analyses whether there are significant inter-specific differences in species' responses to habitat loss and fragmentation. Am. J. Primatol. 72:1–16, 2010. © 2009 Wiley-Liss, Inc.

INTRODUCTION

Hunting, emergent diseases, habitat conversion and fragmentation are the main reasons for the global decline of primate populations [Cowlishaw & Dunbar, 2000; Nunn & Altizer, 2006; Oates, 1996] and, as a consequence of their effects, more than half of the world's primate species are currently threatened by extinction [Chapman & Peres, 2001]. Despite the extensive literature analyzing the effects of habitat fragmentation and disturbance on primates [e.g. Marsh, 2003], no clear patterns have yet emerged, most probably because the responses to habitat modification depend, among other factors, on the biological characteristics of each taxon [see Ewers & Didham, 2006]. In this study, we review the literature analyzing the effects of habitat fragmentation on a single taxon: the genus *Alouatta* (Primates: Atelidae). Although this genus represents a radiation of at least ten species [e.g. Cortés-Ortiz et al., 2003], they all share anatomical, physiological and behavioral characteristics that allow a collective assessment of their responses to habitat modification.

Howlers (*Alouatta* spp.) are one of the most studied Neotropical primates in forest patches

*Correspondence to: Víctor Arroyo-Rodríguez, Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México (UNAM), Antigua Carretera a Pátzcuaro No. 8701, Ex-Hacienda de San José de la Huerta, Morelia 58190, Michoacán, México. E-mail: victorarroyo_rodriguez@hotmail.com

[Crockett & Eisenberg, 1987; Estrada et al., 2006; Marsh, 2003], but almost all studies are centered on only four species (*A. caraya*, *A. palliata*, *A. pigra* and *A. seniculus*). Howlers have been cited as a relatively tolerant taxon to habitat disturbance [e.g. Bicca-Marques, 2003; Garber et al., 2006; Lovejoy et al., 1986; Schwarzkopf & Rylands, 1989; Van Belle & Estrada, 2006], as they are present in patches where other Neotropical primate species (e.g. *Ateles* spp.) cannot persist [Estrada & Coates-Estrada, 1996; Gilbert, 2003]. However, they may be more sensitive than is usually considered to the loss, transformation and fragmentation of tropical forests, as all howler species are arboreal, have a folivore–frugivore diet, and their ability to move between forest patches is limited, particularly when the surrounding matrix is composed of cattle pastures or croplands [Estrada & Coates-Estrada, 1996; Mandujano et al., 2004, 2006]. As a probable consequence of habitat fragmentation and disturbance, several howler species and subspecies are classified as threatened by the IUCN [e.g. Vulnerable: *A. palliata aequatorialis*; Endangered: *A. pigra*; Critically Endangered: *A. guariba guariba*, *A. palliata mexicana*; IUCN, 2009]. Therefore, it is important to assess our current understanding of the effects of habitat fragmentation and disturbance on howlers.

This review is focused on studies that explicitly analyze the effects of habitat fragmentation on howlers. Nevertheless, we complement the review with studies analyzing other habitat disturbance effects, such as deforestation, logging and hunting, that can be facilitated by habitat fragmentation (see Fig. 1). Thus, we hope this review will stimulate a more comprehensive understanding of the ecology, management and conservation of primates in modified landscapes. Our aims include (1) provide a summary of the literature; (2) synthesize data on processes that negatively affect howler populations in modified landscapes; (3) identify empirical evidence supporting predictions of theoretical approaches used in fragmentation studies and (4) suggest directions for future research and conservation priorities for this taxon.

Although different processes resulting from habitat fragmentation and disturbance can interact synergistically to decrease the viability of primate populations [see Chapman et al., 2006], to simplify our analysis, and following Fischer and Lindenmayer [2007], we have grouped these effects into exogenous and endogenous threatening processes (Fig. 1). Exogenous threats are those that are independent of the species' biology, whereas endogenous threatening processes emerge as part of the species' biology. Within the exogenous group of threats, we review the effects of changes in habitat pattern (e.g. decrease in patch size, increase in patch isolation), changes in vegetation structure and food availability, and post-fragmentation anthropogenic pressures (Fig. 1). When considering endogenous threats, the main emphasis of this review is on changes in biology (i.e. physiological stress and genetic diversity), changes in social organization and behavior (i.e. dispersal patterns, grouping patterns, social interactions and activity patterns), and changes in species interactions (i.e. competition, predation and parasitism).
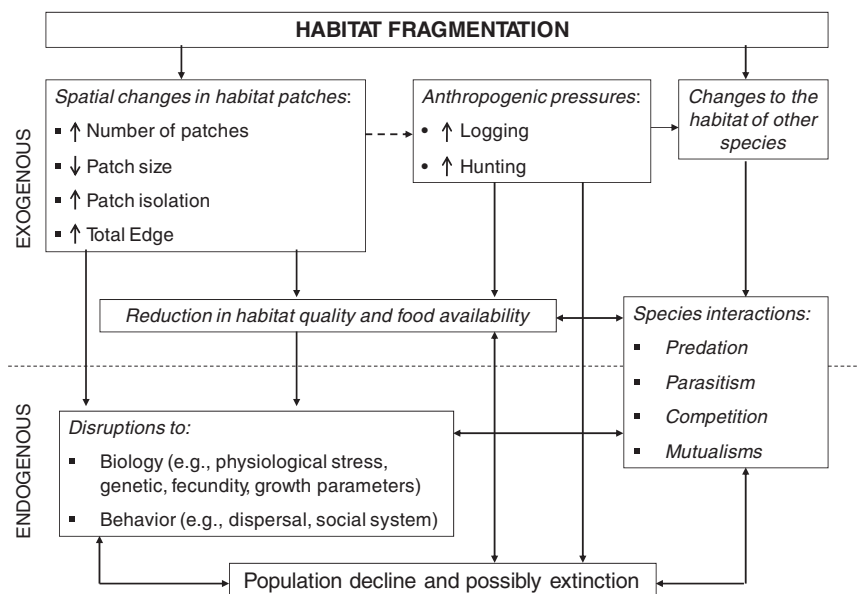

Fig. 1. Deterministic threatening processes arising from habitat fragmentation as experienced by a declining animal species. Threatening processes are broadly classified as exogenous (i.e. external to a species' biology) and endogenous (i.e. as part of a species' biology). Anthropogenic pressures are not a direct consequence of habitat fragmentation, but are facilitated by this process and can exacerbate the negative effects of habitat fragmentation on populations [modified from Fischer & Lindenmayer, 2007].

EFFECTS OF HABITAT FRAGMENTATION AND DISTURBANCE ON HOWLER POPULATIONS

Habitat fragmentation [i.e. the breaking apart of continuous habitat; Fahrig, 2003] is a landscape-scale process that implies habitat loss and its subdivision into a variable number of patches dispersed in a matrix of modified habitat [Fischer & Lindenmayer, 2007]. Typically, as the process of habitat fragmentation advances, there is an increase in the number of isolated or semi-isolated patches, a decrease in patch size and an increase in inter-patch distance and novel habitat boundaries (Fig. 1). Habitat boundaries can vary in structure and composition, from the abrupt boundaries composed mainly of cattle pastures, to more gradual boundaries composed of regenerating vegetation at different growth stages. Additionally, fragmentation modifies the microclimate within and around the patches [e.g. increase in radiation, temperature and wind, and decrease in humidity; Saunders et al., 1991], leading to changes in plant composition and structure. These changes include a sharply elevated rate of tree mortality, and a loss of tree biomass [e.g. Arroyo-Rodríguez & Mandujano, 2006; Laurance et al., 1997], which can promote the proliferation of young secondary vegetation, dominated by disturbance-adapted vines and pioneer trees, and cause a concomitant decline of old-growth, forest-interior trees [Laurance et al., 1998]. Therefore, primates in fragmented habitats are confronted with a habitat of reduced size, highly isolated from other habitat remnants, with few emergent trees and dominated by secondary vegetation (Fig. 1).

Exogenous Threatening Processes

Removal of suitable habitat

The removal or loss of habitat is expected to reduce both the distribution range and population size of a given primate species [metapopulation theory: Hanski, 1999; island biogeography theory: MacArthur & Wilson, 1967]. Supporting these predictions, a landscape-scale study with A. palliata in Los Tuxtlas, Mexico, based on 208 rainforest patches across a total area of ca. 15,000 ha, shows that the proportion of occupied patches is positively correlated ($r = 0.84$) with the abundance of individuals, and that landscapes with a greater proportion of suitable habitat contain more individuals (row 1 in Table I; ref 5 in Table II). Similarly, at the patch scale, studies of howler species such as A. palliata, A. guariba and A. seniculus in several forest types, including tropical wet, moist and dry forests, report that larger patches contain more individuals than smaller ones, and that the proportion of occupied patches (i.e. the distribution range) decreases with patch size (rows 2 and 3 in Table I). Each of these

studies is based on a sample size of greater than nine forest patches (mean = 94 patches) (see Table II). For example, in a study of 119 forest patches located in northern Chiapas, Mexico, Anzures-Dadda and Manson [2007] find that 19% of the patches are occupied by A. palliata, and that both the number of individuals (slope = 0.02, $P < 0.001$) and occupancy (whole model; $\chi^2 = 6.30$, $P = 0.04$) are positively correlated with patch size.

As an exception to these trends, for A. palliata populations living in six forest patches (7–9,571 ha) in Costa Rica (row 2 in Table I; ref 12 in Table II), the density of individuals was unrelated to patch size ($r = 0.29$, $P = 0.21$). Kowalewski and Zunino [1999] also report that when three forest patches in Argentina were deforested and reduced in size by 32.1%, the population size of A. caraya remained unchanged. Similarly, Estrada et al. [2002] studied 18 A. pigra groups living in 44 patches (1.9 to 86 ha) in Mexico (row 2 in Table I; ref 14 in Table II), and found that forest patches with and without howlers did not differ in size ($t = 0.31$, $P > 0.1$). These contrasting results could be due to the small sample sizes (only six patches were studied in Costa Rica and three patches in Argentina), and/or the fragmentation history at these locations (e.g. sampling effects, age of isolation and local historical factors such as recent clearing processes, and hunting), which could mask the effect of habitat area on howler populations. For example, Estrada et al. [2002] argued that the hunting history could explain the lack of a relationship between patch occupancy and patch size, whereas DeGamma-Blanchet and Fedigan [2006] argued that the large sizes (up to 95.7 km^2) of most of the patches they surveyed in Costa Rica may explain why this variable makes no explanatory contribution in their study.

Changes in Habitat Patterns

An increase in the number of habitat patches, decrease in patch size and increase in patch isolation can initially result in a random occupancy (i.e. without a specific pattern) of the remaining patches [Marsh, 2003]. However, over time primates may disappear from some patches owing to their small size and limited resources, whereas they may recolonize other suitable patches [Chapman et al., 2003; Mandujano et al., 2006]. Metapopulation theory predicts that the probability of local extinction in fragmented habitats increases with decreasing patch size and increasing isolation [i.e. ''first-order'' factors; sensu Hanski, 1999], whereas the probability of colonization follows the opposite trend [Hanski, 1999]. Five studies of A. palliata, A. seniculus and A. caraya support these predictions (row 3 in Table I). For instance, Arroyo-Rodríguez et al. [2008a] studied 208 isolated patches (ranging from 0.9 to 266 ha) in three landscapes with

TABLE I. Summary of Both Habitat and Population Attributes (HPA) Analyzed in Fragmentation Studies With Howlers (*Alouatta* spp.), Predictions Tested From Fragmentation Theory (see Text), the Species Analyzed, and Empirical Evidence (EE): +prediction supported; −prediction not supported; in parentheses: indirect inference or rarely tested

Rows	HPA	Predictions	Species	EE	Refs.
1	Landscape forest cover	Landscapes with a greater proportion of suitable habitat support more individuals	*A. palliata*	+	5,26
2	Patch size	Larger patches contain more individuals than smaller ones	*A. palliata*	+	2,5,10,15,26
				−	12
			A. guariba	+	11
			A. caraya	+	40
				−	42
3		The distribution range (% occupied patches) decreases with patch size	*A. palliata*	+	5,10,24
			A. seniculus	+	18
			A. pigra	−	14
4		Reduced patch size and increased isolation result in higher population densities	*A. palliata*	+	8,10,25
			A. pigra	+	14,37
			A. seniculus	+	35
				−	17
			A. caraya	+	42
5	Patch isolation	The least isolated patches contain more individuals than more isolated ones	*A. palliata*	+	15
				−	10,12
6		Distribution range (% occupied patches) decreases with increasing patch isolation	*A. palliata*	+	24
7	Shape complexity	Complex patches are colonized more frequently than compact ones	*A. palliata*	(+)	5
8	Habitat productivity	More productive patches represent a source of emigrants that migrate towards less productive fragments (sinks)	*A. palliata*	(+)	4,5
9	Food sources	Individuals can move between patches to supplement their diet	*A. palliata*	+	3,24
			A. caraya	+	40
10		Smaller and more irregularly shaped patches contain less food sources	*A. palliata*	+	6,21
			A. pigra	+	27,32
			A. seniculus	+	22
11		Changes in vegetation affect distribution and abundance of populations	*A. palliata*	+	2,4,10,15
			A. caraya	+	43
12	Physiological stress	Populations living in forest patches are more stressed than those living in large forest tracks	*A. palliata*	+	13
			A. pigra	+	28
13	Genetic diversity	Habitat disturbance, mainly through the reduction in dispersion rates of individuals between patches, reduces genetic diversity	*A. palliata*	+	23
			A. pigra	+	20
				−	16,39
			A. seniculus	+	31
			A. caraya	+	30, 41
14	Social organization	Group size decreases with decreasing patch size and conservation	*A. palliata*	+	7,8,9,29
				−	25
			A. pigra	−	14
				+	37
			A. caraya	−	40
			A. seniculus	−	17
			A. sara	−	19
15	Parasitism	The transformation of original habitat, reduction in food availability and presence of humans in disturbed patches increases the vulnerability of individuals to parasite infestations	*A. palliata*	+	1,34,36
			A. pigra	+	38
			A. seniculus	+	17
			A. caraya	+	33

1. Aguilar-Cucurachi et al. [2007]; 2. Anzures-Dadda & Manson [2007]; 3. Asensio et al. [2009]; 4. Arroyo-Rodríguez et al. [2007]; 5. Arroyo-Rodríguez et al. [2008a]; 6. Arroyo-Rodríguez & Mandujano [2006]; 7. Chapman & Balcomb [1998]; 8. Clarke et al. [2002b]; 9. Clarke & Zucker [1994]; 10. Cristóbal-Azkarate et al. [2005]; 11. Chiarello [2003]; 12. DeGamma-Blanchet & Fedigan [2006]; 13. Dunn [2009]; 14. Estrada et al. [2002]; 15. Estrada & Coates-Estrada [1996]; 16. García del Valle et al. [2005]; 17. Gilbert [1994]; 18. Gilbert [2003]; 19. Goffard et al. [2008]; 20. James et al. [1997]; 21. Juan et al. [2000]; 22. López et al. [2005]; 23. Malgrem & Brush [1978]; 24. Mandujano et al. [2006]; 25. Mandujano & Escobedo-Morales [2008]; 26. Mandujano & Estrada [2005]; 27. Marsh & Loiselle [2003]; 28. Martínez-Mota et al. [2007]; 29. McCann et al. [2003]; 30. Oklander et al. [2006]; 31. Pope [1992]; 32. Rivera & Calmé [2006]; 33. Santa-Cruz et al. [2000]; 34. Stuart et al. [1990]; 35. Terborgh et al. [2001]; 36. Trejo-Macías et al. [2007]; 37. Van Belle & Estrada [2006]; 38. Vitazkova & Wade [2007]; 39. Winkler et al. [2004]; 40. Zunino et al. [2007]; 41. Nascimento et al. [2007]; 42. Kowalewski & Zunino [1989]; 43. Zunino et al. [2001].

TABLE II. Characteristics of Fragmentation Studies with Howlers[a]

Ref.	Species	Site[b]	Habitat[c]	Months	Groups	Design
1	Apa	Tux	TWF	6	4	Analyzed 4 small patches (<8 ha)
2	Apa	Chi	TWF	–	23	Analyzes 119 patches (0.2–43.4 ha) in a 12,500 ha landscape
3	Apa	Tux	TWF	23	2	Analyzes 2 groups in 2 different patches (1.3–40 ha)
4	Apa	Tux	TWF	16	9	Analyzes 18 <10 ha patches, 9 occupied and 9 unoccupied by howlers
5	Apa	Tux	TWF	16	42	Analyzes 208 patches (0.9–266 ha) in 3 landscapes with different forest cover
6	Apa	Tux	TWF	6	8	Analyzes 15 patches (1–76 ha) in a 4,960 ha landscape
7	Apa	–	TDF & TWF	–	80	Reviews 80 howler populations from Mexico to Argentina
8	Apa	Pac	TDF	4	34	Surveys a 1,180 ha farm with ca. 25% of remaining forest cover
9	Apa	Pac	TDF	1	30	Surveys a 1,180 ha farm with ca. 25% of remaining forest cover
10	Apa	Tux	TWF	17	43	Analyzes 55 patches (<1–244 ha) in a 7,500 ha landscape
11	Agu	Esp	TDF	–	–	Analyzes 14 patches (210–35,000 ha)
12	Apa	ACG	TDF & TWF	6	–	Analyzes 6 patches (7–9,571 ha)
13	Apa	Tux	TWF	12	2	Analyzes 2 groups in 2 different patches (7.2 and 244 ha)
14	Api	Pal	TWF	10	18	Analyzes 44 patches (1.9–86 ha)
15	Apa	Tux	TWF	–	60	Analyzes 126 patches (2–1,000 ha) and 44 agricultural sites
16	Api	Lac	TWF	>3	–	Analyzes a continuous forest and 3 patches (1–1,700 ha)
17	Ase	Man	TMF	16	13	Analyzes 3 10 ha and 2 100 ha patches, and a continuous forest
18	Ase	Man	TMF	–	–	Analyzes a continuous forest and 9 patches (1–100 ha)
19	Asa	San	TWF	12	23	Analyzes populations of a reserve and 3 cattle ranches
20	Api	CBS	TMF	2	10	Analyzes a population living in highly disturbed conditions
21	Apa	Tux	TWF	6	3	Analyzes 3 patches (3.2–250 ha)
22	Ase	Lag	TDF	9	3	Analyzes 2 islands (0.6 and 190 ha)
23	Apa	Pac	TDF	9	17	Surveys a 1,180 ha farm with ca. 25% of remaining forest cover
24, 25	Apa	Tux	TWF	28	17	Analyzes 92 patches (<1–76 ha) in a ca. 4,960 ha landscape
26	Apa	Tux	TWF	–	≥36	Analyzes 130 patches (0.5–150 ha) in 2 landscapes with different forest cover
27	Api	CBS	TMF	12	6	Analyses 6 patches occupied and one unoccupied by howlers (1.3–75 ha)
28	Api	T & C	TMF	8	4	Analyzes 2 patches (<2 ha) and two sites in continuous forest
29	Apa	Fll	TDF	8	97	Analyzes coffee plantations (25–225 ha)
30	Aca	Cor	TDF	–	–	Analyzes 9 patches
31	Ase	Hat	TDF	–	≥18	Analyzes 2 populations inhabiting a large cattle ranch
32	Api	Cal	TDF	8	5	Analyzes 2 sites in a >700,000 ha forest reserve and 2 patches (11.6 and 13.9 ha) outside the reserve
33	Aca	C & C	TDF	–	–	Analyzes 44 individuals in 3 areas with different fragmentation degree
34	Apa	Pac & ACG	TDF	>4	>20	Analyzes a 450 ha forested farm and a continuous forest (50,000 ha)
35	Ase	Lag	TDF	–	14	Analyzes 6 small (0.25–0.9 ha), 4 medium (4–12 ha) and two large islands (150 ha), and 2 sites in mainland (>350 ha)
36	Apa & Api	Tux & Lac	TWF	12	110	Analyzes 6 protected forests (>1,400 ha each) and 6 patches (1–40 ha).
37	Api	M & G	TDF & TWF	–	120	Analyzes 5 large patches (850–2,700 ha) and 3 reserves (57,600–700,000 ha).
38	Api	M & B	TWF & TDF	7	9	Analyzes 5 patches (80 ha) and 4 continuous forests (100 ha)
39	Apa & Api	N & B	TDF	3	4	Analyzes 3 groups of *A. palliata* in an island and one group of *A. pigra* living in a patches
40	Aca	Cor	TDF	4	34	Analyzes 24 patches in a 4,500 ha landscape
41	Aca	B & B	TWF	–	–	Analyzes 4 sites, three in Brazil and one in Bolivia
42	Aca	Cor	TDF	–	3	Analyzes 3 patches between 1984 and 1995
43	Aca	C & M	TDF	–	61	Analyzes 5 sites

[a]We indicate the study species (Aca, *Alouatta caraya*; Agu, *A. guariba*; Apa, *A. palliata*; Api, *A. pigra*; Asa, *A. sara*, Ase, *A. seniculus*), study sites, habitat type, number of months, number of groups, and study design. Reference numbers correspond to those in Table I.
[b]Sites: Area de Conservación Guanacaste, Costa Rica (ACG); Several locations in Central Brazil and one site in Bolivia (B & B); Calakmul, Campeche (Cal); Chiapas, Mexico (Chi); Community Baboon Sanctuary, Bermudian Landing, Belize (CBS); Corrientes and Chaco Provinces, Argentina (C & C), Corrientes Province, Argentina (Cor); Corrientes and Misiones provinces, Argentina (C & M); Espiritu Santo, Brazil (Esp); Finca La Luz, Mombacho Volcano, Nicaragua (Fll); Hato Masaguaral, Los Llanos, Venezuela (Hat); Lacandon rainforest, Mexico (Lac); Lago Guri, Venezuela (Lag); Manaus, Brazil (Man); Several places in shoutern Mexico and Belize (M & B); Shoutern Mexico and northern Guatemala (M & G); Isla de Ometepe, Nicaragua, and the Scotland Half Moon area, Belize (N & B); La Pacifica, Costa Rica (Pac); Palenque, Chiapas, Mexico (Pal); Los Tuxtlas, Mexico (Tux); Santa Cruz, Bolivia (San); States of Tabasco and Campeche, Mexico (T & C).
[c]Habitats: We recognized three broad vegetation types based on annual rainfall: tropical wet forest (TWF), tropical moist forest (TMF) and tropical dry forest (TDF) [Gentry, 1982].

differences in forest cover (ranging from 4 to 24%), and found that patch size was the best predictor (with a positive effect) of patch occupancy by *A. palliata* in each landscape. Similarly, patch size has been consistently described as the best predictor for population size [Cristóbal-Azkarate et al., 2005] and viability [Mandujano et al., 2006] of *A. palliata* in Los Tuxtlas (refs. 10 and 24 in Table II). The fact that patch isolation is not a strong predictor of patch occupancy could be due to a number of methodological problems associated with the metrics used to define and describe patch isolation [see Arroyo-Rodríguez & Mandujano, 2009]. Nearly all fragmentation studies with howlers use distance-based isolation metrics such as the distance to the nearest patch. This 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, which can provide food and facilitate inter-patch movements [e.g. Arroyo-Rodríguez & Mandujano, 2009; Asensio et al., 2009]. Future studies should test the effects of isolation by using area-based isolation metrics, such as the amount of available habitat within a given radius of a patch, as these metrics are a more reliable measure of patch isolation [Arroyo-Rodríguez & Mandujano, 2009].

Evidence from *A. palliata, A. pigra, A. seniculus* and *A. caraya* in tropical dry and wet forests indicates that population density can increase in smaller and more isolated patches (row 4 in Table I). Thus, howlers may be resistant to the initial phases of disturbance, and concentrate in a small number of isolated forest patches [e.g. Estrada et al., 2002; Rosales-Meda et al., 2007]. The regulatory effect that natural predators have on howler populations may be less intense in fragmented habitats, as large predators (e.g. *Harpia harpyja, Panthera onca*) are usually among the first animals to disappear from disturbed areas [e.g. Terborgh et al., 2001]. This absence has been suggested as a factor contributing to the initial or short-term high population densities of howlers living in small patches [Chiarello, 2003; Gilbert, 2003; Lovejoy et al., 1986; Terborgh et al., 2001]. The proliferation of highly productive secondary vegetation in small patches has been suggested as an additional factor that could help to maintain high population densities in small patches [e.g. Kowalewski & Zunino, 1999; Lovejoy et al., 1986]. Although populations living at high densities may respond better to stochastic threats, particularly when populations are large [Fischer & Lindenmayer, 2007], enduring high densities could have negative consequences for the long-term persistence of howlers [see the ''Changes to Species Interactions'' section].

Changes in the habitat pattern (e.g. decrease in patch size, increase in patch isolation) are related to two processes that may explain the distribution, abundance and inter-patch movements of howler populations in fragmented landscapes [Dunning et al., 1992]: landscape supplementation and source/sink relationships. Landscape supplementation occurs when animals use a number of neighboring patches because they contain supplementary resources. For instance, when a patch is very small but is also very close to another patch(es) with supplementary resources, individuals may use several patches to meet their dietary requirements (row 9 in Table I). For example, Zunino et al. [2007] observed five groups of *A. caraya* using more than one forest patch separated by grasslands in northern Argentina, and these groups occupied the smallest patches (<5 ha) in the area. A similar pattern of multi-patch use was observed by Mandujano et al. [2006] and Asensio et al. [2009] in groups of *A. palliata* inhabiting very small patches (<3 ha) in Los Tuxtlas, Mexico. These observations highlight the ability of howlers both to exploit small forest patches and to move between isolated forest patches [also see Pozo-Montuy & Serio-Silva, 2007], and agree with the frequently cited behavioral flexibility that is thought to allow howlers to cope with habitat disturbance [e.g. Bicca-Marques, 2003]. Nevertheless, when howlers are required to descend to the ground, they face an increase in predation risk from dogs [Pozo-Montuy & Serio-Silva, 2007] and other animals (see the ''Changes to Species Interactions'' section).

Source/sink relationships occur when a more productive patch represents a source of emigrants that migrate toward less productive patches, usually named sinks [Pulliam, 1988]. As sink patches have insufficient food, populations living in sinks may go extinct without immigration of individuals from source patches. Source/sink dynamics may be at work in highly fragmented landscapes occupied by *A. palliata* at sites such as Los Tuxtlas, Mexico, as some groups are living in patches that do not present the characteristics required for their long-term survival (e.g. they are very small, highly isolated and with few large (DBH > 60 cm) trees and few food plant species) (row 8 in Table I; refs. 4 and 5 in Table II). In these studies, it has been suggested that such patches may functionally be sinks, as it has been argued for other primate species [e.g. *Procolobus rufomitratus*: Mbora & Meikle, 2004].

Habitat fragmentation can also increase the total amount of habitat boundaries through the increment of the perimeter-to-area relationship (i.e. shape complexity) of the patches. Patch shape complexity offers advantages and disadvantages to howlers in fragmented landscapes. For example, complexly shaped patches can be colonized more easily than compact (e.g. round) patches due to the fact that they have a proportionally greater amount of edge, increasing the likelihood that a patch will be

encountered by a moving individual, either by chance [Ewers & Didham, 2006] or deliberately [Boinski & Garber, 2000]. This hypothesis has been used to explain why patch occupancy by *A. palliata* was positively related to both patch size and shape complexity in a landscape dominated by live fences and vegetation corridors in Los Tuxtlas, Mexico (row 7 in Table I). However, as we describe below, irregularly shaped patches experience higher edge effects, affecting plant composition and vegetation structure within the patch, which could in turn decrease food availability for howlers.

Changes in vegetation attributes and food availability

Food availability in patches depends on patch size, home range size and the composition and structure of vegetation. Studies of *Alouatta* [reviewed by Bicca-Marques, 2003] and particularly *A. palliata* [Cristóbal-Azkarate & Arroyo-Rodríguez, 2007] have shown that home range size decreases with decreasing patch size ($r = 0.51$, $P = 0.001$; $r = 0.96$, $P = 0.01$, respectively), limiting the amount of resources available to each group. However, a small home range does not always result in low food availability [see Gillespie & Chapman, 2001]. This depends on the specific composition of the forest fragment.

Two main processes affect the vegetation in patches, namely, sampling effects and edge effects [i.e. environmental changes near patch edges; Saunders et al., 1991]. Although sampling effects result in different patterns of the presence/absence/ dominance of particular species in remnants, environmental changes alter plant composition and vegetation structure within the patches. Usually these environmental changes result in higher mortality rates of large old-growth tree species near patch edges [Laurance et al., 1997], decreasing tree biomass in the smallest and most irregularly shaped patches [e.g. Arroyo-Rodríguez & Mandujano, 2006]. Changes in vegetation structure that can reduce food availability to howlers in patches include the loss of emergent trees [Arroyo-Rodríguez & Mandujano, 2006; Dunn et al., 2009; Juan et al., 2000; Rivera & Calmé, 2006] and the reduction of plant species richness [Arroyo-Rodríguez & Mandujano, 2006; Juan et al., 2000; López et al., 2005; row 10 in Table I]. These patterns have been reported for tropical wet, moist and dry forests (refs. 6, 21, 22, 27 and 32 in Table II). For example, after analyzing the top food plant species (i.e. those contributing >80% of feeding time) of *A. palliata* in Los Tuxtlas, Arroyo-Rodríguez & Mandujano [2006] found that the basal area of these plant species was negatively related to patch size ($R^2 = 0.50$, $P < 0.01$). Similarly, López et al. [2005] analyzed the vegetation of two islands (0.6 and 190 ha) inhabited by *A. seniculus* in Lago Guri, Venezuela, and reported that the number of plant species found on the smaller island (46 species) was half the number found on the larger island (>100 species).

The changes in vegetation in highly fragmented habitats may affect the distribution and abundance of howlers. The presence and abundance of howlers have been positively correlated with the diversity, abundance and basal area of important food resources (row 11, Table I). Nevertheless, it is still unclear which of these vegetation attributes has the greatest influence on howler populations. Although Cristóbal-Azkarate et al. [2005] and Estrada and Coates-Estrada [1996] show that plant species diversity is related to the population size of *A. palliata* in Los Tuxtlas, Mexico, Arroyo-Rodríguez et al. [2007] and Anzures-Dadda and Manson [2007] demonstrate that the density of large trees is the best predictor of the distribution of *A. palliata* in Los Tuxtlas and Chiapas, Mexico. Further studies are necessary to identify which attributes have the largest influence on different howler populations in different forest types, as current evidence comes almost exclusively from studies with *A. palliata* in tropical wet forests (Tables I and II). This information has critical implications for howler conservation in altered habitats.

Postfragmentation anthropogenic pressures

Anthropogenic pressures (e.g. logging, hunting) are not a direct consequence of habitat fragmentation, but can be facilitated by this process, exacerbating the negative effects of habitat fragmentation on populations (Fig. 1). Poaching and capturing live primates for pets have been considered two of the most important threats for primate survival in fragmented habitats [Chapman & Peres, 2001; Oates, 1996; Peres, 2000], largely because primates may be more vulnerable to poachers in the smallest and most accessible sites [Chiarello & de Mello, 2001; Peres, 1990, 2001]. Hunting may have had an important negative effect on howler populations [*A. caraya*: Agoramoorthy & Lohmann, 1999; *A. guariba*: Chiarello & Galetti, 1994; *A. palliata*: Duarte-Quiroga & Estrada, 2003; *A. pigra*: Watts et al., 1986; *A. sara*: Goffard et al., 2008; *A. seniculus*: Peres, 1990, 2000, 2001], but it should be noted that the effects of hunting on howlers may be context-dependent. For instance, in Central Amazonia, Brazil, howlers are intensively harvested for meat [e.g. Peres, 2000], whereas at other locations such as Los Tuxtlas, Mexico, people only occasionally hunt them for the pet trade [V.A.R. & P.A.D.D, pers. obs.]. Therefore, the impact of hunting on howlers will vary as a function of local historical and socio-economic factors. However, it remains to be demonstrated whether hunting rates are higher in fragmented forests.

The postfragmentation extraction of forest products can lead to additional loss of food resources important to howlers (Fig. 1). For example, in Los Tuxtlas, Mexico, the inhabitants often remove understory plants to allow the cattle to enter the patches [Arroyo-Rodríguez & Mandujano, 2006]. Tree felling also has been observed in this and other regions, where local populations log wood species such as *Albizia purpusii* (Fabaceae), *Ampelocera hottlei* (Rubiaceae) and *Araucaria* sp. (Araucariaceae) to build their houses and for fuel [Arroyo-Rodríguez & Mandujano, 2006; Kowalewski & Zunino, 1999; Zunino et al., 2007]. These trees are among the most common trees in the howler diet [Bicca-Marques, 2003; Cristóbal-Azkarate & Arroyo-Rodríguez, 2007]. However, no studies to date have directly quantified the effects of logging on howler population sizes, structure or persistence. A few studies have attempted to indirectly measure these effects [Arroyo-Rodríguez et al., 2008a; Kowalewski & Zunino, 1999; Zunino et al., 2007]. For instance, Arroyo-Rodríguez et al. [2008a] found that small patches located at greater distances from villages are more likely to be occupied by *A. palliata* than are larger patches located nearer to villages, and argue that this pattern may be related to logging. Further studies relating different intensities of selective logging to population sizes, structure and persistence are necessary to assess to what extent logging affects howler populations.

Endogenous Threatening Processes

In addition to the exogenous threatening processes described above, the distribution and population structure of howlers in fragmented habitats may be affected by changes in their biology, behavior and interactions with other species (Fig. 1). As Fischer and Lindenmayer [2007: 269] noted, "these changes are often triggered by exogenous threats, but may constitute threatening processes in their own right."

Changes in biology

Biological changes have been reported for howlers living in fragmented habitats, including increased physiological stress and loss of genetic diversity (rows 12 and 13 in Table I). For instance, in a recent study of *A. pigra*, 16 individuals living in forest patches had significantly higher levels of stress (as measured in fecal cortisol) than 17 individuals living in a continuous forest, suggesting that physiological stress may increase as a result of forest fragmentation [Martínez-Mota et al., 2007; Tables I and II]. Similarly, Dunn [2009] reports that fecal glucocorticoid concentrations (a measure of stress) are higher (127.1 ± 31.5 ng/g, mean $\pm$ SD) among an *A. palliata* group of six individuals inhabiting a small (7.2 ha) forest patch, than in a group of six individuals inhabiting a larger (244 ha) patch

(105.2 ± 18 ng/g). The increase in the number of solitary males living in isolated patches has also been suggested to result in an increase in the concentration of testosterone, for males, and cortisol, for females, in a population of *A. palliata* [Cristóbal-Azkarate et al., 2006, 2007]. As higher levels of both hormones increase energetic demands, and food availability is expected to be reduced in smaller and isolated patches (see above), individuals living in fragmented habitats may experience compromised nutrition, fecundity and survivorship.

Additional studies on the effects of habitat fragmentation on physiological stress are necessary to assess how this factor affects the health (e.g. parasite incidence) and persistence of wild populations. This information is critical to identify factors singly and in combination that may affect the survival of primates in fragmented landscapes [see Chapman et al., 2006, 2007]. For instance, crowding in small patches may lead to higher rates of aggression, which in turn could lead to increased social stress [Honess & Marin, 2006]. Under these circumstances, higher stress levels in individuals living in disturbed habitats could be a byproduct of fragmentation, rather than a direct consequence of it.

Other negative consequences of population isolation are inbreeding and genetic drift. Both processes are more intense in smaller patches, as these usually have smaller populations, and result in lower genetic diversity. The effects of these processes may reduce the response capacities of individuals to natural or human-induced changes [Jump et al., 2009]. Although studies of *A. caraya*, *A. palliata*, *A. pigra* and *A. seniculus* suggest that habitat disturbance—mainly through the reduction in dispersal rates of individuals between patches—could reduce genetic diversity (row 13 in Table I; refs. 20, 23, 30, 31 and 41 in Table II), recent studies conducted with *A. pigra* populations living in fragmented habitats found higher average heterozygosis than that reported in previous studies (refs. 16 and 39 in Table II). This may be associated with differences in the methodologies used in each study, the small sample sizes or with the recent separation of the populations, and suggests that further long-term genetic studies are required to demonstrate the effect of isolation on the genetic diversity of howler populations.

Changes in social organization and behavior

Habitat fragmentation can also lead to disruptions to the social organization and behavior of howlers such as changes in: (1) dispersal patterns; (2) grouping patterns; (3) social interactions; and (4) activity patterns. As patches become smaller and more isolated, howlers' ability to disperse successfully decreases. Quantitative data on male and female dispersal patterns in red howlers [e.g.

Crockett & Pope, 1993] and mantled howlers [e.g. Clarke & Glander, 2004] are available. However, little is specifically known concerning the movement of individuals between particular forest patches, the frequency of such events, the routes that are used, or the criteria used by howlers to select which patch to disperse to. Although there are several observations of howlers traveling on the ground [*A. palliata*: Asensio et al., 2009; Clarke et al., 2002a; Estrada & Coates-Estrada, 1996; *A. pigra*: Crockett, 1998; Pozo-Montuy & Serio-Silva, 2007], their dispersal abilities in disturbed matrices are likely restricted. Specifically, studies with fragmented populations of *A. palliata* and *A. pigra* in Mexico suggest that there may be isolation thresholds that limit dispersal between patches along the ground. These thresholds may vary as a function of the mortality risk associated with long distance travel, energetic costs and predation [Mandujano & Escobedo-Morales, 2008; Mandujano & Estrada, 2005; Mandujano et al., 2004; Van Belle & Estrada, 2006]. The constraints associated with limited dispersal from small and isolated patches may result in increases in population density [e.g. *A. pigra*: Van Belle & Estrada, 2006], and inbreeding and loss of genetic variability [*A. palliata*: Arroyo-Rodríguez et al., 2008b; *A. guariba*: Fortes & Bicca-Marques, 2008].

We could not identify a clear pattern in the effects of habitat fragmentation on the size and composition of howler groups. Although five studies of *A. pigra* and *A. palliata* show that group size tends to decrease with decreasing patch size, no such relationship was found in other howler populations (*A. caraya*, *A. palliata*, *A. seniculus* and *A. sara*; row 14 in Table I). Regarding group composition and social interactions, evidence is only available from studies analyzing habitat disturbance effects. For instance, in more disturbed habitats, defined as habitats transformed by anthropogenic (e.g. logging) or natural (e.g. hurricanes, droughts) events, the number of males per group is lower and the proportion of unimale groups increases [*A. palliata*: Clarke et al., 2002a,b; McCann et al., 2003; *A. pigra*: Estrada et al., 2002; Van Belle & Estrada, 2006; *A. seniculus*: Rudran & Fernandez-Duque, 2003]. In addition, fission–fusion dynamics [defined as temporal variation in spatial cohesion and individual membership in a group over time; see Aureli et al., 2008] become more prevalent [*A. palliata*: Dias & Rodríguez-Luna, 2005, 2006], and both the rates of social interactions [0.010 interactions/ind/hr vs. 0.004 interactions/ind/hr: Clarke et al., 2002a] and the proportion of time spent in social activity [1.2% vs. 0.55%: Behie & Pavelka, 2005] decrease. Overall these data indicate that habitat disturbance may affect the social organization of howlers; however, other studies of *A. palliata* [Mandujano & Escobedo-Morales, 2008], *A. caraya* [Zunino et al., 2007] and *A. sara* [Goffard et al., 2008] dispute this possibility.

Thus, further studies specifically designed to measure the effects of fragmentation on group composition, social interactions and social organization are needed [see Arroyo-Rodríguez & Mandujano, 2009].

Changes in the activity patterns of individuals (i.e. proportion of daily activity spent resting, feeding and moving) have been reported in relation to habitat disturbance and fragmentation. Clarke et al. [2002a] found that after the partial deforestation of their home range, a group of 10 adult mantled howlers increase feeding time from 18 to 22.3%, possibly to compensate for reduction in food availability. Asensio et al. [2007b] observed that a group of 59 mantled howlers living in an area of extremely high population density (9.5 ind/ha) spent a greater amount of time feeding and traveling (29 vs. 24% and 14 vs. 6%, respectively) and reduced time spent resting (55% vs 69%), relative to another group of six howlers that lived in a small (1.3 ha) patch at lower density (4.6 ind/ha). In contrast, Juan et al. [2000] observed no differences in activity patterns among three groups of *A. palliata* living in habitats of different sizes. Similarly, in their meta-analysis of the diet and activity patterns of *A. palliata* in Los Tuxtlas, Cristóbal-Azkarate and Arroyo-Rodríguez [2007] found that neither patch size nor population density had a significant effect on the activity patterns of howlers. Similarly, after examining all studies with howlers (with duration > 9 months), Bicca-Marques [2003] reported that activity patterns did not vary with patch size.

These contrasting results suggest howlers can exploit habitats that vary in size, degree of disturbance, isolation and population density with relatively minor adjustments in the time they engage in feeding, traveling and resting. In this regard, an evaluation of habitat quality, with specific emphasis on the presence, abundance and nutritional contents of important plant species in the howlers' diet, will help interpret fine-grained variation in activity patterns. Finally, howler activity budgets seem to be constrained by energy-saving behavioral adaptations, associated with resting and related to their digestive physiology [Milton, 1998]. Thus, perhaps howlers' abilities to modify their activity patterns are limited, in which case nutritional stress is expected to particularly affect populations living in the less productive habitats and habitats lacking preferred plant species.

Unfortunately, we still do not know how overall shifts in social organization (e.g. increases in the proportion of unimale groups in populations) and behavior (e.g. reduction in dispersal rates) of howlers are affected by habitat fragmentation. Long-term studies of *A. palliata* and *A. seniculus* suggest that when the amount of habitat increases, howler populations tend to expand, mainly through the formation of new groups, which are usually small

and unimale [Fedigan et al., 1998; Rudran & Fernández-Duque, 2003]. These important findings indicate how howler populations respond to increases in forest cover, but do not necessary explain the long-term response of howler populations and groups to habitat loss and fragmentation.

Changes to species interactions

Changes in species interactions include competition, predation and exposure to parasites (Fig. 1). As indicated above, population density usually increases in the smallest patches, and this could increase intra-specific competition. High population densities have been associated with reductions in food availability and the exploitation of alternative nontree food resources [Cristóbal-Azkarate & Arroyo-Rodríguez, 2007; Rodríguez-Luna et al., 2003]. For example, Rodríguez-Luna et al. [2003] observed that after significant population increase (from 1.2 ind/ha to 6.9 ind/ha), a population of mantled howlers began to intensively exploit alternative food sources (mainly lianas and vines; from 8.8% of feeding time to 21%) and the duration of feeding bouts tended to decrease (from 3.1 to 2.1 min). Similarly, Cristóbal-Azkarate et al. [2005] speculate that immature mortality in a fragmented population of *A. palliata* (43 groups living in 15 fragments) increased at high population densities, as none of the populations living at densities higher than 0.71 ind/ha had juveniles. These authors propose that this trend is possibly mediated by lower food availability under high-density conditions. There also is evidence that reproduction is suppressed in howler populations living at densities of 10 ind/ha [*A. seniculus*: Terborgh et al., 2001]. Terborgh et al. [2001] report that on a 0.6 ha island, a group of howlers containing two adult females (population density of 10 ind/ha) produced only one young in 4 years (0.125 birth per female-year), whereas on a 350 ha island, 10 adult females belonging to two groups (0.3 ind/ha) produced five infants in a single year (0.5 birth per female-year). Finally, increased inter- and intra-specific competition over food is expected to occur in smaller patches, where food resources are limited and feeding encounters may be more common [Dias & Strier, 2000; Rose et al., 2003; Stevenson et al., 2000]. However, there is only weak evidence for the occurrence of direct inter- and intra-specific competition for food in howlers [but see Asensio et al., 2007a; Cristóbal-Azkarate et al., 2004].

Although habitat fragmentation may negatively affect the presence of large predator populations, these same habitats are often characterized by an increase in the number of wild mid-level predators (e.g. coyotes, foxes) and/or domestic dogs and cats [e.g. Crooks & Soul, 1999; May & Norton, 1996]. Although this hypothesis needs further investiga-

tion, primates are expected to be more vulnerable in open environments, such as those present in fragmented landscapes [Santamaría, 2004]. For instance, Pozo-Montuy and Serio-Silva [2007] and Camargo and Ferrari [2007] observed a coyote (*Canis latrans*) and four tayras (*Eira barabara*), respectively, attacking a juvenile of *A. pigra* and a subadult female of *A. belzebul*, respectively, traveling on the ground. Similarly, Ludwig et al. [2007] argue that the presence of howlers (*A. caraya*) in successional vegetation with a low forest canopy can facilitate the predation by cougars (*Puma concolor*). Estrada and Coates-Estrada [1996] and Pavelka et al. [2003] also argue that habitat disturbance promoted by fragmentation and hurricanes, respectively, may force howlers to travel on the ground, increasing their predation risk from terrestrial predators such as boas and dogs.

A topic of growing concern is the potential effect of emerging infectious diseases (EIDs) on endangered primate populations [Nunn & Altizer, 2006]. For instance, the transformation of original habitat, increase of inbreeding, reduction in food availability, the presence of humans and domesticated animals in disturbed patches, or even some management actions, such as the building of corridors connecting forest fragments, may increase the vulnerability of individuals to EIDs infestations. In *A. palliata*, *A. caraya* and *A. seniculus* higher endoparasite loads have been related to higher population density in small patches [Aguilar-Cucurachi et al., 2007; Gilbert, 1994; Santa-Cruz et al., 2000; Stuart et al., 1990], and in *A. caraya*, *A. palliata* and *A. pigra* parasite prevalence is higher in individuals living in fragmented habitats (prevalence: *A. caraya* = 50.7% of individuals infected; *A. palliata* = 45.7%; *A. pigra* = 24.0%) compared with more continuous forest (*A. caraya* = 7.14%; *A. palliata* = 23.7%; *A. pigra* = 13.0%) [Santa-Cruz et al., 2000; Trejo-Macías et al., 2007]. In addition, several groups of *A. pigra* were infected with a parasite (*Giardia duodenalis*) most probably transmitted to them through human feces [Vitazkova, 2009; Vitazkova & Wade, 2007]. It is possible that, as shown for *P. rufomitratus* [Chapman et al., 2007], parasitism co-varies with temporal fluctuations in food abundance, and for howler populations living in disturbed habitats this could lead to decreases in the fitness of infected individuals. To date, no study has demonstrated conclusively that such changes in host–parasite dynamics are detrimental to howlers.

CONCLUSIONS AND FUTURE DIRECTIONS

A complex picture about our current understanding of the effects of habitat fragmentation and disturbance on howlers emerges from this review. Howlers are among the most studied Neotropical primate taxa [e.g. Di Fiore & Campbell, 2007], and

many efforts have been directed toward studying howlers in fragmented and disturbed habitats. Thus, the information we have for howlers allows us to develop best modeling approaches of primate responses to habitat fragmentation and disturbance.

Howlers are known for their ability to persist in both conserved and disturbed habitats, including naturally fragmented landscapes [e.g. *A. seniculus* in Los Llanos, Venezuela; Braza et al., 1981] and very small forest patches (<5 ha) where other primate species cannot survive [Chiarello, 2003; Estrada & Coates-Estrada, 1996; Lovejoy et al., 1986]. Nevertheless, in our review, we found evidence indicating that habitat loss negatively affects the distribution and abundance of howlers. In particular, studies with *A. caraya*, *A. guariba*, *A. palliata*, *A. pigra* and *A. seniculus* indicate that patch size is an important factor negatively affecting the presence, abundance and persistence of howler populations in fragmented habitats. Thus, we propose that habitat loss probably has larger consistent negative effects on howler populations than habitat fragmentation per se [see Fahrig, 2003]. Habitat area is positively related to food availability [e.g. Arroyo-Rodríguez & Mandujano, 2006; Cristóbal-Azkarate & Arroyo-Rodríguez, 2007], and negatively related to anthropogenic pressures [e.g. Peres, 2000, 2001], physiological stress [e.g. Martínez-Mota et al., 2007] and parasite risk [e.g. Gilbert, 1994]. Therefore, we believe that the most important management recommendations for howler populations in disturbed habitats are to increase the remaining habitat area and to conserve the largest habitat remnants. In larger habitats the negative effects of shape complexity (e.g. edge effects) are lower, whereas the positive effects (e.g. increased patch accessibility) are higher (see the "Changes in Habitat Patterns" section).

The reduction of population sizes in smaller forest patches could negatively affect howlers' persistence. Small populations are more susceptible to stochastic threatening processes such as disease epidemics [Agostini et al., 2008; Nunn & Altizer, 2006], environmental catastrophes (e.g. hurricanes) and demographic (e.g. year-to-year variability in reproductive success) and genetic (e.g. genetic drift) stochasticity [Cowlishaw & Dunbar, 2000; Fischer & Lindenmayer, 2007; Gilpin & Soulé, 1986]. Additionally, threatening processes usually have the potential to interact with, and magnify the effects of each other, creating what have been described as "extinction vortices" [Gilpin & Soulé, 1986]. Thus, although the high resilience and "pioneer" capacity of *Alouatta* spp. [Bicca-Marques, 2003; Garber et al., 2006; Lovejoy et al., 1986; Schwarzkopf & Rylands, 1989; Van Belle & Estrada, 2006] may allow them to survive in highly impacted habitats, the current rate of habitat transformation associated with human activities [countries like Bolivia, Brazil or Ecuador had annual rates of forest lost in the period of 1990–2005 of more than 0.5%; FAO, 2007] will eventually result in local extinction of many howler populations.

In this sense, a major focus of future studies should be the identification of threshold values for habitat amount under which the long-term persistence of individual howler species and populations will be compromised [e.g. Andrén, 1994]. These data have important management implications for endangered primates, although it is important to highlight that it is more responsible to require governments to use reference values for habitat amounts well above minimum thresholds (i.e. resilience thinking). In addition, landscape-scale studies offer the most effective means of determining management policies [Arroyo-Rodríguez & Mandujano, 2009]. This approach has been applied in a study with *A. palliata* in three fragmented landscapes in Los Tuxtlas, Mexico [Arroyo-Rodríguez et al., 2008a]. In this study, it was determined that both the proportion of occupied patches and the abundance of primates decreased significantly in landscapes with less than 15% of remaining habitat, suggesting that population persistence could be compromised in the long term in highly fragmented landscapes [Arroyo-Rodríguez et al., 2008a]. For one of these landscapes, it was estimated that with an annual deforestation rate of 4%, the population of *A. palliata* had an extinction probability of 35% in the next 30 years [Mandujano et al., 2006]. Nevertheless, if 112–170 ha are restored in this 5,000 ha landscape, by connecting large patches with low population sizes, the authors predict that the extinction probability would drop to 1%. This example illustrates how the persistence of howlers in altered landscapes depends on the management actions promoted over the coming years.

Our review reveals that patch isolation is not a strong predictor of either patch occupancy or population size for howlers. As we discussed in the text (see the "Changes in Habitat Patterns" section), this could be related to a number of methodological problems of the most commonly used isolation metrics [see Arroyo-Rodríguez & Mandujano, 2009]. However, this result could also reflect the ability of howlers to move among patches, highlighting the ecological plasticity of these primates. For example, a number of studies with *A. palliata*, *A. pigra* and *A. caraya* report that howlers can travel on the ground, along live fences, and other landscape elements such as isolated trees, and that some groups can supplement their diets by making use of resources from several forest patches [e.g. Asensio et al., 2009; Pozo-Montuy & Serio-Silva, 2007]. In fact, we found several papers indicating that howlers may be resistant to the initial phases of disturbance and concentrate in a small number of isolated forest patches, in which other primate species (e.g. *Ateles*) cannot persist [e.g. Estrada & Coates-Estrada, 1996; Gilbert, 2003]. Among other factors, the success of

howlers in coping with habitat disturbance has been related to their capacity to (1) feed from many different plant species and adapt their diet to the species available in the habitat [e.g. Pinto et al., 2003; Rivera & Calmé, 2006], (2) increase the amount of leaves in their diet [Asensio et al., 2007b; Juan et al., 2000; Rodríguez-Luna et al., 2003], (3) consume exotic and secondary species frequent in disturbed habitats [Bicca-Marques & Calegaro-Marques, 1994], (4) use small home ranges [Estrada & Coates-Estrada, 1996; Lovejoy et al., 1986] and (5) utilize energy-saving activity budgets [Milton, 1998].

We found however that in several other areas our current knowledge is, at best, fragmentary. Among these, we highlight two. First, we are lacking direct quantification of the effects of postfragmentation anthropogenic pressures, such as hunting and logging, on howlers living in patches. Although many studies have suggested that hunting has strong detrimental effects on howler populations [e.g. Chiarello & Galetti, 1994; Duarte-Quiroga & Estrada, 2003; Goffard et al., 2008; Peres, 2000], we cannot currently determine how fragmentation facilitates the penetration of human hunters in patches. Furthermore, several studies have speculated that selective logging and wood extraction are affecting the availability of food resources to howlers, but no studies have directly analyzed this assertion. Actually, it is still unclear which vegetation attributes have the biggest influence on howler populations. Vegetation composition and structure may be strongly related to patch size, shape and isolation and hence, the influence of vegetation on howlers should be evaluated through designs that allow discrimination between the effects of habitat spatial patterns and those of vegetation per se. We should do this with several howler species, in different habitat types, and in landscapes with different levels of fragmentation.

Second, regarding the endogenous threatening processes, evidence for how the distribution and population structure of howlers in patches are being affected by changes in their biology, behavior and interactions with other species is vague. For instance, additional studies are needed to assess to what extent increases in physiological stress of individuals inhabiting small patches affects their health (e.g. parasite incidence) and population persistence. Similarly, in the future, it will be important to conduct long-term studies on population genetics to evaluate the possibility that a loss of genetic diversity has already occurred in fragments. Additionally, the impact of EIDs must be investigated more thoroughly. In particular, we need to improve our measures of disease presence in natural and modified habitats. We also need to develop models to predict how host–parasite dynamics will change in response to climate change, and how will this affect the survival of howler populations.

Finally, it is important to highlight that the information presented in this article comes almost exclusively from four (*A. caraya*, *A. palliata*, *A. pigra* and *A. seniculus*) of the ten species of howlers currently recognized [Cortés-Ortiz et al., 2003], and that virtually nothing is known about the effects of habitat fragmentation on *A. belzebul*, *A. coibensis*, *A. guariba*, *A. macconelli*, *A. nigerrima* and *A. sara*. As some of these species inhabit highly disturbed areas in South America—like *A. guariba* in Brazilian Atlantic forests—in the short-term research efforts must be directed toward assessments of the current status of their habitats, population dynamics and behavioral ecology. Additionally, future studies should assess inter-specific differences in species' responses to habitat loss and fragmentation. As howler species differ in group size and composition [Bicca-Marques, 2003; Chapman & Balcomb, 1998; Crockett & Eisenberg, 1987] and inhabit different habitats (from tropical wet to tropical dry forests), their responses to habitat alteration are expected to vary [Ewers & Didham, 2006].

ACKNOWLEDGMENTS

REFERENCES

Agoramoorthy G, Lohmann R. 1999. Population and conservation status of the black-and-gold howler monkeys, *Alouatta caraya*, along the Rio Riachuelo, Argentina. Neotrop Primates 7:43–44.

Agostini I, Holzmann I, Di Bitetti MS. 2008. Infant hybrids in a newly formed mixed-species group of howler monkeys (*Alouatta guariba clamitans* and *Alouatta caraya*) in northeastern Argentina. Primates 49:304–307.

Aguilar-Cucurachi MS, Canales-Espinosa D, Paéz-Rodríguez M. 2007. Parásitos gastrointestinales en mono aullador (*Alouatta palliata*) en la región de Los Tuxtlas, Veracruz, México. In: Bicca-Marques JC, editor. A primatologia no Brasil, Vol. 10. Porto Alegre, RS: Sociedade Brasileira de Primatologia. p 225–237.

Andrén H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportion of suitable habitat: a review. Oikos 71:340–346.

Anzures-Dadda A, Manson RH. 2007. Patch- and landscape-scale effects on howler monkey distribution and abundance in rainforest fragments. Anim Conserv 10:69–76.

Arroyo-Rodríguez V, Asensio N, Cristóbal-Azkarate J. 2008b. Demography, life history and migrations in a Mexican mantled howler group in a rainforest fragment. Am J Primatol 70:114–188.

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 habitat fragmentation from the primates' prespective. Int J Primatol 30:497–514.

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

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.

Asensio N, Arroyo-Rodríguez V, Cristóbal-Azkarate J. 2007a. Feeding encounters between howler monkeys and white-nosed coatis at Los Tuxtlas, Mexico. J Trop Ecol 23:253–255.

Asensio N, Arroyo-Rodríguez V, Dunn JC, Cristóbal-Azkarate J. 2009. Conservation value of landscape supplementation for howler monkeys living in forest patches. Biotropica, in press. DOI: 10.1111/j.1744-7429.2009.00533.x.

Asensio N, Cristóbal-Azkarate J, Dias PAD, Veà JJ, Rodríguez-Luna E. 2007b. Foraging habits of Alouatta palliata mexicana in three forest fragments. Folia Primatol 78:141–153.

Aureli F, Schaffner CM, Boesch C, Bearder SK, Call J, Chapman CA, Connor RC, Di Fiore A, Dunbar RIM, Henzi SP, Holekamp KE, Korstjens AH, Layton RH, Lee PC, Lehman J, Manson JH, Ramos-Fernandez G, Strier KB, van Schaik CP. 2008. Fission-fusion dynamics. Curr Anthropol 49:627–654.

Behie AM, Pavelka M. 2005. The short-term effects of a hurricane on the diet and activity of black howlers (Alouatta pigra) in Monkey River, Belize. Folia Primatol 76:1–9.

Bicca-Marques JC. 2003. How do howler monkeys cope with habitat fragmentation? In: Marsh LK, editor. Primates in fragments: ecology and conservation. New York: Kluwer Academics/Plenum Publishers. p 283–303.

Bicca-Marques JC, Calegaro-Marques C. 1994. Exotic plant species can serve as staple food sources for wild howler populations. Folia Primatol 63:209–211.

Boinski S, Garber PA. 2000. On the move: how and why animals travel in groups. Chicago: University of Chicago Press.

Braza F, Alvarez F, Azcarate T. 1981. Behaviour of the red howler monkey (Alouatta seniculus) in the Llanos of Venezuela. Primates 22:459–473.

Camargo CC, Ferrari SF. 2007. Interactions between tayras (Eira barbara) and red-handed howlers (Alouatta belzebul) in eastern Amazonia. Primates 48:147–150.

Chapman CA, Balcomb SR. 1998. Population characteristics of howlers: ecological conditions or group history. Int J Primatol 19:385–403.

Chapman CA, Lawes MJ, Naughton-Treves L, Gillespie T. 2003. Primate survival in community-owned forest fragments: are metapopulation models useful amidst intensive use? In: Marsh LK, editor. Primates in fragments: ecology and conservation. New York: Kluwer Academic/Plenum Publishers. p 63–78.

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

Chapman CA, Saj TL, Snaith TV. 2007. Temporal dynamics of nutrition, parasitism, and stress in colobus monkeys: implications for population regulation and conservation. Am J Phys Anthropol 134:240–250.

Chapman CA, Wasserman MD, Gillespie TR, Speirs ML, Lawes MJ, Saj TL, Ziegler TE. 2006. Do food availability, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? Am J Phys Anthropol 131:525–534.

Chiarello AG. 2003. Primates of the Brazilian Atlantic forest: the influence of forest fragmentation on survival. In: Marsh LK, editor. Primates in fragments: ecology and conservation. New York: Kluwer Academic/Plenium Publishers. p 99–121.

Chiarello AG, Galetti M. 1994. Conservation of the brown howler monkey in south-east Brazil. Oryx 28:37–42.

Chiarello AG, de Melo FR. 2001. Primate population densities and sizes in Atlantic forest remnants of northern Espírito Santo, Brazil. Int J Primatol 22:379–396.

Clarke MR, Collins AD, Zucker EL. 2002a. Responses to deforestation in a group of mantled howler (Alouatta palliata) in Costa Rica. Int J Primatol 23:365–381.

Clarke MR, Crockett CM, Zucker EL, Zaldivar M. 2002b. Mantled howler population of Hacienda La Pacifica, Costa Rica, between 1991 and 1998: effects of deforestation. Am J Primatol 56:155–163.

Clarke MR, Glander KE. 2004. Adult migration patterns of the mantled howlers of La Pacifica. Am J Primatol 62:87.

Clarke MR, Zucker EL. 1994. Survey of the howling monkey population of La Pacifica: a seven-year follow-up. Int J Primatol 15:29–41.

Cortés-Ortiz L, Bermingham E, Rico C, Rodríguez-Luna E, Sampaio I, Ruiz-García M. 2003. Molecular systematics and biogeography of the Neotropical monkey genus, Alouatta. Mol Phyl Evol 26:64–81.

Cowlishaw G, Dunbar R. 2000. Primate Conservation Biology. Chicago, IL: The University of Chicago Press.

Cristóbal-Azkarate J, Arroyo-Rodríguez V. 2007. Diet and activity pattern of howler monkeys (Alouatta palliate) in Los Tuxtlas, Mexico: effects of habitat fragmentation and implications for conservation. Am J Primatol 69:1013–1029.

Cristóbal-Azkarate J, Chavira R, Boeck L, Rodríguez-Luna E, Veà J. 2006. Testosterone levels of free-ranging resident mantled howler monkey males in relation to the number and density of solitary males: a test of the challenge hypothesis. Horm Behav 49:261–267.

Cristóbal-Azkarate J, Chavira R, Boeck L, Rodríguez-Luna E, Veà J. 2007. Glucocorticoid levels in free ranging resident mantled howlers: a study of coping strategies. Am J Primatol 69:866–876.

Cristóbal-Azkarate J, Dias PAD, Veà J. 2004. Causes of intraspecific aggression in Alouatta palliata mexicana: evidence from injuries, demography and habitat. Int J Primatol 25:939–953.

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

Crockett CM. 1998. Conservation biology of the genus Alouatta. Int J Primatol 19:549–578.

Crockett CM, Eisenberg JF. 1987. Howlers: variation in group size and demography. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RR, Struhsaker TT, editors. Primate societies. Chicago: Chicago University Press. p 54–68.

Crockett CM, Pope TR. 1993. Consequences of sex differences in dispersal for juvenile red howler monkeys. In: Pereira ME, Fairbanks LA, editors. Juvenile primates: life history, development, and behavior. New York: Oxford University Press. p 104–118.

Crooks KR, Soul ME. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563-566.

DeGamma-Blanchet H, Fedigan LM. 2006. The effects of forest fragment age, isolation, size, habitat type, and water

availability on monkey density in a tropical dry forest. In: Estrada A, Garber P, Pavelka M, Luecke L, editors. New perspectives in the study of Mesoamerican primates: Distribution, ecology, behavior and conservation. New York: Kluwer Academic/Plenium Publishers. p 165–188.

Di Fiore A, Campbell CJ. 2007. The atelines: variation in ecology, behavior, and social organization. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK, editors. Primates in perspective. New York: Oxford University Press. p 155–185.

Dias LG, Strier KB. 2000. Agonistic encounters between muriquis, *Brachiteles arachnoides hypoxanthus* (Primates, Cebidae), and other animals at the Estacão Biológica de Caratinga, Minas Gerais, Brazil. Neotrop Primates 8:138–141.

Dias PAD, Rodríguez-Luna E. 2005. Organización espacial y dominancia social en machos *Alouatta palliata* en la Isla Agaltepec, Veracruz, México. Univ Ciencia s.i. II:45–53.

Dias PAD, Rodríguez-Luna E. 2006. Seasonal changes in associative behavior and subgrouping patterns of mantled howler monkey males living on an island. Int J Primatol 27:1635–1651.

Duarte-Quiroga A, Estrada A. 2003. Primates as pets in Mexico City: an assessment of the species involved, source of origin, and general aspects of treatment. Am J Primatol 61:53–60.

Dunn JC. 2009. La estrategia de forrajeo de *Alouatta palliata*: variaciones en la dieta y conducta alimenticia asociadas a la disponibilidad de alimentos (tamaño de hábitat y estacionalidad), y los efectos sobre su salud fisiológica. PhD Thesis. Universitat de Barcelona, Barcelona.

Dunn JC, Cristóbal-Azkarate J, Vea J. 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. DOI 10.1002/ajp.20700.

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, Garber P, Pavelka M, Luecke L. 2006. New perspectives in the study of Mesoamerican primates: distribution, ecology, behavior and conservation. New York: Kluwer Academic/Plenum Publishers.

Estrada A, Mendoza A, Castellanos L, Pacheco R, Van Belle S, García Y, Munoz D. 2002. Population of the black howler monkey (*Alouatta pigra*) in a fragmented landscape in Palenque, Chiapas, Mexico. Am J Primatol 58:45–55.

Ewers RM, Didham RK. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev 81:117–142.

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. Ann Rev Ecol Evol Syst 34:487–515.

Food and Agriculture Organization of the United Nations (FAO). 2007. State of the World's forests 2007. Rome: FAO.

Fedigan LM, Rose LM, Avila RM. 1998. Growth of mantled howler groups in a regenerating Costa Rican dry forest. Int J Primatol 19:405–431.

Fischer J, Lindenmayer DB. 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecol Biogeogr 16:265–280.

Fortes VB, Bicca-Marques JC. 2008. Abnormal pelage color in an isolated population of *Alouatta guariba clamitans* Cabrera, 1940, in South Brazil. Int J Primatol 29:717–722.

Garber PA, Estrada A, Pavelka MSM. 2006. New perspectives in the study of Mesoamerican primates: concluding comments and conservation priorities. In: Estrada A, Garber PA, Pavelka M, Luecke L, editors. New perspectives in the study

of Mesoamerican primates: distribution, ecology, behavior and conservation. New York: Kluwer Academic/Plenum Publishers. p 563–584.

García del Valle Y, Estrada A, Espinoza E, Lorenzo C, Naranjo E. 2005. Genética de poblaciones de monos aulladores (*Alouatta pigra*) en hábitat continuo y fragmentado en la selva Lacandona, México: un estudio preliminar. Univ Ciencia s.i. II:55–60.

Gentry AH. 1982. Patterns of Neotropical plant species diversity. Evol Biol 15:1–85.

Gilbert KA. 1994. Endoparasitic infection in red howling monkeys (*Alouatta seniculus*) in the central Amazonian basin: a cost of sociality? PhD Dissertation. Rutgers University, New Brunswick.

Gilbert KA. 2003. Primates and fragmentation of the Amazon forest. In: Marsh LK, editor. Primates in fragments: ecology and conservation. New York: Kluwer Academic/Plenum Press. p 145–157.

Gillespie TR, Chapman TA. 2001. Determinants of group size in the red colobus monkey (*Procolobus badius*): an evaluation of the generality of the ecological-constraints model. Behav Ecol Sociobiol 50:329–338.

Gilpin ME, Soulé ME. 1986. Minimum viable populations: processes of species extinctions. In: Soulé ME, editor. Conservation biology. The science of scarcity and diversity. Sunderland, Massachusetts: Sinauer Associates. p 19–34.

Goffard DA, Arroyo-Rodríguez V, Aguirre LF. 2008. Poblaciones de monos aulladores (*Alouatta sara*) en cuatro sitios de Santa Cruz, Bolivia. Mastozool Neotrop 15:285–295.

Hanski I. 1999. Metapopulation ecology. New York: Oxford University Press.

Honess PE, Marin CM. 2006. Behavioral and physiological aspects of stress and aggression in nonhuman primates. Neurosci Biobehav Rev 30:390–412.

IUCN. 2009. IUCN red list of threatened species. www.redlist.org.

James RA, Leberg PL, Quattro JM, Vrijenhoek RC. 1997. Genetic diversity in black howler monkeys (*Alouatta pigra*) from Belize. Am J Phys Anthropol 102:329–336.

Juan S, Estrada A, Coates-Estrada R. 2000. Contrastes y similitudes en el uso de recursos y patrón diarios de actividades en tropas de monos aulladores (*Alouatta palliata*) en fragmentos de selva en Los Tuxtlas, México. Neotrop Primates 8:131–135.

Jump AS, Marchant R, Peñuelas J. 2009. Environmental change and the option value of genetic diversity. Trends Plant Sci 14:51–58.

Kowalewski MM, Zunino GE. 1999. Impact of deforestation on a population of *Alouatta caraya* in northern Argentina. Folia Primatol 70:163–166

Laurance WF, Laurance SG, Ferreira LV, Rankin-de Merona JM, Gascon C, Lovejoy TE. 1997. Biomasa collapse in Amazonian forest fragments. Science 278:1117–1118.

Laurance WF, Ferreira LV, Rankin-de Merona JM, Laurance SG, Hutchings R, Lovejoy TE. 1998. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. Conserv Biol 12:460–464.

López GO, Terborgh J, Ceballos N. 2005. Food selection by a hyperdense population of red howler monkeys (*Alouatta seniculus*). J Trop Ecol 21:445–450.

Lovejoy TE, Bierregaard Jr RO, Rylands AB, Malcolm JR, Quintela CE, Harper LH, Brown KS, Powell AH, Schubart HOR, Hays MB. 1986. Edge and other effects of isolation on Amazon forest fragments. In: Soulé ME, editor. Conservation biology. The science of scarcity and diversity. Sunderland, Massachusetts: Sinauer Associates. p 257–285.

Ludwig G, Aguiar LM, Miranda JMD, Teixeira GM, Svoboda WK, Malanski LS, Shiozawa MM, Hilst CLS, Navarro IT, Passos FC. 2007. Cougar predation on black-and-gold howlers on Mutum Island, Southern Brazil. Int J Primatol 28:39–46.

MacArthur RH, Wilson EO. 1967. The theory of island biogeography. Princeton, NY: Princeton University Press.

Malgrem LA, Brush AH. 1978. Isoenzymes and plasma proteins in eight groups of golden mantled howling monkeys (*Allouatta palliata*). In: Chivers DJ, Joysey KA, editors. Recent advances in primatology. New York: New York Academic Press. p 283–285.

Mandujano S, Escobedo-Morales LA. 2008. Population viability analysis of howler monkeys (*Alouatta palliata mexicana*) in a highly fragmented landscape in Los Tuxtlas, Mexico. Trop Conserv Sci 1:43–62.

Mandujano S, Estrada A. 2005. Detección de umbrales de área y distancia de aislamiento para la ocupación de fragmentos de selva por monos aulladores, *Alouatta palliata*, en Los Tuxtlas, México. Univ Ciencia s.i. II:11–21.

Mandujano S, Escobedo-Morales LA, Palacios-Silva R. 2004. Brief report of movements of *Alouatta palliata* among fragments in Los Tuxtlas. Neotrop Primates 12:126–131.

Mandujano S, Escobedo-Morales LA, Palacios-Silva R, Arroyo-Rodríguez V, Rodríguez-Toledo EM. 2006. A metapopulation approach to conserving the howler monkey in a highly fragmented landscape in Los Tuxtlas, Mexico. In: Estrada A, Garber PA, Pavelka M, Luecke L, editors. New perspectives in the study of Mesoamerican primates: distribution, ecology, behavior and conservation. New York: Kluwer Academic/Plenium Publishers. p 513–538.

Marsh LK. 2003. Primates in fragments: ecology and conservation. New York: Kluwer Academic/Plenum Publishers.

Marsh LK, Loiselle B. 2003. Recruitment of black howler fruit trees in fragmented forests of northern Belize. Int J Primatol 24:65–85.

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.

May SA, Norton TW. 1996. Influence of fragmentation and disturbance on the potential impact of feral predators on native fauna in Australian forest ecosystems. Wild Res 23:387–400.

Mbora DN, Meikle DB. 2004. Forest fragmentation and the distribution, abundance and conservation of the Tana river red colobus (*Procolobus rufomitratus*). Biol Conserv 118:67–77.

McCann C, Williams-Guillén K, Koontz FW, Roque-Espinoza AA, Martínez-Sánchez JC, Koontz C. 2003. Shade coffee plantations as wildlife refuge for mantled howler monkeys (*Alouatta palliata*) in Nicaragua. In: Marsh LK, editor. Primates in fragments: ecology and conservation. New York: Kluwer Academics/Plenum Publishers. p 321–341.

Milton K. 1998. Physiological ecology of howlers (*Alouatta*): energetic and digestive considerations and comparison with the Colobinae. Int J Primatol 19:513–547.

Nascimento FF, Bonvicino CR, Seuanez HN. 2007. Population genetic studies of *Alouatta caraya* (Alouattinae, Primates): inferences on geographic distribution and ecology. Am J Primatol 69:1093–1104.

Nunn CL, Altizer S. 2006. Infectious diseases in primates. New York: Oxford University Press.

Oates JF. 1996. African primates status survey and conservation action plan. IUCN/SSC Primate Specialist Group.

Oklander LI, Kowalewski MM, Zunino GE, Corach D. 2006. Genetic consequences of habitat fragmentation in *Alouatta caraya*. Int J Primatol 27:334.

Pavelka MSM, Brusselers OT, Nowak D, Behie AM. 2003. Population reduction and social disorganization in *Alouatta pigra* following a hurricane. Int J Primatol 24:1037–1055.

Peres CA. 1990. Effects of hunting on western Amazonian primate communities. Biol Conserv 54:47–59.

Peres CA. 2000. Evaluating the impact and sustainability of subsistence hunting at multiple Amazonian Forest Sites. In: Robinson JG, Bennett EL, editors. Hunting for sustainability in tropical forests. New York: Columbia University Press. p 31–56.

Peres CA. 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. Conserv Biol 15:1490–1505.

Pinto ACB, Azevedo-Ramos C, de Carvalho Jr O. 2003. Activity patterns and diet of the howler monkey *Alouatta belzebul* in areas of logged and unlogged forest in Eastern Amazonia. Anim Biodiv Conserv 26:39–49.

Pope TR. 1992. The influence of dispersal patterns and mating system on genetic differentiation within and between populations of the red howler monkey (*Alouatta seniculus*). Evolution 46:1112–1128.

Pozo-Montuy G, Serio-Silva JC. 2007. Movement and resource use by a group of *Alouatta pigra* in a forest fragment in Balancán, Mexico. Primates 48:102–107.

Pulliam HR. 1988. Sources, sinks, and population regulation. Am Nat 132:652–661.

Rivera A, Calmé S. 2006. Forest fragmentation and its effects on the feeding ecology of black howlers (*Alouatta pigra*) from the Calakmul area is Mexico. In: Estrada A, Garber PA, Pavelka M, Luecke L, editors. New perspectives in the study of Mesoamerican primates: distribution, ecology, behavior and conservation. New York: Kluwer Academic/Plenum Publishers. p 189–213.

Rodríguez-Luna E, Domínguez-Domínguez LE, Morales-Mavil J, Martinez-Morales M. 2003. Foraging strategy changes in *Alouatta palliata Mexicana* trop released on an island. In: Marsh LK, editor. Primates in fragments: ecology and conservation. New York: Kluwer Academics/Plenum Publishers. p 229–250.

Rosales-Meda M, Estrada A, López JE. 2007. Demographic survey of black howler monkey (*Alouatta pigra*) in the Lachuá Eco-Region in Alta Verapaz, Guatemala. Am J Primatol 70:231–237.

Rose LJ, Perry S, Panger MA, Jack K, Manson JH, Gros-Louis J, Mackinnon KC, Vogel E. 2003. Interspecific interactions between *Cebus capuchinus* and other species: data from three Costa Rican sites. Int J Primatol 24:759–794.

Rudran R, Fernández-Duque E. 2003. Demographic changes over thirty years in a red howler population in Venezuela. Int J Primatol 24:925–947.

Santa-Cruz ACM, Borda JT, Patiño EM, Gómez L, Zunino GE. 2000. Habitat fragmentation and parasitism in howler monkeys (*Alouatta caraya*). Neotrop Primates 8:146–150.

Saunders DA, Hobbs RJ, Margules CR. 1991. Biological consequences of ecosystem fragmentation: a review. Conserv Biol 5:18–32.

Schwarzkopf L, Rylands AB. 1989. Primate species richness in relation to habitat structure in Amazonian rainforest fragments. Biol Conserv 48:1–12.

Stevenson PR, Quinõnes MJ, Ahumada JA. 2000. Influence of fruit availability on ecological overlap among four neotropical primates at Tinigua National Park, Colombia. Biotropica 32:533–544.

Stuart MD, Greenspan LL, Glander KE, Clarke M. 1990. A coprological survey of parasites of wild mantled howling monkeys, *Alouatta palliata palliata*. J Wildl Dis 26:547–549.

Terborgh J, López L, Nuñez P, Rao M, Shahabuddin G, Orihuela G, Riveros M, Ascanio R, Adler GH, Lambert TD, Balbas L. 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923–1926.

Trejo-Macías G, Estrada A, Cabrera MA. 2007. Survey of helminth parasites in populations of *Alouatta palliata mexicana* and *A. pigra* in continuous and in fragmented habitat in southern Mexico. Int J Primatol 28:931–945.

Van Belle S, Estrada A. 2006. Demographic features of *Alouatta pigra* populations in extensive and fragmented forest. In: Estrada A, Garber PA, Pavelka M, Luecke L, editors. New perspectives in the study of Mesoamerican primates: distribution, ecology, behavior and conservation. New York: Kluwer Academic/Plenum Publishers. p 121–142.

Vitazkova SK. 2009. Overview of parasites infecting howler monkeys, *Alouatta* sp., and potential consequences of human-howler interactions. In: Huffman MA, Chapman CA, editors. Primate parasite ecology: the dynamics and study of host-parasite relationships. New York: Cambridge University Press. p 371–385.

Vitazkova SK, Wade S. 2007. Effects of ecology on the gastrointestinal parasites of *Alouatta pigra*. Int J Primatol 28:1327–1343.

Watts ES, Rico-Gray V, Chan C. 1986. Monkeys if the Yucatan peninsula, Mexico: preliminary survey of their distribution and status. Primate Conserv 7:17–22.

Winkler LA, Zhang X, Ferrell R, Wagner R, Dahl J, Peter G, Sohn R. 2004. Geographic microsatellite variability in Central American howling monkeys. Int J Primatol 25:197–210.

Zunino GE, Gonzalez V, Kowalewski MM, Bravo SP. 2001. *Alouatta caraya*. Relations among habitat, density and social organization. Primate Report 61:37–46.

Zunino GE, Kowalewski MM, Oklander LI, González V. 2007. Habitat fragmentation and population size of the black and gold howler monkey (*Alouatta caraya*) in a semideci duous forest in northern Argentina. Am J Primatol 69:966–975.