

The relative impact of forest patch and landscape attributes on black howler monkey populations in the fragmented Lacandona rainforest, Mexico

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Abstract Land-use change is forcing many animal populations to inhabit forest patches in which different processes can threaten their survival. Some threatening processes are mainly related to forest patch characteristics, but others depend principally on the landscape spatial context. Thus, the impact of both patch and landscape spatial attributes needs to be assessed to have a better understanding of the habitat spatial attributes that constraint the maintenance of populations in fragmented landscapes. Here, we evaluated the relative effect of three patch-scale (i.e., patch size, shape, and isolation) and five landscape-scale metrics (i.e., forest cover, fragmentation, edge density, mean inter-patch isolation distance, and matrix permeability) on population composition and structure of black howler monkeys (*Alouatta pigra*) in

the Lacandona rainforest, Mexico. We measured the landscape-scale metrics at two spatial scales: within 100 and 500 ha landscapes. Our findings revealed that howler monkeys were more strongly affected by local-scale metrics. Smaller and more isolated forest patches showed a lower number of individuals but at higher densities. Population density also tended to be positively associated to matrices with higher proportion of secondary forests and arboreal crops (i.e. with greater permeability), most probably because these matrices can offer supplementary foods. The immature-to-female ratio also increased with matrix permeability, shape complexity, and edge density; habitat characteristics that can increase landscape connectivity and sources availability. The prevention of habitat loss and isolation, and the increment of matrix permeability are therefore needed for the conservation of this endangered Neotropical mammal.

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Introduction

Because of continued deforestation and forest fragmentation in the tropics (FAO 2011), an increasingly higher number of animal populations are forced to inhabit human-dominated landscapes (Peres et al. 2006; Gardner et al. 2009). Within these landscapes, several

processes acting at different spatial scales can threaten species' maintenance (Ewers and Didham 2006; Fischer and Lindenmayer 2007; Gardner et al. 2009). For example, for large canopy-dwelling mammals, such as many primates, canopy modifications related to changes in forest patch spatial attributes (e.g., patch size, shape and isolation) can negatively affect habitat quality and resource availability (Arroyo-Rodríguez and Mandujano 2006). However, at a larger spatial scale, changes in the landscape spatial configuration can alter metapopulation dynamics (Hanski 1999), source-sink dynamics (Pulliam 1988), and other landscape processes, such as landscape complementation and supplementation (Dunning et al. 1992). Therefore, a multi-scale approach is required in fragmentation studies to identify the patch and/or landscape spatial attributes with stronger influence on the maintenance of animal populations in human-dominated landscapes (McGarigal and Cushman 2002; Fahrig 2003; Arroyo-Rodríguez and Mandujano 2009; Thornton et al. 2011).

This approach is particularly needed to improve management and conservation policies (Sutherland et al. 2004; Lindenmayer and Fischer 2007). For example, if species/populations are particularly vulnerable to changes in forest cover in the landscape, conservation plans should prioritize the creation of large forest reserves and the increment of forest cover in the landscape throughout forest restoration (Fahrig 1999). However, if species/populations are negatively affected by increasing fragmentation degree and/or by the loss of landscape connectivity, management plans should be focused on the creation of landscape corridors (Fahrig 1999). Therefore, conservation efforts may be misguided unless we assess the relative impact of different patch and landscape characteristics on the persistence of species in fragmented tropical landscapes (Fahrig 2003; Gardner et al. 2009; Chazdon et al. 2011).

Forest fragmentation can result in different changes in landscape configuration (e.g., increase in number of forest patches, decrease in patch sizes, and increase in forest edge density; Fahrig 2003). Yet fragmentation studies have been focused on testing the impact of patch-scale metrics (mainly patch size and isolation), without evaluating (nor controlling) the effects of landscape-scale characteristics (Fahrig 2003). This caveat is particularly evident in fragmentation studies with primates (Arroyo-Rodríguez et al. 2013). Thus, although arboreal primates can be particularly vulnerable to changes in both forest patch and landscape attributes

(Chapman and Peres 2001; Harcourt and Doherty 2005; Estrada et al. 2006; Anzures-Dadda and Manson 2007), we likely have inaccurate and biased assessments of the effects of habitat configuration on primates (Arroyo-Rodríguez et al. 2013). This is particularly evident in howler monkeys (*Alouatta* spp.), an exclusively arboreal primate. Although evidence indicates that howler monkeys can be negatively affected by high levels of habitat loss and degradation (Arroyo-Rodríguez and Dias 2009), no study to date has simultaneously tested the effect of patch and landscape attributes to identify which habitat spatial attributes have the greatest influence on howler monkey populations.

The main objective of our study was to evaluate the relative effect of three patch-scale (i.e., patch size, shape, and isolation) and five landscape-scale metrics (i.e., forest cover, fragmentation, edge density, mean inter-patch isolation distance, and matrix permeability) on population composition and structure of black howler monkeys (*Alouatta pigra*) in the Lacandona rainforest, Mexico. Because species responses to habitat configuration can be scale dependent (primates: Anzures-Dadda and Manson 2007; birds: Smith et al. 2011; terrestrial mammals: Thornton et al. 2011), we measured the landscape-scale metrics at two spatial scales; within 100 and 500 ha landscapes. This information is particularly valuable to improve our understanding of the spatial extent to which management plans should be designed and implemented (Smith et al. 2011). We hypothesized that *A. pigra* populations will be affected by both forest patch and landscape metrics (Anzures-Dadda and Manson 2007; Arroyo-Rodríguez and Días 2009); however, because this species have a relatively small home range size (e.g., 9.6–18.7 ha: Ostro et al. 1999; 15.3 ha: Gavazzi et al. 2008), have a relatively low vagility, and largely depend on local habitat characteristics (e.g., for feeding, locomotion, and refuge; Alexander et al. 2006; Rivera and Calmé 2006; Arroyo-Rodríguez et al. 2007), this species will be more strongly affected by local-scale metrics, such as forest patch metrics and 100 ha landscape metrics.

Methods

Study species

The black howler monkey has a restricted distribution range, from southeastern Mexico, to Belize and

northern and central Guatemala (Rylands et al. 2006). Reported densities for *A. pigra* range from 0.1 to 0.4 ind./ha in continuous forests, and from 1.1 to 1.2 ind./ha in fragmented landscapes (Van Belle and Estrada 2006). This primate lives in sex-mixed groups, usually from 2 to 10 individuals (Van Belle and Estrada 2006). Their diet consists mainly of mature fruits and young leaves (e.g., Bicca-Marquez 2003; Rivera and Calmé 2006). The species is classified as ‘Endangered’ in the IUCN red list since 2003 (Marsh et al. 2008).

Study area

The study area is located in the Lacandona rainforest, Mexico ($16^{\circ}05'58''N$, $90^{\circ}52'36''W$), in two areas separated by the Lacantún river: the Marqués de Comillas region (MCR, eastern side of the river) and the Montes Azules Biosphere Reserve (MABR, western side) (Fig. 1). The protected area of MABR was created in 1978, and consists of approximately

300,000 ha of undisturbed forest, encompassing the largest remnant of tropical rainforest in Mexico (Dirzo 1994). However, this area is highly threatened by land-use changes in the reserve’s boundaries (e.g., MCR; Mora 2008), and is nowadays considered a main conservation concern by the Mexican government (Arriaga et al. 2000). The climate is hot and humid, with annual precipitation averaging 2,500–3,500 mm, and average monthly temperatures of 24–26 °C.

We selected 20 forest patches (from 3 to 92 ha) in MCR, and three areas within MABR separated by at least 4 km among each other and located at least 1 km from the MABR edge (Fig. 1). With recent SPOT 5 satellite images (March 2011) and the GIS GRASS program (GRASS 2011), we characterized the spatial configuration of the landscapes surrounding each site at two spatial scales: within a 100 ha buffer and within a 500 ha buffer from the center of each sampling site (i.e., 100 and 500 ha landscapes, respectively; Fig. 1). We used a supervised classification with GIS SPRING (Camara et al. 1996) considering six land cover types:

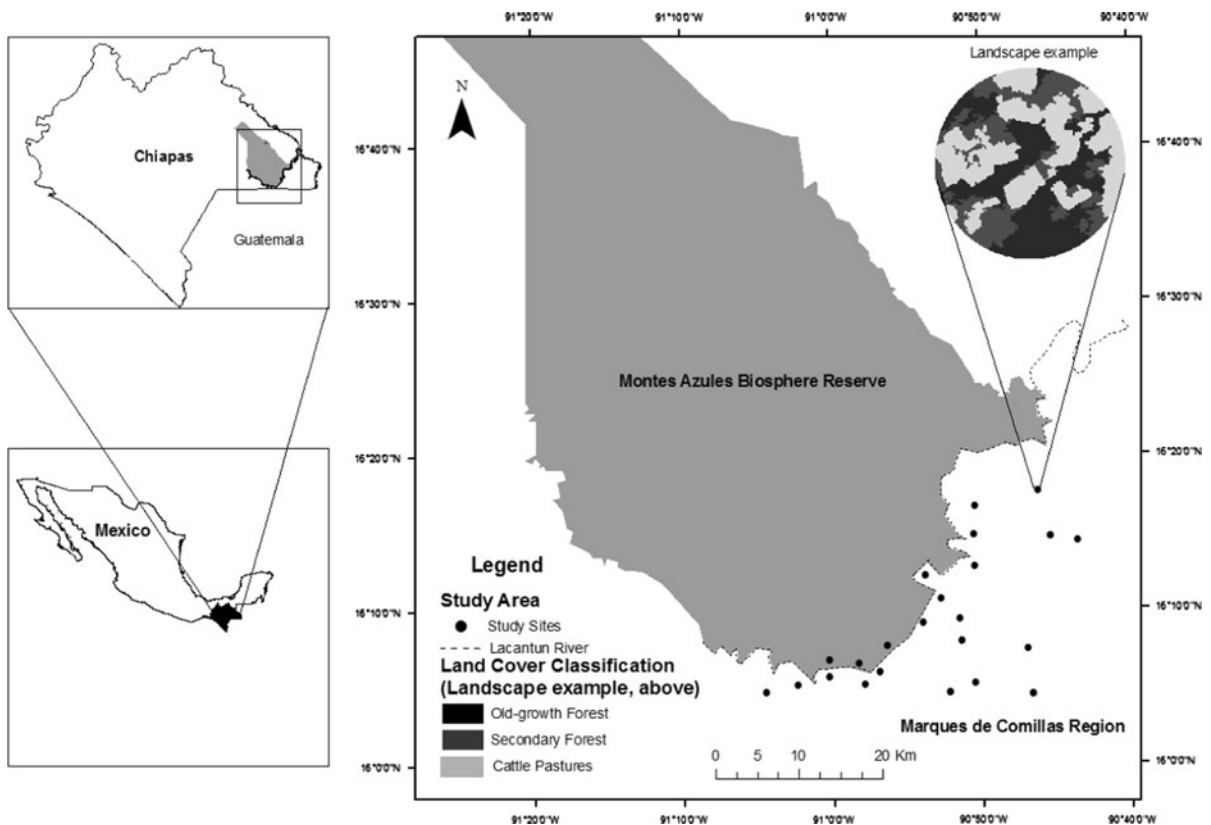


Fig. 1 Location of the study sites in the Lacandona rainforest, southeastern Mexico. We described the landscape spatial pattern of all sites as showed in the example located in the *up right side*

old-growth forests, secondary forests, arboreal crops (i.e., palm and rubber plantations), shrub crop (i.e., corn and bean plantations), cattle pastures, and human settlements. Overall classification accuracy was 77 %.

Habitat configuration

We estimated the size, shape and isolation (i.e., Euclidian distance to the nearest neighbor forest patch) of all patches. Patch shape was estimated with the shape index (Forman and Godron 1986): $SI = P/\sqrt{A\pi}$, where P and A are the patch perimeter and area measured in meters, respectively. The higher the SI values, the higher the shape complexity (perfect circle, $SI = 1.0$). Within both the 100 and 500 ha landscapes, we estimated the percentage of remaining forest cover, fragmentation level (i.e., number of forest patches), edge density (i.e., length of all old-growth forest borders within the landscape, expressed as meters per hectare), mean inter-patch isolation distance (i.e., mean nearest-neighbor distance from all patches to the focal patch in the landscape), and matrix permeability. Matrix permeability was estimated using an index that relates the percentage of each land cover type within the landscape matrix to their relative permeability. The relative permeability was ranked, based on the vegetation structure of each land cover type in the matrix, on a five-point scale: 1 (human settlements, lowest permeability), 2 (cattle pastures), 3 (shrub crops), 4 (arboreal crops), and 5 (secondary forests, highest permeability). Then, the permeability index was calculated as: $PI = [(1 \times \% \text{ human settlements}) + (2 \times \% \text{ cattle pastures}) + (3 \times \% \text{ shrub crops}) + (4 \times \% \text{ arboreal crops}) + (5 \times \% \text{ secondary forests})]/5$. PI can thus vary between 20 (100 % of the matrix composed by human settlements) and 100 (100 % of the matrix composed by secondary forests).

Primate surveys

Surveys were conducted between March and September 2011 in the 23 sites following methods used in other survey research of *A. pigra* (e.g., Van Belle and Estrada 2006; Rosales-Meda et al. 2007). At least two people walked slowly (1 km/h) around and inside each patch and control site at the time of the day when howler monkeys are usually more active, from 6:00 to 12:00 h, and from 16:00 to 18:00 h. The complete area was

walked continuously until it was assumed all groups in a given area were sighted. Long distance vocalization of *A. pigra* helped to locate the groups within the sites.

In addition, we interviewed the local people who lived and worked in the proximity of the sites about the presence or absence of primates in the area. If after several days no monkeys were heard in a patch, and the local people reported that the patch is not occupied by monkeys, it was considered empty. Each site was surveyed only once, but search time was adjusted to site size, with two consecutive days being dedicated to survey small patches (<10 ha), 3 days in medium-sized patches (10–50 ha), 4 days in larger patches (50–100 ha), and 5 days in control sites. Surveys within the control sites were restricted to an area of approximately 100 ha. Once visual contact was established, the geographical position of the group or that of solitary individuals was recorded with a GPS, and we made a count of all individuals in the group. Groups were thus recognized by their location and composition, including the estimated age-sex classes and natural markings on each group member. Individuals were classified into the following categories: adults (males and females), juveniles (males and females), and infants (Rosales-Meda et al. 2007).

Statistical analysis

We first compared the composition and structure of populations between forest patches ($n = 20$) and control sites ($n = 3$) with U-Mann–Whitney tests. We evaluated the following response variables: number of groups, number of individuals, population density (i.e., number of individuals per hectare), number of adult males and females, number of juvenile males and females, and number of infants. We also evaluated differences in the immature-to-female ratio as an indicator of reproductive success. Population density was estimated by dividing the number of recorded individuals by the survey area. In control sites, density was estimated considering a survey area of 100 ha.

To identify the forest patch and landscape attributes with stronger influence on population composition and structure we used multiple linear regressions analyses (Crawley 2002). To reduce the probability of incorrectly reject true null hypotheses (Type I statistical error) related to multiple testing, we reduced the number of response variables by discarding those that were redundant. In particular, we evaluated the

number of individuals (which was significantly correlated to the number of groups, number of adult males and females, number of juveniles and number of infants; $p < 0.001$ in all cases; Table 1), population density, and the immature-to-female ratio. In all cases, control sites were included in the regression models, considering them as having 100 ha, zero isolation, circular shape ($SI = 1.0$), 100 % forest cover, zero fragmentation, zero edge density, and maximum matrix permeability ($PI = 100$).

To identify the factors with stronger influence on each response variable we used REVS (Regression with Empirical Variable Selection); a new approach that has proven to be more effective than full, stepwise and all-subsets models (Goodenough et al. 2012). REVS uses sophisticated branch-and-bound all-subsets regression to quantify the amount of empirical support for each factor. Regression models are created and compared post hoc with R^2 and Akaike Information Criterion (AIC) values. Delta (Δ) AIC values are calculated for each model as $AIC_i - AIC_{min}$; where AIC_{min} is the AIC value of the model that has the lowest AIC score from a series of candidate models. Models with $\Delta AIC < 2$ can be considered with strong support (highly feasible), whereas models with $\Delta AIC > 10$ have essentially no support (Burnham and Anderson 2002). REVSs were run in R with the script published by Goodenough et al. (2012) which uses the R library LEAPS (Lumley 2009). See Goodenough et al. (2012) for further details.

To ensure our results were not overly dependent on statistical artifacts (Smith et al. 2009), the best REVS model was compared with the best stepwise model following the protocol described by Goodenough et al. (2012). For each model, we calculated the adjusted R^2 , AIC, ΔAIC and p values. We also assessed the predictive accuracy of each model by estimating the mean square prediction error with leave-one-out cross-validation with the R library BOOT. The leave-one-out cross-validation involves using a single observation from the original sample as the test (or validation) data, and the remaining observations as the training data. This is repeated such that each observation in the sample is used once as the validation data, and then it is possible to judge the goodness of the prediction of each model by estimating its average square prediction error. To assess the collinearity between the predictor variables and multivariate models, we also checked each predictor’s variance inflation factor (Neter et al. 1990). Variance inflation factors (VIF) were calculated for each predictor as the inverse of the coefficient of non-determination [$1/(1-R^2)$] for a regression of that predictor on all others. Generally, $VIF > 10$ indicate “severe” collinearity (Neter et al. 1990). Although we also tested full models, we do not include the results of these models because in all cases they had severe multicollinearity problems, lower model fit (i.e., smaller R^2 values), and ΔAIC values higher than 14.8 in all cases.

Table 1 Correlations between different population characteristics of howler monkeys (*Alouatta pigra*) in the Lacandona rainforest, Mexico

	No. ind.	Density	Adult M	Adult F	Juv. M	Juv. F	Infants	Immatures	I/F ratio
No. groups	0.83***	0.30 n.s.	0.86***	0.81***	0.65**	0.51*	0.64**	0.74**	0.15n.s.
No. ind.		0.48*	0.95***	0.97***	0.85***	0.73***	0.78***	0.97***	0.17n.s.
Density			0.49*	0.43*	0.34 n.s.	0.46 n.s.	0.43*	0.49*	0.21n.s.
Adult M				0.87***	0.83***	0.63**	0.67***	0.89***	0.23n.s.
Adult F					0.76***	0.72***	0.77***	0.92***	-0.00n.s.
Juv. M						0.41 n.s.	0.57**	0.87***	0.24n.s.
Juv. F							0.48*	0.76***	0.26n.s.
Infants								0.79***	0.14n.s.
Immatures									0.27n.s.

We evaluated the number of groups, total number of individuals, population density, number of adult males and females, number of juveniles males and females, number of infants, number of immatures (considering both juveniles and infants), and the immature-to-female ratio

In all cases, we indicate Pearson’s correlation coefficients and significance levels (* $p < 0.05$; ** $p < 0.01$, *** $p < 0.001$; n.s. $p > 0.05$)

Results

Population composition and structure

Overall, all control sites were occupied by howler monkeys, but we did not find monkeys in 4 out of 20 forest patches. Considering the sites occupied by howler monkeys ($n = 19$), a total of 225 individuals were recorded, belonging to 41 mixed-sex groups, 1 male group, 1 female group and two solitary males. In general, the composition and structure of populations did not differ between forest patches and sites within the continuous forest, but the density of individuals was five times higher in forests patches (mean \pm SD, 0.5 ± 0.4 ind./ha) than within the continuous forest (0.1 ± 0.01 ind./ha) (U-Mann–Whitney test, $Z = 2.68$, $p = 0.007$; Table 2).

Spatial attributes impacting population structure and composition

In general, REVS models included a similar set of factors than the stepwise models, and revealed that howler monkeys' populations responded principally to changes in patch-scale metrics and 100-ha landscape metrics (Table 3). When analyzing the immature-to-female ratio, the best REVS and the best stepwise model were synonymous. Nevertheless, when analyzing the number and density of individuals, the REVS model demonstrated to be more effective (with greater predictive accuracy) than the stepwise model. In fact, the best stepwise model for density of individuals included several collinear

factors (VIF >10), which resulted in a higher p value (Table 3).

Both the REVS and stepwise models indicated that the number of individuals was negatively and significantly related to inter-patch isolation distances in 100 ha landscapes (Table 3). However, the REVS model showed that edge density in 100 ha landscapes also tended to have a positive effect on the number of individuals ($p = 0.08$), whereas the best stepwise model showed that the number of individuals tended to increase in larger patches ($p = 0.08$; Table 3). Although the predictive accuracy of the best stepwise model was slightly lower than the best REVS model, it showed similar Δ AIC, R^2 and p values (Table 3).

Regarding the density of individuals, the best REVS model indicated that smaller patches located in landscapes with lower inter-path isolation distances, greater matrix permeability, and higher fragmentation level showed a higher density of individuals (Table 3). Nevertheless, the immature-to-female ratio increased in patches with more complex shapes and located in landscapes with greater matrix permeability. This response variable also tended to be positively associated to landscapes with higher edge density, both at the 100 and 500 ha landscape scales ($p = 0.06$ and $p = 0.07$, respectively; Table 3).

Discussion

This paper support the idea that not only patch-scale metrics, but also the landscape spatial context need to considered to have a better understanding of the main

Table 2 Composition and structure of black howler monkey (*Alouatta pigra*) populations in 16 forest patches and three sites within a continuous forest in the Lacandona rainforest, Mexico

	Forest patches	Continuous forest	Z	p
Number of groups	2.8 (1.9)	2.7 (0.6)	-0.45	0.655
Number of individuals	12.1 (9.3)	10.7 (1.2)	-0.73	0.467
Density (ind./ha)	0.5 (0.4)	0.1 (0.0)	2.68	0.007
Number of adult males	3.8 (2.8)	4.3 (1.5)	-0.89	0.371
Number of adult females	4.1 (3.6)	2.7 (0.6)	-0.17	0.867
Number of juvenile males	1.8 (1.8)	2.3 (0.6)	-1.17	0.240
Number of juvenile females	1.6 (1.2)	0.3 (0.6)	1.79	0.074
Number of infants	0.9 (1.0)	0.7 (0.6)	0.28	0.780
Immature-to-female ratio	1.3 (0.7)	1.3 (0.6)	-0.17	0.867

Mean and standard deviations (in parenthesis) are indicated. Differences between habitats were assessed with U-Mann–Whitney tests

Table 3 Habitat spatial attributes with stronger influence on composition and structure of black howler monkey (*Alouatta pigra*) populations in the fragmented Lacandona rainforest, Mexico

Response variable/Model ^a	Parameter	SE	t	p	VIF	AIC	ΔAIC	Adj R ²	p	MSE ^d
Population size										
Best REVS model						99.0	0.00	0.18	0.05	74.8
Intercept	8.55	3.49	2.45	0.02						
Inter-patch distance (100)	−0.01	0.01	−2.53	0.02	1.33					
Edge density (100)	0.10	0.05	1.83	0.08	1.33					
Best stepwise model						99.0	0.00	0.18	0.05	83.0
Intercept	8.56	3.48	2.45	0.02						
Inter-patch distance (100)	−0.01	0.01	−2.53	0.02	1.33					
Patch size	0.10	0.05	1.84	0.08	1.33					
Population density										
Best REVS model						45.1	0.00	0.30	0.03	0.20
Intercept	−0.51	0.62	−0.83	0.42						
Inter-patch distance (100)	0.00	0.00	2.42	0.03	1.7					
Fragmentation (500)	0.12	0.05	2.27	0.04	3.5					
Patch size	−0.01	0.00	−2.17	0.04	2.6					
Matrix permeability (100)	0.01	0.01	1.89	0.07	2.0					
Best stepwise model						47.5	2.44	0.36	0.09	0.71
Intercept	−2.20	0.96	−2.30	0.04						
Inter-patch distance (100)	0.00	0.00	2.74	0.02	7.2					
Fragmentation (500)	0.33	0.14	2.26	0.04	28.3					
Patch isolation	0.00	0.00	2.45	0.03	3.6					
Matrix permeability (100)	0.02	0.01	1.97	0.07	18.7					
% Forest cover (500)	−0.01	0.01	−1.84	0.09	12.2					
Patch size	−0.01	0.01	−1.10	0.29	13.6					
Fragmentation (100)	0.18	0.12	1.55	0.15	3.9					
% Forest cover (100)	−0.01	0.01	−1.84	0.09	3.6					
Inter-patch distance (500)	0.00	0.00	1.26	0.23	13.1					
Immature-to-female ratio						16.3	0.00	0.33	0.03	0.88
Intercept	−3.18	1.14	−2.78	0.01						
Matrix permeability (100)	0.03	0.01	2.67	0.01	2.4					
Shape index	0.49	0.16	3.09	0.01	5.4					
Edge density (100)	0.02	0.01	2.01	0.06	4.8					
Edge density (500)	0.00	0.00	1.92	0.07	1.6					
% Forest cover (100)	0.01	0.01	1.33	0.20	2.4					

^a Spatial factors included in the best REVS (Regression with Empirical Variable Selection) and best stepwise models are indicated (from a total of 13 factors). When analyzing the immature-to-female ratio we indicate only one model, as both best models were synonymous. With (100) and (500) we indicate the predictor variables estimated within 100-ha and 500-ha landscapes, respectively. The sign of each parameter indicates the relationship (positive or negative) between each factor and the response variable. The Variance Inflation Factor (VIF), Akaike Information Criterion (AIC), delta AIC, adjusted R², p values, and prediction accuracy of each model (MSE mean squared error) are also indicated

drivers of species maintenance in fragmented landscapes (Anzures-Dadda and Manson 2007; Smith et al. 2011; Thornton et al. 2011; Arroyo-Rodríguez et al. 2013). In general, both forest patch and landscape

metrics affected *A. pigra* populations in the study area; however, as predicted, howler monkeys were more affected by local-scale metrics, such as patch size, patch shape, and inter-patch isolation distance,

edge density, and matrix permeability within 100-ha landscapes.

The abundance of howler monkeys was principally associated to the spatial context of the neighboring landscapes (100-ha landscapes). In particular, patches located in landscapes with lower mean inter-patch distances and higher edge density had more individuals. These landscape spatial patterns increase the landscape connectivity, facilitating inter-patch movements (Ewers and Didham 2006), and favoring thus several landscape-scale processes that can be critical for populations' maintenance in fragmented landscapes (e.g., source/sink dynamics and landscape complementation; Dunning et al. 1992). Source/sink dynamics can be present in highly fragmented landscapes occupied by howler monkeys (reviewed in Arroyo-Rodríguez and Dias 2009), and can prevent the local extirpation of populations inhabiting patches with insufficient food (sinks) if individuals immigrate from more productive patches (sources) (Pulliam 1988). Primates can persist in forest patches with scarce resources if they can supplement their diet with sources located in neighboring patches and/or in different elements in the landscape matrix (e.g., isolated trees, live fences), as has been observed in howler monkeys inhabiting fragmented landscapes (*A. caraya*: Zunino et al. 2007; *A. palliata*: Asensio et al. 2009; *A. pigra*: Pozo-Montuy and Serio-Silva 2007).

We also found evidence that the number of individuals was positively related to patch size (best stepwise model; Table 3); a result that has also been found in other studies with howler monkeys (reviewed in Arroyo-Rodríguez and Dias 2009) and other primates (e.g., colobus and mangabeys: Wiczowski 2004; Wahungu et al. 2005). This can be related to the fact that larger patches may support more resources (Arroyo-Rodríguez and Mandujano 2006). Also, threats such as vegetation degradation (Estrada and Coates-Estrada 1996; Cristóbal-Azkarate et al. 2005; Arroyo-Rodríguez and Mandujano 2006; Rivera and Calmé 2006; Arroyo-Rodríguez et al. 2007), parasitic infections (Martínez-Mota et al. 2007; Trejo-Macías and Estrada 2012), physiological stress (Cristóbal-Azkarate et al. 2007), and hunting pressures (Watts et al. 1986; Peres 2001; Estrada et al. 2002) can be less intense in larger patches.

The density of individuals increased in more isolated and smaller forest patches, a finding consistent with that of other studies (*A. palliata*: Cristóbal-Azkarate et al. 2005; *A. pigra*: Estrada et al. 2002; Van

Belle and Estrada 2006; *A. seniculus*: Terborgh et al. 2001). In fact, the average density of individuals found within the patches (0.5 ind./ha, range = 0.1–1.4 ind./ha) was similar to the figures reported for *A. pigra* existing in other fragmented landscapes (Van Belle and Estrada 2006). High densities can have negative consequences for the long-term persistence of howler monkeys, as higher population densities in small patches can result in the reduction in food availability, the increment of inter- and intra-specific competition for resources, and higher endoparasite loads (reviewed by Arroyo-Rodríguez and Dias 2009). These processes can represent important threats to howler monkeys in our study area. Hence, although howler monkeys seems to be relatively resistant to the initial phases of disturbance, concentrating in small and isolated forest patches, the sharp increase in population density in these patches might suggest that there is an extinction debt to be paid in these patches (Cowlshaw 1999; Laurance et al. 2008; Metzger et al. 2009).

The absence of large predators (e.g., *Harpia harpyja*, *Panthera onca*) in smaller patches can favor the maintenance of high population densities of howler monkeys in small patches (Lovejoy et al. 1986; Chiarello 2003; Terborgh et al. 2001). Also, the proliferation of highly productive secondary vegetation in small patches has been suggested as an important factor that can contribute to maintain high population densities in small patches (e.g., Kowalewski and Zunino 1999; Lovejoy et al. 1986). In this sense, the density of individuals tended to be higher in patches surrounded by landscapes with higher matrix permeability (i.e., with higher proportion of secondary forests and arboreal crops). These kinds of matrices can offer important supplementary food sources for howler monkeys that can favor the maintenance of individuals within the patches (Estrada et al. 2012). In fact, the immature-to-female ratio increased significantly with matrix permeability, suggesting that this factor could also improve the reproductive success of females. Other important factors that were positively related to immature-to-female ratio were shape complexity and edge density within 100-ha and 500-ha landscapes. As reviewed by Ewers and Didham (2006), these habitat spatial characteristics can increase landscape connectivity facilitating the interchange of individuals and the availability of resources.

Overall, our findings support previous assumptions that conservation of large canopy-dwelling Neotropical

mammals, such as primates, requires the prevention of habitat loss (Fahrig 2003; Harcourt and Doherty 2005; Arroyo-Rodríguez and Dias 2009). By increasing the remaining habitat area and conserving the largest habitat remnants, we can preserve larger populations and at lower densities, preventing thus the potential deleterious effects of high population densities in small forest patches. With these management actions we can, at the same time, contribute to the maintenance of habitat quality and food availability for howler monkeys (Arroyo-Rodríguez and Mandujano 2006), as well as to the reduction of some potential health problems (e.g., physiological stress: Martínez-Mota et al. 2007; parasite risk: Gilbert 1994) and hunting pressures (Peres 2001).

Our results however suggest that the reduction of habitat isolation and the increment of matrix permeability can also favor the maintenance of howler monkeys in fragmented landscapes. These two management practices can increase landscape connectivity (Castellón and Sieving 2006; Ewers and Didham 2006), and favor the access to different sources (Asensio et al. 2009; Estrada et al. 2012), increasing thus the persistence of populations in fragmented landscapes. Because howler monkeys are effective seed dispersers for many plant species, with important consequences for plant communities and forest regeneration (Arroyo-Rodríguez et al. in press), plans directed to conserve howler monkeys also could be valuable for the conservation of their habitat.

Finally, it is important to recognize that additional studies with comparable sampling methods are necessary to determine if our results represent general responses of *A. pigra* populations in fragmented landscapes. Because each site was surveyed only once, future studies in the area should monitor population trends over time to have a better understanding of the impact of land use changes on species' persistence.

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