

## Chapter 28

# Landscape Attributes Affecting the Natural Hybridization of Mexican Howler Monkeys

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**Abstract** Natural hybridization can be affected by genetic and environmental factors. For instance, genetic incompatibilities may impede the formation of hybrids, or cause infertility of hybrid offspring, whereas anthropogenic habitat disturbance can promote the contact between formerly isolated species, and therefore, increase the probabilities of hybrid formation. Although there are a number of studies addressing endogenous factors affecting hybridization, little is known about the effects of environmental factors, such as habitat fragmentation, on hybridization in animals. Here we evaluate whether habitat configuration in a fragmented landscape affects the process of natural hybridization between Mexican howler monkeys (*Alouatta palliata* and *Alouatta pigra*), and which attributes of the fragmented landscape, if any, are likely responsible for this effect. Based on the genetic and morphological identification of purebred and hybrid individuals, we assessed the relationship between several metrics of habitat configuration (number of habitat fragments, fragment size, fragment isolation, and fragment shape) and the demographic characteristics and occupancy patterns of groups in areas where exclusively purebred individuals occur and in areas of hybridization in Macuspana, Tabasco. Our results indicate that forest fragmentation is more severe where hybridization occurs, where there is a larger number of small, though less isolated, fragments. Additionally, there are differences in group size and composition between purebred groups in areas with just purebred animals and in areas where hybridization is occurring. In areas of hybridization, purebred groups tended occupy the largest fragments,

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whereas in the only area where groups of the two parental species and hybrids co-exist, groups that included hybrid individuals tended to occupy more isolated fragments than groups of purebreds. These results are congruent with the hypothesis that hybridization between Mexican howlers is facilitated in fragmented landscapes. Although we could not discover the mechanisms that underlie this hypothesis, it is possible that in a landscape with more fragments, which are also smaller but rather connected, individuals move more frequently between forest remnants, increasing the probabilities of interspecific encounters.

## Introduction

Hybrid zones are affected by both endogenous (hybrid viability and fecundity) and exogenous (environmental) selection (Arnold 1997). It has been long assumed that most hybrid zones are maintained by a balance between dispersal of parental genotypes into the zone and selection against hybrids (Barton and Hewitt 1985). However, it is also recognized that the habitat configuration may play an important role in structuring hybrid genotypes within a hybrid zone (Cruzan and Arnold 1993). In areas where the habitat has been disturbed due to natural or anthropogenic events, hybridization may be favored (Anderson 1948) and hybrids can use niches unoccupied by purebred individuals, or even compete with parental forms if hybrids are equivalent to, or more fit than, the parental taxa (Arnold 1997).

Many instances of hybridization associated with human disturbance have been reported in both plants (Bleeker and Hurka 2001; Lamont et al. 2003) and animals (Docker et al. 2003; Heath et al. 2010; Keller et al. 2008; Schwarz and McPherson 2007). In primates, anthropogenic factors have also been suggested to augment the incidence of hybridization (Detwiler et al. 2005). However, further research based on field-based studies is required to understand how habitat configuration affects primate hybridization, and which particular spatial metrics affect this process in fragmented landscapes.

An excellent opportunity to investigate the effect of habitat configuration on hybridization in primates is the natural hybridization occurring between the two species of howler monkeys in Mexico (Cortés-Ortiz et al. 2007). These species (*Alouatta palliata* and *Alouatta pigra*) have allopatric distributions in most of their range, but live in sympatry in a small region in the state of Tabasco (Smith 1970). The landscape in this area has been severely transformed by human activities and the remaining habitat is highly fragmented (Sánchez-Colón et al. 2009).

The two species of Mexican howler monkeys diverged approximately 3 mya (Cortés-Ortiz et al. 2003), and can be distinguished on the basis of genetic (Cortés-Ortiz et al. 2003), cytogenetic (Steinberg et al. 2008), and morphological characters (Smith 1970). Additionally, they present marked differences in their social systems. For example, group size and sex ratios are higher in *A. palliata*, and unimale groups are common among *A. pigra* in contrast to the typical multimale groups of *A. palliata* (Di Fiore and Campbell 2007). Genetic studies on a number of populations of *A. palliata* throughout Mesoamerica show a clear decline of genetic variation from

south to north, implying a recent expansion in that direction (Cortés-Ortiz 2003; Ellsworth and Hoelzer 2006), and suggesting a secondary contact as the origin of the hybrid zone between these species (Cortés-Ortiz et al. 2003).

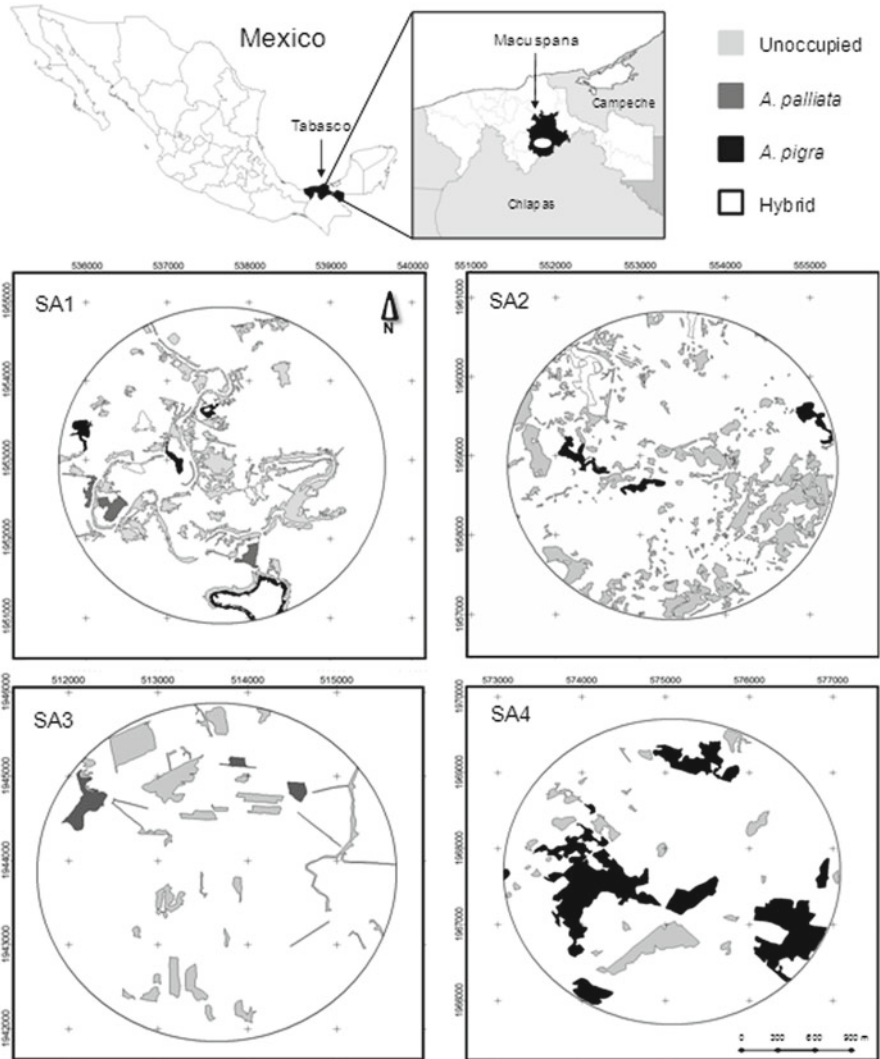
The fact that many cases of primate hybridization have occurred in areas where the habitat is fragmented due to human disturbance (Detwiler et al. 2005) raises the questions of whether human-induced forest fragmentation promotes the contact and subsequent hybridization between different primate species, and if so, which attributes of the landscape affect the hybridization process. In particular, Cortés-Ortiz et al. (2007) noted that human-induced forest fragmentation may promote contact between *A. palliata* and *A. pigra*, by confining members of both species to small areas and limiting access to conspecific mates. Under this scenario, natural hybridization of Mexican howlers would be facilitated in highly fragmented landscapes.

Here we examine the process of hybridization between *A. palliata* and *A. pigra* by comparing landscape configuration (see Chap. 2) and group size and composition of howler groups of the Macuspana hybridization area (HY) to those in the adjacent areas where only purebred *A. palliata* or *A. pigra* occur (PB). We expect that, if hybridization is facilitated in highly fragmented landscapes, the following conditions should be met: (1) Forest fragments in HY should be smaller, more isolated, and more irregular—attributes usually associated with a high degree of fragmentation (Fahrig 2003). (2) If fragmentation is more severe in HY, (A) groups of purebred *A. palliata* and *A. pigra* should be smaller than groups in PB. This is because, as Arroyo-Rodríguez and Dias (2010) report, in fragmented habitats population size of howler monkeys decreases, dispersion rates are reduced, groups are smaller and grouping patterns are altered. Also, as group size is reduced while male to female ratios are maintained, (B) a larger proportion of unimale groups should occur in HY than in PB for both species (as has been observed in fragmented habitats for *A. palliata* by: Clarke et al. 2002; McCann et al. 2003; and for *A. pigra* by: Estrada et al. 2002; Van Belle and Estrada 2006). (3) If habitat configuration affects the contact between parental species, (A) groups containing hybrid individuals should occupy smaller, more isolated and more irregular fragments than purebred groups in the same area (HY), and (B) hybrid groups should exhibit similar group size and composition among themselves. Additionally, (C) the spatial attributes that predict the probability of fragment occupancy by purebred or hybrid groups should differ.

## Methods

### *Study Sites*

This study was carried out in the state of Tabasco, which is located in southeastern Mexico (Fig. 28.1). Its original vegetation included large tracts of tropical evergreen and semievergreen forests (Rzedowski 2006), but native vegetation has been severely disturbed and destroyed due to human activities. Currently, the remaining



**Fig. 28.1** Location of the four sampling areas (SA) studied in the Macuspana area, Tabasco. Occupation of forest fragments by purebred and hybrid groups is indicated in the map. Coordinates provided at the edge of the maps are in UTM

tropical forests in the area are immersed in a matrix of pasturelands, agricultural fields, and human settlements (Sánchez-Colón et al. 2009).

Previous surveys of *A. palliata* and *A. pigra* in their contact zone, and the associated genetic evidence suggested that the Macuspana hybridization area follows a southwest (*A. palliata*)–northeast (*A. pigra*) gradient (Cortés-Ortiz et al. 2007, LCO unpublished). Therefore, we selected four sampling areas following this gradient:

two sampling areas where sympatry and hybridization have been confirmed (sampling area 1 and sampling area 2 in Fig. 28.1), and two sampling areas where only purebred individuals have been found (sampling area 3 for *A. palliata* and sampling area 4 for *A. pigra*, Fig. 28.1). In each sampling area, we positioned a 2 km-radius circle that included at least one location for which we had genetic evidence for purebred or hybrid individuals, resulting in an area of 1,257 ha per sampling area. Sampling areas were approximately 20 km apart.

### ***Spatial Attributes of Sampling Areas***

We digitized vegetation fragments in the four sampling areas with ArcGIS 9.3.1 (ESRI Inc., Redlands, CA, USA), using orthophotos (1:10,000, resolution 1 m) taken between 2004 and 2008 and obtained from the National Institute of Statistics and Geography of Mexico (INEGI). We corroborated the current presence of fragments with field surveys. We defined a fragment as a patch of forest with a surface area  $\geq 0.5$  ha. This choice was based on previous studies that have identified a 0.5 ha criterion as the minimum habitat requirement for fragment occupation by howler monkeys (Arroyo-Rodríguez et al. 2008; Cristóbal-Azkarate et al. 2005). However, we also digitized and visited smaller patches of vegetation to confirm the absence of howler monkeys. We calculated size, isolation, and shape of each fragment using Patch Analyst 3.12 for ArcView 3.2 and Patch Analyst 4.2 for ArcGIS 9.3.1, as well as self-developed geostatistical processes created in ModelBuilder for ArcGIS (ESRI Inc., Redlands, CA, USA). Three isolation metrics were used: (1) distance to the nearest fragment, (2) number of fragments in a radius of 200 m from each fragment, and (3) the amount of available habitat in the neighborhood of each fragment within a 200 m radius. The 200 m criterion was used because this distance has been previously defined as a maximum threshold for interfragment dispersion of howler monkeys in other populations (Mandujano and Estrada 2005). In addition, we calculated the shape of each fragment using the index proposed by Forman and Godron (1986):  $SI = P/\sqrt{A\pi}$ ; where  $P$  is the perimeter and  $A$  is the area of the fragment. This index varies from 1, for a circular shape, to 5 for a highly irregular shape. Irregular fragments can be colonized more easily than compact (e.g., round) patches, as they have a proportionally greater amount of edge, increasing the likelihood that a patch will be encountered by a moving individual (Ewers and Didham 2006).

### ***Sampling of Howler Monkey Populations***

*Genetics.* We captured and collected blood samples from 40 individuals in HY (for a description of the capture and handling techniques that were used see Rodríguez-Luna and Cortés-Ortiz 1995). All individuals were genetically characterized based on sequence data for the mitochondrial control region, the SRY gene

**Table 28.1** Number and identity of groups sampled in the hybridization area

Sampling area	Species/group	No. of groups
1	<i>A. palliata</i>	3 (1)
1	<i>A. pigra</i>	4 (2)
1	Hybrid	3 (3)
2	<i>A. pigra</i>	4 (2)
2	Hybrid	2 (2)

Numbers in brackets denote the number of groups for which genetic data was available

and genotype data from 20 microsatellite loci (Cortés-Ortiz et al. 2007, 2010). Individuals with discordant mtDNA and SRY haplotypes were considered hybrids. To identify hybrid individuals based on their microsatellite genotype, we used the Bayesian methods implemented in the program STRUCTURE v2.3 (Pritchard et al. 2000). We used this method to assign individuals to one of two populations ( $K=2$ ). The program was run with 100,000 iterations as burn-in period and 100,000 iterations for convergence. Individuals were classified as hybrids if they had an assignment value  $\leq 0.90$ . Analyses were carried out using the groups as the unit of study. Groups were considered as “pure” if they only contained purebred individuals of one of the species, and “hybrid” if they contained at least one genetically confirmed hybrid individual. We could only capture 62.5 % of all groups (Table 28.1). Within HY, groups that were not captured were classified based on their phenotype. Given that the phenotype usually resembles the genotype (Cortés-Ortiz et al. 2007), phenotypic identifications are reasonably confident.

*Demography.* Between May and August 2010 we visited all fragments in the four sampling areas. Two trained observers walked slowly around and inside each fragment between 6:00 and 19:00 h, to detect visual cues (e.g., movement in the canopy, feces, consumed food items) or vocalizations of howler monkeys. Once a group was located, we recorded the species, and the number of adult males, adult females, subadults, juveniles, and infants following the age–sex classifications of Balcells and Veà (2009) for *A. palliata*, and Rosales-Meda (2003) for *A. pigra*.

### ***Data Analyses***

To compare the proportion of available habitat and the number of fragments between PB and HY, we used chi-square tests for similar expected frequencies. To compare the spatial attributes of fragments between PB and HY, we used ANODEV with generalized linear models corrected for overdispersion. In these models, we nested fragments within sampling areas to control for spatial dependency of measures taken from fragments belonging to the same sampling area. To compare group size and composition of purebred groups between PB and HY, and of hybrid groups between sampling areas, we used Mann–Whitney tests, and to compare the

percentage of unimale groups of purebreds between PB and HY, we used Z tests for two proportions. We compared the spatial attributes of fragments occupied by purebred and hybrid groups in HY with Kruskal–Wallis ANOVA (sampling area 1) and Mann–Whitney tests (sampling area 2). Finally, to identify the spatial attributes that explained the probability of occupancy (i.e., presence/absence of groups) of fragments by purebred and hybrid groups in HY, we used logistic regressions with generalized linear models. We used the Akaike’s information criterion to first select the most parsimonious model, that is, the combination of spatial attributes that better explained the probability of a fragment being occupied (Motulsky and Christopoulos 2003). We then reran the regressions with the selected variables to generate occupancy models for purebred and hybrid groups.

## Results

### *Prediction 1: Difference in landscape attributes between HY and PB*

We sampled a total of 349 fragments for the presence of howler monkey groups; 196 fell within the category of forest fragments (i.e.,  $\geq 0.5$  ha). None of the fragments with less than 0.5 ha was occupied. The proportion of available habitat was similar between PB and HY ( $\chi^2=0.155$ ,  $p=0.693$ ), but the number of forest fragments was significantly higher in HY ( $\chi^2=41.32$ ,  $p<0.001$ ). All spatial variables differed significantly between PB and HY (Table 28.2). In PB fragment size and distance to nearest fragment were larger, whereas in HY the number of neighboring fragments, available habitat and shape index were higher.

### *Prediction 2: (A) Group size and composition of purebred groups differ between HY & PB, and (B) there is a larger proportion of unimale groups in HY than in PB*

We found *A. palliata* groups in sampling area 1 (3 groups, 15 individuals) and sampling area 3 (3 groups, 30 individuals). In sampling area 3 (i.e., PB for this species) groups were significantly larger ( $Z=1.993$ ,  $p=0.046$ ) than in sampling area 1, and included more females ( $Z=1.993$ ,  $p=0.046$ ) and subadults ( $Z=2.121$ ,  $p=0.034$ ;

**Table 28.2** Comparisons of landscape spatial attributes between HY and PB

	Hybridization	Purebred	$\chi^2$	<i>P</i>
Proportion of remaining habitat	15.1 %	12.9 %	0.155 <sup>a</sup>	0.693
Number of fragments	143	53	41.32 <sup>a</sup>	<0.001
Fragment size (ha)	2.7±3.2	6.2±12.2	13.51 <sup>b</sup>	<0.001
Distance to the nearest fragment (m)	42.6±74.6	114.8±118.2	22.12 <sup>b</sup>	<0.001
Number of neighboring fragments	4.5±2.5	1.6±1.3	71.04 <sup>b</sup>	<0.001
Available habitat in the neighborhood of each fragment (ha)	5.2±3.4	1.9±2.1	49.78 <sup>b</sup>	<0.001
Shape index	2.9±1.1	2.2±1.2	11.31 <sup>b</sup>	<0.001

<sup>a</sup>Analyzed with chi-square goodness-of-fit tests

<sup>b</sup>Used in GLM analysis

**Table 28.3** Group size and composition of purebred and hybrid groups

	<i>Alouatta palliata</i>		<i>Alouatta pigra</i>		Hybrid
	HY	PB	HY	PB	
Group size	3.7±1.2	11.3±5.9	4±1.7	5.3±1.7	5.4±3.4
No. of males	1.3±0.6	2.3±0.6	1.1±0.8	1.1±0.4	1±0
No. of females	1.3±0.6	4.3±1.5	1.5±1.1	1.6±0.7	2±1.4
No. of subadults	0	1.7±1.2	0.1±0.4	0.8±0.9	0.8±0.8
No. of juveniles	0.7±0.6	2±1.7	0.5±0.8	1.3±0.5	0.8±0.8
No. of infants	0.3±0.6	1±1	0.8±0.7	0.5±0.8	0.8±1.3
% unimale groups	33.3	0	42.9	87.5	100

Table 28.3). In sampling area 1, 33.3 % of the groups were unimale and 66.7 % had two adult males. In sampling area 3, 66.7 % of the groups included two adult males and 33.3 % included three adult males.

We observed *A. pigra* in sampling area 1 (4 groups, 16 individuals), sampling area 2 (4 groups, 16 individuals) and sampling area 4 (PB for this species, 8 groups, 42 individuals). There were significantly more juveniles per group in PB ( $Z=2.176$ ,  $p=0.029$ ; Table 28.3) than in HY. In HY, 42.9 % of the *A. pigra* groups had only one male, 42.9 % had two males and 14.2 % did not include adult males; whereas in PB, 87.5 % of the groups were unimale and a single group had two males. Nonetheless, the proportion of unimale groups did not significantly differ between PB and HY ( $Z=1.281$ ,  $p>0.05$ ).

*Prediction 3: (A) Groups containing hybrids use smaller, more isolated and more irregular fragments than purebred groups; (B) groups that include hybrids have similar size and composition, and (C) different attributes of landscape configuration predict the occupancy of hybrids and purebred groups in HY*

We observed groups that included hybrid individuals in sampling area 1 (HY, 3 groups, 15 individuals) and sampling area 2 (HY, 2 groups, 12 individuals). In sampling area 1—the only one that includes both hybrids and both species of purebreds—, hybrid groups occupied fragments that had higher DNF than fragments occupied by purebred groups ( $H_{2,10}=6.746$ ,  $p=0.034$ ). In sampling area 2, there were no differences between *A. pigra* and hybrid groups in the spatial attributes of occupied fragments (all Mann–Whitney tests  $p>0.05$ ). There were no significant differences in group size and composition among hybrid groups between sampling areas (all Mann–Whitney tests  $p>0.05$ ). All hybrid groups were unimale.

When modeling the data with Akaike's information criterion to identify the attributes that better explain the probability of fragment occupancy in HY, the most parsimonious model explaining the occupancy of fragments by hybrid individuals retained four variables: fragment size, number of neighboring fragments, available habitat, and shape. The logistic model including these four variables was significant ( $\chi^2_{4,143}=9.791$ ,  $p=0.041$ ,  $R^2=0.23$ ), but only size ( $\chi^2_{1,143}=4.14$ ,  $p=0.041$ , estimate=-0.33), number of neighboring fragments ( $\chi^2_{1,143}=5.53$ ,  $p=0.019$ , estimate=0.81), and available habitat ( $\chi^2_{1,143}=4.72$ ,  $p=0.029$ , estimate=0.82) had significant effects on occupancy. Therefore, the probability of fragment occupancy



by hybrid groups increased in smaller fragments that had more neighboring fragments and available habitat. For *A. pigra*, fragment occupancy was best explained by fragment size and available habitat ( $\chi^2_{2, 166}=19.928$ ,  $p<0.001$ ,  $R^2=0.19$ ). However, only fragment size had a significant positive effect on the model ( $\chi^2_{1, 166}=9.56$ ,  $p=0.002$ , estimate=0.16), indicating that fragment occupancy by *A. pigra* in HY increased with fragment size. Finally, for *A. palliata* fragment occupancy depended on fragment size, number of neighboring fragments and shape ( $\chi^2_{3, 102}=9.429$ ,  $p=0.024$ ,  $R^2=0.21$ ). Yet, again, only fragment size had a significant positive effect on the model ( $\chi^2_{1, 166}=3.95$ ,  $p=0.047$ , estimate=1.49) indicating that in HY, the probability of finding *A. palliata* groups increased in larger fragments.

## Discussion

We found evidence suggesting that in the Macuspana area, hybridization between *A. palliata* and *A. pigra* is likely associated with particular attributes of the habitat configuration. First, there were differences in spatial attributes of the landscape between the hybridization area (HY) and the areas where only purebred individuals occur (PB). Although the proportion of total available habitat was similar between HY and PB, in HY there were more fragments, which were smaller and more irregular. However, in contrast to our prediction, in HY forest fragments were less isolated, as distance to nearest fragment was shorter and number of neighboring fragment and available habitat were larger. Second, as predicted, we found differences in group size and composition of purebred groups between HY and PB. For *A. palliata*, PB groups were larger mainly due to a significantly higher number of females and subadult individuals; whereas *A. pigra* groups in PB were similar in size to *A. pigra* groups in HY, but included more juveniles. Third, in the sampling area 1 (HY), where *A. palliata*, *A. pigra* and hybrid groups were present, hybrid groups occupied more isolated fragments than purebred groups. Also, there were differences between purebred and hybrid groups in the spatial attributes that predicted their occupancy patterns: whereas purebred groups tended to occupy larger fragments, hybrid groups were usually present in smaller fragments that had higher values for number of neighboring fragments and available habitat. These results are consistent with our hypothesis that hybridization in howler monkeys is affected by habitat configuration associated with human-induced habitat fragmentation; however which mechanisms are responsible for these associations is still unclear.

Comparing the landscape of the sampled areas with studies of Mexican howler monkeys in other fragmented areas, both HY and PB are severely disturbed. For instance, the proportion of available habitat is significantly lower in our study area than in fragmented landscapes in Veracruz occupied by populations of *A. palliata* (Arroyo-Rodríguez et al. 2008), or in southeast Tabasco occupied by *A. pigra* (Pozo-Montuy et al. 2008). Although the origin of the hybrid zone in Mexico is likely the product of a secondary contact between two species that have not achieved complete reproductive isolation (Cortés-Ortiz et al. 2003; Smith 1970),

the current occurrence of hybridization in HY might be facilitated by the presence of a highly disturbed landscape with a large number of small fragments in close proximity. In smaller fragments the access to food for howler monkeys is constrained (Arroyo-Rodríguez and Dias 2010), and as a consequence, groups will have to move between fragments to meet their dietary requirements (Asensio et al. 2009). Such movements would be facilitated in HY by the large number of fragments and their proximity. Thus, individuals of both parental species living in sympatry in this landscape would have higher probability of encounter than those living in a less disturbed setting.

There is evidence that group size is positively related to fragment size in howler monkeys (Arroyo-Rodríguez and Dias 2010), so it is expected that in HY fragments may only sustain small groups of purebreds. For *A. palliata*, group size was nearly three times smaller in HY, whereas in PB group size was similar to that reported for both extensive and fragmented forests (12.9 individuals; Chapman and Pavelka 2005). However, for *A. pigra* there were no differences in group size between PB and HY, and the observed values are similar to those reported for this species in both extensive and fragmented landscapes throughout its distributional range (reviewed in Van Belle and Estrada 2006). Consequently, the small fragment size in HY seems to pose a major effect on group size and composition to groups of *A. palliata*, limiting the number of potential mates. Therefore *A. palliata* groups in HY may experience increased intraspecific competition that would drive *A. palliata* individuals to leave their natal groups, and promote higher rate of encounter with *A. pigra* groups. Furthermore, even when there were no significant differences in size between *A. pigra* groups in HY and PB, there remains an observed trend (Arroyo-Rodríguez and Dias 2010) that in smaller fragments there are smaller groups. Therefore, the small size of fragments in the area could also restrict the potential number of mates for *A. pigra*. The additive effects of lower food availability and fewer reproductive opportunities must therefore promote higher rates of natal and secondary dispersal by individuals in HY, facilitating encounters between individuals of the two parental species and favoring the occurrence of interspecific matings.

Another important consideration is the possible influence of interspecific differences in responses to disturbance and competitive abilities. In agreement with what has been suggested by Van Belle and Estrada (2006), habitat size seems to have limited effects on the grouping patterns of *A. pigra*, probably because small group sizes have been evolutionarily favored in response to conspecific competition (Chapman and Pavelka 2005). In contrast, group size in *A. palliata* was severely reduced in small fragments. This suggests that, given their usually large size, *A. palliata* groups are more likely to change their social organization in response to habitat constraints than *A. pigra* groups. Thus, when facing similar environmental conditions, group size and composition tend to be similar for both species, as it is shown in the present study. A social element that is likely to play a role in the dynamics of the hybridization in this fragmented landscape is the fact that howler monkey males employ alternative mating tactics, which usually involve evading female-guarding by dominants (Horwich et al. 2000; Jones 1995). Such opportunities are reduced in small groups, as the effectiveness of mate-guarding is expected

to increase when group size is reduced (Nunn 1999). However, given that *A. pigra* are significantly larger in body mass than *A. palliata* individuals (Kelaita et al. 2011), it is possible that the former are at an advantage during interspecific encounters. This could result in the eviction of *A. palliata* males from their own groups by *A. pigra* males in the context of group takeovers, facilitating hybridization, as well as the displacement of *A. palliata* groups from preferred fragments (i.e., larger and less isolated fragments).

Even if some of the groups that were classified morphologically as purebreds included hybrid individuals, the fact that hybrid groups were mainly present in the smallest and more isolated fragments in the area where groups of both of purebred species exist, suggests that either (1) hybridization occurs in fragments where it is less probable to find purebreds, (2) that hybrids may be more fit to occupy highly disturbed habitat than purebreds, or (3) that hybrids are displaced by purebreds from better quality fragments. To understand the mechanisms that are determining the distribution of hybrid groups and individuals within this fragmented landscape, we are expanding our genetic and demographic samplings and establishing long-term behavioral and demographic investigations of howler monkeys in the area.

In conclusion, we found evidence concordant with the hypothesis that natural hybridization between Mexican howlers is associated with highly fragmented landscapes in the Macuspana area, as groups that included hybrid individuals were present in small and more isolated fragments. Furthermore, these findings suggest that the genetic make-up of this hybrid zone is affected by the configuration of the habitat, and that the prevalence of hybridization in the area may be a consequence of repeated encounters between parental species favored by a landscape where the movements of individuals between forest fragments are more frequent, and influenced by the social dynamics among *A. palliata*, *A. pigra* and hybrid individuals.

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