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Group Structure and Dynamics in Black Howlers (*Alouatta pigra*): A 7-year Perspective

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Abstract The long-term monitoring of group structure and dynamics is critical to the study of primate ecology and evolutionary processes, as well as to understand the responses of individuals to changes in their environments. We monitored individually recognized black howlers (*Alouatta pigra*) belonging to 11 groups for 7 yr in different habitats and landscapes in Campeche (Mexico). Our aims were 1) to describe group structure and dynamics; 2) to determine whether group structure and dynamics changed significantly over time; and 3) to evaluate which habitat and landscape-scale attributes best predicted variation among groups in structure and dynamics. Each year we surveyed the groups twice in each climatic season (wet and dry season), resulting in a total of 10,083 sampling days. Although group size increased over time, mostly as a result of moderate to high infant survival rates and increases in the number of juveniles in groups, other demographic parameters, such as the number of adults and infants per group, were stable. We observed no group takeovers involving two or more males and infrequent takeovers by solitary males; frequent disappearances of individuals of both sexes from their natal groups around the age of sexual maturation, suggesting a bisexual dispersal pattern; concentration of births in the wet season; male-biased sex ratios at birth but female-biased immature survival. Group structure and dynamics were affected by both habitat and landscape-scale attributes, but factors acting at the habitat scale had an overall higher impact on demographics. Besides reporting new life history and demographic data for this species, the results from this study suggest that black howlers may be more sensitive to habitat disturbance than previously reported.

Keywords *Alouatta pigra* · Campeche · Census · Demographics · Group size and composition · Long-term monitoring

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Introduction

The long-term monitoring of individually recognizable animals is critical to the study of animal ecology and evolutionary processes (Clutton-Brock and Sheldon 2010). It allows, among others, the study of individual development and life history, and when it involves monitoring temporal variation in the size and composition of social groups, the description of the social structure and organization of a species (Kappeler and Watts 2012). Because the monitoring of the current responses of individuals to changes in their environment is required to predict their future responses to selective pressures, long-term studies are also very important in a conservation context (Kappeler *et al.* 2012). If long-term monitoring is conducted in environments with different anthropogenic activities, we can determine which activities have a higher impact on populations, and improve our ability to predict future persistence of the study species (Chapman *et al.* 2000; Stouffer and Borges 2001).

Howlers (*Alouatta* spp.) have been studied for 80 yr. Many short-term studies have focused on population structure (i.e., how the population is organized by sex and age classes, as well as the spatial organization of the population into social groups and other units: Lawler 2011) of several howler species in multiple locations (e.g., *A. caraya*, black-and-gold howler monkeys: Kowalewski and Zunino 1999; *A. clamitans*, brown howler monkeys: Strier *et al.* 2001; *A. palliata*, mantled howler monkeys: Cristóbal-Azkarate *et al.* 2005; *A. pigra*, black howler monkeys: Estrada *et al.* 2002). Long-term studies, defined as those that encompass more than one generation (i.e., the age at which members of a given cohort are expected to reproduce, which in howler monkeys corresponds to ca. 3.6-8 years: Di Fiore *et al.* 2011), have been conducted on populations of three species: mantled howlers (Arroyo-Rodríguez *et al.* 2008a; Clarke *et al.* 1986; Fedigan *et al.* 1998; Milton *et al.* 2005), ursine red howlers (*Alouatta arctoidea*: Rudran and Fernández-Duque 2003), and black howlers (Horwich *et al.* 2001); providing information on population dynamics (i.e., population parameters that change over time: Lawler 2011). Overall, there is evidence that howler populations undergo fluctuations with population reduction, stability and growth being linked to food shortages and disease (Milton *et al.* 2005; Rudran and Fernández-Duque 2003), parasitism and density-dependent regulation (Horwich *et al.* 2001; Milton 1996), and increases in the amount of available habitat (Fedigan *et al.* 1998; Horwich *et al.* 2001; Rudran and Fernández-Duque 2003), respectively.

The population structure of howlers is affected by habitat disturbance (i.e., transformation, loss or fragmentation of the habitat) at both a habitat and a landscape scale. In general, the number of individuals in fragmented landscapes and habitats is positively related to the proportion of suitable habitat and forest fragment size, but negatively related to the isolation of forest fragments (Arroyo-Rodríguez and Dias 2010). It is less clear, however, which factors are more important in determining population structure and dynamics in disturbed habitats. In one of the first attempts to address this problem, it was recently demonstrated that populations of black howlers living in Chiapas (Mexico) are more affected by habitat-scale metrics, such as fragment size, shape, and isolation, than by landscape-scale variables, such as forest cover and interfragment distance (Arroyo-Rodríguez *et al.* 2013; see also Anzures-Dadda and Manson 2007; Mandujano *et al.* 2006). Because each site was surveyed only once, Arroyo-Rodríguez *et al.* (2013) could not assess whether variation in the effects of habitat disturbance on population structure is associated with changes in population dynamics over time. Therefore, although there are abundant data on the demographics of howlers (including black howlers: Horwich *et al.* 2001), we lack information about the effects of habitat disturbance, measured at different spatial scales, on the structure and dynamics of howler populations over time.

To address this gap, we report 7 yr of monitoring of individually recognized black howlers belonging to groups that lived in different habitats and landscapes in the Mexican state of Campeche. Black howlers have a geographic distribution restricted to the Yucatan Peninsula in Mexico and Belize, and some parts of northern and central Guatemala, and are endangered (Marsh *et al.* 2008). Previous research indicated that fragment size is positively related to food availability and negatively related to anthropogenic pressures, physiological stress, and parasite loads in howlers (Arroyo-Rodríguez and Dias 2010). Therefore, to increase the probability to detecting significant effects of habitat disturbance on the demographics of black howlers, we selected groups living in habitats of different size, ranging from 5 to 140,000 ha. Our study had three aims: 1) to describe group structure and dynamics; 2) to determine whether group structure and dynamics changed significantly over time; and 3) to evaluate which habitat and landscape-scale parameters best predicted variation in structure and dynamics among groups.

Methods

Study Area and Sites

We studied 11 groups of black howlers that lived in different locations in Campeche, Mexico (Table I). Mean annual rainfall in Campeche is 1300 mm, with a dry season from November to May (mean monthly rainfall ± SD = 43.7 ± 25.8 mm), and a wet season between June and October (218.9 ± 14.1 mm). Mean annual temperature is 26°C.

The size of Campeche is 57,924 km^2, of which *ca.* 40% are protected. Black howlers are found in large protected areas, such as the Calakmul Biosphere Reserve and the Laguna de Términos Reserve, where original habitat availability is high and primates face low anthropogenic pressures (Escamilla *et al.* 2000). The majority of the remaining nonurban Campeche consists of highly anthropogenically modified landscapes, where original forest habitats have been converted into forest-agricultural mosaics. Black howlers living in these landscapes occupy forest fragments of variable size where they face multiple anthropogenic disturbances, such as livestock grazing, predation threat by domestic animals such as dogs, and forest fires associated with slash-and-burn agriculture (Rangel-Negrín *et al.* 2011, 2014b).

Census

Census of black howler groups began in February of 2006 and ended in February of 2012. The site Chicbul was an exception, as the fragment was logged in February 2011 and the group could not be located. All groups were part of complementary projects that included intensive observations of the behavior and ecology of black howlers as

Table I Habitat and landscape-scale predictors of group structure and dynamics in 11 groups of black howlers from 2006 to 2012 in Campeche, Mexico

Group	Latitude	Longitude	Sampling effort (days)	Habitat-scale attributes								Landscape-scale attributes			
				Spatial attributes					Vegetation attributes of hábitats			AH (ha)	NF	MFS (ha)	MIID (m)
				Size (ha)	SI^a	DNH (m)	DNR (m)	DNHS (m)	Sp. richness	Sum of DBH (cm)	Tree density				
AA Álamo	18°48′45.44″ N	90°58′54.61″ W	1008	86.0	2.3	2.6	299.0	190.0	17	2334.8	1,060.0	193.1	6.0	32.2	1043.7
Calakmul S	18°19′0.28″ N	89°51′28.92″ W	1025	140,000	3.0	30.0	0.0	200.6	33	3353.7	660.0	1200.0	1.0	1200.0	0.0
K9 Calakmul	18°27′49.89″ N	89°53′57.24″ W	807	140,000	3.0	30.0	0.0	0.0	22	3003.9	523.9	1190.8	1.0	1190.8	0.0
Calaxchil	18°51′15.38″ N	91°18′41.70″ W	1004	3000.0	2.6	4.3	1000.0	1432.8	24	2578.0	480.0	985.6	2.0	492.8	76.2
Chicbul	18°46′51.66″ N	90°56′13.45″ W	600	5.0	2.8	6.2	0.0	323.0	16	1436.2	910.0	33.7	4.0	8.4	999.4
Manantiales	18°42′55.39″ N	91°4′42.07″ W	927	50.0	3.1	94.0	95.0	0.0	22	1626.1	740.0	268.5	8.0	33.6	1356.5
Oxcabal	18°51′44.34″ N	90°57′39.45″ W	906	7.0	2.9	339.1	0.0	73.8	5	1436.2	140.0	52.6	4.0	13.1	356.6
R Álamo	18°48′42.15″ N	90°58′58.69″ W	857	35.3	2.7	50.7	0.0	0.0	25	1656.2	820.0	161.2	7.0	23.0	1468.8
T61Calax	18°50′52.35″ N	91°18′27.12″ W	984	300.0	1.7	164.6	1500.0	2488.7	25	2238.0	600.0	540.1	4.0	135.0	911.1
Tormento N	18°36′50.68″ N	90°48′25.93″ W	987	600.0	2.0	38.8	0.0	218.7	26	1920.8	1110.0	1017.4	2.0	508.7	38.8
Tormento S	18°36′27.29″ N	90°48′51.44″ W	978	800.0	2.3	38.8	30.0	932.0	29	2650.4	1120.0	1097.5	3.0	365.8	76.1
Total (mean)			916.6	25,898.5	2.6	72.6	265.8	532.7	22.2	2203.1	742.2	612.8	3.8	364.0	575.2
Total (± SD)			125.3	56,419.9	0.5	100.2	507.2	789.2	7.5	649.0	303.2	486.8	2.4	453.6	584.5

SI = shape index; DNH = distance to nearest habitat; DNR = distance to nearest road; DNHS = distance to nearest human settlement; Sp. richness = plant species richness; DBH = diameter at breast height of trees; AH = amount of habitat; NF = number of fragments; MFS = mean fragment size; MIID = mean interpatch isolation distance.

well as genetic and morphometric sampling. All monkeys were individually recognizable by researchers via ankle bracelets or their natural anatomical and physiognomic characteristics, such as body size and proportions, scars, broken fingers, and genital morphology and pigmentation. During each sampling day we determined group size by counting group members repeatedly until several consistent totals were obtained. We recorded the number of adult males, adult females, juveniles, and infants following the age–sex classification of Rosales-Meda (2003). Each year, each group was sampled at least twice in each climatic season, i.e., dry and wet season. Each season sampling encompassed a mean (±SD) of 67 (±5.4) d (range = 57–73 d). We accumulated a total of 10,083 sampling days, with a mean (±SD) of 918.5 (±125.3) sampling days per group (Table I).

Habitat Characterization

We defined habitat as a forest tract occupied by at least one group of black howlers, and landscape as a 1200-ha circle around the center of the home range of each group (Rangel-Negrín *et al.* 2014a). To assess the effects of habitat and landscape-scale factors on the demographics of black howler groups we estimated the following variables. First, at the landscape scale we characterized the spatial configuration of landscapes. Each landscape was digitized with ArcGIS 9.3.1 (ESRI Inc., Redlands, CA), using orthophotos (1:10,000, resolution 1 m), where we classified land cover types as forest, pasture lands or crops, human settlements, and roads. For each landscape we calculated total amount of habitat as the sum of forested areas (in ha); number of forest fragments; mean fragment size (in ha); and mean isolation distance among fragments, i.e., mean Euclidian distances among fragments measured from the edge of each fragment, in m. For these calculations we used Patch Analyst 3.12 for ArcView 3.2 and Patch Analyst 4.2 for ArcGIS 9.3.1, as well as geostatistical processes created in ModelBuilder for ArcGIS (ESRI Inc., Redlands, CA). Mean (± SD) distance between any two landscapes was 62.4 (±52.2) km.

Second, at the habitat scale we studied spatial and vegetation attributes. We studied the following habitat spatial attributes: habitat size, shape, and distance to nearest habitat, road, and human settlement. These spatial attributes were calculated with the same GIS procedures described previously. Habitat shape was estimated with the shape index (Forman and Godron 1986): $\mathrm{SI} = P/\sqrt{A\pi}$; 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). To study vegetation attributes, in each habitat we randomly located ten 50 × 2 m linear transects inside each group's home range (Gentry 1982). In each transect, we measured the diameter at breast height (DBH; 1.3 m) of all trees with DBH >10 cm, which we identified at the species level based on morphology. We previously demonstrated that the performance of this method is relatively insensitive to variation in the total forest area that is sampled (Dias *et al.* 2014). From these data we calculated species richness as the total number of sampled plant species, tree density as the estimated number of trees per hectare, and the sum of basal areas of all sampled trees in each group's habitat. These seven habitat measures have been frequently used to describe the habitats of howlers (Arroyo-Rodríguez *et al.* 2013; Arroyo-Rodríguez and Mandujano 2006; Cristóbal-Azkarate *et al.* 2005; Dias *et al.* 2013, 2014; Dunn *et al.* 2009).

Habitat characterization is based on GIS measurements performed with 2006 orthophotos and vegetation transects were conducted in 2006. To determine if habitat characterization needed to be repeated during the study, we compared the sizes of the study habitats among 2006, 2008, and 2010 orthophotos. The mean (±SD) biannual change in habitat size was -0.18 ± 0.7 ha, indicating very low variation. Therefore, with the exception of Chicbul, we assume that only minor changes in both the habitats and the landscapes occurred during the 7 yr encompassed by this study.

Data Analyses

We describe the demographics of the study groups using the following parameters: group size; number of adult males, adult females, juveniles, and infants in groups; the ratio of adult females to adult males (i.e., socionomic sex ratio; hereafter sex ratio); the ratio of infants (i.e., individuals <12 mo old) to females and the ratio of immatures (i.e., individuals <36 mo old) to adult females; finite growth ratio; number of births; interbirth interval; infant survival rate; immigrations; emigrations (disappearance of healthy individuals of >3 yr of age). We calculated the finite growth ratio (λ) by dividing the group size in the first sample of the dry season of a given year (which usually happened between January and March) by the group size in the first sampling of the dry season of the previous year. $\lambda > 1$ indicates that group size is increasing, $\lambda < 1$ indicates group decline, and $\lambda = 1$ that the group is stable. Infant survival rate was calculated as the percentage of infants born in each year that reached 12 mo of age.

To analyze variation in births between climatic seasons we calculated the number of births for each season and compared them with a Wilcoxon matched pairs test. To analyze temporal variation in group size and composition we used generalized linear mixed models (GLMM) (Rabe-Hesketh *et al.* 2005). In these analyses we used mean annual values for group size, number of adult males, adult females, juveniles, and infants, as well as sex ratio, infant survival rate, and λ for each group as dependent variables. We ran one model for each dependent variable, including year as a fixed predictive factor and group as a random factor to account for repeated sampling of each group over time. To model group size and λ we used a normal distribution with an identity link function, whereas for all other variables we used a Poisson distribution with an identity link function. The underlying assumptions of the models were assessed visually by QQ plots. These analyses were performed in SPSS 22.0 (IBM Corp.).

To analyze which habitat and landscape-scale factors had a stronger effect on group structure and dynamics we used multiple linear regression analysis (Crawley 2002). Because we had more predictors (13 variables) than cases (11 habitats), which would limit parameter estimations (Quinn and Keough 2002), we reduced the number of predictive variables in the models. To this end, we ran Pearson correlations, which indicated that amount of habitat in the landscape correlated with the number of fragments ($r = -0.79$, $P = 0.004$), mean fragment size ($r = 0.86$, $P = 0.001$), mean isolation distance among fragments ($r = -0.82$, $P=0.002$), plant species richness ($r = 0.71$, $P = 0.015$), and DBH ($r = 0.84$, $P = 0.001$). Distance to nearest road correlated with distance to nearest human settlement ($r = 0.92$, $P < 0.001$). Therefore, we retained amount of habitat, tree density, habitat size, SI, distance to nearest habitat, and distance to nearest road as predictors. Habitat sizes were log transformed to reduce the influence of its very high variation in the analyses. 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 $\mathrm{AIC_i} - \mathrm{AIC_{min}}$; where $\mathrm{AIC_{min}}$ is the AIC value of the model with the lowest AIC score from a series of candidate models. Models with $\Delta\mathrm{AIC} < 2$ can be considered to have strong support (highly feasible), whereas models with $\Delta\mathrm{AIC} > 10$ 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). 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 (Canty and Ripley 2014). 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. In each model we calculated each predictor's variance inflation factors (VIF; Neter *et al.* 1990) as the inverse of the coefficient of nondetermination $[1/(1 - R^2)]$ for a regression of that predictor on all others. Generally, $\mathrm{VIF} > 10$ indicate severe multicollinearity (Neter *et al.* 1990; *cf.* O'Brien 2007). Sex ratio and infant survival rate models revealed that habitat size had a high VIF (caused by correlation with habitat amount in the landscape: $r = 0.60$, $P = 0.051$), so we reran models without this variable.

Ethical Note

Our research protocols complied with the legal requirements of the Estados Unidos Mexicanos and were approved in permits SEMARNAT/SGPA/DGVS/01273/06 and SEMARNAT/SGPA/DGVS/04949/07.

Results

Group Size and Composition

We observed a total of 161 individuals, of which 23% were adult males, 33% were adult females, 25% were juveniles, and 19% were infants. On average, groups included 7 individuals, of which 1.6 were adult males, 2.3 were adult females, 1.8 were juveniles, and 1.3 were infants (Table II; Table SI). There were usually more adult females than males in the groups (1.7 females per male), but the sex ratio was highly variable (range = 0.7–3 females per male; Table SI). In 52% of all group/years the grouping pattern was unimale–multifemale, and with the exception of Tormento S, all groups were at some point unimale–multifemale. With the exception of a single group (AA Álamo), there was always more than one immature per adult female, the majority of which were juveniles.

Table II Mean group size and composition in 11 groups of black howlers from 2006 to 2012 in Campeche, Mexico

Group	Group size	No. of males	No. of females	Sex ratio	No. of juveniles	No. of infants	Infant survival rate (%)
AA Álamo	4.9	1.1	2.1	2	0.9	0.7	66.7
Calakmul S	8.9	1.6	2.4	1.8	2.9	1.9	79.2
K9 Calakmul	6.1	1.4	2.1	1.7	1.7	0.9	100
Calaxchil	8.4	1.9	2.7	1.9	2	1.6	86.1
Chicbul[a]	6.6	1	2	2	2.2	1.4	37.5
Manantiales	3.4	1.3	1	0.9	0.6	0.6	25
Oxcabal	6.6	1.9	2	1.2	1.4	1.3	62.5
R Álamo	7.1	1.6	2.6	1.9	1.7	1.3	80
T61Calax	6.9	0.7	2.7	2.4	2	1.4	100
Tormento N	10.9	2.4	3.3	1.9	3.3	1.9	93.3
Tormento S	7.6	2.4	2.1	0.9	1.7	1.3	70
Mean±SD	7.0±2.0	1.6±0.5	2.3±0.6	1.7±0.5	1.8±0.8	1.3±0.4	72.8±24.2

[a] This group was observed only from 2006 to 2010.

Group size varied for each group across years, and among groups throughout the study (Table II; Table SI). Annual finite growth ratios were in general highly variable both within groups across the study, and among groups in each sampling year (Table III). However, finite growth ratio during the study across all groups indicated demographic stability (λ = 1.05 ± 0.1).

Table III Finite rate of increase (λ) in 11 groups of black howlers from 2006 to 2012 in Campeche, Mexico

	2007[a]	2008	2009	2010	2011	2012	Mean ± SD
AA Álamo	1.00	1.00	1.00	1.50	1.00	1.00	1.08 ± 0.2
Calakmul S	0.78	1.00	1.29	1.00	1.11	1.10	1.05 ± 0.2
K9 Calakmul	1.00	1.20	1.00	1.33	0.75	1.17	1.08 ± 0.2
Calaxchil	1.13	0.78	1.00	1.14	1.25	1.00	1.05 ± 0.2
Chicbul[b]	1.33	0.88	1.00	0.71	—	—	0.98 ± 0.3
Manantiales	0.80	0.75	1.33	0.50	1.50	1.00	0.98 ± 0.4
Oxcabal	0.83	1.60	1.00	0.75	1.17	0.86	1.03 ± 0.3
R Álamo	1.14	0.75	1.17	1.14	0.88	1.00	1.01 ± 0.2
T61Calax	1.17	1.00	0.86	0.67	2.00	1.25	1.16 ± 0.5
Tormento N	1.38	1.09	0.83	1.30	0.85	1.00	1.07 ± 0.2
Tormento S	1.20	1.33	0.88	1.29	1.11	0.80	1.10 ± 0.2
Mean±SD	1.07 ± 0.2	1.03 ± 0.3	1.03 ± 0.2	1.03 ± 0.3	1.16 ± 0.4	1.02 ± 0.1	

[a] Light gray shading when λ < 1.00, i.e., group declines; white shading when λ = 1.00, i.e., group is stable; dark gray shading when λ > 1.00, i.e., group increases.

[b] This fragment was logged in January 2011 and the group could not be located.

Births and Deaths

We recorded 96 births, of which 63% were of male infants and 37% were of females. Overall, there were 2.1 male births per female birth. Across years, the number of births recorded in the wet season was significantly higher than the number of births in the dry season ($Z_7 = 3.29$, $P < 0.001$), with 71.9% of all births occurring during June–October, i.e., wet season. The mean interbirth interval was 16.4 ± 5.9 mo ($N = 74$). This value ranged from 14, when the previous infant died before reaching 1 yr, to 37 mo.

The mean survival rate of infants varied among groups from 25 to 100% (Table II; Table SI): 31.7% of all infants disappeared during their first year of life (Table IV); 15.9% and 12.7% of immatures disappeared during the second and third year of age, respectively. The proportion of male disappearances was higher than that of females during the first, second, and third year of age (Table IV).

Dispersal

With the exception of R Álamo, there were immigrations in all groups. We recorded a total of 18 immigration events (Table V): three (16.7%) corresponded to the immigration of adult females, nine (50%) to adult male immigrations, and six (33.3%) to immature immigrations. Usually, individuals entered groups alone. The exceptions to this pattern were Calakmul S and Chicbul. In 2009, one adult male, one adult female, and two female juveniles joined Calakmul S together, and in 2010 one adult female and a female juvenile entered Chicbul. On two occasions we observed the immigration of lone immatures, which were juvenile females *ca.* 2 yr old that entered Manantiales and Tormento N. The Tormento N juvenile immigrant, as well as the juvenile females that immigrated into Calakmul S, reached sexual maturity, reproduced, and stayed in their new groups until the end of the study. The Manantiales juvenile immigrant was not present in the next census. Adult male immigrations were associated with the disappearance of immatures (three infants <10 mo and one 36 mo juvenile) in three groups. In AA Álamo the immigration of an adult male resulted in the disappearance of the resident male. Similarly, the immigration of a new adult male to Calaxchil resulted in the disappearance of two young adult males (4 and 5 yr). In 2008, an adult male entered Tormento S, which had two resident males. One of the resident males disappeared, and the other remained in the group until the end of the study. In 2009 a new male invaded Tormento S, and after an intense fight, the male that had immigrated in 2008 disappeared. The body of this male was found a week later and showed several wounds

Table IV The fate of immatures observed in 11 groups of black howlers from 2006 to 2012 in Campeche, Mexico: percentage of males, females, and total individuals that disappeared or stayed in natal groups ($N = 96$, 60 males and 36 females)

Fate of immature		% Males	% Females	% Total
Disappeared during year	1	34.2	27.3	31.7
	2	19.5	9.1	15.9
	3	14.6	9.1	12.7
	4	9.8	31.8	17.5
	5	14.6	0	9.5
Stayed in natal group[a]		7.3	22.7	12.7

[a] Males with ≥5 yr and females with ≥4 yr.

Table V Dispersal events per age/sex class in 11 groups of black howlers from 2006 to 2012 in Campeche, Mexico

	Emigrations	Immigrations	Total
Adult males	11	9	20
Adult females	9	3	12
Immature females	1	5	6
Immature males	0	1	1
Total	21	18	39

typical of male–male fights in howlers (Cristóbal-Azkarate *et al.* 2004). In 2011 a new male immigrated into this group and the male that had joined the group in 2009 also disappeared. Some adult individuals disappeared from groups when no immigration occurred: two young adult males (5 yr old) disappeared from Calakmul S in 2007; an adult female and her putative juvenile daughter (3 yr old) left Calaxchil in 2008. These females from Calaxchil were observed on several occasions during 2009 without other individuals.

Of the 96 individuals that were born during the study, 25 could be followed after they were 4 yr old. Of these, 13 were males and 12 were females. Four males disappeared from their groups during their fourth year (two males disappeared together from T61 Calax) and six during their fifth year. Seven females disappeared during their fourth year and one during her fifth year. As none of these 18 individuals showed signs of injury or illness before disappearing, it is probable that they emigrated. One adult female that was present in Tormento N at the beginning of the study disappeared in 2009, but rejoined the group during 2010 with a male infant with *ca.* 2 mo of age. One male that was born in Oxcabal in 2006 remained in the group until the end of the study, when he was >7 yr old. In R Álamo, one male that was *ca.* 3 yr old at the beginning of the study disappeared in 2009, when he was 7 yr old. In the same group, one male born in 2008 was still in group by the end of the study, when he 5 yr old and fully grown. Four females remained and reproduced in their natal groups, AA Álamo, Calaxchil, Oxcabal and T61 Calax. In all cases the adult male composition of their groups had changed with respect to when they were born. These females were between 4.7 and 5.3 yr of age when their first infants were born, suggesting that they were all at least four years old at conception (assuming a gestation of 6 mo: Van Belle *et al.* 2009).

Temporal Variation in Group Size and Composition

Group size ($F_{6,68} = 2.25$, $P = 0.049$), the number of juveniles in groups ($F_{6,68} = 6.05$, $P < 0.001$), and infant survival rate ($F_{5,44} = 28.17$, $P < 0.001$) varied significantly across years. *Post hoc* tests revealed that group size was significantly smaller in 2006 than in both 2011 and 2012, and in 2007 than in 2012 (all tests $P < 0.05$; Fig. 1a). There were fewer juveniles in groups during 2006 than in all other years (all tests $P < 0.05$; Fig. 1b). Infant survival rate was higher in 2006 than in 2007–2009; 2010 than 2007–2009 and 2011; 2011 than in 2007–2008 (all tests $P < 0.05$; Fig. 1c). There were no significant differences among years in the number of adults (males $F_{6,68} = 0.246$, $P = 0.959$; females $F_{6,68} = 2.07$, $P = 0.069$) and infants ($F_{6,68} = 1.44$, $P = 0.212$) in groups, sex ratio ($F_{6,66} = 0.992$, $P = 0.438$), and λ ($F_{5,58} = 0.45$, $P = 0.814$).

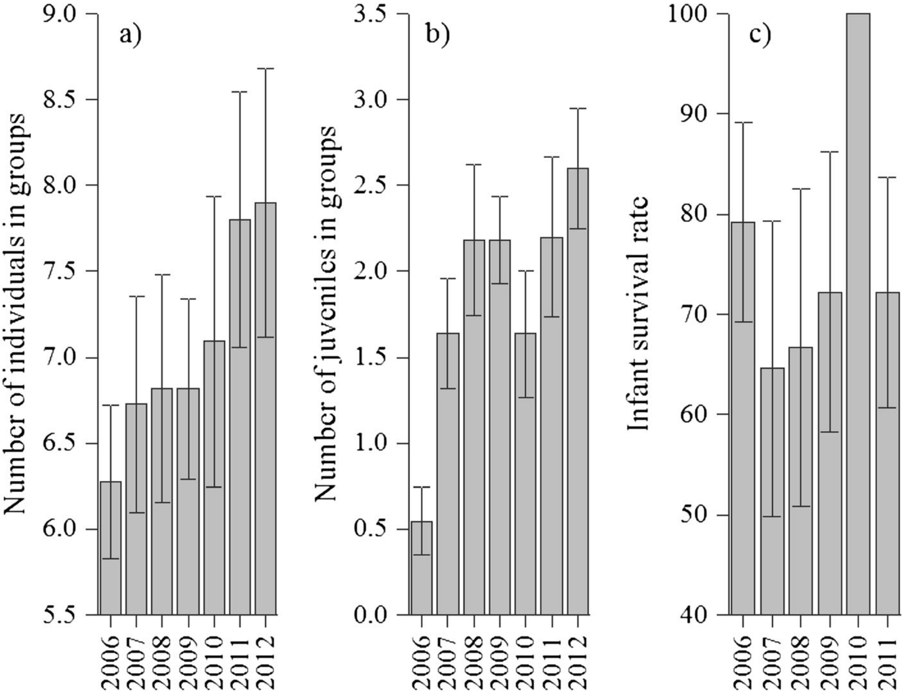

Fig. 1 Variation in mean (±SE) group size (**a**), number of juveniles in groups (**b**), and infant survival rate (**c**) among years in 11 groups of black howlers from 2006 to 2012 in Campeche, Mexico.

Effects of Habitat and Landscape Attributes on Group Dynamics

Larger groups lived in habitats with less complex shapes that were closer to roads (Table VI). Groups included more males in smaller forest fragments located in landscapes with more available habitat. In contrast, the number of females in groups increased in habitats with less complex shapes that were closer to roads and other fragments, and had low tree density. The presence of juveniles in groups was negatively related to distance to roads. Population growth was higher in habitats with less complex shapes. The proportion of females to males increased in groups that lived in habitats with less complex shapes, lower tree density, that were closer to roads and other fragments, and in landscapes with less available habitat. Infant survival was higher in habitats with lower shape complexity, tree density, and distance to nearest fragment. Finally, dispersal was more frequent in landscapes with more available habitat (Table VI). No significant model could be determined for the number of infants and immatures in groups or for infant-to-female and immature-to-female ratios.

Discussion

We documented variation in the size and composition of 11 groups of black howlers over 7 yr. Although group size, the number of juveniles in groups, and infant survival rates varied through time, most groups showed demographic stability. There were more

Table VI Significant effects calculated with Regression with Empirical Variable Selection (REVS) of habitat and landscape-scale factors on group dynamics in 11 groups of black howlers from 2006 to 2012 in Campeche, Mexico

Response variable/model	Parameter[a]	SE	t	P	VIF	AIC	ΔAIC	Adj R^2	P	MSE
Group size						9.75	0	0.54	0.04	6.43
Intercept	13.4	3.1	4.3	0.004						
Habitat amount	0.0	0.0	2.3	0.056	1.02					
SI	–2.6	1.1	–2.4	0.048	1.30					
DNR	–0.8	0.4	–2.3	0.054	1.29					
Males						–21.3	0	0.65	0.054	1.08
Intercept	1.2	0.8	1.5	0.198						
Habitat amount	0.0	0.0	3.9	0.011	7.81					
Habitat size	–0.7	0.2	–3.7	0.014	8.31					
SI	0.4	0.3	1.4	0.215	1.79					
DNR	–0.1	0.1	–1.2	0.301	1.42					
Females						–24.8	0	0.77	0.009	0.348
Intercept	8.5	1.1	7.7	<0.001						
SI	–1.7	0.3	–6.0	<0.001	2.05					
DNR	–0.3	0.1	–3.9	0.008	1.48					
DNH	–0.0	0.0	–3.4	0.015	2.33					
Tree density	–0.0	0.0	–3.4	0.014	2.91					
Juveniles						–10.4	0	0.52	0.045	1.26
Intercept	4.2	1.3	3.5	0.012						
SI	–0.9	0.4	–2.2	0.068	1.3					
DNR	–0.4	0.1	–2.6	0.036	1.29					
Habitat amount	0.0	0.0	2.1	0.073	1.02					
Lambda						–67.8	0	0.646	0.007	0.003
Intercept	1.3	0.1	17.6	<0.001						
SI	–0.1	0.0	–4.4	0.002	1.01					
Habitat size	0.013	0.0	1.5	0.176	1.01					
Sex ratio						5.35	31.95	0.75	0.03	0.145
Intercept	8.0	1.1	7.1	<0.001						
SI	–1.4	0.3	–5.4	0.003	2.41					
DNH	–0.0	0.0	–4.9	0.005	3.38					
Habitat amount	–0.0	0.0	–3.1	0.030	1.48					
Tree density	–0.0	0.0	–4.6	0.004	3.55					
DNR	–0.2	0.1	–2.8	0.040	1.60					
Infant survival rate						–15.1	35.3	0.82	0.029	0.033
Intercept	2.8	0.5	6.0	0.004						
SI	–0.5	0.1	–4.6	0.010	2.43					
Tree density	–0.0	0.0	–3.7	0.022	3.57					
DNR	–0.1	0.0	–2.7	0.056	1.70					
DNH	–0.0	0.0	–2.8	0.051	3.41					
Habitat amount	0.0	0.0	0.3	0.816	2.55					

Table VI (continued)

Response variable/model	Parameter[a]	SE	t	P	VIF	AIC	ΔAIC	Adj R^2	P	MSE
Dispersal						8.5	0	0.52	0.021	4.27
Intercept	–0.1	1.1	–0.1	0.902						
Habitat amount	0.0	0.0	3.6	0.007	1.77					

SI = shape index; DNR = distance to nearest road; DNH = distance to nearest habitat.

[a] 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 (ΔAIC), adjusted R^2, P values, and prediction accuracy of each model (MSE, mean squared error) are also indicated.

male than female births, but the proportion of males that disappeared before reaching sexual maturity was notably higher. We also found that variation in demographic structure and dynamics among groups was affected by habitat and landscape-scale factors. Although the study was performed at the group level, rather than at a population level, we are confident that our results are representative of the population dynamics of this species in this region because the study encompassed several years and included both several groups and habitats.

Group Composition and Size

Over the course of more than one generation, group structure tended to be stable, and the composition of the studied groups was comparable to that reported by previous studies for both this and other howler species, except for mantled howlers (Di Fiore *et al.* 2011). Group size increased over the years, mostly due to moderate to high infant survival rates and an increase in the number of juveniles. There was no temporal variation in the number of adults and infants in groups, ratios of infants to adult females and immatures to adult females, sex ratio and λ. The reduced annual variation in these demographic parameters, combined with the frequent disappearance of individuals resulted in total finite growth ratios indicating equilibrium.

In addition to births and deaths (discussed later) group size and composition varied through dispersal events. As reported for other black howler populations (Brockett *et al.* 2000) and other howler species (Clarke and Glander 2008; Crockett 1984) only a small proportion of individuals stayed in their natal groups, and we could not identify any clear difference in emigration between the sexes. It is possible that female philopatry occurs only when inbreeding probabilities are low, because all cases of females remaining in natal groups were associated with changes in adult male group composition with respect to when they were born. Most females disappeared from their natal group during their fourth year, whereas male disappearances after the juvenile stage mostly occurred during their fifth year, suggesting that emigration was associated with sexual maturity. This sex difference in dispersal age is similar to that reported in ursine howlers (Pope 2000). We observed aggression directed toward young adult females by nonmother females and males preceding some female emigrations (Rangel-Negrín *unpubl. data*), supporting the suggestion that aggression may be the proximate cause of female dispersal in howlers (Brockett *et al.* 2000; Crockett 1984).

This observation and the rarity of female immigrations indicate that adult female residence is very stable in this species. In fact, in all groups some individuals were present throughout the entire study, indicating group tenure for males and females of ≥7 yr. Concerning male immigrations, the takeover of groups by male coalitions was never observed, but we found evidence that young adult males sometimes emigrated together from their natal groups. The invasion of groups by solitary males was infrequent, but when it occurred, it usually did not result in the expulsion of resident males (the exception was AA Álamo in 2009), a pattern that had been previously observed in this species (Horwich *et al.* 2001; Van Belle *et al.* 2008) as well as in ursine howlers (Crockett and Sekulic 1984).

Births and Deaths

We identified a very significant concentration of births in the wet season. Future studies should focus on determining birth distribution within each season and relate it to variation in biotic and abiotic factors known to affect infant survival in primates (e.g., food availability and climate: Janson and Verdolin 2005). There is evidence that the wet season is a period of high fruit abundance in the Yucatan Peninsula (Schaffner *et al.* 2012), and that lactating black howler females spend more time consuming fruits as a possible strategy to offset the energetic demands of lactation (Dias *et al.* 2011). Black howlers are more frugivorous than other species of this genus (Behie and Pavelka 2015; Dias and Rangel-Negrín 2015) for which no reproductive seasonality has been found (e.g., brown howlers: Strier *et al.* 2001). It is therefore possible that birth seasonality in the current study is the result of synchronization of lactation with high fruit availability, as observed in other primates (van Schaik and van Noordwijk 1985).

Almost one-third of all infants observed during the study disappeared, indicating high mortality in this age class. The most common causes of mortality affecting infant howlers are infanticide and food restrictions. In ursine, brown, and red howlers infanticide is estimated to account for 25, 44, and 53% of infant deaths, respectively (Crockett 2003). In black howlers only two infanticides have been directly observed (Van Belle *et al.* 2010). In the present study we did not observe infanticide, but infant disappearance was associated with male immigrations on at least three occasions. Therefore, the impact of infanticide on infant mortality rates in this species remains to be determined, although the fact that group size was consistently small supports the suggestion that in large groups individual reproductive success may decrease as a consequence of higher infanticide risk (Crockett and Janson 2000; Van Belle and Estrada 2008).

It has been suggested that immature mantled howlers may be vulnerable to dietary stress during periods of scarcity, leading to a higher death rate of infants compared to other age classes (Cristóbal-Azkarate *et al.* 2005; Froehlich *et al.* 1981; Milton 1982). In this sense, infant mortality may be a sensitive indicator of changes in habitat quality, particularly food availability (Altmann *et al.* 1985). This possibility is supported by the negative relationship we found between infant survival and tree density. In the tropics, low tree density occurs in mature old-growth forests (Laurance *et al.* 1998b), where fruit abundance is higher compared to secondary forests because trees are larger (Arroyo-Rodríguez and Mandujano 2006; Laurance *et al.* 2000). As immature black howlers rely on lactation as their main food supply for at least their first 10 mo of life

(Dias *et al.* 2011), the putative negative effects of vegetation disturbance on infant survival are probably linked to a reduction in nursing quality by mothers that face reduced access to food resources (e.g., low fat stores: Emery Thompson 2013). For instance, we found that in several of the same groups sampled in the present study, the amount of leaves consumed is negatively predicted by habitat size (Dias *et al.* 2014). This effect of dietary stress on immature survival could also explain why almost 30% of individuals disappeared during the juvenile stage. The number of juveniles in groups tended ($P = 0.07$) to increase with increasing plant species richness and DBH, which reflect diversity and abundance of food, respectively. Therefore, increased availability of easily harvested and highly digestible foods (i.e., weaning foods: Altmann 1980) during the weaning period could favor juvenile survival in some of the larger habitats.

In addition, juvenile mammal males show higher vulnerability to nutritional stress and starvation due to faster growth rates and lower levels of fat reserves than females, and as a consequence have higher mortality rates (Clutton-Brock *et al.* 1985). The body mass of adult black howler males is between 22 and 41% higher than that of females (Kelaita *et al.* 2011), and adult body size is reached at 5 yr by males and 4 yr by females (Kitchen 2000), indicating that growth rates must vary significantly between sexes during the juvenile period. Because there are no apparent behavioral differences between female and male juveniles that could result in higher male mortality due to predation or physical injury, the fact that males disappeared more frequently than females suggests a higher mortality rate in male black howler juveniles associated with the interaction between food restrictions and the physiological costs of growth. Despite of such strong male biased immature mortality, the sex ratio in the groups was low and quite constant through time. This trend was probably associated with the fact that many more males than females were born. Male biased sex ratios have been reported for ursine howlers and were associated with high population density (Rudran and Fernández-Duque 2003), although in black howlers living at very high densities no such bias was observed (Horwich *et al.* 2001). Adaptive explanations for the causes of skewed sex ratios at birth are unclear (Silk and Brown 2004). There is, however, evidence suggesting that local resource competition may contribute to variation in sex ratios at birth. In spider monkeys (*Ateles geoffroyi*), for instance, when habitat productivity is low, resource competition is higher within groups, and fewer individuals of the philopatric sex (i.e., males) are produced (Chapman *et al.* 1989). In the current study, a higher proportion of females than males stayed in their natal groups, suggesting that, some level of local resource competition may arise among females in this species, which could favor male biased sex ratios at birth.

Finally, predation and disease are important mortality causes in howlers (Bianchi and Mendes 2007; Collias and Southwick 1952; Holzmann *et al.* 2010; Milton 1996). There is no evidence for age–sex differences in susceptibility to predation in howlers. Both yellow fever infections and botfly infestations are easy to identify in the field as howlers are highly susceptible to yellow fever, so they rapidly develop the disease and die (Holzmann *et al.* 2010) and larval pores are easily observed in individuals infected with botfly. We observed neither a mortality event that could be associated with a yellow fever outbreak nor botfly infestations. Therefore, because infanticide, predation, and disease did not exert an important effect on the studied groups, it is possible that frequent immature disappearance reflects mortality caused by food deprivation.

Habitat and Landscape-Scale Influences on Black Howler Group Structure and Dynamics

Group structure and dynamics were affected by both habitat and landscape attributes, supporting the idea that the analysis of the persistence of arboreal primates in disturbed habitats must be performed at multiple spatial scales (Anzures-Dadda and Manson 2007; Arroyo-Rodríguez *et al.* 2013; Ordóñez-Gómez *et al.* 2014). Most demographic parameters were affected by habitat-scale attributes, such as shape, size and isolation, distance to nearest road and human settlement, and tree density. For instance, the past (λ and infant survival rate) and current (number of adult females) reproductive potential of the groups were exclusively predicted by habitat-scale attributes. Therefore, although processes occurring at a landscape-scale may influence the maintenance of black howler populations (Anzures-Dadda and Manson 2007; Asensio *et al.* 2009; Mandujano and Estrada 2005; Pozo-Montuy *et al.* 2013), group demographics are affected mainly by factors acting at a local scale. This is probably related to the fact that although howlers can move through highly disturbed matrices to supplement their diet (Asensio *et al.* 2009; Pozo-Montuy *et al.* 2013), groups mostly rely on food resources present in their habitats. Thus, vegetation attributes of habitats are expected to impact the behavior, nutritional status, and ultimately, reproduction of individuals. Accordingly, our analyses revealed that shape (a proxy for edge effects and consequent vegetation disturbance: Laurance *et al.* 1998a; Saunders *et al.* 1991) and tree density (discussed previously) affected demographic parameters as predicted under the hypothesis that vegetation disturbance has negative effects on howler populations (Arroyo-Rodríguez and Dias 2010). Furthermore, proximity to roads and human settlements resulted in fewer females and juveniles in groups, as well as lower infant survival, suggesting that anthropogenic activities occurring inside some habitats could negatively affect howlers (Arroyo-Rodríguez *et al.* 2008b). In our study Chicbul represents a prime example of such effects. People used the fragment on a daily basis, usually to collect wood or to access other properties. Logging was also recurrent, although before 2011 was usually of low intensity (*ca.* 10 trees per year: Rangel-Negrín *unpubl. data*). In 2011 the owner of the property decided to log the entire forest to establish a palm plantation for oil production (a relatively new threat to forests in Campeche that has grown considerably during the last decade). As a result of reports of black howler infants being sold in the area around the moment of infant disappearances in this group, and changes in the behavior of fully habituated individuals in response to the presence of researchers, we also suspect that people captured infants from this group on at least two occasions.

Dispersal events were infrequent, so we were unable to perform independent analyses of immigration and emigration patterns. Overall, dispersal was more frequent in landscapes with more habitat, fewer fragments, and fewer isolated fragments. At the habitat scale, habitat size and vegetation attributes (plant species richness and DBH) had positive effects on dispersal, whereas distance to nearest habitat was negatively related to dispersal. If, as in other howler populations (Cristóbal-Azkarate *et al.* 2005), in this area population size is positively related to habitat size, the likelihood of dispersal should increase in larger habitats and in landscapes with more habitat due to a higher number of individuals moving within their habitats. However, the negative effects of habitat and landscape isolation on dispersal also suggest that individuals may move between habitats, supporting previous evidence that the probabilities of dispersal of howlers in fragmented landscapes depend on the ability of individuals to cross nonforested areas (Cristóbal-Azkarate *et al.* 2004; Dias *et al.* 2013; Estrada and Coates-Estrada 1996; Mandujano and Estrada 2005). Therefore, our results suggest that black howlers are dispersing both within and among fragments.

Interestingly, several parameters usually employed to quantify female reproductive success in howlers (number of infants and immatures in groups, ratio of infants to females, and ratio of immatures to females: Arroyo-Rodríguez *et al.* 2008a; Cristóbal-Azkarate *et al.* 2005; Horwich *et al.* 2001) did not vary significantly among groups according to the analyzed factors (i.e., habitat and landscape-scale attributes). We suggest that this is the result of a highly significant correlation in our sample between the number of females in groups and both the number of infants (Pearson $r = 0.76$, $P = 0.006$) and immatures ($r = 0.79$, $P = 0.004$), which suggests that females reproduced at similar rates across groups, and of the fact that interbirth intervals did not show a significant reduction when infants died before reaching 1 yr (14 mo) compared with infants that survived (16 mo). Therefore, female fertility did not vary significantly with habitat type, whereas female fecundity did, as there were significant differences among groups in infant survival. This result questions previous speculations of reduced fertility of female howlers in highly disturbed habitats (Cristóbal-Azkarate *et al.* 2005; Martínez-Mota *et al.* 2007; Terborgh *et al.* 2001). Future research should investigate the possibility that female reproductive output is not affected by habitat disturbance.

Conservation Implications

Howlers are commonly considered to be highly resilient to habitat disturbance, and sometimes described as a pioneer or colonizing genus (e.g., Rosenberger *et al.* 2009). These ideas are based on the observation that howlers are frequently encountered in habitats where other primate and nonprimate mammals are absent, usually due to anthropogenic disturbance (Rangel-Negrín *et al.* 2014a). However, our results indicate that population growth and infant survival were negatively related to habitat disturbance, whereas dispersal was dependent on the amount of habitat in the landscapes. Therefore, populations of black howlers that are found in highly disturbed habitats may be composed of many adult individuals born before disturbance occurred, and/or by individuals that come from less disturbed habitats. Concluding that howlers are highly resistant to habitat disturbance because they are present in disturbed habitats without considering the historical context of populations may therefore be a dangerous oversimplification and lead to erroneous conservation decisions, such as lack of conservation action where it is necessary. In this context, our results emphasize the importance of gathering long-term data on population structure and dynamics for planning actions directed at conserving howler populations.

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