THE INFLUENCE OF STOCHASTIC EVENTS ON THE EXTINCTION RISK OF BLACK HOWLER MONKEY (*ALOUATTA PIGRA*) POPULATIONS IN CAMPECHE, MEXICO

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Abstract

Population viability analysis (PVA) allows assessing extinction risk, which is of paramount importance for conservation and natural resource management practices. In addition to the modeling of the influence of deterministic demographic processes on the extinction risk of populations, PVA allows simulating the consequences of stochastic factors. The aim of the present study was to model the potential effects of two stochastic sources of variation, anthropogenic disturbance events (ADE) and hurricanes, on demographic parameters of extinction risk for 11 populations of the Endangered black howler monkey, in Campeche, Mexico. Models were built using information collected during a seven-year demographic monitoring of the populations, as well as on published life history data. We used the software VORTEX to study four extinction parameters: population growth rate; final population size; probability of extinction; years to extinction. For each population we ran five models: a baseline model; one model with 5% increase in the frequency of ADE; one model with 10% increase in ADE; one model with 5% increase in hurricanes; one model with 10% increase in hurricanes. We ran a sixth model excluding ADE for populations that were known to be exposed to ADE in baseline models. Hurricanes did not impact extinction parameters. As ADE increased, population growth rate, final population size, and years to extinction decreased, whereas probabilities of extinction increased. When ADE was removed, population growth decreased more slowly, populations included more individuals, and extinction became less probable and was delayed. Small populations that were not affected by ADE faced high extinction risk. ADE is thus predicted to be a major stochastic factor influencing the extinction risk of black howler monkeys in Campeche, although population size is also determinant for long-term viability. Through PVA based on long-term demographic data, this study is the first to ascertain that decreasing anthropogenic disturbance may benefit the persistence of threatened populations of this species.

Keywords: Anthropogenic disturbance, conservation, extinction, hurricanes, population viability analysis

Resumen

Los análisis de viabilidad poblacional (AVP) permiten establecer el riesgo de extinción, lo cual es sumamente importante para la conservación y manejo de los recursos naturales. Además de permitir conocer la influencia de procesos demográficos determinísticos en el riesgo de extinción de las poblaciones, los AVP permiten simular las consecuencias de factores estocásticos. El objetivo de este estudio fue modelar los efectos potenciales de dos fuentes de variación estocástica, eventos de disturbio antrópico (EDA) y huracanes, en los parámetros demográficos de extinción de 11 poblaciones de monos aulladores negros en Campeche, México. Los modelos fueron construidos con base en información colectada durante el monitoreo demográfico de las poblaciones durante siete años, así como en datos publicados sobre la historia de vida de esta especie. Usamos el software VORTEX para estudiar cuatro parámetros de extinción: tasa de crecimiento poblacional; tamaño poblacional final; probabilidad de extinción; años hasta la extinción. Corrimos cinco modelos para cada población: un modelo base; un modelo con un incremento del 5% en la frecuencia de EDA; un modelo con un incremento del 10% en la frecuencia de EDA; un modelo con un incremento del 5% en la frecuencia de huracanes; un modelo con un incremento del 10% en la frecuencia de huracanes. Corrimos un sexto modelo excluyendo EDA para aquellas poblaciones que sabíamos que estaban expuestas a EDA. Los huracanes no afectaron los parámetros de extinción. A medida que los EDA aumentaron, la tasa de crecimiento poblacional, el tamaño poblacional final, y los años hasta la extinción disminuyeron, mientras que la probabilidad de extinción aumentó. Cuando excluimos los EDA, la disminución en el crecimiento poblacional fue más lenta, las poblaciones incluyeron más individuos, y la extinción se volvió menos probable o fue demorada. Las poblaciones pequeñas no afectadas por EDA enfrentaron un riesgo de extinción alto. Por lo tanto, se predice que los EDA son un factor estocástico que influye de manera importante sobre el riesgo de extinción de los monos aulladores negros en Campeche, aunque el tamaño poblacional es también determinante para la viabilidad a largo plazo. Con base en un AVP en el que usamos datos demográficos de largo plazo, este estudio es el primero que establece que una reducción en la perturbación antropogénica puede favorecer la persistencia de poblaciones amenazadas de esta especie.

Palabras clave: Disturbio antrópico, conservación, extinción, huracanes, análisis de viabilidad poblacional

Introduction

The International Union for Conservation of Nature and Natural Resources (IUCN) defines a taxon as extinct "when there is no reasonable doubt that the last individual has died" (IUCN, 2016). In practice, however, extinction may effectively occur when individuals belonging to only one sex remain in species with sexual reproduction (usually termed quasi-extinction, e.g., *Chelonoidis nigra abingdonii*: Nicholls, 2006), or when population size is inferior to that required to assure persistence (Shaffer, 1981). Given the numerous current threats to biodiversity (Laurance, 1999), understanding extinction processes and assessing extinction risk are of paramount importance in the context of conservation and natural resource management practices (Regan et al., 2005; Cardillo et al., 2008; Mace et al., 2008).

Deterministic models have been used for more than 40 years to study the effects of demographic fluctuations on the extinction risk of many species (Miller et al., 1974). In these models, demographic parameters (e.g., population growth rate) are deterministic functions of environmental variables, and variability in demographic parameters is considered negligible. In contrast, stochastic models focus on the effects of factors of uncertain nature on demographic parameters, such as demographic, environmental, and genetic stochasticity, as well as natural catastrophes (Shaffer, 1981). Both types of models have been used in the implementation of population viability analysis (PVA), which aims at calculating the probability that a population persists for some particular time (Beissinger and McCullough, 2002). Currently, demographic modeling through PVA represents a powerful tool for biodiversity conservation and management, and has been conducted to predict the extinction risk of a wide range of animal populations (e.g., Pe'er et al., 2014), including several primate species (e.g., King et al., 2013; Zeigler et al., 2013).

Black howler monkeys (*Alouatta pigra*) are arboreal Neotropical primates with a geographic distribution restricted to the Yucatán Peninsula in Mexico, Belize and north and eastern Guatemala (Cortés-Ortiz et al., 2015). This species is currently classified by the IUCN as Endangered and there is a trend for decreasing population sizes (Marsh et al., 2008), which, similarly to other howler monkey species, is strongly associated to anthropogenic disturbance (Arroyo-Rodríguez and Dias, 2010; Estrada, 2015). We have recently reported seven years of demographic data for 11 groups of black howler monkeys living in distinct populations in the Mexican state of Campeche (Dias et al., 2015). Campeche represents the state with the largest potential amount of suitable habitat for black howler monkeys in Mexico (Tobón et al., 2012), and likely, the largest population. Our results indicate that several habitat (e.g., habitat size, tree density, distance to human settlements) and landscape-scale attributes (the amount of available habitat, number of forest fragments) affect group structure and dynamics in this region (Dias et al.,

2015). For instance, infant survival is negatively related to tree density, shape of the fragments and distance to human settlements, and population growth is negatively affected by vegetation disturbance. Thus, extinction risk could vary among populations according to stochastic anthropogenic disturbance events, such as logging, fires, or hunting.

Campeche is affected by hurricanes originating in the north Atlantic Ocean basin (CONAGUA, 2016). Hurricanes have the potential to cause extreme environmental disturbance, and there are several accounts of the impact of these climatic events on animal populations (e.g., Lugo, 2008). For black howler monkeys, 88% reduction in the size of a population that lived in the path of a Category 4 hurricane (Saffir–Simpson Scale: NOAA, 2016) has been documented (Pavelka et al., 2007). Therefore, in addition to anthropogenic disturbance hurricanes may represent an important source of stochastic variation in demographic parameters in populations of this species living in Campeche, and as a consequence, affect their extinction risk. Furthermore, there is evidence that the frequency of intense hurricanes (Categories 4 and 5 of the Saffir–Simpson Scale: NOAA, 2016) in the Atlantic basin has been increasing (Webster et al., 2005), suggesting that in the future these extreme climatic events may pose stronger threats to black howler monkeys.

The aim of the present study was to perform a PVA to determine the potential effects of two stochastic sources of variation in demographic parameters on the extinction risk of 11 populations of black howler monkeys living in Campeche. To this end, we modeled the effects of variation in the frequency of hurricanes and anthropogenic disturbances on four extinction parameters: population growth rate; final population size; probability of extinction; years to extinction. Specifically, we expected that, as the frequency of hurricanes and anthropogenic disturbances increased, population growth rate, final population size, and years to extinction would decrease, whereas the probability of extinction would increase. To better understand which factors besides demographic stochasticity could relate to the observed results, we also explored the relationship between habitat size and extinction parameters, as habitat size has been found to consistently predict population size and distribution range of howler monkeys (Arroyo-Rodríguez and Dias, 2010).

Methods

Study site and subjects
We studied 11 groups of black howlers that lived in different locations in Campeche, Mexico (spatial and ecological attributes of the study sites are thoroughly described in Dias et al., 2014, 2015; Fig. 1). 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 study
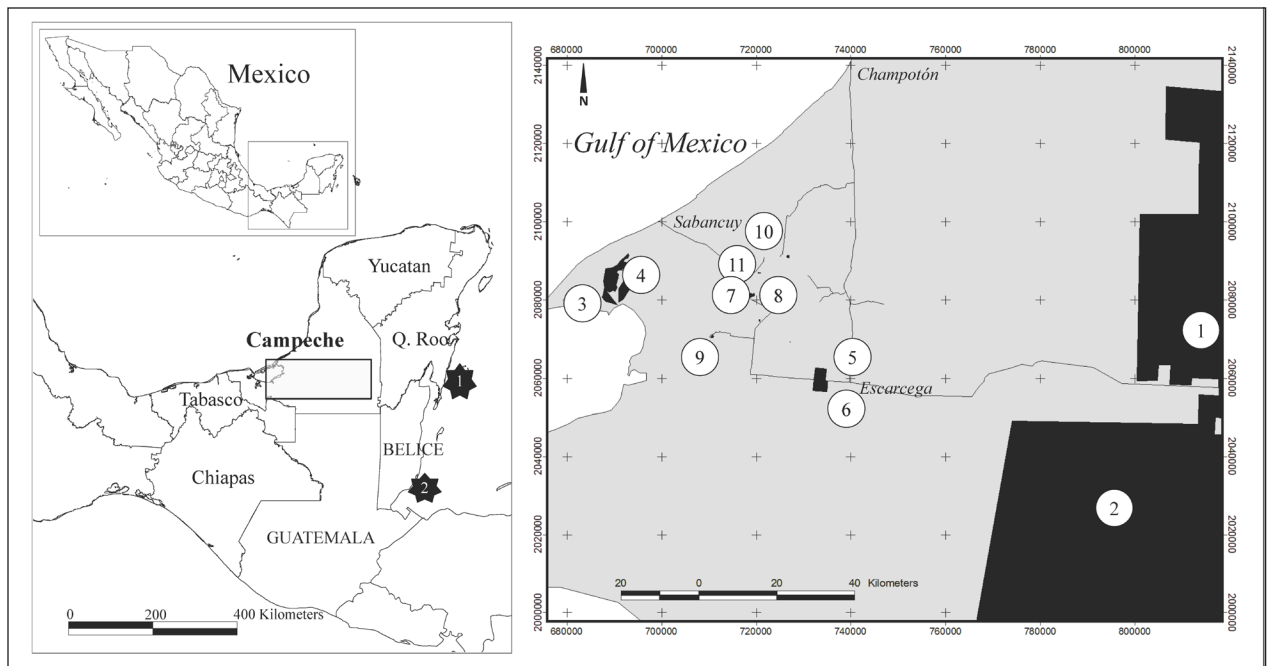
Figure 1. Location of the 11 populations of black howler monkeys studied in the state of Campeche (Mexico). The approximate location of the study area is represented in the map on the left by a light grey rectangle. Groups: 1 = Calakmul N, 2 = Calakmul S, 3 = Calaxchil, 4 = Calaxchil, 5 = Tormento N, 6 = Tormento S, 7 = AA Álamo, 8 = Chicbul, 9 = Manantiales, 10 = Oxcabal, 11 = R Álamo. Black stars in the map on the left represent approximate locations of (1) hurricane Dean landfall, and (2) the Monkey River study site.

encompassed total area of approximately 20,000 km² (Fig. 1), where original forest cover is mainly composed of medium to high semi-evergreen vegetation (Escalona-Segura and Vargas-Contreras, 2010).

Demographic data

Censuses of black howler monkey groups were carried out between February 2006 and February 2012, except for Chicbul (location 8 in Fig. 1) where the fragment was logged in February 2011 and we could not locate the group anymore. We recognized all individuals via ankle bracelets or their natural anatomical and physiognomic characteristics, such as body size and proportions, scars, broken fingers, and genital morphology and pigmentation (Dias et al., 2015). Each year, we sampled each group at least twice in each climatic season (i.e., dry and wet season). Each season sampling included a mean (±SD) of 67 (±5.4) days, and we accumulated a total of 10,083 sampling days, with a mean (±SD) of 918.5 (±125.3) per group.

Five of the 11 study groups (T61 Calax, AA Álamo, Chicbul, Oxcabal, R Álamo) lived in forest fragments that did not contain any other groups. In these cases, demographic data represented population-level demographics. For the remaining fragments, our data represents a sample of population-level demographics. We are, however, confident that our results for those groups are representative of population-level demographics because 1) the study encompassed several years and 2) sampled groups lived under ecological and social conditions similar to those of other groups within their habitats (Dias et al., 2015; Dias, unpublished data).

Our demographic monitoring allowed acquiring data on reproductive system, reproductive rates, mortality rates, catastrophes, and initial population size, which are essential for PVA modeling (Table 1; Lacy et al., 2015). Mortality rates for individuals > 4 years of age could not be directly estimated, because the disappearance of both males and females at this age could result from emigration (Dias et al., 2015). Therefore, we assumed a constant annual mortality rate of 1% for females and 1.5% for males of ages > 4 years in all groups and a standard deviation (SD) due to environmental variation of 0, as used before in studies of other Ateline species lacking direct estimations of mortality for the adult class (Britto and Grelle, 2006). By setting SD to 0, we omitted the effect of environmental variability on mortality rates of adult individuals (Lacy et al., 2015), although they were still affected by the severity of catastrophes (see below). To calculate initial population size, during the first sampling of each group we conducted censuses of the entire fragments for the presence of black howler monkeys following the methods described in Estrada et al. (2002) and Dias et al. (2013). Population density was calculated by dividing the total number of censused individuals by the area of the fragments that were surveyed, and population size was calculated by multiplying population density by the size of the fragment. These fragment-scale censuses were repeated three times during the study period, and we used mean values for the three censuses in simulations. Because there is not a quantitative estimation for carrying capacity in *Alouatta* (Mandujano and Escobedo-Morales, 2008), we followed previous PVA for other primates in assuming that all populations lived at carrying capacity (e.g., Holst et al., 2006; Ziegler et al., 2013). Thus, in this study

initial population size equates carrying capacity. Similarly, because there are no estimations of migration rates in black howler monkeys, all models were run under a single population scenario, not allowing dispersion to occur.

Stochastic events data
We modeled two types of stochastic events: hurricanes and anthropogenic disturbance events. In the period of 1924 to 2014, seven intense hurricanes (Categories 4 and 5: NOAA, 2016) made landfall in Mexico (CONAGUA, 2016). Of these, only three passed through Campeche (NHC, 2016). Therefore, the annual rate of occurrence of intense hurricanes in Campeche for this 90-year period was 0.03 (Table 1). In August 2007, a Category 5 hurricane (hurricane Dean) made landfall in the Yucatán Peninsula, ca. 200 km from our easternmost field site (Calakmul N; Fig. 1). In the aftermath of the storm we observed an increase in infant mortality in all sampled populations (Dias et al., 2015), and therefore defined in our models survival in hurricane years as 60% of that recorded in non-hurricane years. Although we did not notice a direct effect of the hurricane on the reproduction of individuals in Campeche, it is possible that it actually had an effect and our sampling

scheme did not allow us to detect it. Other researchers have observed occasional adult female mortality during storms, and suggested that food shortages resulting from habitat modification could reduce adult female fecundity (e.g., Behie and Pavelka, 2015). We therefore considered that 95% of the reproduction recorded in non-hurricane years should occur after a hurricane.

We defined anthropogenic disturbance events (ADE) as: the destruction or modification of the habitat (logging, fires) caused by human activities, hunting, road-kills, and attacks by dogs (e.g., Rangel-Negrín et al., 2011). We recorded these events while sampling the groups, and calculated an annual frequency of ADE per group as the number of days in which ADE were observed divided by the number of sampling days. ADE were only observed in AA Álamo, Chicbul, Manantiales, Oxcabal, and R Álamo, so for simplicity of presentation of the models, we used a mean frequency of occurrence of ADE among these groups (Table 1). As in the case of hurricanes, we did not observe an effect of ADE on the reproduction of individuals; following the same reasoning explained above for the effects of hurricanes on reproduction, we considered that after an

Table 1. Simulation input derived from demographic data collected during seven years in 11 groups of black howler monkeys in Campeche, Mexico

Simulation input		Group a										
		1	2	3	4	5	6	7	8	9	10	11
Reproductive system	Sex ratio at birth (% of males)	57.1	58	47	50	53.8	50	60.7	85.7	60	77.8	62.5
Reproductive rates	% of adult females breeding	59.5	50	40.5	47.6	41.6	40.5	69	30	42.9	39.5	50
	SD in % breeding due to EV b	34.5	33.1	30.2	10	36	34	29	27	53.5	15.2	13
Mortality rates: females	0-1 years	10	10	10	10	15	10	30	13	35	20	30
	1-2 years	1	1	14	0	12	12	10	0	15	10	15
	2-3 years	1	15	1	5	15	0	15	20	2	9	10
	3-4 years	1	1	1	3	4	0	8	7	5	8	5
	> 4 years	1	1	1	1	1	1	1	1	1	1	1
Mortality rates: males	0-1 years	5	25	35	4	20	20	45	80	66.7	35	44.2
	1-2 years	1	1	16	0	14.4	10	0	0	15	18	15
	2-3 years	1	15	1	0	15	11	0	20	2	12	0
	3-4 years	5	1	1	5	4	2	15	7	5	8	5
	> 4 years	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5
Catastrophes: hurricanes	Frequency (%)	3	3	3	3	3	3	3	3	3	3	3
	Impact in reproduction	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95
	Impact in survival	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6
Catastrophes: anthropogenic disturbance	Frequency (%)	0	0	0	0	0	0	5	5	5	5	5
	Impact in reproduction	1	1	1	1	1	1	0.95	0.95	0.95	0.95	0.95
	Impact in survival	1	1	1	1	1	1	0.8	0.8	0.8	0.8	0.8
Initial population size/carrying capacity		2750	8884	57	6.9	60.6	127.2	44.8	6	14	7	10.6

[a] 1 = Calakmul N; 2 = Calakmul S; 3 = Calaxchil; 4 = T61 Calax; 5 = Tormento N; 6 = Tormento S; 7 = AA Álamo; 8 = Chicbul; 9 = Manantiales; 10 = Oxcabal; 11 = R Álamo.

[b] EV is environmental variation. EV is the annual variation in the probabilities of reproduction that arises from random variation in environmental conditions (Lacy et al., 2015). We used mean interannual SD in % of adult females breeding in each group.

ADE 95% of the reproduction should occur. Concerning survival, our observations indicated that between 0 and 90% of individuals could die after ADE, with a mean value of 20% (i.e., 80% of individuals survive; Table 1).

PVA models

We used VORTEX (version 10.0.7.0; Lacy and Pollak, 2014) to run our PVA. VORTEX is a free software program that allows modeling the impact of deterministic forces and stochastic events on wildlife population dynamics. Besides the demographic data described above, VORTEX requires additional information on the genetics, reproductive system, and mating behavior of the species (Table 2). For genetics, there is no information on the occurrence and consequences of inbreeding depression in black howler monkeys. We therefore used in our models the default severity of inbreeding depression suggested by Lacy et al. (2015). Concerning the reproductive system of the species, our data indicates that age of first offspring for female black howler monkeys is 5 years of age and 7 years for males (Dias et al., 2015). There is currently no data on the maximum lifespan of this species, but a closely related howler monkey species (*A. palliata*) has a lifespan of 30 years and females reproduce at least until 25 years of age (Glander, 2006). Due to close phylogenetic relatedness and similarity in the ecological conditions faced by these species (Cortés-Ortiz et al., 2015; Dias and Rangel-Negrín, 2015), we used lifespan and maximum age of reproduction reported for *A. palliata*. Female black howler monkeys give birth to a single infant, and produce a maximum of one infant per year (Dias et al., 2015). Although some adult males may be excluded from reproduction due to mating competition (Van Belle et al., 2012), they can potentially contribute to the breeding pool, so we considered that 100% of males can compete for mates (Table 1).

All models were run for 1,000 iterations and 100 years: 1,000 iterations allow for a rigorous description of the simulated population's behavior (Lacy et al., 2015); and 100 years is a time span sufficiently long to allow for the simulation of the occurrence of several infrequent stochastic events (i.e., hurricanes in the case of our simulations), but short enough to allow discussing realistic conservation and management actions (Fieberg and Ellner, 2000). Finally, we defined extinction as the absence of one sex, which is the most common choice when modeling the extinction process of sexually reproducing species (Lacy et al., 2015).

We started our modeling by running a baseline model for each population with the data described in Tables 1 and 2. We explored the relationship between habitat size and extinction parameters calculated for these baseline models with linear (population growth rate) and non-linear (final population size and extinction probabilities) regressions. We then ran four additional models with 5% and 10% increases in the frequency of hurricanes and ADE, respectively. For populations with baseline models that included ADE, we ran a sixth model excluding ADE. For each model we recorded four extinction parameters: population growth rate; final population size; probability of extinction; years to extinction. Population growth rate was calculated as:

$$r = \sum l_x m_x e^{-rx}$$

where l_x and m_x are the age-specific mortality and fecundity rates, respectively for age class x to $x+1$ (Lacy et al., 2015). Final population size was defined as the mean number of individuals in the population across all iterations, including those in which the population went extinct. Probability of extinction was calculated as the proportion of iterations in which the population went extinct. Years to extinction were calculated as the mean time to first population extinction

Table 2. Simulation input derived from the literature.

Simulation input		
Scenario settings[a]	Number of iterations	1,000
	Number of years	100
	Duration of each year	365 days
	Extinction definition	Only one sex remains
Species description	Lethal equivalents	6.29[a]
	Percent due to recessive lethal alleles	50[a]
Reproductive system		Polygynous[b]
	Age of first offspring females	5 years[c]
	Age of first offspring males	7 years[c]
	Maximum lifespan	30 years[d]
	Maximum number of broods per year	1[c]
	Maximum number of progeny per brood	1[c]
	Maximum age of reproduction	25 years[d]
Mate monopolization	% males in breeding pool	100[e]

[a] Lacy et al. (2015); [b] Van Belle et al. (2012); [c] Dias et al. (2015); [d] Glander (2006); [e] This study

considering iterations in which the population became extinct (Lacy et al., 2015). We describe the results by calculating percentage of change in extinction parameters between models as:

$$Percentage\ of\ change = \frac{I - F}{I} \times 100$$

where I is the initial and F is the parameter value.

Results

Baseline models
Only four of the 11 modeled populations showed a positive population growth rate and were extant by the end of the 100-year simulation (Table 3). Of these, three populations, Calakmul N, Calakmul S and Tormento S showed a -0.6%, a -2.2% and a -15% change from their initial to their final population sizes, respectively. The probabilities of extinction of the eight remaining populations varied from 33% (Calaxchil) to 100% (Chicbul and Oxcabal). Conversely, time to extinction varied notably, from 4.7 years in Chicbul to 84.5 years in Calaxchil (Table 3). Habitat size was associated positively with population growth ($R^2 = 0.81$, $P < 0.001$; Fig. 2a) and final population size ($R^2 = 0.98$, $P < 0.001$; Fig. 2b), and negatively with the probability of extinction ($R^2 = -0.94$, $P = 0.002$; Fig. 2c).

Effects of hurricanes on extinction parameters
Variation in hurricane frequency resulted in minor variation in extinction parameters in all populations (Table 3). With a 5% increase in hurricane frequency the mean proportion of decrease was 3.4±5.8% for population growth rate, 0.7±4.1% for final population size, 3.4±16.5% for probability of extinction and 0.1±1.7% for years to extinction. With a 10% increase in hurricane frequency this variation remained similar: 4.3±7.4% reduction in population growth rate; 1.2±3.6% reduction in final population size; 3.5±13.1% increase in probability of extinction; 1.02±2.4% reduction in years to extinction.

Effects of anthropogenic disturbance events on extinction parameters
With a 5% increase in ADE there was a mean proportion of decrease in population growth of 84.7±90.1%, and this decrease was particularly pronounced in some of the populations living in large habitats, such as Calaxchil (400% decrease), Tormento N (109%) and Tormento S (109%). Final population size decreased a mean of 18.2±18.3%, or 22.3±17.8% after excluding populations that had a final population size of 0 individuals in baseline models (i.e., Chicbul and Oxcabal). The probabilities of extinction increased on average 96.5±189% across all populations. This increase in ADE resulted in seven, four, and two-fold increases in extinction probabilities in Calaxchil, Tormento N and AA Álamo, respectively. With the exception of the Calakmul populations and Tormento S, 5% more frequent ADE reduced time to extinction by 9.7% (or a mean of 4.4±2.6 years). For instance, in Manantiales extinction

changed from 44 to 37 years. Of particular interest in this scenario was the change observed in Tormento S, which in the baseline model was extant after 100 years, but presented a probability of extinction of 0.4% with 5% increase in ADE, being predicted to become extinct in 80.3 years.

With a 10% increase in ADE, mean population growth decreased by 162.5±230%, final population size (for populations extant by the end of the simulation time) was 36.4±23.1% smaller, probabilities of extinction for
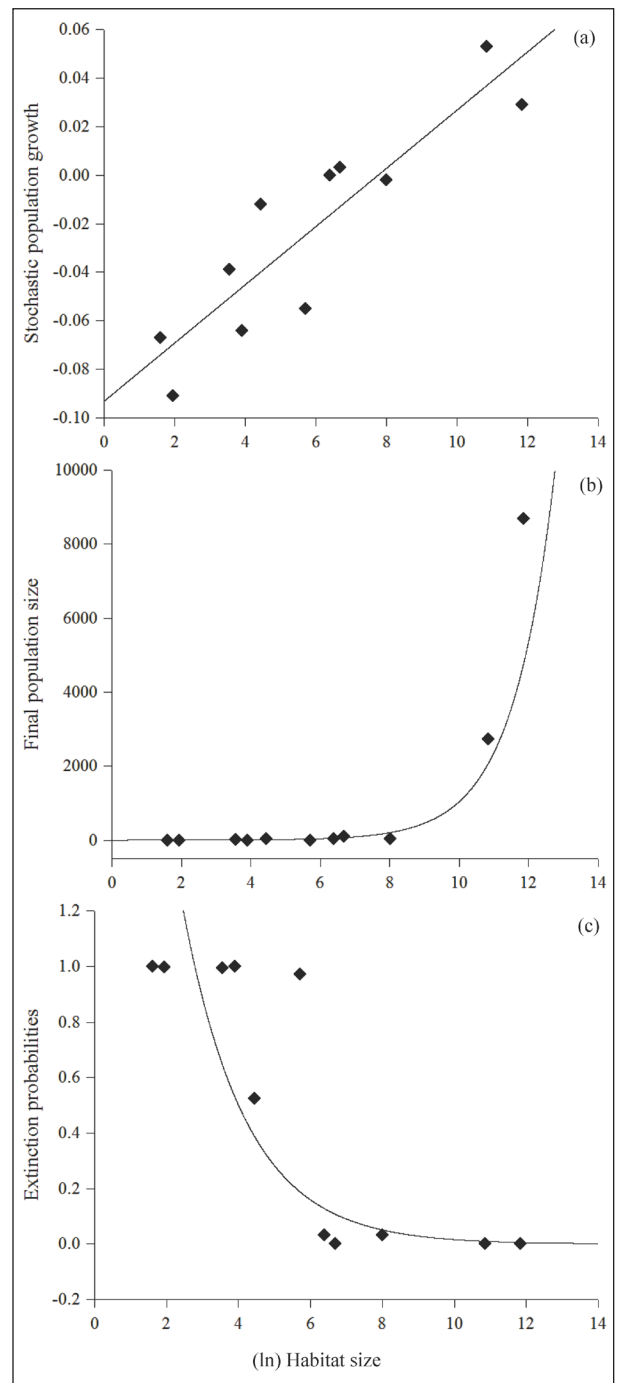

Figure 2. The relationships between habitat size and extinction parameters calculated using VORTEX (v. 10.0.7.0) for 11 populations of black howler monkeys in Campeche, México.

Table 3. Simulation (1,000 iterations) of the extinction process of 11 populations of black howler monkeys (*Alouatta pigra*) in Campeche (Mexico) over a 100-year period.

Population	Scenario [a]	Population growth rate (r) [mean(SD)]	Final population size [mean(SD)]	Probability of extinction	Years to extinction [b]
Calakmul N	Baseline	0.053 (0.05)	2732.3 (139.6)	0	>100
	5% more H	0.053 (0.05)	2733.4 (46.45)	0	>100
	10% more H	0.053 (0.05)	2731.1 (66.8)	0	>100
	5% more ADE	0.042 (0.07)	2665.5 (178.4)	0	>100
	10% more ADE	0.030 (0.09)	2535.8 (321.9)	0	>100
Calakmul S	Baseline	0.029 (0.05)	8692.9 (358.5)	0	>100
	5% more H	0.029 (0.05)	8681.2 (405.2)	0	>100
	10% more H	0.029 (0.05)	8694.4 (327.9)	0	>100
	5% more ADE	0.017 (0.73)	7984.3 (1208.5)	0	>100
	10% more ADE	0.007 (0.86)	6587.3 (2054.9)	0	>100
Calaxchil	Baseline	-0.003 (0.06)	33.98 (15.5)	0.033	84.5
	5% more H	-0.003 (0.06)	34.15 (15.4)	0.028	85.1
	10% more H	-0.003 (0.06)	34.72 (15.1)	0.030	85.0
	5% more ADE	-0.015 (0.09)	20.17 (13.6)	0.223	79.0
	10% more ADE	-0.026 (0.11)	13.07 (10.4)	0.533	72.2
T61Calax	Baseline	0.026 (0.12)	5.16 (1.52)	0.902	36.7
	5% more H	0.026 (0.12)	5.19 (1.42)	0.882	38.3
	10% more H	0.025 (0.12)	5.2 (1.5)	0.895	37
	5% more ADE	0.017 (0.14)	4.84 (1.29)	0.957	34.1
	10% more ADE	0.010 (0.15)	4.00 (1.41)	0.986	29.1
Tormento N	Baseline	-0.011 (0.08)	25.6 (15.5)	0.118	80.9
	5% more H	-0.012 (0.08)	25.23 (14.9)	0.178	81.4
	10% more H	-0.013 (0.08)	24.21 (15.2)	0.167	80.6
	5% more ADE	-0.023 (0.11)	14.7 (11.7)	0.441	74.5
	10% more ADE	-0.034 (0.12)	9.7 (8.22)	0.736	67.1
Tormento S	Baseline	0.011 (0.06)	108.15 (19.3)	0.000	>100
	5% more H	0.011 (0.06)	109.44 (17.3)	0.000	>100
	10% more H	0.011 (0.06)	109.69 (18.3)	0.000	>100
	5% more ADE	-0.001 (0.08)	77.04 (33.5)	0.004	80.3
	10% more ADE	-0.014 (0.1)	42.28 (31.9)	0.076	82.2
AA Álamo	Baseline	-0.016 (0.09)	18.3 (11.4)	0.33	70.6
	5% more H	-0.017 (0.09)	17.4 (11.6)	0.338	70.5
	10% more H	-0.017 (0.09)	17.9 (11.5)	0.352	69.1
	5% more ADE	-0.029 (0.11)	11.1 (8.0)	0.667	63.7
	10% more ADE	-0.040 (0.13)	8.1 (6.4)	0.882	56.6
	5% less ADE	-0.004 (0.05)	29 (12.5)	0.093	75.1
Chicbul	Baseline	-0.285 (0.18)	0.00 (0.0)	1	4.7
	5% more H	-0.286 (0.18)	0.00 (0.0)	1	4.7
	10% more H	-0.287 (0.18)	0.00 (0.0)	1	4.7
	5% more ADE	-0.296 (0.19)	0.00 (0.0)	1	4.5
	10% more ADE	-0.297 (0.19)	0.00 (0.0)	1	4.5
	5% less ADE	-0.064 (0.14)	0.00 (0.0)	1	24.4

Table 3. *continued from previous page*

Population	Scenario [a]	Population growth rate (r) [mean(SD)]	Final population size [mean(SD)]	Probability of extinction	Years to extinction [b]
Manantiales	Baseline	-0.029 (0.13)	5.71 (3.59)	0.951	44.3
	5% more H	-0.030 (0.13)	4.93 (2.35)	0.954	44.1
	10% more H	-0.030 (0.13)	6.13 (3.1)	0.944	43.3
	5% more ADE	-0.038 (0.14)	5.6 (2.67)	0.985	37.2
	10% more ADE	-0.047 (0.16)	4.6 (3.21)	0.995	31.6
	5% less ADE	-0.021 (0.12)	7.11 (3.19)	0.86	51.2
Oxcabal	Baseline	-0.064 (0.15)	0.00 (0.0)	1	13.2
	5% more H	-0.064 (0.15)	0.00 (0.0)	1	12.9
	10% more H	-0.067 (0.15)	0.00 (0.0)	1	12.2
	5% more ADE	-0.070 (0.16)	0.00 (0.0)	1	11.7
	10% more ADE	-0.079 (0.17)	0.00 (0.0)	1	10.4
	5% less ADE	-0.060 (0.14)	0.00 (0.0)	1	14.3
R Álamo	Baseline	-0.011 (0.14)	5.33 (2.16)	0.951	36.5
	5% more H	-0.013 (0.14)	5.97 (2.49)	0.964	35.8
	10% more H	-0.013 (0.14)	4.79 (1.79)	0.961	36.4
	5% more ADE	-0.021 (0.15)	3.61 (1.54)	0.982	31.3
	10% more ADE	-0.029 (0.16)	4.60 (2.07)	0.995	26.8
	5% less ADE	-0.004 (0.12)	5.8 (2.16)	0.901	41.6

[a] H is hurricanes; ADE is anthropogenic disturbance events; [b] Models were run for a 100-year period. Therefore, time to extinction for populations that were not extinct in this period is represented as >100 years.

populations predicted to become extinct in baseline models increased 370.8±463%, and time to extinction was reduced 19.1±10.1 years. Under this scenario, only two populations would be extant in 100 years, 45.5% of all populations would become extinct in approximately 30 years and 81.8% in approximately 80 years. When ADE were removed from models of populations known to be exposed to their effects (AA Álamo, Chicbul, Manantiales, Oxcabal, R Álamo), population growth increased 50±31.6%, population size increased 30.6±25.4% (excluding Chicbul and Oxcabal, which were still predicted to include no individuals by the end of the simulation), probabilities of extinction decreased 28.9±30.7%, and time to extinction increased 92.7±182%, compared to baseline. In this scenario it was noteworthy the change in time to extinction in Chicbul, which increased approximately 20 years.

Discussion

Variation in the frequency of anthropogenic disturbance events (ADE), but not hurricanes, affected the extinction parameters analyzed for black howler monkey populations observed in Campeche. As ADE increased, population growth rate, final population size, and years to extinction decreased, whereas probabilities of extinction increased, with only two of 11 populations being extant after 100 years. Conversely, when ADE was removed from the model for populations that are known to have experienced ADE, extinction was still predicted for all populations at the end of the simulation, but as the decrease in population growth was not as fast, the populations ended with a larger number of individuals, and extinction became less likely and was delayed for all the populations. Therefore, the occurrence of ADE is a major stochastic factor predicting the extinction risk of black howler monkeys in Campeche.

Similar to other howler monkey species, black howler monkeys may be found in highly disturbed environments, where the available habitat is reduced and food resources are limited when compared to pristine forests (e.g., Arroyo-Rodríguez and Dias, 2010; Pozo-Montuy and Serio-Silva, 2007). This observation, combined with evidence of behavioral flexibility in response to anthropogenic disturbance (Dias and Rangel-Negrín, 2015) and with the presence of individuals in habitats where other mammals are absent (Rangel-Negrín et al., 2014), has led to the idea that howler monkeys are highly resilient to habitat disturbance (e.g., Rosenberger et al., 2009). However, we have previously demonstrated that population growth and infant survival in black howler monkeys living in Campeche are negatively related to habitat disturbance (Dias et al., 2015), and the present study suggests that if current disturbance conditions are maintained, populations living in more disturbed habitats (i.e., those exposed to ADE in baseline

models) will go extinct during the next 100 years. For some populations (Chicbul and Oxcabal) current conditions were sufficient to predict extinction in the short-term, and variation in ADE had no impact in extinction parameters (in fact, the Chicbul group does not exist anymore due to the complete destruction of its habitat). We have previously speculated that, based on the demographic trends observed in populations living in highly disturbed habitats (lower population growth and infant survival in highly disturbed habitats; dispersal patterns positively related to amount of habitat in the landscape), many adult individuals may have been born before disturbance occurred, and/or come from less disturbed habitats (Dias et al., 2015). The predictions generated in the present study support this speculation, as it is possible that the smaller and more disturbed habitats represent sinks where populations go extinct. It is therefore possible that such habitats are being recolonized by individuals that move between forest fragments (Pulliam, 1988). By continuing to monitor these populations in the long-term, we will be able to validate our PVAs and to document ecological processes affecting populations in disturbed landscapes (Dunning et al., 1992).

Some populations where we did not record ADE were also predicted to go extinct. Calaxchil and Tormento N had low extinction probabilities in baseline models, but were predicted to go extinct in *ca*. 80 years and had negative population growth; and T61 Calax had a very high baseline extinction probability. The interaction between small population size and vital rates may explain why populations in protected areas still faced extinction risk. For instance, the population size of Tormento N was half of that in Tormento S and mortality rates of females and males during the first three years of age were on average 4.7% higher in the former than in the later. Calaxchil and Tormento N populations comprised approximately 50 individuals each, and T61 Calax was a single group living in a 300 ha habitat. Small populations are more vulnerable to the effects of demographic and environmental stochasticity, genetic drift, inbreeding depression, and Alleé effects (i.e., co-dependency between population size and gross population growth or some fitness component) (Fischer and Lindenmayer, 2007). At the individual level, these factors may lead to a reduction in survival and reproduction, whereas at the population level may derive in reduced population sizes and genetic diversity (Fahrig, 2003). Although habitat size has been reported as the main factor constraining howler monkey populations in disturbed habitats (Arroyo-Rodríguez and Dias, 2010), we found a non-linear relationship between habitat size and both final population size and extinction probabilities. Therefore, our results suggest that the persistence of some populations may be linked to demographic processes derived from small population size, which are not directly linked to habitat size. It is possible that the management of these populations through translocations and reinforcements (Baker, 2002; e.g., King et al., 2013) could decrease their extinction risk.

An additional indirect evidence for the strong effect exerted by small population size on extinction probabilities is the low impact that the removal of ADE had on the probability of extinction of populations known to be exposed to these types of events. Still, it is important to acknowledge that without ADE, predicted time to extinction increased by a mean of 7.5 years. From a conservation and management perspective, this additional time may be sufficient to develop actions aimed at promoting population growth and persistence (Grantham et al., 2009). For instance, two years was considered a time span long enough to evaluate the success of an environmental education program developed with human populations living in proximity with six primate species in Uganda (Kuhar et al., 2010); and seven years were sufficient to implement conservation and management actions recommended by a population and habitat viability assessment of lion tamarins (*Leontopithecus* spp.; Holst et al., 2006). Therefore, it is important to study more thoroughly ADE faced by black howler monkeys in Campeche, and develop strategies for their mitigation in order to avoid local extinctions.

In one of the best studied populations of black howler monkeys, high mortality was recorded after the occurrence of a Category 4 hurricane (Pavelka et al., 2007). It was recently suggested that hurricanes could represent a stronger threat to the persistence of mantled howler monkeys (*A. palliata*) living near the Gulf of Mexico than anthropogenic disturbance (Ameca y Juárez et al., 2015). We therefore included hurricanes as a source of stochastic variation in the demography of our study populations. Hurricanes, however, had a marginal impact in our models of extinction risk. Differences between the results of the present and of the above mentioned studies could be related to two main aspects. First, in contrast with the Monkey River population (Pavelka et al., 2007; Fig. 1), which is located near the Caribbean Coast where several hurricanes make landfall (NOAA, 2016), the majority of the Campeche territory is located inland, and its coast faces the southernmost portion of the Gulf of Mexico (Fig. 1). Therefore, hurricanes originating in the Atlantic basin never make direct landfall in Campeche, usually reach its territory with decreased intensity (CONAGUA, 2016), and are thus less destructive (as observed in the aftermath of hurricane Dean). Therefore, the level of severity we used to model the impact of hurricanes in Campeche was lower than that directly observed in Monkey River. Second, in contrast with Ameca y Juárez et al. (2015), we only modeled the frequency of hurricanes with the potential to cause an actual effect on individuals and their habitat (i.e., we did not include hurricanes in Categories 1-3 in our analyses), and estimated hurricane frequency for our study area based on the actual trajectories of hurricanes. Therefore, although intense hurricanes affect the survival of infants in our populations, they do not seem to pose a threat to the current or future persistence of black howler monkeys in the state of Campeche, even if hurricane frequency increases (Webster et al., 2005).

Despite several shortcomings (e.g. Reed et al., 2002), PVA represents an important tool for assessing the extinction risk of populations. When PVA are based on long-term data, their predictive value is expected to increase significantly (Brook et al., 2000), and are therefore of high value for policy development and management planning. This study is grounded on a 7-year monitoring of 11 black howler monkey groups, representing a reliable approach to model the future of black howler monkeys in Campeche. In sum, our results suggest that: 1) anthropogenic disturbance is a major source of stochastic variation in extinction risk; 2) small populations not currently affected by such disturbance face high extinction risk as well; and 3) the lessening of anthropogenic disturbance may benefit the persistence of threatened populations.

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