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Source: Tropical Conservation Science, 1(1) : 43-62

Published By: SAGE Publishing

URL: https://doi.org/10.1177/194008290800100104

Mongabay.com Open Access Journal - Tropical Conservation Science Vol. 1:43-62, 2008

Research Article

# Population viability analysis of howler monkeys (*Alouatta palliata mexicana*) in a highly fragmented landscape in Los Tuxtlas, Mexico

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**Abstract**

We performed a population viability analysis (PVA) using a stochastic population model employing RAMAS/Metapop software: 1) to evaluate the contribution of demographic parameters to population growth, and 2) to simulate group trend and local extinction probability of the Mexican mantled howler monkeys *Alouatta palliata mexicana* in Los Tuxtlas, Mexico, under two landscape scenarios: isolated populations (IPS) and patchy population or metapopulation (MPS). We found that as the number of adult females per fragment increased, the rate of fecundity and relative reproductive success increased. As a consequence, the finite growth rate depended mainly on the survival of adult females. In both IPS and MPS the simulations suggested that the probability of extinction was exponentially dependent on fragment size. An estimation of 60% of extinction was predicted when fragment size is lower than 15 ha. Simulations suggest that in MPS the expected population change could be lower than in IPS. The value of these analyses for conservation of the primate populations studied is discussed.

**Resumen**

Realizamos análisis de viabilidad poblacional (PVA) usando modelos demográficos estocásticos con el programa RAMAS/Metapop para: 1) evaluar la contribución de parámetros demográficos en el crecimiento poblacional, y 2) simular la tendencia poblacional y probabilidad de extinción del mono aullador *Alouatta palliata mexicana* en Los Tuxtlas, México, bajo dos escenarios de paisaje: poblaciones asiladas (IPS) y poblaciones parchadas o metapoblación (MPS). Encontramos que conforme el número de hembras adultas por fragmento aumenta, la tasa de fecundidad y el éxito reproductivo también aumenta. Por lo tanto, la tasa finita de crecimiento poblacional depende principalmente de la sobrevivencia de las hembras. En ambos escenarios las simulaciones sugieren que la probabilidad de extinción depende exponencialmente del tamaño del fragmento. Se estimó una probabilidad del 60% de extinción cuando el tamaño de los fragmentos es menor a 15 ha. Las simulaciones sugieren que en el MPS el cambio es menor en comparación al IPS. Se discute al valor de este tipo de análisis para la conservación de las poblaciones de primates investigadas.

Cite this paper as: Mandujano, S. and Escobedo-Morelos, L. A. 2008. Population Viability Analysis of Howler Monkey (*Alouatta palliata mexicana*) in a Highly Fragmented Landscape in Los Tuxtlas, Mexico. *Tropical Conservation Science* 1:43-62. Available online: tropicalconservationscience.org.

## Introduction

One of the most powerful and pervasive tools in conservation biology is population viability analysis (PVA) [1-4]. In fact, PVA has been used in conservation biology for approximately 25 years. The principal motivation behind the development of PVA is to assess the threats to a species' survival, and to intervene before population declines become inevitable [5]. In general, PVA is the study of all factors that might cause a species to go extinct [6]. Specifically, PVA could be defined as an analysis that uses data in an analytical or simulation model to calculate the risk of extinction after some specified period of time [7]. In practice, biologists use a wide variety of PVA models to interpret past population trends, to evaluate likely threats to a population, and to project future population trends [7]. Actually, there exist software programs (e.g.,Vortex, RAMAS/metapop, ALEX) that could be used to answer specific questions about population trends under different simulation scenarios. In consequence, PVA helps us not only to assess the risk of extinction but also to identify the most promising management strategies [3,6,8]. Of course, criticisms and caveats exist around PVA, defined in part by data availability and theoretical and biological understanding, and in part by social, regulatory, and political contexts [9].

The population abundance and sex-specific age structure of a primate population is the result of extrinsic natural factors (habitat, predation, competition, disease, and catastrophes) and intrinsic factors (fecundity, mortality, immigration and emigration), all of which help determine the long-term trend of population dynamics [10]. However, human-induced factors such as hunting, deforestation, and fragmentation, negatively affect population dynamics of many primate species [11]. As population size decreases, the population is more vulnerable to extinction due to demographic and environmental stochasticity, loss of heterozygosity, and disruption of social structure [12]. In this context, the PVA is a valuable analytical approach for proposing management recommendations to increase the persistence of a target primate population and species [13]. The use of PVA in primate studies has been done using different approaches [14-19]. In particular, the effect of demographic parameters on population growth has been used as an index to evaluate the importance of certain life stages for conservation [13,20]. For example, the elasticity analysis of matrix projection models examines the effects of proportional changes in demographic parameters, such as survival and fecundity rates on population growth rates [21,22]. Thus, PVA uses matrix models that require relatively few data and can be generalized for populations with a wide variety of life-history traits [20-22].

Los Tuxtlas, a region located in the Mexican state of Veracruz, is the northernmost area of lowland tropical rainforest in America [23]. These forests are inhabited by the Mexican mantled howler monkey, *Alouatta palliata mexicana*, and the Spider monkey, *Ateles geoffroyi*, both classified as critically endangered by the IUCN [24]. The reduction in distribution and abundance of primates in Los Tuxtlas is principally due to deforestation of the tropical rainforest: 75% of native habitat has been lost, and 20% has become isolated. Only 5% consists of continuous rainforest at high elevations (>800 m) [25]. As a result, the remaining population is spread across archipelagoes of forest fragments that vary in size, isolation distance, age, and quality, resulting in precarious demographic and ecological conditions [26-29]. Studies at Los Tuxtlas have shown that the presence and abundance of howlers monkeys are positively related to fragment size and quality, and negatively related to fragment isolation [18,19,25,29,30]. However, little is known about the population viability in this region. The principal objectives of the present study were development of a PVA in order to: 1) evaluate the contribution of demographic parameters to population growth, and 2) to simulate group trend and local extinction probability of Mexican mantled howler monkeys under two landscape scenarios – isolated populations and patchy population or metapopulation – in Los Tuxtlas. We discuss the PVA implications for conservation of this species.

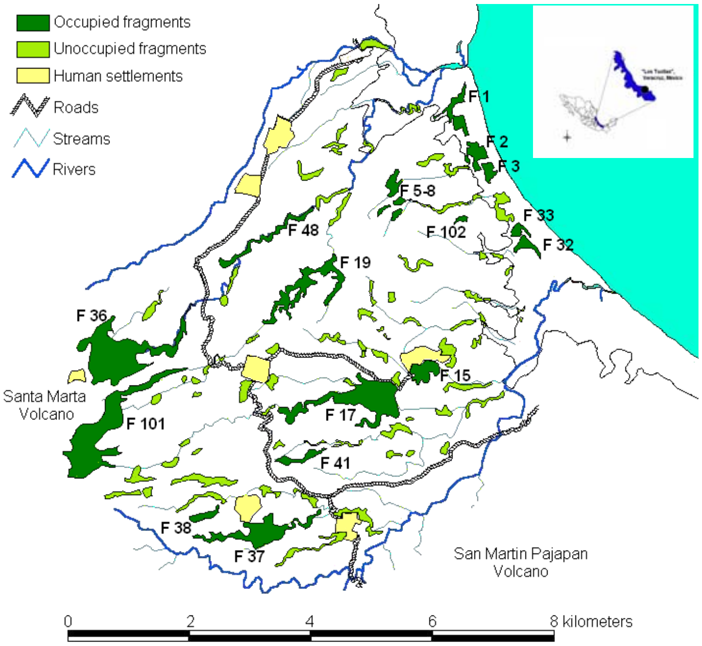

Figure 1. Location of the study site in Los Tuxtlas, Mexico, and forest fragments containing howler monkeys. The numbers refer to forest fragments listed in Table 1.

## Methods

### *Study Area*

Los Tuxtlas, Veracruz, Mexico (18° 18' N and 94° 45' W), was decreed a Special Biosphere Reserve in 1998. It covers 155,122 ha and has an elevation from 0 to 1780 m. The mean annual temperature is 25º C and annual rainfall varies from 1850 to 4600 mm [31]. The study area is located at the base of the Santa Marta and San Martin Pajapan volcanoes and includes eight tracts of communal land in the municipality of Tatahuicapan de Juarez. It is bordered by the Tecuanapa and Tilapa Rivers, the Mexican Gulf Coast, and the skirts of the Santa Marta Sierra at an altitude of 800 m (Fig. 1). The landscape is characterized by an irregular topography with slopes that often exceed 30°. Gentle slopes are only found on lowlands near the Gulf Coast, which also has permanent flooding. Since the establishment of communal lands in the 1960s, deforestation has increased, with an annual rate of vegetation loss from 4% to 7% [32]. Approximately 17,000 Zoque-Popoluca indigenous people inhabit the Sierra and neighboring areas [33]. The landscape has been severely altered by human activity: only 547 ha (11%) of the 4960 ha total area represents tropical forests. The matrix surrounding forest fragments is mainly pasture and corn.

We digitized the landscape with ArcView 3.2 (ESRI®) software, using aerial photographs (1:20,000; INEGI 1999), orthophotos (INEGI 1996), and digital (INEGI 1990), and field data. We defined "fragment" as a remnant of the original forest, with a mean canopy height > 10 m, and a surface area > 0.5 ha, which appear to be the minimum parameters for patch occupation by *A.p.mexicana* in Los Tuxtlas [29,34]. We calculate size and isolation for all fragments using the Patch Analysis 2.2 extension. Three isolation parameters were used: nearest fragment, nearest town, and nearest continuous forest.

### *Study species*

Howler monkeys (*Alouatta*) are known for their ability to survive in both intact and disturbed habitats of varying sizes [35]. Their broad tolerance to changes in habitat quality has been related to a high degree of folivory, a diverse and flexible diet, and the use of small home ranges [36-40]. *Alouatta* populations are divided into social groups that act as semi-closed reproductive units [41]. Dispersal is a reproductive strategy that is often adopted by both juveniles and adults of both sexes [42,43], possibly to avoid inbreeding and may result in maintaining the genetic variability of populations [44]. In consequence, the size and composition of the social groups vary notably in response to variation in the habitat resources and population density [41,45]. This feature has permitted howlers to survive in very small habitat fragments where other species have been unable to do so [46,47]. However, howlers are more vulnerable to hunting, diseases, and predation in a fragmented habitat [35].

### *Census*

To determine the presence and size/composition of howler monkey groups, the fragments were sampled from 07:00 to 12:00 and 16:00 to 18:00 h, during: April 2002 (10 days, 197 h), June 2002 (15 d, 260 h), October 2002 (13 d, 125 h), February 2003 (9 d, 225 h), April 2003 (7 d, 88 h), June 2003 (11d, 166 h), February 2004 (11 d, 182 h) and April 2004 (10 d, 166 h). A group was defined as a social unit having at least one adult male and one adult female. Each group encountered was followed and counted repeatedly the same day until a consensus of group size and age and sex composition was reached. All groups were followed on subsequent days to confirm their composition. Recounting groups helped to reduce the probability of counting a group more than once. The isolated nature of the forest fragments in the landscape also greatly reduced this probability. Individuals in each group were recognized by pigmentation of the hands and feet, face scars, and by patches of blond hair on hands, feet, tail, and lower back. Individuals were classified as infants (< 1 year old), juveniles (>1 year, < 3 years), adult females, and adult males (> 3 years, distinctive sexual characters). We did not distinguish sex in infants and juvenile individuals.

### *Demographic parameters*

For the purposes of demographic analysis we calculated the average group composition based on the annual census from 2002 to 2004 (Appendix 1), and 24 demographic parameters for each group (Appendix 2). The complete subpopulation of animals in each occupied fragment was counted; thus sex and age composition were unbiased. The density was estimated for each occupied fragment as the number of individuals per surface area of the fragment. The ratios of female per male, and immatures per female were calculated following standardized procedure [48]. The relative reproductive success (RRS) was estimated following Jones [47]. In this case, RRS estimation was based on the average number of juveniles and infants per female group size. Thus, we calculated the RRS for groups with two, three, or more females. Fecundity and survival rates were estimated according to Akçakaya [8]. In *Alouatta* the births can happen during the whole year [46]. In consequence, it is possible that some infants have been born in months of the year when we didn't visit the fragments. However, these records are not relevant to fecundity rate estimation if these breedings didn't survive from $t$ to $t+1$-. Thus, fecundity ($F_x$) is the number of newborns at time $t$ produced by individuals in the age class $x$ at time $t-1$. Specifically, $F_x = S_x \times m_x$, where $S$ = survival and $m$ = fertility. Fertility is the average number of offspring produced by an individual of age $x$ per unit time. Thus, fertility is not the same thing as fecundity. The fecundity values incorporate two kinds of mortality over the time step. Some of the mothers that were alive during the last census die before reproducing, and some of the offspring that are born die before they can be counted in the next census [8]. Data from April sampled from 2002 to 2004 were used in demographic analysis. A correlation analysis was performed among demographic parameters in order to know relationships.

### *Simulation model*

To simulate deterministic and stochastic factors affecting howler group dynamics, the RAMAS/Metapop Program [8] was used. The model used in the simulations considers a transition matrix as proposed by Caswell [49], which is a variation of the Lefkovitch [50] stage-structured model. In this matrix the population is coarsely divided into three stage classes: infants, juveniles, and adults. The matrix considers the probability that an individual remains in the same stage class from one year to the next.

To simulate the number of infants, juveniles, and adults that could be expected in the following year [8], we used the equation:

$$\begin{bmatrix} I \\ J \\ A \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & Fec \\ S_i & G_j & 0 \\ 0 & S_j & G_a \end{bmatrix} \times \begin{bmatrix} I \\ J \\ A \end{bmatrix}_{t} \qquad \text{Eq. 1}$$

where *I*, *J* and *A* are, infants, juveniles, and adults, respectively; while *Fec* is the fecundity rate (infants born alive in the year $t+1$ in relation to the adult females in the previous year $t$), $S_i$ is the survival rate from infant to 1 y-old juvenile category, $S_j$ is the survival rate from 2 y-old juvenile to adult category, $G_i$ is the survival rate from 1 y-old juvenile to 2 y-old juvenile, and $G_a$ is the survival rate of adult individuals. According to Eq. 1, the animals estimated in the year $t+1$ are the product of the transition matrix by the animals in the year $t$ [8]. This procedure was repeated 1,000 times and two forecast variables were estimated: the expected number of individuals and the probability of extinction. We considered probability of extinction as the probability that group size will be below a threshold of one individual at the end of the 30 years.

In population ecology the finite growth rate (λ) is calculated as the dominant eigenvalue of the stage matrix [8], and we used RAMAS/Metapop Program to estimate it. Robinson and Redford [51] give the maximum finite growth rate ($\lambda_{\max}$) for *Alouatta palliata* as 1.162 [see 52]. Note that $\lambda = e^r$ where $r$ is the instantaneous population growth rate. When value of λ is greater than 1 the population increases in size, when λ is lower than 1 the population declines, and when λ is equal to 1 the population is stable.

We used a density-dependent model in population trend simulations, taking into account the Ricker equation [52] in which the finite growth rate depends on abundance, fecundity, and survival rates, and carrying capacity (*K*) (Table 1). In population ecology *K* is the population size above which the population growth tends to decline [8]. However, estimation of *K* is difficult because it is an estimation of the maximum number of individuals per surface that the habitat can support according to available food resources. In fact, this parameter varied depending on the regional climatic conditions, local habitat composition and structure, and annual and stational variations [8]. As an indirect measure of *K*, the density in a low disturbed populations could be used. Because we did not find a quantitative estimation of carrying capacity for *Alouatta*, in this study we define *K* as the maximum density found in the fragments, which corresponds to 1.4

individuals/ha. This is a relaxed assumption and the consequence in the simulation is the possibility that more individuals could inhabit fragments. The general results and conclusions were not affected by this assumption since it is a constant number affecting similarly all fragments.

In order to simulate environmental stochasticity, two types of catastrophes were considered: hurricanes and diseases. In Los Tuxtlas, the climatic conditions are influenced partly by tropical hurricanes; however, very few of them had a considerable impact in this region [A.Estrada, personal communication]. In previous PVA for *A. p. mexicana*, Rodríguez-Luna et al. [18] used an annual probability of 0.1, with a negative impact of 10% in the reproduction and 30% in the survival. In our analysis we suppose that hurricanes diminish the carrying capacity because they affect directly the canopy tree structure. Thus, in this study we considered an annual probability incidence of 0.1 with a reduction of 30% on *K*. With respect to diseases as a catastrophic event, it has been shown that this is a non-frequent event but one that could have a devastating effect on the populations of howler monkeys [36]. We used data of Rodríguez-Luna et al. [18] to simulate this event. In the case of diseases a probable annual impact of 0.01 was considered, resulting in a 40% reduction on reproduction and of 60% on survival rate.

Table 1. Average structure, vital rates, elasticity analysis, and population viability analysis of occupied fragments by the howler monkey in the landscape during the period 2002-2004. For abbreviations and details of calculation of each demographic parameter, see Appendix 2.

| | Average structure | | | | | Vital rates | | | | | | | | | Elasticity analysis | | | | | Population Viabili Analysis [b] | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *M* | *F* | *J* | *I* | *N* | *D* | *F:M* | *I:F* | *Im:F* | *RRS* | *Fec* | *Sad* | *Sj* | *Si* | *%Fec* | *%Sm* | *%Sh* | *%Sj* | *%Si* | *λ* | *Pe IPS* | *Pe MP* |
| Groups | | | | | | | | | | | | | | | | | | | | | | |
| F1 | 1 | 2.3 | 0 | 0 | 3.3 | 0.30 | 2.3 | 0 | 0 | 0.00 | 0 | 0.88 | - | - | - | - | - | - | - | - | ? | 0.5 |
| F2 | 2 | 3 | 0 | 0 | 5 | 0.54 | 1.5 | 0 | 0 | 0.00 | 0 | 1.00 | - | - | - | - | - | - | - | - | ? | 0.5 |
| F3 | 1 | 3.7 | 1.3 | 0.7 | 6.7 | 1.42 | 3.7 | 0.19 | 0.58 | 0.54 | 0.13 | 1.00 | 0.75 | 1.00 | 3 | 2 | 86 | 6 | 3 | 0.98 | 0.59 | 0.8 |
| F5-8[a] | 2 | 3 | 1 | 1.3 | 7.3 | 0.76 | 1.5 | 0.44 | 0.78 | 0.77 | 0.67 | 1.00 | 0.50 | 0.5 | 0 | 29 | 71 | 0 | 0 | 0.95 | 0.65 | 0.5 |
| F15 | 3.7 | 5.7 | 2.3 | 2.3 | 14 | 1.19 | 1.6 | 0.43 | 0.86 | 0.81 | 0.44 | 0.90 | 0.50 | 1.00 | 0 | 27 | 73 | 0 | 0 | 0.90 | 0.62 | 0.5 |
| F17 | 2 | 3 | 0.3 | 0.3 | 5.6 | 0.10 | 1.5 | 0.11 | 0.22 | 0.20 | 0.17 | 1.00 | - | 1.00 | - | - | - | - | - | - | ? | 0.1 |
| F19 | 4.3 | 4.3 | 3 | 2 | 13.6 | 0.46 | 1.0 | 0.54 | 1.41 | 1.16 | 0.48 | 0.71 | 0.58 | 1.00 | 8 | 0.1 | 64 | 21 | 8 | 0.78 | 0.21 | 0.3 |
| F32 | 2 | 2 | 0 | 0.3 | 4.3 | 0.82 | 1.0 | 0.17 | 0.17 | 0.15 | 0.25 | 1.00 | - | - | - | - | - | - | - | - | ? | 0.8 |
| F33 | 1 | 2.3 | 1 | 0.7 | 5 | 1.35 | 2.3 | 0.28 | 0.72 | 0.74 | 0.25 | 1.00 | 1.00 | 0 | 10 | 4 | 45 | 0 | 0 | 0.95 | 0.89 | 0.8 |
| F41 | 1 | 4 | 0 | 0 | 5.3 | 0.77 | 4.0 | 0 | 0 | 0.00 | 0 | 1.00 | - | - | - | - | - | - | - | - | ? | 0.6 |
| Solitaries | | | | | | | | | | | | | | | | | | | | | | |
| F36 | 1 | 0 | 0 | 0 | 1 | 0.01 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.00 | 1.0 |
| F37 | 1 | 0 | 0 | 0 | 1 | 0.04 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.00 | 1.0 |
| F38 | 1 | 0 | 0 | 0 | 1 | 0.13 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.00 | 1.0 |
| F48 | 1 | 0 | 0 | 0 | 1 | 0.08 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.00 | 1.0 |
| F101 | 2 | 0 | 0 | 0 | 2 | 0.03 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.00 | 0.2 |
| F102 | 1 | 0 | 0 | 0 | 1 | 0.67 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 1.00 | 1.0 |

[a] Fragments 5, 6, 7, and 8 were used by one group.

[b] Probability of local extinction in the isolated populations scenario (IPS) and metapopulation scenario (MPS).

### *Simulated scenarios*

In this study we performed a PVA simulating two possible scenarios: “isolated populations” and “patchy population or metapopulation.” In the first scenario, we assumed that occupied fragments were totally isolated from other occupied fragments. Consequently, the finite population growth rate is only affected by particular density-dependent processes occurring in each fragment. The simulation was performed using the specific transition matrix obtained for each group in Equation 1. Simulations were only performed in those groups where it was possible to estimate all elements of the matrix during the study period 2002-2004. In fragments occupied by adult individuals of both sexes, but not immatures, simulations were not performed. There was also no simulation in those fragments occupied by only one solitary individual or individuals of the same sex. In the metapopulation scenario we assumed that all groups and solitary individuals inhabiting different fragments were affected by similar environmental conditions, thus assuming complete dispersal between fragments. To simulate we used the average vital rates estimated for all groups. Thus an average transition matrix was obtained and substituted in Equation 1. In this case, all occupied fragments (by group or solitaries) were analyzed. In both simulated scenarios the forecast-predicted variables were the expected number of individuals and the probability of extinction of selected howler monkeys groups over the next 30 years. A non-linear regression model was used to explore the relationships between fragment size and probability of extinction in each scenario.

## Results

### *Fragment occupation*

In the studied landscape, 75 to 77 howler monkeys inhabited 17.5% of fragments (19 out of 92 fragments; 348 ha of total forest area). Nine fragments were each inhabited by a separate group; four fragments were used by one group; five fragments were each inhabited by a separate solitary male; and one fragment was occupied by two males (Appendix 1). Some relatively large fragments (F36, F101 and F37) were occupied only by solitary individuals; while a small fragment (F15 = 11.8 ha) was occupied by the largest group (N = 14). Consequently, the number of individuals per group was not significantly related to the size of the fragment (Fig.2a, $r^2 = 0.04$, $P = 0.59$). The average population density was 0.53 ± 0.48 individuals/ha (range 0.10 to 1.42 ind/km$^2$, Table 1). As fragment size decreased, the density increased. In fact, the density showed a significant non-linear relationship with the fragment size (Fig. 2b, $r^2 = 0.70$, $P = 0.03$).

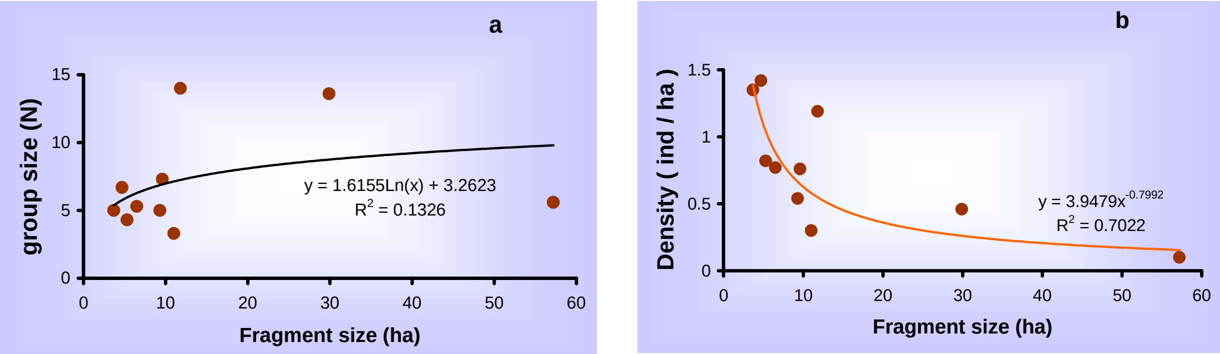

Fig. 2. Relationship between group size (a) and population density (b) with fragment size.

### *Group structure*

Inter-annual and average age and sex structure of each group are presented in Appendix 1 and Table 1, respectively. The average group size was 7.0 ± 3.8 (range 3 to 14) individuals, including mean 2.0 ± 1.2 adult males, 3.3 ± 1.1 adult females, 0.9 ± 1.1 juveniles, and 0.8 ± 0.8 infants. The adult sex ratio was 2.04 ± 1.05 females per male; while the ratio of infants per adult female was 0.22 ± 0.20, and immatures per adult female 0.47 ± 0.47. Group size was positively related to the number of adult females ($r^2$ = 0.72, P = 0.002), and the number of immatures ($r^2$ = 0.90, P = 0.0001). Consequently, the number of adult females related significantly to the number of juveniles ($r^2$ = 0.50, P = 0.02).

### *Vital rates*

The average fecundity rate was 0.24 ± 0.23 infants per female, while the relative success in reproducing (RRS) was 0.44 ± 0.42 (Table 1). In three fragments (F1, F2 and F41), no infants or juveniles were registered and the fecundity rate and RRS were therefore zero. A significant non-linear relationship between the group size and fecundity rate (Fig. 3a, $r^2$ = 0.41, P = 0.04) and RRS ($r^2$ = 0.62, P = 0.006); and between the number of females per group and fecundity rate (Fig. 3b, $r^2$ = 0.75, P = 0.13) and RRS ($r^2$ = 0.95, P = 0.02), was found. The survival rate of adults from one year to the next was 0.95 ± 0.10, juveniles 0.67 ± 0.21, and infants 0.75 ± 0.42 (Table 1). The elasticity analysis showed that the survival of adult females contributed 45% to 86% of the group growth rate (Table 1), while the survival of adult males, juveniles, and infants contributed 2-29%, 0-21% and 0-8%, respectively. The contribution of fecundity rate to population growth was 0 to 10%.

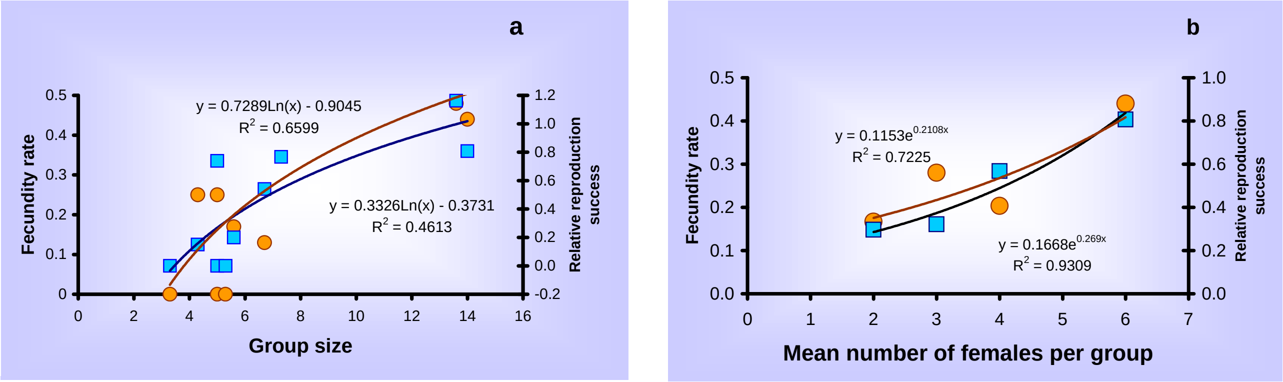

Fig. 3. Relationships between fecundity rate (●) and relative reproductive success (■) with group size (a) and mean number of females per group (b).

### *Simulation of population viability*

In the isolated populations scenario, the simulated 30-year trends for the five groups with at least one immature, are presented in Fig. 4a. All groups are predicted to decline in numbers except for F19 which is predicted to increase slightly. From an initial 12 individuals in F19 we could expect a slight increase to 18 individuals at the end of the 30 years simulated. The carrying capacity could limit the growth of this group since it inhabits a medium size fragment (29.9 ha). The tendency for the other four groups is to diminish in number.

In the metapopulation scenario, trends for each of the 10 groups with at least one adult male and one adult female showed that F17 was the group which tends to increase (Fig. 4b). From an initial group size of five, the group could be expected to increase to 35 individuals due to the large size of this fragment (57.2 ha). The expectation of F19 is to maintain approximately the same initial number of individuals. The tendency for the other eight groups is to diminish in number.

A comparision of a total population change indicated that in the isolated populations scenario the expected number of individuals decreased, while in the metapopulation scenario no change is expected in the total number of indivuals (Fig. 5). In both the isolated populations ($r^2$ = 0.91, P = 0.01) and metapopulation ($r^2$ = 0.97, P = 0.01) scenarios, the probability of extinction was significantly related to the fragment size according to an exponential model (Fig. 6). As fragment size decreased, the probability of extinction increased exponentially. Fragment size less than15 ha had a 60% or more extinction probability. The largest fragments in the studied landscape (F36 = 75.5 ha, F101 = 71.0 ha, and F37 = 32.6 ha) were inhabited by solitary males; thus the contribution of these fragments to population viability is null in the actual situation.

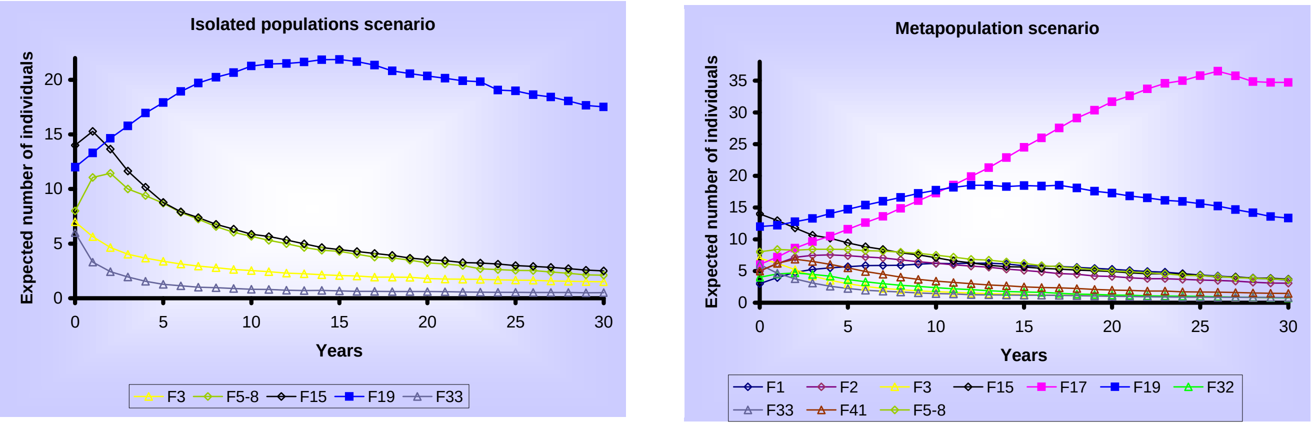

Fig. 4. Simulation of group size expectations of howler monkeys in the next 30 years in the isolated population and metapopulation scenarios.

## Discussion

### *Parameters affecting population growth*

The sex-specific age structure of howler monkeys varied notably among the groups in the study area. This pattern has been reported for *A. palliata*, *A. pigra*, and *A. seniculus* inhabiting both continuous and fragmented habitats [e.g.,26,41,53]. In particular, the average composition of groups in this study was similar to that reported in fragmented habitats in Los Tuxtlas (Table 2) [25,29,32]. In contrast, the group size was smaller and its composition different compared with data from Central America [36-38]. Social, ecological, geographical, and historic factors should interact to explain any differences and similarities within or between locations and groups [45,54].

Table 2. Average density, age structure, and vital rates of howler monkeys groups in different habitats and locations.

| Habitat | Population structure and vital rates | | | | | | | | Site/Source |
|---|---|---|---|---|---|---|---|---|---|
| | *D* | *M* | *F* | *J* | *I* | *N* | *F:M* | *Im:F* | |
| *A. palliata* in the south of Los Tuxtlas, Mexico | | | | | | | | | |
| Fragmented | 0.8 | 1.6 | 2.7 | 0.8 | 0.7 | 5.8 | 1.9 | 0.7 | Los Tuxtlas, This study |
| Fragmented | 1.0 | 1.6 | 2.4 | 1.0 | 0.7 | 5.7 | 1.8 | 0.6 | Los Tuxtlas, 32 |
| *A. palliata* in the north of Los Tuxtlas, Mexico | | | | | | | | | |
| Continuous | 0.2 | 3.0 | 4.1 | 0.9 | 1.2 | 9.2 | 1.5 | 0.5 | Los Tuxtlas, 60 |
| Fragmented | 0.1 | 1.9 | 3.3 | 0.7 | 1.2 | 7.0 | 1.9 | 0.5 | Los Tuxtlas, 25 |
| Island | 11.4 | - | - | - | - | - | 1.3 | 0.9 | Los Tuxtlas, 71 |
| *A. palliata* in Central America | | | | | | | | | |
| Continuous | 0.8 | 3.9 | 6.7 | 2.6 | 3.1 | 16.3 | 1.5 | 0.9 | Santa Rosa, 38 |
| Continuous | - | 2.7 | 4.7 | 2.8 | 1.9 | 12.1 | 1.6 | 1.0 | Santa Rosa, 72 |
| Fragmented | 1.0 | 2.5 | 6.8 | - | - | 12.6 | 2.8 | 0.5 | La Pacífica, 37 |
| Fragmented | 0.3 | 1.6 | 4.8 | 1.5 | 2.3 | 10.2 | 3.0 | 0.8 | La Pacífica, 39 |
| Continuous | - | 3.9 | 8.4 | 2.6 | 7.0 | 21.3 | 2.2 | 1.1 | Barro Colorado, 36 |

Our data suggest that as the number of adult females increases, the fecundity rate and relative reproductive success increase. Several studies support the importance of adult females in population growth rates [20,22,36,55]. Because female fertility directly affects population growth rates, strategies to increase female fitness have implications on the probability of persistence [47]. Elasticity analysis suggests that adult female survival is the most critical parameter contributing to population growth trends in howler monkey populations. Cristobal-Azkarate *et al.* [29] suggest that immature mortality due to reduced food availability resulting from high population densities is the principal demographic factor affecting fragmented populations of howlers in the northern part of Los Tuxtlas (at least 60 km from our study area). In contrast, our elasticity analysis showed that the survival of immatures was not the principal factor that determines the finite growth rate (λ) in the groups studied. The number of immatures presented at any determined moment is the result of the demographic dynamics (variation in fecundity, survival, and dispersal rates) in previous years. Thus, what elasticity analysis means is that even with a high mortality rate of adult males and immatures, the growth potential of a group mainly depends on the survival rate of adult females. High survival means a high fecundity rate and RRS, which in turn increases the growth rate and future group size. Our results agree with data reported by Akkoç and Williams [22] and Dobson and Lyles [20] which emphasizes the importance of female survival.

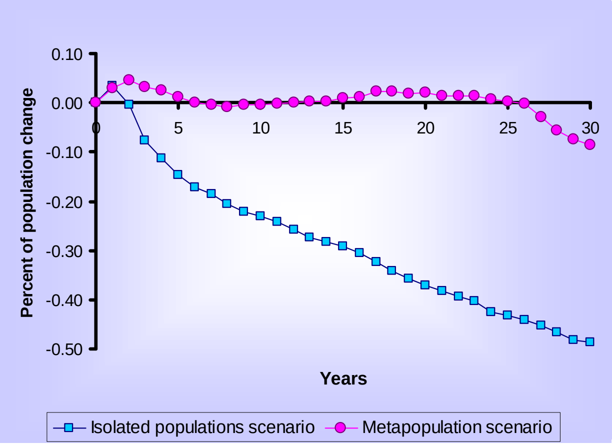

Fig. 5. Comparison of expected population change during the simulation of isolated populations and metapopulation scenarios. Note that y-axes units are in percent, where a positive value indicates a population increase and negative value represents a decreasing population.

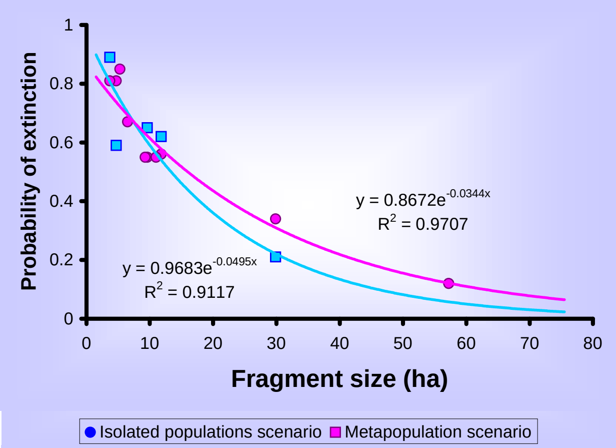

Figure 6. Exponential decreasing of probability of extinction of howler monkey groups as fragment size increase in both isolated populations and metapopulation scenarios.

Solitary males represented 26% of the total adult males in the study area and inhabited 32% of the 19 occupied fragments. A crucial aspect is that the largest fragments were inhabited only by solitary males. Solitary animals are common in continuous habitats and they represent dispersed individuals with a potential of entering other groups or forming a new group [56]. In fact, the dispersal of individuals of both sexes is common in the *Alouatta* species [42,57-59]. In Los Tuxtlas, solitary males and females have been reported in continuous [60] and fragmented habitats [25]. However, Cristobal-Azkarate *et al*. [29] suggested that the migration patterns of howlers may be depressed in the fragmented landscapes of Los Tuxtlas, and they reported only solitary adult males. Our results agree with these findings and the possibility that the solitary animals are transients searching for a non-natal group. However, the low connectivity of the landscape, estimated at less than 30% [30], severely limits the possibility of moving between fragments and groups. In fact, preliminary data suggest that when isolation distances between fragments reach 100 m, the probability of movement diminishes exponentially [61]. Thus, the spatial configuration and connectivity of habitat could severely limit dispersal movements [62]. In consequence, from a demographic perspective, solitary individuals inhabiting isolated fragments represent a “wasted-life” individual for population growth and viability, except in those cases where these animals can join another group or form a new group.

### *Population persistence*

Our PVA suggests that the probability of extinction increases exponentially as fragment size decreases. A 60% of extinction probability was estimated when fragment size is lower than 15 ha. Evidence from several primate species, including howler monkeys, suggests that<10-ha fragments have little probability of being occupied [63,64]. For instance, Cowlishaw and Dunbar [10] reported that extinction rates of three primate species increased sharply when primates inhabited < 10-ha forest fragments in the Tana River, Kenya. In Manaus, Brazil, Gilbert [63] found higher numbers of primate species and groups in 10-ha and 100-ha fragments than in 1-ha fragments. Small forest fragments support lower number of individuals [25,27,29], and as fragment size decreases the habitat quality decreases also [28,65]. In consequence, even though howler monkeys have the ability to live in small fragments for several years, our PVA suggests that viability of local population increases as fragment size and quality increase.

The comparison of isolated populations and metapopulation scenarios showed that in the second the overall expected population change could be lower, due to the possibility of dispersal among fragments. Although there have been many studies on primates that inhabit fragments [11], few have addressed the problem of primate population conservation from a metapopulation perspective [10,66,67]. Metapopulation theory has been the focus of much discussion in population and conservation biology in fragmented habitats [68]. The essence of the metapopulation approach is that the presence of a given species in an area depends on the balance between the rates at which local populations become extinct and those at which new ones are established by migrants from other populations in the landscape. In consequence, metapopulations exist as various local populations within a fragmented system surrounded by a matrix. According to predictions based on metapopulation theory, if the landscape has been so severely transformed by deforestation that the number, size, quality, and connectivity of fragments are all quite low, the probability of persistence on a regional scale will decrease due to limited fragment occupation and reduced colonization of empty fragments [68]. This type of scenario clearly indicates the pressing need for a proposal of measures to mitigate and reverse fragmentation.

## Implications for Conservation

Our PVA was based on the analysis of a single landscape and three years of census; in consequence it is necessary to continue monitoring for several years in order to have more precise estimates of demographic paramters [15]. However, PVA simulation suggests that the howler monkey population in this highly fragmented landscape is at a high local extinction risk, and conservation strategies from a metapopulation perspective are urgently required. The strategy must deal with the protection of large, occupied fragments, avoiding further loss of area and must implement habitat restoration programs. We suggest two strategies for conserving howler monkeys in the study landscape. The first is to protect priority fragments, that is, those that maintain the largest groups of howlers and that have the greatest surface area, connectivity, and habitat quality. The second is to develop reforestation strategies in order to recover and restore habitat by increasing the area of certain occupied fragments and by establishing corridors and/or stepping stones.

PVA simulation suggests conserving fragments larger than 15 ha. Large fragments can sustain a greater number of individuals due to an increase in carrying capacity, decreasing the likelihood of local extinction. Several studies have illustrated that an increase in the area and number of protected sites is vital to conserving endangered populations. For example, Gilbert [63] suggested that areas larger than 100 ha are necessary for the conservation of six primate populations, *Alouatta seniculus* among them, in the Amazon. Chapman et al. [67] determined that *Colobus guereza* populations, despite their ability to colonize and survive in altered habitats, might disappear due to the rapid habitat loss. Furthermore, Lawes et al. [69] found that *Cercopithecus mitis* populations are more vulnerable to extinction due to habitat loss and their limited dispersal ability, as they form a metapopulation in an imbalanced state. Harcourt [17] indicated that the main threat to mountain gorilla populations was habitat loss. For *Brachyteles* *arachnoides*, Strier [15] also found that the persistence probability after 100 years was maximized by increasing available habitat and allowing the population to expand naturally.

The second strategy reflects the need to restore monkey habitat. For this, two measures are necessary: increasing the size of small (< 15 ha) fragments that are presently occupied and increasing the connectivity of fragments inhabited by monkeys. For example, according to Gilbert [63], secondary vegetation corridors are important for primate populations in Central Amazonia. Swart and Lawes [66] evaluated different management strategies designed to create corridors connecting patches in a *C. mitis* metapopulation and concluded that in the long run (> 200 years), corridors would increase metapopulation persistence. In particular, some data suggest that howler movements may follow a stepping stone pattern when they travel from one fragment to another [42]. For primates, a stepping stone can be a group of isolated trees, live fences, riparian zones, or remnants of arboreal vegetation and/or habitat patches that are substantially smaller than an animal's home range [70].

In a previous paper, Mandujano et al. [30] estimated the number of hectares that must be reforested in order to create a scenario in which the probability of extinction at the metapopulation level is under 1%. The total reforestation area, taking into account both increased fragment size and connectivity, could vary from 112-170 ha. Species that are particularly useful are those trees that are vital to howler monkeys as sources of food and shelter; they should also serve some use to the area's human inhabitants. The possible native species for restoration of the study landscape, could be: *Ficus yoponensis* Desv., *Cecropia obtusifolia* Bertol., *Brosimum alicastrum* Sw., *Pseudolmedia oxyphyllaria* Donn Smith, *Dialium guianense* (Aubl.) Sandwith, *Poulsenia armata* (Miq.) Standl., *Spondias mombin* L., *Nectandra ambigens* (Blake) Allen, and *Bursera simaruba* (L.) Sarg. The majority of these tree species are also used by local inhabitants for various purposes (e.g., construction, medicinal, ornamental, forage, etc).

In conclusion, our results stress the urgency of implementing conservation approaches in which increases in area of habitat fragments and connectivity are of fundamental importance for persistence of primates in the landscape. In this scenario it would be important to involve the local communities. In an on-going study we are evaluating the feasible of restoration programs considering the local human perspective. Briefly, local people are interested in conservation programs because they perceive the usefulness of the biodiversity in the fragments [Bernal Robles, personal communication]. However, socio-cultural and economic restrictions could limit any restoration program if local people don't obtain some immediate economic benefit. The negative experience of local people with previous government forestry programs has resulted in reservations in their responses to further initiatives. However, emphasizing the possible ecological services that conservation and expansion of area of forest fragments would have in capturing water, decreasing erosion, and enhancing availability of medicinal, alimentary, ornamental and woody species reservoirs, among other benefits, are aspects that are easily understood by local rural inhabitants [33]. The parallel implementation of environmental education programs would help in raising awareness among local people regarding the importance of preserving the primates in their forests.

## Acknowledgments

We would like to thank M. Gutierrez, A. Cuarón, E. J. Naranjo, M. Equihua, and F. Garcia-Orduña, and L. G. Luecke for their comments- Thanks are also due the Consejo Nacional para la Ciencia y Tecnología and the American Society of Primatologists and Primate Conservation, Inc., who provided financial support for this study. The Departamento de Biodiversidad y Ecología Animal of the Instituto de Ecología A. C. additionally supported this project. We are grateful to three anonymous reviewers for constructive comments to improve this paper.

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## Appendix 1. Annual abundance and group composition of howler monkeys, and of forest fragment characteristics in the study area.

| Fragment | Size (ha) | Isolation distances (m) | | | 2001[a] | 2002 | | | | | 2003 | | | | | 2004 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Nearest fragment | Nearest town | Nearest continuous forest | Tot | M | F | J | I | Tot | M | F | J | I | Tot | M | F | J | I | Tot |
| 1 | 11 | 96 | 1,438 | 6,704 | 3 | 1 | 3 | 0 | 0 | 4 | 1 | 2 | 0 | 0 | 3 | 1 | 2 | 0 | 0 | 3 |
| 2 | 9.3 | 34 | 2,125 | 6,169 | 5 | 2 | 3 | 0 | 0 | 5 | 2 | 3 | 0 | 0 | 5 | 2 | 3 | 0 | 0 | 5 |
| 3 | 4.7 | 34 | 2,542 | 5,900 | 7 | 1 | 5 | 0 | 2 | 8 | 1 | 4 | 1 | 1 | 7 | 1 | 4 | 1 | 1 | 7 |
| 15 | 11.8 | 115 | 4 | 3,675 | 10 | 3 | 7 | 3 | 2 | 15 | 4 | 5 | 3 | 2 | 14 | 4 | 5 | 2 | 3 | 14 |
| 17 | 57.2 | 18 | 307 | 3,364 | 5 | 2 | 3 | 0 | 0 | 5 | 2 | 3 | 0 | 1 | 6 | 2 | 3 | 1 | 0 | 6 |
| 19 [b] | 29.9 | 196 | 562 | 3,197 | 11 | 4 | 7 | 2 | 1 | 14 | 4 | 3 | 2 | 2 | 11 | 3 | 3 | 4 | 2 | 12 |
| 32 | 5.3 | 24 | 1,988 | 4,426 | 6 | 2 | 3 | 0 | 0 | 5 | 2 | 3 | 1 | 0 | 6 | 2 | 2 | 0 | 0 | 4 |
| 33 | 3.67 | 12 | 2,186 | 4,817 | 6 | 1 | 1 | 0 | 1 | 3 | 2 | 1 | 1 | 0 | 4 | 1 | 3 | 1 | 1 | 6 |
| 36 | 75.5 | 75 | 81 | 144 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| 37 | 32.6 | 50 | 6 | 1,164 | 1 | 2 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| 38 | 5 | 23 | 192 | 1,184 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| 41 | 6.5 | 57 | 625 | 2,850 | 5 | 1 | 4 | 0 | 0 | 5 | 1 | 4 | 0 | 0 | 5 | 1 | 4 | 0 | 0 | 5 |
| 48 | 13 | 15 | 557 | 2,660 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| 5-8[c] | 14.6 | 43 | 1,941 | 5,634 | 10 | 2 | 3 | 1 | 1 | 7 | 2 | 3 | 1 | 2 | 8 | 2 | 3 | 1 | 2 | 8 |
| 101[d] | 71.0 | 75 | 438 | 206 | ? | | | | | ? | | | | | 2 | | | | | ? |
| 102[d] | 1.4 | 171 | 1,976 | 6,624 | ? | | | | | ? | | | | | 1 | | | | | ? |

M = adult males, F = adult females, J = juveniles, I = infants, Tot = total of individuals

[a] during 2001 specific data (sex, age) were not observed in detail in each group by Rodríguez-Toledo et al. [34]

[b] fragment 19 inhabited 3 groups,

[c] fragments 5 to 8 were used by one group, therefore the size is the sum of each fragment and isolation is the mean distance,

[d] fragment 101 and 102 was sampled only once in 2003, thus is lacking precise data.

Appendix 2. Definitions and equations used to calculate the demographic parameters in this study.

| Symbol | Definition | Calculation |
|---|---|---|
| $M$ | Male, all large and robust individuals | Census |
| $F$ | Female, all large and robust individuals | Census |
| $J$ | Juvenile, independent of mother and ¼ - ½ the size of adults | Census |
| $I$ | Infant, clinging to mother | Census |
| $Im$ | Immature | $\mathrm{Im} = J + I$ |
| $N$ | Total number of individuals in a fragment | $N = M + F + J + I$ |
| $D$ | Ecological density (ind/ha; number of individuals per occupied fragment area; A). | $D = \frac{N}{A}$ |
| $F : M$ | Sex ratio | $F : M = \frac{F}{M}$ |
| $I : F$ | Infants per adult female | $I : F = \frac{I}{F}$ |
| $Im : F$ | Immatures per adult female | $\mathrm{Im} : F = \frac{I + J}{F}$ |
| $RRS$ | Relative reproductive success | $RRS = \frac{mean\left(J + I\right)}{female\ group\ size}$ |
| $Fec$ | Fecundity rate (infants alive in the year $t+1$ per adult female in the previous year $t$) | $Fec_t = \frac{I_{t+1}}{F_t}$ |
| $S_i$ | Survival rate infant to 1 yr juvenile | $S_{i\,t} = \frac{J_{1y\,t+1}}{I_t}$ |
| $S_j$ | Survival rate 2 yr juvenile to adult | $S_{j\,t} = \frac{F_{t+1} + M_{t+1}}{J_{2y\,t}}$ |
| $G_j$ | Survival rate 1 yr juvenile to 2 yr juvenile | $G_{j\,t} = \frac{J_{2y\,t+1}}{J_{1y\,t}}$ |
| $G_a$ | Survival rate of adult individuals | $G_{a\,t} = \frac{F_{t+1} + M_{t+1}}{F_t + M_t}$ |
| λ | Finite population growth rate between time steps in simulations (Ricker [52]) | $\lambda(t) = \lambda_{\max}^{\left(1 - \frac{N(t)}{K}\right)}$ |
| $\%Fec$ | Percent contribution of fecundity rate to the population increase rate λ | Elasticity analysis |
| $\%S_i$ | Percent contribution of infant survival to the population increase rate λ | Elasticity analysis |
| $\%S_j$ | Percent contribution of juvenile survival to the population increase rate λ, $S_j + G_j$ | Elasticity analysis |
| $\%S_{am}$ | Percent contribution of adult male survival to the population increase rate λ | Elasticity analysis |
| $\%S_{af}$ | Percent contribution of adult female survival to the population increase rate λ | Elasticity analysis |
| $Nf$ | Number of individuals expected after 30 yr simulation | Simulation, RAMAS/Metapop software |
| $Pe$ | Probability of extinction | Simulation, RAMAS/Metapop software |