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A ten-year demographic history of a population of howler monkeys (*Alouatta palliata*) living in a fragmented landscape in Mexico

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Long-term field studies of primates are critical for our understanding of life history and the processes driving changes in demography. Here, we present the first long-term demographic data for the northernmost population of the mantled howler monkey (*Alouatta palliata*). We followed 10 groups of howler monkeys living in a highly fragmented landscape between 2000 and 2011. Forest fragmentation did not seem to play a major role in the dynamics of our population, as the population size remained relatively stable over the 10-year study period, and birth rates and inter-birth intervals were comparable to those of howler monkeys at other sites. Moreover, dispersal events were commonplace, particularly secondary dispersal (individuals emigrating from groups that they had previously immigrated into), which supports the suggestion that this may be an important component of the reproductive strategy of the mantled howler monkey. Finally, we found a marked effect of seasonality on the population dynamics of our study population. In particular, the period of lowest temperatures and resource scarcity between November and March was associated with higher mortality and reproductive inhibition, while the period of resource abundance between April and May was associated with the majority of conceptions and weaning of offspring. This, in turn, could be influencing dispersal patterns in our study area, as male howler monkeys seem to time some of their immigrations into new groups to coincide with the start of the period of higher fertility, while females preferentially joined new groups several months before the onset of this period.

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27 **INTRODUCTION**

28

29 Long-term field studies of primates are critical for our understanding of life history and the processes
30 driving changes in demography (Kappeler & Watts, 2012). Such studies are particularly important in
31 modified habitats, where monitoring demographic parameters in threatened populations may be critical
32 for primate conservation. However, very few field studies have lasted long enough to provide data
33 spanning several generations and the long-term studies that do exist are usually limited to one or a
34 handful of sites across the species' distribution.

35 Long-term data on howler monkey (*Alouatta* spp.) demography is limited to studies of red
36 howler monkeys in Venezuela (*A. arctoidea*) (Crockett & Rudran, 1987; Rudran & Fernandez-Duque,
37 2003) and mantled howler monkeys in Panama (*A. palliata aequatorialis*) (Milton, 1982, 1990, 1996)
38 and Costa Rica (*A. palliata palliata*) (Glander, 1992; Clarke et al., 2002; Zucker & Clarke, 2003;
39 Clarke & Glander, 2010). However, demographic patterns in primates are contingent on local climate
40 and vegetation, and consequently a comprehensive understanding of the factors determining dispersal
41 processes, mortality and fertility in howler monkeys requires long-term studies to be conducted not
42 only in different taxa, but also in different landscapes and locations.

43 Here, we present ten years of demographic data from ten groups of mantled howler monkeys
44 (*Alouatta palliata mexicana*) residing in a highly fragmented landscape in the north of the Los Tuxtlas
45 Biosphere Reserve, Veracruz, Mexico, which represents the northernmost limit of mantled howler
46 monkey distribution and is near the northern limit of the distribution of the genus (Rylands et al.,
47 2006). *Alouatta palliata mexicana* is a critically endangered subspecies (Cuarón et al., 2008), which
48 has been studied since the 1980s in Los Tuxtlas (Cristóbal-Azkarate, Dunn & Cristobal-Azkarate,
49 2013). However, paradoxically, our knowledge of reproduction, mortality and migration in this

50 subspecies is very limited, and what data is available is mostly based on indirect evidence from single
51 population censuses and anecdotal observations (Estrada & Coates-Estrada, 1996; Cristóbal-Azkarate,
52 Dias & Veà, 2004; Cristóbal-Azkarate et al., 2005). Only two studies have examined demographic
53 change in this subspecies, both of which are limited in scope: the first studied demographic changes in
54 only one group of howler monkeys over a ten year period (Arroyo-Rodríguez, Asensio & Cristóbal-
55 Azkarate, 2008), and the second compared data from two primate population censuses carried out in
56 1985 and 2008 (Solórzano-García & Rodríguez-Luna, 2010). Consequently, there is an urgent need for
57 long-term demographic data for this taxon. Such information is crucial for monitoring the conservation
58 status of *A. p. mexicana* populations and to further our understanding of the ways in which forest
59 fragmentation may affect population dynamics in primates.

61 **METHODS**

63 *Ethics statement*

64 This study is based on observational data and there was no direct interaction with the study subjects.
65 We were granted access to the study site by local communities, landowners, and the Los Tuxtlas
66 Biosphere Reserve, part of the National Commission of Natural Protected Areas of Mexico
67 (CONANP). All research adhered to the American Society of Primatologists Principles for the Ethical
68 Treatment of Non-Human Primates and to the legal requirements of Mexico. We also obtained
69 approval from the ethics committees of the University of Barcelona and Universidad Veracruz.

71 *Study species*

72 Five subspecies of mantled howler monkeys (*Alouatta palliata*) are currently listed in the IUCN Red
73 List of Threatened Species (Cuarón et al., 2008): *A. p. mexicana*, *A. p. palliata* and *A. p. aequatorialis*,

74 *A. p. coibensis*, and *A. p. trabeata*. These subspecies are distributed from south-east Mexico to
75 northwest Peru (Rylands et al., 2006). Owing to widespread habitat loss and fragmentation throughout
76 its range, the remaining population of *A. p. mexicana* has declined drastically over the last 30 years and
77 this subspecies is now restricted to highly fragmented forested areas in the Mexican states of Veracruz,
78 Tabasco, Oaxaca and Chiapas. As a result, this subspecies is currently listed as critically endangered by
79 the IUCN (Cuarón et al., 2008).

80 These primates are seasonally folivorous, with leaves contributing over 80 % of food intake
81 when fruit is scarce (Milton, 1980; Glander, 1981; Cristóbal-Azkarate & Arroyo-Rodríguez, 2007).
82 This degree of folivory has been associated with their small home range size compared to other more
83 frugivorous species (Milton, 1976) and primates living in small home ranges are considered to be more
84 resistant to habitat fragmentation (Cowlshaw & Dunbar, 2000).

85 Gestation lasts 6 months in mantled howler monkeys (Glander, 1980; Crockett & Rudran, 1987;
86 Strier, Mendes & Santos, 2001), and weaning occurs at approximately 18-20 months of age (Carpenter,
87 1934; Clarke, 1990; Domingo-Balcells & Veà-Baró, 2009). This species is characterized by bisexual
88 emigration of juveniles; males typically emigrate at around 22 months of age and females typically
89 emigrate at around 33 months of age (Glander, 1992). However, it has been suggested that in Los
90 Tuxtlas juveniles may occasionally emigrate as early as 14 months of age (Domingo-Balcells & Veà-
91 Baró, 2009). Recent evidence indicates that secondary dispersal (individuals emigrating from groups
92 that they have previously immigrated into) also exists in mantled howler monkeys and that this can be
93 driven by the availability of individuals of the opposite sex (Clarke & Glander, 2010). Dispersal
94 patterns can be disturbed by relatively low levels of fragmentation (Chiarello & de Melo, 2001), as
95 howler monkeys are highly arboreal and spend almost all of their time in the upper canopy, very rarely
96 coming to the ground (Mendel, 1976).

97

98 ***Study site***

99 The Los Tuxtlas Biosphere Reserve represents the northernmost limit of tropical rainforest distribution
100 in the Americas (Guevara-Sada, Laborde & Sánchez-Ríos, 2004). Our study site (18° 39' 21" – 18° 31'
101 20" N and 95° 9' 14" – 95° 1' 45" W; elevation 0 – 400 m a.s.l) covers approximately 7, 500 hectares,
102 and like many other regions throughout the tropics, it has suffered from extensive habitat loss,
103 transformation, and fragmentation, principally as a result of cattle farming (Fig. 1). Nevertheless,
104 compared to many other fragmented landscapes, it retains a relatively high level of connectivity, with
105 live fences (i.e., several strands of barbed wire held up by a line of trees), riparian vegetation and
106 isolated trees found between many fragments. It also contains areas of continuous forest in close
107 proximity to the fragments (Fig. 1).

108 The climate in Los Tuxtlas is warm and humid with a mean annual temperature of 25 °C and
109 rainfall of 4,900 mm (Soto, 2004). There is a dry season between March and May and a wet season
110 from June to February. During the wet season there is also a period of strong winds and a considerable
111 reduction in temperature between October and February (Fig. 2a). Long-term records of phenological
112 data in the region show that there are two distinct peaks in fruit production in the region: a primary
113 peak at the end of the dry season—beginning of the rainy season (April–June), and a shorter, less intense
114 secondary peak in the wet season (August–October), while fruit production abruptly falls to very low
115 levels between November and March (Fig. 2b). The howler monkeys in Los Tuxtlas respond to the
116 reduction in temperature and fruit availability between November and March by increasing their
117 consumption of leaves and their foraging effort (Dunn, Cristóbal-azkarate & Veà, 2010), which, in
118 turn, has been associated to higher levels of physiological stress (Dunn et al., 2013). Therefore, we
119 refer to this period as the “period of energetic stress”.

120

121 ***Study groups***

122 We carried out the first census of our study site in 2000. Of the 55 forest fragments that are found in
123 our study site, we found 21 to be inhabited with at least one howler monkey and recorded a total
124 population of 316 individuals living in 43 groups (Cristóbal-Azkarate et al., 2005). We began studying
125 four of these groups intensively in 2000. Over the following 10 years, we studied six more groups as
126 part of a programme of interdisciplinary research, for a total of 10 groups, which provided the data for
127 our analyses (e.g. (Cristóbal-Azkarate et al., 2006, 2007; Dunn, Cristóbal-azkarate & Veà, 2010; Dunn
128 et al., 2013)). Despite the wide-ranging nature of the research, we gathered basic demographic data,
129 such as the number of individuals, age-sex composition, births, deaths and migrations, whenever
130 possible over the 10 year period.

131

132 ***Data collection***

133 We present demographic data from 10 groups of howler monkeys, representing 454 monthly group
134 visits, which were carried out between 2000 and 2011 (Table S1; further details about our demographic
135 records are available upon request). Given that the data has been pooled across several different
136 studies, there is some discontinuity, with certain groups being studied for longer and/or more
137 frequently than others (mean \pm SD = 45.1 \pm 29.7 monthly visits per group; Table S1). The study groups
138 inhabited eight different forest fragments, which varied in size, shape and connectivity (Fig. 1).

139 During each visit, we identified group members on the basis of characteristic patterns on the fur
140 and skin, scars, and other distinguishing features. Each time we recorded a new individual in a group,
141 we determined its age and sex using the classification system developed by Balcells and Veà
142 (Domingo-Balcells & Veà-Baró, 2009), which allows an age range to be estimated on the basis of
143 morphological and behavioural characteristics.

144

145 ***Demographic events***

146 Throughout the study, we registered all demographic events in the groups, including: emigration,
147 immigration, birth and death. However, given the low probability of observing these events directly,
148 some of the events were also assumed to have occurred on the basis of changes in group composition
149 and supporting evidence.

150

151 *Birth*

152 We assumed a new individual had been born in a group when a new dependent infant, which was
153 strongly associated with one of the group females, was observed in a group, and that had a younger
154 estimated age than the time that had passed since we last visited the group.

155 To calculate the mean annual birth rate for each group, we determined the number of births that
156 had taken place per year for the mean number adult females in the group. This allowed us to control for
157 the effect of the number of females on birth rate. We defined the inter-birth interval (IBI) as the time
158 that occurred between births for any given female.

159

160 *Emigration*

161 We assumed an individual had emigrated from a group when all of the following criteria were met: 1)
162 we had not observed the individual in the group for more than one month; 2) the last time we observed
163 the individual it showed no sign of disease or injury; and 3) the last time we observed the individual it
164 was fully weaned (unless emigrating with its mother). We also classified an individual as having
165 emigrated if it was observed in a new group or as a solitary individual.

166 When an individual emigrated from the group it was born in, we defined this as 'natal
167 emigration'. When an individual emigrated from a group that it had previously immigrated into, we
168 defined this as 'secondary emigration'.

169

170 *Immigration*

171 We assumed a new individual had immigrated into a group when, on first sighting, its estimated age
172 was greater than the time passed since our last visit to the group (e.g., a new individual with an
173 estimated age of 12 months was observed for the first time in a group, but the group was last visited 2
174 months ago).

175

176 *Death*

177 We assumed an individual had died when at least one of the following criteria was met: 1) we found
178 the body; 2) the individual went missing while still dependent on its mother's milk and its mother
179 remained in the group; or 3) the individual went missing fully weaned, but was showing serious signs
180 of injury or disease the last time it was observed.

181

182 *Disappeared*

183 For some individuals it was not possible to determine with any confidence whether they had emigrated
184 or died. Therefore, we recorded these individuals as disappeared.

185

186 *Statistical analyses*

187 For the calculation of the seasonality of demographic events, IBI and birth rates, we considered only
188 those events that were registered during periods in which the study groups were observed continuously
189 and that could be assigned to a date with a maximum error of one month (see Table S1). In order to
190 control for the effect that our slightly unbalanced sampling effort could have on the seasonality data,
191 we weighted the original data by dividing the frequency of events per month by the total number of
192 times observations were conducted each month (mean \pm SD average visits per month = 37.6 ± 3.1 ,

193 range = 35 – 42; Table S1). We used these weighted values to calculate the % of demographic events
194 in each month.

195 We used a Kruskal-Wallis test to analyse the difference in annual birth rate among groups. We
196 also used a Mann-Whitney U test to test the hypothesis that the death of a suckling offspring (≤ 14
197 months of age (Domingo-Balcells & Veà-Baró, 2009)) shortens the IBI by comparing the mean IBI of
198 females with surviving and non-surviving offspring.

199 To test for differences in the frequency of demographic events between the season of energetic
200 stress (November – March, see above) and the rest of the year, as well as to test for significant
201 differences between peaks in demographic events at certain times of year compared to the rest of the
202 year, we conducted G-tests, with expected values being proportionally calculated according to the
203 number of months used in the analysis.

204 Furthermore, in order to account for the underlying continuity of the time variable, we also used
205 circular statistics to test for seasonality of demographic events (Batschelet, 1981). This approach has
206 several advantages over those traditionally used by primatologists to test for seasonality (Janson &
207 Verdolin, 2005; Gogarten et al., 2014). The mean vector length (r) obtained from circular statistics is
208 well suited as an index of seasonality, as it provides a measure of how evenly events are distributed
209 throughout the year. When events are spread evenly across months (not seasonal), r is close to zero and
210 when events are highly clustered at the same time of year (highly seasonal), r is close to one. We tested
211 the significance of the r statistic using the Rayleigh test (Batschelet, 1981), which compares the data
212 with the null hypothesis that demographic events have a random distribution across months. As we
213 used monthly data for demographic events, rather than specific dates, we also used a correction factor
214 ($c = 1.0115$) when calculating the r statistic (Batschelet, 1981). To test for bimodal distribution in the
215 data, we also calculated r by doubling the angle calculated for each demographic event (Batschelet,

216 1981; Janson & Verdolin, 2005; Gogarten et al., 2014). We carried out analyses in R 2.13.1 (Team
217 Development Core, 2008), testing for normality in the data and considering $p < 0.05$ as significant.

218

219 **RESULTS**

220

221 Overall, we observed an increase in the number of individuals in our population between 2000-2011.
222 Most of the study groups showed little change in the total number of individuals and in the number of
223 adult individuals from the start to the end of the ten-year study period. However, two groups showed a
224 substantial increase in number (Table 1). Migration was the principal cause of change in group size and
225 composition, followed by births, then deaths.

226

227 *Births*

228 We registered a total of 75 births and at least two births were observed in all 10 of our groups (Table
229 1). Of these, we were able to determine the date of birth to within one month on 49 occasions.

230 The mean birth rate per group was 0.40 ± 0.33 births per female per year ($N = 39$ births; Table
231 2). There were groups with no births in some years, while other groups had a birth rate as high as 1 in
232 some years (indicating that all females of reproductive age gave birth in that year). We found no
233 significant differences in mean birth rate among groups (Kruskal-Wallis Test $H = 5.74$, $p = 0.76$).

234 The mean IBI was 21.61 ± 13.27 months (Table 2), with 12 cases in which the offspring from
235 the first birth had survived until weaning (mean = 26.08 ± 14.05 months) and six cases in which the
236 offspring from the first birth had died before weaning (mean = 12.67 ± 4.54 months). There was a
237 significant reduction in IBI when the first offspring had died before weaning (Mann-Whitney $U = 8.0$,
238 $p = 0.007$).

239 Although we observed births throughout the whole year, births were clearly seasonal. Seventy
240 four per cent of births occurred between October and March (Fig. 3a), with a main peak in November
241 and a second peak in February. The bimodal r statistic was highly significant (unimodal $r = 0.20$, $p =$
242 0.14 ; bimodal $r = 0.43$, $p < 0.001$), suggesting a bimodal distribution and a strong effect of seasonality
243 on birth. As the gestation time of howler monkeys is 6 months, these data indicate that conceptions
244 leading to births peaked in May, after the period of energetic stress. In fact, the number of conceptions
245 leading to births was significantly lower during the period of energetic stress than in the rest of the year
246 ($G = 9.9$, $p < 0.001$).

247

248 *Emigration*

249 We recorded emigrations in all but one of our study groups, with a total of 62 individuals emigrating
250 from groups (Table 1). Thirty-four of these were adults (13 adult males and 21 adult females), 7 were
251 sub-adults (2 males, 2 females, and 3 of unknown sex), 13 were juveniles and 8 were infants.

252 We recorded 24 natal emigrations (52.8% of total number of emigrations of known origin). One
253 by an adult male, 6 by adult females, 3 by subadults, 11 by juveniles and 7 by infants. Of these, 4 left
254 the group soon after the birth of a sibling and 8 left the group soon after one or more individuals had
255 immigrated into their group.

256 We recorded 22 secondary emigrations (47.8% of total number of emigrations of known
257 origin). Nineteen of these were adults (11 males and 8 females), 1 was a male sub-adult, 1 was a
258 juvenile and 1 was an infant that transferred to the group together with her mother, and then left with
259 her after one month of permanence in the group. The mean time that the individuals spent in a group
260 prior to secondary transfer was 18.4 ± 21.1 months (range = 1 – 90 months).

261 On 16 occasions, we were not able to determine whether the emigrating individuals were born
262 in the group they emigrated from or whether they had previously immigrated into the group.

263 Accordingly these emigrations were of unknown origin and were not classified as natal or secondary.

264 Emigrations occurred throughout the year, but there were clear differences in emigration
265 patterns among the age-sex classes (Fig. 3b). Male emigration peaked in August (33.1% of cases) and
266 January-February (43.9%), but the r statistic was not significant (unimodal $r = 0.34$, $p = 0.23$; bimodal
267 $r = 0.40$, $p = 0.13$). Female emigration showed a very clear peak in August-September (49.6% of
268 cases), when significantly more emigrations occurred than during the rest of the year ($G = 10.8$, $p <$
269 0.001). The unimodal r statistic showed a trend towards seasonality, and was close to significant
270 (unimodal $r = 0.34$, $p = 0.08$; bimodal $r = 0.27$, $p = 0.19$). Subadult and juvenile emigration showed a
271 peak in November-December (38.9% of cases), when significantly more emigrations happened than
272 during the rest of the year ($G = 6.9$, $p < 0.001$). However, the r statistic was not significant (unimodal r
273 $= 0.15$, $p = 0.62$; bimodal $r = 0.29$, $p = 0.23$).

274

275 *Immigration*

276 We recorded immigrations in the all forest fragments that we studied and in all but one of our study
277 groups (this group was only followed for one year). In total we recorded 57 individuals immigrating
278 into new groups (Table 1); 46 were adults (22 males and 24 females), 6 were sub-adults (3 males and 3
279 females), 3 were juveniles and 2 were infants. Of these, we were able to determine the date of
280 immigration to within one month in 41 cases (Table S1).

281 Immigration occurred throughout the year, but there were clear differences in immigration
282 patterns among the age-sex classes (Fig. 3c). Adult male immigrations peaked between April-May
283 (40.5% of cases) and September-December (52.2%), and while the bimodal r statistic showed a trend
284 towards seasonality, it was not significant (unimodal $r = 0.20$, $p = 0.56$; bimodal $r = 0.38$, $p = 0.11$).

285 Female immigration showed a clear peak between September and December (79.3% of cases), when
286 significantly more immigration occurred than in the rest of the year ($G = 12.1$, $p < 0.001$). The bimodal
287 r statistic showed a trend towards seasonality, but was not significant (unimodal $r = 0.20$, $p = 0.58$;
288 bimodal $r = 0.39$, $p = 0.11$). Subadults and juveniles showed a peak in immigration between August
289 and September (65.3% of cases), and significantly more immigrations occurred in this period than in
290 the rest of the year. However, the r statistic was not significant (unimodal $r = 0.36$, $p = 0.74$; bimodal r
291 $= 0.23$, $p = 0.65$).

293 *Deaths*

294 We registered a total of 18 deaths, and at least one death was registered in eight of the 11 groups (Table
295 1). Thirteen of these individuals were infants that were not weaned when they disappeared, of which
296 eight went missing before four months of age, three between four and eight months, and two at 10
297 months of age. Of these infants, we observed one death directly, which happened when the infant was
298 one month old and another howler monkey seemingly killed its mother (see below) and we assumed
299 another infant to have died shortly after its mother had died and it was observed falling in a tree. We
300 assumed one juvenile to have died having shown signs of physical weakness and struggling to keep up
301 with the group. The remaining 4 deaths were all adults. We recovered the body of one female, which
302 had several serious bite marks. Post-mortem examination by a veterinarian found the cause of death to
303 be lung perforation, consistent, in terms of bite shape, breadth and depth, with an attack by another
304 howler monkey (Escorcia-Quintana, personal communication). One adult male probably died after we
305 observed it with severe open wounds resulting from an attack by two immigrating males. Another adult
306 male showed signs of paralysis and lethargy before his assumed death. A further adult male showed
307 signs of old age, lack of appetite and was unable to keep up with the group.

308 We registered deaths in most months of the year, but there was a clear peak between November
309 and March when 75.3% of deaths occurred (Fig. 3d). There were significantly more deaths during the
310 period of energetic stress than in the rest of the year ($G = 9.8$, $p < 0.001$). However, the r statistic was
311 not significant (unimodal $r = 0.08$, $p = 0.89$; bimodal $r = 0.25$, $p = 0.30$).

312

313 *Disappeared*

314 We were unable to interpret the history of 27 individuals from the data, which we recorded as
315 disappeared (Table 2).

316

317 **DISCUSSION**

318

319 Our data show a dynamic population with frequent demographic change, including a large number of
320 migrations, births and deaths.

321 While births were distributed throughout the year, they were highly seasonal, with a clear peak
322 between October and December and a secondary peak in February. Another study carried out in a
323 different area of Los Tuxtlas found similar results (Carrera- Sánchez, Medel-Palacios & Rodríguez-
324 Luna, 2003). This suggests that the majority of conceptions that lead to births occur between April and
325 June (Fig. 3a), coinciding with the annual peak in fruit availability and increase in ambient temperature
326 (Figs. 2a & 2b). Accordingly our data suggests that the higher energetic stress between November and
327 March may be inhibiting the reproduction of females and that the improved conditions from April to
328 June results in an increase in fertility. Other studies have also reported that the time of conception is
329 associated with the availability of food and temperature in howler monkeys (Kowalewski & Zunino,
330 2004). This supports the idea that howler monkeys are income breeders (rather than capital breeders)
331 and that they use energy acquired during the reproductive period for reproduction instead of stored

332 energy (Brockman & van Schaik, 2005; Janson & Verdolin, 2005). Similarly, the weaning of offspring
333 would also occur in April and May, supporting the idea that the weaning of offspring in howler
334 monkeys occurs at times of year in which the availability of high quality food is higher and the climate
335 is more benign (Kowalewski & Zunino, 2004).

336 The mean birth rate of the study groups is within the range reported for other growing
337 populations in the Neotropics (*Alouatta palliata*: (Cortés Ortiz et al., 1994); *A. arctoidea*: (Crockett &
338 Rudran, 1987)), which suggests that, in principle, our study population is not constrained by its
339 reproductive output. The IBI is also within the range previously reported for the species (Glander,
340 1980; Milton, 1982; Fedigan & Rose, 1995; Carrera- Sánchez, Medel-Palacios & Rodríguez-Luna,
341 2003; Arroyo-Rodríguez, Asensio & Cristóbal-Azkarate, 2008) and genus (*Alouatta guariba*: (Strier,
342 Mendes & Santos, 2001); *A. arctoidea*: (Crockett & Rudran, 1987); *A. caraya*: (Rumiz, 1990); *A.*
343 *pigra*: (Horwich et al., 2001)). The death of an infant significantly reduced the IBI, a phenomenon also
344 reported for other primate species (Fedigan & Rose, 1995).

345 We recorded numerous migration events, with both emigration and immigration being observed
346 in almost all of the study groups. Surprisingly, all of the groups that were the only group in a forest
347 fragment received immigrants, and all but one were a source of emigrants. This suggests that, in our
348 study landscape, howler monkeys are able to transfer between forest fragments. This behaviour has
349 also been reported elsewhere for howler monkeys, and the probability of dispersal has been negatively
350 related to the isolation distance of the fragment and positively related to the connectivity of the
351 fragment and heterogeneity of the landscape (Glander, 1992; Mandujano, Escobedo-Morales &
352 Palacios-silva, 2004; Estrada et al., 2006; Mandujano et al., 2006; Asensio et al., 2009). Accordingly,
353 we believe that the high levels of dispersal recorded in our study population are probably related to the
354 high level of landscape connectivity.

355 The high number of migratory events that we observed is a good sign for the long-term viability
356 of the population, as transfer among forest fragments may serve to mitigate the negative effects of
357 forest fragmentation on howler monkeys, by improving access to resources and promoting outbreeding.
358 Unfortunately, we were unable to determine the exact origin and destination of most migrations.
359 Determining which groups and fragments are in migratory contact with each other, in addition to
360 identifying important dispersal routes, would allow for better modeling of the dynamics of our study
361 population and help identify priority areas for conservation. This gap in our knowledge should be
362 addressed in the future with research focused on molecular genetic methods in addition to telemetry to
363 follow the movement of individuals in the landscape.

364 Both natal and secondary emigration was common in our population. The fact that most
365 juveniles leave their natal group is well described in the literature (Glander, 1992), but it was not until
366 very recently that it was proposed that secondary dispersal may be a common and important
367 component of the reproductive strategy of mantled howler monkeys (Clarke & Glander, 2010). The
368 fact that almost half of all emigrations in our study population were secondary dispersals provides
369 strong support for this hypothesis. While emigration was not found to be strongly seasonal, males and
370 females showed clear peaks (males in January-February and August; females August-September)
371 which preceded by less than two months the peaks in immigration (Figs. 3b & 3c), while the
372 emigration of subadults and juveniles peaked in November, coinciding with the beginning of the period
373 of fruit scarcity and higher levels of physiological stress (Dunn et al., 2013). This could suggest that
374 the timing of emigration might be associated with factors determining the best time for transferring to a
375 new group (e.g., resource availability and reproduction), while the emigration of subadults and
376 juveniles might be driven by competition for food. However, this is speculative and without more
377 information on the life of solitary individuals in Los Tuxtlas, including data on the duration of this
378 period for males and females, it is not possible to draw any solid conclusions from our data.

379 Like emigration, immigration was not found to be strongly seasonal. However, for both sexes
380 these events were more common during the primary and secondary peaks in fruit availability and
381 consumption by howler monkeys in Los Tuxtlas (Dunn, Cristóbal-azkarate & Veà, 2010), which
382 suggests that resident individuals may be more willing to accept immigrants during periods of relative
383 resource abundance. Moreover, the primary peak in male immigration (April-May) coincides with the
384 time when most conceptions leading to births occurred. It is not clear whether in Los Tuxtlas
385 immigrating males achieve alpha status immediately upon immigration as described in *Alouatta*
386 *palliata palliata* in Costa Rica (Glander, 1980). However, several males were observed mating with
387 females shortly after immigration (pers. communication) and, nonetheless, mantled howler males are
388 not reported to monopolize reproduction (Jones, 1995; Wang & Milton, 2003). Therefore, the
389 availability of fertile females may be driving, at least in part, the timing of immigration of males. On
390 the other hand, by joining the group several months before the onset of the period with the highest
391 number of conceptions leading to births (April-May), the females may have more time to achieve an
392 adequate position in the group to maximise their chances for successful reproduction when the
393 environmental conditions are optimal.

394 The fact that we only recorded 3 immigrations by juveniles, but recorded 13 emigrations,
395 suggests that the mortality of juveniles may be high during these periods, and/or that immigration into
396 groups is easier for fully grown adults and juveniles may need to spend several years as solitary
397 individuals before forming a new group or joining an established group (Glander, 1992). Although
398 intense fighting has previously been reported between resident males and adult male immigrants
399 (Clarke & Glander, 2004a; Dias et al., 2010), and evidence from facial scarring and injuries suggests
400 that fighting may be common in howler monkeys in Los Tuxtlas (Cristóbal-Azkarate, Dias & Veà,
401 2004), we only observed one such fight during our study, and apart from this occasion, we did not
402 observe any males with injuries following an immigration event. Therefore, male transfers in Los

403 Tuxtlas might be more pacific than previously thought (Cristóbal-Azkarate, Dias & Veà, 2004), and
404 than has been reported for other sites (Clarke & Glander, 2004b).

405 We registered 18 assumed deaths, which were predominantly infants, although we were unable
406 to determine the cause of death for most of the cases. The fact that a group female was, seemingly,
407 killed by a conspecific while carrying a 1-month-old infant is noteworthy, and may have been the result
408 of an attempted infanticidal attack. However, this is speculative and, without more information of the
409 context and details of the event, it is difficult to interpret. One male probably died after we observed it
410 with severe open wounds resulting from an attack by two immigrating males. Ignoring these cases,
411 which were seemingly the result of intraspecific aggression, deaths showed a clear pattern with 75% of
412 total deaths, and 100% of adult deaths, occurring in the period of energetic stress. Thus, it seems that
413 energetic constraints may be an important factor regulating the population dynamics of howler
414 monkeys in the region.

415 Overall, our results suggest that the population of howler monkeys in Los Tuxtlas has neither
416 increased nor decreased in the last ten years. Moreover, we found migration events to be frequent
417 between groups and fragments, despite the isolating effects of forest fragmentation. However, the study
418 period was short relative to the long life span and slow life-history of howler monkeys, and the
419 fragmentation history is relatively recent in the region, meaning that group size and composition may
420 not yet be well suited to the current environmental conditions. Only longer-term studies, which
421 incorporate indices of health, reproduction and fitness (e.g., ecophysiology, molecular genetics) in
422 conjunction with intensive data on demographic evolution, would allow us to fully examine the long-
423 term conservation prospects of this population.

424

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426

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431

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592 **FIGURE LEGENDS**

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594 **Figure 1.** Ortophoto obtained from INEGI (<http://www.inegi.org.mx>) of our 7,500 ha study area in the
595 Los Tuxtlas Biosphere Reserve, Veracruz, Mexico, indicating the forest fragments inhabited by the 10
596 study groups. Areas in dark green represent forest, light green pasture and black the sea. Note that the
597 RH fragment has recently connected to continuous forest through regrowth of secondary vegetation,
598 but during the period that this group was studied there was no such connection.

599

600 **Figure 2.** A) Monthly average temperature and rainfall in the study area for the study period; and B)
601 Plant phenology in Los Tuxtlas adapted from Dunn et al. (Dunn, Cristóbal-azkarate & Veà, 2010)
602 showing the mean percentage of tree species containing fruit and young leaves.

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604 **Figure 3.** Seasonality of demographic events (A = birth, B = emigration, C = immigration, D = natural
605 death, i.e., not associated with aggression) for 10 groups of mantled howler monkeys in the Los
606 Tuxtlas Biosphere Reserve, Mexico. Dispersal events of infants are not considered because the always

607 occurred in the company of their mothers. Values are weighted by dividing the frequency of
608 demographic events by the number of observations conducted each month.

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615 **Table 1.** Demographic data from 10 groups of mantled howler monkeys in Los Tuxtlas, Mexico, between 2000 and 2011

Group	Fragment size (ha)	Study Period	Adults Start	Total Start	Birth	Emigration	Immigration	Death	Disappeared	Adults end	Total end	Adult growth	Total growth
MT (1)	63.8	2000-2011	2	2	16	23	24	3	0	11	16	9	14
MT (2)	63.8	2000-2011	13	18	13	12	12	3	10	11	18	-2	0
RC3	7.2	2000-2011	5	6	10	7	5	4	4	4	6	-1	0
2AB	3.6	2001-2011	5	5	8	9	4	1	2	3	5	-2	0
JIC	6.9	2001-2011	2	2	3	0	4	0	0	7	9	5	7
RH	244	2001-2011	5	6	12	3	1	3	4	6	9	1	3
RC5	5.9	2007-2011	3	4	3	3	1	1	0	3	4	0	0
RC2	5.3	2004-2005	11	12	5	3	2	2	0	10	14	-1	2
RC4 (1)	17.5	2004-2005	6	8	2	1	4	0	7	5	5	-1	-3
RC4 (2)	17.5	2004-2005	5	5	3	1	0	1	0	5	6	0	1
TOTAL		2000-2011	57	68	75	62	57	18	27	65	92	8	24

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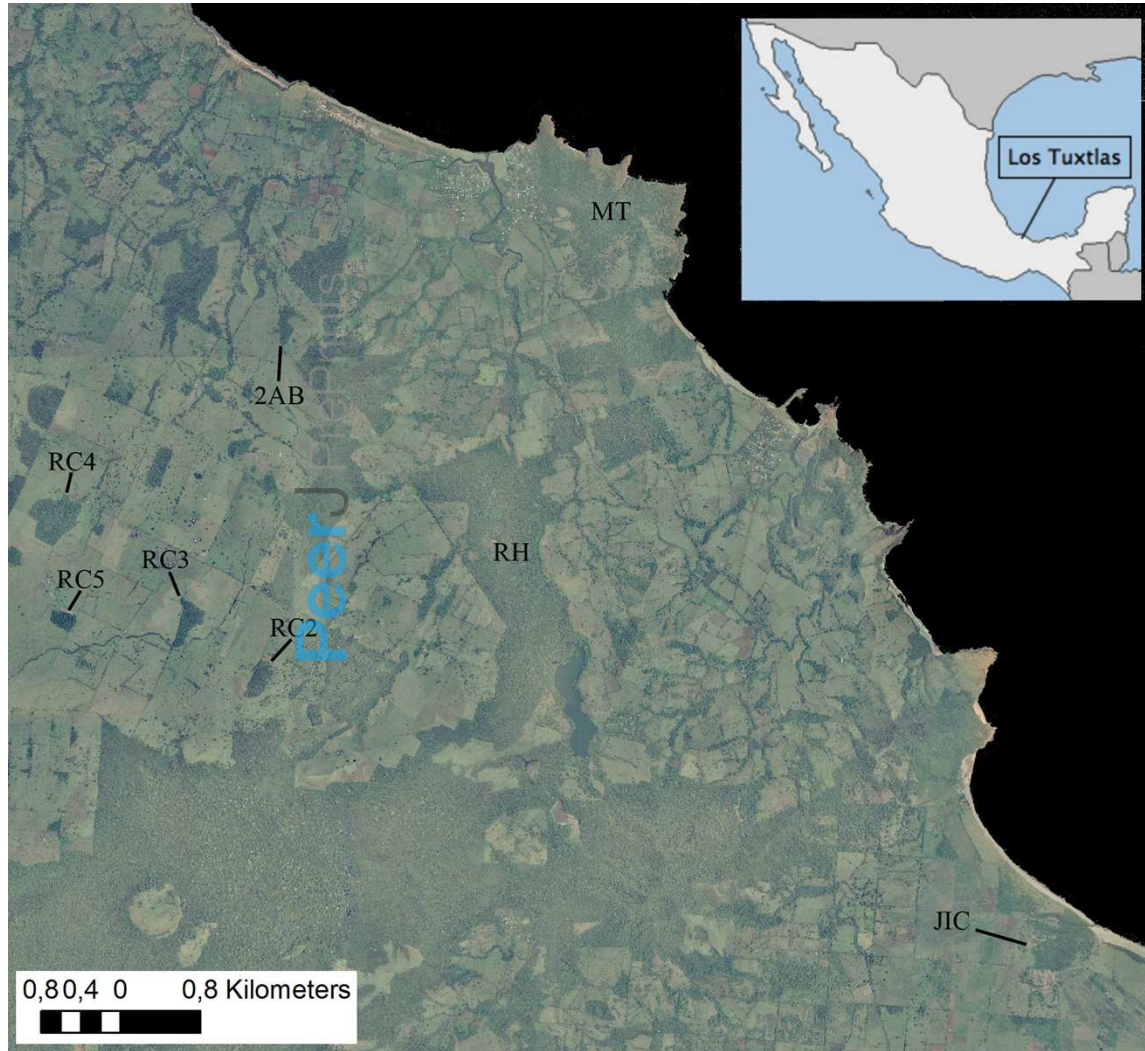
624 **Table 2.** Mean birth rate and inter-birth interval for 10 groups of mantled howler monkeys in Los Tuxtlas, Mexico, between 2000 and 2010,
 625 as well as other studies of howler monkeys in the Neotropics

Study	Taxon	Group	Birth Rate (births per female per year)			Inter-birth interval (IBI) (months)		
			Mean ± SD	N (years)	Range	Mean ± SD	N (cases)	Range
Present Study	<i>A. palliata mexicana</i>	MT (1)	0.36 ± 0.26	6	0.00 - 0.80	11.0	2	8 - 14
Present Study	<i>A. palliata mexicana</i>	MT (2)	0.50 ± 0.25	2	0.32 - 0.68	20.6 ± 9.9	5	8 - 35
Present Study	<i>A. palliata mexicana</i>	RC3	0.56 ± 0.40	7	0.00 - 1.00	23.33 ± 13.5	6	13 - 50
Present Study	<i>A. palliata mexicana</i>	2AB	0.47 ± 0.32	6	0.00 - 1.00	39.5 ± 24.7	2	15 - 57
Present Study	<i>A. palliata mexicana</i>	JIC	0.18 ± 0.24	4	0.00 - 0.50	-	-	-
Present Study	<i>A. palliata mexicana</i>	RH	0.52 ± 0.17	4	0.33 - 0.75	15 ± 4.3	3	12 - 20
Present Study	<i>A. palliata mexicana</i>	RC5	0.25 ± 0.35	2	0.00 - 0.50	-	-	-
Present Study	<i>A. palliata mexicana</i>	RC2	0.35 ± 0.33	2	0.11 - 0.58	-	-	-
Present Study	<i>A. palliata mexicana</i>	RC4 (1)	0.33 ± 0.58	3	0.00 - 1.00	-	-	-
Present Study	<i>A. palliata mexicana</i>	RC4 (2)	0.33 ± 0.33	3	0.00 - 0.67	-	-	-
Total		-	0.42 ± 0.32	39	0.00 - 1.00	21.6 ± 13.3	18	8 - 57
Cortés Ortiz et al., 1994	<i>A. palliata mexicana</i>	-	0.62	5	-	15.79	19	10 - 21
Carrera- Sánchez, Medel-Palacios & Rodríguez-Luna, 2003	<i>A. palliata mexicana</i>	-	≈ 0.5	14	0.25 - 1.00	20.4	20	8 - 50
Arroyo-Rodríguez, Asensio & Cristóbal-Azkarate, 2008	<i>A. palliata mexicana</i>	-	-	-	-	25.0 ± 3.0	4	23 - 29
Glander, 1980	<i>A. palliata palliata</i>	-	0.22	7	0.07 - 0.40	22.5 ± 0.6	16	18 - 25
Fedigan & Rose, 1995	<i>A. palliata palliata</i>	-	≈ 0.5	8	0.00 - 1.00	19.90	24	9 - 40
Milton, 1982	<i>A. palliata aequatorialis</i>	-	-	-	-	17	3	-
Crockett & Rudran, 1987	<i>A. arctoidea</i>	-	0.68	8	0.55 - 0.88	17.4 ± 4.5	135	10 - 35
Strier, Mendes & Santos, 2001	<i>A. guariba</i>	-	-	-	-	22.8 ± 6.6	12	11 - 38
Rumiz, 1990	<i>A. caraya</i>	-	0.89	4	-	15.9 ± 3.7	30	12 - 22
Horwich et al., 2001	<i>A. pigra</i>	-	-	-	-	19.4	64	10 - 35

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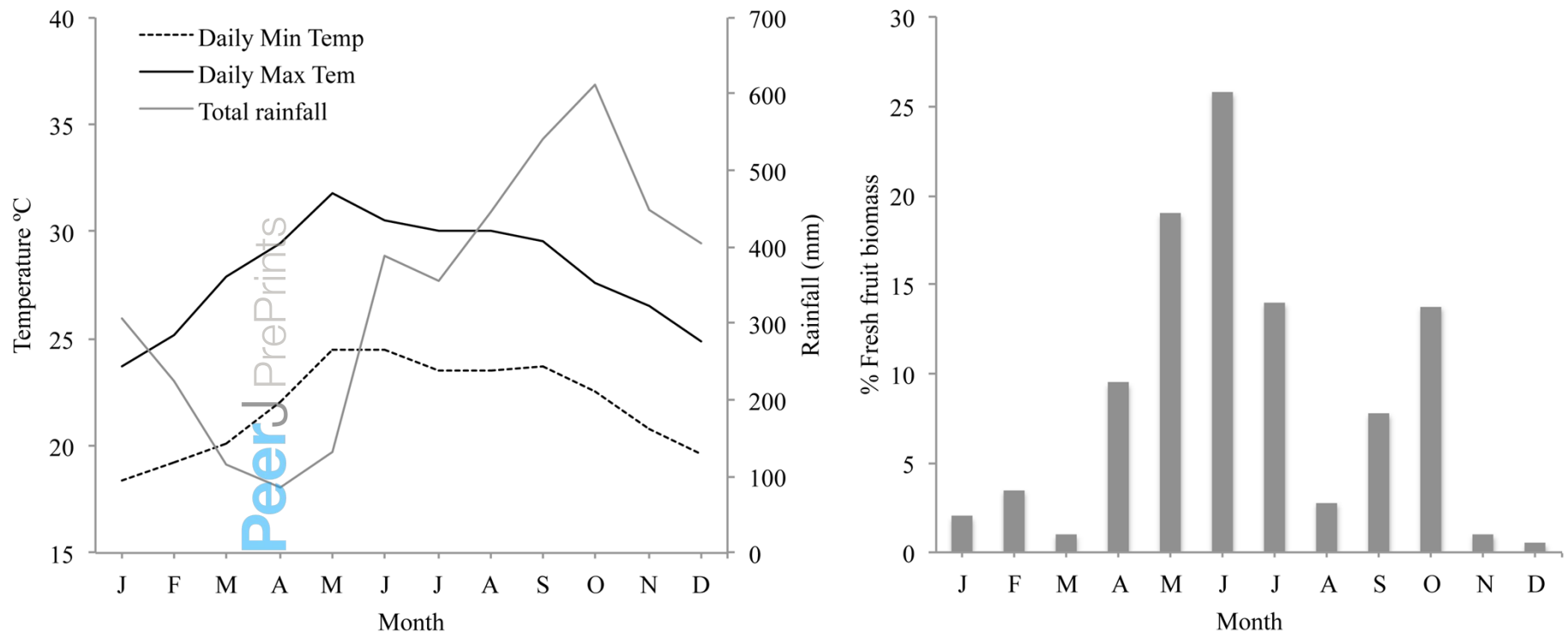
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Figure 1.



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Figure 2.



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Figure 3.

