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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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INTRODUCTION

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

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

Here, we present ten years of demographic data from ten groups of mantled howler monkeys (*Alouatta palliata mexicana*) residing in a highly fragmented landscape in the north of the Los Tuxtlas Biosphere Reserve, Veracruz, Mexico, which represents the northernmost limit of mantled howler monkey distribution and is near the northern limit of the distribution of the genus (Rylands et al., 2006). *Alouatta palliata mexicana* is a critically endangered subspecies (Cuarón et al., 2008), which has been studied since the 1980s in Los Tuxtlas (Cristóbal-Azkarate, Dunn & Cristobal-Azkarate, 2013). However, paradoxically, our knowledge of reproduction, mortality and migration in this subspecies is very limited, and what data is available is mostly based on indirect evidence from single population censuses and anecdotal observations (Estrada & Coates-Estrada, 1996; Cristóbal-Azkarate, Dias & Veà, 2004; Cristóbal-Azkarate et al., 2005). Only two studies have examined demographic change in this subspecies, both of which are limited in scope: the first studied demographic changes in only one group of howler monkeys over a ten year period (Arroyo-Rodríguez, Asensio & Cristóbal-Azkarate, 2008), and the second compared data from two primate population censuses carried out in 1985 and 2008 (Solórzano-García & Rodríguez-Luna, 2010). Consequently, there is an urgent need for long-term demographic data for this taxon. Such information is crucial for monitoring the conservation status of *A. p. mexicana* populations and to further our understanding of the ways in which forest fragmentation may affect population dynamics in primates.

METHODS

Ethics statement

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

Study species

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

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

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

Study site

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

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

Study groups

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

Data collection

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

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

Demographic events

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

Birth

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

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

Emigration

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

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

Immigration

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

Death

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

Disappeared

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

Statistical analyses

For the calculation of the seasonality of demographic events, IBI and birth rates, we considered only those events that were registered during periods in which the study groups were observed continuously and that could be assigned to a date with a maximum error of one month (see Table S1). In order to control for the effect that our slightly unbalanced sampling effort could have on the seasonality data, we weighted the original data by dividing the frequency of events per month by the total number of times observations were conducted each month (mean ± SD average visits per month = 37.6 ± 3.1, range = 35 – 42; Table S1). We used these weighted values to calculate the % of demographic events in each month.

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

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

Furthermore, in order to account for the underlying continuity of the time variable, we also used circular statistics to test for seasonality of demographic events (Batschelet, 1981). This approach has several advantages over those traditionally used by primatologists to test for seasonality (Janson & Verdolin, 2005; Gogarten et al., 2014). The mean vector length (r) obtained from circular statistics is well suited as an index of seasonality, as it provides a measure of how evenly events are distributed throughout the year. When events are spread evenly across months (not seasonal), r is close to zero and when events are highly clustered at the same time of year (highly seasonal), r is close to one. We tested the significance of the r statistic using the Rayleigh test (Batschelet, 1981), which compares the data with the null hypothesis that demographic events have a random distribution across months. As we used monthly data for demographic events, rather than specific dates, we also used a correction factor ($c = 1.0115$) when calculating the r statistic (Batschelet, 1981). To test for bimodal distribution in the data, we also calculated r by doubling the angle calculated for each demographic event (Batschelet, 1981; Janson & Verdolin, 2005; Gogarten et al., 2014). We carried out analyses in R 2.13.1 (Team Development Core, 2008), testing for normality in the data and considering $p < 0.05$ as significant.

RESULTS

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

Births

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

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

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

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

Emigration

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

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

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

On 16 occasions, we were not able to determine whether the emigrating individuals were born in the group they emigrated from or whether they had previously immigrated into the group. Accordingly these emigrations were of unknown origin and were not classified as natal or secondary.

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

Immigration

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

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

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

Deaths

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

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

Disappeared

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

DISCUSSION

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

While births were distributed throughout the year, they were highly seasonal, with a clear peak between October and December and a secondary peak in February. Another study carried out in a different area of Los Tuxtlas found similar results (Carrera- Sánchez, Medel-Palacios & Rodríguez-Luna, 2003). This suggests that the majority of conceptions that lead to births occur between April and June (Fig. 3a), coinciding with the annual peak in fruit availability and increase in ambient temperature (Figs. 2a & 2b). Accordingly our data suggests that the higher energetic stress between November and March may be inhibiting the reproduction of females and that the improved conditions from April to June results in an increase in fertility. Other studies have also reported that the time of conception is associated with the availability of food and temperature in howler monkeys (Kowalewski & Zunino, 2004). This supports the idea that howler monkeys are income breeders (rather than capital breeders) and that they use energy acquired during the reproductive period for reproduction instead of stored energy (Brockman & van Schaik, 2005; Janson & Verdolin, 2005). Similarly, the weaning of offspring would also occur in April and May, supporting the idea that the weaning of offspring in howler monkeys occurs at times of year in which the availability of high quality food is higher and the climate is more benign (Kowalewski & Zunino, 2004).

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

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

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

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

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

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

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

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

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

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BIBLIOGRAPHY

Arroyo-Rodríguez V, Asensio N, Cristóbal-Azkarate J. 2008. Demography, life history and migrations in a Mexican mantled howler group in a rainforest fragment. *American Journal of Primatology* 70:114–118.

Asensio N, Arroyo-Rodríguez V, Dunn JC, Cristóbal-Azkarate J. 2009. Conservation value of landscape supplementation for howler monkeys living in forest patches. *Biotropica* 41:768–773.

Batschelet E. 1981. Circular statistics in biology. In: Academic Press, 371.

Brockman DK, van Schaik CP. 2005. Seasonality and reproductive function. In: Brockman DK, van Schaik CP eds. *Seasonality in primates*. Cambridge, UK: Cambridge University Press, 270–305.

Carpenter CR. 1934. A field study of the behavior and social relations of howling monkeys (*Alouatta palliata*). *Comparative Psychology Monographs* 10:1–168.

Carrera- Sánchez E, Medel-Palacios G, Rodríguez-Luna E. 2003. Population study of mantled howler monkeys (*Alouatta palliata mexicana*) of Agaltepec Island, Veracruz, Mexico. *Neotropical Primates*:176–180.

Chiarello A, de Melo F. 2001. Primate population densities and sizes in Atlantic forest remnants of northern Espirito Santo, Brazil. *International Journal of Primatology* 22:379–396.

Clarke MR. 1990. Behavioral development and socialization of infants in a free-ranging group of howling monkeys (*Alouatta palliata*). *Folia Primatologica* 54:1–15.

Clarke MR, Crockett CM, Zucker EL, Zaldivar M. 2002. Mantled howler population of Hacienda La Pacifica, Costa Rica, between 1991 and 1998: Effects of deforestation. *American Journal of Primatology* 56:155–63.

Clarke MR, Glander KE. 2004a. Adult migration patterns of the mantled howlers of La Pacifica. *American Journal of primatology* 62:Suppl. 87.

Clarke MR, Glander KE. 2004b. Adult migration patterns of the mantled howlers of La Pacifica. *American journal of primatology* 62:87.

Clarke MR, Glander KE. 2010. Secondary transfer of adult mantled howlers (*Alouatta palliata*) on Hacienda La Pacifica, Costa Rica: 1975 – 2009. *Behaviour* 51:241–249.

Cortés Ortiz L, Rodríguez Luna. E, Martínez Morales M, Carrera Sánchez E. 1994. Parámetros demográficos y reproductivos de un grupo de monos aulladores (*Alouatta palliata*) en semilibertad. *La Ciencia y el Hombre* 1:151–166.

Cowlishaw G, Dunbar RIM. 2000. Primate conservation biology. In: University Of Chicago Press, 498.

Cristóbal-Azkarate J, Arroyo-Rodríguez V. 2007. Diet and activity pattern of howler monkeys (*Alouatta palliata*) in Los Tuxtlas, Mexico: effects of habitat fragmentation and implications for conservation. *American Journal of Primatology* 69:1013–1029.

Cristóbal-Azkarate J, Chavira R, Boeck L, Rodríguez-Luna E, Veà JJ. 2007. Glucocorticoid levels in free ranging resident mantled howlers: a study of coping strategies. *American Journal of Primatology* 69:866–876.

Cristóbal-Azkarate J, Chavira R, Boeck L, Rodríguez-Luna E, Veàl JJ. 2006. Testosterone levels of free-ranging resident mantled howler monkey males in relation to the number and density of solitary males: a test of the challenge hypothesis. *Hormones and behavior* 49:261–7.

Cristóbal-Azkarate J, Dias PAD, Veà JJ. 2004. Causes of intraspecific aggression in *Alouatta palliata mexicana*: Evidence from injuries, demography, and habitat. *International Journal of Primatology* 25:939–953.

Cristóbal-Azkarate J, Dunn JC, Cristobal-Azkarate J. 2013. Lessons from Los Tuxtlas: 30 years of research into primates in fragments. In: Marsh LK, Chapman CA eds. *Primates in fragments: complexity and resilience*. New York, NY: Springer, New York, 75–88.

Cristóbal-Azkarate J, Veà JJ, Asensio N, Rodríguez-Luna E, Vea JJ. 2005. Biogeographical and floristic predictors of the presence and abundance of mantled howlers (*Alouatta palliata mexicana*) in rainforest fragments at Los Tuxtlas, Mexico. *American Journal of Primatology* 67:209–222.

Crockett CM, Rudran R. 1987. Red howler monkey birth data II: Interannual, habitat, and sex comparisons. *American Journal of Primatology* 13:369–384.

Cuarón A, Shedden A, Rodríguez-Luna E, de Grammont PC, Link A. 2008. *IUCN Red List of Threatened Species. Version 2012.2 <www.iucnredlist.org>. Downloaded on 05 April 2013.*

Dias PAD, Rangel-Negrin A, Veà JJ, Canales-Espinosa D. 2010. Coalitions and male-male behavior in *Alouatta palliata*. *Primates; journal of primatology* 51:91–4.

Domingo-Balcells C, Veà J. 2009. Developmental stages in the howler monkey, subspecies *Alouatta palliata mexicana*: A new classification using age-sex categories. *Neotropical Primates* 16:1–8.

Domingo-Balcells C, Veà-Baró JJ. 2009. Developmental stages in the howler monkey, subspecies *Alouatta palliata mexicana*: A new classification using age-sex categories. *Neotropical Primates* 16:1–8.

Dunn JC, Cristóbal-Azkarate J, Schulte-Herbrüggen B, Chavira R, Veà JJ, Vea JJ. 2013. Travel time predicts fecal glucocorticoid levels in free-ranging howlers (*Alouatta palliata*). *International Journal of Primatology* 34:246–259.

Dunn JC, Cristóbal-azkarate J, Veà JJ. 2010. Seasonal variations in the diet and feeding effort of two groups of howlers in different sized forest fragments. *International Journal of Primatology* 31:887–903.

Estrada A, Coates-Estrada R. 1996. Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. *International Journal of Primatology* 17:759–783.

Estrada A, Sáenz-Méndez, Joel Cris.; Harvey CA., Naranjo E., Muñoz-Guerrero, Diego Rosales-Meda A, Marleny M. 2006. Primates in agroecosystems: conservation value of some agricultural practices in Mesoamerican landscapes. In: Estrada A, Garber PA, Pavelka MSM, Luecke L eds. *New perspectives in the study of Mesoamerican primates: Distribution, ecology, behavior, and conservation.* Springer, New York, 437–470.

Fedigan LM, Rose LM. 1995. Interbirth interval in three sympatric species of neotropical monkey. *American journal of primatology* 37:9–24.

Glander KE. 1980. Reproduction and population growth in free-ranging mantled howling monkeys. *American Journal of Physical Anthropology* 53:25–36.

Glander KE. 1981. Feeding patterns in mantled howling monkeys. In: Kamil AC, Darsent TD eds. *Foaging behavior: Ecological, ethological and psychological approaches*. New York: Garland Press, 231–259.

Glander KE. 1992. Dispersal patterns in Costa Rican mantled howling monkeys. *International Journal of Primatology* 13:415–436.

Gogarten JF, Brown LM, Chapman CA, Cords M, Doran- D, Fedigan LM, Grine FE, Perry S, Pusey AE, Doran-Sheehy D et al. 2014. Seasonal mortality patterns in non-human primates: implications for variation in selection pressures across environments. *Evolution* 66:3252–3266.

Guevara-Sada S, Laborde J, Sánchez-Ríos G. 2004. Los Tuxtlas: El paisaje de la sierra. In: Instituto de Ecología A. C. and European Union, 287.

Horwich RH, Brockett RC, James RA, Jones CB. 2001. Population growth in the Belizean black howling monkey (*Alouatta pigra*). *Neotropical Primates* 9:1–7.

Janson CH, Verdolin J. 2005. Seasonality of primate births in relation to climate. In: Brockman DK, van Schaik CP eds. *Seasonality in primates: studies of living and extinct human and non-human primates*. Cambridge, UK: Cambridge University Press, 307–350.

Jones CB. 1995. Howler subgroups as homeostatic mechanisms in disturbed habitats. *Neotropical Primates* 3:7–8.

Kappeler P, Watts DP. 2012. Long term field studies of primates. In: Springer, New York, 460.

Kowalewski M, Zunino GE. 2004. Birth seasonality in *Alouatta caraya* in Northern Argentina. *International Journal of Primatology* 25:383–400.

Mandujano S, Escobedo-Morales, L. A., Palacios-Silva R, Arroyo-Rodríguez V, Rodriguez-Toledo EM. 2006. A metapopulation approach to conserving the howler monkeys in highly altered landscape in Mexico. In: Estrada A, Garber P, Pavelka MSM, Luecke L eds. *New perspectives in the study of Mesoamerican primates: Distribution, ecology, behavior, and conservation.* Springer, New York, 513–538.

Mandujano S, Escobedo-Morales LA, Palacios-silva R. 2004. Movements of *Alouatta Palliata* among forest fragments in Los Tuxtlas, Mexico. *Neotropical Primates* 12:126–131.

Mendel F. 1976. Postural and locomotor behavior of Alouatta palliata on various substrates. *Folia Primatologica*:36–53.

Milton K. 1976. Body weight, diet and home range area in primates. *Nature* 259:459–462.

Milton K. 1980. The foraging strategy of howler monkeys: A study of primate economics. In: New York: Columbia University Press, 165.

Milton K. 1982. Dietary quality and demographic regulation in a howler monkey population. In: Leigh E, Rands SA, Windsor D eds. *The ecology of a tropical forest: Seasonal rhythms and long-term changes*. Washington, DC, 273–289.

Milton K. 1990. Annual mortality patterns of a mammal community in central Panama. *Journal of Tropical Ecology* 6:493–499.

Milton K. 1996. Effects of bot fly (*Alouattamyia baeri*) parasitism on a free-ranging howler monkey (*Alouatta palliata*) population in Panama. *Journal of Zoology* 239:39–63.

Rudran R, Fernandez-Duque E. 2003. Demographic changes over thirty years in a red howler population in Venezuela. *International Journal of Primatology* 24:925–947.

Rumiz DI. 1990. *Alouatta caraya*: population density and demography in northern Argentina. *American Journal of Primatology* 21:279–294.

Rylands AB, Groves CP, Mittermeier RA, Cortés-Ortiz L, Hines J. 2006. Taxonomy and distribution of Mesoamerican primates. In: Garber PA, Pavelka MSM, Luecke L eds. *New perspective in Mesoamerican primates: Distribution, ecology, behaviour, and conservation.* Springer, New York, 29–79.

Solórzano-García B, Rodríguez-Luna E. 2010. Cambios demograficos en poblaciones de primates de la region sur de Los Tuxtlas, Mexico: analisis longitudinal 1985–2008. *Neotropical Primates* 17:1–6.

Soto M. 2004. El Clima. In: Laborde J, Sánchez G eds. *Los Tuxtlas: El paisaje de la Sierra*. Instituto de Ecología A. C. and European Union, 195–200.

Strier KB, Mendes SL, Santos RR. 2001. Timing of births in sympatric brown howler monkeys (*Alouatta fusca clamitans*) and northern muriquis (*Brachyteles arachnoides hypoxanthus*). *American journal of primatology* 55:87–100.

Team Development Core R. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Wang E, Milton K. 2003. Intragroup social relationship of male Alouatta palliata on Barro Colorado Island, Republic of Panama. *International Journal of Primatology* 24:1227–1243.

Zucker EL, Clarke MR. 2003. Longitudinal assessment of immature-to-adult ratios in two groups of Costa Rican *Alouatta palliata*. *International Journal of Primatology* 24:87–101.

FIGURE LEGENDS

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

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

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

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

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**

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

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

Figure 1.

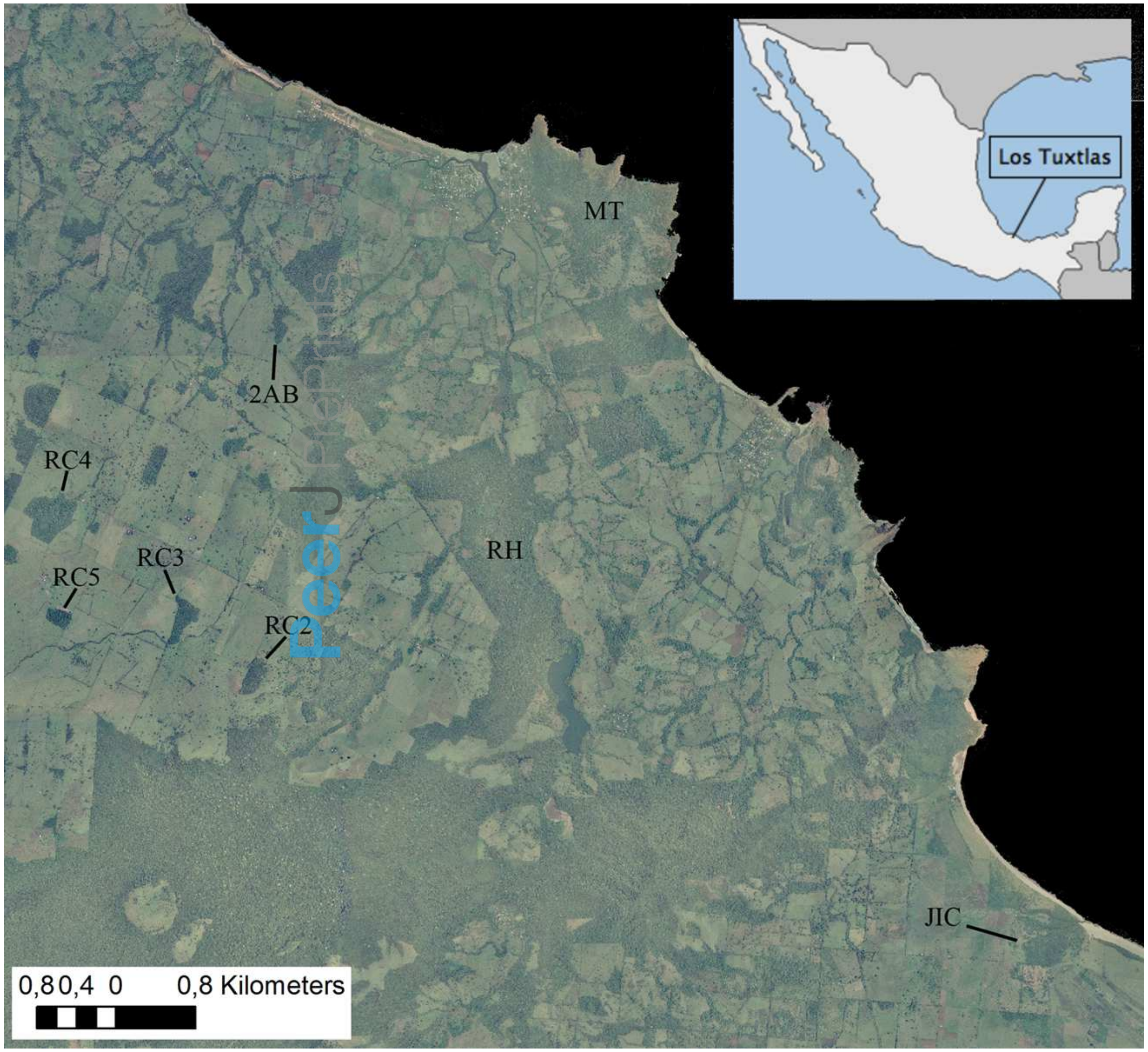


Figure 2.

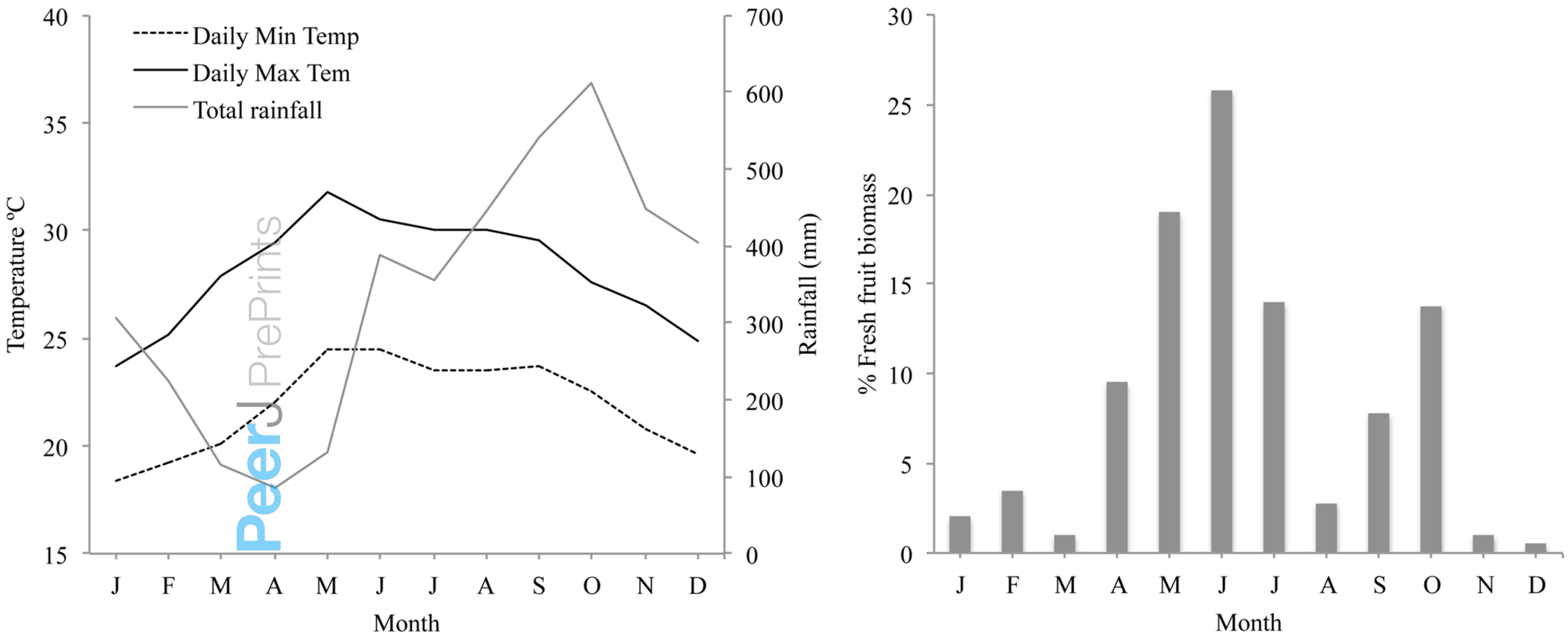
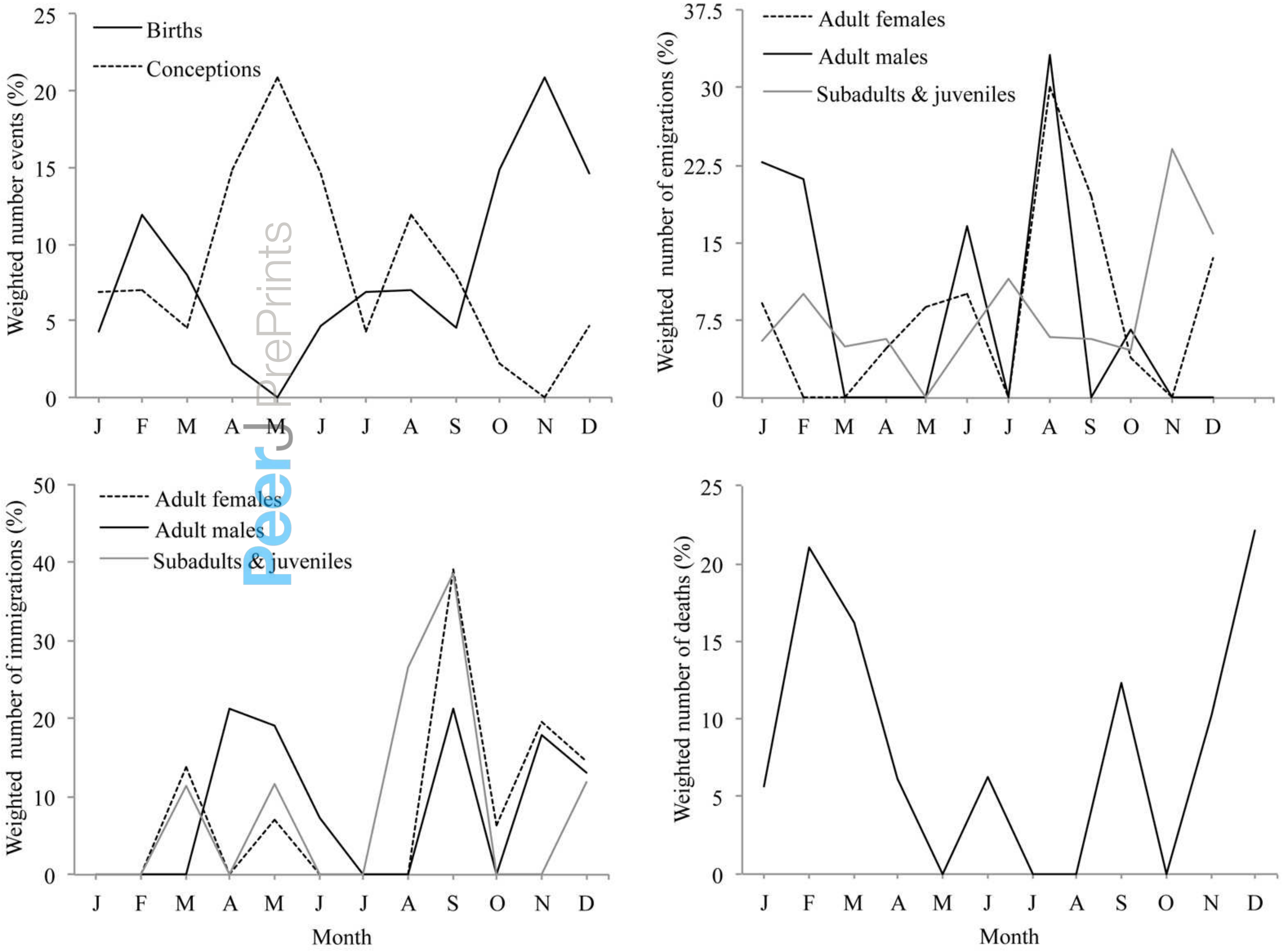

Daily Min Temp
Daily Max Tem
Total rainfall
Temperature °C
40
35
30
25
20
15
Rainfall (mm)
700
600
500
400
300
200
100
0
J
F
M
A
M
J
J
A
S
O
N
D
Month
% Fresh fruit biomass
30
25
20
15
10
5
0
J
F
M
A
M
J
J
A
S
O
N
D
Month

Figure 3.


25
20
15
10
5
0
Weighted number events (%)
Births
Conceptions
J F M A M J J A S O N D
37.5
30
22.5
15
7.5
0
Weighted number of emigrations (%)
Adult females
Adult males
Subadults & juveniles
J F M A M J J A S O N D
50
40
30
20
10
0
Weighted number of immigrations (%)
Adult females
Adult males
Subadults & juveniles
J F M A M J J A S O N D
Month
25
20
15
10
5
0
Weighted number of deaths (%)
J F M A M J J A S O N D
Month