

Factors Influencing the Reproductive Success of Female Black Howlers (*Alouatta pigra*)



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Abstract Measuring reproductive success is necessary to determine an organism's fitness, and thus, to address evolutionary processes. In this study we determined the effects of social, ecological, and individual attributes on the reproductive success of black howlers (*Alouatta pigra*) measured through infant survival and interbirth intervals (IBIs). From 2006 to 2012 we studied 29 black howler (*A. pigra*) females living in 11 groups in Campeche (Mexico), and recorded 82 births. We recorded group size and composition and the sex of infants during weekly surveys. We calculated a food availability index based on rainfall levels and on the size of preferred food resources. Daughters had a 30 % higher probability of surviving than sons, and the survival of the latter was positively related to food availability. IBI decreased when the first infant in the interval died, and when considering only IBIs in which the first infant survived, IBIs were longer following the birth of a daughter. These results suggest that, even if the production of daughters reduces reproductive output due to longer IBIs, female black howlers may still accrue higher reproductive success through their daughters due to differences between sexes in survival.

Keywords Food availability · Infant sex · Infant survival · Interbirth interval

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Introduction

Measuring reproductive success is necessary to determine an organism's fitness, and thus, to address evolutionary processes (Falconer and Mackay 1996). There is evidence that the reproductive success of female primates is affected by ecological and social factors, in addition to intrinsic attributes of the individuals. Food availability is a major ecological factor constraining female reproductive success, as it influences the occurrence of ovulation (e.g., Bronson and Manning 1991; humans: Ellison 2001; chimpanzees, *Pan troglodytes schweinfurthii*: Emery Thompson and Wrangham 2008) and conception (e.g., Assamese macaques, *Macaca assamensis*: Heesen *et al.* 2013; Hanuman langurs, *Presbytis entellus*: Koenig *et al.* 1997), as well as the sustaining of pregnancy (e.g., humans: Ceesay *et al.* 1997; Moore *et al.* 1997; marmosets, *Callithrix jacchus*: Tardif *et al.* 2004; baboons, *Papio hamadryas*; Antonow-Schlorke *et al.* 2011) and lactation (e.g., baboons: Roberts *et al.* 1985; marmosets: Tardif *et al.* 2001). As a result, food availability generally positively correlates with reproductive success (e.g., baboons: Altmann and Alberts 2003; long-tailed macaques, *Macaca fascicularis*: van Noordwijk and van Schaik 1999; Japanese macaques, *Macaca fuscata*: Suzuki *et al.* 1998; Bornean orangutans, *Pongo pygmaeus*: Knott 2001).

Social competition affects female reproductive success (Chapman *et al.* 2012; Schülke and Ostner 2012). When large group size confers competitive advantages over small groups (Wrangham 1980) the reproductive success of females is positively related to group size (Cheney and Seyfarth 1987; Robinson 1988). However, intragroup feeding competition may increase in large groups, either directly through more frequent contests for food or indirectly by a faster depletion of food patches (Silk 2007; Snaith and Chapman 2007; van Schaik 1983), and have therefore a negative effect in female reproductive success (e.g., baboons: Altmann and Alberts 2003; black howler monkeys, *Alouatta pigra*: van Belle and Estrada 2008; long-tailed macaques: van Noordwijk and van Schaik 1999; mantled howler monkeys, *A. palliata*: Ryan *et al.* 2008; Phayre's leaf monkeys, *Trachypithecus phayrei*: Borries *et al.* 2008). In addition to group size, variation in group composition is likely to affect female reproductive success. When groups with more females are more attractive to extragroup males, takeover attempts may be more frequent, and successful takeovers may lead to infanticide (e.g., ursine howler monkeys, *A. arctoidea*: Crockett and Janson 2000; Hanuman langurs: Treves and Chapman 1996), which has a negative impact on female reproductive success (Cheney *et al.* 2004). This effect is particularly evident in groups with female-biased sex ratios, suggesting that large groups including several males are more successful in deterring takeover attempts, as attested by higher female reproductive success under these circumstances (e.g., mantled howler monkeys: Ryan *et al.* 2008; white-faced capuchins, *Cebus capucinus*: Fedigan and Jack 2011; *cf.* Bădescu *et al.* 2016).

Intrinsic attributes that influence reproductive success of female primates include rank, age, and sex of the infant produced. First, when females establish dominance-based relationships, priority of access to resources is expected to be positively related to rank, and dominant females usually have higher reproductive success (Pusey 2012). Second, different age-related patterns in female

reproductive success have been identified (*cf.* Robbins *et al.* 2006), and the causes for such variation include tradeoffs between investment in growth vs. reproduction (e.g., mandrills, *Mandrillus sphinx*: Setchell *et al.* 2002), parity status and rearing experience (e.g., bonnet macaques, *M. radiata*: Silk 1990; baboons: Altmann and Alberts 2005), and senescence (e.g., Milne-Edwards sifaka, *Propithecus edwardsi*: King *et al.* 2005; chimpanzees: Emery Thompson *et al.* 2007). Third, the reproductive success of females may also depend on the sex of their offspring. Depending on the impact that maternal investment will have on offspring reproductive success, infant sex ratios may be biased in favor of males or females (Silk and Brown 2004). In polygynous species, for instance, maternal investment is expected to have a stronger effect on the reproductive success of sons than on that of daughters, and mothers in good physical condition are expected to produce more sons (Trivers and Willard 1973). However, under local resource competition maternal condition may be transmitted to offspring (Clark 1978; Leimar 1996). For instance, when rank is inherited along matriline, high-ranking females tend to produce more daughters, as the impact of maternal investment in their offsprings' reproductive success will be higher for daughters than for sons (Altmann 1980; Silk *et al.* 1981; Simpson and Simpson 1982). Therefore, whereas the fitness benefits associated with producing either a son or a daughter depend on the interplay of maternal physical condition and the social and ecological contexts of a population, in several species females in good physical condition bias sex ratios at birth in favor of the sex that provide higher reproductive benefits (Schino 2004; *cf.* Silk and Brown 2004).

As in other primates, the reproductive success of female howlers is affected by ecological, social, and intrinsic factors. Food availability and social stability, for instance, are positively related to infant survival (mantled howlers: Clarke and Glander 1984; ursine howler monkeys: Crockett and Janson 2000). In this context, social stability refers to the occurrence of male immigrations, which frequently result in infanticide (Crockett 2003). Male immigrations depend on 1) the expected reproductive payoff of group membership (Crockett and Janson 2000); 2) the ability of resident males to defend their groups (Kitchen 2004; Pope 1990; Rangel-Negrín *et al.* 2011; Van Belle *et al.* 2009a,b); and 3) the competitive abilities of dispersing males (Pope 1990). Accordingly, groups including more females are more attractive to dispersing males, and infanticide associated with male takeovers increases with increasing number of females per group in ursine howlers (Crockett and Janson 2000). In this species, groups with more males are more efficient in deterring intrusions by extragroup males (Crockett and Janson 2000; Rudran and Fernandez-Duque 2003; see also Treves 2001), and the reproductive success of female mantled howlers increases with increasing number of males per group (Ryan *et al.* 2008). However, the reproductive success of female black howlers is unrelated with either the number of males per group or sex ratios. In this species, it is negatively correlated to the number of females per group, suggesting that intragroup resource competition could also account for variation in female reproductive success in howler monkeys (Van Belle and Estrada 2008; *cf.* Snaith and Chapman 2007).

There is some evidence suggesting that female howlers may accrue higher reproductive success through their daughters than through their sons. In mantled howlers, the survival of daughters doubles that of sons, which are usually produced only under unfavorable contexts (e.g., during social instability, when food availability is low), and maternal investment is higher for daughters (Clarke and Glander 1984). In ursine howlers, reproductive success increases for females residing in groups with related females, probably because the degree of kinship within female coalitions is higher in established than in recently formed groups, and the former occupy higher quality territories (Pope 2000). In this species maternal investment is also higher in daughters, especially in those who eventually become natal breeders (Crockett and Rudran 1987). It is therefore possible that local resource competition leads to biased sex ratios at birth in howlers in favor of daughters.

To investigate in detail the influence of ecological, social, and intrinsic factors on female reproductive success in howlers, we studied the effects of food availability, group size and composition, the occurrence of male immigrations, and infant sex on infant survival and interbirth intervals (IBIs) in free-ranging black howlers. Based on the available evidence, we predicted that infant survival should increase 1) when food availability was higher; 2) in smaller groups comprising fewer females (i.e., lower intragroup resource competition), but more males (i.e., higher ability to deter takeover attempts and potential infanticidal attacks); 3) when no male immigrations occurred; and 4) for daughters. We predicted that IBIs would be shorter 1) when food availability was higher; 2) in smaller groups comprising fewer females (i.e., lower intragroup resource competition); 3) groups with fewer males (i.e., lower ability to deter takeover attempts and potential infanticidal attacks); 4) when male immigrations occurred; and 5) for sons.

Methods

Study Sites, Demographic Sampling, and Subjects

From February 2006 to February 2012 we studied 11 groups of black howlers in different locations in the Mexican state of Campeche. Mean annual rainfall in Campeche is 1300 mm, with a dry season from November to May (mean monthly rainfall \pm SD = 43.7 \pm 25.8 mm), and a rainy season between June and October (218.9 \pm 14.1 mm). Mean annual temperature is 26 °C. Black howlers living in Campeche live in extensive and fragmented lowland evergreen and semideciduous tropical forests. We have described the study sites in detail elsewhere (Dias *et al.* 2011, 2014, 2015; Electronic Supplementary Material [ESM] Table SI).

We recognized all individuals via ankle bracelets or their natural anatomical and physiognomic characteristics, such as body size and proportions, scars, broken fingers, and genital morphology and pigmentation. During the 7 yr of demographic monitoring, we tracked a total of 29 adult females that had at least one infant (Table 1) whose birth date could be determined and that could be followed until it reached 12 mo old or died. Because infants (i.e., individuals <12 mo), are highly dependent on their mothers and cannot survive alone, when

Table 1 Reproductive success of adult female black howlers in Campeche (Mexico) studied between 2006 and 2012

Female ID	Number of infants born during the study	Proportion of infants surviving to 1 yr	Mean IBIs (mo)	Number of surviving infants
1	5	0.60	18.0	3
2	5	0.40	16.4	2
3	4	0.75	17.2	3
4	4	0.50	21.0	2
5	4	1.00	17.1	4
6	4	0.50	20.5	2
7	3	0.67	17.5	2
8	3	1.00	18.0	3
9	3	0.33	21.8	1
10	3	0.67	20.1	2
11	3	0.67	15.8	2
12	3	1.00	15.4	3
13	3	0.67	17.7	2
14	3	0.00	20.1	0
15	3	0.33	19.3	1
16	3	0.67	16.9	2
17	3	0.33	14.4	1
18	2	0.50	16.2	1
19	2	0.50	16.2	1
20	2	1.00	21.2	2
21	2	0.50	23.5	1
22	2	0.50	21.7	1
23	2	0.50	16.0	1
24	2	1.00	21.5	2
25	2	0.50	17.3	1
26 ^a	2	1.00	15.8	2
27 ^a	2	0.50	17.1	1
28 ^a	2	0.50	14.8	1
29 ^{a,b}	1	0.00	—	0

^a Female that had her first infant during the study (i.e., primipara)

^b Only one infant from this primiparous female was born during the study, so we could not calculate an IBI for her

an infant could not be located for more than 2 sampling days, but the mother was still in the group, we considered that it died. We recorded the sex of newborns. In this species, the contrast of the white scrotum of male infants against their black pelage allows for the easy discrimination of sex from birth.

We sampled all groups for 2–3 days each week. Therefore, error in birth dates varied ± 5 days. The forest fragment in which one of the study groups lived was logged in 2010 and we could not relocate the monkeys. We accumulated a total of 10,083

sampling days, with a mean (\pm SD) of 918.5 (\pm 125.3) sampling days per group. We also recorded group size and composition on each sampling day by performing repetitive counts of individuals until consistent results were obtained.

Assessment of Reproductive Success

The two measures of female reproductive success used in the present study were infant survival up to 1 yr of age and IBIs. Up to 32 % of all offspring die during the first 12 mo of life in these groups (Dias *et al.* 2015). Furthermore, female black howlers face the costliest portion of rearing in energetic terms during this period, as they 1) spend less time resting, but more time feeding and moving; 2) socialize more; and 3) forage more intensively (i.e., range over longer distances and use more feeding trees and feeding species) (Dias *et al.* 2011). Therefore, although the infant age class includes individuals between 0 and 20 mo (Bolin 1981), survival of infants during their first year of life is expected to have a critical effect on female fecundity and fertility.

Predictive Variables

We used the following variables as predictors of infant survival: food availability, group size, group composition, adult male immigration, and sex of infant. To determine food availability during the first year of life of each infant we used an index based on the basal area of food species preferred by black howlers and monthly rainfall levels. As part of complementary projects that included intensive observations of the behavior and ecology of black howlers as well as genetic and morphometric sampling, the behavior of black howlers was studied for a total of *ca.* 260 h per group (for details see Dias *et al.* 2011, 2014). Based on these observations, we determined the top food species for each group, defined as the five plant species with overall highest ingestion per group (Dias *et al.* 2014). The percentage of ingested food from top food species among our study groups varies between 47.8 % and 98.9 %, with a mean (\pm SD) of 71.3 \pm 14.9 % (Dias *et al.* 2014). In addition, during behavioral sampling each tree used by black howlers for feeding, resting, or moving was identified at the species level. Because the basal area of tropical trees has been found to correlate positively with both fruit and leaf biomass (Sorensen and Fedigan 2000), we calculated the sum of the basal areas of all trees belonging to top food species used by black howlers during behavioral observations to obtain an estimation of the potential food biomass available to each group. We could not estimate temporal variation in the availability of fruits and young leaves, the main foods consumed by howlers (Dias and Rangel-Negrín 2015). However, as in other tropical forests (Chapman *et al.* 2000; Janson and Chapman 2000), the production of fruits and young leaves correlates positively with rainfall in the Yucatán Peninsula (e.g., fruits: Schaffner *et al.* 2012; young leaves: Valdez-Hernández *et al.* 2010), so we used monthly rainfall levels (reported by CONAGUA/SMN—Mexican National Water Committee/National Weather Service) as a proxy for plant productivity. We calculated monthly food availability per group by multiplying the sum of the basal areas of all trees belonging to top food species by rainfall levels. We then calculated food

availability during the first year of life of each infant as the sum of monthly food availability for the first 12 mo following each birth.

Group size was calculated as the mean number of group members (both adult and immature) during the first 12 mo of life of each infant or, when it died <12 mo, during the period in which it lived. We used three variables related to group composition: 1) number of adult females per group; 2) number of adult males per group; 3) the ratio of adult females to adult males (i.e., socioeconomic sex ratio; hereafter sex ratio). Adult male immigration was defined as the occurrence (i.e., a yes/no measure) of adult male immigrations during the first 12 mo of life of each infant or, when it died <12 mo, during the period in which it lived. To analyze variation in IBIs, in addition to the aforementioned factors we considered whether the infant at the beginning of the interval survived or not.

Statistical Analyses

In the analysis of factors affecting infant survival we used 82 births (for 29 females) for which birth dates were recorded with a ± 5 day accuracy and infants could be followed during their first 12 mo of life or until they died. Fourteen additional births that were considered in a previous analysis of this database (Dias *et al.* 2015) were not analyzed here, as four correspond to births that occurred outside the ± 5 day range and ten correspond to births that occurred <12 mo before the end of the study. We analyzed 81 complete IBIs for 28 females, and 48 complete IBIs for which the infant at the beginning of the interval survived. The exclusion of births from primiparous females ($N = 4$, Table 1) from analyses described in the text that follows did not lead to different results.

We used a generalized linear mixed model (GLMM) (Baayen 2010) with binomial error structure and logit-link function to analyze the effects of food availability, group size, number of females per group, number of males per group, sex ratio, occurrence of male immigrations, and infant sex on infant survival. Analyses of IBIs were twofold. First, we analyzed variation in IBIs as a function of food availability, group size, number of females per group, number of males per group, sex ratio, occurrence of male immigrations, sex of the infant at the beginning of the interval, and survival of the infant at the beginning of the interval. Second, because IBIs were shorter when the infant at the beginning of the interval died, we ran another GLMM considering only IBIs when infants at the beginning of the interval survived past 12 mo of life. IBIs were transformed to their natural logarithms and analyzed with GLMMs adjusted with Gaussian error structure and identity link function. We included significant interactions between predictors in all models. We diagnosed model validity through distribution of residuals and quantile–quantile plots to verify normality and residuals plotted against predicted values to assess homogeneity. Female identity nested within group identity was used as a random variable in all models to account for repeated observations of females belonging to the same group contributing more than one birth to the dataset. We used the `lmer` function from the `lme4` package (Bates and Maechler 2010) in R 3.3.1 (R development Core Team 2016) to run GLMMs. We used the `perturb` package (Hendrickx 2015) to assess collinearity among predictive

variables and found that number of males, number of females, and sex ratio had significant effects on parameter estimations of other predictors, as well as the sex of the infant at the beginning of the interval in the first IBI model described previously, so they were excluded.

We performed significance testing by comparing full models (i.e., all fixed variables and their significant interactions, as well as the random variable) with null models including only the intercept and the random variable, using likelihood ratio tests (Dobson 2002) implemented with the R function `anova`. When likelihood ratio tests were significant, we calculated *P*-values using the Markov Chain Monte Carlo (MCMC) procedure (Baayen 2011) using the functions `pvals.fnc` of the R-package language R (Baayen 2011).

Ethical Note

Our research protocols complied with the legal requirements of the Estados Unidos Mexicanos and were approved in permits SEMARNAT/SGPA/DGVS/01273/06 and SEMARNAT/SGPA/DGVS/04949/07. Our study also complied with the “Guidelines for the treatment of animals in behavioural research and teaching” of the Association for the Study of Animal Behaviour and the Animal Behavior Society.

Results

Infant Survival

Sixty percent of all newborn infants survived to 1 yr of age ($N = 82$ births). The full model explaining variation in infant survival (Table II) was significantly different from the null model ($\chi^2 = 45.73$; $df = 9$; $P < 0.001$). Female infants had a 30 % higher probability of surviving during their first year of life than males, and the survival of male infants, but not females, was positively related to food availability during the first 12 mo following birth (Fig. 1).

Table II Results of the generalized linear mixed model examining variation in infant survival in black howlers in Campeche (Mexico) studied between 2006 and 2012

Variable	Estimate \pm SEM	<i>t</i>	<i>P</i> _{MCMC} ^a
Intercept	5.64 \pm 22.49	3.25	0.009
Food availability	2.84 \pm 1.42	3.48	0.067
Group size	-0.04 \pm 0.19	-0.12	0.467
Male immigrations	0.21 \pm 0.45	1.22	0.649
Infant sex	-1.84 \pm 1.44	-4.65	0.005
Infant sex \times food availability	-1.12 \pm 0.01	-5.37	<0.001

^a *P*_{MCMC} are *P*-values based on Markov Chain Monte Carlo sampling

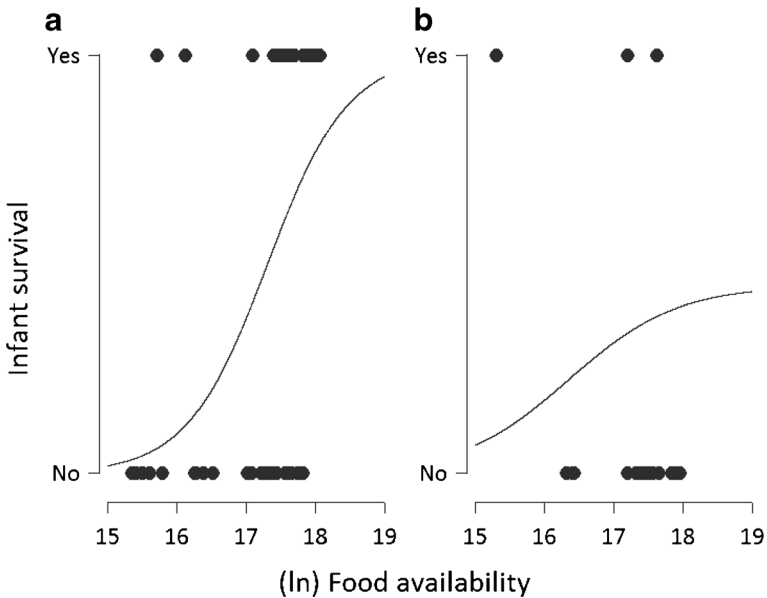


Fig. 1 The survival probabilities of infant black howlers in Campeche (Mexico) studied between 2006 and 2012 as a function of variation in food availability (ln transformed): (a) males, (b) females.

IBIs

IBIs varied between 12.1 and 27.0 mo, with a mean of 18 mo (median = 16.6, SD = 3.7 months, $N = 81$). The majority (66.7 %) of IBIs ranged between 14 and 18 mo (Fig. 2). The full model for variation in IBIs (Table III) was significantly different from the null model ($\chi^2 = 50.01$; $df = 7$; $P < 0.001$). IBIs decreased from a mean of 19.0 mo (median = 17.0, SD = 3.6 mo) when the first infant in the interval survived to 16.6 mo (median = 15.3, SD = 3.3 mo) when it died before reaching 12 mo (Fig. 3a). When considering only IBIs in which the infant at the beginning of the interval survived, the

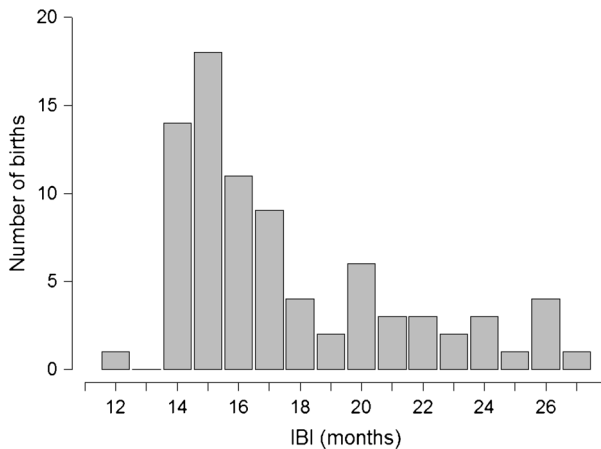


Fig. 2 The distribution of interbirth intervals (IBIs; in months) in black howlers studied in Campeche (Mexico) between 2006 and 2012.

Table III Results of the generalized linear mixed model examining variation in IBIs in black howlers in Campeche (Mexico) studied between 2006 and 2012

Variable	Estimate \pm SEM	<i>t</i>	P_{MCMC} ^a
Intercept	3.77 \pm 0.57	6.67	<0.001
Food availability	-0.05 \pm 0.03	-1.36	0.179
Group size	-0.01 \pm 0.01	-0.79	0.467
Male immigrations	-0.01 \pm 0.04	-0.26	0.795
Infant survival	-0.61 \pm 0.05	-3.56	0.001

^a P_{MCMC} are *P*-values based on Markov Chain Monte Carlo sampling

full model (Table IV) was also significantly different from the null model ($\chi^2 = 43.31$; $df = 7$; $P < 0.001$). The IBI following the birth of a female was 21.1 mo (median = 20.5, SD = 3.2 mo), nearly 4 mo longer than the IBI following a male birth (mean = 17.6; median = 16.4; SD = 3.4 mo; Fig. 3b).

Discussion

In this study we examined the influence of ecological, social, and intrinsic factors on the reproductive success of female black howlers. As predicted, infant survival and IBI were affected by food availability and the sex of the infant: infant survival was lower for male infants, especially when food availability during their first year of life was low, and IBIs in which the infant at the beginning of the interval survived to 1 yr of age were shorter for male infants. Therefore, females can produce male infants more rapidly but at a lower probability of success. However, group structure and composition, as well as the occurrence of male immigrations, which affected variation in female reproductive success in other populations of howlers (Clarke and Glander 1984; Ryan *et al.* 2008; Treves 2001; Van Belle and Estrada 2008) and other primates (Fedigan *et al.* 2008), did not have significant effects in this population. The low variation in the size and composition of black howler groups (Dias *et al.* 2015; Van Belle and Estrada 2006), infrequent male replacements (Dias *et al.* 2015; Rangel-Negrin *et al.* 2011), and inconclusive evidence for the occurrence of infanticide (Dias *et al.* 2015), could account for such differences. In the absence of long-term data that allow for the analysis of lifetime reproductive success, these results provide insight into the reproductive strategies of female black howlers.

Although behavioral variation in maternal investment according to offspring sex remains to be described in howlers, longer IBIs suggest that mothers invest more in rearing their daughters, a pattern that has been previously described in other primates (e.g., Japanese macaques: Takahata *et al.* 1995; rhesus macaques: Maestripieri 2001). Proximally, longer IBIs could result from the physiological impact of an extended nursing period on maternal energy balance (e.g., lactational amenorrhea: Emery Thompson 2013; Gittleman and Thompson 1988; Valeggia and Ellison 2004), whereas functionally longer IBIs may emerge from local resource competition (Clark 1978; Leimar 1996; Silk 1984). Black howlers of both sexes may disperse, but there is

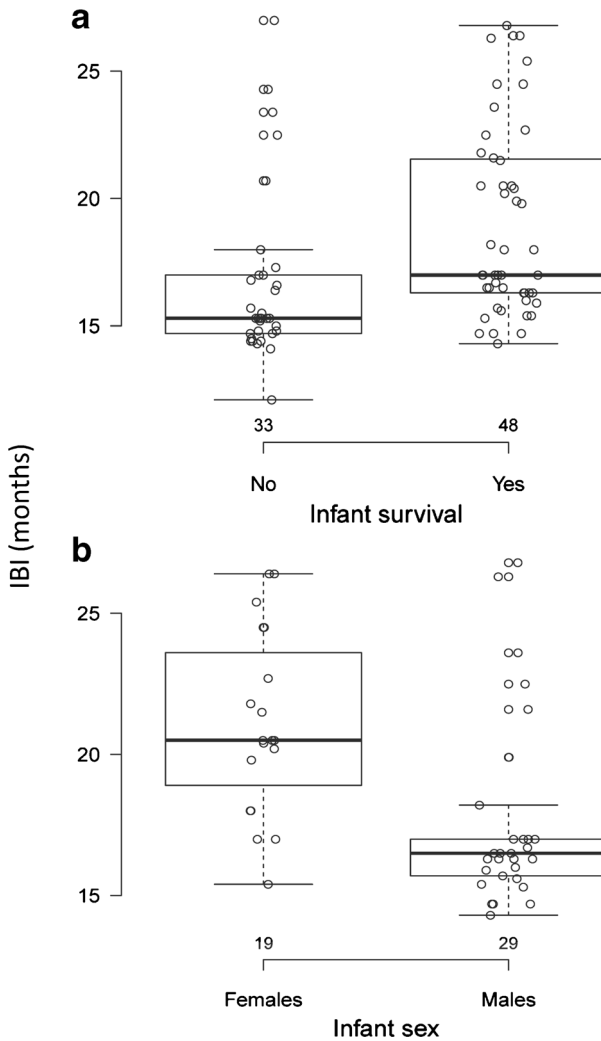


Fig. 3 The duration of interbirth intervals (IBIs; in months) in black howlers studied in Campeche (Mexico) between 2006 and 2012 as a function of infant survival (**a**) and as a function of infant sex when the first infant in the interval survived (**b**). Center lines show the medians; box limits indicate the 25th and 75th percentiles; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles. Number of births per infant survival (**a**) and sex (**b**) are shown above the x-axis.

observational (Dias *et al.* 2015) and genetic (Van Belle *et al.* 2012) evidence that some females stay and reproduce in their natal groups. Furthermore, resident females prevent the immigration of other females (Brockett *et al.* 2000; Van Belle *et al.* 2011), a pattern that resembles that observed in ursine howlers (Crockett 1984; Crockett and Pope 1993). In that species, the degree of relatedness among females increases over time and with increasing resource competition (measured through population density) because some females successfully recruit their daughters while forcing the emigration of other females' daughters (Crockett 1984; Pope 2000). In addition, maternal investment is higher for daughters that eventually become natal breeders (Crockett and Rudran

Table IV Results of the generalized linear mixed model examining variation in IBIs when the first infant in the interval survived in black howlers in Campeche (Mexico) studied between 2006 and 2012

Variable	Estimate \pm SEM	<i>t</i>	P_{MCMC} ^a
Intercept	2.66 \pm 0.86	3.08	<0.004
Food availability	0.01 \pm 0.05	0.23	0.819
Group size	0.00 \pm 0.01	0.13	0.900
Male immigrations	-0.03 \pm 0.05	-0.68	0.503
Infant sex	0.18 \pm 0.05	3.48	0.001

^a P_{MCMC} are *P*-values based on Markov Chain Monte Carlo sampling

1987), and the reproductive success of females increases when they live in groups with related females (Pope 2000). Therefore, it is possible that, as in ursine howlers and other primates (e.g., baboons: Altmann 1980; bonnet macaques: Silk *et al.* 1981; chimpanzees: Nishida *et al.* 2013; rhesus monkeys, *Macaca fuscata*: Simpson and Simpson 1982), black howler females skew investment in favor of the sex that does not disperse, because the inheritance of attributes related to maternal condition (e.g., access to resources: Silk and Brown 2004) benefits their fitness.

Evolutionary theory indicates that mothers in good physical condition should bias sex ratios at birth in favor of the sex that provides higher fitness returns (Trivers and Willard 1973). In our study population, however, although mothers invest more in their daughters, sex ratios at birth are strongly biased in favor of males. In a parallel analysis based on the same data set, we found that when a female conceived a new infant while still suckling the previous infant, the probability that the new infant was a daughter increased, and this effect was determined mainly by a positive relationship between male infant mortality and the conception of sons (Dias *et al.* in press). Owing to sex differences in postnatal growth patterns, age of maturation, and adult body size (Raguet-Schofield and Pavé 2014), the production of male black howlers is probably costlier than that of females, and therefore, as observed in other primates (e.g., toque macaques, *Macaca sinica*: Dittus 1998), the probabilities of conceiving a male should increase with increasing maternal condition. Therefore, high mortality of sons, and the consequent interruption of nursing, could lead to better maternal condition around conception and higher production of males in this population. Future research on the physiological mechanisms underlying these findings should allow understanding the significance of sex allocation in black howlers, because the described interplay of potential reproductive output per offspring sex, sex ratio at birth, and infant mortality patterns is highly counterintuitive.

Milk from their mothers is the main food of black howler infants during the first 10 mo of life (Dias *et al.* 2011) and, although no data are available for howlers, in other primates milk output and quality vary as a function of maternal nutritional condition (Hinde and Milligan 2011; Roberts *et al.* 1985; Tardif *et al.* 2001), which in turn depends on food availability (Heesen *et al.* 2013; Koenig *et al.* 1997). The interaction between presumed nursing quality and nutritional demands for postnatal growth (Raguet-Schofield and Pavé 2014; *cf.* Hinde 2007) could explain why only male

mortality was affected by food availability in the present study. We have previously reported a birth peak in this population in the rainy season (Dias *et al.* 2015), a period of high young leaf and fruit abundance in the Yucatán Peninsula (Schaffner *et al.* 2012; Valdez-Hernandez *et al.* 2010). Based on the observation that black howler females feed intensively on fruits during early lactation (Dias *et al.* 2011), we had speculated that birth seasonality could occur in this population as a strategy to offset the energetic demands of lactation (Dias *et al.* 2015). However, according to IBIs calculated in the current study, which were longer than an annual cycle, if in a particular year a female had an infant during the rainy season, it would be unlikely that her next infant would also be born on a rainy season, whether it survived or not. In this species, as well as in mantled howlers, infant loss leads to a quick resumption of sexual behavior (1 day to 3 weeks after infant loss: Glander 1980; Van Belle *et al.* 2009a), and to a consequent shortening of IBIs (Crockett 2003; Crockett and Sekulic 1984; Dias *et al.* 2015; Fedigan and Rose 1995; Pavé *et al.* 2012; Van Belle and Bicca-Marques 2014). As a consequence, in our study population several infants can be born when food availability is low. These results further indicate that females do not delay reproduction to synchronize lactation with high food abundance (i.e., strict seasonal breeding: Brockman and van Schaik 2005), perhaps as a consequence of the mechanism linking the occurrence of lactation around the time of conception, maternal condition, and offspring sex. Finally, for 73.3 % of all female births the sex of the next infant was a male. The sum of mean female and male IBIs is 39 and 37 mo, depending on whether the male survives or dies, respectively. After a 39-mo IBI, there is a 60 % probability that the next infant will be born during the rainy season, and this probability increases to 100 % after a 37-mo IBI (Fig. 4). Considering the reproductive advantages associated with the production of daughters, this raises the intriguing possibility that mothers are hedging a bet on the survival of sons (a “gamble” son, as posed by Clarke and Glander 1984) to synchronize the lactation of valuable daughters with the season of high food abundance.

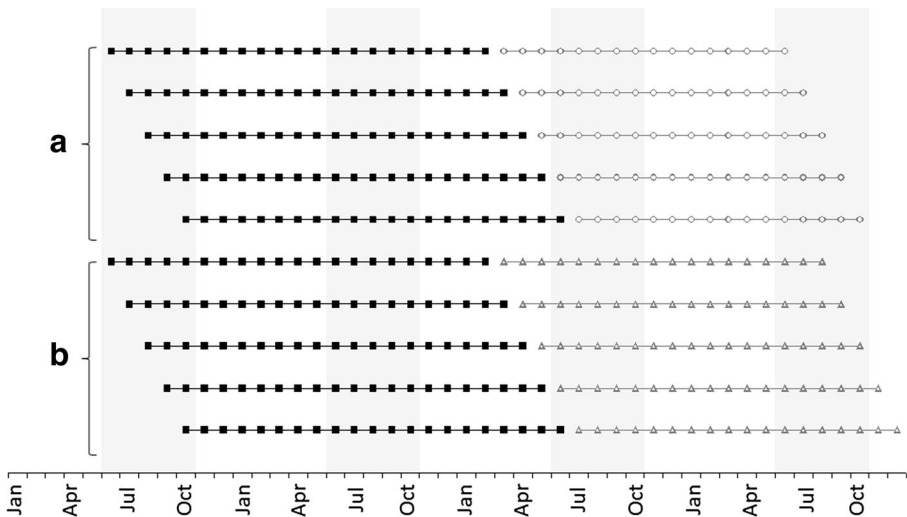


Fig. 4 IBIs of consecutive daughter (solid black squares) and son (open gray circles and triangles) births as a function of seasonality (rainy season in light gray shading) in black howlers studied in Campeche (Mexico) between 2006 and 2012. (a) Sons died before reaching 1 yr of age. (b) Sons survived to 1 yr of age.

In summary, our results indicate that female black howlers may accrue higher reproductive success by having more daughters than sons due to differences between sexes in survival and reproductive strategies. Furthermore, mothers invest more in daughters than in sons, probably owing to local resource competition. We propose, however, that the lower survival of sons is linked to sex differences concerning the interaction between nursing quality and infant nutritional demands during periods of low food availability, rather than to lower maternal investment in sons. More detailed studies are required to further understand the causes of infant mortality in this population and to quantify maternal investment through behavioral evidence.

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