

RESEARCH ARTICLE

Factors influencing infant sex ratio in howler monkeys (*Alouatta* spp.): A literature review and analysis

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Abstract

Objective: Frequency-dependent selection is expected to maintain infant sex ratios around parity over evolutionary time. However, over ecological time periods, infant sex ratios vary, and it has been proposed that this variation may reflect adaptive processes. In primates, there are consistent patterns of variation in infant sex ratios, although their adaptive significance remains contentious. In addition to design issues, contrasting results could have derived across primates from variation in the fitness benefits accrued through sons or daughters associated with the specific social, ecological, and demographic context of populations. Thus, different sex allocation tactics could occur within species over time and space.

Methods: We reviewed the literature to describe variation in infant sex ratio in howler monkeys (genus *Alouatta*) and to examine whether such a variation could be associated with adaptive sex allocation. We found 26 studies that provided data for this review. These studies yielded 96 infant sex reports, corresponding to 1,477 sexed infants.

Results: Infant sex ratio across howler monkey species tends to parity, but females produce more sons under high group densities and more daughters when rainfall increases.

Discussion: Based on these results, as well as on information on howler monkey dispersal patterns, demography, and within-group genetic relatedness, we speculate that, depending on population growth stage, sex allocation is explained by (a) local resource enhancement, that is, more cooperative philopatric daughters are produced when populations are growing; and (b) local resource competition, that is, more dispersing sons are produced when populations are saturated. Thus, there is evidence suggestive of adaptive variation in infant sex ratios in howler monkeys.

KEYWORDS

infant sex ratio, competition, population growth, rainfall, sex allocation, sex ratio

1 | INTRODUCTION

Following what was perhaps the first systematic review of variation in infant sex ratios across animal groups, Darwin concluded that “I formerly thought that when a tendency to produce the two sexes in equal numbers was advantageous to the species, it would follow from natural selection, but I now see that the whole problem is so intricate

that it is safer to leave its solution for the future” (Darwin, 1871, pp. 259–260). It was later argued that, under natural selection, infant sex ratios of sexually reproducing species should tend to unity (e.g., Bodmer & Edwards, 1960; Fisher, 1958; Kolman, 1960), but subsequent theoretical (Trivers & Willard, 1973) and empirical (Hamilton, 1979; Wilson & Colwell, 1981) studies questioned such arguments. Currently, skewed infant sex ratios have been documented in all

vertebrate classes (e.g., Bonier, Martin, & Wingfield, 2007; Brown, 2001; Hewison & Gaillard, 1999; Ryan, Anderson, Berkvens, & Hare, 2014; Ryan, Anderson, Gardiner, & Hare, 2012; Schino, 2004; Sheldon & West, 2004). Given that the relative number of individuals from each sex in a population affects reproductive strategies, sex allocation remains a key topic in evolutionary research.

Although there is growing evidence that fathers can affect infant sex ratios (e.g., Edwards & Cameron, 2014; Lavoie, Tedeschi, García-González, & Firman, 2019; Tanaka, Fukano, & Nakamura, 2019; reviewed in Douhard, 2018), variation in mammalian infant sex ratios has been found to be mostly linked to maternal physical condition, proxied by age (e.g., Martin & Festa-Bianchet, 2011; Packer, Collins, & Eberly, 2000; Saltz, 2001), body mass (e.g., Borowik & Jędrzejewska, 2017), access to food resources (e.g., Schwanz & Robert, 2014), dominance rank (e.g., Schino, 2004; van Schaik & Hrdy, 1991), occurrence of lactation at the time of conception (e.g., Dias, Coyohua-Fuentes, Canales-Espinosa, & Rangel-Negrín, 2018a; Rutberg, 1986), rainfall (e.g., Kruuk, Clutton-Brock, Albon, Pemberton, & Guinness, 1999; Law, Fike, & Lent, 2014), or sex of preceding offspring (e.g., Hogg, Hass, & Jenni, 1992). It is assumed that these factors affect maternal reproductive physiology, and thus, sex allocation, an assumption now supported by the observation of covariation between maternal glucose or hormonal concentrations and offspring sex (Cameron, Lemons, Bateman, & Bennett, 2008; Gutiérrez-Adán, Granados, Pintado, & De la Fuente, 2001; Rangel-Negrín, Coyohua-Fuentes, Canales-Espinosa, Chavira-Ramírez, & Dias, 2018; Ryan et al., 2012). Ultimately, variation in infant sex ratios is expected when fitness returns vary between sexes and parents are able to couple offspring sex with investment potential and local conditions (Altmann & Altmann, 1991; Clark, 1978; Trivers & Willard, 1973; but see Booksmythe, Mautz, Davis, Nakagawa, & Jennions, 2017; Cockburn, Legge, & Double, 2002). Given that the fitness returns provided by offspring of each sex may vary with the social, ecological, and demographic contexts of populations (e.g., Aars, Andreassen, & Ims, 1995; Altmann & Altmann, 1991; Perret, 1990, 1996), different sex allocation tactics may occur within species over time (Schindler et al., 2005). Thus, infant sex ratios may offer insight into the particular constraints faced by populations at a particular moment in time (Clutton-Brock, 1991).

Sex allocation in nonhuman primates (henceforth primates) has been thoroughly researched. Tests of adaptive hypotheses for variation in infant sex ratio have yielded contrasting results, with some studies reporting positive and others reporting negative effects of maternal condition on the proportion of produced sons (reviewed in Schino, 2004; Silk, Willoughby, & Brown, 2005). Assuming that sex allocation in primates is adaptive, these conflicting results may stem from low statistical power, stochastic variation associated with small sample sizes, and/or the use of surrogate measures that do not proxy maternal condition (Silk & Brown, 2004). A robust meta-analysis of 102 species (Silk & Brown, 2008) has demonstrated that variation in infant sex ratios is associated with dispersal patterns and breeding cooperation. On the one hand, more infants of the sex that disperses are produced in species that do not breed cooperatively, as expected under the Local Resource Competition hypothesis (Clark, 1978; Silk,

1984). On the other hand, more offspring of the sex that helps with rearing is produced in species with cooperative breeding, supporting the Local Resource Enhancement hypothesis (Emlen, Emlen, & Levin, 1986; Lessells & Avery, 1987; Pen & Weissing, 2000). Still, the proportion of individuals from each sex that disperses may vary within and between populations (e.g., Boinski, Ehmke, Kauffman, Schet, & Vreedzaam, 2005; Di Fiore, Link, Schmitt, & Spehar, 2009; Minhós et al., 2013), and a large proportion of primates do not have cooperative breeding (e.g., in 192 of 219 species, paternal care is absent: Opie, Atkinson, Dunbar, & Shultz, 2013a). Therefore, further testing of adaptive explanations for primate sex allocation is required.

Alouatta (howler monkeys) is a platyrrhine radiation of at least 12 species that distributes from southern Mexico to northern Argentina (Cortés-Ortiz, Rylands, & Mittermeier, 2015). Howler monkeys occupy a wide range of habitat types from evergreen rainforests with annual rainfall up to 4,900 mm (e.g., mantled howler monkeys [*A. palliata*] at Los Tuxtlas, Mexico: Cristóbal Azkarate, Dunn, Domingo-Balcells, & Veà, 2017) to dry forests receiving less than 800 mm of rain per year (e.g., black-and-gold howler monkeys [*Alouatta caraya*] at Caatinga, Brazil: Moura & McConkey, 2007). Howler monkeys usually live in groups of less than 10 individuals, including 1–5 adult males, 1–5 adult females, and variable numbers of immatures (Di Fiore, Link, & Campbell, 2010). Bisexual dispersal, male philopatry, and female philopatry have been reported in this genus (Calegario-Marques & Bicca-Marques, 1996; Crockett & Pope, 1993; Di Fiore et al., 2010; Dias, Coyohua-Fuentes, Canales-Espinosa, & Rangel-Negrín, 2015; Oklander, Kowalewski, & Corach, 2010). Cooperative rearing of infants has been seldom described in this genus (Raguette-Schofield & Pavé, 2015).

Although howler monkeys are a thoroughly studied primate genus (e.g., Bezanson & McNamara, 2019; Kowalewski, Garber, Cortés-Ortiz, Urbani, & Youlatos, 2015a, 2015b), variation in infant sex ratios has seldom been addressed. Longitudinal surveys of ursine (*Alouatta arctoidea*; 8 years) and brown (*Alouatta guariba*; 4 years) howler monkey populations indicate that infant sex ratio tends to unity (0.9 sons per daughter: Crockett & Rudran, 1987; Strier, Mendes, & Santos, 2001), whereas in black howler monkeys (*Alouatta pigra*; 7 years) it is skewed in favor of sons (1.7: Dias et al., 2015). In black howler monkeys, sons are born more often to mothers with higher glucocorticoid hormone metabolite concentrations around the time of conception (Rangel-Negrín, Coyohua-Fuentes, Canales-Espinosa, et al., 2018). This association appears to be mediated by environmental conditions, such that fewer daughters are born to mothers living in anthropogenically disturbed habitats. In disturbed habitats, sons are produced more than daughters (Rangel-Negrín, Coyohua-Fuentes, Canales-Espinosa, et al., 2018). A bias toward the production of sons in disturbed habitats supports the Local Resource Competition hypothesis for sex allocation (Clark, 1978) as sons are more likely to disperse than daughters (Rangel-Negrín, Coyohua-Fuentes, Canales-Espinosa, et al., 2018) and disturbed habitats may have lower food availability and thus increased food competition. In ursine howler monkeys, daughters are produced more than sons at low population densities (Crockett, 1996; Crockett & Pope, 1993; Rudran & Fernández-Duque, 2003), supporting the Local

Resource Enhancement hypothesis, as lower population densities are expected to reduce food competition. Thus, infant sex ratios in howler monkeys may be linked to food availability and maternal physical condition, but these relationships have not been formally tested.

Given that sex allocation is proximately affected by maternal physical condition (Cameron et al., 2008; Gutiérrez-Adán et al., 2001; Rangel-Negrín, Coyohua-Fuentes, Canales-Espinosa, et al., 2018; Ryan et al., 2012), we reviewed the literature to assess variation in infant sex ratio relative to maternal condition in howler monkeys. As there are very few data on the physical condition of female howler monkeys (Cano-Huertes et al., 2017; Dias et al., 2018b; Rangel-Negrín, Coyohua-Fuentes, Chavira-Ramírez, Canales-Espinosa, & Dias, 2018), we indexed maternal condition by annual rainfall and the potential for resource competition. In tropical forests, rainfall levels are positively correlated with habitat productivity such that where rainfall is higher, net primary productivity, plant biomass, and plant species diversity are higher (e.g., Lewis et al., 2013; Malhi et al., 2004; Quesada et al., 2009; Ter Steege et al., 2003; Toledo et al., 2011). Thus, compared to sites where rainfall is lower, where rainfall is higher individuals should have more access to food resources, and, as a consequence, higher physical condition. Resource competition may occur both within and between groups, and it is expected to increase as a function of group size and group density, respectively (e.g., Sterck, Watts, & van Schaik, 1997; van Schaik, 1989). Under high intra- and intergroup competition, differences among individuals in access to food resources, via contest competition, are expected to increase (Sterck et al., 1997; van Schaik, 1989), leading to variation in physical condition (e.g., Abbott et al., 2003). Habitat loss (Rangel-Negrín, Coyohua-Fuentes, Chavira-Ramírez, Canales-Espinosa, & Dias, 2014), human noise (Cañadas-Santiago et al., 2019), and habitat fragmentation (Martínez-Mota, Valdespino, Sánchez-Ramos, & Serio-Silva, 2007; but see Rimbach et al., 2013) affect glucocorticoid hormone concentrations in howler monkeys, a likely

consequence of decreased access to food resources and higher psychosocial stress in disturbed habitat (Cañadas-Santiago et al., 2019; Dias & Rangel-Negrín, 2015; Gómez-Espinosa, Rangel-Negrín, Chavira-Ramírez, Canales-Espinosa, & Dias, 2014). Thus, if a glucocorticoid hormone-mediated mechanism is associated with the facultative adjustment of infant sex in howler monkeys (Rangel-Negrín, Coyohua-Fuentes, Canales-Espinosa, et al., 2018), anthropogenic disturbance could affect infant sex ratio. Given previous evidence that female howler monkeys may adaptively adjust infant sex ratios in response to Local Resource Competition (Rangel-Negrín, Coyohua-Fuentes, Canales-Espinosa, et al., 2018), we hypothesized that mothers should produce more sons as food competition increases. We thus predicted that more daughters than sons should be produced when rainfall increases, but that more sons than daughters should be produced in when group size, group density, and habitat disturbance increase.

2 | METHODS

In all species except mantled howler monkeys, infant sex is easily identified at a young age in the field by a highly conspicuous scrotum in males (e.g., Clarke, Zucker, Ford, & Harrison, 2007; Strier et al., 2001; Thorington Jr, Ruiz, & Eisenberg, 1984; Figure 1). For this reason, we excluded mantled howler monkeys from our analyses. This study complies with the legal requirements of Mexico, where the research was conducted.

2.1 | Literature review

We systematically reviewed all published articles and book chapters reporting information on group size and composition of howler

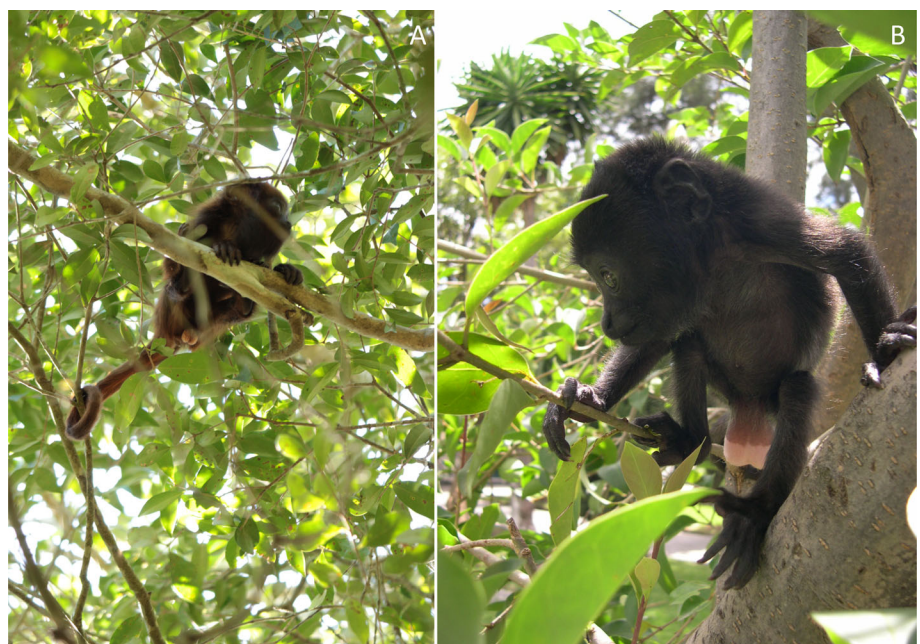


FIGURE 1 Images of male howler monkey infants illustrating that infant sex may be visually assessed through the observation of the scrotum: (a) 3-month-old *A. guariba* (photo by G. Pacheco Hass); (b) 3-month-old *A. pigra* (photo by A. Rangel Negrín)

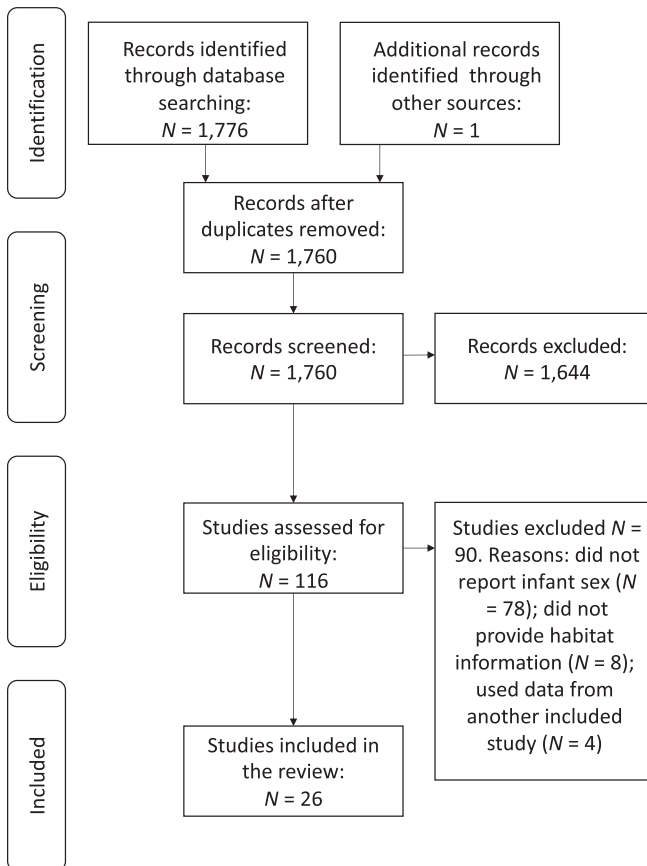


FIGURE 2 Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flow chart of our literature search and data collection process

monkeys up to September 2019. We searched the SCOPUS database using the following terms in all reference topics: [(alouatta OR "howl* monkey*" OR howler*) AND ("group composition" OR "survey" OR "demograph*" OR "sex allocation" OR "infant sex")]. Additionally, we consulted dissertations available on ProQuest Dissertations & Theses: Global (ProQuest LLC, Ann Arbor, MI) as well as those in digital libraries of Latin American universities and repositories (e.g., Prima-T, INECOL, Xalapa, México; CAPES, Ministério da Educação, Brasil). When data from these were published, we only used information presented in the publication. From each source, we extracted the following information: (a) species that was studied (according to the taxonomy of Cortés-Ortiz et al., 2015); (b) group size and age–sex composition of each studied group; (c) habitat size (in ha), defined as the amount of continuous habitat available to each group; (d) the presence of humans or signals of human activities (e.g., logging) inside the forest; (e) information on the fragmentation/continuity of the habitat; (f) annual rainfall levels at the site (in mm; Table S1); and (g) study type, defined as census (demographic data obtained during short-term visits, such as a few days to a few weeks) or longitudinal (data collected for each group for at least 1 year). In this process, we followed the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines (<http://www.prisma-statement.org/>; Figure 2).

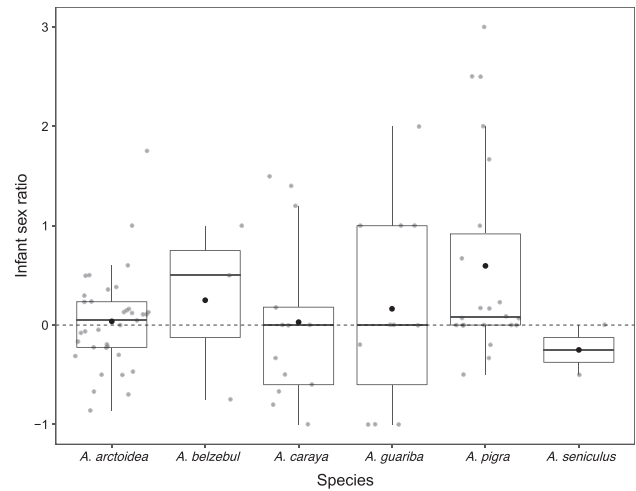


FIGURE 3 Variation among howler monkey species (*Alouatta* spp.) in infant sex ratios. For illustration purposes, infant sex ratios are represented as the number of male infants divided by the number of female infants minus 1. Therefore, a 1:1 sex ratio corresponds to zero, illustrated as the dotted line. Sex ratios >0 indicate more males, whereas those <0 indicate more females. Thick lines inside the boxes are the medians; black circles are the means; box limits are the 25th and 75th percentiles; whiskers indicate $1.5 \times$ interquartile ranges. Data points are plotted as gray circles

2.2 | Data organization and analysis

To assess the influence of anthropogenic disturbance on infant sex ratio, we built an habitat disturbance index based on three categorical variables: habitat size, classified as large/small; presence of humans or signs of human activities inside the forest, classified as yes/no; habitat fragmentation, classified as yes/no. We discretized habitat size with an unsupervised method based on the frequency of observations. Based on this analysis, we classified habitat sizes <156 ha as small and those >155 ha as large. We assigned a value of 1 each for small habitat size, human presence, and fragmented habitats, and 0 each for large habitat size, no human presence, and no habitat fragmentation. Thus, this habitat disturbance index ranged from 0 (large continuous habitat without human presence) to 3 (small fragmented habitat with human presence).

Our analysis was twofold. First, we used a generalized linear model (GLM) to assess whether infant sex ratio varied among species. We applied a binomial distribution and logit-link function, added the number of male infants and the number of female infants as a two-vector response variable (Crawley, 2013) using the "cbind" function in R (R Core Team, 2019), and used species identity as the predictive variable.

Second, we ran a GLM with a binomial distribution, in which infant sex ratio was the two-vector response variable and annual rainfall, group size, group density (defined as the number of groups living in the same habitat divided by habitat size), and the habitat disturbance index were the predictors. When we had data from several groups belonging to the same population, we summed infant numbers.

TABLE 1 Summary of data used in this study to assess the influence of anthropogenic disturbance, social, and ecological factors on the infant sex ratios of howler monkeys (*Alouatta* spp.)

Species	Infant sex ratio	Group size	Group density	Rainfall	No. of cases	No. of studies
<i>Alouatta arctoidea</i>	1.04 (0.5)	7.81 (1.2)	0.14 (0.1)	2,000 (0.0)	35	2
<i>Alouatta belzebul</i>	1.25 (0.9)	7.33 (1.6)	0.03 (–)	2,338 (400.1)	3	2
<i>Alouatta caraya</i>	1.03 (0.8)	10.07 (4.2)	0.39 (0.6)	2,046 (756.8)	13	6
<i>Alouatta guariba</i>	1.17 (1.2)	7.26 (2.1)	0.18 (0.2)	1,294 (92.9)	20	7
<i>Alouatta pigra</i>	1.78 (1.4)	6.19 (1.7)	0.15 (0.2)	1,499 (239.8)	23	7
<i>Alouatta seniculus</i>	0.75 (0.4)	6.90 (0.1)	0.25 (0.3)	2,791 (269.4)	2	2
Total	1.24 (1.0)	7.49 (2.5)	0.19 (0.3)	1,766 (467.9)	96	26

Note: Infant sex ratio calculated as the number of male infants divided by the number of female infants. Group density calculated as the number of groups divided by habitat size, in ha. Rainfall in mm. With the exception of number of cases and number of studies, numbers are means \pm SDs (in parenthesis). The dash indicates that a single value for group density was found for *A. belzebul*.

TABLE 2 Results of information-theoretic based model selection and multimodel inference for assessing the influence of anthropogenic disturbance, social and ecological factors on the infant sex ratios of howler monkeys (*Alouatta* spp.)

Predictor	β	SE	95% CI		$\sum w_i$
			Lower	Upper	
Group size	–0.16	0.19	–0.62	0.14	0.57
Group density	0.86	0.64	0.07	2.18	0.82
Rainfall	–0.45	0.18	–0.79	–0.14	0.96
Habitat disturbance	0.04	0.19	–0.46	1.35	0.05

Note: The model-averaged parameter estimate (β) and its 95% confidence interval are indicated. The sign of each parameter represents the direction of the effect (positive or negative) of each predictor on the response variable. Importance ($\sum w_i$) was calculated as the sum of Akaike weights of predictors in the set of models having a 95% probability of containing the best model.

We standardized all continuous predictors by subtracting the mean and dividing the result by the standard deviation of the original variables. Given that we obtained infant sex ratios from both longitudinal and census studies, and that the latter could yield biased data (e.g., lower number of infants from the sex with higher mortality rate), we assessed whether infant sex ratios in our data set were affected by study design. Specifically, we compared a model of variation in infant sex ratios including the predictors described above with a model in which study design was included as an additional predictor with a likelihood ratio test. These models were not significantly different (LR = 8, $p > .05$). Thus, as variation in study design did not affect results, for simplicity we present model results without further reference to this factor.

To determine the relative effect of each predictor on infant sex ratio, we used a multimodel inference approach (Burnham & Anderson, 2002). We first verified independence among predictors with the variance inflation factor (VIF) and found that none had VIF > 2, indicating no collinearity. We then ran models for each isolated and additive combinations of predictors (Table S2). For each model, we

calculated Akaike's information criterion corrected for small samples (AIC_c) and obtained model-averaged parameter weights using Akaike weights (w_i). The set of models for which $\sum w_i$ is 0.95 has a 95% probability of containing the best model (Burnham & Anderson, 2002). The best predictors of infant sex ratio were those that: (a) had high $\sum w_i$ considering all candidate models in which they were included; and (b) had 95% confidence intervals of the estimate that did not include zero. We also calculated the percentage of explained deviance by the complete model as a measure of goodness-of-fit.

All analyses were performed with R 3.6.0 (R Core Team, 2019) using packages “base” (R Core Team, 2019), “car” 3.0-3 (Fox, Weisberg, & Price, 2019), “lme4” 1.1-21 (Bates, Maechler, Bolker, & Walker, 2019), and “MuMIn” 1.43.6 (Bartoń, 2019).

3 | RESULTS

We found data on infant sex for six howler monkey species in 26 studies, of which the majority (56%) reported data for a single group (Table 1; Table S1). The remaining studies provided data for several groups surveyed in the same ($N = 4$) or different ($N = 3$) areas, or groups sampled through time ($N = 5$). From the 26 studies, we gathered 96 infant sex ratio reports, corresponding to 1,477 infants, of which 717 were females and 760 were males. Infant sex ratio across the sample was 1.1, with a mean \pm SD of 1.2 ± 1 females per male (range = 0–6). Variation in infant sex ratio among species was not significant ($\chi^2_5 = 6.8$, $p = .235$; Figure 3).

Sixty-one percent of the deviance in infant sex ratio was explained by the predictors. The most important predictor in this model was rainfall, followed by group density, group size, and habitat disturbance (Table 2). However, only rainfall and group density had estimates with 95% CI that did not include zero, suggesting that the remaining factors had limited influence on infant sex ratio. Infant sex ratio decreased (i.e., more females) with increasing rainfall, but increased (i.e., more males) with increasing group density (Figure 4).

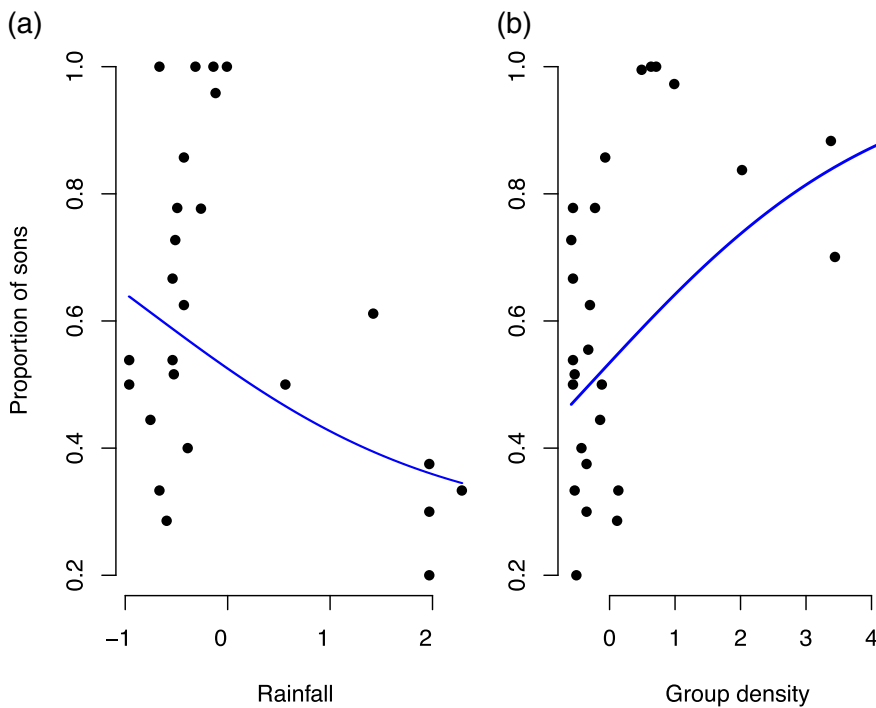


FIGURE 4 The effects of rainfall (a) and group density (b) on infant sex ratio in howler monkeys (*Alouatta* spp.). Predictors were standardized before analysis

4 | DISCUSSION

We reviewed the literature to describe variation in infant sex ratios in howler monkeys (genus *Alouatta*) and to determine if such variation could be associated with adaptive sex allocation. Infant sex ratio data coming from census studies represent snapshots in time of populations under demographic fluctuation. As a consequence, and in contrast with longitudinal data, it may be subjected to much stochasticity. Additionally, these studies do not allow a reliable estimation of infant mortality, which may have a strong impact on female reproductive strategies (e.g., Dias, Coyohua-Fuentes, Canales-Espinosa, & Rangel-Negrín, 2018a). With this in mind, and given that census studies did not yield different infant sex ratio results than longitudinal studies, we found that, regardless of species, on average infant sex ratios tend to unity, as expected under frequency-dependent selection (Fisher, 1958; Frank, 1990). There is, however, considerable variation in this parameter, which is mostly influenced by rainfall and group density: as predicted, females produce more daughters when rainfall increases and more sons under high group densities. We propose that this variation reflects adaptive sex allocation, as posed by both the Local Resource and the Local Resource Enhancement (cooperation) hypotheses.

As with other primate taxa, the generalized lack of information on the physical condition of howler monkeys precludes the direct testing of sex allocation hypotheses that are based on variation in parental condition (Altmann & Altmann, 1991; Booksmythe et al., 2017; Burley, 1981, 1986; Trivers & Willard, 1973). Still, rainfall and group density may influence maternal physical condition—and sex allocation—through their effects on food availability and resource competition (Berkeley & Linklater, 2010; Kruuk et al., 1999; Weladji & Laflamme-Mayer, 2010; Wells & Van Vuren, 2017). Thus, our results converge

with previous suggestions that, as in other organisms (e.g., Chason et al., 2012; Moore, Hayward, & Robert, 2015; Ryan et al., 2012; Schwanz & Robert, 2014), sex allocation in howler monkeys may be based on a mechanism that transduces environmental information to maternal physiology, such as glucocorticoid hormone modulation (Rangel-Negrín, Coyohua-Fuentes, Canales-Espinosa, et al., 2018).

Local resource competition and cooperation may affect sex allocation: skewing infant sex ratio in favor of the sex that is less likely to compete or more likely to cooperate locally may accrue fitness benefits for parents (Clark, 1978; Emlen et al., 1986; Johnson, 1988; Schwarz, 1988; Taylor, 1994). The commonly reported bisexual dispersal patterns of howler monkeys (Di Fiore et al., 2010) could lead to the expectation that usually only unrelated individuals co-reside. Under this scenario, local resource competition and cooperation should have a minor influence on sex allocation. In well-studied populations, however, related individuals often live in the same groups and kinship relationships affect social relationships (e.g., Cristóbal Azkarate et al., 2017; Dias et al., 2015; Lecompte, Bouanani, de Thoisy, & Crouau-Roy, 2017; Nidiffer & Cortés-Ortiz, 2015; Pope, 1990, 2000; Rudran & Fernández-Duque, 2003; Van Belle, Estrada, & Di Fiore, 2014; Van Belle, Estrada, Strier, & Di Fiore, 2012). For instance, in both black and ursine howler monkeys, females actively recruit females from their own matriline and force the daughters of other females to emigrate (Crockett, 1984; Horwich, Brockett, James, & Jones, 2001; Rumiz, 1992). In ursine howler monkeys, female reproductive success is positively related with the degree of genetic relatedness among group females (Pope, 2000). Additionally, some male ursine howler monkeys remain in the natal groups and help their fathers defend groups against extragroup males (Pope, 1990). Thus, nonrandom dispersal patterns according to sex, matrilineal cooperation, and enhanced reproductive success in the presence of

relatives occur in howler monkeys, complying with the basic premises of the Local Resource Enhancement hypothesis for sex allocation (Clark, 1978; Emlen et al., 1986; Lessells & Avery, 1987; Pen & Weissing, 2000; Silk, 1984).

Nevertheless, given that social, ecological, and demographic factors affect reproductive strategies (e.g., Kokko & Jennions, 2008; Kokko & Rankin, 2006), and that howler monkeys live under a large array of socio-ecological conditions (Crockett, 1998), it is unlikely that a single sex allocation tactic occurs in *Alouatta*. When howler monkey populations are growing, most groups include two to three adult females (Rudran & Fernández-Duque, 2003). It is during this stage that females recruit their daughters (Crockett, 1984; Pope, 2000; Rumiz, 1992), and our results suggest that an overproduction of daughters under low densities may be a component of female reproductive strategies under a local resource enhancement scenario. As populations saturate (i.e., reach carrying capacity, proxied in this study by group density), competition among females for both food resources and group membership increases (Crockett & Janson, 2000; Horwich et al., 2001), and a shift toward the production of dispersing sons (i.e., higher infant sex ratio under higher group density) could decrease such competition. The negative relationship between rainfall (a proxy for habitat productivity) and infant sex ratio also aligns with the possibility that females produce more sons when resource competition is potentially higher. An additional selective pressure against the production of philopatric daughters is a positive correlation between infanticide rates and the number of resident females (Crockett & Janson, 2000), which seems to set an upper limit of five adult females per group (Di Fiore et al., 2010). Thus, Local Resource Competition is a better explanation than Local Resource Enhancement for sex allocation in howler monkeys living in stable populations. As previously demonstrated in theoretical (e.g., Julliard, 2000; Reinhold, 1996) and empirical (e.g., Robinson & O'Brien, 1991) studies with other organisms, howler monkey females may facultatively adjust infant sex ratios to prevailing environmental conditions and have varying sex allocation tactics.

In summary, infant sex ratio across howler monkey species tends to parity, but its variation is positively correlated with group density and negatively correlated with rainfall. Thus, we provide evidence suggestive of adaptive variation in infant sex ratios in howler monkeys. Based on these results, as well as on previous information on dispersal patterns, demography, and within-group genetic relatedness, we speculate that, depending on population growth stage, sex allocation is explained by the Local Resource Enhancement (more philopatric daughters produced when populations are growing) and the Local Resource Competition (more dispersing sons when populations are saturated) hypotheses.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

I.L. Montero-Domínguez and P.A.D. Dias built the database; A. Rangel-Negrín and P.A.D. Dias performed the analysis; I.L. Montero-Domínguez, A. Rangel-Negrín, and P.A.D. Dias wrote the manuscript.

DATA AVAILABILITY STATEMENT

Data analyzed in this study is presented in supporting information.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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