




Mother's Age and Social Integration Modulate Sex-biased Maternal Investment in Wild Spider Monkeys (*Ateles geoffroyi*)

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Abstract

In many mammal species, mothers are crucial for the survival and development of young offspring. In primates, maternal investment may ensure immatures' survival and also foster their social integration in the group, providing long-term fitness benefits. In this study, we analysed maternal investment in a wild group (N = 49) of male philopatric spider monkeys (*Ateles geoffroyi*). We assessed whether maternal investment is biased toward sons (compared with daughters) and which factors modulate this relation. We studied 20 mother–offspring dyads, measuring the time mothers spent in body contact, nursing, carrying, grooming, and playing with their offspring, for a total of 359 focal samples from February to July 2022. We then ran generalized linear mixed models to assess how these responses varied depending on the two-way interactions of offspring sex with offspring age, maternal age, and maternal centrality. Our results showed that mothers were more likely to nurse, carry, and have body contact with younger than older offspring, regardless of their sex. However, we also found that mothers invested more in male than female offspring; differences were mediated by mothers' age and social integration in the group. Older mothers, in particular, were more likely to carry sons than daughters, whereas the contrary was true for younger mothers. Moreover, socially more central mothers were more likely to be in body contact with sons than daughters. Overall, our study shows that some maternal behaviours are sex-biased in male-philopatric species, although maternal experience and social integration may modulate this relation.

Keywords Male philopatry · Maternal care · Platyrrhines · Social experience · Primates

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Inclusion and diversity statement: While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list.

Extended author information available on the last page of the article

Introduction

In mammals, mothers are crucial for the survival and development of their young offspring. First, mothers provide immatures with food, warmth, and protection against predators and other dangers (Bales, 2017; Broad *et al.*, 2006; Mogi *et al.*, 2011; Okabe *et al.*, 2012). Second, mothers may offer important opportunities for social learning to their offspring, fostering the acquisition of novel skills and knowledge (Gilbert, 1999; Holekamp & Smale, 1991; Lee & Moss, 1999; Sargeant & Mann, 2009). In species with long lifespans, large brains, and slow development, such as primates, offspring are dependent on their mothers for long periods, and the relationship to their mothers may be even more significant than in other taxa (Barton & Capellini, 2011; Keller & Chasiotis, 2008; Powell *et al.*, 2019; van Noordwijk, 2012).

The effort expended by mothers towards their young offspring is usually referred to as maternal investment. It can increase offspring fitness by positively affecting survival and reproductive success (Trivers, 1972). In primates, maternal investment includes a variety of behaviours that have an immediate beneficial function for the offspring's survival, such as nursing and carrying (Brown, 2001). Moreover, maternal investment may include behaviours that are important to foster immatures' socioemotional development (Mason & Mendoza, 1998; Mendoza & Mason, 1999). By socially interacting with their offspring, for instance, primate mothers provide immediately reassuring physical contact (Mandalaywala *et al.*, 2014; van de Rijt-Plooij & Plooij, 1987) but also contribute to forming strong emotional bonds that will affect the development of species-typical behaviours and foster their gradual integration in the social network (Amici *et al.*, 2019; Jaeggi *et al.*, 2010; Maestripieri, 2018; Mikeliban *et al.*, 2021; Rosati *et al.*, 2014; Whiten & van de Waal, 2018), with long-term fitness benefits (Archie *et al.*, 2014; Kulik *et al.*, 2012; Schülke *et al.*, 2010; Silk *et al.*, 2003, 2006, 2009, 2010).

Maternal investment posits high costs to mothers and reduces their ability to produce other offspring, so that mothers should maximize their reproductive success by adjusting the time and energy allocated to immatures based on the specific conditions they face (Bercovitch, 2002; Clutton-Brock, 1991; Daly & Wilson, 1995; Trivers & Willard, 1973). Factors that may affect maternal investment include both mother and offspring characteristics. Mothers, for instance, may bias the time they spend in social interactions with their offspring, depending on the latter's sex. In female-philopatric rhesus macaques (*Macaca mulatta*), mothers are more likely to be aggressive and less likely to groom and be in body contact with their sons, who will leave the natal group at sexual maturity, than their daughters, who will remain in the natal group (Kulik *et al.*, 2016). In this way, mothers foster the integration of the philopatric sex in the social network, while promoting independence in the nonphilopatric sex (Kulik *et al.*, 2016; Timme, 1995). In male-philopatric chimpanzees (*Pan troglodytes*), in contrast, mothers invest more in sons than daughters (Boesch, 1997), weaning male offspring later than female offspring (Lonsdorf *et al.*, 2020; Bădescu *et al.*, 2022), providing them with a higher proportion of milk in their diets, and showing longer interbirth

intervals after sons than daughters (Bădescu *et al.*, 2022). Mothers of black spider monkeys (*Ateles paniscus*) also invest more in philopatric males than in females, weaning sons later than daughters (Symington, 1987).

These findings suggest that mothers may invest more in the philopatric sex, because this provides higher fitness returns (Bădescu *et al.*, 2022). However, sex differences also may reflect the need to temporally tailor maternal investment to the specific needs of the offspring. Mothers of sons in rhesus macaques, for instance, produce higher-quality milk (i.e., containing more fat and protein, and less sugar) than mothers of daughters but in lower quantity (Hinde, 2007), suggesting an adjustment to the sex-specific physiological needs of the offspring (Eckardt *et al.*, 2016; Hinde, 2009). In line with this, the link between maternal investment and offspring sex is not always clear (Brown, 2001, for a review), possibly because this relation is modulated by other factors (Packer *et al.*, 2000). First, maternal investment may vary depending on the interaction of offspring sex with their age. Mothers generally decrease their investment as offspring become older, but this decrease may follow different developmental patterns for sons and daughters. In rhesus macaques, for example, mothers are more likely to engage in social interactions with philopatric daughters rather than nonphilopatric sons. However, when offspring approach sexual maturity, the probability of some behaviours also decreases more quickly for nonphilopatric sons than for philopatric daughters (Kulik *et al.*, 2016). Second, maternal investment may vary depending on the interaction of offspring sex and maternal condition. According to Trivers and Willard (1973), mothers in good physical condition should invest more in the sex that provides higher fitness returns (e.g., in polygynous species, mothers should invest more in sons than in daughters), so that mothers' condition should modulate sex-biased investment. In primates, however, evidence supporting this theory is inconsistent (for a review, see Brown, 2001). Third, maternal investment may vary depending on the interaction of offspring sex and maternal experience. In baboons (*Papio spp.*), for example, sons generally provide higher fitness returns to mothers, but it is only more experienced (i.e., older) mothers who invest more in sons than daughters (Packer *et al.*, 2000).

To date, research on sex-biased maternal investment in wild primates has been mostly conducted in catarrhines, whereas much less is currently known about plathyrrines (for good exceptions, see Arbaiza-Bayona *et al.*, 2022; Pavé *et al.*, 2015; Pavé, 2016; Verderane *et al.*, 2020; Yamamoto *et al.*, 1996). Geoffroy's spider monkeys (*Ateles geoffroyi*) are a male philopatric plathyrrine species, in which females usually migrate to other groups upon reaching sexual maturity (Symington, 1987), whereas males remain in the group and form strong affiliative bonds with each other (Fedigan & Baxter, 1984). Mothers have long interbirth intervals (2–4 years), and individuals reach sexual maturity relatively late (around 4 years for females and 5 years for males; Chapman & Chapman, 1990; Vick, 2008). For some authors, this extended period of dependency on the mother reflects the sociocognitive complexity of a species with high levels of fission–fusion dynamics (Arbaiza-Bayona *et al.*, 2022). Given that spider monkeys share the same male-philopatric and fission–fusion social characteristics of chimpanzees, it is possible that maternal investment also follows a pattern of sex-biased maternal investment similar to that in chimpanzees. So far, however, only one study has systematically studied mother–infant

relationships in spider monkeys, showing a decrease of maternal investment through offspring's development, and the presence of important developmental milestones around 10 and 20 months of age, when infants become more independent and mothers more rejecting (Arbaiza-Bayona *et al.*, 2022).

We aimed to assess whether maternal investment differs depending on the offspring's sex, and whether sex-biased maternal investment is modulated by maternal and offspring characteristics. We hypothesized that maternal investment (operationalized as the probability of nursing, carrying, being in body contact, grooming or playing with the offspring) would be biased in favour of the philopatric sex, but that offspring age, maternal integration in the social network (as a measure of maternal condition) and maternal age (as a proxy of experience) would mediate this relationship (Table I). In particular, we predicted that mothers would generally decrease their investment when offspring become older but that this decrease would happen more quickly for nonphilopatric daughters than philopatric males (Prediction 1). We further predicted that socially more integrated mothers (Prediction 2) and more experienced mothers (Prediction 3) would be more likely to invest in philopatric sons than in nonphilopatric daughters compared with socially less integrated and less experienced mothers.

Methods

Ethical Note We obtained the permission to conduct this study by the Mexican institutions CONANP (Comisión Nacional de Áreas Naturales Protegidas) and SEMARNAT (Secretaría de Medio Ambiente y Recursos Naturales). This study was purely observational and in line with the Principles for the Ethical Treatment of Nonhuman Primates by the American Society of Primatologists (2001).

Data Availability The datasets analysed during the current study are available from the corresponding author on reasonable request.

Conflict of Interest The authors declare that they have no conflict of interest.

Field Site and Study Subjects We conducted our study in the Otoch Ma'ax Yetel Kooch protected area in Yucatan, Mexico (20° 38' N, 87° 38' W), characterized by a lake, old-growth, semi-evergreen medium forest, 30–50-year-old successional forest and patches of younger regenerating forest (Ramos-Fernández & Ayala-Orozco, 2003). We observed a group of 49 Geoffroy's spider monkeys, who were well-habituated to the presence of human observers, and could be individually recognized by observing their hair and facial features. The group included 13 adult females, 9 adult males, 3 subadult females, 2 subadult males, 9 juvenile females, 5 juvenile males, 3 infant females, and 5 infant males (see Shimooka *et al.*, 2008 for age categories; Table II). Demographic records spanning over several years allowed us to establish

Table 1 Predictions of our study on a wild group of spider monkeys (*Ateles geoffroyi*) in the Oloch Ma'ax Yetel Koooh protected area in Yucatan, Mexico, from February to July 2022, together with the responses analysed in different models, significant test predictors, and whether predictions were confirmed

Predictions	Response	Model	Confirmed?	Significant test predictors
1 Mothers decrease their investment through offspring's age, but more quickly for daughters than sons	Nursing	1	Partially	Offspring's age
	Carrying	2	Partially	Offspring's age
	Body contact	3	Partially	Offspring's age
	Grooming	4	No	-
	Playing	5	No	-
2 Socially more integrated mothers invest more in sons than daughters, as compared to socially less integrated mothers	Nursing	1	No	-
	Carrying	2	No	-
	Body contact	3	Yes	Offspring's sex * Maternal integration
	Grooming	4	No	-
	Playing	5	No	-
3 More experienced mothers invest more in sons than daughters, as compared to less experienced mothers	Nursing	1	No	-
	Carrying	2	Yes	Offspring's sex * Maternal experience
	Body contact	3	No	-
	Grooming	4	No	-
	Playing	5	No	-

Table II Individuals belonging to a wild group of spider monkeys (*Ateles geoffroyi*) observed in the Otoch Ma'ax Yetel Kooch protected area in Yucatan, Mexico, from February to July 2022, including their sex, mother identity (for infants and juveniles), age and age class assigned (i.e., infants: < 2 years; juveniles: 2–5 years; subadults: 6–7 years; adults: < 8 years). Study subjects are marked with an asterisk. The two individuals whose mother was not present in the group and are not included as focal subjects are marked with two asterisks

Subject	Mother	Sex	Age (yr)	Age class
Alma*	Antena	Male	0	Infant
Andrés		Male	8	Adult
Antena		Female	15	Adult
Apolo		Male	8	Adult
Aura*	Antena	Female	3	Juvenile
Bekech		Female	7	Subadult
Boxhuevos		Male	11	Adult
Braga*	Tanga	Female	4	Juvenile
Cacao*	Xibalba	Male	0	Infant
Canela*	Verónica	Female	2	Juvenile
Chaac*	Ikil	Male	1	Infant
China		Female	39	Adult
Chikich*	Tanga	Female	1	Infant
Covid*	Pancha	Male	0	Infant
Digit		Male	9	Adult
Eek*	Mich	Female	5	Juvenile
Eulogio		Male	18	Adult
Fabrizio*	Rwanda	Male	2	Juvenile
Yuli*	Lola	Female	1	Infant
Ikil		Female	8	Adult
Ixchel*	Xibalba	Female	5	Juvenile
Joanne		Female	24	Adult
Juan		Male	19	Adult
Lola		Female	21	Adult
Luna*	Joanne	Female	2	Juvenile
Luz*	Lola	Female	4	Juvenile
Mandíbula		Female	18	Adult
Marcos		Male	15	Adult
Marylin		Female	13	Adult
Mich		Female	13	Adult
Morita		Female	6	Subadult
Nacho		Male	7	Subadult
Nit		Female	7	Subadult
Pancha		Female	20	Adult
Pekín*	China	Male	3	Juvenile
Poncho*	Pancha	Male	4	Juvenile
Puma**		Male	2	Juvenile
Rwanda		Female	9	Adult
Sacbe*	Joanne	Female	5	Juvenile
Sancho		Male	10	Adult
Selva*	Marylin	Female	0	Infant
Sol*	Joanne	Male	0	Infant
Tanga		Female	20	Adult

Table II (continued)

Subject	Mother	Sex	Age (yr)	Age class
Valentín		Male	6	Subadult
Verónica		Female	38	Adult
Voldemort*	Mandíbula	Male	3	Juvenile
WiguiBERTO		Male	12	Adult
Xibalba		Female	9	Adult
Yalit**		Female	4	Juvenile

the age of the monkeys. The mothers with juvenile offspring were 20 ± 9.7 years old, and mothers with infant offspring were 17.5 ± 5.9 years old.

Data Collection We collected data from February to July 2022, for 5 days a week, either from 6:00 to 13:30 or from 15:00 to 19:30. We used 15-min focal animal samples with continuous sampling (Altmann, 1974) and recorded data with CyberTracker devices (Blackview BV9700 PRO and Blackview BV9900). One to two observers dictated, and the third wrote in the device. Before the study started, all the researchers received training about how to record behavioural data, and data collection started only after reaching 85% interobserver reliability on the observed behaviours. We conducted focal samples on all the individuals of the group, pseudo-randomizing the order in which they were observed (i.e., we conducted the observations on the first available individual from a list with all the randomly ordered group members).

We conducted two types of focal samples. First, to assess maternal investment, we observed all the individuals who were younger than 6 years, whose mother was present in the group ($N=20$). Two individuals (Table II) were younger than 6 years, but their mother was no longer present in the group, so we did not include them as focal individuals. We conducted 359 focal samples (mean \pm SD: 4.5 ± 0.3 h per focal animal), continuously recording the exact duration of all the following behaviours performed by the focal sample: (i) time visible; (ii) time being nursed by the mother (i.e., the offspring held the mother's nipple in the mouth), (iii) time being carried by the mother (i.e., the mother moved with the offspring clinging to her back), (iv) time in body contact with the mother (i.e., any part of the offspring's body was adjacent to any part of the mother's body, but no grooming or play took place), (v) time being groomed by the mother (i.e., the mother manipulated the offspring's hair with her hands or mouth), or (vi) time playing with the mother (i.e., any behaviour between the mother and her offspring associated to behavioural indicators of play, such as play faces).

Second, to assess individual social integration in the group, we also observed all the individuals in the group who were older than 6 years ($N=27$). On these older individuals, we conducted a total of 443 focal samples (mean \pm SD: 4.5 ± 0.6 h per focal animal) by recording: (i) the duration of the focal sample; (ii) the duration in which the focal individual was grooming or receiving grooming

by another individual, specifying the partner identity; (iii) the duration in which the focal individual was cofeeding with another individual (i.e., the focal animal and a partner fed on the same food within 1 m from each other); and (iv) every 2 min, the identity of all the individuals who were within 5 m proximity from the focal animal.

Finally, to estimate food availability (which might affect individual energetic income and thus maternal investment in the offspring), we followed Schaffner and colleagues (2012) and used a phenological transect, including 111 trees from the 17 main species in the spider monkeys' diet (Ramos-Fernández & Ayala Orozco, 2003). Two observers walked the transect approximately every month and recorded whether more than one fruit was visible on each tree.

Statistical Analyses First, for each possible dyad older than 6 years, we calculated the proportion of time that the dyad spent grooming (i.e., the total time in which each individual groomed the other, divided the total time in which we observed both individuals), the proportion of time that the dyad spent co-feeding, and the proportion of scans in which the dyad was in proximity. For each of these three behaviours, we then rescaled all dyadic values to vary between 0 and 1 and then used the mean of each dyad to construct an undirected weighted matrix with all the possible dyads. By rescaling the three behaviours, we ensured that they all contributed equally to the final matrix, despite some behaviours being more frequent than others. We then used this matrix to run social network analyses with the following packages in R: *vegan* (Oksanen *et al.*, 2018), *asnipe* (Farine, 2018), and *igraph* (Csardi & Nepusz, 2006). As a measure of social centrality, we assessed individuals' eigenvector centrality in the social network, which measures individuals' direct and indirect contacts (so that individuals with many contacts or with contacts having many contacts have high centrality) and is considered a proxy of individuals' importance as social hubs (Davis *et al.*, 2018; Farine, 2017; Farine & Whitehead, 2015).

Second, every time we walked the phenological transect, we calculated the proportion of trees in the transect that contained fruit. We then divided the period between two transects in three (so that each period was approximately 10 days long), and we operationalized fruit availability as the proportion assessed during each transect (for the parts of the period temporally closer to the transect) and as the mean of the two proportions (for the part of the period between two transects).

Finally, we ran five generalized linear mixed models (Baayen *et al.*, 2008) in R (R Core Team, 2020), with the package *glmmTMB* (Brooks *et al.*, 2017) to test for different effects on maternal investment. In our data-set, we entered one line for each focal sample of individuals younger than 6 years ($N = 359$). We considered the following binomial responses as dependent variables: whether the mother nursed (Model 1), carried (Model 2), was in body contact (Model 3), groomed (Model 4), or played (Model 5) with the focal immature individual during each focal sample. Although we had coded the exact proportion of time spent in each of these behaviours during each focal sample, the low frequency with which these

behaviours happened led us to use binomial distributions to obtain stronger models. All models included as test predictors the three 2-way interactions of offspring's sex with offspring's age (in days), maternal age (in years), and maternal centrality (with a score ranging from 0 to 1, where 1 meant highest centrality in the social network). We entered offspring's age in days to better capture variation in maternal behaviour during development. The terms of the 2-way interactions also were included as main terms in the model. In all models, we further included fruit availability as a control, the duration of the focal sample as offset term, and maternal identity nested in offspring identity as random factor.

We z -transformed all the continuous predictors (i.e., offspring's age, maternal age, maternal centrality, and food availability) to facilitate model convergence and interpretation of model estimates. We use a likelihood ratio test to compare each full model to a corresponding null model, which was identical to the full one but did not include test predictors (Dobson & Barnett, 2018). If the full and null model were significantly different, we used the `drop1` function to assess which test predictors were significant. If interactions were not significant, we re-run the model removing the nonsignificant interactions and only entering their terms as main effects. We did not detect any convergence, overdispersion, or underdispersion issues in any of our models. We further used the performance package (Lüdtke *et al.*, 2021) to check for multicollinearity, which was low (maximum variance inflation factors across models after removing the interactions = 2.66; Miles, 2005).

Results

On average (mean \pm SD), in each focal sample, mothers nursed their offspring for a $1.3 \pm 1.8\%$ of the time. In Model 1, the full model significantly differed from the null model (GLMM, $\chi^2 = 21.77$, $df = 7$, $p = 0.003$; Table III), with offspring's age having a significant effect. In particular, mothers were more likely to nurse younger than older offspring, with no differences depending on the offspring's sex: for each additional year of age, the odds of an offspring being nursed (i.e., the probability of being nursed over the probability of not being nursed) decreased by approximately 55%.

In each focal sample, on average, mothers carried their offspring for $7.1 \pm 14.1\%$ of the time. In Model 2, the full and null model significantly differed (GLMM, $\chi^2 = 43.74$, $df = 7$, $p < 0.001$; Table III), with both offspring's age and the 2-way interaction of offspring's sex with maternal age having a significant effect. In particular, mothers were more likely to carry younger than older offspring: for each additional year of age, the odds of an offspring being carried decreased by approximately 13%. Moreover, older mothers were more likely to carry males than females, whereas the contrary was true for younger mothers (Fig. 1).

In each focal sample, on average, mothers were in body contact with their offspring for a $17.6 \pm 25.4\%$ of the time. In Model 3, the full model significantly differed from the null model (GLMM, $\chi^2 = 34.37$, $df = 7$, $p < 0.001$; Table III), with offspring's age and the 2-way interaction of offspring's sex with maternal centrality having a significant effect. In particular, mothers were more likely to be in body contact with younger than older offspring, with no differences depending on

Table III Results of five models run to assess sex-biased maternal investment in a wild group of spider monkeys (*Ateles geoffroyi*), which was observed in the Otoch Ma'ax Yetel Kooh protected area in Yucatan, Mexico, from February to July 2022, including *p* values for test and control predictors (in italics), with reference categories in parentheses

MODEL	Estimate	SE	2.5% to 97.5% CI	LRT	df	<i>P</i>
1: probability of mothers nursing their infants						
Intercept	-9.99	0.52	-11.00 to -8.97	-	-	-
Offspring's sex (male)	0.58	0.50	-0.40 to 1.56	1.49	1	0.222
Offspring's age	-1.05	0.35	-1.73 to -0.38	13.18	1	< 0.001*
Maternal age	0.30	0.24	-0.18 to 0.78	1.56	1	0.212
Maternal centrality	-0.56	0.31	-1.17 to 0.05	3.61	1	0.057
<i>Fruit availability</i>	0.12	0.19	-0.25 to 0.49	0.38	1	0.535
2: probability of mothers carrying their infants						
Intercept	-16.12	6.88	-29.60 to -2.64	-	-	-
Offspring's sex (male) * Maternal age	7.35	9.24	-10.77 to 25.47	4.51	1	0.034*
Offspring's sex (male)	5.83	6.76	-7.42 to 19.08	-	-	-
Maternal age	-7.30	9.24	-25.42 to 10.81	-	-	-
Offspring's age	-3.64	0.61	-4.85 to -2.44	32.88	1	< 0.001*
Maternal centrality	0.28	0.38	-0.47 to 1.03	0.57	1	0.450
<i>Fruit availability</i>	-0.03	0.23	-0.47 to 0.41	0.02	1	0.900
3: probability of mothers being in body contact with their infants						
Intercept	-8.19	0.33	-8.84 to -7.53	-	-	-
Offspring's sex (male) * Maternal centrality	1.88	0.67	0.56 to 3.21	9.01	1	0.003*
Offspring's sex (male)	0.50	0.51	-0.49 to 1.49	-	-	-
Maternal centrality	-0.61	0.36	-1.32 to 0.10	-	-	-
Offspring's age	-1.31	0.27	-1.84 to -0.79	16.21	1	< 0.001*
Maternal age	-0.08	0.22	-0.52 to 0.36	0.12	1	0.730
<i>Fruit availability</i>	-0.10	0.16	-0.42 to 0.21	0.41	1	0.523
4: probability of mothers grooming their infants						
Intercept	-9.66	0.34	-10.33 to -8.98	-	-	-
Offspring's sex (male)	-0.17	0.55	-1.24 to 0.91	0.09	1	0.761
Offspring's age	0.08	0.26	-0.44 to 0.59	0.08	1	0.772
Maternal age	-0.19	0.27	-0.72 to 0.34	0.52	1	0.473
Maternal centrality	-0.01	0.26	-0.52 to 0.51	0.00	1	0.977
<i>Fruit availability</i>	0.30	0.21	-0.11 to 0.71	1.92	1	0.166
5: probability of mothers playing with their infants						
Intercept	-11.31	0.73	-12.75 to -9.88	-	-	-
Offspring's sex (male)	0.49	0.94	-1.35 to 2.33	0.28	1	0.597
Offspring's age	-0.58	0.49	-1.53 to 0.38	1.48	1	0.224
Maternal age	-0.49	0.57	-1.61 to 0.63	0.85	1	0.357
Maternal centrality	-0.05	0.53	-1.10 to 0.99	0.01	1	0.912
<i>Fruit availability</i>	-0.01	0.37	-0.73 to 0.71	0.00	1	0.974

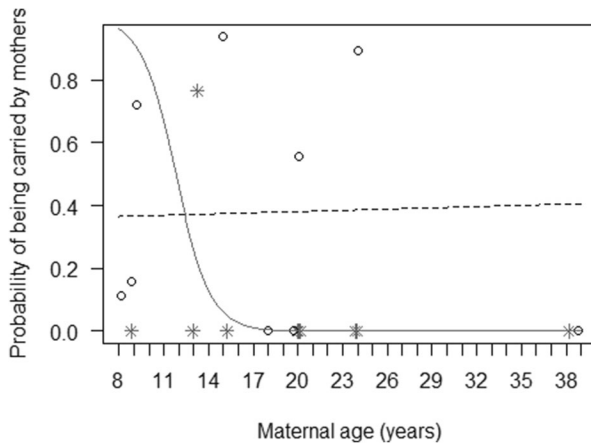


Fig. 1 Probability that mothers carried their offspring as a function of maternal age, separately for male and female immatures, in a wild group of spider monkeys (*Ateles geoffroyi*), in the Otoch Ma'ax Yetel Kooch protected area in Yucatan, Mexico, from February to July 2022. For each study subject, black circles represent the mean probability of being carried by mothers for male offspring, whereas dark grey asterisks represent the mean probability of being carried by mothers for female offspring. Two lines represent the fitted model (black dashed for males; dark grey continuous for females), which is like Model 2, except that observational effort is expressed in 5-h intervals (rather than seconds) to increase visual clarity. On the x-axis, data points are slightly jittered to avoid overlapping

the offspring's sex: for each additional year of age, the odds of an offspring being in body contact sex decreased by approximately 47%. However, the more central the mother, the more likely it was that she would be in body contact with male rather than female offspring (Fig. 2).

Finally, in each focal sample, mothers groomed their offspring for $0.7 \pm 0.7\%$ of the time, and played with them for $0.2 \pm 0.7\%$ of the time, on average. In Model 4 (GLMM, $\chi^2 = 2.13$, $df = 7$, $p = 0.952$; Table III) and in Model 5 (GLMM, $\chi^2 = 6.00$, $df = 7$, $p = 0.539$; Table III), we found no significant difference between the full and the null model, suggesting that the probability of receiving grooming or playing with the mother was not predicted by any of the terms included in the models.

Discussion

Our study provided evidence of sex-biased maternal investment in spider monkeys, which was partially mediated by the mothers' characteristics. Regardless of offspring sex, mothers were more likely to nurse, carry, and be in body contact with younger than older offspring. However, older mothers were more likely to carry males than females, whereas the contrary was true for younger mothers. Moreover, more central mothers were also more likely to be in body contact with sons than daughters. Finally, the probability that mothers groomed or played with their offspring did not significantly vary depending on offspring's sex or age, maternal age, or centrality, or their interactions.

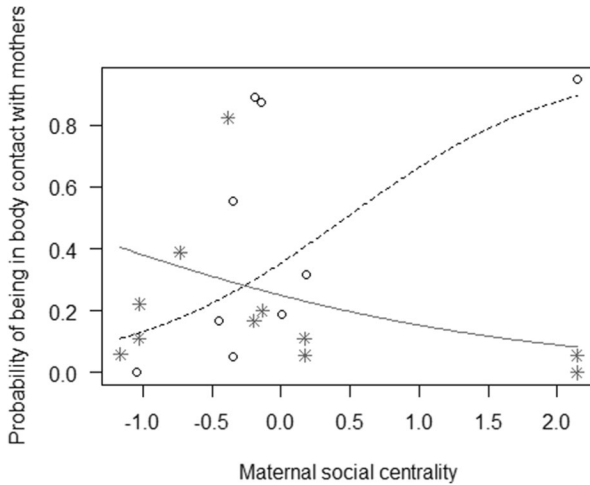


Fig. 2 Probability that mothers were in body contact with their offspring as a function of maternal integration in the group (i.e., social centrality), separately for male and female immatures, in a wild group of spider monkeys (*Ateles geoffroyi*), which was observed in the Otoch Ma'ax Yetel Kooh protected area in Yucatan, Mexico, from February to July 2022. For each study subject, black circles represent the mean probability of being in body contact with their mothers for male offspring, whereas dark grey asterisks represent the mean probability of being in body contact with their mothers for female offspring. Two lines represent the fitted model (black dashed for males; dark grey continuous for females), which is like Model 3, except that observational effort is expressed in 20-min intervals (rather than seconds) to increase visual clarity. On the x-axis, data points are slightly jittered to avoid overlapping

Our results provided no support for our first prediction that maternal investment would decrease more quickly in daughters compared with sons as offspring became older. Mothers decreased their investment through offspring age when immatures became increasingly independent. In particular, mothers become gradually less likely to nurse, carry, and be in body contact with their offspring, possibly also as a result of younger siblings being born, and mothers diverting their investment toward younger offspring. However, the decrease was similar for daughters and sons, with the offspring's sex having no modulating effect. Nursing, carrying, and body contact are crucial behaviours for the offspring's survival, because they provide immatures with food, warmth, and immediate protection against dangers (Brown, 2001). Therefore, it is possible that mothers engage in these behaviours similarly with offspring of the same age, independently of their sex, because they fulfil basic primary needs that cannot be neglected. Moreover, we did not find a significant effect of offspring sex (neither as main term nor in interaction with other terms) on the probability that mothers would groom or play with their offspring. Unlike many other primate species, however, it is possible that at least grooming has little importance for social interactions in spider monkeys, especially in females (Ahumada, 1992; Fedigan & Baxter, 1984; Klein & Klein, 1971; Schaffner & Aureli, 2005; Slater *et al.*, 2007; Symington, 1990).

Our findings provided partial support for our second prediction that socially more integrated mothers would invest more in philopatric sons than in nonphilopatric daughters compared with less integrated mothers. In particular, more central mothers were more likely to engage in body contact with their male offspring compared

with fewer central mothers, although we found no significant effect for other maternal behaviours. Maternal physical condition may mediate the link between maternal investment and offspring sex; healthier mothers invested more in sons than daughters in polygynous species (Trivers & Willard, 1973). Like physical condition, maternal dominance rank also may mediate the link between maternal investment and offspring's sex (Boesch, 1997; Symington, 1987). In male-philopatric chimpanzees, for instance, higher-ranking mothers invest more in sons than daughters, whereas the opposite is true for lower-ranking mothers (Boesch, 1997). However, other studies with chimpanzees show that lower-ranking mothers weaned their offspring later than higher-ranking ones, although the age of weaning was more variable for sons than daughters (Lonsdorf *et al.*, 2020). Higher-ranking females of black spider monkeys also preferentially invest in sons than daughters (Symington, 1987). Therefore, it is possible that other factors linked to maternal physical condition, such as rank and perhaps social integration, might have a similar mediating function on sex-biased maternal investment. This is not unlikely, because social integration may provide crucial fitness benefits to primates (Silk *et al.*, 2003, 2006, 2009, 2010), decreasing individual stress levels (Wittig *et al.*, 2016) and increasing others' tolerance over resources (Amici *et al.*, 2020; Dell'Anna *et al.*, 2020), so that more integrated individuals might also have better physical condition. Our results therefore provide evidence that socially more integrated mothers might invest more in sons than daughters, at least in terms of body contact, and suggest that maternal social integration might have a similar mediating function as physical condition (Trivers & Willard, 1973), modulating sex-biased investment in wild primates. Future studies should better disentangle the link between these variables (i.e., physical condition, rank, social integration) and (sex-biased) maternal investment and ideally also explore the mediating function that other factors might have, such as mothers' and offspring personality.

Finally, our study provided partial support for our third prediction that older mothers would be more likely than younger ones to bias their investment toward sons (Table D). As expected, older mothers were more likely to carry sons than daughters compared with younger ones. This is in line with a study in baboons, also showing that older mothers are more likely than younger ones to preferentially invest in sons (Packer *et al.*, 2000). Investing in males may provide mothers with crucial benefits in terms of fitness returns (Trivers & Willard, 1973), but only more experienced mothers may reliably do that (Fairbanks, 1996; Hooley, 1983; Hooley & Simpson, 1981; Packer *et al.*, 2000). In the future, it would be interesting to assess the role of maternal age and number of previous offspring separately, as maternal experience is likely to increase not only through age, but also proportionally to the number of offspring that mothers have. Moreover, the number of previous offspring could be an important indicator of maternal condition, affecting the time at which mothers wean their offspring (Eckardt *et al.*, 2016). In this study, it was unfortunately not possible to assess the role of maternal age and number of previous offspring separately, because there was a high correlation between these two variables.

Our study has several limitations. First, we only observed a few mother-offspring dyads over a short period of time. Longitudinal studies, including more dyads across more groups, will be necessary to confirm our preliminary

findings. In spider monkeys, moreover, behaviours like grooming happen at relatively low frequencies (Schaffner & Aureli, 2005), so that longer-term observations will be crucial to detect possible variation in these uncommon behaviours. Second, we did not include measures of maternal physical condition. Future studies should ideally include measures, such as C-peptide levels in urine as a proxy of energy balance (de la Torre *et al.*, 2021; Dias *et al.*, 2018), to assess whether physical condition might be a more reliable mediator than social integration in the relationship between offspring's sex and maternal investment, or at least include a visual assessment of maternal physical condition. Third, we recorded nursing every time an infant held the mother's nipple into the mouth. Although it reduces the ability of mothers to conceive again, implying direct costs for the mother (Brown, 2001), nipple contact does not necessarily imply that the offspring is actually obtaining milk, and direct measures of milk transfer might provide different results (Lonsdorf *et al.*, 2020; reviewed by Cameron, 1998; Mendl & Paul, 1989). In the same line, mothers may not only show sex-differences in the quantity of milk provided to offspring but also in its quality (Hinde, 2007, 2009). Therefore, even though we did not find any sex-differences in nursing patterns, finer-grained analyses are needed to rule out a sex-bias in lactational investment. Fourth, mothers in our study became gradually less likely to nurse, carry, and be in body contact with their offspring, possibly also as a result of younger siblings being born. Future studies should ideally separately assess the developmental patterns of maternal investment for offspring with and without younger siblings, specifically assessing how the birth of younger offspring affects maternal investment in older ones. Unfortunately, the limited number of dyads did not allow us to run these analyses. Finally, in our study, we assumed that maternal investment has costs for mothers, although we provided no direct assessment of these potential costs (Clutton-Brock, 1991; Trivers, 1972). Therefore, future studies should provide a direct assessment of maternal costs and ideally a longitudinal evaluation of the fitness benefits related to these behaviours (Bercovitch, 2002).

Overall, our study showed that some maternal behaviours are likely sex-biased in wild spider monkeys, despite an important mediating role of maternal experience and social integration. In particular, mothers preferentially invested in the philopatric sex, especially when they were socially more integrated (Prediction 2) and when they were more experienced (Prediction 3), although maternal investment largely decreased through immatures' development regardless of the offspring's sex (Prediction 1). Our study improves our understanding of patterns of sex-biased maternal investment in wild primates and the factors that may affect it, and therefore, it provides a significant contribution to the few existing studies on maternal investment in wild plathyrrines.

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