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Are male orangutans a threat to infants? Evidence of mother-offspring counterstrategies to infanticide in Bornean orangutans (Pongo pygmaeus wurmbii)

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ABSTRACT

Sexually selected infanticide by males is widespread in primates. Female primates employ a variety of strategies to reduce infanticide risk. While infanticide has never been directly observed in wild orangutans (*Pongo* spp), their slow life history makes infants vulnerable to infanticide. The mating strategies of female orangutans include polyandrous and post-conceptive mating which may serve to increase paternity confusion, an infanticide avoidance strategy. Here, we investigate whether female orangutans alter their social interactions with males as another infanticide avoidance strategy. We hypothesize that females with younger offspring avoid males and that the distance between mother and offspring decreases in the presence of males. We use long-term behavioral data collected between 1994 and 2016 from Bornean orangutans (*Pongo pygmaeus wurmbii*) in Gunung Palung National Park, Indonesia, to test whether the sexual selection hypothesis for infanticide helps explain aspects of orangutan social behavior. We found that mothers with offspring under six years old both encountered fewer males and spent less time with males during social interactions than did mothers with offspring over six years old and females without offspring. Additionally, the distance between a mother-offspring dyad showed a statistically significant decrease in the presence of males, but not females. Our results are consistent with the hypothesis that female orangutans employ strategies to reduce infanticide risk in their social interactions. Because orangutans have a high fission-fusion dynamic, they have flexibility in manipulating social interactions as a counter-infanticide strategy. Our results suggest that infanticide by males is a selective pressure shaping female orangutan social behavior.

KEYWORDS

great apes; male infanticide; sexual selection hypothesis; male avoidance; orangutan sociality

INTRODUCTION

Infanticide is the killing of an infant by an individual of the same species (Hrdy and Hausfater 1984). Infanticide committed by males is widespread across primate species, documented in the wild in 36 primate species and inferred in the wild in an additional 17 species (Alvarez et al. 2015; Gursky-Doyen 2011; Kane and Gnépa 2016; Palombit 2012; van Schaik 2000a). The widespread prevalence of infanticide in primates has necessitated its inclusion in socioecological models explaining patterns of primate sociality and group fission-fusion dynamics (Aureli et al. 2008; Janson 2000; Koenig et al. 2013; Sterck et al. 1997). Thus, the risk of infanticide plays a major role in determining social relationships in primates.

The sexual selection hypothesis for infanticide posits that members of one sex kill the offspring of their competitors to increase access to mates of the opposite sex (Hrdy 1979). Female primates' reproductive output is constrained by gestation and lactation, and male primates are typically the infanticidal sex (van Schaik 2000a). This hypothesis predicts that infanticidal males kill other males' offspring to return females to cycling and, as a consequence, increase infanticidal males' chances of siring offspring (Hrdy 1979, but see Bartlett et al. 1993; Sussman 1994 who questioned the limited dataset available at the time). Subsequent review of cases of infanticide by males across primates supports the sexual selection hypothesis by showing that infanticide significantly shortens the period of time it takes for a female to return to cycling and increases the odds that the infanticidal male has access to the female when she returns to cycling (van Schaik 2000a). Therefore, the age of the infant and the length of the period of lactational amenorrhea are critical in determining whether infanticide occurs (Hrdy 1979). The sexual selection hypothesis also predicts that males have a low probability of being the father of infants they kill (Hrdy 1979).

Life history and reproductive parameters make some species vulnerable to sexually selected infanticide (van Shaik 2000b; Lukas and Huchard 2014). Because infanticide is more common in mammalian taxa where the length of lactation is longer than the length of gestation, van Schaik (2000b) defines a vulnerable species as a species in which lactation is longer than gestation. Infanticide is only adaptive if it shortens the time it takes for a female to return to cycling. If gestation is longer than lactation and females can conceive immediately following the birth of offspring, then infanticide will not shorten the time that it takes a female to reproduce again (van Schaik 2000c). Likewise, in species with strict annual breeding season, males will not gain anything through killing infants, and infanticide is not predicted to occur (van Schaik 2000b). Across mammalian species, non-seasonal and non-annual breeding is most closely associated with the incidence of infanticide by males (Lukas and Huchard 2014). If breeding is seasonal, but the interbirth interval is longer than one year, then males will still gain by killing the infant, and infanticide may still be selected for (Palombit 2012). Additionally, high reproductive skew is also associated with infanticide in mammals (Lukas and Huchard 2014).

Females can employ a variety of strategies to reduce infanticide risk. Mating with multiple males is argued to be a counter-infanticide strategy (Hrdy 1979; van Schaik et al. 2004). Van Schaik et al. (1999) argue that female primates reduce infanticide risk by employing a mixed mating strategy which involves mating with multiple males to confuse paternity while concentrating mating with preferred males during the periovulatory period to increase the likelihood that a preferred male is the sire. Post-conceptive mating is part of this strategy because it confuses paternity by mating when females cannot become pregnant (van Noordwijk and van Schaik 2000). Sexually selected infanticide by males has also been proposed to shape maternal behavior in primate species (Palombit 2012). For instance, increased maternal aggression in response to new males has been documented in some primate species with low sexual dimorphism in body size (ring-tailed lemurs, *Lemur catta:* Ichino 2005; western tarsiers, *Tarsius bancanus*: Roberts 1994). “Males turnover” in vervets, *Chlorocebus pygerythrus,* was associated with increased maternal vigilance and protection (Fairbanks and McGuire 1987). Females may also form coalitions against intruder and immigrant males (blue monkeys, *Cercopithecus mitis*: Cords and Fuller 2010; Milne-Edward's sifaka, *Propithecus edwardsi*: Morelli et al. 2009; and red colobus, *Procolobus badius*: Starin 1994). In species with a high fission-fusion dynamic, females with vulnerable infants may avoid males (chimpanzees, *Pan troglodytes*: Matsumoto-Oda 1999; Otali and Gilcrest 2006). Females may also change social groups to reduce infanticide risk. Mothers may transfer with an evicted male (presumably the sire of the infant) (white-faced capuchins, *Cebus capucinus:* Fedigan and Jack 2009; purple-faced langur, *Semnopithecus vetulus*: Rudran 1973; Hanuman langur, *Semnopithecus entellus:* Hrdy 1977) or cycling females may transfer to a group with a stronger male (gorillas, *Gorilla* spp: Stokes et al. 2003, Yamagiwa et al. 2009; Robbins et al. 2009).

While there are no direct observations of infanticide in wild orangutans, many features of orangutan life history and reproduction make them potentially vulnerable to infanticide as a male reproductive strategy (van Schaik 2000b). One record of a captive male orangutan killing his own infant (Mallinson 1984) demonstrates that males are capable of killing infants. Additionally, infanticide is suspected in the disappearance of a 3-month old infant whose mother suffered an injury to her foot at the same time (Knott et al. 2019). The slow life history traits of orangutans are associated with vulnerability to infanticide (Lukas and Huchard 2014; van Schaik 2000b). They are non-seasonal breeders who have the longest interbirth interval, 7.6 years (van Noordwijk et al. 2018) of any primate (Galdikas and Wood 1990). They also have a much longer period of lactation, 5.75-7.5 years, (van Noordwijk et al. 2013) than gestation, approximately 8 months (Graham 1988). Orangutans are unique among apes in that offspring are beginning to develop independence when the next offspring is born because multiple offspring traveling with their mother is not the norm for this species (van Noordwijk and van Schaik 2005). It is not known whether orangutans have high male reproductive skew, which is associated with infanticide (Lukas and Huchard 2014). While there is high male-male competition in orangutans (Galdikas 1985b; Utami Atmoko et al. 2009; van Schaik and van Hooff 1996), the degree of male reproductive skew varies across studies (high reproductive skew: Banes et al. 2015; low reproductive skew: Goossens et al. 2006; Utami et al. 2002). Orangutans exhibit male bimaturism, in which there are two fully mature male morphs, flanged males and unflanged males. Flanged males are twice the size of unflanged males, who are the size of adult females and flanged males possess secondary sexual characteristics including an enlarged throat pouch, large check flanges, and the ability to produce long calls (Knott and Kahlenberg 2011).

Orangutan female mating strategies indicate that female orangutans employ infanticide avoidance strategies (Knott 2009; Knott et al. 2010; Stumpf et al. 2008). Females employ a mixed mating strategy, mating preferentially with flanged males during the periovulatory period and mating with unflanged males when the risk of conception is low (Knott et al. 2010; Stumpf et al. 2008). Bornean females display the most proceptive behaviors during the early stages of pregnancy (Knott et al. 2010). Furthermore, adult females with dependent offspring rarely associate with conspecifics (Rijksen 1978), and offspring seek out their mother after hearing playback recordings of unfamiliar males' long calls (Delgado 2003). There is mounting evidence that infanticide risk may be an important, albeit rare, event that influences behavior in female orangutans with young infants. However, additional tests of the female strategy of avoiding potentially infanticidal conspecifics are needed to assess infanticide risk in orangutans (Beaudrot et al. 2009).

Due to their semi-solitary social structure (Galdikas 1985a; Mitra Setia et al. 2009; van Schaik and van Hoof 1996), female orangutans may also employ the strategy of altering their social interactions to reduce infanticide risk. In this study we address the question of whether female orangutans with offspring employ the counter-infanticide strategy of avoiding potentially infanticidal males and further examine mother-offspring proximity in the presence of male conspecifics to determine whether the sexual selection hypothesis of infanticide helps explain aspects of social interactions in orangutans. Here, we analyze orangutan behavioral data collected between 1994 and 2016, to determine whether the behavior of mothers with vulnerable offspring is consistent with infanticide avoidance strategies. We predict that if males are a threat to infants, females with younger offspring who are vulnerable to infanticide will 1) encounter males less often and 2) spend less time in the presence of males than females with older offspring and females without dependent offspring. Since encounter rates and time in association may be driven by either infanticide avoidance or mating interest, we also examine how the distance between mother and dependent offspring changes in the presence of males. We predict that if males represent a threat to offspring, mother-offspring dyads will react to the presence of males by decreasing the distance between the mother-offspring dyad. By contrast, we predict no change in distance between mother and offspring in the presence of female conspecifics.

METHODS

Study Site and Population

We conducted our study in the Cabang Panti Research Site in Gunung Palang National Park, West Kalimantan, Borneo, Indonesia (1°13´S, 1107´E). The wild orangutan (*Pongo pygmaeus wurmbii*) population in the park constitutes approximately 2500 individuals (Johnson et al. 2005). The field site consists of primary rainforest and contains a mosaic of habitats (Marshall et al. 2009; Marshall et al. 2014). No former captives have been released in the park. Orangutans in the study site are habituated to human presence, although unhabituated individuals do travel through the study site. We analyzed data collected from 1994-2003 and from 2008-2016. The break in data collection occurred when the field site was closed due to the threat of illegal logging.

Data Collection

We collected behavioral data during full day focal follows of habituated adolescent and adult female orangutans (Table 1). While we collected focal data only on habituated individuals, our focal animals did encounter or associate with unhabituated orangutans. We classified orangutans as in a social interaction when they were within 50 meters of each other (Mitani et al. 1991; Knott et al. 2008). We recorded the presence of conspecifics and social interactions using all-occurrence sampling (Altmann 1974). We classified females into maternal status categories based on the presence or absence of an offspring and the age in years of the youngest accompanying offspring (Table 1). We estimated offspring ages based on known conception or birth date approximations or through observations by experienced field assistants. Females without offspring include both nulliparous and parous females.

Fruit Availability

Because fruit availability impacts many aspects of orangutan behavior (Knott and Kahlenberg 2011), we controlled for fruit availability in our analyses. We calculated fruit availability as the mean monthly kilocalories available to orangutans following the method outlined in Knott (2005) and Emery Thompson and Knott (2008). We calculated Z-scores from the mean monthly kilocalories of fruit available.

Encounter Rates

To test the prediction that females with younger offspring will encounter males less often, we examined full day follows of independent females from September 1994 through April 2003 and November 2008 through December 2016 (N_{days} = 2721; $N_{females}$ = 98). Encounters can last from a few minutes to an entire day. We also examined whether male morph played a role in encounter rates by considering only the encounters that occurred (N_{days}=544; $N_{females}$=47). From this dataset of encounters, we compared the proportion of flanged and unflanged males encountered by females based on their maternal status. If male morph does not impact encounter rates, we would expect that all female categories encounter both male morphs in the same proportion. We compared female maternal categories to each other, we did not examining absolute encounter rates of flanged vs unflanged males, thus we do not control for the proportion of flanged to unflanged males in the study population.

Time in Association

To test the prediction that females with younger infants spend less time associated with males, we examined the minutes per day that females spent in association with one or more males from September 1994 through April 2003 and November 2008 through December 2016. We only considered full day follows of independently-ranging females who encountered one or more males for these analyses ($N=454_{days}$, $N_{females}=43$).

Mother-Offspring Distance

We recorded the distance between mother and offspring at 5 minute intervals throughout focal follows. For this analysis we examined days from September 1994 through April 2003 and November 2008 through December 2016 in which mother-offspring dyads were alone for a portion of the day and within 50 meters of conspecifics for a portion of the day ($N_{days}=194$, $N_{dyads}=24$). We compared the mean distance between the mother-offspring dyad when they were alone, when they associated with male conspecifics (flanged and unflanged males) ($N_{days}=115$, $N_{dyads}=19$), and when they associated with female conspecifics (adolescent females and adult females with or without dependent offspring) ($N_{days}=79$, $N_{dyads}=19$). We excluded any females who were known to be related to the mother-offspring dyad from this analysis, although we cannot rule out the possibility that the mothers' sisters or nieces were included as female conspecifics in this dataset. We did not include data when young infants (under 6 months) maintained constant contact with the mother. We included partial day follows when orangutans were found after leaving the nest (N=20), but we excluded follows in which the focal was lost while in association because these social distance data were incomplete.

Statistical Analysis

To investigate the most meaningful way to categorize females for the encounter rate analysis, we preformed pairwise comparisons of proportions to test whether total male, flanged male, and unflanged male encounter rates differed across five female maternal status categories: mothers with offspring ages 0 to 2 years, mothers with offspring ages 2 to 4 years, mothers with offspring ages 4 to 6 years, mothers with offspring over age 6 years, and females without offspring. We used the Holm-Bonferonni correction in the pairwise comparisons of proportions to reduce type I errors associated with multiple pairwise tests (Holms 1979). To investigate the most meaningful way to categorize females for the analysis of the amount of time that females spend in association with males, we preformed Tukey-Kramer (Nemenyi) test for pairwise comparisons to compare time spent associated with males across the same five maternal status categories. This test corrects for type 1 errors associated with multiple comparisons and uses a chi-square distribution when ties are present (Pohlert 2014). In the models and data visualizations, we grouped together maternal status categories which were not statistically significantly different from each other.

We used a binomial generalized linear mixed model (GLMM) to test whether the presence and age of offspring predicted whether a female encountered a male. Data exploration and model residuals revealed no violations of the assumptions of the GLMM. The response variable was presence or absence of an encounter with one or more males. Due to the binomial nature of the encounter data, we reported descriptive statistics of the encounter rate (median and range) among females, for only females with five or more follow days (N_{days}=2644, $N_{females}$=33). From the subset of the data in which encounters did occur, we used two binomial GLMMs to test whether presence and age of offspring predicted whether the encounter was with a flanged or unflanged male. Because there were some encounters in which male type was not recorded, we ran two binomial GLMMs, one in which the response variable was whether or not the male encountered was known to be flanged and one in which the response variable was whether or not the male encountered was known to be unflanged. For each binomial GLMM, we included the identity of the female focal as a random effect, and we included fruit availability as a control variable in the model. For each binomial GLMM we used a likelihood ratio test to compared the full model to the null model, which uses only the random and control variables as predictors (Dobson and Barnett 2008; Forstmeier and Schielzeth 2011). Due to the binomial nature of the encounter data, we reported descriptive statistics (median and range) of the proportion of flanged and unflanged males encountered, only for females with four or more encounters (N_{days}=472, $N_{females}$=27).

We used a linear mixed model (LMM) to analyze whether male type and the presence and age of offspring predicted the number of minutes that a female spent associated with a male. The response variable, minutes of association, was log transformed to fit the distribution assumptions of the model. Data exploration and model residuals revealed no violations of the assumptions of the LMM. We included the identity of the female focal as a random effect and fruit availability as a control variable in the model. We used a likelihood ratio test to compare the full model to the null model, which uses only the random and control variables as predictors (Dobson and Barnett 2008; Forstmeier and Schielzeth 2011). We report descriptive statistics (median and range) of the mean time spent with males among females.

To test the prediction that the distance between mother and offspring differs in the presence of a conspecific we ran one-tailed Wilcoxon matched pair tests to test whether the mean distance between a mother-offspring dyad was shorter when they were alone compared to when they were in the presence of a conspecific (male or female) within the same day. We used a Kruskal-Wallis test and post-hoc Tukey-Kramer (Nemenyi) test for pairwise comparisons to compare the mean distance between mother and offspring when they were alone, with female conspecifics, and with flanged and unflanged male conspecifics. This posthoc test corrects for type 1 errors associated with multiple comparisons (Pohlert 2014). For posthoc tests, when ties were present, the chi-square distribution was used (Pohlert 2014).

We used a linear mixed model (LMM) to assess the significance of conspecific presence (no conspecific, female, flanged male, unflanged male, and unknown male morph) on the mean distance (meters) between a mother-offspring dyad. We transformed the response variable, by adding 1 and log transforming that value, to fit distribution assumptions of the model. Data exploration and model residuals revealed no violations of the assumptions of the LMM. We included the identity of the mother-offspring dyad as a random effect, and we included fruit availability and offspring age (in days) as control variables in the model. We used a likelihood ratio test to compare the full model to the null model (Dobson and Barnett 2008; Forstmeier and Schielzeth 2011). We report descriptive statistics (median and range) on the mean distance among mother and offspring dyads.

We performed all statistical procedures in R (R Core Team 2018). For the nonparametric post-hoc tests, we used in the package PMCMR (Pohlert 2014). For the binomial GLMMs, we used the package lme4 (Bates et al. 2011), and for the LMMs we used the package lmerTest (Kuznetsova et al. 2018).

Data Availability

The datasets generated during and/or analyzed during the current study are available from the authors on reasonable request.

Ethical Note

This study was non-invasive and observational. All protocols were approved by the Standing Committee on the Use of Animals in Research and Teaching at Harvard University (Protocol no. 95-04), Boston University IUCAC (protocol no. 11-045 and 14-043), or deemed exempt by Boston University IUCAC. All protocols were approved by Indonesian government authorities.

RESULTS

Encounter rates

The pairwise comparisons of proportions showed that for total male encounter rates, maternal status categories grouped together into three categories: females without offspring, females with offspring under 6 years old, and females with offspring over 6 years old (Table S1). The full binomial GLMM, assessing the effect of maternal status category on male encounter rates was statistically significantly different from the null model (ANOVA: $\chi^2 = 89.65$, df = 2, $P<0.001$) (Table 2). The proportion of days in which females with offspring under 6 years old encountered males ($N_{females} = 26$, median = 0.096 days, range = 0–0.4 days) was statistically significantly lower than the proportion of days in which females with offspring over 6 years old ($N_{females} = 12$, median = 0.310 days, range=0–1.0 days) and females without offspring ($N_{females}=14$, median=0.143 days, range=0–0.8 days) encountered males (Fig. 1).

Table S1 P values of pairwise comparisons of female encounter rates with males across maternal status categories of female Bornean orangutans at Gunung Palung National Park (data collected from September 1994 through April 2003 and November 2008 through December 2016). Significant p values are shown in *italics*.

	Mother with infant 0 to 2 years old	Mother with infant 2 to 4 years old	Mother with infant 4 to 6 years old	Mother with infant over 6 years old
Mother with infant 2 to 4 years old	1.000			
Mother with infant 4 to 6 years old	0.062	0.062		
Mother with infant over 6 years old	*<0.001*	*<0.001*	*<0.001*	
Non-mother	*<0.001*	*<0.001*	*0.048*	*<0.001*

Table 2 Results of GLMM testing influence of offspring presence and age on male encounter rates for female Bornean orangutans at Gunung Palung National Park (data collected from September 1994 through April 2003 and November 2008 through December 2016). Random effects standard deviation = 0.808.

	Estimate	SE	95% Confidence Interval	P value
(Intercept)	*-1.911*	0.203	0.503; 1.282	<0.001
Predictor Variables:				
Non-Mother[a]	*0.875*	0.232	0.462; 1.341	<0.001
Offspring Over 6 years[a]	*1.370*	0.150	1.127; 1.709	<0.001
Control Variables:				
Fruit Availability	*0.339*	0.047	0.244; 0.430	<0.001

[a] Reference category: Offspring Under 6 years

Significant effects are shown in *italics*

SE standard error

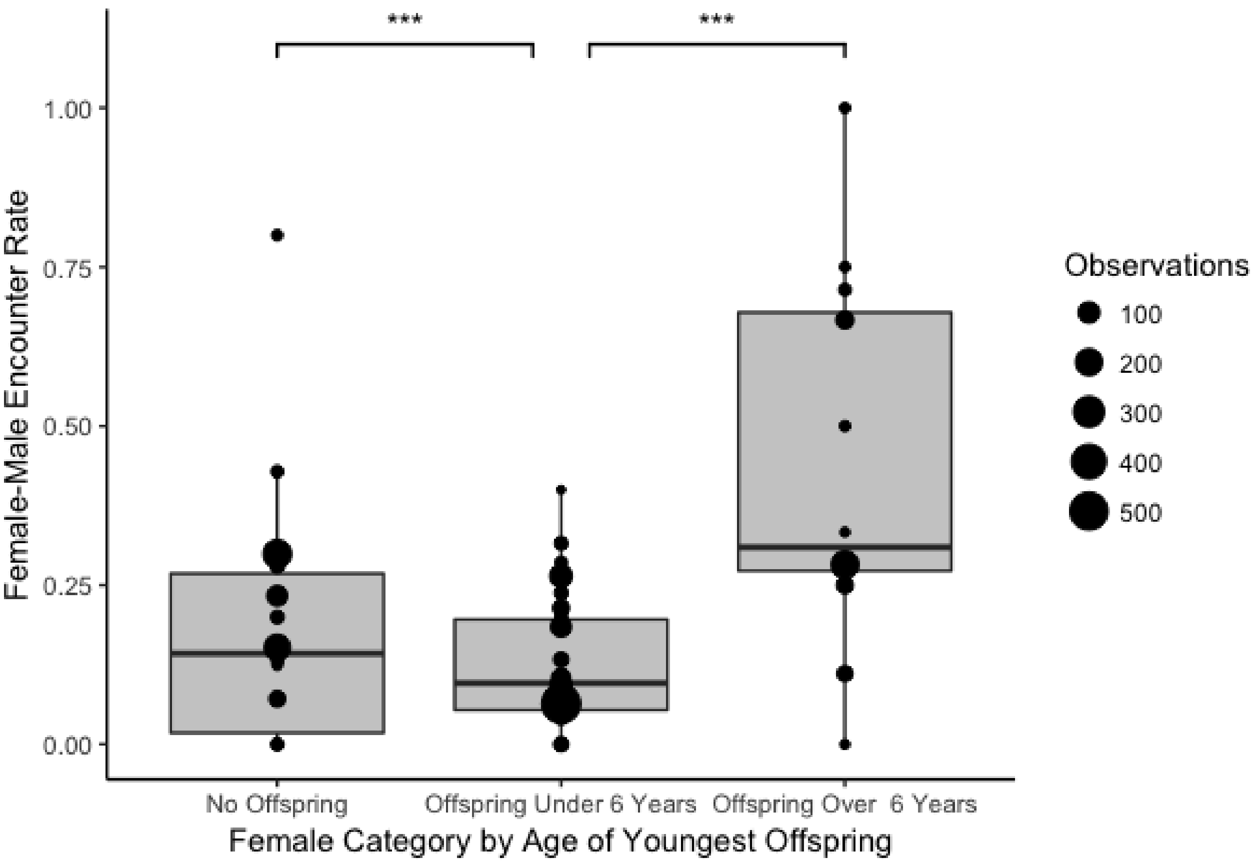

Fig. 1 Male encounter rates by maternal status category of Bornean orangutans at Gunung Palung National Park (data collected from September 1994 through April 2003 and November 2008 through December 2016). Boxplots are based on individual female encounter rates for females who had five or more full-day observation days. For each boxplot, the middle line represents the median, the box represents the interquartile range (IQR), the whiskers represent all values that are within 1.5 x IQR, and outliers are plotted individually. The size of the dot shows the number of observation days. Significance values are from a GLMM (*** = P<0.001).

The pairwise comparisons of proportions revealed that for flanged and unflanged male encounter rates, maternal status categories should be grouped together into 3 categories: non-mothers, mothers with offspring ages 0-4 years and over 6 years, and mothers with offspring ages 4-6 years (Table S2 and S3). The full binomial GLMM, assessing the effect of female maternal status category on the proportion of male encounter rates that are with flanged males was statistically significantly different from the null model (ANOVA: $\chi^2 = 26.651$, df = 2, $P<0.001$) (Table 2). The proportion of male encounters that were with flanged males was statistically significantly lover for females with offspring ages 4-6 years old ($N_{Females} = 5$, median = 0.125 encounters, range = 0–0.313 encounters) than the proportion of male encounters that were with flanged males for females with offspring ages 0-4 and over 6 years ($N_{Females} = 15$, median = 0.405 encounters, range = 0.167–0.839 encounters) and females without offspring ($N_{Females} = 7$, median = 0.483 encounters, range = 0–0.778 encounters). Likewise, the full binomial GLMM, assessing the effect of female maternal status category on the proportion of male encounter rates that are with unflanged males was statistically significantly different from the null model (ANOVA: $\chi^2 = 25.787$, df = 2, $P<0.001$) (Table 2). The proportion of male encounters that were with an unflanged male was statistically significantly higher for females with offspring ages 4-6 years old ($N_{Females} = 5$, median = 0.750 encounters, range = 0.563–1.0 encounters) than the proportion of male encounters that were with an unflanged male for females with offspring ages 0-4 years and over 6 years ($N_{Females} = 15$, median = 0.568 encounters, range = 0.100–0.833 encounters) and females without offspring ($N_{Females} = 5$, median = 0.500 encounters, range = 0.318–1.0 encounters).

Table S2 P values of pairwise comparisons of proportion of male encounters that are with a flanged male across maternal status categories of Bornean orangutans at Gunung Palung National Park (data collected from September 1994 through April 2003 and November 2008 through December 2016). Significant p values are shown in *italics*.

	Mother with infant 0 to 2 years old	Mother with infant 2 to 4 years old	Mother with infant 4 to 6 years old	Mother with infant over 6 years old
Mother with infant 2 to 4 years old	1.000			
Mother with infant 4 to 6 years old	*0.006*	*0.017*		
Mother with infant over 6 years old	1.000	1.000	*<0.001*	
Non-mother	0.595	1.000	0.078	0.196

Table S3 P values of pairwise comparisons of proportion of male encounters that are with an unflanged male across maternal status categories of Bornean orangutans at Gunung Palung National Park (data collected from September 1994 through April 2003 and November 2008 through December 2016). Significant p values are shown in *italics*.

	Mother with infant 0 to 2 years old	Mother with infant 2 to 4 years old	Mother with infant 4 to 6 years old	Mother with infant over 6 years old
Mother with infant 2 to 4 years old	0.781			
Mother with infant 4 to 6 years old	*0.001*	*0.034*		
Mother with infant over 6 years old	1.000	1.000	*0.001*	
Non-mother	0.112	1.000	0.112	0.117

Table 3 Results of GLMMs testing the influence of maternal status category on whether a male encountered was a flanged male or an unflanged male by female Bornean orangutans at Gunung Palung National Park (data collected from September 1994 through April 2003 and November 2008 through December 2016). Random effects standard deviation for flanged males = 0.672. Random effects standard deviation for unflanged males = 0.780.

	Estimate	SE	95% Confidence Interval	P value
Outcome: Male Encountered is Flanged				
(Intercept)	*-1.937*	0.426	-2.827; -1.141	<0.001
Predictor Variables:				
Non-Mother[a]	*1.394*	0.498	0.419; 2.401	0.005
Mother with offspring ages 0-4 or over 6 years[a]	*1.905*	0.410	1.137; 2.756	<0.001
Control Variables:				
Fruit Availability	-0.062	0.081	-0.222; 0.097	0.447
Outcome: Male Encountered is Unflanged				
(Intercept)	*1.734*	0.421	0.941; 2.604	<0.001
Predictor Variables:				
Non-Mother[a]	*-1.504*	0.499	-2.517; -0.538	0.003
Mother with offspring ages 0-4 or over 6 years[a]	*-1.868*	0.393	-2.671; -1.122	<0.001
Control Variables:				
Fruit Availability	0.048	0.084	-0.118; 0.213	0.571

[a] Reference category: Mother with offspring ages 4-6 years

Significant effects are shown in *italics*

SE standard error

Time Spent in Association

The pairwise comparisons of time spent in association with males across the five maternal status categories showed that maternal status categories grouped together into three categories: females without offspring, females with offspring under 6 years old, and females with offspring over 6 years old (Table S4). On days when a female orangutan encountered one or more males, they spent a median of 170 ± SD 254 minutes associated with males (range: 1-830 minutes). The full linear mixed model (LMM), assessing the effect of maternal status category and male morph on the time that females spent associated with males was statistically significantly different from the null model (ANOVA: $\chi^2 = 48.359$, df = 5, $P<0.001$). Females with offspring under 6 years old ($N_{females} = 25$, median = 118 minutes, range=22–684 minutes) spent statistically significantly less time with males than females with offspring over 6 years old ($N_{females} = 12$, median = 287.38 minutes, range=75–641 minutes), and there was no difference in time spent with males between females without offspring ($N_{Ffmales} = 21$, median = 238.67 minutes, range=21–653 minutes) and females with offspring over 6 years old (Table 5). There was no difference in time spent with flanged versus unflanged males, but when multiple males were present at the same time, females associated with males for a statistically significantly longer time than when only a flanged male was present (Table 4).

Table S4 P values of pairwise comparisons time (minutes) spent with males across maternal status categories of Bornean orangutans at Gunung Palung National Park (data collected from September 1994 through April 2003 and November 2008 through December 2016). Significant p values are shown in *italics*.

	Mother with infant 0 to 2 years old	Mother with infant 2 to 4 years old	Mother with infant 4 to 6 years old	Mother with infant over 6 years old
Mother with infant 2 to 4 years old	0.998			
Mother with infant 4 to 6 years old	0.837	0.637		
Mother with infant over 6 years old	*0.003*	*0.003*	*<0.001*	
Non-mother	*0.021*	*0.025*	*<0.001*	0.924

Table 4 Results of LMM testing influence of male type and offspring presence and age on time that females spend in association with males in Bornean orangutans at Gunung Palung National Park (data collected from September 1994 through April 2003 and November 2008 through December 2016). Random effects standard deviation = 0.256.

	Estimate	SE	95% Confidence Interval	P value
(Intercept)	*5.443*	0.187	5.081; 5.807	<0.001
Predictor Variables:				
Offspring Under 6[a]	*-0.739*	0.165	-1.070; -0.419	<0.001
No Offspring[a]	-0.359	0.234	-0.825; 0.099	0.129
Multiple Males[b]	*0.793*	0.278	0.252; 1.336	0.005
Unflanged Male[b]	0.089	0.135	-0.172; 0.356	0.508
Unrecorded Males type[b]	*-0.766*	0.231	-1.224; -0.319	<0.001
Control Variables:				
Fruit Availability	0.052	0.052	-0.051; 0.153	0.319

[a] Reference category: Offspring Over 6

[b] Reference category: Flanged Male

Significant effects are shown in *italics*

SE standard error

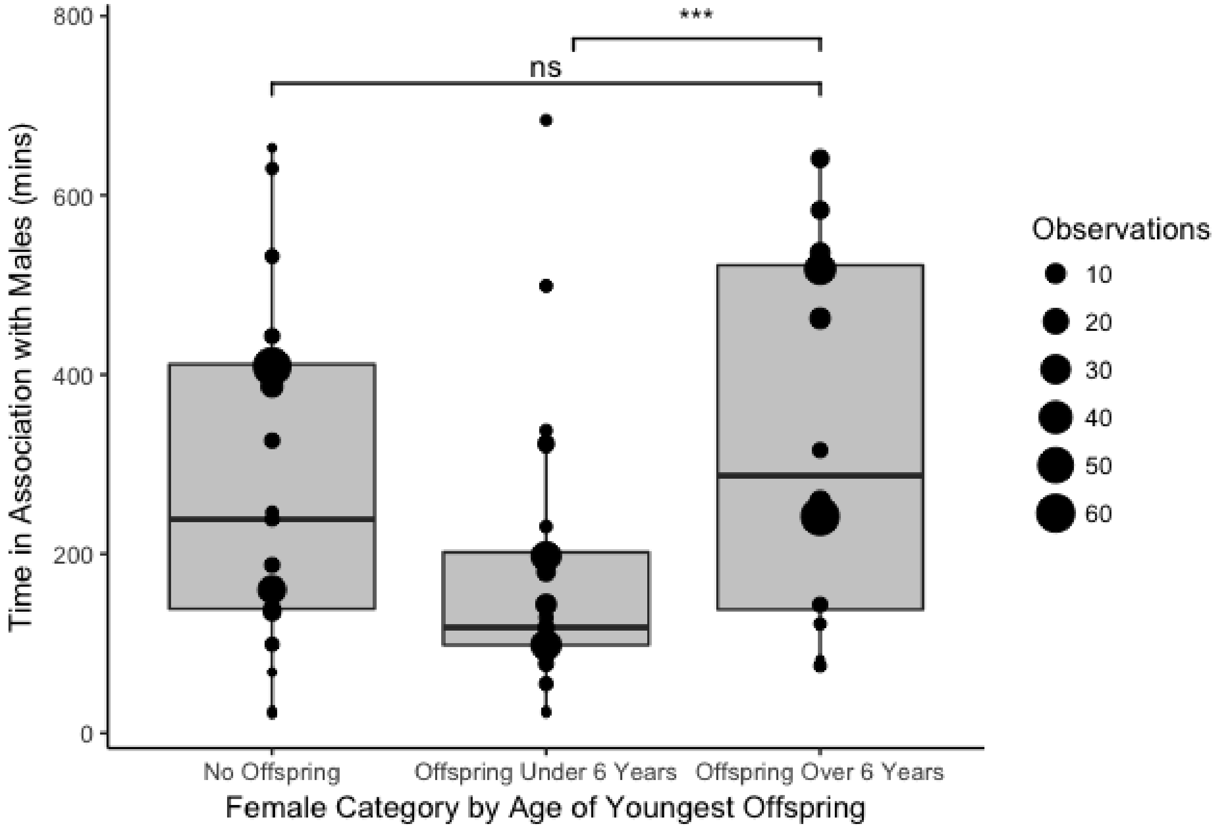

Fig. 2 Time spent in association with males by maternal status category of Bornean orangutans at Gunung Palung National Park (data collected from September 1994 through April 2003 and November 2008 through December 2016). Boxplots are based on individual female means. For each boxplot, the middle line represents the median, the box represents the interquartile range (IQR), the whiskers represent all values that are within 1.5 x IQR, and outliers are plotted individually. The size of the dot shows the number of observation days for each female. Significance values are from a LMM (ns= $P>0.05$, *** = $P<0.001$).

Mother-Offspring distance

The distance between a mother-offspring dyad significantly decreased in the presence of male conspecifics (One-tailed Wilcoxon Matched Pair Test: $V=639$, $P<0.001$, $N=115$) (Fig. 3a), but did not decrease in the presence of a non-related female conspecific (V=1352.5, P=0.2845, N=79). (Fig. 3b). The presence of both flanged and unflanged males was associated with a decrease in distance between the mother-offspring dyad (Kruskal-Wallis: $\chi^2 = 36.587$, df = 3, P<0.001, N=382) (Fig. 4). Our full LMM, assessing the effect of conspecific type on the distance between mother and offspring, was statistically significantly different from the null model (ANOVA: $\chi^2 = 102.09$, df=4, p<0.001). When controlling for offspring age and fruit availability, the mean distance between mother and offspring ($N_{dyads} = 19$, median = 1.95 m, range=0–12.5 m) was statically significantly shorter when males were present than when the mother-offspring dyad was alone ($N_{dyads} = 25$, median = 3.16 m, range=0.3–13.18 m). When controlling for offspring age and fruit availability, the mean distance between mother and offspring did not change when non-related females were present ($N_{dyads} = 19$, median = 2.48 m, range = 0.8–26.6m) compared to when the mother-offspring dyad was alone (Table 5; Fig. 5).

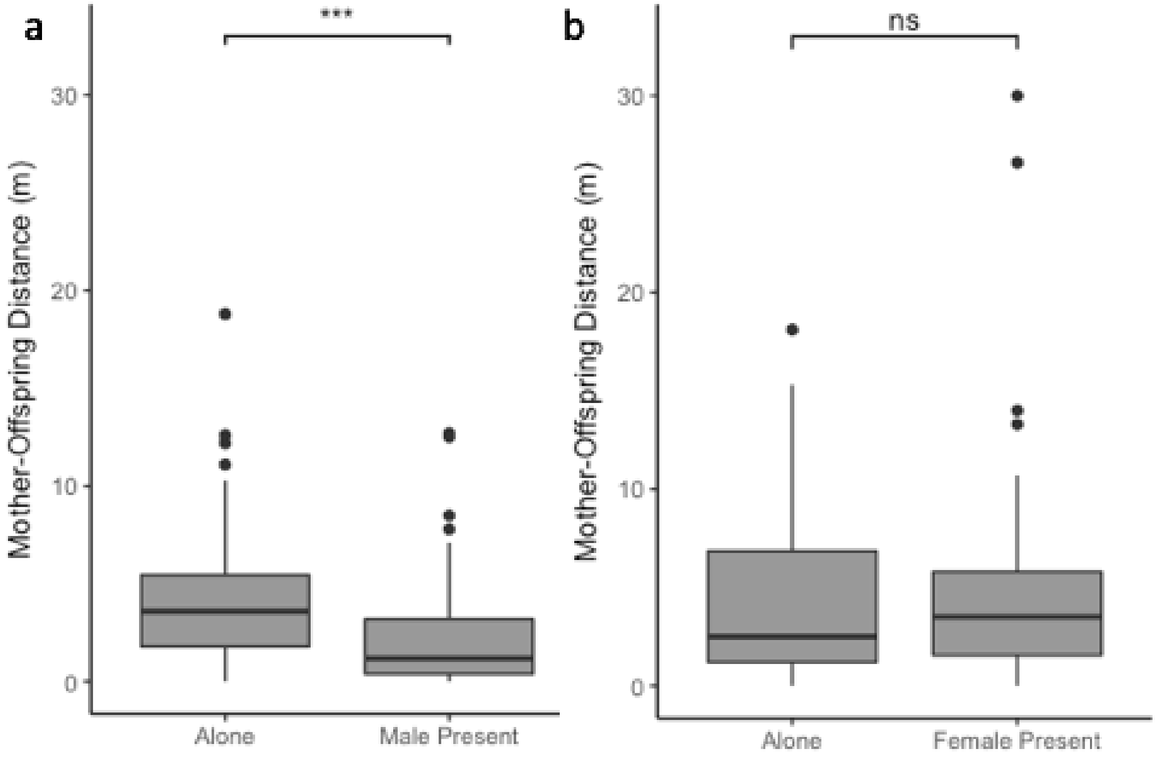

Fig. 3 Matched comparisons of the distance between mother and offspring dyads during the same day when the dyad was alone and in the presence of **a.** a male conspecific (***=P<0.001) or **b.** a female conspecific in Bornean orangutans at Gunung Palung National Park (data collected from September 1994 through April 2003 and November 2008 through December 2016). Boxplots are based on the mean distance between a mother-offspring dyad, when a conspecific was and was not present within the same day. For each boxplot, the middle line represents the median, the box represents the interquartile range (IQR), the whiskers represent all values that are within 1.5 x IQR, and outliers are plotted individually.

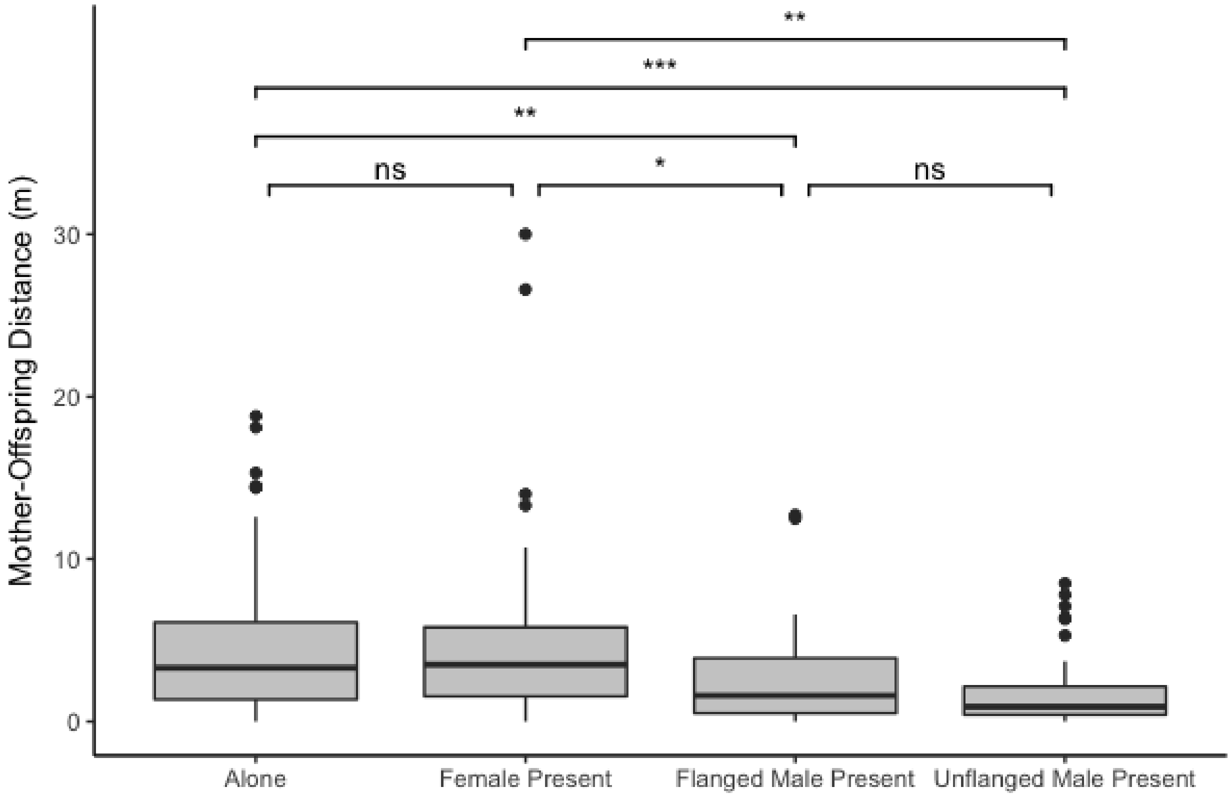

Fig. 4 Comparison of distance between mother-offspring dyad in different social associations in Bornean orangutans at Gunung Palung National Park (data collected from September 1994 through April 2003 and November 2008 through December 2016). (ns= P>0.05, *= P<0.05, **=P<0.01, ***=P<0.001) Alone: N=194; Female: N=70; Flanged: N=65; Unflanged: N=47. Boxplots are based on the mean daily distance between a mother-offspring dyad, when a conspecific was or was not present. For each boxplot, the middle line represents the median, the box represents the interquartile range (IQR), the whiskers represent all values that are within 1.5 x IQR, and outliers are plotted individually.

Table 5 Results of a LMM of the factors effecting the mean distance between a mother and offspring in Bornean orangutans at Gunung Palung National Park (data collected from September 1994 through April 2003 and November 2008 through December 2016).

	Estimate	SE	95% Confidence Interval	P value
(Intercept)	0.176	0.112	-0.043; 0.393	0.119
Predictor Variables:				
Female Present[a]	-0.040	0.063	-0.163; 0.082	0.512
Flanged Male Present[a]	*-0.344*	0.067	-0.475; -0.212	<0.001
Unflanged Male Present[a]	*-0.687*	0.077	-0.838; -0.536	<0.001
Male Type Unknown Present[a]	*-1.394*	0.277	-1.933; -0.852	<0.001
Control Variables:				
Offspring age (days)	*0.001*	0.0001	0.0007; 0.0009	<0.001
Fruit Availability	*-0.054*	0.021	-0.094; -0.014	0.009

[a] Reference category: Mother-Offspring Dyad Alone

Significant effects are shown in *italics*

SE standard error

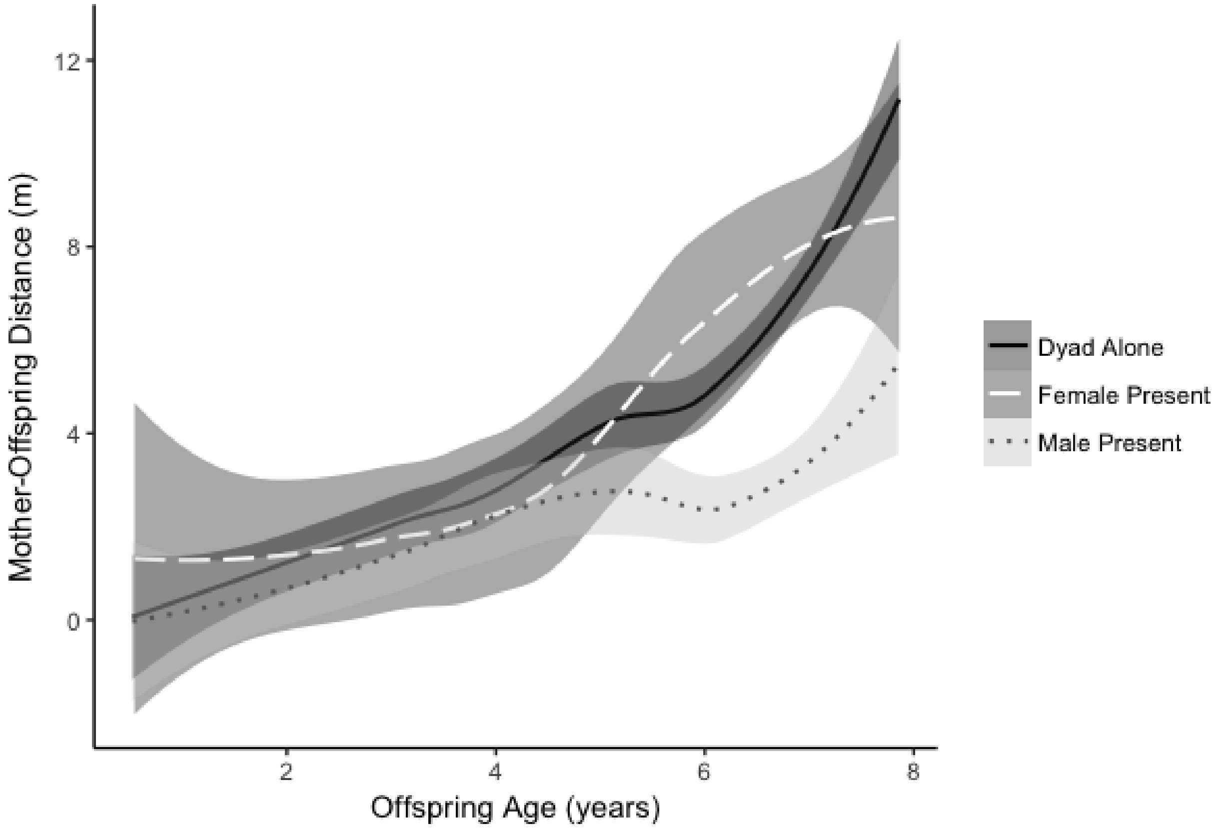

Fig. 5 Predicted distance between mother-offspring dyad in different social associations in Bornean orangutans at Gunung Palung National Park (data collected from September 1994 through April 2003 and November 2008 through December 2016). Dyad Alone: N=194; Female Present: N=70; Male Present: N=115. Lines represent the smoothed conditional mean distance values using the loess method. Shading represents standard error.

DISCUSSION

Our results show that presence or absence of dependent offspring and the age of dependent offspring impact the interactions of female Bornean orangutan with males. The long interbirth interval of orangutans creates a long period during which offspring are potentially vulnerable to infanticide. Consistent with our predictions, our results show that mothers with offspring under 6 years old encounter males less often than mothers with offspring over 6 years old and females without dependent offspring. Mothers with offspring under 6 years old also spend less time with males than mothers with offspring over 6 years old. Since the mean orangutan interbirth interval is 7.6 years (van Noordwijk et al. 2018) and gestation is approximately 8 months (Graham 1988), it is not surprising that mating effort would increase when offspring reach 6 years old, as the mother's fecundity is expected to be increasing and offspring vulnerability will also be decreasing. This difference in encounter rates and time spent in association with males may be due to infanticide avoidance behavior or an increase in mating effort by males and/or females. Female chimpanzees, show similar patterns of gregariousness, with higher levels of gregariousness in cycling females compared to lactating females and non-mothers compared to mothers (Matsumoto-Oda 1999; Otali and Gilcrest 2006; Sakura 1994). Lactating female chimpanzees specifically avoid groups with males but not with other lactating females (Sukura 1994). Among the Kanyawara chimpanzee community, the probability of associating with a male increased with increasing offspring age (Otali and Gilcrest 2006). Further analysis of initiators and terminators of orangutan interactions could be used to distinguish whether these differences are due to mating effort or infanticide avoidance by female orangutans.

Additionally, the distance between mother and offspring when they are alone compared to when they are with conspecifics can aid in distinguishing between whether mating effort or infanticide avoidance is driving the change in encounter rates and time spent in association with males. Consistent with our predictions, our results show that mother-offspring dyads respond to the presence of males, but not unrelated females, in a protective manner by decreasing the distance between mother and offspring. Because it has been suggested that unrelated females pose a threat to female orangutans and their infants (Marzec et al. 2016; van Noordwijk et al. 2012), we excluded females who are known relatives of the mother-offspring dyad. Even when considering only non-related females, mother-offspring dyads did not react to the presence of females in a protective manner, they only reacted to the presence of males in a protective manner. In Kanyawara chimpanzees, where males commit infanticide, the distance between mother and offspring is shorter when males are present compared to when mother-offspring dyads are alone or with conspecific females (Otali and Gilcrest 2006). Not surprisingly, our results showed that the distance between mother and offspring increases as offspring age and develop independence. Yet even as offspring age, the distance between the mother-infant dyad continues to decrease in the presence of males as long as offspring continue traveling with their mother. This indicates that mothers and offspring perceive males as a threat, but our data do not allow us to distinguish whether it was the mother and/or the offspring who decreased this distance when males were present. In the presence of new males, who present a potential infanticide threat, vervet mothers, but not infants, alter their behavior in a protective manner, increasing both contact initiation and restraint of infants (Fairbanks and McGuire 1987). Future studies should examine proximity maintenance, contact initiation and termination, and infant restraint in orangutans to determine whether the mother or offspring is responsible for the change in proximity in the presence of males.

Mothers and offspring dyads shortened the distance between themselves in the presence of both flanged and unflanged males, suggesting that both male morphs are treated as a potential threat. Male morph did not affect the time that females spent associating with males but it did impact encounter rates. Given that an encounter occurred, females of different maternal status categories encountered flanged and unflanged males at different rates. This difference was driven by the category of mothers with offspring ages 4 to 6 years, who encountered a lower proportion of flanged males and a higher proportion of unflanged males compared to the other female categories. This finding may be driven by male competition and female attractivity. The mothers in the category “mothers with offspring age 4 to 6 years” are approaching the time when they are ready to conceive again, although their monthly probability of conception is still low. If flanged males have limited energy to devote to mating (Knott and Emery Thompson 2013), they are unlikely to concentrate mating effort with these females who are unlikely to conceive. Since flanged males have priority of access to females (Fox 2002), unflanged males may monitor these females (with offspring ages 4 to 6 years) to take advantage of this mating opportunity if flanged males are not interested in these females.

While infanticide has never been directly observed in orangutans, our results are consistent with the hypothesis that females employ the infanticide counterstrategy of avoiding males. It has been argued that due to unpredictable food availability, polyandrous mating, and a dispersed social system infanticide is not an adaptive male strategy in orangutans because the likelihood that an infanticidal male orangutan will sire the next offspring is not greater than the likelihood that he sired the current offspring (Beaudrot et al. 2009). Yet, sexual selection theory suggests that orangutan males would benefit from infanticide (Delgado 2003; Delgado and van Schaik 2000; van Schaik and Kappeler 1997). Additionally, female orangutans employ mating strategies that are consistent with infanticide avoidance (Knott et al. 2010; Stumpf et al. 2008). Infanticide is extremely costly for females, so even a low-level threat can shape female behavior. The reproductive and energetic cost of losing an infant may be even higher in orangutans than other primates due to the long interbirth interval (Galdikas and Wood 1990; Knott 2009; van

Noordwijk et al. 2018) and supra-annual fluctuations in fruit availability due to mast fruitings (Ashton et al. 1998; Medway 1972; van Schaik 1986). The unpredictable environment means that it may be longer before female energy balance and corresponding ovarian hormone levels (Knott 1998) allow a female to become pregnant again. Low infant mortality in orangutans (van Noordwijk et al. 2018; Wich et al. 2004) means that if infanticide occurs it must be rare. Nevertheless, the large reproductive cost attached to infanticide predicts that mothers and offspring will employ behaviors to avoid infanticide when infanticide is an adaptive male strategy (Treves 2000). Our results provide evidence that female orangutans employ the infanticide counterstrategies of altering their social behavior to avoid males and increased protection in the presence of males.

Taken together, our results are consistent with the hypothesis that the threat of infanticide by males affects aspects of female orangutan social behavior, including female-male encounter rates, the length of social interactions with males, and mother-offspring proximity during a social interaction. Infanticide risk is hypothesized to shape primate group structure influencing both the existence of long-term male-female associations (Sterck et al. 1997) and flexibility in group size, composition and cohesiveness (Aureli et al. 2008). For instance, it has been argued that infanticide threat is the reason that mountain gorillas and Thomas langurs are group-living because females group themselves around protective males (Sterck et al. 1997). Due to the lack of long-term male-female associations, female orangutans employ different strategies to reduce the risk of infanticide compared to female primates who live in groups with males. This may be similar to the observation that female chimpanzees with young offspring are less gregarious than cycling females (Matsumoto-Oda 1999; Nishie & Nakamura, 2018; Otali and Gilcrest 2006; Pusey et al. 2008; Sakura 1994). Protecting offspring from potentially infanticidal male and female chimpanzees has been suggested as the reason that female chimpanzees with dependent offspring are less gregarious than females without dependent offspring (Nishie & Nakamura, 2018; Otali and Gilcrest 2006; Pusey et al. 2008). Orangutans provide another example of how a high fission-fusion dynamic allows mothers to alter social interactions, which may serve to protect infants from potentially infanticidal males. Although infanticide may be extremely rare in orangutans, the potential for this behavior still exists, and our data are consistent with the hypothesis that mothers alter their social interactions with males because males are perceived as a threat to offspring.

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