Are Male Orangutans a Threat to Infants? Evidence of Mother–Offspring Counterstrategies to Infanticide in Bornean Orangutans (Pongo pygmaeus wurmbii)

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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 postconceptive mating that 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 <6 yr. old both encountered fewer males and spent less time with males during social interactions than did mothers with offspring >6 yr. old and females without offspring. In addition, 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 counterinfanticide strategy. Our results suggest that infanticide by males is a selective pressure shaping female orangutan social behavior.

Keywords Great apes · Male avoidance · Male infanticide · Orangutan sociality · Sexual selection hypothesis

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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; cf. Bartlett *et al.* 1993 and Sussman 1994, who questioned the limited data set 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 (Lukas and Huchard 2014; van Schaik 2000b). 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 an offspring, then infanticide will not shorten the time that it takes a female to reproduce again (van Schaik 2000c). Likewise, in species with a 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, nonseasonal and nonannual 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 1 yr., then males will still gain by killing the infant, and infanticide may still be selected for (Palombit 2012). In addition, 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 counterinfanticide 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 that 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. Postconceptive 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 Gilchrist 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.: Robbins *et al.* 2009; Stokes *et al.* 2003; Yamagiwa *et al.* 2009).

Although 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. In addition, infanticide is suspected in the disappearance of a 3-mo-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 nonseasonal breeders who have the longest interbirth interval, 7.6 yr. (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 yrs. (van Noordwijk *et al.* 2013) than gestation, ca. 8 mo. (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 unclear whether all orangutan populations 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, which 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 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).

Owing to their semisolitary social structure (Galdikas 1985a; Mitra Setia *et al.* 2009; van Schaik *et al.* 1999), 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 counterinfanticide 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. As 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 ca. 2500 individuals (Johnson *et al.* 2005). The field site consists of primary rainforest and contains a mosaic of habitats (Marshall *et al.* 2009, 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 to 2003 and from 2008 to 2016. The break in data collection occurred when the field site was closed because of the threat of illegal logging.

Data Collection

We collected behavioral data during full day focal follows of habituated adolescent and adult female orangutans (Table I). 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 ≤ 50 m of each other (Knott *et al.* 2008; Mitani *et al.* 1991). 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 I). 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 orangutan 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 ($N_{\text{days}} = 2721$; $N_{\text{females}} = 98$). 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 ($N_{\text{days}} = 544$; $N_{\text{females}} = 47$). From this data set 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 examine absolute encounter rates of flanged vs. unflanged males; thus we did not control for the proportion of flanged to unflanged males in the study population.

Time Spent 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 considered only full-day follows of independently ranging females that encountered one or more males for these analyses ($N = 454_{\text{days}}$, $N_{\text{females}} = 43$).

Table I Sample sizes used to determine if female orangutan behavior is consistent with infanticide avoidance strategies

	Encounter rates: All days	Encounter rates: Male type	Time in association	Mother–offspring distance[b]	Mother–offspring distance: Male[b]	Mother–offspring distance: Female[b]
Observation days	2721	544	454	194	115	79
Females	74	47	43	25	20	19
Median (range)[a]	5.5 (1–534)	3 (1–120)	4 (1–60)	3 (1–50)	2.5 (1–30)	2 (1–17)
Mothers with offspring <6 yr	38	–	25	23	17	15
Median (range)[a]	16.5 (1–534)	–	3 (1–32)	2 (1–34)	2 (1–17)	2 (1–17)
Mothers with offspring >6 yr	15	–	12	8	8	6
Median (range)[a]	8 (1–216)	–	7 (1–60)	4.5 (1–42)	3.5 (1–24)	1 (1–18)
Nonmothers	45	23	21	–	–	–
Median (range)[a]	2 (1–234)	2 (1–73)	3 (1–58)	–	–	–
Mothers with offspring 0–4 and > 6 yr	–	11	–	–	–	–
Median (range)[a]	–	3 (1–99)	–	–	–	–
Mothers with offspring 4–6 yr	–	25	–	–	–	–
Median (range)[a]	–	3 (1–19)	–	–	–	–

The number of individuals in each mother and nonmother category does not add up to the number of individuals because some individuals appear in multiple categories

[a] Median and range for the number of observation days of each female

[b] Number of individuals refers to number of mother–offspring dyads

Mother–Offspring Distance

We recorded the distance between mother and offspring at 5-min 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 in a social association (≤ 50 m of conspecifics) for a portion of the day ($N_{\text{days}} = 194$, $N_{\text{dyads}} = 24$). We compared the mean distance between the mother–offspring dyad when they were alone, when they associated with male conspecifics (flanged and unflanged males) ($N_{\text{days}} = 115$, $N_{\text{dyads}} = 19$), and when they associated with female conspecifics (adolescent females and adult females with or without dependent offspring) ($N_{\text{days}} = 79$, $N_{\text{dyads}} = 19$). We excluded any females that 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 (<6 mo) 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 0–2 yr., mothers with offspring ages 2–4 yr., mothers with offspring ages 4–6 yr., mothers with offspring age > 6 yr., and females without offspring. We used the Holms–Bonferonni correction in the pairwise comparisons of proportions to reduce type I errors associated with multiple pairwise tests (Holm 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 the time females spent associated with males across the same five maternal status categories. This test corrects for type I 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 that 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. Owing to the binomial nature of the encounter data, we reported descriptive statistics of the encounter rate (median and range) among females, only for females with five or more follow days ($N_{\text{days}} = 2644$, $N_{\text{females}} = 33$). 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 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). Owing 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 ($N_{\text{days}} = 472$, $N_{\text{females}} = 27$).

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 post hoc test corrects for type I errors associated with multiple comparisons (Pohlert 2014). For post hoc tests, when ties were present, the chi-square distribution was used (Pohlert 2014).

We used an 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 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 mother–offspring dyad as a random effect, and 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 between mother and offspring in each dyad.

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

Ethical Note

This study was noninvasive 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. The authors declare no conflict of interest.

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 <6 yr. old, and females with offspring >6 yr. old (Electronic Supplementary Material [ESM] Table SI). 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 II). The proportion of days in which females with offspring <6 yr. old encountered males ($N_{\text{females}} = 26$, median = 0.096 days, range = 0–0.4 days) was statistically significantly lower than the proportion of days in which females with offspring >6 yr. old ($N_{\text{females}} = 12$, median = 0.310 days, range = 0–1.0 days) and females without offspring ($N_{\text{females}} = 14$, median = 0.143 days, range = 0–0.8 days) encountered males (Fig. 1).

The pairwise comparisons of proportions revealed that for flanged and unflanged male encounter rates, maternal status categories should be grouped together into three categories: nonmothers, mothers with offspring ages 0–4 yr. and > 6 yr., and mothers with offspring ages 4–6 yr. (ESM Tables SII and SIII). 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 III). The proportion of

Table II 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)

	Estimate	SE	95% Confidence interval	*P* value
(Intercept)	*−1.911*	0.203	0.503; 1.282	<0.001
Predictor variables				
Nonmother[a]	*0.875*	0.232	0.462; 1.341	<0.001
Offspring >6 yr[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

Random effects standard deviation = 0.808. Significant effects are shown in *italics*. SE = standard error

[a] Reference category: Offspring <6 yr

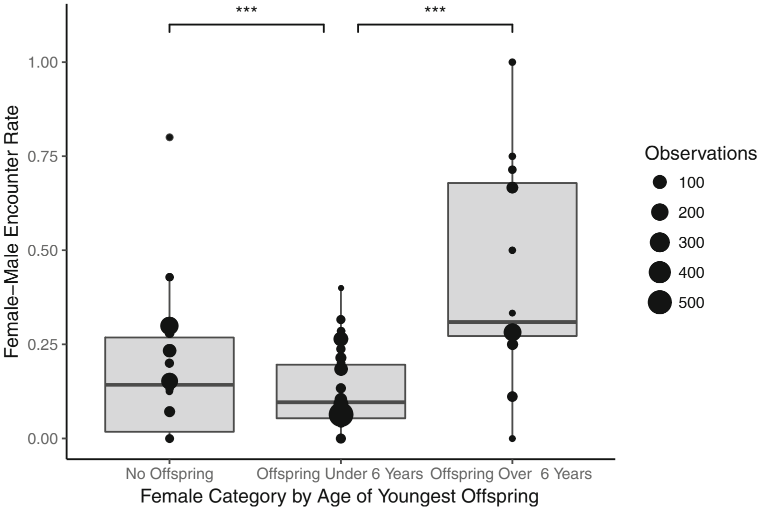

Fig. 1 Male encounter rates by maternal status category of Bornean orangutans at Gunung Palung National Park (data collected from September 1994 through April 2003 and November 2008 through December 2016). Boxplots are based on individual female encounter rates for females that had five or more full-day 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 × IQR, and outliers are plotted individually. The size of the dot shows the number of observation days. Significance values are from a GLMM ($*** = P < 0.001$).

male encounters that were with flanged males was statistically significantly lower for females with offspring ages 4–6 yr. old ($N_{\mathrm{females}} = 5$, 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 > 6 yr. ($N_{\mathrm{females}} = 15$, median = 0.405 encounters, range = 0.167–0.839 encounters) and females without offspring ($N_{\mathrm{females}} = 7$, 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 III). The proportion of male encounters that were with an unflanged male was statistically significantly higher for females with offspring ages 4–6 yr. old ($N_{\mathrm{females}} = 5$, 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 yr. and > 6 yr. ($N_{\mathrm{females}} = 15$, median = 0.568 encounters, range = 0.100–0.833 encounters) and females without offspring ($N_{\mathrm{females}} = 5$, median = 0.500 encounters, range = 0.318–1.0 encounters).

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 <6 yr. old, and females with offspring >6 yr. old (ESM Table SIV). On days when a female orangutan encountered one or more males, she spent a median of 170 ± SD 254 min associated with males (range: 1–830 min). The full LMM, assessing the effect of maternal status category and

Table III 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)

	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				
Nonmother[a]	*1.394*	0.498	0.419; 2.401	0.005
Mother with offspring ages 0–4 or > 6 yr[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				
Nonmother[a]	*−1.504*	0.499	−2.517; −0.538	0.003
Mother with offspring ages 0–4 or > 6 yr[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

Random effects standard deviation for flanged males = 0.672. Random effects standard deviation for unflanged males = 0.780. Significant effects are shown in *italics*. SE = standard error

[a] Reference category: Mother with offspring ages 4–6 yr.

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 <6 yr. old ($N_{\text{females}} = 25$, median = 118 min, range = 22–684 min) spent statistically significantly less time with males than females with offspring >6 yr. old ($N_{\text{females}} = 12$, median = 287.38 min, range = 75–641 min), and there was no difference in time spent with males between females without offspring ($N_{\text{females}} = 21$, median = 238.67 min, range = 21–653 min) and females with offspring >6 yr. old (Table IV; Fig. 2). There was no difference in time spent with flanged vs. 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 IV).

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 nonrelated female conspecifics ($V = 1352.5$, $P = 0.2845$, $N = 79$) (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, $P < 0.001$).

Table IV Results of LMM testing the 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)

	Estimate	SE	95% Confidence interval	*P* value
(Intercept)	*5.443*	0.187	5.081; 5.807	<0.001
Predictor variables				
Offspring <6 yr[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

Random effects standard deviation = 0.256. Significant effects are shown in *italics.* SE = standard error

[a] Reference category: Offspring >6 yr.

[b] Reference category: Flanged male

When controlling for offspring age and fruit availability, the mean distance between mother and offspring ($N_{\text{dyads}} = 19$, 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 ($N_{\text{dyads}} = 25$, median = 3.16 m, range = 0.3–13.18 m). (Table V; Fig. 5). When controlling for offspring age and fruit availability, the mean distance between mother and offspring did not change when nonrelated females were present ($N_{\text{dyads}} = 19$,

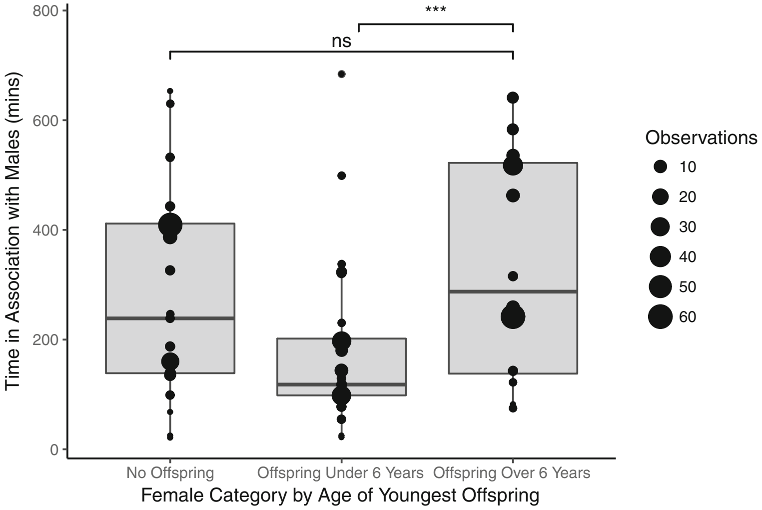

Fig. 2 Time spent in association with males by maternal status category of Bornean orangutans at Gunung Palung National Park (data collected from September 1994 through April 2003 and November 2008 through December 2016). Boxplots are based on individual female means. For each boxplot, the middle line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

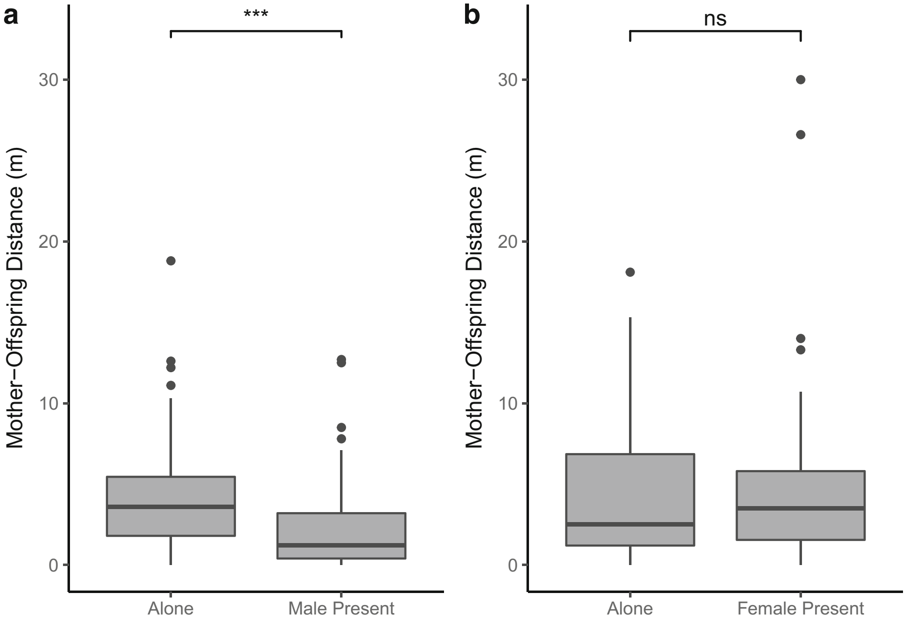

Fig. 3 Matched comparisons of the distance between mother and offspring dyads during the same day when the dyad was alone and in the presence of **(a)** a male conspecific (*** = $P < 0.001$) or **(b)** a female conspecific (ns = $P > 0.05$) in Bornean orangutans at Gunung Palung National Park (data 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 × IQR, and outliers are plotted individually.

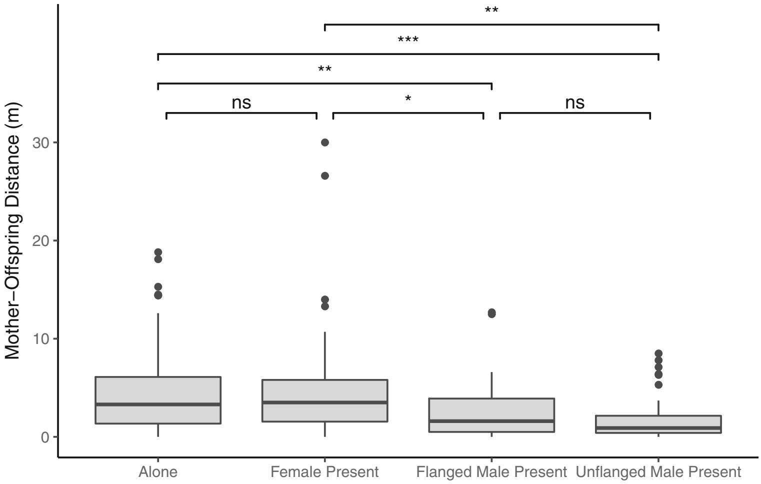

Fig. 4 Comparison of distance between mother–offspring dyad in different social associations in Bornean orangutans at Gunung Palung National Park (data collected from September 1994 through April 2003 and November 2008 through December 2016) (ns = $P > 0.05$, * = $P < 0.05$, ** = $P < 00.01$, *** = $P < 0.001$). 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 × IQR, and outliers are plotted individually.

median = 2.48 m, range = 0.8–26.6 m) compared to when the mother–offspring dyad was alone (Table V; Fig. 5).

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 <6 yr. old encounter males less often than mothers with offspring >6 yr. old and females without dependent offspring. Mothers with offspring <6 yr. old also spend less time with males than mothers with offspring >6 yr. old. As the mean orangutan interbirth interval is 7.6 yr. (van Noordwijk *et al.* 2018) and gestation is ca. 8 mo. (Graham 1988), it is not surprising that mating effort would increase when offspring reach 6 yr. 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 nonmothers compared to mothers (Matsumoto-Oda 1999; Otali and Gilchrist 2006; Sakura 1994). Lactating female chimpanzees specifically avoid groups with males but not with other lactating females (Sakura 1994). Among the Kanyawara chimpanzee community, the probability of associating with a male increased with increasing offspring age (Otali and Gilchrist 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.

Table V Results of an LMM of the factors affecting 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

Significant effects are shown in *italics.* SE = standard error

[a] Reference category: Mother–offspring dyad alone

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: $N = 79$; Male Present: $N = 115$. Lines represent the smoothed conditional mean distance values using the loess method. Shading represents standard error.

In addition, 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), our analysis does not include females that are known relatives of the mother–offspring dyad. Even when considering only nonrelated females, mother–offspring dyads do not react to the presence of females in a protective manner; they only react 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 Gilchrist 2006). Not surprisingly, our results show 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 that decreases this distance when males were present. In the presence of new males, which 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 shorten 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 does not affect the time that females spent associating with males but it does impact encounter rates. Given that there is an encounter with a male, females of different maternal status categories encounter flanged and unflanged males at different rates. This difference is driven by the category of mothers with offspring ages 4–6 yr., which encounter 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 4–6 yr" are approaching the time when they are ready to conceive again, although their monthly probability of conception is still low (Knott et al. 2009) . 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 that are unlikely to conceive. As flanged males have priority of access to females (Fox 2002), unflanged males may monitor these females (with offspring ages 4–6 yr) to take advantage of this mating opportunity if flanged males are not interested in these females.

Although 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 owing 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). In addition, 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 in other primates owing to the long interbirth interval (Galdikas and Wood 1990; Knott 2009; van Noordwijk *et al.* 2018) and supraannual fluctuations in fruit availability due to mast fruitings (Ashton *et al.* 1988; 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 increase infant 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). Owing to the lack of long-term male–female associations, female orangutans employ different strategies to reduce the risk of infanticide compared to female primates that 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 and Nakamura 2018; Otali and Gilchrist 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 and Nakamura 2018; Otali and Gilchrist 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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Author Contributions AMS and CDK formulated the idea. CDK supported and supervised the collection of data and maintains the long-term database. TWS contributed to field supervision and data collection. CDK and AMS prepared data for analysis. AMS analyzed data and wrote the majority of the manuscript. CDK provided guidance and assisted with data analysis and writing of the manuscript.

Data Availability The data sets generated during and/or analyzed during the current study are available from the authors on reasonable request.

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