Title: Countering infanticide: chimpanzee mothers are sensitive to the relative risks posed by males on differing rank trajectories

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Running title: Female sensitivity to infanticide risk

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Abstract

Objectives

Infanticide by males is common in mammals. According to the sexual selection hypothesis, the risk is inversely related to infant age because the older the infant, the less infanticide can shorten lactational amenorrhea; risk is also predicted to increase when an infanticidal male's chance of siring the replacement infant is high. Infanticide occurs in chimpanzees (*Pan troglodytes*), a species in which male dominance rank predicts paternity skew. Infanticidal male chimpanzees (if low-ranking) are unlikely to kill their own offspring, while those who are currently rising in rank, particularly when this rise is dramatic, have a increased likelihood of fathering potential future infants relative to any existing ones.

Given that mothers should behave in ways that reduce infanticide risk, we predicted that female chimpanzees, and specifically those with younger, more vulnerable infants, would attempt to adjust the exposure of their infants to potentially-infanticidal males. Specifically, mothers of young infants should reduce their association with adult males in general, and to a greater extent, with both low-ranking males and those rising in rank from a position where paternity of current infants was unlikely, to a rank where the probability of siring the next infant is significantly higher. We also investigated the alternative possibility that rather than avoiding all adult males, mothers would increase association with males of stable high rank on the basis that such males could offer protection against infanticide.

Materials and Methods

We examined data on female association patterns collected from the Budongo Forest, Uganda, during a period encompassing both relative stability in the male hierarchy and a period of instability with a mid-ranking male rising rapidly in rank.

Results

Using linear mixed models, we found that mothers reduced their association with the rank-rising male, contingent on infant age, during the period of instability. We also found evidence that females preferentially associated with a potential protector male during the high-risk period.

Discussion

Our results support the sexually-selected hypothesis for infanticide, and demonstrate that female chimpanzees are sensitive to the relative risks posed by adult males.

Introduction

Infanticide by males is common in mammals (Lukas and Huchard, 2014). According to the sexually-selected infanticide hypothesis (Hrdy, 1979; Sommer, 1987), the risk of infanticide increases when (a) males can kill unrelated infants; (b) infanticide reduces the interbirth interval of the targeted infant's mother; and (c) infanticide increases the male's likelihood of achieving paternity (i.e. the chance of siring the replacement infant relative to the infant killed). Infanticide should generate significant selective pressure, and so females are expected to employ counterstrategies, such as promiscuity and post-conceptive swellings to confuse paternity, as well as maternal vigilance and aggression (Hrdy, 1979; van Schaik, 2000a; Treves et al., 2003; Wolff and Macdonald, 2004; Parmigiani et al., 2010).

Infanticide occurs in multiple communities of East African chimpanzees, with most cases perpetrated by males (*Pan troglodytes schweinfurthii*: Arcadi and Wrangham, 1999; Newton-Fisher, 1999a; Murray et al., 2007; Newton-Fisher and Emery Thompson, 2012). Female promiscuity is conventionally interpreted as a strategy aimed at confusing paternity and protecting against male-committed infanticide (Hrdy, 1981). However, adult males may be able to track variation in the size of female sexual swellings, suggesting that ovulation is not entirely concealed (Deschner et al., 2003), and in some communities male coercive aggression may place restrictions on females' ability to determine the males with whom they mate (Muller et al., 2007; Feldblum et al., 2014), although the use of coercion varies between sites (Kaburu and Newton-Fisher, 2015a). More critically, however, male dominance rank typically predicts paternity across multiple communities, including our study group (Boesch et al., 2006; Wroblewski et al., 2009; Newton-Fisher et al., 2010; Langergraber et al., 2013). This raises a particular problem for females: while promiscuity might reduce rank-related paternity skew (and might be responsible for the relatively moderate degree of skew: 60% of paternities achieved by males of ranks 1 – 3 in our study community: Newton-Fisher et al., 2010), it cannot protect fully against infanticide by confusing paternity. Infanticide becomes an adaptive strategy where the chances of a male having sired an existing infant are low, and when changes in social dominance rank increase the probability of him siring a replacement infant (the value of *P* in van Schaik's [2000a] model of adaptive infanticide). As a consequence of the probabilistic relationship between rank and paternity, males who employ infanticide as a strategy contingent on their relative dominance rank (and recent changes thereof) will do so, on average, in an adaptive fashion. At a proximate level, tracking outcomes of recent agonistic interactions with other males and thus relative rank is likely to be less challenging than tracking mating history, or estimating likelihood of paternity, under a fission-fusion social system with promiscuously mating females. While such a reliance on rank as a proxy may in some cases be negated by specific mating strategies such as consortships (in which mating is restricted and paternity certainty is potentially high), the existence of a statistical relationship between rank and paternity, itself the outcome of the interplay of male and female mating strategies, will in most cases provide males with a reliable cue (at least considered from the perspective of the evolution of the strategy) which females cannot directly counter. The proposed female strategy of concentrating mating efforts, when most likely to conceive, on preferred males (Stumpf and Boesch, 2005) will only worsen this problem if these preferred males are high ranking, as it will reinforce or exacerbate the rank-related skew in paternity. If females cannot fully reduce paternity skew through promiscuous and frequent copulation, either because they cannot overcome male coercive aggression (Muller et al., 2007, 2011), or because they seek high quality mates (Tutin, 1979; Stumpf and Boesch, 2005, 2006), additional or alternative strategies will be needed to counter the risk of infanticide.

A consequence of this link between male rank and paternity skew is the correlated link between male rank and infanticide risk. While low-ranked males generally have a low likelihood of siring any given infant, and would have less to lose by pursuing an infanticidal strategy, the greatest risk to females comes, however, from males who rise in rank, all other factors being equal (cf. *Macaca fuscata*: Soltis et al., 2000). In particular, those males who rise from a rank at which paternity was unlikely when an infant was conceived to a sufficiently high rank that the probability of siring the next infant is non-negligible have both little to lose and a lot to gain (van Schaik, 2000b). Female chimpanzees, who are 20 – 25% lighter than males (Goodall, 1986; Bean, 1999) and socially subordinate (Goodall, 1986; Goldberg and Wrangham, 1997), are in a poor position to defend their infants directly from attacks by males, although in some cases they may receive coalitionary support (Newton-Fisher, 2006; Kahlenberg et al., 2008).

These arguments assume that male chimpanzees are not able to identify paternity directly, and while recent studies of chimpanzee from communities in both Taï and Gombe (Lehmann et al., 2006; Murray et al., 2016) have shown that male chimpanzees bias socially-positive interactions towards their offspring, these studies did not explore males' knowledge of paternity. The statistical dependency between rank and paternity, which we argue allows males to be adaptively infanticidal, may allow males to provide paternal investment without offspring recognition by biasing behavior according to their expected probability of paternity according to rank, although other factors, such as previous association with the mother, may also be involved (Langergraber et al., 2013). Furthermore, the nature of this paternal biasing differs between Taï and Gombe: although males at both sites bias social behaviour (play, reduced aggression) towards their own infants and those infants' mothers, only males at Gombe preferentially associate with their own infants (Lehmann et al., 2006; Murray et al., 2016). Preliminary data from our study community suggests a different pattern again, with paternity having no effect on either association or aggression rates, with adult male-infant play too infrequent to be analysed (Lowe & Newton-Fisher, forthcoming). The preferential association of male chimpanzees with maternal, but not paternal, siblings (Langergraber et al., 2007) further questions direct recognition of kin: paternal siblings may be valuable coalition partners rather than reproductive rivals. We suggest, therefore, that it is premature to assume that male chimpanzees have direct knowledge of paternity.

Chimpanzees have a social system characterized by high fission-fusion dynamics, whereby individuals associate with one another in sub-groups ('parties': Sugiyama, 1968) of variable composition and duration (Goodall, 1986; Boesch and Boesch-Achermann, 2000). Fission-fusion grouping is thought to be a response to managing feeding competition across dispersed patches, particularly of ripe fruit (Symington, 1968), but it also provides individuals with opportunities to adjust their social environment (Newton-Fisher, 1999b; Pepper et al., 1999; Murray et al., 2014), subject to the conditions that others may do likewise, and that individuals must satisfy their foraging demands. We suggest that females may make use of this flexibility to counter infanticide risk, as the association of dependent infants with other community members is the direct consequence of decisions made by their mothers to join or leave parties.

We consider three non-exclusive possibilities for female counterstrategies to infanticide risk: (1) that females seek protection from high-ranking males who generally have a greater likelihood of having sired their infants, (the *male protector hypothesis*: (Borries et al., 1999; Palombit et al., 2000; Kahlenberg et al., 2008); (2) that females adjust the exposure of their infants to potentially-infanticidal males: specifically, that they reduce association with low-ranking and males who are currently rising in rank, contingent on infant age, as vulnerability and desirability as targets are inversely related to infant age (the *risky-male-avoidance hypothesis*); and (3) that females seek protection for their infants by associating with other mothers (potentially benefiting from both dilution and selfish herd effects: Hamilton, 1971). We also consider the *infant safety hypothesis* (Otali and Gilchrist, 2006), which proposes that low female gregariousness is due to females avoiding association with males in general, due to their potential for aggression. To test these hypotheses, we take advantage of prior work identifying the link between paternity and rank in our study community (Newton-Fisher, Thompson et al., 2010) and the rapid rise in rank of one of the adult males (NK) in June 2004, from mid/low ranking (rank 5 of 8 adult males) to rank 2 within one month (Newton-Fisher, 2017). As paternity in this community is concentrated in the top three ranks, and rare below rank 5, this increase in rank represents a significant shift in the likelihood of siring infants, as well as in the level of infanticide risk. Intracommunity infanticide is well documented for this community, with 10 recorded incidents between 2004 – 2013 (Wilson et al., 2014). Of the 4 infanticides for which the attacker's identity was confirmed, two were committed by males, one by females and one involved both sexes.

Methods

Data Collection

We used data on the Sonso community of chimpanzees from the Budongo Forest, Uganda, collected between October 2003 and January 2005. This community inhabits around 7km^2 (Newton-Fisher, 2002) of the 428km^2 semi-deciduous tropical forest within the reserve (Eggeling, 1947; Plumptre, 1996; Reynolds, 2005), and has been studied continuously since 1994 (Newton-Fisher, 1997; Reynolds, 2005)]. During data collection, the community consisted of 63 individuals, including eight adult males (by definition, ≥ 16 years old), six adolescent males (ranging from 9–14 years old) and 21 adult females (≥ 14 years old). Age categories follow Goodall (1986). Seven of these females had infants under one year of age during the study period; these mothers are our focal mothers. Infants of this age are always in the presence of their mothers (Boesch and Boesch-Achermann, 2000). Of these seven females (ID codes: BN, KG, KU, ML, NB, RH, ZM), two (KU and ZM) had male infants, while five (BN, KG, ML, NB and RH) had female infants. All focal mothers were multiparous, with between one and four known prior infants. Two infants were of unknown paternity; of the remaining five, adult male BK was the father of three, while MA and BB were fathers of one each (all adult males are listed in Figure 1). Data were recorded by NNF and field assistants using a focal-behaviour sampling regime: parties were followed for as long as possible from first encounter until nesting, with pre-selected focal animals followed when parties fissioned. If contact with chimpanzees was lost due to terrain and/or chimpanzee movement patterns, data were collected from the next party encountered that contained one of the predetermined focal animals. We defined a party following Newton-Fisher's (1999) operational definition: "a collection of independently associating individuals showing coordination in behaviour; a cluster of individuals with a radius of around 35m". Party composition was recorded using 5-minute-interval instantaneous scan sampling. Given that a chimpanzee could travel >240m between scan samples (assuming an average travel speed of 2.95 km/h: Newton-Fisher 2003, calculated from data in Wrangham, 1977), and easily leave a party in < 1 min, an individual's presence in consecutive scans of the same party is not because they are unable to leave within the 5-minute period, and so represents an active decision to remain in the same party (for example when a party leaves a feeding patch and travels together without changes in membership). All occurrence sampling was used to record aggressive interactions within the focal party (Kaburu and Newton-Fisher, 2015b; Newton-Fisher, 2017).

Our research complied with regulations set by the Ethics Committee of the University of Kent, the protocols of the Budongo Forest Project (now BCFS) and the legal requirements of Uganda. In addition, it complied with the American Association of Physical Anthropologists Code of Ethics as it pertains to living human and nonhuman subjects.

Data analysis

We distinguished a new party whenever one or more individuals joined and/or left a party (i.e. at each change in party composition). For the purposes of analysis, we accorded each of the 1040 parties a unique identifier. This was used to control for multiple observations of the same party. The duration for which party composition remained unchanged was highly variable, with parties lasting between 1 and 47 scans (mean = 2.82 ± 4.07 scans, median = 2). To generate a cardinal measure of social rank we constructed Elo-ratings from wins and losses of directed aggressive interactions (Newton-Fisher, 2017). We identified several categories of aggression: static threats, approach threats, charging displays, chases and attacks, scaling the impact that these had on Elo-ratings (for further details see Newton-Fisher (2017). We used these Elo-ratings (Fig. 1) to identify two consecutive 8-month periods in our dataset: the first, when adult male ranks were relatively stable (October 2003 – May 2004), the second when a mid-ranking (rank 5 of 8) adult male (NK) rose rapidly and held high (2nd) rank (June 2004 – January 2005). NK then remained high ranking, holding the alpha position from 2006 until 2013. We considered ranks 1-3 to be "high", 4 & 5 to be "mid" and 6-8 to be "low." Predicted infanticide risk was low during the stable period and higher during the unstable period. We also calculated aggression rates for each male: (1) aggressive interactions per hour towards all members of the community, and (2) aggressive interactions per hour towards our focal mothers.

FIGURE 1

Since infant age is a proxy for infanticide risk (Hrdy, 1979), and mothers should be sensitive to this, we looked at the relationship between the age of the focal's infant and party composition. This process allowed us to investigate whether female decisions to participate in parties, based on the composition of those parties, varied as a function of infant age. Given that 86% of chimpanzee infanticide victims with confirmed male attackers were under 1 year of age (Wilson et al., 2014), we restricted our analysis to the behaviour of mothers with infants younger than 1 year. We used linear mixed-model (LMM) analyses to test our predictions, using the function 'lmer' from the R package 'lme4' (Bates et al., 2015) to constructed . We used mixed models with REML and random intercepts to see how the presence of particular individuals related to the age of the focal mother's infant. We produced two models. In model 1, age of the focal mother's infant was the dependent variable, with the number of adult males and number of mothers of infants <1 year of age in the party as the predictors. This model was designed to show whether mothers of younger (i.e. more vulnerable) infants spent time in parties with more/fewer adult males and other mothers. In model 2, we again set the age of the focal mother's infant as the dependent variable, this time with the presence (Y/N) of each adult male and time period (low/elevated risk) as predictors, along with an interaction between these. This model, specifically the interaction between male presence and low/elevated risk, was designed to show whether, after taking into account the fact that infants will necessarily be older in the second of these two periods, younger (more vulnerable) infants were more or less likely to be in the presence of particular males in the unstable versus the stable period. We included, as random effects, the ID of the focal mother to account for repeated observations and possible idiosyncratic variation in behaviour, and party ID to account for multiple samples from the same parties. We tested the significance of the predictors on the dependent variable by using the ‘drop1’ function to compute a likelihood ratio test.

Age of the focal mother’s infant was calculated at each scan sample from either a known birth date or otherwise the midpoint of an estimated date range. Birthdate estimated ranges were 0-14 days, mean: 5.6 days, sd: 6.2.

Results

Our focal mothers spent the majority of their time (52.3% of scans) in parties with no adult males, while one male was present in 19.6% of scans, two males in 9.5% and three to seven males in 18.6% of scans. Mothers were alone, except for their dependent infants for 28.9% of scans. The proportion of time which our focal mothers spent in parties with other mothers of infants <1 year of age was similar to that spent with males. They were with no other mothers of young infants in 58.0% of scans, one other mother in 21.8% of scans, two other mothers in 13.9% of scans and three to six other mothers in 6.3% of scans. We recognise that these percentages may underestimate the total time mothers spend alone, as following lone individuals, in particular females, is typically harder than following larger parties (personal observations). Therefore, time spent with other individuals, or in small all-female parties, may be overrepresented in the data. The mean number of adults in a party was 3 (sd: 4), with a mean of 1 males (sd: 2), and 2 females (sd: 2). On average, 1 of these two females (mean: 1, sd: 1) were mothers of infants <1 year of age.

During the study period, we recorded a mean rate per male of 0.4 (sd: 0.2) aggressive interactions per hour (h^{-1}), but these ranged from 0.1 to 0.7 (median =). Our three lowest ranking males (GS, TK, and BB) were the least aggressive overall, initiating aggressive interactions at rates of 0.1, 0.1, and 0.3 times per hour of observation respectively. NK was the most aggressive, directing aggression towards other individuals at a rate of 0.7 h^{-1}. The second most aggressive male was BK, who spent the majority of the study period at either rank 2 or 3, with a rate of 0.6 h^{-1}. The other mid- to high-ranking males (ranks 1-5) had rates between 0.3 h^{-1} and 0.4 h^{-1}.

When considering just aggression towards our focal mothers, two low-ranking males (TK and GS) were, again, the least aggressive, with rates of 0.004 h^{-1}, and 0.005 h^{-1}, respectively. MA, ZF and BB (high, mid and low-ranking males) had mid-range aggression rates of 0.009 h^{-1}, 0.2 h^{-1} and 0.03 h^{-1} respectively. The male most aggressive towards mothers (0.053 h^{-1}) was the high-ranking BK, followed by NK, our rank-rising male (0.050 h^{-1}). Aggression rates by the alpha male DN (0.03 h^{-1}) were lower, comparable to the low-ranking BB.

Male intervention was not observed in any of the 567 recorded attacks or threats towards adult females by other adult males. Two females were observed approaching adult males when threatened and chased by another male, on three separate occasions. On one occasion, this female was a mother; the other two occasions involved the same non-mother. The male aggressor was the rank-rising NK in all three instances, while the approached males were all mid- to high-ranking, and in all cases were higher ranking than NK. The mother approached the alpha male, who was not the father of her infant. Approached males did not offer active support in any of the three incidences, and adult males typically ignored aggression directed towards females by other males.

We found no evidence of a relationship between either the number of adult males (Model 1: $\beta \pm SE = 8.18e-03 +/- 6.51e-03, p = 0.21$), or the number of other mothers of infants <1 year (Model 1: $\beta \pm SE = 2.29e-03 +/- 1.27e-03, p = 0.07$), in the party and the age of the focal mother's infant.

However, we did find (Model 2) statistically significant relationships between the age of the focal's infant and the interaction between the shift from low to elevated infanticide risk and the presence of two of the eight adult males (BK & NK). This reflects which mothers (those with older vs younger infants) were in the presence of these males. Of the three high-ranking males, there was an effect only for BK, who spent time in parties with mothers of comparatively younger infants during the period of elevated risk than before this period (Model 2: $\beta \pm SE = -0.12 \pm 0.03, p < 0.0001$). The presence of the male who posed the most likely source of infanticide risk (NK) had the greatest influence: mothers in his presence had infants which were 67.5 days older when risk was elevated compared to the low risk period (Model 2: $\beta \pm SE = 0.19 \pm 0.03$; $p < 0.0001$).

Discussion

The *infant safety hypothesis* suggests that adult males, by virtue of being potentially aggressive, are a physical and psychological risk to infants, a risk that is heightened when infants are younger (Otali and Gilchrist, 2006). However, our results suggest that, when considered as a group, male chimpanzees in the Sonso community were not necessarily treated as dangerous by mothers, or at least that that any danger posed did not vary with infant age in infants under 1 year old.

Instead, mothers of young infants reacted most strongly to the rapid rise in social dominance rank of the male NK, supporting our *risky-male-avoidance hypothesis*. While we cannot exclude the possibility that our results were the product of this male tending to spend more time with mothers of ‘older’ infants, during and after his rise in rank, we find no convincing explanation why this would be so. It would be difficult to account for such behaviour in terms of future mating effort, since all the infants in our dataset are under 1 year of age and therefore the mothers of even the oldest are several years away from being sexually receptive: the average interbirth interval (IBI) for chimpanzees, when infants survive, is around 5 years (Goodall, 1986; Kappeler, P and Pereira, M, 2003), while the shortest recorded IBI for our study community is 47 months. Furthermore, previous work at Gombe has found that male-female association in chimpanzees does not reflect future mating effort (Murray et al., 2016), while evidence that males may seek out contact with mothers of specific infants was associated with paternity of those infants (Murray et al., 2016). In this study, NK was not the father of any of the 5 infants under 1 year of age for whom paternity was known. By contrast, interpreting these results as attempts by mothers to avoid this male is consistent with the *sexually selected infanticide hypothesis* (Hrdy, 1979; Sommer, 1987). Under this hypothesis, the risk posed by a male depends on the change in his likelihood of achieving paternity with the female’s next infant as compared to being the father of her current infant. Risks are greater for younger infants as their death has a greater impact in reducing lactational amenorrhoea (Hrdy, 1979; Sommer, 1987; van Schaik, 2000b). An infanticidal male chimpanzee rising in rank will increase his likelihood of achieving future paternities if this rise is post conception and before weaning of the infant(s) at risk. This was precisely the situation for the adult male NK, who was ranked fifth during the first period of our study, only to rise rapidly and sustain high rank in the second period: data from the Sonso community suggest that males of rank 5 or below have only a low probability of achieving paternity, with most paternity concentrated in males of the top four, and particularly the top three ranks (Newton-Fisher et al., 2010). According to the *sexually selected infanticide hypothesis*, NK's rise should have made him the greatest source of infanticide risk, and the male towards whom mothers should therefore respond most strongly. This is precisely what we found.

Our interpretation is supported by our results with respect to males who consistently held high rank: it was the *change* from low to high rank, and thus change in likelihood of achieving paternity, that appeared to be the important factor. Males whose ranks are unchanging between conceptions should not pose an infanticide risk, because without a substantive rise in rank between successive conceptions of a given female, their chance of siring a second infant will be unchanged from that of siring the first, and so they cannot expect to increase their reproductive success through infanticide.

Despite an expectation of higher rates of aggression among high-ranking males (Muller and Wrangham, 2004), and thus the likelihood that infants may be at risk from redirected or unintended violence, we found no evidence that mothers reduced association with higher-ranking males when NK was challenging for high rank. Given that rates of aggression by Sonso community males conform to this general expectation, we would have expected such a reduction if females were concerned primarily about their infants falling victim to inadvertent aggression. Even if high-ranking males were only aggressive when around rank-rising males, this male strategy would result in increased levels of aggression during the second period (when NK was rising in rank) and so we would still expect a reduction in mother-male association as females seek to avoid male aggression, which we did not find. Instead, we found opposite effects for the two most aggressive males: while NK was avoided by mothers of young infants, BK, the second most aggressive male, associated more with younger infants during the unstable period. Danger of misdirected aggression cannot explain these patterns of behaviour. We also note that while female chimpanzees will shepherd dependent infants to safety when faced with aggressive males, typically they do not flee from parties under these conditions (personal observations), and it is their older, more independent infants and juveniles who appear to be at most at risk from inadvertent or redirected aggression: the youngest infants – those most vulnerable to infanticide – are more likely to be bodily contact with their mother. Thus, our findings suggest it is the likelihood of infant-directed attacks, rather than misdirected aggression, to which mothers are sensitive. Given that we find both decreased and increased association with particular males, and no general differences in mothers' associations with adult females compared to their association with adult males, we have no reason to suggest that variation in female association patterns is due to infant socialisation (Horvat and Kraemer, 1981). Such patterns may be apparent across the period of infancy (0-5years), but for infants < 1 year, it seems that mothers are attempting to reduce infanticide risk.

We found some support for the *protector male hypothesis* (Borries et al., 1999; Palombit et al., 2000). Of the high-ranking males, the expected effect (an increase in association when infanticide risk was elevated) was seen only for BK, who was father to 3 of the 5 infants <1yr old for whom paternity is known. We found no evidence of a 'protector' role for the alpha male, although this might have been because the two infants whom he was confirmed to have sired were already over 4 years old at the start of the study period and therefore at low risk of being victims of an infanticidal attack. Although these results are suggestive of a link between paternity and protector male effect, it is not clear why this was not evident for the other fathers in our dataset, unless the effect is small, visible only because of the cumulative effect of multiple infants, or perhaps because BK had higher paternity certainty than might typically be the case due to coercive curtailing of the mother's promiscuity or through fathering an infant during a consortship. Unfortunately, mating history for the relevant period is not available to test these ideas.

Alternatively, and perhaps more plausibly since it does not require identification of paternity, mothers may have been using BK as a shield, regardless of paternity, on the basis that he could deter potentially infanticidal males. Mothers are unlikely to gain active defence – neither BK nor any other male, was observed intervening in an attack by an adult male on an adult female during this study – but may benefit if the presence of aggressive high-ranking males deters aggression from other males. If males interpret aggressive displays from others as rank challenges, this is potentially something that mothers could exploit. However, since BK was also aggressive towards females, such a strategy would be potentially costly, but tolerating high rates of displays, threats and even contact aggression could be beneficial if linked to protection from infanticidal attacks.

In summary, our results suggest that eastern female chimpanzees in our study community with young infants are sensitive to male rank shifts and respond adaptively to reduce the exposure of their infants to infanticide risk. Mothers reduced their association with (and thus the exposure of their infants to males who have incentives to commit infanticide, as well as associating with safer, potentially protective males, supporting our *risky-male-avoidance hypothesis* and, possibly, the *male-protector hypothesis*. We predict that these findings will be generalisable to other chimpanzee communities with rank-based paternity skew, as this generates potential fitness differentials and associated risks of infanticidal behaviour. Our findings support the *sexually-selected infanticide hypothesis* for within-community infanticide by male eastern chimpanzees.

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