RESEARCH ARTICLE

WILEY AGGRESSIVE BEHAVIOR

# Aggression by male bonobos against immature individuals does not fit with predictions of infanticide

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The selective advantage of male infanticide is enhancement of reproductive success of the aggressor. This implies that aggression is directed at individuals sired by others, infant loss shortens the mother's inter-birth interval, and the aggressor has a greater likelihood of siring the next offspring of the victims' mother. As these conditions are not always met, the occurrence of male infanticide is expected to vary, and hominoid primates offer an interesting example of variation in male infanticide. Infanticide has been reported in gorillas and chimpanzees but appears to be absent in orangutans and bonobos. One argument for the absence of infanticide in bonobos is reduction of male aggression. However, given that male aggression against immature individuals occurs and that females engage in behavior that is considered to be counterstrategy against male infanticide, the risk of male infanticide may pose a potential threat. Here, we explored whether aggression by male bonobos fits predictions of male infanticide. Male aggression toward immature individuals was rare and did not have lethal consequences, but the majority of observed cases exposed targets to risks of injury. Males did not target their own offspring less frequently than unrelated immatures, and the risk of being the target of male aggression increased with the targets' age. Overall, these results do not match the predictions of the adaptive male infanticide hypothesis. Instead, aggression by males may promote the emigration of the targets and older males may reinforce their superior status toward individuals that will soon compete for the same resources.

**KEYWORDS**
bonobo, counter strategies, Great apes, infanticide, male aggression

## 1 | INTRODUCTION

In many cases, the occurrence of aggression between individuals can be ultimately explained by its fitness enhancing effect for the aggressor (Archer, 2004; MacCormick et al., 2012; Muller, Kahlenberg, & Wrangham, 2009; Smuts & Smuts, 1993). This applies to both sexes, but physical aggression is generally more common among males, where intra-sexual competition for access to fertile females drives the

investment in physical power, risk-taking, and development of weaponry (Clutton-Brock & Huchard, 2013 but see Björkqvist & Niemelä, 1992). Males may also use physical aggression against females if aggression enhances mating opportunities and reproductive success (Drea, 2005; Lindenfors & Tullberg, 2011; Stockley & Campbell, 2013). While male aggression against both adult males and females can be very intense, lethal aggression is rare and escalation of fights is usually prevented by behavior that signals asymmetries in

physical strength, group size, or motivation (Clutton-Brock & Albon, 1979; Hammerstein, 1981; Maynard Smith & Parker, 1976). This type of aggression differs from male aggression against infants. Killing of small infants evolved as a male reproductive strategy and has been reported in various vertebrate species (such as voles (Horne & Ylönen, 1996), lions (Pusey & Packer, 1994), non-human primates (van Schaik & Kappeler, 1997), and humans (Voland & Stephens, 2000). The selective advantage of male infanticide is contingent on a number of conditions. First, the male aggressor did not sire the victim. Second, females who lose a small infant resume reproductive cycling earlier than they would have, had they nursed until weaning. Third, the male committing infanticide is likely to sire the next offspring of the mother of the victim. While evidence from a large number of species does confirm that these conditions promote aggression by males against immature individuals, there is evidence that males may gain benefits when the above predictions are not met. For example male lions may attack immatures at the age of weaning and females with cubs at this age tend to segregate temporarily from males, behavior that has been interpreted as a strategy to prevent infanticide (Palombit, 2015). Furthermore, data from non-human primates and humans indicate that close kinship between the male aggressor and the immature victim does not necessarily prevent lethal male aggression (Arcadi & Wrangham, 1999; Brewis, 1992; Daly & Wilson, 1994). Finally, in some species, males have been observed to kill infants of a different species (Rimbach, Pardo-Martinez, Montes-Rojas, Di Fiore, & Link, 2012). Instead of promoting the reproductive success of the male aggressor, the behavior may be triggered by intense resource competition or represent redirected aggression (Rimbach et al., 2012).

Male aggression against immature individuals can be accompanied by vigorous movements and noisy chases, making behavioral observations of the interactions between aggressor and victim difficult. Moreover, due to the poor visibility in many natural habitats, the actual outcome of an aggressive encounter between a male and an immature individual and/or its mother is not always easy to detect. Therefore, the lethal consequences of male aggression are often inferred and the impact of infanticide on mortality rates are likely underestimated (van Schaik, 2000). Infanticide is costly to both the mother of the infant as well as the putative father and both are likely to respond with defensive strategies and counter aggression. In some species, these counter strategies can be so effective that in spite of frequent attacks, infanticide rarely occurs (Fruteau, Range, & Noë, 2010). In other species, infanticide does not require aggressive acts, as the presence of a new male may be sufficient to induce prenatal resorption of fetuses, leading to indirect or deterrent infanticide (Bruce, 1960; Hackländer, 1999). Another reason that the detection of infanticide is difficult is that aggressive acts are not always immediately linked to the death of the target. In humans, children may die because of insufficient nutrition, parental neglect, or repeated non-lethal assaults (Guggenheim, Davis, & Figueredo, 2007), and similar cases are known from non-human primates (Maestripieri & Carroll, 2000). Finally, in wild populations, infanticide may escape the attention of human observers because of environmental conditions (e.g., poor visibility or when subjects are not habituated and avoid human observers). Therefore, the absence of direct evidence for infanticide is not evidence for the absence of infanticide, and a close look at the cases of male aggression against immature individuals can help to assess the potential for male infanticide in species without confirmed cases of this behavior. This is particularly relevant in species were the social system and the reproductive strategies are such that males derive benefits from infanticide (Lukas & Huchard, 2014).

In spite of the difficulty of detection in some cases, male infanticide is particularly prominent in non-human primates (van Schaik & Kappeler, 1997). The behavior occurs in all clades of the primate order and is responsible for a considerable proportion of infant mortality (Sommer, 1994; Watts, 2010). In primates, the risk of male infanticide has shaped grouping patterns (Opie, Atkinson, Dunbar, & Shultz, 2013; van Schaik & Dunbar, 1990), social relations (Palombit, 1999; van Schaik & Kappeler, 1997), and the reproductive physiology of females (van Schaik, 2000).

Hominoid primates offer an interesting example for the extent of variation in terms of the frequency and context of male infanticide across close related species. Orangutans have been studied at multiple sites and for long periods but evidence for male infanticide is so far lacking. One explanation for the absence of infanticide is that killing a dependent offspring would not induce cycling in the mother, because environmental conditions and related changes in energy status, rather than nursing, constrain the reproductive physiology of female orangutans. In other words, even the loss of a small infant would not reduce inter-birth intervals (Beaudrot, Kahlenberg, & Marshall, 2009). In gorillas, male infanticide resembles the pattern observed in other primates. Infanticide occurs when a new male takes over a group of females, during group encounters or when groups disintegrate (Robbins et al., 2013). Under such circumstances, it is unlikely that the victim and the male aggressor are closely related. Moreover, females that lose an infant resume cycling earlier than females that nurse until weaning (Robbins, Robbins, Gerald-Steklis, & Steklis, 2006), making male infanticide a potentially advantageous reproductive strategy. Evidence for male infanticide in chimpanzees comes from multiple populations (Wrangham, Wilson, & Muller, 2006). Infant killing occurs during encounters between members belonging to different communities (Watts, Sherrow, & Mitani, 2002) and sometimes when females with offspring migrate into existing communities (Nishida & Hiraiwa-Hasegawa, 1985). In some chimpanzee populations infants have also been killed by resident males, and in some cases males may have actually killed their own offspring (Arcadi & Wrangham, 1999; Hamai, Nishida, Takasaki, & Turner, 1992).

Evidence for male infanticide is also lacking for the fourth hominoid species, the bonobo. This lack of evidence is puzzling as females exhibit traits that have been considered to be counter-strategies against male infanticide in other species (Ebensperger, 1998; Lukas & Huchard, 2014). For example, in bonobo communities the number of adult females exceeds the number of males (Hohmann & Fruth, 2002), females mate with many or all males within a given reproductive cycle and may solicit mating with multiple males in close succession (Takahata, Ihobe, & Idani, 1996), likely leading to confusion over paternity. Females exhibit cyclic changes of sexual swellings that

attract the attention of males, increase male mate competition, and affect male mating effort (Douglas, Hohmann, Murtagh, Thiessen-Bock, & Deschner, 2016; Hohmann & Fruth, 2003; Surbeck, Deschner, Schubert, Weltring, & Hohmann, 2012). Although females transfer between communities, there is evidence for differentiated social relationships (Moscovice et al., 2017) and coalitional support (Nurmi, Hohmann, Goldstone, Deschner, & Schülke, 2018; Tokuyama & Furuichi, 2016). Moreover, females losing small infants resume cycling much earlier than females who nurse their offspring until weaning age (own observations), which suggests that killing an infant would actually shorten the inter-birth interval. Finally, long-term records from the field site of LuiKotale include several cases when infants either disappeared from their mothers or were found dead with the hints to infant mortality remaining ambiguous.

Compared to chimpanzees, bonobos are often portrayed as being peaceful and less is known regarding the circumstances in which aggression occurs and what function it serves in bonobos. As in other animals, male bonobos tend to be more aggressive than females (Furuichi, 1997; Hohmann & Fruth, 2003). However, certain forms of male aggression that are common in primates and other mammals such as sexual coercion or territorial aggression seem to be absent or rare in bonobos (Hohmann & Fruth, 2003; Sakamaki, Ryu, Toda, Tokuyama, & Furuichi, 2018). Moreover, unlike chimpanzees, bonobos appear to refrain from lethal aggression (Wilson et al., 2014), and neither females nor males direct aggression against immigrant females (Furuichi, 2011). On the other hand, bonobos tend to be less tolerant than chimpanzees when competing for access to lumped food sources (Jaeggi, Stevens, & Van Schaik, 2010) and in the context of food competition, females may launch cooperative charges against males (Nurmi et al., 2018; Tokuyama & Furuichi, 2016). Moreover, a recent study found that every sixth case (13%) of male aggression was directed against immature group members (Surbeck & Hohmann, 2013). The goal of this study is to explore the extent to which male aggression against immature individuals fits with predictions of the adaptive male infanticide hypothesis. This hypothesis explains infanticide as a strategy of intra-sexual competition for mating opportunities among males. The rationale is that by killing immature individuals, male perpetrators reduce the fitness of competing males and enhance mating opportunities by inducing the victims' mother to resume cycling. This way, males do not only eliminate the offspring of another male but they shorten the time until the female can conceive again.

If the aim of male aggression against immature individuals is infanticide, one would expect that males: (i) only target infants sired by other males; (ii) focus aggression on young infants that require an extended period of maternal care which is likely to prevent the mother from resuming cycling; and (iii) use physical force that is likely to have lethal consequences. Although the adaptive male infanticide hypothesis does not predict variation with the infants' sex, data from spider monkeys (Alvarez et al., 2015), chimpanzees (Hiraiwa-Hasegawa & Hasegawa, 1994; Wrangham et al., 2006), and humans (Hrdy, 1979) indicate a bias of male infanticide toward male offspring. Therefore, we also examine whether offspring sex plays a role in infanticide.

There are other forms of aggression from adults against immature individuals that serve different functions. Resident males and females direct aggression against immature intruders of the same sex (MacCormick et al., 2012) and may also use aggression to evict natal immatures of the migrating sex (Isbell & van Vuren, 1996). Adult males may evict immature natal females to recruit unrelated mating partners (Pusey & Packer, 1987). Adult males may target older immature individuals to enforce their superior status over immature individuals (Horrocks & Hunte, 1983). Unlike infanticide, these forms of aggression do not aim at killing the target and involve immatures of older age rather than dependent infants. There are species-differences in terms of age and sex of targets as well as the context of aggression. Yet, the inferred function of aggressive acts against older immatures is resource competition, in which the targets of aggression soon compete with the aggressor for the same resources (MacCormick et al., 2012).

## 2 | METHODS

### 2.1 | Study site and subjects

We collected data from habituated bonobos at LuiKotale (2°45.610′S, 20 ° 22.723′E), Democratic Republic of Congo (Hohmann & Fruth, 2003). During the data collection period (2007–2012) the study community comprised 29–41 individuals including 3–5 adult (15 years and older) and 2–4 sub-adult (8–14 years) males, 9–11 parous and 2–7 nulliparous females, and 11–17 immature individuals (<8 years) that were offspring of resident females. The average party size of adult individuals was 8.48 (range 4–14) and party composition was biased toward females (average # adult males = 2.64, average #adult females = 5.89). Age estimates for most individuals born before the year 2007 were based on physical characteristics such as body size, dentition, and (in females) genital swellings (Hohmann, Gerloff, Tautz, & Fruth, 1999). Long-term records from LuiKotale enabled us to assign the age of younger individuals to the day or the month of birth. Males engaging in aggression against immature individuals were resident members of the study community since the beginning of the project and were estimated to be between 10 and 35 years of age.

### 2.2 | Paternity assessment

We used genetic paternity assignments to determine whether males were less aggressive toward immature individuals they had sired. We detailed the genotyping of 39 bonobos and the process of paternity assignment for five offspring in a previous study (Schubert et al., 2013). In brief, DNA was extracted from noninvasively-collected fecal samples and genotyped at 19 highly-variable microsatellite loci with replication to ensure accurate results (Arandjelovic et al., 2009; Schubert et al., 2013). We recently genotyped 31 bonobos at a subset of 13 of these microsatellite loci (Surbeck, Langergraber, Fruth, Vigilant, & Hohmann, 2017) using an updated multiplex protocol described in detail by McCarthy et al. (2015). Four of these individuals were previously genotyped, and were retyped to ensure that allele identification was consistent between studies. Paternity analysis was

conducted as previously described by using both mismatch analysis and likelihood analysis approaches in CERVUS 3.0 (Kalinowski, Taper, & Marshall, 2007). The five previous paternity assignments (Schubert et al., 2013) were confirmed and paternity was newly assigned to 15 group offspring (Surbeck, Langergraber et al., 2017). Of the 60 cases of male aggression against immature individuals analyzed in this study, 17 cases involved targets for which the paternity was unknown. However, comparison of genotypes of the immature and the aggressor revealed in all these cases a mismatch, that is, the aggressor could always be excluded as being the father of the target.

## 2.3 | Behavioral observations

As elsewhere, LuiKotale bonobos engage in fission–fusion grouping with the majority of subgroups (parties) consisting of both sexes (Hohmann & Fruth, 2002; Surbeck, Girard-Buttoz et al., 2017). Events of male aggression against immature individuals were recorded either during individual focal follows or during party follows as all occurrence data (Altmann, 1974). Focal follows lasted for 10 min (2007–2009) or 5 min (2010–2012), respectively, and follows of the same individual were separated by at least 1 hr. Party follows ranged from 4–12 hr. There were 2112 hr of party follows and 470 hr of focal follows during the first period (2007–2009) and 2656 hr of party follows and 525 hr of focal follows during the second period (2010–2012). Dominance relations were linear among resident males (Surbeck et al., 2012), stratified among females (Moscovice et al., 2017), and co-dominant between the sexes (Surbeck & Hohmann, 2013).

## 2.4 | Aggression

For the purpose of this study aggression refers to aggressive behavior with physical contact such has hitting, tearing, biting, or dragging. Chases that induced escape and submissive vocalizations of the victim were considered as attempts by the aggressor to engage in physical contact and were also recorded.

## 2.5 | Age of targets

The age of targets of male aggression was either known from the records of the LuiKotale Bonobo Project (e.g., day, week, or month of birth), or, for older individuals, estimated based on observed mother-infant interactions such as nursing and other types of maternal care such as carrying, joint nest use, and coordination of travel at an earlier time. In bonobos, maternal care can be extensive and may exceed the time of weaning. Nursing is thought to be intensive for the first 12 months but it may take several more years until an offspring is entirely weaned. Reports of inter-birth intervals range from 4.8 at Wamba (Furuichi, 1989) to 9 years in Lomako (Knott, 2001). In the absence of more precise information on the duration of lactation amenorrhoea, we included all events when the target of aggression by males was estimated to be up to 8 years, as this coincides with the estimated time of conception given the largest inter-birth intervals.

## 2.6 | Data analysis

To test the influence of infant age and relatedness on the probability in aggression of males against immatures we used a Generalized Linear Mixed Model (GLMM; Baayen, 2008). The response variable was whether or not a given immature individual received aggression when an aggressive act by a male toward an immature individual in the same party was observed. Hence, the model was fitted with binomial error structure and logit link function (McCullagh & Nelder, 1989). Consequently, the model was fitted on a data set conditional on that an aggression against an immature took place, that is, each aggressive event of a male against an immature was included in the data, whereby all potential targets (i.e., all immature individuals present in the same party) were included as potential targets in the data set. To test whether males were less likely to aggress their own offspring, we included whether or not the immature individual was the offspring of the aggressor as a fixed effect (factor with levels no or yes) in addition to the fixed effect of infant age.

We controlled for the particular event (i.e., party ID), as well as the identities of the males, the immatures, and their mothers by including them as random effects in the model. We also included the identities of the male-female dyad and the male-immature dyad as random effects since it seemed possible that aggression rates varied due to special relationships such as friendships (e.g., Smuts, 1985). To control for the number of immatures in the party trivially leading to the finding that the smaller the party the more likely any given immature was to be the target of aggression, we included the log-transformed inverse of the number of immatures present in the party as an offset term into the model (McCullagh & Nelder, 1989). To keep type I error rates at the nominal level of 0.05 we included the needed random slopes components (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009) of infant age within all random effects as well as that of own-offspring within mother ID. To rule out a lack of power due to the model being too complex we fitted a reduced model lacking all random slopes, which revealed in essence identical results. As an overall test of the effects of immature age and the kinship between aggressor and target we compared the initial full model as described above with a null model lacking these terms (Forstmeier & Schielzeth, 2011) but comprising all others present in the full model using a likelihood ratio test (Dobson & Barnett, 2008). We derived significance for paternity and infant age by comparing the full model with respective reduced models lacking these effects but being otherwise identical to the full model (Barr et al., 2013). To test for the influence of the sex of the target of male aggression on the occurrence of male aggression and a potentially differentiated influence of immature age depending on its sex, we fitted an additional model with all parameters of the initial full model including sex of the offspring and its two-way interaction with offspring-age as fixed effect, but without random slopes (we decided against including sex of the immature and its interaction with immature age in the original full model to avoid over-parametrization). The sample for all models encompassed a total of 60 aggressive events by six males with a total of 321 potential targets

(23 immature individuals of 11 mothers, forming 86 male-immature dyads, and 49 male–female dyads.

All models were fitted in R (version 3.4.1; R Core Team, 2013) using the function glmer of the R package lme4 (version 1.1-13; (Bates, Mächler, Bolker, & Walker, 2014). We determined model stability by excluding levels of random effects (i.e., individual party IDs, males, immature individuals, females, male–female as well as male-immature dyads) one at a time. Such an approach allows the identification of levels of random effects which are highly influential on the model results and account for non-independence of observations from the same respective level of a random effect (Bates, Maechler, Bolker, & Walker, 2013; Nieuwenhuis, te Grotenhuis, & Pelzer, 2013). This revealed large uncertainty but consistent signs of model estimates for the intercept and infant age. However, the model estimates concerning the effects of whether it was the own offspring of the aggressor were associated with a large uncertainty and inconsistency (see Table 1). We derived confidence intervals by means of a parametric bootstrap (function bootMer provided by the R-packet lme4; Bates et al., 2013).

# 3 | RESULTS

The 60 observed cases of aggression by males against immature individuals were committed by six males, with the alpha male accounting for 58% and another high-ranking male for 23% of all cases. In all cases male aggression was clearly directed at immature individuals, unidirectional, and apparently unprovoked. Aggression was directed 24 times against four different male offspring (average number of male offspring present in party during aggression against immatures ± SD = 2.27 ± 0.47), and 36 times against six different female offspring (average number of female offspring present in party during aggression against immatures ± SD = 3.08 ± 0.47). The average age of the targets of male aggression was 5.9 years (range 3–7.9 years), and males were never seen to direct aggression against dependent infants.

## 3.1 | Nature of male aggression

Considering the relative intensity of male aggression (see Table 2 for a tentative classification of aggressive events), we found that the attempts of males to physically aggress to infants resulted in most cases in actual physical aggression (N = 54), and in only a few cases the

targets of male aggression managed to escape (N = 6). Looking only at the former cases, the majority (N = 38) included forceful acts such as grabbing an immature by the leg or arm and dragging it along the ground and up into trees (N = 16), biting (N = 6), and hitting (N = 16). In one case, a male pushed the immature target out of a tree and in two other cases, immature individuals fell out of trees when chased. In these cases, immature individuals fell from heights of up to 10 m, hitting the ground very hard, and in two out of the three cases they were apparently unable to move and had to be retrieved by the mother. In nine cases males held on to their targets for up to 40 min and engaged in repeated aggressive acts such as dragging them on the ground and up into trees, biting, hitting, and twisting limbs. Taken together, the majority of observed cases (N = 41 or 68%) involved physical force, exposed targets to risks of injury, and in some cases, had the potential of inflicting lethal damage. In all cases of male aggression against immature individuals, targets screamed, tried to escape from males, and showed other signs of stress and discomfort.

## 3.2 | Kinship between aggressor and target

Males attacked their own offspring in six cases and offspring sired by other males 54 times. While there were more cases of aggression by unrelated males, males did not target their offspring significantly less than unrelated immatures (GLMM: estimates ±SE, 1.44 ± 0.95, $\chi^2 = 1.04$, df = 1, p = 0.31; Table 1). The full model was significantly different from the null model ($\chi^2 = 15.10$, df = 2, p = 0.001).

## 3.3 | Age of targets of male aggression

The age of the immatures had a significant influence on the likelihood of being the victim of male aggression (GLMM estimates ±SE, 2.27 ± 0.40, $\chi^2 = 15.09$, df = 1, p < 0.001; Table 1). The older the immature individual the more likely it was to be the target of aggression (Figure 1).

## 3.4 | Sex of target of male aggression

There was no significant difference in terms of the age at which immature females and males became target of male aggression (GLMM estimates ±SE, −0.58 ± 1.00, $\chi^2 = 0.37$, df = 1, p = 0.54). Likewise, the sex of targets of male aggression had no significant influence on the likelihood of being targeted by males (GLMM estimates ±SE, −0.12 ± 0.74, $\chi^2 = 0.03$, df = 1, p = 0.87; assessed from model lacking

**TABLE 1** Results from the General Linear Mixed Model examining the effects of age and relatedness of target on male aggression

| | Estimate | SE | Lower CI | Upper CI | $\chi^2$ | df | p | Min | Max |
|---|---|---|---|---|---|---|---|---|---|
| Intercept | −1.454 | 0.598 | −5.681 | −0.552 | | | [a] | −2.192 | −1.135 |
| Age[b] | 2.273 | 0.398 | 1.583 | 4.358 | 15.091 | 1 | <0.001 | 1.988 | 2.741 |
| Offspring[c] | 1.441 | 0.948 | −9.330 | 4.622 | 1.036 | 1 | 0.309 | −16.198 | 2.150 |

[a]Not indicated because of having a very limited interpretation.
[b]Z-transformed; mean and sd of the original variable were 1,458 and 803 days.
[c]Dummy coded with not offspring being the reference category.

**TABLE 2** Type and distribution of male aggression against immature individuals

| Type | Type of aggression | Age | Sex |
| --- | --- | --- | --- |
| Intense physical attack (N = 16) | Repeated attacks, often of long duration, aggression inflicts visible wounds | 4–6 | Males |
| Physical aggression (N = 38) | Single attacks that stop after brief contact between target and aggressor | 3–7 | Both sexes |
| Directed chase= (N = 6) | Directed aggression against specific target without physical contact | 4–8 | Both sexes |

The two last columns refer to the targets age (in years) and the sex.

the interaction). However, immature males were more likely to receive intense aggression from adult males than immature females (Table 2).

## 4 | DISCUSSION

In this study representing 5763 hr of field observations we observed male aggression against immature individuals 60 times, showing that such aggression is infrequent but not absent in bonobos. With regard to male infanticide, the evidence presented in this study does not support predictions of the hypothesis: First, although males grabbed and forcefully held on to the victims, they did not kill them. Second, males did not direct aggression significantly more frequently at offspring sired by other males. Third, males preferentially directed aggression toward weaned offspring.

Although the majority of cases reported here involved physical contact, and although victims of male aggression were sometimes exposed to a high risk of physical damage, male aggressors did not mutilate their victims. This is in contrast to what has been described from common chimpanzees, in which males kill their victims by biting, tearing them apart, or hitting them against tree trunks. Moreover, in chimpanzees infanticide is often followed by cannibalism, behavior that appears to be absent from infanticide in gorillas and most other primate species. By contrast, aggression by male bonobos was modest and appeared to be assaults rather than attempts to kill. This raises two



**FIGURE 1** Probability of being the target of male aggression as a function of the immature individual's age in years. Shown are the observed probabilities per year of age (open circles), the model estimates (dashed line), and the 95%CI (dotted lines). The area of the circles corresponds to the sample size per year of age (N = 15–65 potential targets)

questions: (i) what prevents male infanticide in bonobos and (ii) why do adult males engage in physical aggression against immature individuals?

### 4.1 | What prevents male infanticide in bonobos?

In bonobos, females can copulate with multiple males during a single reproductive cycle (Furuichi & Hashimoto, 2002). Copulations are sometimes advertised by copulation calls; behavior that may induce mating with multiple males (Clay & Zuberbühler, 2011). Furthermore, changing states of fecundity are ambiguous as: (i) females show cyclic changes of sexual swellings even at times when fecundity is low such as during pregnancy and early lactation (Douglas et al., 2016); (ii) the duration of maximum swelling phase (MSP) varies within and between females (Douglas et al., 2016); and (iii) ovulation is often outside the MSP (Douglas et al., 2016; Reichert, Heistermann, Hodges, Boesch, & Hohmann, 2002). In combination, these female traits provide conditions that are likely to reduce the ability of individual males to monopolize mating and to focus mating effort to the time when fecundity is highest. These strategies should be sufficient to confuse paternity in a way to prevent male infanticide. Adopting the general concept of paternity confusion as outlined above, one could argue that the absence of male infanticide in bonobos is the result of female sexual behavior and a reproductive physiology that has evolved as a counter strategy to male infanticide. Given this, other questions emerge. Does the mating behavior of female bonobos lead to a low paternity skew, and why are female bonobos more successful in adopting mating strategies that prevent male infanticide than female chimpanzees? First, a recent assessment of the genealogy of the bonobo community involved in this study revealed an unexpected paternal skew toward the alpha male (Surbeck, Langergraber et al., 2017), the same individual accounting for more than 50% of cases of male aggression against immature individuals. Thus, while the mating of female bonobos with multiple males may prevent mating skew, it does not necessarily prevent skew in paternity. Second, there is evidence that male chimpanzees show selective paternal care (Lehmann, Boesch, & Fickenscher, 2006; Murray, Stanton, Lonsdorf, Wroblewski, & Pusey, 2016) suggesting that in spite of mating with multiple males by females, paternity confusion is not complete. If the ability of male chimpanzees to identify their own offspring exceeds that of male bonobos, this could explain species-differences in within-group infanticide. If male bonobos are not able to identify their own offspring, the benefits from male infanticide would be diminished and males may refrain from killing immature individuals. The fact that there is evidence for both paternity confusion and paternal investment
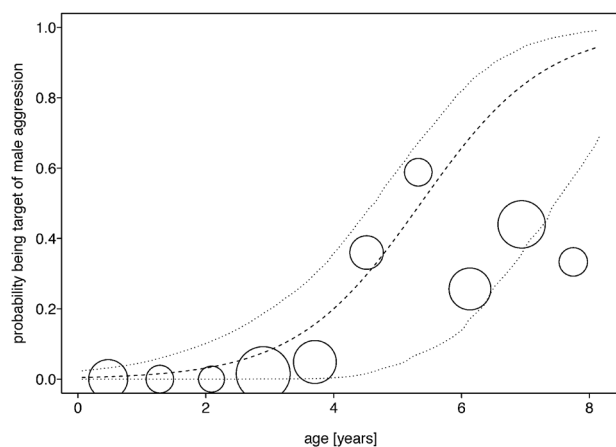
offers an interesting topic for future work, as it suggests that female chimpanzees may use alternative mating strategies to prevent male infanticide and/or that male chimpanzees have means for book keeping of their mating activities. What remains unresolved is that bonobos show a suit of traits that is found in those species in which males do benefit from infanticide (Lukas & Huchard, 2014) on one hand, and the absence of this behavior on the other.

## 4.2 | Why do male bonobos direct aggression against immature individuals?

One common function of non-lethal aggression against immature individuals in other species is to enforce dispersal. While both females and males may use severe aggression in this context, it is often biased toward the migrating sex (Lawson Handley & Perrin, 2007). In bonobos, migration is female biased (Gerloff, Hartung, Fruth, Hohmann, & Tautz, 1999), targets of male aggression were weaned individuals, and, in case of females, close to the age when females are likely to transfer to other communities. This suggests that aggressive acts by males against immature and weaned females may enhance early transfer of the targets. Yet, as our analyses suggests, the sex of immature individuals did not affect the probability of males directing aggression against them. If the aim of male aggression against young females is to evict offspring, what could explain aggression against immature males? One possibility is that adult males gain by evicting both sexes. Eviction of the philopatric sex has been observed in red fronted lemurs and banded mongooses, and in these cases it has been explained as a strategy that decreases reproductive competition (Kappeler & Fichtel, 2012; Thompson et al., 2016). In our study, one juvenile male who had been repeatedly targeted by his putative father and other males separated from his mother and the rest of the community and eventually disappeared. The long-term records from LuiKotale note some cases in which unknown juvenile males visited the study group without becoming resident members, one case of immigration of an adult male into an existing community was reported from another site (Hohmann, 2001), and genetic data suggest occasional male transfer (Schubert et al., 2013). While these data do not allow firm conclusions, they hint at the possibility that male philopatry in bonobos may be facultative. This behavior could explain why resident males challenging immatures refrain from exerting lethal aggression and why this strategy is targeted specifically at individuals who are able to meet their nutritious requirements.

Another possibility is that male aggression against immature males serves as a means to maintain dominance relations. Although the pattern of male philopatry requires a certain degree of tolerance among males, it does not eliminate intra-sexual competition for access to resources. Recent analyses revealed that the effect of kinship is restricted to close relatives (e.g., sons of the same female) and is not a driving force for cooperation and alliance formation in this species, confirming the evidence that the advantages deriving from inter- actions among close kin may be limited (West, 2002). Male bonobos show a linear dominance hierarchy that is reinforced by physical aggression and displays (Surbeck et al., 2012). Rates of male aggression increase with dominance status (Surbeck et al., 2012) and a recent analysis of kin relationships indicated that paternity success is skewed toward the alpha male (Surbeck, Langergraber et al., 2017). By directing non-lethal aggression toward young males, older males may reinforce their superior status toward individuals that will soon compete for the same resources. In chimpanzees, intra-community infanticide is heavily biased toward male offspring (Wrangham et al., 2006), which may also suggest that aggression by adult males toward immature males reflects intra-sexual competition.

An entirely different approach in exploring the function of male aggression against immature individuals would be to test whether the aim of male aggression is to elicit a response from the victims' mother. In this case the behavior could resolve ambiguity in inter- sexual dominance relations or provide information about the probability that a given female is able to be recruited for agonistic support. The rationale for this argument is that in species in which grouping patterns fluctuate due to fission–fusion, aggressive interactions are rare (de Silva, Schmid, & Wittemyer, 2017) and the strength of social relations among females varies with context (Moscovice et al., 2017). Moreover, information about female alliances may be more difficult to obtain than in species with stable grouping patterns and frequent dominance interactions. Exploring these and related questions can contribute to a better understanding of the function of male aggression in a social system that is obviously different from that of closely related species. As in the case of other primates, bonobos use aggressive behavior in contexts such as resource competition, male-male competition, and during encoun- ters with individuals from neighboring groups (Jaeggi et al., 2010; Sakamaki et al., 2018; Surbeck et al., 2012). Instead of assuming an overall lower level of aggression in bonobos, the discrepancy in aggressive behavior between bonobos and chimpanzees may reflect differences in function. Female coalitionary support and the lack of male bonding are likely to increase the costs of male aggression against females and may render aggressive mating strategies less efficient. How males adjust their behavior to that of females and what benefits derive from male aggression are interesting topics for future studies on the aggressive behavior of bonobos.

## ETHIC STATEMENT

The data collection protocol used in the field was in compliance with the regulations of the Congolese Wildlife Authority (ICCN) and adhered to the ethical guidelines of the Max-Planck-Society.

## CONFLICTS OF INTEREST

The authors declare that they have no conflicts of interest.

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