



## Male aggression and sexual coercion in wild West African chimpanzees, *Pan troglodytes verus*

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Sexual conflict has an important selective influence on mating strategies, particularly in promiscuous species such as chimpanzees. Males may coerce females to mate and aggression may inhibit female choice. The effect of male coercion on females has rarely been examined in primates. The present study focuses on male aggression towards females and the influence of male coercion on female choice in two communities of wild chimpanzees in the Tai National Park, Côte d'Ivoire to determine (1) whether male-to-female aggression increases in a sexual context, (2) the frequency, context and efficacy of male-female aggression and (3) the influence of male coercion on female choice.

Our results suggest that direct male coercion was relatively rare, was used by less preferred males, and did not seem to function effectively to constrain female mate preferences as neither (1) a general measure of overall male-female aggression nor (2) a specific measure of direct sexual coercion corresponded to male mating success, and (3) male aggression did not correspond to increased female proceptivity or decreased female resistance rates. Lastly, variation in male-female sexual strategies appears to be yet another important realm for behavioural diversity in chimpanzees. This detailed examination of chimpanzee male-to-female aggression emphasizes the importance of carefully distinguishing male and female influences on sexual interactions in light of their disparate reproductive interests.

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Across many species, sexual conflict exists between females and males for control of mating opportunities (Arnqvist & Rowe 2005). Because of sex differences in gamete availability and parental investment, males in most species attempt to mate with multiple females to increase their reproductive success, while females attempt to mate selectively and invest in their offspring (Darwin 1871; Trivers 1972). These differences in the evolutionary interests between males and females lead to intersexual conflict (Parker 1979), most notably manifested through female choice and male sexual coercion. Male sexual coercion, defined as the use or threat of force in a sexual context (Smuts & Smuts 1993), is one strategy that a male may use to constrain female choice. Male coercion may serve either to increase the probability that a female will mate with the aggressor or to decrease the chances that she will mate with other males, at some cost to herself (Smuts & Smuts 1993). Factors such as female choice and male sexual coercion are increasingly recognized as causes of differential mating and reproductive

success among individuals (Cunningham 1986; Smuts & Smuts 1993; Clutton-Brock & Parker 1995; Wiley & Poston 1996; Stumpf & Boesch 2005) and thus are thought to be under strong selective pressure. Examining sexual conflict, particularly the influence of male and female strategies on the outcomes of sexual interactions, is challenging, yet fundamental to our understanding of these important evolutionary mechanisms. In previous studies, we examined the nature and effectiveness of female mating preferences in wild chimpanzees in the Tai National Park, Côte d'Ivoire (Stumpf & Boesch 2005, 2006), and in the present study, we examined the nature and efficacy of male coercion in the same study population.

Male aggression towards females is prevalent across many mammalian taxa and is expressed in many forms (Hrdy & Hausfater 1984; Smuts & Smuts 1993; Clutton-Brock & Parker 1995; Andersson & Iwasa 1996; Watts 1998; Kokko et al. 2008). Some male-female aggression is associated with sexually active, oestrous females and/or with mating (i.e. the use of threat or force in a sexual context), whereas male aggression can also be directed towards nonoestrous females. Coercion in a sexual context can be labelled 'direct' or 'indirect', based on how it may influence the actor's mating success. Direct coercion can increase the chances that a female will mate with the aggressor in three ways: through

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forced copulation (when a male mates by physically restraining a resisting female), harassment (when a male's aggressive or persistent mating attempts cause a female to lessen such a high cost by mating with the male), and intimidation (when a male punishes a resistant female, thereby increasing the chance of mating with her in the future) (Clutton-Brock & Parker 1995). Indirect coercion occurs when males attempt to decrease the relative mating success of other males through mate guarding, punishment of females that attempt to mate with other males, copulation interference, herding and sequestering females, and even infanticide (Hrdy & Hausfater 1984; Smuts & Smuts 1993). Nonsexual aggression refers to male aggression towards females in contexts other than mating (e.g. feeding competition, social dominance, displaced aggression, male pawns, policing). Here, we examine general male–female aggression (including both sexual and nonsexual aggression) as well as specifically focus on direct coercion alone.

A greater understanding of the influence of male coercion is valuable for several reasons. Male coercion has only relatively recently been recognized as an important, sexually selected male strategy (Smuts & Smuts 1993), yet the nature, context and function of male–female aggression lacks consensus (Smuts & Smuts 1993; Clutton-Brock & Parker 1995; van Schaik et al. 2004; Wrangham & Muller 2009) and few empirical studies exist (van Schaik et al. 2004). Little is known about factors contributing to the occurrence, timing and frequency of male–female aggression generally and specifically during sexual interactions. Because females are often smaller and subordinate to males, male coercion can potentially affect the expression and efficacy of female choice. Moreover, male coercion holds the potential to impede our recognition of female choice, (i.e. to determine whether female mate preferences are real or simply a response to male coercion). For example, while female choice appears to be an effective and important component of sexual selection in chimpanzees (Stumpf & Boesch 2006), if male aggression influences the expression of female choice, what appears to be female preference may actually be risk avoidance response. Alternatively, female proceptivity and resistance behaviours may be honest indicators of female mating preferences. Examining both male and female sexual strategies and evaluating their effectiveness is important for understanding sexually antagonistic coevolution and the evolutionary influences of sexual selection. To this end, we closely examined wild chimpanzees male–female aggression and specifically male–female aggression in the context of mating.

Wild chimpanzees live in stable, multimale, multifemale communities, where males are philopatric and females generally emigrate during adolescence and remain within their new community throughout their lifetime (Goodall 1986; Boesch & Boesch-Achermann 2000). Chimpanzee association patterns are characterized as fission–fusion, whereby individuals within a community come together and separate several times throughout the days, weeks or months, such that subgrouping patterns are flexible and variable. Chimpanzee males are dominant to females, aggression is frequently observed, and females are often victims (Goodall 1986; Muller 2002). In this study, we closely examined chimpanzee direct coercion in order to evaluate its function and efficacy and to test the predictions of the sexual coercion hypothesis (Smuts & Smuts 1993). According to Smuts & Smuts (1993), since male aggression against females occurs in various contexts, to be considered sexual coercion, male aggression should (1) increase in reproductive contexts, (2) correspond to increased male mating success and (3) incur a cost to females. In one of the most thorough studies to date of male coercion in wild chimpanzees (*P.t. schweinfurthii*) of the Kibale National Park, Uganda, Muller et al. (2007) found support for the male coercion hypothesis. However,

behavioural diversity across chimpanzee populations is extensive, with abundant cross-population differences ranging from variation in grooming habits to social organization (Whiten et al. 2001; Boesch 2009). For example, the Tai chimpanzee population (*P.t. verus*) is considered 'bisexually bonded' (Boesch & Boesch-Achermann 2000; Lehmann & Boesch 2005), whereby males and females associate and socialize together frequently, in contrast to the male-bonded social organization characteristic of eastern chimpanzees (*P.t. schweinfurthii*) (Wrangham 1975; Boesch 2009). In light of these differences in male–female relationships across chimpanzee sites, the pattern and function of male aggression towards females may also differ.

In this investigation of patterns of male aggression towards females in Tai chimpanzees, if male aggression functions as sexual coercion, we expected it to (1) increase in sexual contexts, (2) influence female behaviour and (3) result in increased mating success by aggressive males. To this aim, we examined the following four questions.

#### (1) *When are Males Aggressive towards Females?*

If male–female aggression functions to coerce females and increase male mating success, it should increase in sexual contexts, specifically (1) during the sexually active phase, and more specifically, during the periovulatory period (POP) when conception is most likely. We examined the timing of all male–female aggression to shed light on its functional significance.

#### (2) *How Effective is Direct Coercion and When Does it Occur?*

If male sexual aggression is effective, it should be relatively common and result in increased mating success for the aggressor. Male aggression towards females may function to threaten females into mating. If so, aggression should occur prior to the sexual interaction, which may then increase the likelihood that the female mates with the coercive male (Clutton-Brock & Parker 1995). Alternatively, male aggression after female mating resistance may function to intimidate females by punishing resistance, thus inducing future cooperation (Clutton-Brock & Parker 1995). Thus, we closely examined male aggression in the context of mating (direct coercion) to shed further light on its function.

#### (3) *Does Male Aggression Influence Female Preference and Female Choice?*

The male coercion hypothesis predicts that male aggression constrains female choice. Because conception likelihood is highest in the periovulatory period (POP), sexual conflict should be particularly active in this phase. Thus, male sexual aggression should correlate with decreased female resistance, increased female proceptivity and mating success during the POP. If general (sexual and nonsexual) male–female aggression functions as coercion, we should also expect similar effects. We also examined whether greater female proceptivity, lower resistance rates and higher mating success are better explained as indexes of male coercion than as indexes of female preference.

#### (4) *Which Males are Sexually Aggressive?*

More aggressive males may be more likely to manipulate, coerce and intimidate females into mating with them against their will. Higher-ranking males may be more aggressive towards females than are lower-ranking males. Consequently, we examined the relationship between male sexual aggression and male rank.

## METHODS

### Observation Methods

Data were collected on two habituated chimpanzee (*Pan troglodytes verus*) communities in the Tai National Park, Cote d'Ivoire (see Boesch & Boesch-Achermann 2000 for a detailed description of the study site). Over 2600 h of all-day, continuous focal follows (Altmann 1974) were conducted on 14 parous, cycling females interacting with seven sexually mature males (Table 1) during oestrous and nonoestrous days. Data from multiple menstrual cycles were collected for 10 females. Chimpanzee male sexual maturity occurs around 10 years of age (when spermatogenesis begins and males are capable of siring offspring; see Tutin 1979; Boesch et al. 2006). As male coercion is defined as aggression by sexually mature males against estrous females (Smuts & Smuts 1993; van Schaik et al. 2004), we included all sexually mature males. Although it is possible that frequencies or forms of male–female aggression potentially may differ by male age, rates of aggression (both sexual and nonsexual) by younger males in the present study were intermediate between those of other males, suggesting that inclusion or exclusion of these younger males does not alter the patterns and conclusions. Male aggressive behaviour was defined as hitting, biting, slapping, pounding, kicking, chasing, dragging, manhandling or displaying a female. Although sexual coercion refers specifically to aggression in a sexual context (Smuts & Smuts 1993), any male–female aggression (sexual or nonsexual) might also function as sexual coercion (Smuts & Smuts 1993; Wrangham & Muller 2009). Thus, we included detailed observations of all instances of male aggression towards females (oestrous and nonoestrous), with specific attention to aggressive behaviour within sexual interactions. Sexual interaction data included: (1) premating interactions between the dyad, (2) the sexual initiator (male or female), (3) detailed response (resist or

cooperate), (4) the outcome (copulation or not), (5) postmating interactions between the dyad, (6) other individuals present, and (7) the behaviour of other individuals towards the dyad. Behavioural observations were recorded using a Psion Workabout™ handheld computer (Psion LTC, London, U.K.), with Observer 3.0 software (Noldus Information Technology, Wageningen, The Netherlands).

Sexual interactions initiated by males generally all follow the same pattern in chimpanzees. Males solicit matings, females respond by either accepting or resisting the solicitation, and mating either occurs or does not occur (Tutin 1979; Stumpf & Boesch 2005; for a detailed description of chimpanzee courtship and copulatory behaviour, see Tutin 1980). In sexual interactions, male–female aggression can occur in the context of the solicitation ('aggressive solicitation'), after a female has resisted a solicitation (i.e. 'intimidation'; Clutton-Brock & Parker 1995), or even after mating. We defined 'aggressive solicitation' as aggression aimed at the target female within 5 min before a solicitation, and we defined 'resistance aggression' and 'postmating aggression' as aggression aimed at the target female within 5 min after her resistance or mating, respectively. The end of a sexual interaction sequence was marked by copulation, by initiation of a different activity (such as feeding), or by one of the two subjects leaving the party. Within the same dyad, successive male solicitation or aggression was counted independently if separated by more than 10 min from the last solicitation or aggression.

Male aggression rates for each dyad were measured in two ways: (1) a count of male-initiated sexual interactions involving aggression divided by all of that dyad's sexual interactions and (2) a count of all dyadic male–female aggression divided by (a) the dyadic association (presence in the party) time or (b) the observation time for each female. Although male–female aggression in a sexual context is termed sexual coercion, it is possible that male–female aggression in a nonsexual context may also be considered sexual coercion. Thus, this second measurement takes into account all male aggression aimed at females, not just during sexual interactions.

### Dominance Rank

Ranks of males and females were determined by the unidirectionality of pant-grunts, which are submissive vocalizations (Bygott 1979; Wittig & Boesch 2003). Ranks in males were linear. Females were grouped into five rank categories, from high to low, based on all group females. When relative rank between two females could not be determined, they were regarded as occupying the same rank ( $N = 8$  dyads). Males and females were grouped into four age categories based on long-term data records (Table 1).

### Determination of Oestrous Phase

During their cyclical sexually active phases, chimpanzee females develop large perineal swellings. The swelling phase lasts an average of 10–12 days (Tutin & McGinnis 1981; Stumpf 2007) and can be divided into two parts: a longer nonperioovulatory phase (non-POP), during which conception is unlikely, and a 3–4-day perioovulatory period (POP) during which conception most likely occurs (Elder & Yerkes 1936; Stumpf & Boesch 2005). Urine from estrous females was collected daily and ovulation and the delineation of POP was determined noninvasively using ovulatory test kits (Ovuquick™; Quidel Corp., San Diego, CA, U.S.A.) shown accurate and reliable for chimpanzees (Stumpf & Boesch 2005). The perioovulatory period (POP) was defined as 3 days prior to and including ovulation (see Stumpf & Boesch 2005). Nonoestrous females were nontumescent and nonsexually active.

**Table 1**  
Female and male chimpanzees included in the present study

Individuals	Group	Rank	Age	Oestrous phase cycles		
				Total	Non-POP	POP
<b>Females</b>						
Duna	South	High	1	4	3	4
Sumatra	South	High	2	3	2	2
Tita	South	Middle-high	2	2	1	2
Zora	South	Middle-high	1	1	1	1
Isha	South	Middle-high	2	1	1	0
Margot	South	Middle	3	3	3	3
Atra	South	Middle	3	4	3	2
Mandy	South	Middle-low	3	1	1	1
Coco	South	Middle-low	3	2	2	1
Yucca	South	Low	2	3	3	1
Wapi	South	Low	2	2	2	0
Mystere	North	High	2	2	2	2
Belle	North	Middle	3	1	1	1
Perla	North	Middle	3	3	3	2
<b>Males</b>						
Zyon	South	1	2			
Kaos	South	2	3			
Mkubwa	South	3	1			
Sagu	South	4	4			
Macho	North	1→2	1			
Marius	North	2→1	3			
Nino	North	3	4			

Female rank: high; high-middle; middle; middle-low; low. Age (estimated): 1 = 35+ years; 2 = 25–34 years; 3 = 15–24 years; 4 = 10–14 years. Total cycle count may differ from non-POP and POP because not all phases were sampled from every cycle. Two males (Macho and Marius) exchanged ranks halfway through the study.

## Data Analyses

Female proceptivity was calculated as female-initiated sexual behaviour towards a male, with no preceding male sexual invitation (Stumpf & Boesch 2005). Proceptivity rates were calculated for each female–male dyad as the total number of unsolicited presentations by a female to a male, standardized by the dyadic association time during oestrus. Female resistance was calculated as female response to a male solicitation, either by cooperating (rapidly approaching the soliciting male and presenting for copulation; Tutin 1979), or resisting a male (ignoring the solicitation, avoiding the male, screaming, or leaving). Female resistance does not imply that copulation did not occur. It indicates just the female's initial response to a male's solicitation, to control for the potential influence of male coercion on the outcome of the sexual interaction. Following a failed male solicitation (i.e. successful female resistance), males solicited again  $88.4 \pm 23.6$  min later, or  $143.3 \pm 44.1$  min later when including data from days when no subsequent solicitations occurred (averaged across  $N = 7$  males, 14 females). Resistance rates were calculated for each female–male dyad as the total number of female resistance events divided by the number of male solicitations (Stumpf & Boesch 2005). Because male copulation counts (and rates) may be influenced by male mating effort (e.g. the number of male solicitations, whether aggressive or not), mating effort must be accounted for in any analyses of the relationship between male aggression and mating success. Thus, we quantified male sexual aggression rate for each dyad as a count of male aggressive sexual interactions divided by the total count of sexual interactions. We also quantified male sexual aggression rate for each dyad as a count of male aggressive sexual interactions divided by male solicitations, to control for the influence of male mating effort, but results were consistent with the above measure.

To take individual variation into account, dyadic rates of male sexual aggression towards females were correlated with copulation rates and counts as well as female proceptivity and resistance using the  $K_r$  row-wise matrix partial correlation test (Hemelrijk 1990). A second matrix test was done to compare general aggression (sexual and nonsexual) rates with copulation rates and counts and female proceptivity and resistance. Missing values (6/44, 13% for proceptivity, copulation counts and rates; 10/44, 23% for resistance) were partialled out of the correlations by creating a 'dummy' matrix containing a constant for missing values and a zero for nonmissing values (Hemelrijk 1990). We also added the same constant to missing values within the data matrices, and calculated a test statistic with the dummy matrix partialled out. Matrix tests were conducted only on the larger of the two study groups (South Group) because statistical significance for the  $3 \times 3$  table derived from the other group (North Group) could not be assessed (Hemelrijk & Ek 1991). We used Matman 1.1 software (Noldus Information Technology) to calculate the probability of the observed value following Mantel's (1967) procedure based on 10 000 permutations.

To determine whether changes in female behaviour are influenced by male behaviour, we used Spearman rank correlation coefficient tests (Spearman's rho) on data from both groups to examine whether male aggression was negatively and positively correlated with female resistance and proceptivity, respectively. We assessed differences in male aggression and solicitation rates between POP, non-POP and nonswelling phases using Friedman tests. First, to avoid pseudoreplication, we compared aggression rates between the three phases for individual females. We used post hoc Wilcoxon exact tests to determine whether male aggression rates differed across oestrous phases. Nonparametric tests were applied using (SPSS version 13.0; SPSS Inc., Chicago, IL, U.S.A.). For all tests, the  $\alpha$  level of significance was 0.05 (two tailed).

## RESULTS

Results are based on more than 2600 observation hours with data from 1449 sexual interactions and 1120 copulations. Individual females received aggression from males at a mean  $\pm$  SE rate of  $0.245 \pm 0.327$  occurrences/h (of dyadic association time) or  $0.078 \pm 0.24$  occurrences/h (of female observation).

### When Does Male Aggression towards Females Occur?

If male–female aggression functions to increase male mating and reproductive success, we predicted that more male aggression would occur during oestrus (and particularly during the POP) than during nonoestrus. Standardizing male aggression by female observation time (Fig. 1a), we found significant differences between oestrous phases (Friedman test:  $\chi^2_2 = 7.714$ ,  $P = 0.021$ ), with significantly more male aggression occurring during POP and non-POP than during nonoestrus (Wilcoxon post hoc tests: POP–nonoestrus:  $T = 7$ ,  $N = 6$ ,  $P = 0.016$ ; non-POP–nonoestrus:  $T = 7$ ,  $N = 7$ ,  $P = 0.008$ ; POP–non-POP:  $T = 4$ ,  $N = 7$ ,  $P = 0.469$ ). However, after standardizing male aggression by the dyadic association time, we found no significant difference in male aggression across the phases (based on females:  $\chi^2_2 = 4.255$ ,  $P = 0.119$ ; based on males:  $\chi^2_6 = 2.000$ ,  $P = 0.368$ ; Fig. 1b). This finding suggests that the significant differences in male aggression rates based on female observation time can be explained by greater male association with females during oestrus than during nonoestrus.

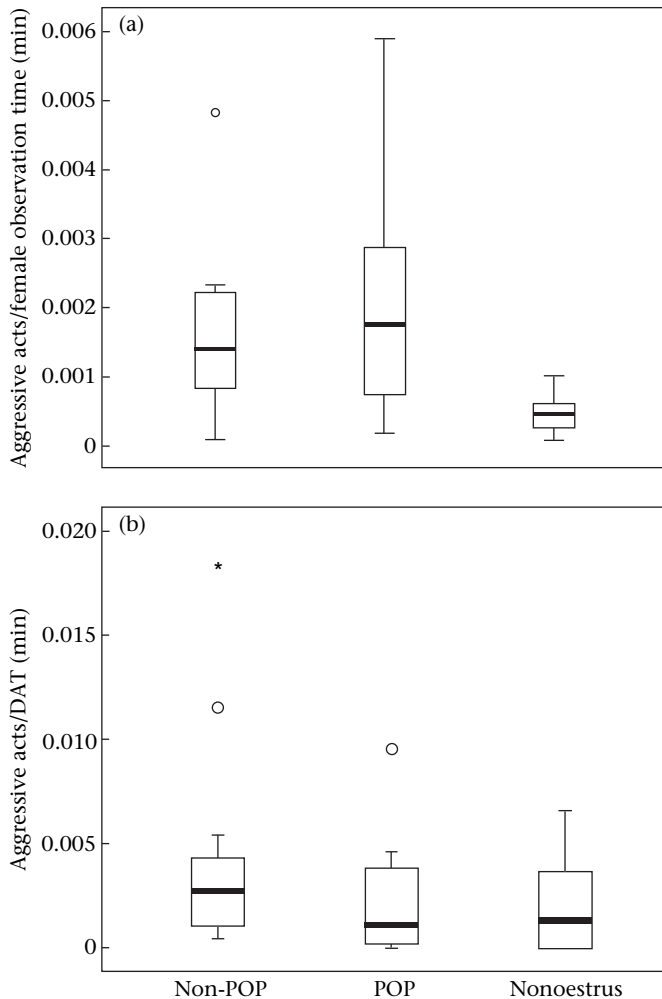
### What Is the Nature, Frequency and Efficacy of Direct Male Coercion?

Averaging across all males, only 11.6% of sexual interactions involved direct coercion (1449 sexual interactions, range 2.2–30%;  $T = 7$ ,  $N = 7$  males, 14 females,  $P = 0.018$ ; Fig. 2a). Male–female sexual aggression (direct coercion) occurred at three main junctures within a sexual interaction: (1) during solicitation, (2) after female resistance to solicitation and (3) after copulation. Based on individual averages for all males, 77.2% of male aggression towards females in a sexual interaction occurred in conjunction with the solicitation ( $\chi^2 = 11.185$ ,  $N = 2$ ,  $P = 0.004$ ; Fig. 2b). On average, 18.1% of aggression towards females occurred following resistance to solicitation, and 7% occurred after mating (Fig. 2b).

We then determined the efficacy of male sexual aggression (direct coercion) in attaining copulations, which is important if aggression has a potential reproductive benefit. When aggression occurred during solicitation (Fig. 2c), females responded by resisting over half (56%) of these cases, while mating cooperatively in 44%. When males aggressed after females resisted mating (i.e. intimidation), resistance was successful and mating did not occur in 78% of cases (Fig. 2d).

### Is Male Aggression towards Females Effective?

Male sexual aggression was not significantly correlated with female proceptivity ( $K_r$  matrix partial correlation:  $\tau_{rw;xy,z} = 0.08$ ,  $N = 11$  females, 4 males,  $P = 0.38$ ). Based on average male aggression rates towards females for all males in both communities, we found a strong negative correlation with female proceptivity (Spearman's rho:  $r_s = -0.821$ ,  $N = 7$ ,  $P = 0.023$ ; Fig. 3a). Similarly, we found no significant correlation between male sexual aggression and female resistance ( $K_r$  matrix partial correlation:  $\tau_{rw;xy,z} = -0.05$ ,  $N = 11$  females, 4 males,  $P = 0.49$ ). Correlating averages for all males in both communities, male sexual aggression showed a strong positive correlation with female resistance (Spearman's rho:  $r_s = 0.893$ ,  $N = 7$ ,  $P = 0.007$ ; Fig. 3b). Male sexual aggression and mating success were not significantly correlated



**Figure 1.** Box plots of median, upper and lower quartiles and whiskers indicating the range of variation in male aggression towards females during nonperiovulatory (non-POP), periovulatory (POP) and nonoestrous phases standardized by (a) female observation time and (b) dyadic association time.

(copulation count:  $K_r$  matrix partial correlation:  $\tau_{rw;xy,z} = 0.18$ ,  $N = 11$  females, 4 males,  $P = 0.29$ ; copulation rate:  $\tau_{rw;xy,z} = 0.00$ ,  $N = 11$  females, 4 males,  $P = 0.49$ ; averages across all males from both groups:  $r_s = -0.429$ ,  $N = 7$ ,  $P = 0.337$ ; Fig. 4), suggesting that more aggressive males did not obtain higher mating success.

Male-to-female aggression (both sexual and nonsexual) could induce females to mate more cooperatively in the future. If so, we predicted a positive correlation between general male aggression and female proceptivity and a negative correlation between male aggression and female resistance. However, we found no significant correlation between dyadic rates of generalized (sexual or nonsexual) male aggression towards females and female resistance ( $K_r$  matrix partial correlation:  $\tau_{rw;xy,z} = -0.06$ ,  $N = 11$  females, 4 males  $P = 0.46$ ) or proceptivity ( $\tau_{rw;xy,z} = 0.24$ ,  $N = 11$  females, 4 males,  $P = 0.33$ ). In addition, no relationship was found between general male aggression and copulation counts ( $\tau_{rw;xy,z} = 0.24$ ,  $N = 11$  females, 4 males,  $P = 0.33$ ) or rates ( $\tau_{rw;xy,z} = 0.25$ ,  $N = 11$  females, 4 males,  $P = 0.27$ ).

#### *Does Male Sexual Aggression (Direct Coercion) Correspond to Male Rank?*

Figure 5a shows a plot of the percentage of aggressive sexual interactions for each male from both communities. We found no

relationship between direct coercion and male rank (Spearman's rho:  $r_s = -0.243$ ,  $N = 7$ ,  $P = 0.599$ ). When we examined the percentage of aggressive sexual interactions for each male in which male aggression occurred during the solicitation (aggressive solicitation), we also found no relationship with male aggressive solicitations and male rank ( $r_s = -0.083$ ,  $N = 7$ ,  $P = 0.860$ ; Fig. 5b). Similarly, we found no relationship between intimidation (aggressive sexual interactions in which the aggression occurred after females resisted the solicitation) and male rank ( $r_s = -0.327$ ,  $N = 7$ ,  $P = 0.474$ ; Fig. 5c).

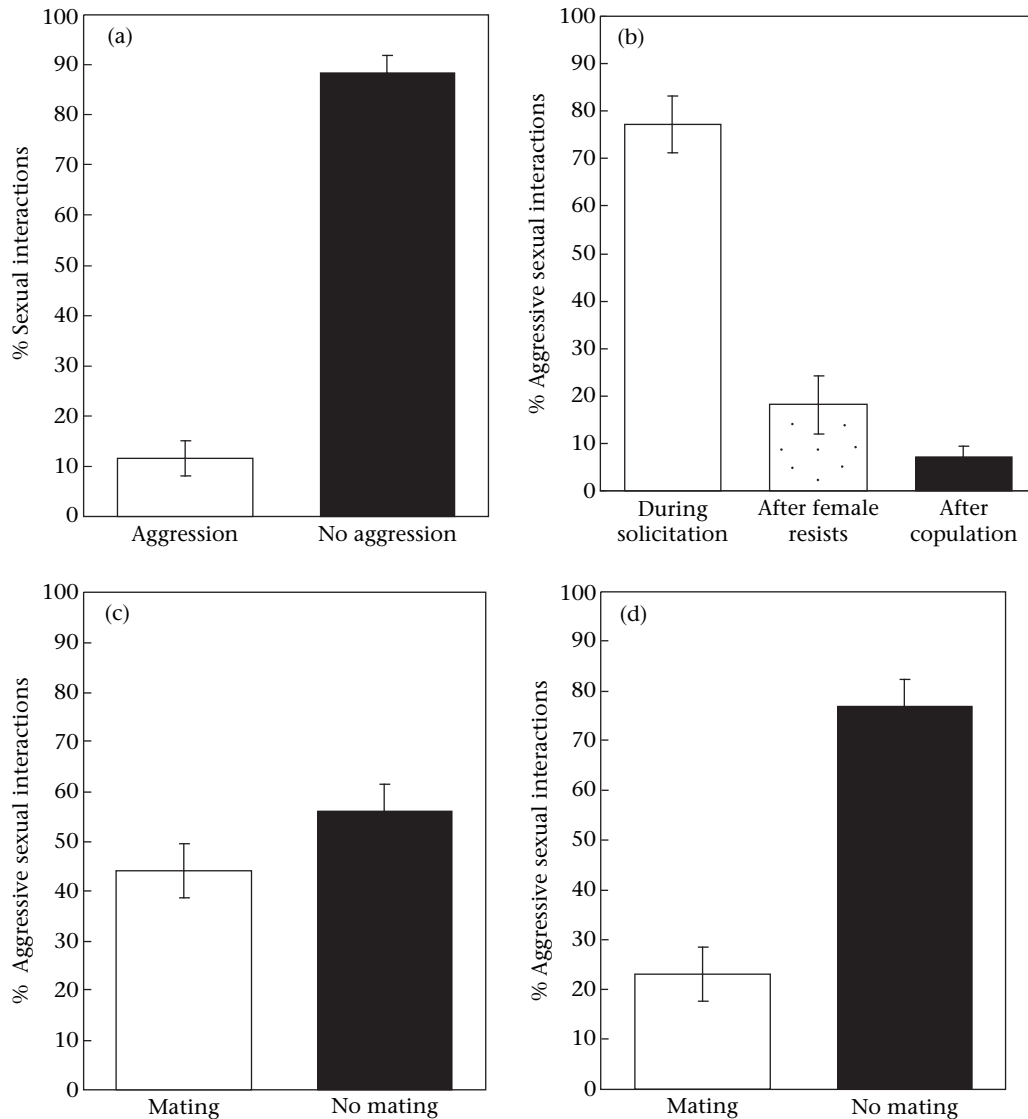
#### **DISCUSSION**

While chimpanzee male aggression against females is prevalent, noticeable and creates considerable reactions from females, detailed studies of patterns of male aggression towards females remain scarce. This study investigated patterns of male aggression towards females in two chimpanzee communities of Tai to determine (1) whether male-to-female aggression increases in a sexual context, (2) the frequency, context, influence and efficacy of male-to-female aggression, and finally, (3) whether direct coercion corresponds to male rank. In summary, results of our study of Tai chimpanzees suggest that direct male coercion is relatively rare, is used by less preferred males and does not seem to function effectively to constrain female choice. Male coercion did not deter females from expressing their mate preferences, as neither (1) a general measure of overall male–female aggression, nor (2) a specific measure of direct sexual coercion corresponded to male mating success, and (3) male aggression did not correspond to increased female proceptivity or decreased female resistance rates.

If most male-to-female aggression functions as sexual coercion, we predicted that it would increase when females were in oestrus and, in particular, during the periovulatory period. Although we found that females received more aggression from males during oestrus, males are also more likely to associate with females during this time (Tutin 1979; Goodall 1986; see also Soltis et al. 1997). Controlling for male–female dyadic association time, male aggression towards females was evenly distributed across the oestrous phases. In other words, in the presence of a male, a female incurred the same risk of aggression regardless of her oestrous state.

Because male aggression towards females occurred with equal frequency relative to time in association with oestrous and non-oestrous females, and thus did not increase in a sexual context, this leads to one of several possible conclusions: chimpanzee male-to-female aggression serves a multitude of functions, not just sexual coercion (sensu Smuts & Smuts 1993). Among Gombe chimpanzees, male aggression towards females occurs most often during reunions than in other contexts such as foraging, meat eating, or sex (Goodall 1986). At Gombe, acts of male aggression towards females (threats and attacks or just attacks) in sexual contexts are rare (less than 4% of all adult male aggression and ~10% of all aggression received from adult males; Goodall 1986). The rarity of sexual aggression is further supported at other chimpanzee sites as it was usually observed only during possessive mating (or consortship), which is considerably less common than other types of mating (e.g. opportunistic: 2% versus 73%; Tutin 1979; Goodall 1986; see also Matsumoto-Oda 1999).

Campbell's (2003) study of spider monkeys similarly found no increase in male aggression when females were periovulatory versus during other times in the female cycle, and other researchers found that most attacks by males are not directly associated with sexual contexts (Fedigan & Baxter 1984; Symington 1987). Consequently, it has been argued that, rather than coercion, most male aggression functions to maintain dominance (Campbell 2003; see



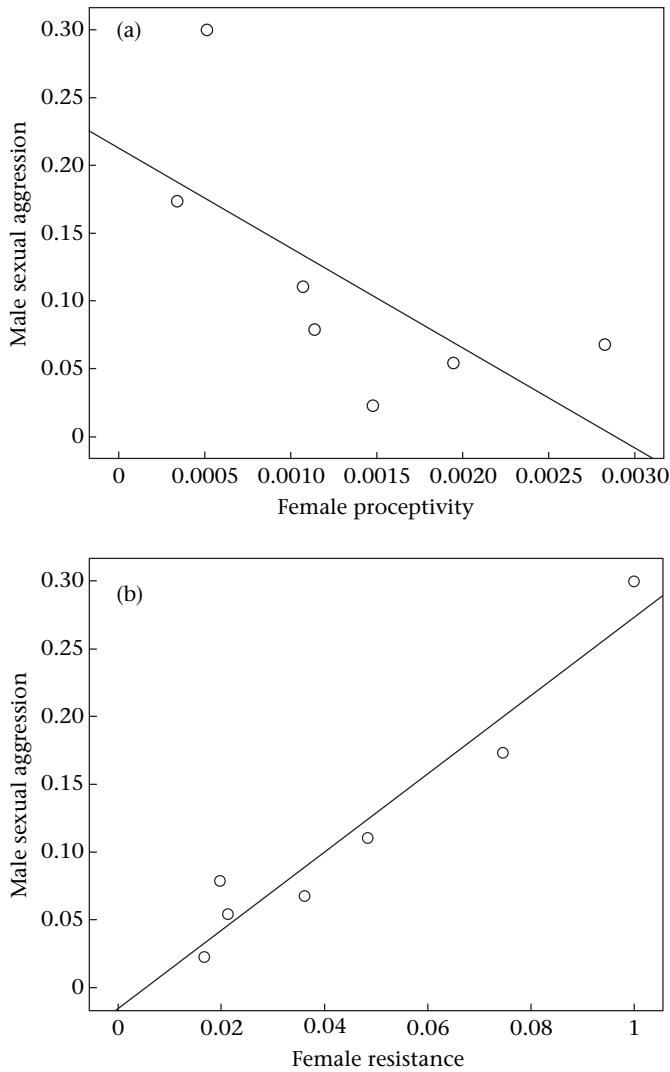
**Figure 2.** (a) Mean  $\pm$  SE percentage of sexual interactions with (open bar) and without (solid bar) male aggression towards females ( $N = 14$  females, 7 males). (b) Mean percentage of aggressive sexual interactions in which male aggression occurred during solicitation (open bar), after female resistance (grey bar) and after copulation (solid bar) ( $N = 14$  females, 7 males). (c) Mean percentage of male aggressive sexual interactions that led to mating (open bar) or did not lead to mating (closed bar) after aggressive solicitation ( $N = 14$  females, 7 males) and (d) after female resistance ( $N = 14$  females, 7 males).

also Strier 1994). Alternatively, male-to-female aggression (sexual or nonsexual) may function to intimidate females long before they come into oestrus (cf. Goodall 1986), which may then affect female behaviour during oestrus and increase the likelihood of mating with the aggressive male (e.g. Smuts & Smuts 1993; Clutton-Brock & Parker 1995; see also Muller & Wrangham 2009b). If so, then the definition of sexual coercion would need to expand beyond force or threat of force solely in a sexual context (sensu Smuts & Smuts 1993).

Despite clear male dominance and sexual dimorphism among chimpanzees, we found little evidence for effective direct coercion (harassment, forced copulation, aggressive solicitation and intimidation). Male direct coercion in Tai chimpanzees is relatively rare, occurring in less than 12% of all sexual interactions (see Fig. 2). Forced copulation, an extreme form of direct coercion, is exceedingly rare across chimpanzee populations (Tutin 1979; Stumpf et al. 2008). When direct coercion does occur, it is predominantly during the solicitation phase of the sexual interaction. However, the

majority of the time, direct coercion does not successfully lead to copulation. In fact, aggressive sexual solicitations lead to copulation considerably less often (44%) than do sexual solicitations in general (69.2%; Stumpf & Boesch 2006). Thus, direct male coercion is not very common and not very successful. These findings concur with related studies in other primate species (Manson 1992; Soltis et al. 1997).

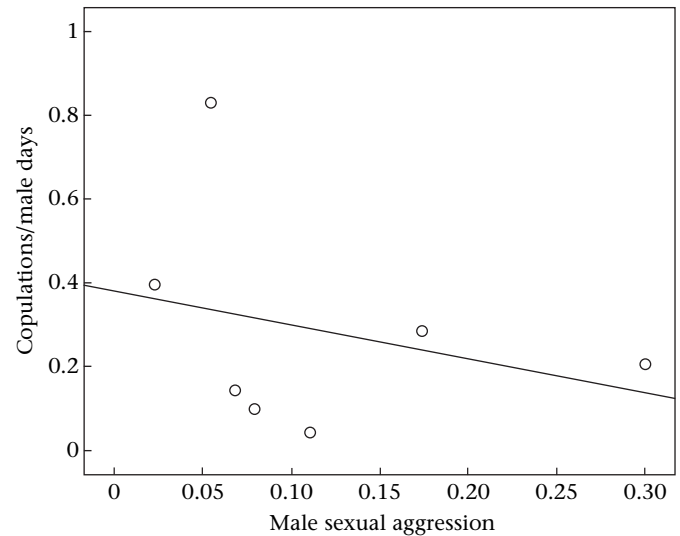
While male aggression (sexual or nonsexual) may theoretically function to condition females, more aggressive males did not obtain higher mating success than less aggressive males (see also Soltis et al. 1999; Campbell 2003; Link et al. 2009; but see Muller et al. 2007). Moreover, if most male coercion functions to influence a female's behaviour in the future, male punishment of female resistance might be expected to be a common and effective strategy for modifying female behaviour in response to the actions of known males (Clutton-Brock & Parker 1995). However, punishment for female resistance was not common. Rather, the majority of direct coercion occurred in the context of the solicitation, suggesting that



**Figure 3.** Correlation between male sexual aggression and (a) female proceptivity and (b) female resistance during the periovulatory phase (POP).

male coercion functions to influence female behaviour more in the short term than in the future. In addition, male aggression did not appear to modify female behaviour (by increasing receptivity and proceptivity).

Rather, we found a strong positive correlation between male sexual aggression rates and female resistance and a negative correlation with proceptivity. The positive correlation between male aggression towards females and female resistance rates support three related conclusions: (1) males show sexual aggression towards females that they expect will resist, (2) males that direct most sexual aggression towards females are nonpreferred, and (3) females resist coercive males, and their resistance is often effective. Females often respond submissively to male aggression by screaming, fear grimacing and whimpering, and they suffer costs, including injuries, decreased foraging time (Bercovitch 1983; Smuts 1985; Goodall 1986; Watson et al. 1998; Linklater et al. 1999; Stumpf & Boesch 2006) and increased cortisol levels (Muller et al. 2007). Despite this, chimpanzee females still often risk the costs of resistance (as found in other primates: Enomoto 1981; Huffman 1987, 1991; Soltis et al. 1997, 1999), particularly from more aggressive males, which experienced higher resistance rates in our study. Whereas male coercion could be expected to decrease

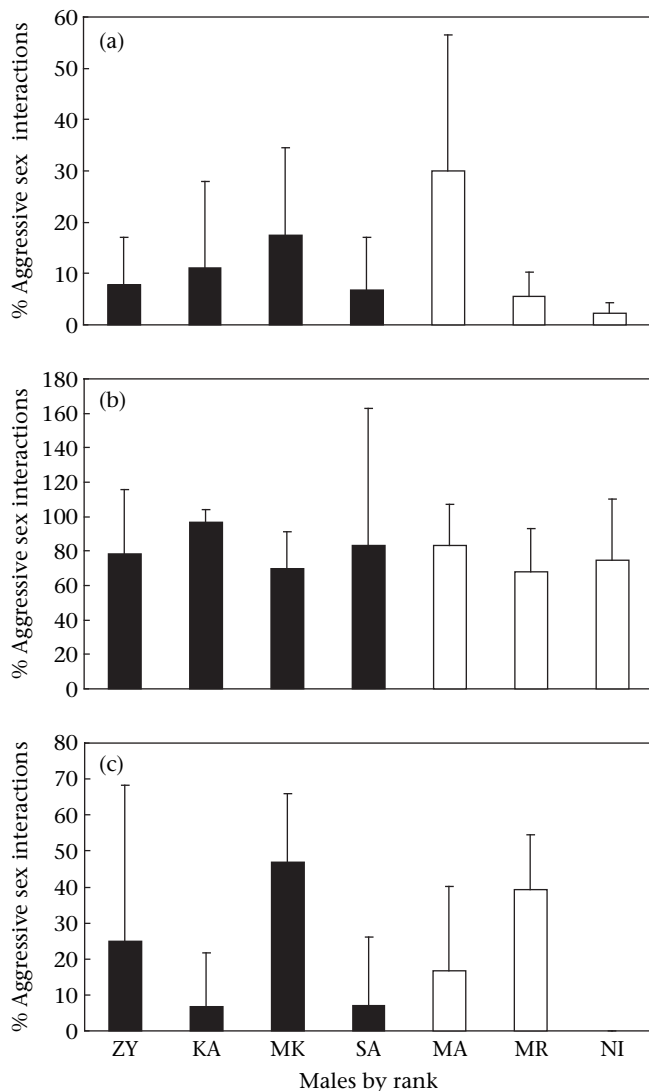


**Figure 4.** Correlation between male sexual aggression and male mating success.

female resistance in future interactions, we found that female resistance was consistent over time (see also Stumpf & Boesch 2005, 2006). Evidence from other species suggests that female resistance remains consistent to particular males, does not decrease over time and affects male mating success (Fox 1998, 2002; Cunningham 2003; Campbell 2003). Importantly, these findings also suggest that female proceptivity and resistance are better explained as measures of female preferences than as indexes of male coercion.

Models of coercion by van Schaik et al. (2004) emphasize male sexual aggression towards females as an expression of mating conflict between the female and the dominant male. Results of this study, however, suggest that direct coercion is not correlated with male dominance rank, and instead appears to be a strategy of nonpreferred males (see also Galdikas 1981; Mitani 1985; Utami 2000). These results emphasize the role of nonpreferred and/or lower-ranking males in mating conflict, particularly, although unlikely exclusively, in fission–fusion species such as chimpanzees (see also Clarke et al. 2009).

The lack of a correlation between male rank and aggression towards females may be explained by variation among male ranks in the expression and use of male–female aggression and coercion. Higher-ranking chimpanzee males are often observed to herd and mate-guard females and aggress against other males (Nishida 1997; Watts 1998; Boesch & Boesch-Achermann 2000; Wrangham 2002; Muller & Wrangham 2004). This indirect form of coercion may allow particular males to maintain preferential access to fecund females, and effectively prohibit other males from mating. Thus, these males limit other males' mating opportunities, and thereby, indirectly influence female mating, and it is likely that most effective male coercion functions not directly but indirectly to constrain female choice and limit other male mating opportunities. While indirect coercion is more often expressed by a few higher-ranking males during the limited window of the periovulatory period (e.g. Watts 1998; Wrangham 2002; Muller & Wrangham 2004; see also Manson 1994), generally nonpreferred males use direct coercion throughout the lengthy oestrus, and much of it appears ineffective in modifying female behaviour. Moreover, when not in oestrus, females may receive aggression from males of all ranks for various reasons, potentially including sexual coercion, thus contributing to the lack of a correlation between mating success and male-to-female aggression.



**Figure 5.** Relationships between male rank and (a) male sexual aggression, (b) male solicitation aggression and (c) intimidation (aggressive sexual interactions in which the aggression occurs after females resist sexual solicitation).

Increasing evidence suggests that chimpanzee populations differ substantially in their association patterns and behaviour (Boesch & Boesch-Achermann 2000; Whiten et al. 2001; Boesch 2009), and this is also likely the case for male–female sexual relationships (Lehmann & Boesch 2005, 2008, 2009; Stumpf & Boesch 2005; Newton-Fisher 2006). While rates of male aggression towards females are similar between chimpanzee populations in Kanyawara (mean  $\pm$  SE:  $0.017 \pm 0.004$  acts/h: Muller et al. 2007), Budongo ( $0.07$  acts/h of female observation time: Newton-Fisher 2006) and Tai ( $0.078 \pm 0.24$  acts/h of female observation time: this study), patterns of male sexual aggression differed between these populations. Muller et al. (2007) and Matsumoto-Oda (1999) found that male aggression towards parous cycling females was higher than that towards noncycling females. Coalitionary aggression (male-to-female aggression involving more than one male aggressor and often involving physical assault) has also been noted for the Kanyawara population (Muller & Wrangham 2009a), but not for other populations. In the present study, we found that direct coercion rates were low in Tai chimpanzees, that male aggression rates did not differ between non-POP, POP and nonoestrous females, and that the efficacy of male coercion was low, supporting

the idea that patterns of male aggression differ across chimpanzee populations.

This interpopulation variation may reflect real differences in the nature of sexual interactions between chimpanzee populations. Several possibilities may explain these differences. High female-to-male sex ratios (Tai: 4:1; Gombe: 1.35:1; reviewed in Stumpf 2007), fewer males, and consequent lower levels of male competition for oestrous females may influence the patterns and efficacy of male-to-female aggression in Tai chimpanzees compared to that in some eastern populations. However, male-to-female aggression rates are on a par with rates at other sites, suggesting that male aggression is not diminished despite the demographic differences. Rather, broader differences may be responsible for patterns of aggression across chimpanzee populations. More seasonal habitats characterized by less food availability (such as at Kanyawara and Gombe; Doran et al. 2002) and less seasonal habitats with greater food availability (e.g. Tai and Budongo) suggest that ecology plays a fundamental role in male–female relationships and may explain the diversity in the intensity and efficacy of male aggression towards females across chimpanzee populations. In light of the costs of grouping, females in some eastern chimpanzee populations (Gombe and Kanyawara) have fewer cycles per conception, resulting in scramble competition for females, and consequently, male aggression and coercion are hypothesized to be greater in eastern (*Pan troglodytes schweinfurthii*) than in western (*Pan troglodytes verus*) chimpanzees (Wrangham 2002; Boesch 2009). The bisexual nature of Tai chimpanzees, characterized by frequent associations and coalition between males and females as well as common and long-lasting female–female relationships (Boesch & Boesch-Achermann 2000; Boesch 2009; Lehmann & Boesch 2009), leads to a higher integration of females in the community. Therefore, females in the Tai population may have potentially greater influence in their community than do less social females of some east African populations. Male aggression towards female chimpanzees at Budongo, an eastern population (*P. t. schweinfurthii*), may be less intense than at other sites, potentially because of increased female gregariousness (Newton-Fisher 2006; Emery Thompson & Wrangham 2006), and male aggression towards females may be relatively nonexistent in bonobos because of their more stable and larger groups, greater female social power and more concealed ovulation (Paoli 2009). Thus, growing evidence hints at the possibility that variation in levels and intensity of male aggression towards females among chimpanzees may reflect ecological differences.

Sexual coercion and female choice are both considered mechanisms of sexual conflict and behavioural manifestations of the arms race between males and females and control over paternity. If costs of male coercion get too high for females, there will be selection for counterstrategies until a point where continued sexually antagonistic coevolution may lead to equilibrium, making winners and losers difficult to determine (Parker 2006). While male-to-female aggression is prevalent, conspicuous and clearly threatening, the lack of a significant positive relationship between male coercion and mating success and the inefficacy of direct coercion in this population suggest that male coercion is not uniformly effective. The inclusion of negative results in different species and populations is important to avoid publication bias and will increase our understanding of the factors affecting variation in reproductive strategies and the outcomes of sexual conflict. While this study is limited to male-to-female aggression in one population of chimpanzees, future studies that examine the prevalence, distribution context and agents of male-to-female aggression across different species, habitats and mating systems will enable better understanding of male coercion within the broader context of sexual conflict.

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