



## Maternal rank influences the outcome of aggressive interactions between immature chimpanzees



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For many long-lived mammalian species, extended maternal investment has a profound effect on offspring integration in complex social environments. One component of this investment may be aiding young in aggressive interactions, which can set the stage for offspring social position later in life. Here we examined maternal effects on dyadic aggressive interactions between immature (<12 years) chimpanzees. Specifically, we tested whether relative maternal rank predicted the probability of winning an aggressive interaction. We also examined maternal responses to aggressive interactions to determine whether maternal interventions explain interaction outcomes. Using a 12-year behavioural data set (2000–2011) from Gombe National Park, Tanzania, we found that relative maternal rank predicted the probability of winning aggressive interactions in male–male and male–female aggressive interactions: offspring were more likely to win if their mother outranked their opponent's mother. Female–female aggressive interactions occurred infrequently (two interactions), so could not be analysed. The probability of winning was also higher for relatively older individuals in male–male interactions, and for males in male–female interactions. Maternal interventions were rare (7.3% of 137 interactions), suggesting that direct involvement does not explain the outcome for the vast majority of aggressive interactions. These findings provide important insight into the ontogeny of aggressive behaviour and early dominance relationships in wild apes and highlight a potential social advantage for offspring of higher-ranking mothers. This advantage may be particularly pronounced for sons, given male philopatry in chimpanzees and the potential for social status early in life to translate more directly to adult rank.

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For many animals, high rank affords priority of access to resources and ultimately influences increased survivorship and reproduction (reviewed in: Clutton-Brock, 1988; Ellis, 1995; Majolo, Lehmann, de Bortoli Vizioli, & Schino, 2012). While these benefits are well characterized for adults, the adaptive value of dominance status among immature individuals is poorly understood. One hypothesis is that the formation of dominant–subordinate relationships in early life sets the stage for social status and reproductive success in adulthood. Mothers may therefore increase their inclusive fitness by aiding young offspring in agonistic encounters.

Indeed, maternal intervention on behalf of an offspring is well documented in several species (reviewed in: Maestripietri, 2009;

Mateo, 2009) and often results in the offspring outranking his or her competitor (e.g. vervet monkeys, *Cercopithecus aethiops*: Fairbanks & McGuire, 1985; rhesus monkeys, *Macaca mulatta*: Datta, 1988; spotted hyaenas, *Crocuta crocuta*: Engh, Esch, Smale, & Holekamp, 2000). When mothers aid their offspring in aggressive interactions, maternal intervention can be a mechanism by which matrilineal hierarchies are maintained within social groups (e.g. Harcourt & Stewart, 1987; Pereira, 1995). Maternal interventions may thus be particularly influential for the philopatric sex because social status early in life can translate more directly to adult rank. However, maternal support can also afford immediate benefits to offspring of the dispersing sex via protection and/or access to resources. More broadly, long-term fitness benefits associated with maternal effects in early life have been documented for offspring of the dispersing sex in several social species including spotted hyaenas (Hofer & East, 2003; Höner et al., 2010) and yellow baboons, *Papio cynocephalus* (Altmann & Alberts, 2005; Onyango, Gesquiere, Wango, Alberts, & Altmann, 2008).

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Chimpanzees, *Pan troglodytes*, live in multimale, multifemale communities characterized by male philopatry (Goodall, 1986; Nishida & Hiraiwa-Hasegawa, 1987; Pusey, 1979) and a fission–fusion social organization (Goodall, 1986; Nishida, 1968). Despite nutritional independence at weaning between the ages of 3 and 5 years, offspring continue to travel with their mother for several years thereafter (Pusey, 1983, 1990). Maternal effects can be realized across this long period of dependency. For example, a recent study demonstrated lower survivorship for offspring that were orphaned after weaning (Nakamura, Hayaki, Hosaka, Itoh, & Zamma, 2014). Similar patterns have been observed in other long-lived mammals, including killer whales, *Orcinus orca* (Foster et al., 2012) and red deer, *Cervus elaphus* (Andres et al., 2013).

Although both male and female chimpanzees rely upon prolonged maternal investment, emerging evidence has highlighted sex biases in some components of maternal care. For instance, mothers with sons are more gregarious than mothers with daughters (Murray et al., 2014). Male infants take advantage of these social opportunities by playing and grooming with significantly more individuals than female infants (Lonsdorf, Anderson, et al., 2014; Murray et al., 2014). Together, these studies emphasize the interaction between maternal effects and sex differences in offspring prosocial development. The extent to which mothers influence aggressive interactions in immature offspring, particularly with peers, has not yet been quantified. Furthermore, it is unknown whether maternal effects on aggressive outcomes are more influential for chimpanzee sons or daughters, despite adult sex differences in dispersal and propensity for social interaction (see below).

For many primates, peer interactions provide opportunities to learn essential social and behavioural skills (Pagel & Harvey, 2002; Pereira & Fairbanks, 2002). Early establishment of play and grooming partners may be especially important for male chimpanzees, which remain in their natal communities and form long-lasting bonds that function in dominance rank acquisition, cooperative defence and communal hunting (Gilby & Wrangham, 2008; Mitani, 2009). Adult male dominance rank is correlated with reproductive success, with several studies demonstrating that alpha males sire a disproportionate number of offspring (Boesch, Kohou, Néné, & Vigilant, 2006; Newton-Fisher, Emery Thompson, Reynolds, Boesch, & Vigilant, 2010; Wroblewski et al., 2009). In comparison to males, overt female–female aggression is rare in chimpanzees (Goodall, 1986; reviewed in Murray, 2007). Nevertheless, female dominance rank likewise correlates with reproductive success (Emery Thompson et al., 2007; Pusey, Williams, & Goodall, 1997). Despite the importance of dominance rank later in life, relatively little is known about dominance interactions among immature chimpanzees. However, earlier reports indicate that mothers sometimes support their offspring in aggressive interactions (Goodall, 1968, 1971; Pusey, 1983).

Here, we examined the influence of maternal rank on aggressive interactions between immature chimpanzees to test our overarching hypothesis that high maternal rank benefits immature offspring in competitive contests. Specifically, we tested whether relative maternal rank predicts the probability of an immature offspring winning an aggressive interaction. In addition, we evaluated the behavioural response of mothers following aggressive interactions involving their offspring to determine whether direct interventions explain interaction outcomes. Recognizing the importance of maternal help in offspring contests and its potential implications for rank ‘inheritance’ (e.g. Harcourt & Stewart, 1987), we predicted that higher-ranking mothers would be more likely than lower-ranking mothers to intervene in aggressive interactions involving their offspring.

## METHODS

This study was part of long-term research on wild eastern chimpanzees (*P. t. schweinfurthii*) living in the Kasekela community of Gombe National Park, Tanzania. All chimpanzees within the study population were individually identifiable by field researchers of the Gombe Stream Research Centre, and each mother with her youngest dependent offspring (i.e. ‘family group’) in the community was targeted for detailed observations at least once per month. Each observation day, researchers recorded detailed behavioural observations on activity type and social partners for the focal mother and her youngest dependent offspring using 1 min scans (Altmann, 1974). Observation began when the focal mother descended from her sleeping nest or was first located, and continued (at maximum) until the mother ascended into a sleeping site in the evening. The data presented here were collected from January 2000 through December 2011, a time period for which details on aggressive interactions have been extracted from field notes originally recorded in Swahili. During the study period, the community contained 48–62 total individuals, 19–26 of which were immatures. We defined immatures as individuals younger than 12 years, consistent with previous research on our study population (e.g. Markham et al., 2014; Murray, Eberly, & Pusey, 2006; Murray, Lonsdorf, Eberly, & Pusey, 2009). This age criterion coincides with current, unpublished records for the youngest age of female emigration (9.9 years), first birth for a female (11.1 years) and first fathering of an offspring by a male (12.9 years).

### *Aggressive Interactions and Maternal Interventions*

Data on aggressive interactions among all chimpanzees were recorded ad libitum. Aggressive interactions are typically noisy and conspicuous events, and thus the vast majority of interactions are readily noticeable to field observers; our analytical emphasis on the outcome of observed aggressive interactions (see below) minimizes the effect of any undetected subtle (and therefore atypical) agonistic encounters. Only decided, dyadic aggressive interactions between immature individuals were included in analyses (resulting in the exclusion of two interactions that had undecided outcomes). Extending Goodall (1986), decided aggressive interactions were defined as contests in which only one individual (the ‘winner’) expressed aggressive behaviour (directed threat, display, chase or attack) towards another individual and/or in which only one individual (the ‘loser’) expressed clear submissive behaviour (flee, scream or cry) in response to another individual. We did not include play fighting, which can be distinguished on the basis of facial expressions (e.g. relaxed jaw versus bared teeth). Field assistants regularly record play fighting for the focal of a follow on the 1 min scan but not on an ad libitum basis for all immatures in the party. We therefore did not include play fighting in our analyses, although future work should investigate its relevance to dominance interactions (Paquette, 1994).

When a dyad interacted aggressively more than once on a single observation day, the average  $\pm$  SE duration between consecutive aggressive interactions was  $51 \pm 10.9$  min (range 1–335 min). We considered successive aggressive interactions as a single, ongoing event when they occurred within 10 min of each other. Only one aggressive interaction occurring within 10 min was a ‘reversal’ (i.e. aggressor–recipient roles were inconsistent in the consecutive aggressive interactions); in this case, we included only the outcome of the final interaction in our analyses. Researchers recorded descriptive notes of maternal intervention in the immediate aftermath of immature aggressive interactions. Because data on aggressive interactions were collected on all immatures in the party (i.e. not limited to members of the focal family group), detailed

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