The effect of intergroup competition on intragroup affiliation in primates

B. Majolo [a, *], A. de Bortoli Vizioli [b, c], J. Lehmann [d]

[a] School of Psychology, University of Lincoln, Lincoln, U.K.
[b] Istituto di Scienze e Tecnologie della Cognizione, Consiglio Nazionale delle Ricerche, Rome, Italy
[c] Dipartimento di Psicologia dello Sviluppo e della Socializzazione, Università di Padova, Padua, Italy
[d] Centre for Research in Evolutionary Anthropology, University of Roehampton, London, U.K.

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Researchers from various disciplines have hypothesized a positive correlation between the level of intergroup contest competition (IGCC) and the evolution of behavioural traits, such as cooperation, altruism and friendship, which promote intragroup affiliation. Empirical support for this hypothesis is, however, scarce and mainly available from humans. We tested whether the level of IGCC affects intragroup affiliation (i.e. intragroup grooming exchange) among male and female nonhuman primates. To quantify intragroup affiliation, we used social network measures and a grooming index. Our measure of IGCC combined frequency of intergroup encounters and proportion of aggressive encounters and was calculated separately for males and females. We ran our analyses on 27 wild groups of primates belonging to 15 species (13 Cercopithecinae, one Colobinae and one Cebinae). Our analyses reveal a clear pattern of correlated evolution between grooming network density and interindividual variation in the number of grooming partners on the one hand and the intensity of IGCC on the other in females, but not males. Thus, our results suggest that the exact nature of the relationship between IGCC and intragroup affiliation is sex specific. These results may be explained by the differential costs and benefits males and females experience during aggressive intergroup confrontations and by sex-specific differences in intragroup affiliation.
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Intergroup contest competition (IGCC), where some or all members of one group aggressively attempt to access and monopolize valuable resources (e.g. food or water) at the expense of another group, is a phenomenon observed in many group-living species (e.g. Brown & Crofoot, 2013; Crofoot & Wrangham, 2010; Kitchen & Beehner, 2007; Radford, 2008a; Rubenstein, 1986). The outcome of an aggressive intergroup encounter can affect individual fitness (e.g. Radford & Fawcett, 2014), especially when ecological conditions elicit frequent aggressive interactions between groups (e.g. due to habitat saturation or food scarcity) that impose high cost/benefits payoffs (e.g. Mitani, Watts, & Amsler, 2010). Aggressive intergroup encounters represent a typical example of collective action problems (Nunn & Lewis, 2001; Willems, Hellriegel, & van Schaik, 2013; Willems & van Schaik, 2015): groups in which a larger proportion of animals take part in the aggressive confrontation are expected to have the best chances of

winning a fight (other things being equal; e.g. group size, sex ratio) and thus gain access to the resources at stake. However, because aggressive intergroup encounters also impose potential high costs for individuals (e.g. injuries or death; Mitani et al., 2010), the risk of free riding is high: some individuals could gain the benefits of their group winning a fight with another group, without incurring any potential cost, by not taking an active role in the aggressive confrontation (Crofoot & Gilby, 2012; Nunn & Lewis, 2001; Willems & van Schaik, 2015; Willems et al., 2013).

Researchers have hypothesized that strong intragroup affiliation should reduce the probability that animals in a group free-ride during collective action problems (Alexander & Borgia, 1978; Choi & Bowles, 2007; Puurtinen & Mappes, 2009). Thus, individuals from groups in which intragroup affiliation is strong should outperform groups with weak intragroup affiliation during intergroup confrontations, because everybody is taking part in the interaction. These groups should then gain overall fitness benefits. Under this scenario, individuals in populations/species that face a high level of IGCC should become progressively more affiliative towards their group members over evolutionary time, thereby

* Correspondence: B. Majolo, School of Psychology, University of Lincoln, Brayford Pool, Lincoln, LN6 7TS, U.K.
E-mail address: bmajolo@lincoln.ac.uk (B. Majolo).

increasing the overall intragroup affiliation of the group. Furthermore, individuals in populations/species in which intragroup affiliation is strong should also be more likely to take part in collective actions (such as protecting a food source from other groups) than individuals in populations/species in which intragroup affiliation is weak (Conradt & List, 2009; Miller, Garnier, Hartnett, & Couzin, 2013). Following this logic, researchers from a range of different disciplines, including evolutionary biology (Reeve & Hölldobler, 2007), behavioural ecology (Sterck, Watts, & van Schaik, 1997; Wrangham, 1980), psychology (West et al., 2006; van Vugt & Park, 2009) and anthropology (Choi & Bowles, 2007; Haas, 1990), have predicted that a high level of IGCC should favour the evolution of behavioural traits that promote intragroup affiliation, such as social bonding and parochialism (Alexander & Borgia, 1978; Reeve & Hölldobler, 2007). However, different mechanisms and factors have been proposed to be involved, depending on the discipline and/or study taxon. Genetic similarity among group members (e.g. due to limited dispersal; Reeve & Hölldobler, 2007), environmental conditions (Sterck et al., 1997) and the evolution of social norms (e.g. rules on fairness and punishment of free-riders; e.g. Gintis, van Schaik, & Boehm, 2015) can all affect the relationship between intergroup competition and intragroup affiliation over evolutionary time.

Several mathematical models that support the hypothesis that the level of IGCC has a positive effect on the evolution of intragroup affiliation have been developed (e.g. Bowles, 2009; Reeve & Hölldobler, 2007). However, empirical tests of this hypothesis are rare and have mostly focused on the proximate link between IGCC and intragroup affiliation. There is consistent experimental evidence in humans showing that cooperation increases when groups compete with one another compared to situations without intergroup competition; this effect is independent from kin relationships among group members (Erev, Bornstein, & Galili, 1993; Puurtinen & Mappes, 2009; Tan & Bolle, 2007; West et al., 2006). This evidence has led some authors to propose that the extensive period of warfare that our ancestors faced in the Pleistocene and Holocene has driven the evolution of group-beneficial behaviours, such as in-/out-group categorization in humans (Bowles, 2009; Choi & Bowles, 2007).

For nonhuman species, data on the proximate link between IGCC and intragroup affiliation are relatively scarce (for a review: Grueter, 2013), although the same principles should apply to all taxonomic groups (see e.g. Reeve & Hölldobler, 2007; Wrangham, 1980). A few studies have focused on post intergroup encounter allopreening and allogrooming, as a measure of intragroup affiliation (Radford, 2008a), as these two behaviours have important social functions in many mammals and birds (e.g. they promote agonistic support and food tolerance; Dunbar, 1991; Radford, 2008a; Ventura, Majolo, Koyama, Hardie, & Schino, 2006). In the cooperatively breeding green woodhoopoe, *Phoeniculus purpureus*, the frequency and duration of allopreening between group members increases following a conflict with another group (Radford, 2008a,b, 2011). Conversely, in captive tufted capuchin monkeys, *Cebus apella*, visual interactions between groups did not result in increased grooming exchange within the group (Polizzi di Sorrentino, Schino, Massaro, Visalberghi, & Aureli, 2012). Another measure of affiliation that has been used is spatial proximity between group members. In chimpanzees, *Pan troglodytes*, and spider monkeys, *Ateles geoffroyi*, individuals were found to stay closer together when feeding in the home range of a neighbouring group (i.e. an area where the risk of a conflict with another group is high) than when feeding in their home range (Aureli, Schaffner, Verpooten, Slater, & Ramos-Fernandez, 2006; Mitani et al., 2010). However, all of these studies have tested the immediate effects of intergroup encounters on intragroup affiliation. It remains unclear

whether such effects are only short lived and thus temporary (e.g. an emotional response to the stress of the encounter; Polizzi di Sorrentino et al., 2012; Radford, 2008a, 2011),whether such an increase in affiliative behaviour occurs primarily between already closely bonded partners and/or those that have actively participated to the intergroup encounter (i.e. affiliation is partner specific), or whether such behavioural responses to intergroup encounters would indeed lead to an overall more general increase in intragroup affiliation over evolutionary time.

To our knowledge, only two studies (Cheney, 1992; Grueter, 2013) have attempted to test the generality of the hypothesized relationship between IGCC and intragroup affiliation across a number of different species. Cheney (1992) used allogrooming (hereafter grooming) distribution (averaged across individuals of the same group) as a measure of group affiliation in nonhuman primates. She predicted that animals would increase their effort to distribute their grooming more evenly to their potential grooming partners, instead of mostly grooming with fewer individuals, the higher the level of IGCC they faced. Grueter (2013) also investigated nonhuman primates and used the average grooming time per species as a measure of intragroup affiliation. These two studies hypothesized that the proximate effect of IGCC on intragroup affiliation would extend beyond the first few minutes after an intergroup encounter. Groups facing higher IGCC would have overall stronger intragroup affiliation than groups facing a lower level of IGCC, irrespective of the timing and occurrence of each intergroup encounter (Sterck et al., 1997; Wrangham, 1980). Contrary to what was predicted, IGCC was not found to have a significant effect on either grooming distribution among group members (Cheney, 1992) or total grooming time (Grueter, 2013). However, these two studies could not effectively tackle some important issues. Cheney's (1992) study was restricted to female primates and did not control for the phylogenetic relationship between species. Grueter (2013) used total grooming time to measure group cohesion, without taking into account how animals distributed their grooming among their group members. Moreover, Grueter (2013) used a proxy of IGCC (i.e. home range overlap) that could equally measure intergroup scramble competition (Sterck et al., 1997; Wrangham, 1980). These factors could potentially explain the discrepancy between the human and the nonhuman primate data.

The mixed results available on this topic so far make it difficult to determine whether IGCC affects the evolution of group-beneficial behaviours (Bowles, 2009; Choi & Bowles, 2007) in nonhuman animals. Our aim was to analyse the occurrence of correlated evolution between IGCC and intragroup affiliation across primate social groups, using a phylogenetically controlled analysis and a variety of different measures of intragroup affiliation. We measured the level of IGCC by multiplying the frequency of intergroup encounters with the proportion of aggressive encounters (independently calculated for males and females). Intragroup affiliation, using grooming distribution, was measured by three different variables: (1) the evenness of grooming, assessing the distribution of grooming effort across potential grooming partners (following Cheney, 1992), (2) the interindividual variation in the number of grooming partners and (3) grooming network density. We predicted that species that experience more IGCC will also exhibit more intragroup affiliation, that is, animals would increase their effort to distribute their grooming more evenly to their group companions, interindividual variation in grooming partner numbers would be low, and more individuals would be involved in grooming interactions (high network density). Owing to the scarcity of data available on a wide range of primate taxa our data set is mostly composed of Cercopithecinae (see Supplementary Table S1), i.e. of species in which grooming is the main affiliative behaviour and females are the philopatric sex. Although not ideal, this allowed