

No effect of inter-group conflict on within-group harmony in non-human primates

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It has been a longstanding assumption that the threat of extra-group conflict can promote the expression of socio-positive behavior and cohesion within animal groups. I conducted a comparative analysis on the effect of inter-group conflict (indexed by home range overlap) on within-group affiliation levels (indexed by time engaged in allogrooming) in a sample of 48 primate species. There was no association between the 2 variables in a phylogenetic generalized least squares regression. I conclude that inter-group conflict may at best elicit short-term immediate changes in affiliation levels, but permanently elevated cohesion appears unique to humans with their large-scale social integration and scaled up inter-group conflict.

Introduction

The idea that conflict between groups can cause groups to become internally more cohesive was put forward by sociologists many centuries ago.¹ Darwin² also stated that inter-group hostilities can have an influence on the evolution of socio-positive behavior, a notion that has received empirical support from anthropologists and human evolutionary biologists.³⁻⁵ In birds, levels of social cohesion within units become intensified when collective agonistic support of unit members is required for group defense (for insect societies see 8).^{6,7}

The assumption that within-group affiliation is heightened by increased conflicts between groups is also central to the socioecological model of primate (female) social relationships (see also¹²).⁹⁻¹¹ The underlying principle is that in the face of competition with neighboring groups, individuals experience a relaxation in dominance interactions and will develop strong and often reciprocal affiliative bonds and egalitarian relationships, which will benefit cooperative defense of resources. However, little research focus has been devoted to testing this model in primates, and the findings of the few available studies do not converge.

In a comparative multi-species study, female involvement in inter-group aggression was not found to lead to a larger grooming diversity ratio (see also¹⁴).¹³ Chism and Rogers¹⁵ did not find support for the prediction that time spent grooming among adult female patas monkeys increased on days with inter-group encounters. Experimental manipulation of aggressive interactions between 2 adjacent captive groups of tufted capuchins did not produce changes in affiliative behaviors.¹⁶ Similarly, Lu et al.¹⁷ found that social tolerance among female Hanuman langurs, as evidenced by aggression intensity and counteraggression, was not predicted by

between-group competition (proxied by female participation in between-group encounters). On the other hand, Samango monkey females showed more frequent grooming during and immediately after encounters with other groups.¹⁸ In blue monkeys, aggressive territorial inter-group encounters were followed by intense grooming among females, which was interpreted as a strategy to reinforce “team spirit.”¹⁹ Cheney¹³ also reported intense grooming during inter-group encounters in vervet monkeys.

Using a comparative approach, I ask whether pronounced inter-group competition (of either the food or mating type) affects the frequency of within-group affiliative behavior in primates. The degree of inter-group conflict is proxied via the variable home range overlap among groups. More extensive range overlap leads to more frequent encounters and a higher potential for contest competition between groups. Grooming is considered a good marker of affiliation strength,^{20,21} and engenders a sense of bonding that allows cooperative or collective resource defense when confronted with inter-group conflict.²² Hence time spent in allogrooming is an often-used indicator of affiliation among group members.²³

Methods

Data on time spent allogrooming in primates are largely based on Grueter et al.,²⁴ with a few updates. In the aforementioned study, mean allogrooming time was calculated for each study site, and in case of multiple study sites for a species, the values from different sites were averaged to yield a mean value for each species. For inclusion in the data set, grooming time estimates and home range overlap had to come from the same groups. I included data of only non-food enhanced (unprovisioned) primate populations in the analyses. Data on home range overlap between groups for

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the same primate populations were extracted from the literature (Table S1). My literature search resulted in a total sample size of 48 species. Data were analyzed by means of Phylogenetic Generalized Least Squares Regressions (PGLS),²⁵ which use Pagel's lambda as an estimate of phylogenetic correlation. Data were analyzed with the package *caper*²⁶ in R.²⁷ To comply with normality, percentage of grooming and home range overlap were arcsine square root transformed.

Results

There was no significant relationship between home range overlap and time spent allogrooming in primates ($F_{2,46} = 0.455$, $P = 0.6376$, $R^2 = 0.0098$, $\lambda = 0.759$).

Discussion

My large-scale cross-species evaluation of the hypothesis that grooming time increases in primates with elevated levels of inter-group conflict yielded no supportive evidence, which is in line with 2 previous studies on a select number of primate species that investigated whether grooming distribution is influenced by inter-group conflict.^{13,14} If social grooming was important in promoting group cohesion,^{20,28} one would not only expect a strong effect of group size on grooming frequency (*ibid.*), but also an effect of inter-group conflict. The absence of such a relationship could be taken as further evidence for the marginal importance of grooming as a group cohesion mechanism.²⁴ However, it could be that effects of within-group competition and conflict are the main determinants of affiliation levels and social tolerance, outweighing those of between-group conflict.

Grooming frequency may be a crude measure for bondedness, but previous analyses using grooming diversity/distribution did not find any connection with inter-group conflict either.^{13,14} My

analysis could be repeated with social network measures such as group density, a measure of group cohesiveness.²⁹ I provided sex-independent analyses, so future analyses could also separate males and females, although data on sex-specific grooming allocation are not as readily available as data on time spent grooming. Also home range overlap may not capture all the details of inter-group conflict; level of conflicts and escalation potential depend on various factors such as familiarity with neighbors, sex ratio of interacting groups, and resource availability.³⁰⁻³²

It is well established that the presence of an outside group can elicit collaborative or coordinated defense involving males and/or females in a variety of primate species (e.g.,^{19,33,34}). In a similar vein, it is conceivable that grooming may be an immediate response to antagonistic inter-group interactions that serves a stress-reducing function (*cf.*³⁵) and thus affects only short-term changes in affiliative behavior. While there is some evidence for this proposition in guenons and vervets,^{13,18,19} di Sorrentino et al.¹⁶ reported the opposite effect in capuchins, i.e., more within-group aggression in groups when confronted with inter-group aggression.

The reason why inter-group conflict seems to have a stronger impact on cohesion in humans may lie in the fact that humans exhibit unusually high levels of social integration³⁶ and have to scale up collaborative skills to deal with competition from other groups for ensuring group survival (see 37).

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

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Supplemental Materials

Supplemental materials may be found here: www.landesbioscience.com/journals/CIB/article/26801.

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