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Preparing for battle? Potential intergroup conflict promotes current intragroup affiliation

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Groups of human soldiers increase their affiliative behaviour when moving into combat zones. Despite numerous other species also competing as groups, little is known about how potential intergroup conflict might influence current intragroup affiliative behaviour in non-human animals. Here, I show that allopreening (when one individual preens another) increases in groups of cooperatively breeding green woodhoopoes (*Phoeniculus purpureus*) when they enter areas where conflicts with neighbours are more likely. Self-preening, which is an indicator of stress in other species, did not increase in conflict areas, suggesting that the change in affiliative behaviour is not the simple consequence of greater stress. Instead, because it is the dominant breeding pair that increase their preening of subordinate helpers, it is possible that current affiliative behaviour is being exchanged for agonistic support in any intergroup conflicts that might ensue. These results are important for our understanding of group dynamics, cooperation and the evolution of sociality, but also bring to mind the intriguing possibilities of social contracts and future planning in birds.

Keywords: cooperation; grooming; sociality; primates; group-living; cooperative breeding

1. INTRODUCTION

Groups of soldiers increase their affiliative behaviour when moving into combat zones [1], and human groups in general exhibit greater cohesiveness if they have to contend with rivals [2]. However, despite numerous other species also competing as groups [3,4], and recent empirical evidence from a social bird species indicating that intragroup affiliation increases in the immediate aftermath of intergroup conflict [5,6], we know little about how the likelihood of *future* intergroup conflict influences *current* intragroup behaviour in non-human animals. Considering the impact of potential events can provide insights into the capacity for future planning [7], while elucidating the effect of intergroup interactions on intragroup processes is crucial for our understanding of group dynamics, cooperation and the evolution of sociality [8,9].

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The green woodhoopoe (*Phoeniculus purpureus*), a sub-Saharan bird species, offers an ideal opportunity to investigate how potential intergroup conflict might influence current intragroup affiliation. In South Africa, groups of 2–8 individuals defend linearly arrayed, permanent territories [10] and conflict between neighbours occurs frequently [4]. The vast majority (97%; $n = 488$ interactions, 24 groups) of such interactions take place within 100 m of shared territory boundaries (zones of potential conflict), which constitute $7 \pm 2\%$ of the territory and in which groups spend $9 \pm 4\%$ of their time (means \pm s.e.m.: $n = 24$ territories, 1256 observation hours); intergroup conflict rarely occurs in core territory areas. It is, therefore, possible to examine intragroup affiliative behaviour, specifically allopreening (which is known to play an important social role in this species; [11]), at times when the likelihood of intergroup conflict differs greatly. Moreover, because groups consist of a dominant breeding pair and up to six non-breeding subordinate helpers of both sexes [4], how individuals of different sex and status respond to the threat of intergroup conflict can be compared.

Here, I ask two main questions. First, is there more intragroup allopreening when intergroup conflict is more likely? Second, do all group members exhibit a similar change in allopreening donation and receipt in response to an increased likelihood of intergroup conflict?

2. MATERIAL AND METHODS

(a) *Study species*

Fieldwork was carried out on a colour-ringed population of green woodhoopoes near Morgan's Bay (32°43' S, 28°19' E), Eastern Cape Province, South Africa. Throughout the year, each group defends a stable area of thickly forested riverine valley, and boundaries between neighbouring groups remain remarkably fixed over time [10]. Intergroup conflicts between neighbours involve all adult group members, but individual contributions differ: males and females contribute equally overall, but each sex expends more effort responding to same-sex intruders; helpers contribute more than the breeding pair, perhaps because they have more to lose from the addition of new group members or because they are signalling to particular individuals in the opposing group (see [4] for details). Allopreening involves one individual preening another, and bouts focus on either body parts inaccessible (head allopreening) or accessible (body allopreening) to the recipient [11]. See the electronic supplementary material for further details about the study species.

(b) *Data collection and analysis*

I collected data on affiliative behaviour from 12 groups (mean \pm s.e.m.: adult group size = 3.3 ± 0.3 , range 2–5) between November 2000 and May 2001. Group compositions and the dominance status of group members remained constant throughout the data-collection period. Whenever I was with a group, I recorded the start and finish time of each self-preening and allopreening bout, the individual(s) involved and the territory location (on a 1:10 000 orthophotographic map; see [10]). For allopreening bouts, I also recorded the body parts preened (head or body) and the roles of both participants (donor or recipient). Bouts were considered finished when no (allo)preening had occurred for 30 s.

Because juvenile woodhoopoes (identifiable from their black bills) rarely allopreen [11], I only consider interactions between adult individuals (greater than 11 months post-fledging; nestling period lasts one month). Data were analysed from hours when the group spent the entire time in core territory areas (at least 100 m away from territory boundaries) and hours when at least 70 per cent of time was spent in zones of potential conflict (within 100 m of a territory boundary); territory position was established from maps constructed as part of a previous study [10]. Groups rarely spent an entire 1 h period within 100 m of a territory boundary, so 70 per cent time was used as a cut-off to ensure a suitable sample size for analysis; the results are conservative when considering the

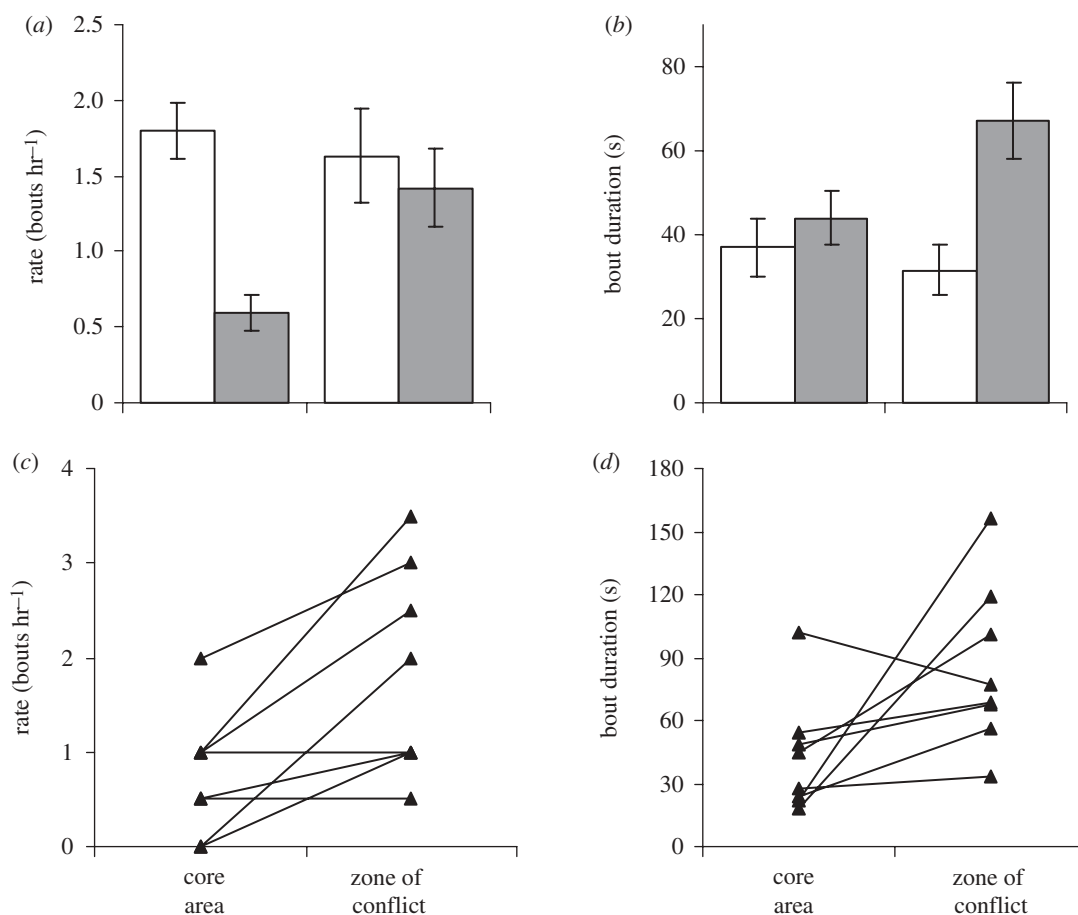


Figure 1. The influence of potential intergroup conflict on current intragroup; (a,c) allopreening rate and (b,d) allopreening bout duration. Shown in (a) and (b) are means \pm s.e.m. from both types of allopreening in all analysis hours ($n = 76$ h, 12 groups); shown in (c) and (d) are individual group values from paired comparisons of body allopreening in consecutive hours ($n = 8$ groups). (a,b) white bar, head; grey bar, body.

impact of time spent in zones of potential conflict on intragroup affiliative behaviour.

(c) Statistical analysis

Datasets containing repeated measures from the same group were analysed using mixed models to allow the inclusion of both random and fixed terms (see the electronic supplementary material for further details). To assess whether intragroup allopreening and self-preening differed depending on the potential threat of intergroup conflict, I used linear mixed models (LMMs) to compare (allo)preening rates and bout durations when groups were in core territory areas and zones of potential conflict. Models controlled for group size and month (see [11]) and were based on hourly (allo)preening rates of the whole group and mean durations of all (allo)preening bouts within an hour ($n = 52$ h in core areas, 24 h in conflict zones; 12 groups). The findings were confirmed by comparing changes in allopreening when the same group moved from one territory location to another in consecutive hours; these paired hours also formed the basis for subsequent analyses (see below).

To assess whether group members of different sex and dominance status (the breeding pair, helpers) altered their allopreening similarly when moving into zones of potential conflict from core territory areas in consecutive hours, I used two generalized linear mixed models (GLMMs) with a Poisson error structure and a log-link function (one for allopreening donation, one for receipt). Both models were based on 30 mean changes in hourly body allopreening rate (total rate in conflict zone minus total rate in core area); one value each from 16 dominants and 14 subordinates in eight groups.

3. RESULTS AND DISCUSSION

Intragroup allopreening rate (LMM: $\chi^2_1 = 8.37$, $p = 0.016$) and bout duration ($\chi^2_1 = 5.02$, $p = 0.028$) were both significantly influenced by the interaction

between territory location and body part preened (electronic supplementary material, table S1): there was no difference in head allopreening (which serves a primarily hygienic function; [11]) depending on territory location, but bouts of body allopreening (which serves a primarily social function; [11]) occurred more frequently and lasted for longer in zones of potential intergroup conflict compared with core territory areas (figure 1a,b). Paired comparisons of the same groups in consecutive hours produced similar results: body allopreening rates (Wilcoxon test: $W = 21$, $n = 8$, $p = 0.036$; figure 1c) and the duration of individual body allopreening bouts ($W = 33$, $n = 8$, $p = 0.042$; figure 1d) increased when groups moved from core areas to zones of potential conflict, but there was no change in head allopreening (rate: $W = 5.0$, $n = 8$, $p = 0.590$; bout duration: $W = 15$, $n = 8$, $p = 0.726$). The change in body allopreening is unlikely to be the consequence of temporal effects or of following the birds for longer because, in all cases for which paired data were available ($n = 4$ groups), body allopreening also decreased when groups moved from zones of potential conflict (mean \pm s.e., rate: 1.9 ± 0.4 bouts h^{-1} ; bout duration: 77 ± 9 s) to core areas (rate: 1.1 ± 0.3 bouts h^{-1} ; bout duration: 39 ± 6 s).

Analyses focused on occasions when there had been no visual or vocal signs of other woodhoopoes for at least 1 h. Moreover, qualitatively, the same results

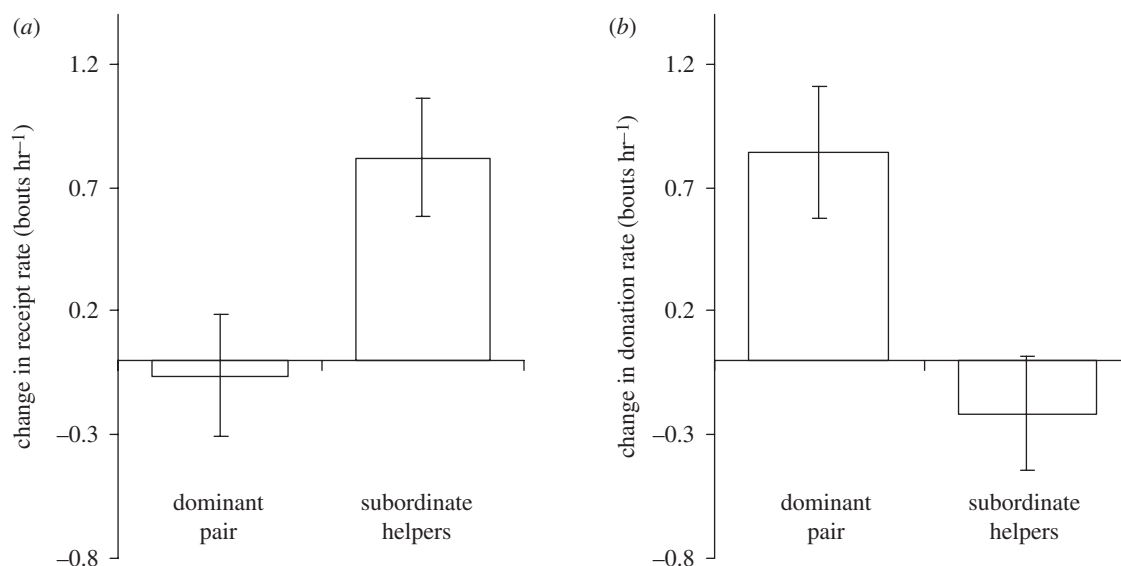


Figure 2. Mean \pm s.e.m. change in rate of all allopreening (a) receipt and (b) donation by individual group members when moving from core territory areas into zones of potential intergroup conflict ($n = 16$ dominants and 14 subordinates in eight groups).

were obtained if even stricter criteria were applied, and the LMMs examining allopreening rate and bout duration included only occasions when no woodhoopoes were seen or heard for at least an additional 1 h after the analysed period (interaction between territory location and body part preened, rate: $\chi^2_1 = 4.80$, $p = 0.031$; bout duration: $\chi^2_1 = 6.73$, $p = 0.012$; $n = 52$ h). It is therefore unlikely that the birds detected direct cues that I did not, and so external indicators of rivals are probably not responsible for the demonstrated increase in intragroup affiliation in zones of potential conflict.

Individuals did not preen themselves more when in zones of potential conflict compared with core areas (LMM, rate: $\chi^2_1 = 0.04$, $p = 0.841$; bout duration: $\chi^2_1 = 1.32$, $p = 0.255$; electronic supplementary material, table S2). Such self-directed behaviour has been shown to be an indicator of stress in other species [12,13]. If that relationship holds true for woodhoopoes, the demonstrated increase in allopreening in zones of potential conflict is also unlikely to be the simple consequence of additional stress.

An alternative explanation is suggested by the allopreening rates of different group members: the change in intragroup affiliative behaviour was the result of a significant increase in the preening received by subordinate helpers (GLMM: $\chi^2_1 = 6.39$, $p = 0.011$; electronic supplementary material, table S3a and figure 2a) and donated by the dominant breeding pair ($\chi^2_1 = 7.72$, $p = 0.010$; electronic supplementary material, table S3b and figure 2b). Dominants might therefore be using allopreening (the receipt of which is likely to reduce stress; [14]) to enhance group cohesiveness (see [15]) or to persuade subordinates to participate in any intergroup conflict that subsequently arises. It remains to be tested whether allopreening does indeed increase the participation of subordinates in this context, but previous work on other species has indicated that current affiliative behaviour might be exchanged for future agonistic support in intragroup conflicts [16]. The potential benefits

to dominants of ensuring the participation of subordinates in intergroup conflicts is clear, at least in woodhoopoes, because the latter contribute the most to such interactions [4] and their outcome is often determined by relative group size [17]. Although dominants might benefit from constantly maintaining social bonds, allopreening reduces the time available for other vital activities such as feeding, so dominants may increase their preening of others only when the likelihood of intergroup conflict is greatest.

Recent work has demonstrated that intragroup affiliative behaviour increases in groups immediately following intergroup conflict [5,6]. By contrast, the change in allopreening reported here is not a response to any actual conflict in the recent past, but rather the potential threat of conflict: allopreening increases when conflict is more likely. My results therefore provide rare and important empirical support in non-human animals for a link between intergroup conflict and intragroup affiliation. However, they also bring to mind the possibility of social contracts and even future planning, a trait that was until recently considered the preserve of humans and other primates but which is now known to be within the capabilities of birds (see [7]).

This work complies with the current laws in the country in which it was conducted, and was approved by the ethics committee of the University of Cambridge.

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