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Conflict Between Groups Promotes

Later Defence of a Critical Resource

in a Cooperatively Breeding Bird

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Running title: Intergroup conflict affects resource use

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Summary

Conflict between groups (intergroup conflict) is common in many social species [1–4] and is widely discussed as an evolutionary driver of within-group dynamics and social structure [2, 5]. However, empirical studies investigating the impacts of intergroup conflict have focused on the immediate aftermath [6–9], when behavioural changes may be the direct result of elevated stress levels [7] or territorial exclusions [9]. Demonstrations of longer-term effects, with behavioural changes persisting once increases in stress have diminished and when full access to resources is again possible, would support proposed links to individual fitness and social evolution. Here we show that conflicts between neighbouring groups of cooperatively breeding green woodhoopoes (*Phoeniculus purpureus*) have a lasting influence on decisions concerning roost cavities, a limiting resource vital for survival and breeding. Groups involved in extended conflicts in the morning were more likely to return to the zone of conflict that evening, roosting closer to territorial borders, than when intergroup interactions were short or did not occur. Extended morning conflicts also increased the likelihood that groupmates roosted together and preened one another at the roost, suggesting that intergroup conflict promotes consensus decision-making, social bonding and group cohesion. Border roost use and allopreening increased more following conflicts that were lost rather than won. Our results demonstrate that both the intensity and outcome of intergroup interactions affect resource defence and associated within-group behaviour many hours later, and begin to bridge the gap between the immediate impacts of intergroup conflict and its role in social evolution.

Results

Green woodhoopoes live in groups consisting of a dominant breeding pair and up to six nonbreeding helpers of both sexes [10]. Each group defends a year-round territory (mean ± SE size = 23.5 ± 1.7 ha) in thickly forested valleys [11] and they generally forage and move around this territory as a single unit [12]. Group members roost communally in tree cavities every night, which yields vital thermoregulatory benefits [13], and use one of the same cavities for nesting [10]. Each territory contains only a small number (mean ± SE = 6.9 ± 2.9) of suitable tree cavities [10] and these represent the limiting resource for woodhoopoe survival and reproduction: groups will rapidly move into previously unoccupied areas of forest if nestboxes are provided [14].

Interactions between groups are common and involve all group members contributing to alternating choruses (or 'rallies') [1], which on rare occasions escalate to physical fighting [15]. Around 97% of intergroup interactions (hereafter IGIs) between neighbours take place within 100 m of shared territory boundaries, termed zones of conflict [16]. We found that cavities in zones of conflict were used for roosting significantly more often than would be expected by chance (Wilcoxon signed-ranks test: Z = 2.05, n = 12, p = 0.041; Figure 1A). Groups with a greater involvement in IGIs, compared to those that interacted less with their neighbours, used zone-of-conflict roosts relatively more often than predicted from their availability (Spearman rank correlation, IGI rate: r_s = 0.59, n = 12, p = 0.042; proportion of time engaged in IGIs: r_s = 0.62, n = 12, p = 0.032; Figure 1B).

Woodhoopoe IGIs are highly variable in duration (1–45 min) and exhibit a bimodal distribution: 'short' IGIs (> 57% of cases), usually on territory boundaries, are decided within 5 min and primarily involve information exchange about current group structure and potential breeding opportunities; while 'extended' IGIs (ca. 30% of cases), which develop when there is a conflict over territory space, take over 15 min to resolve and usually involve a territorial intrusion [15]. We found that self-preening, a potential indicator of stress levels in this species [16, 17], was not significantly affected by the occurrence of short IGIs (linear mixed model (LMM) using mean duration of self-preening bouts: χ^2_2 = 0.23, n = 44, p = 0.900), but there was a highly significant effect of extended IGIs (χ^2_2 = 11.40, n = 42, p = 0.003). Specifically, self-preening bouts lasted significantly longer in the immediate aftermath of an extended IGI

than in the period immediately preceding the conflict (Figure 2). The fact that self-preening was unaffected by short IGIs, and that no diurnal fluctuations in self-preening were evident on days without IGIs (A.N. Radford pers. obs.), strongly suggests that the increase immediately following an extended IGI is a direct response to intense conflict. However, this effect was short-lived: by the start of the afternoon observation session, long before groups roosted (mean ± SE time from start of observation session to roosting: 3.5 ± 0.2 h, range = 2.2–4.5 h, n = 16 days), the duration of self-preening bouts had returned to pre-IGI levels (Figure 2).

Despite no evidence of prolonged stress, and groups always (100% of 134 cases) moving away from the IGI site in the interim, the occurrence and type of IGIs in the morning (none, short IGI, extended IGI) significantly influenced the likelihood of roosting within a zone of conflict at the end of the day (generalised linear mixed model (GLMM): χ^2_2 = 23.30, n = 232, p < 0.001). Specifically, zone-of-conflict roosts were more likely to be chosen on evenings when there had been an extended IGI during that morning compared to days on which there had been a short IGI or no IGI (Figure 3A). Even when controlling for whether a group had roosted in the zone of conflict the night before (by including the location of the previous night's roost for the subset of observations for which this information was known), the effect of IGI categorisation remained highly significant (χ^2_2 = 13.88, n = 153, p = 0.001). Further analysis showed that the effect of IGI categorisation was not because groups were more likely to change roost sites on extended IGI days (χ^2_2 = 4.44, n = 153, p = 0.109), but because groups that changed roost were more likely to move to a roost closer to the shared border on nights following an extended IGI than when there had been a short IGI or no IGIs that morning (χ^2_2 = 9.52, n = 64, p = 0.009; Figure 3B).

When groups roosted within a zone of conflict, their time of arrival at the roost site was significantly affected by IGI categorisation (LMM: χ^2_2 = 6.68, n = 70, p = 0.035): they arrived earlier on days that they had experienced an extended IGI than on other occasions (Fig. 4A). There was, however, no significant difference in the time they entered the roost for the night depending on IGI categorisation (χ^2_2 = 0.13, n = 70, p = 0.938). On most nights all groupmates roosted together in a single cavity, but occasionally groups split up more than 20 min before roosting and spent the night in two different cavities, as found previously in this species [18].

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122   There was a strong, but marginally non-significant, tendency for groups to split less often on

123   days when there had been an extended IGI (GLMM: χ^2_2 = 5.95, n = 70, p = 0.051; Figure 4B).

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125   Allopreening between woodhoopoe groupmates (an established affiliative behaviour [19])

126   has previously been shown to change in the hour following an IGI, with dominant individuals

127   increasing their preening of subordinates [7, 20]. In the current study, we found that the

128   likelihood of groups exhibiting allopreening in the evening when roosting in the zone of

129   conflict was significantly influenced by IGI categorisation that morning (GLMM: χ^2_2 = 8.27, n =

130   70, p = 0.016): allopreening was more likely on extended IGI days than in other cases (Figure

131   4C).

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133   Extended IGIs usually have clear-cut winners and losers; neighbouring groups that intrude and

134   win extended IGIs spend up to an hour in the territory of their opponent, foraging and

135   examining tree cavities [15]. We therefore considered whether roost choice in the evening is

136   affected by the outcome of earlier intergroup conflicts, testing the prediction that there is a

137   stronger response following lost encounters, as is the case with intragroup behaviour in the

138   immediate aftermath of IGIs [7]. Considering only days when there was an occurrence of an

139   extended IGI in the morning, there was a strong though non-significant trend for groups to be

140   more likely to roost in the zone of conflict with their opponents when they had lost rather

141   than won the conflict (GLMM: χ^2_1 = 2.90, n = 54, p = 0.089; Figure 3C). There was no significant

142   difference in arrival time depending on conflict outcome (LMM: χ^2_1 = 0.81, n = 31, p = 0.368),

143   but groups were significantly more likely to exhibit allopreening before roosting when they

144   had lost rather than won the morning conflict (GLMM: χ^2_1 = 3.98, n = 31, p = 0.046; Figure

145   4D).

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148   **Discussion**

149   Our findings provide strong evidence that intergroup conflict can influence group decisions

150   and intragroup behaviour relating to critical resource use. In general, green woodhoopoe

151   groups that interacted more with their neighbours used roosts near territorial borders more

152   often. Use of border roosts was most pronounced when there had been an extended IGI

153   earlier in the day, especially if that conflict had been lost. Extended IGIs in the morning were

154   also associated with a greater likelihood of group members roosting together in one place

155   and allopreening at the roost site in the evening, suggesting that conflict with rivals promotes

156   consensus over roosting decisions and group cohesion. Our results indicate that subsequent

157   behaviour is influenced both by the nature of the interaction with another group (extended

158   but not short IGIs in this case) and the outcome of a conflict (see also [7, 9, 20]). Most

159   importantly, we demonstrate that the behavioural impact of intergroup conflict is longer-

160   lasting than the immediate effect considered in many previous studies [7, 8, 21, but see 9,

161   22], and can occur without territorial exclusions (cf. [9, 22, 23]) and once elevated stress levels

162   have subsided.

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164   Previous work on intergroup conflict has shown that losing groups might be prevented from

165   using certain areas because of exclusion by winners [9, 23], or may avoid areas of agonistic

166   interaction if prior experience reliably predicts future conflict [22]. This reduced involvement

167   in agonistic interactions parallels the 'loser effect' often found in dyadic contests, whereby

168   individuals become less likely to escalate future conflicts following a defeat (reviewed in [24]).

169   Even where loser effects are not found, previous fights can reduce aggression and discourage

170   home-range overlap [25, 26]. Here, however, we found the opposite effect: the woodhoopoe

171   groups in our study used roosts in zones of conflict *more* often following intergroup conflicts,

172   especially those that were lost, and arrived at roost sites earlier on such occasions. This

173   greater usage may represent defence of a limiting resource; as in many other species [23, 27,

174   28], there is a risk that highly productive or important parts of a territory will be annexed by

175   successful rival groups [29]. Despite this risk, groups may continue to use other roosts outside

176   the zone of conflict if they provide greater thermoregulatory benefits [13], provide more

177   protection from predators [29], are less likely to accumulate water on rainy nights [30] or if

178   switching roosts is important for minimising the build-up of parasites [31].

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180   Occasions when members of the same group roost in different places probably reflect

181   unresolved between-individual conflicts of interest over group decisions [32, 33]. Our results

182   suggest that an earlier conflict with a rival group enhances the likelihood that a consensus is

183   reached later on, i.e. that all group members roost together. Since all adult woodhoopoe

184   group members contribute to the majority of IGIs [1] and the outcome of extended IGIs is

185   strongly determined by relative group size [15], an increased need for collective defence may

186 override within-group disagreements about roost site. Previous work on the factors
187 influencing group fissions has focused on environmental variability and uncertainty and
188 within-group factors such as individual energetic state, the social relationships between group
189 members and the ways information is gathered and shared [34–36]. Our study suggests that
190 external factors – in this case, intergroup conflict – also play an important role and should be
191 considered in future work on consensus decision-making.

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193 Extended intergroup conflicts appear to cause short-term increases in stress, which may be
194 responsible for previously documented changes in allopreening and other behaviour in the
195 immediate aftermath [7, 37]. However, our data on self-preening suggest that those
196 increased stress levels have subsided long before groups arrive at the roost site, perhaps
197 because commonly exhibited postconflict affiliative behaviour between groupmates reduces
198 stress for both recipients [38, 39] and donors [17, 40]. Consequently, the greater allopreening
199 at roost sites on days when there had been an extended IGI in the morning is unlikely to be
200 explained by lingering stress from the earlier conflict. One alternative possibility is that
201 returning to the zone of conflict in the evening causes a secondary stress increase, especially
202 since conflicts reliably occur in the same areas. Previous work has indicated that merely being
203 in a zone of conflict can affect intragroup behaviour [16], but here we also found a difference
204 in allopreening depending on the outcome of a conflict occurring many hours earlier. From a
205 functional perspective, allopreening may strengthen social bonds and group cohesion [41] or
206 may be traded in return for some other commodity [42, 43], such as increased involvement
207 in any conflict that subsequently ensues.

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209 Green woodhoopoe roosts are crucial both for survival and reproduction [10, 13]. If
210 intergroup conflict affects the use of such limiting resources, as suggested by our work here,
211 then there are likely implications for individual fitness beyond the obvious consequences of
212 injury or death resulting from aggressive interactions themselves [16, 18]. Moreover, the
213 increasing evidence that intergroup interactions affect intragroup behaviour in a variety of
214 species [7, 20, 37], not just humans [6, 8, 21], suggests broad evolutionary significance. While
215 it has long been suggested that conflict with rival groups is a key selective driver for group
216 dynamics and social structure [2, 5], previous empirical work on behaviour has generally
217 focused on immediate, short-term responses [6, 7, 37, but see 9, 22]. The current study,

showing that there can be a lasting impact of individual conflicts beyond the immediate effect of elevated stress, combined with the possibility that the mere threat of future conflicts also has an influence [16], suggests a stronger mechanism for evolutionary change. Future studies on intergroup conflict will therefore continue to be important in developing our understanding of resource use, sociality and the evolution of cooperation.

Experimental Procedures

Available in online Supplemental Information.

Author Contributions

ANR conceived the research and collected the data. TWF conducted the statistical analysis. ANR and TWF interpreted the data and co-wrote the paper.

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Figure Legends

Figure 1. Relative use of roosts in a zone of conflict.

(A) Expected (relative to total number of roosts available in the territory) and observed proportions of zone-of-conflict roosts used. (B) The difference between observed and expected usage of zone-of-conflict roosts in relation to the proportion of observation time engaged in intergroup conflict; the least-squares regression line is shown. N = 12 groups.

Figure 2. The influence of intergroup interactions (IGIs) on self-preening bouts.

The effect of extended and short IGIs on the duration of self-preening bouts in the 30 min immediately before the IGI ('before'), immediately after the IGI ('aftermath') and at the start of the afternoon observation session 7.7 ± 1.1 h (mean ± SE) later ('afternoon'). Shown are means ± SE, along with p values for significant post-hoc comparisons. N = 8 (extended IGIs) and N = 10 (short IGIs) groups.

Figure 3. The influence of intergroup interactions (IGIs) on roost use.

The effect of IGI categorisation (extended, short or no IGI in the morning) on the proportion of occasions that (A) a zone-of-conflict roost was used that evening and (B) the group chose a roost closer to the relevant territorial border that evening compared to the night before. (C) The effect of extended IGI outcome on the proportion of occasions that a zone-of-conflict roost was used that evening. Shown in all panels are means ± SE, along with p values for significant post-hoc comparisons. N = 12 groups.

Figure 4. The influence of intergroup interactions (IGIs) on roost-related behaviour.

The effect of IGI categorisation (extended, short or no IGI in the morning) on (A) arrival time at the roost site that evening, (B) the proportion of occasions that the group split to roost between different sites and (C) the proportion of occasions that group members allopreened at the roost site. (D) The effect of extended IGI outcome on the proportion of occasions that allopreening occurred. Shown in all panels are means ± SE, along with p values for significant post-hoc comparisons. N = 12 groups.