and developmental disorders such as autism involve disruption of executive function (in ways that may distinguish one group from another). Finally, it is known that prefrontal cortex matures relatively slowly, with some parts continuing to develop through adolescence and into adulthood. The consequences of this for fields such as education are only just beginning to be explored. Thus new developments in the field promise to transform the way that we understand the highest levels of human cognition, its disorders, and development.

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Type of threat influences postconflict allopreening in a social bird

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In many social species, aggressive conflict between individuals in the same group (intragroup conflict) is often followed by increased allogrooming (when one individual grooms another) involving the protagonists and their relatives [1,2]. Although conflict between groups (intergroup conflict) is also common (see [3]), there has been little consideration of its impact on intragroup affiliative behaviour (see [4] for an exception). Moreover, there has been no investigation of whether the different threat posed by different rival groups (for example, neighbours and strangers [5]) influences the level of subsequent affiliative behaviour. Experiments using playbacks to simulate territorial intrusions by green woodhoopoes (*Phoeniculus purpureus*), reported here, show that intragroup allopreening — the avian equivalent of allogrooming — increases significantly in response to strange groups, but not neighbouring groups, and that the increase is due to more allopreening of subordinate helpers by the dominant pair. This is the first experimental evidence for an influence of intergroup conflict on intragroup affiliative behaviour, and lends support to the recent idea that intragroup cooperation should increase most when the intergroup threat is highest [6].

Green woodhoopoes provide an ideal opportunity to investigate how the type of threat posed by rival groups influences intragroup affiliative behaviour. First, allopreening is a common and easily scored affiliative behaviour [7]. Second, groups frequently engage in obvious territorial contests, which involve the combined cackling of adult group members ('rallies') [3], and allopreening increases following these contests (my unpublished data). Third, green woodhoopoes can discriminate between rivals using group-specific signatures in their rallies [8], and they respond more rapidly to the playback of strangers than neighbours [8]. Neighbours may be viewed as less threatening because on winning a contest they only invade the loser's territory temporarily to forage and examine roost holes [9], but no changes in territory boundaries result [10]. In contrast, a strange group may take over the owner's territory permanently if successful in a contest [11].

I recorded allopreening events in the hour before and after simulated intrusions into the territories of 12 groups. Each group received two playback trials: one of a rally from a neighbouring group; the other of a rally from a strange group of the same size and sex ratio as the neighbouring group. I noted the identity of the individual donating and receiving each bout of allopreening, and also whether the bout focused on the head (which cannot be reached by the recipient itself) or the rest of the body (see Supplemental data available on-line with this issue for further details).

Intragroup allopreening rates increased significantly in the hour following simulated intrusions by strange groups, but not those by neighbours (Figure 1A). There was no significant increase in head allopreening, but body allopreening did increase significantly (Figure 1B), supporting the idea that the former serves a primarily hygienic function, while the latter fulfils a social function [7]. The increase in body allopreening following the playback of a strange group resulted from a significant increase in allopreening donation by the dominant pair (Figure 1C) to subordinate helpers (Figure 1D).

Intragroup allopreening may have increased to reduce stress [1], although there is no evidence that third-party affiliation has this effect [2]. And if stress reduction was important, the dominant pair might have been expected to receive, rather than donate, more allopreening, as they have the most to lose (a breeding position, as well as a territory) if a strange group defeats them. Alternatively, the dominant pair might have been attempting to improve affiliative relationships in the group and enhance social cohesion [12], thus maximising the likelihood that subordinate helpers participate in the next contest; relative group size is a key factor determining the outcome

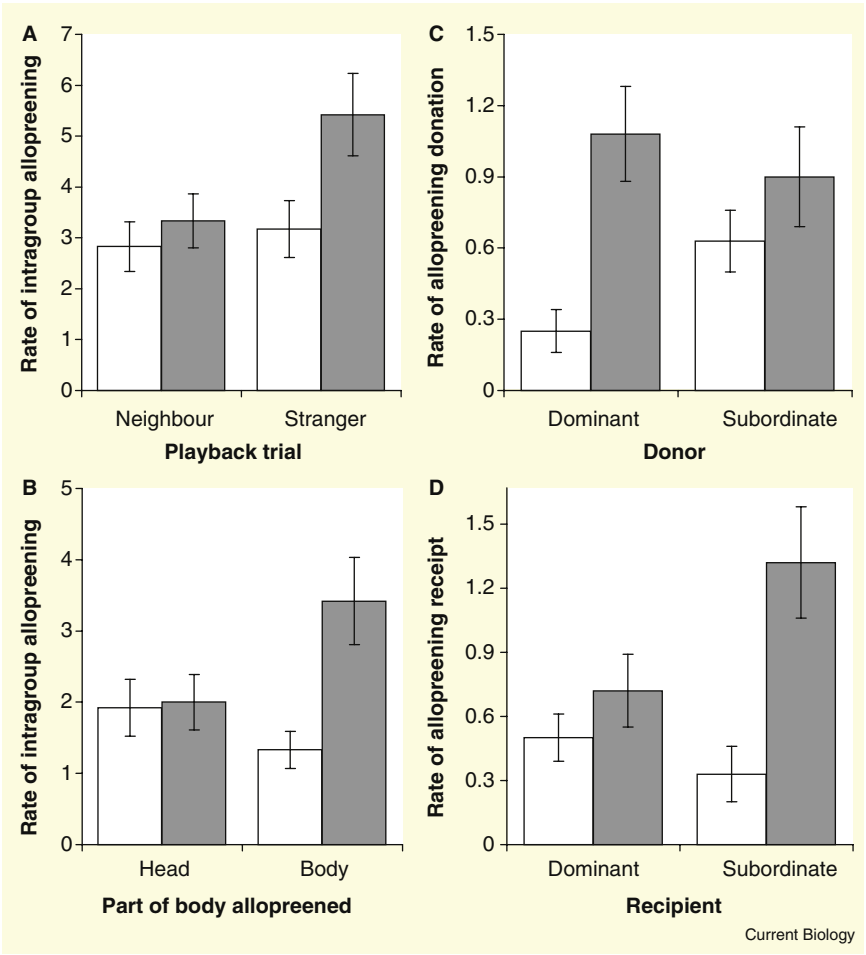

Figure 1. Allopreening by green woodhoopoes in response to simulated territorial intrusions.

(A) Intragroup allopreening increased following the playback of a strange group, but not a neighbouring group (repeated-measures ANOVA, interaction term: $F_{1,33} = 7.07$, $p = 0.012$). (B) Body allopreening, but not head allopreening, increased following the playback of a strange group (interaction term: $F_{1,33} = 10.07$, $p = 0.003$). (C) The dominant pair, but not subordinate helpers, increased their donation of body allopreening following the playback of a strange group (interaction term: $F_{1,29} = 5.65$, $p = 0.025$). (D) Subordinate helpers, but not the dominant pair, received more body allopreening following the playback of a strange group (interaction term: $F_{1,29} = 9.37$, $p = 0.005$). Shown in all cases are mean ± s.e.m. rates of allopreening (bouts per hour) in the hour before (white bars) and after (grey bars) playback trials. In (A) and (B), allopreening rates are for the whole group combined (N = 12 groups). In (C) and (D), allopreening rates are for individuals (N = 10 groups, because two groups contained no subordinate helpers).

of intergroup contests [9]. Although individuals have previously been shown to groom others in exchange for agonistic support in intragroup conflicts (for example [12]), the novel suggestion here is that they might do so to gain help in intergroup conflicts.

While most work on the 'dear-enemy phenomenon' — whereby territory holders respond more strongly to intrusions by strangers than to those by neighbours — has considered individuals [5], my results confirm its occurrence in a group-territorial species [8]. They also provide the first experimental evidence that intergroup conflict can influence intragroup affiliative behaviour, and show the type of threat may affect behaviour beyond the immediate response of territory holders. This is important because an increase in allopreening reduces the time for other vital activities, such as feeding. Because territory holders face more of a threat from strangers than from neighbours, the greater increase in allopreening following simulated intrusions by the former lends support to recent work suggesting that intragroup cooperation should be most apparent when intergroup conflict is highest [6]. In general, the ways in which interactions between groups affect within-group processes is of great importance for our understanding of cooperation and group dynamics.

Supplemental data

Supplemental data are available at http://www.current-biology.com/cgi/content/full/18/3/R114/DC1

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