Post-allogrooming reductions in self-directed behaviour are affected by role and status in the green woodhoopoe

Andrew N. Radford*

School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK
*andy.radford@bristol.ac.uk

Allogrooming occurs in a wide range of species and can serve both hygienic and social functions. While the latter have long been thought to be underpinned by reductions in tension for recipients, recent work has suggested that donors may also benefit in this way. Here, I show that, in cooperatively breeding green woodhoopoes *Phoeniculus purpureus*, involvement in allogrooming is followed by a reduction in self-grooming by both recipients and donors, but that the former exhibit a greater decrease. Moreover, I demonstrate for the first time that the dominance status of the allogrooming participant is important, with subordinate group members reducing subsequent self-grooming to a greater extent than the dominant pair. If avian self-directed behaviour reflects current distress levels in the same way as found in various primates, my results would indicate that allogrooming benefits are not confined to mammals, and would have important implications both for accurate assessments of the true costs and benefits of affiliative behaviour and for our understanding of the evolution of sociality.

1. INTRODUCTION

Allogrooming, whereby one individual grooms another, plays an important hygienic role in many species [1–3]. It also serves a number of social functions, including bond maintenance [4], conflict reconciliation [5] and as a trading commodity [6–8]. Empirical evidence has long supported the assertion that these social functions are based on short-term reductions in tension or distress for allogrooming recipients [9,10]. A recent study has shown that allogrooming donors may also gain through short-term distress reduction [11]. However, it remains unexplored whether both participants benefit to the same extent in this regard. Moreover, there has been little consideration of how groupmates of different sex and dominance status respond to allogrooming. Without such information, it is impossible to assess the true costs and benefits of affiliative behaviour.

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Most work investigating the social functions of allo-grooming has focused on primates [4,12] and other mammals [13,14]. While many birds engage in allogrooming (also called allopreening), it was initially assumed to serve a solely hygienic function, apparently involving only body areas that are difficult or impossible for an individual to reach itself [15]. It has become clear, however, that some bird species allogroom accessible body parts and that avian allogrooming can play an important social role [3,16–19].

Here, I use allogrooming data from a cooperatively breeding bird, the green woodhoopoe *Phoeniculus purpureus*, to answer three questions. First, does avian allogrooming reduce subsequent self-directed behaviour (specifically self-grooming), which reflects distress levels in other taxa (see [20,21])? Second, do donors and recipients reduce their self-grooming to the same extent following allogrooming? Third, how do participants of different sex and dominance status respond in the aftermath of allogrooming?

2. MATERIAL AND METHODS

(a) Study species

I studied a colour-ringed population of green woodhoopoes near Morgan's Bay (32°43′ S, 28°19′ E), Eastern Cape Province, South Africa. Here, groups consist of a dominant breeding pair (hereafter, *dominants*) and up to six non-breeding, subordinate helpers of both sexes (hereafter, *subordinates*) [22]. All adults participate in regular allogrooming, with bouts focusing either on the head (inaccessible to the recipient) or other body parts (accessible to the recipient) [3]. See the electronic supplementary material for additional information.

(b) Data collection

I collected data from 12 groups between November 2000 and May 2001 and from a further eight groups in October and November 2004 (mean ± s.e.m. group size: 3.2 ± 0.3; range: 2–6), whenever they were not engaged in a breeding attempt. Observations were made in either morning (4 h after dawn) or afternoon (3 h before dusk) sessions, during periods of group foraging [23]. Following allogrooming bouts of known duration between identified individuals, I conducted a 10 min post-allogrooming focal watch (PA) on the donor or the recipient. PAs were randomly assigned, up to a maximum of two complete PAs (one for each role) on an individual during an observation session. PAs were abandoned if the focal bird engaged in a new allogrooming bout or the group flew somewhere else. During PAs, I recorded the number and duration of all observed self-grooming bouts; bouts separated by at least 10 s were classified as distinct.

Where possible, I also collected self-grooming data in matched-control (MC) periods. MCs were during the subsequent observation session on the same group (mean ± s.e.m. days between sessions: 2.7 ± 0.6, range: 1–4, $n = 252$ PA–MC pairs), at approximately the same time of the day as the corresponding PA. MCs were not conducted if the individual had been involved in allogrooming during the preceding 15 min. Self-grooming data were collected during MCs in the same way as for PAs. The thick canopy at the study site made it difficult to see birds throughout entire focal periods, but there was no difference in the time birds were in sight during PAs (mean ± s.e.m. duration = 8.6 ± 0.5 min) and MCs (8.7 ± 0.6 min; paired *t*-test: $t = 0.691$, $n = 47$, $p = 0.493$), and no systematic biases in terms of observation durations are apparent in the dataset (see the electronic supplementary material for more information).

(c) Data analysis

All analyses were conducted on the difference between PAs and their MCs in the percentage time spent self-grooming. To assess whether there was any reduction in self-grooming following allogrooming, I used one-sample *t*-tests; mean values were calculated for each individual. I then used a linear mixed model (LMM) to examine the importance of the individual's role (donor versus recipient), sex and dominance status (dominant pair versus subordinate helper), while controlling for potential influences of allogrooming bout duration, group size, month and year (fixed effects) and individual
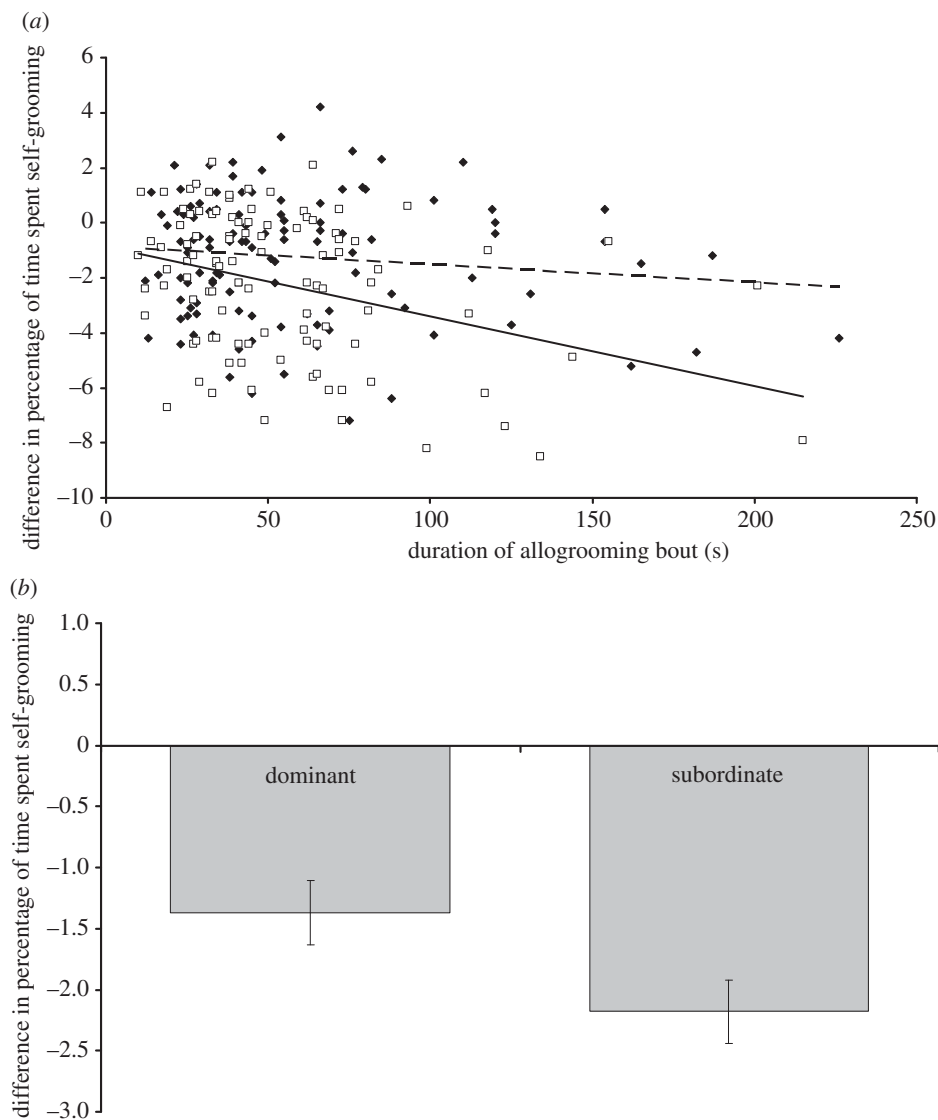
Figure 1. Reduction in self-grooming by green woodhoopoes in post-allogrooming periods (PA) compared with matched-control (MC) periods. Shown are (*a*) values for individual PA–MC pairs (diamonds, allogrooming donors; open squares, allogrooming recipients; *n* = 215) and least-squares regression lines (dashed, donors; solid, recipients), and (*b*) mean ± s.e.m. values for group members of different dominance status (*n* = 27 dominants, 20 subordinates).

and group identity (random effects). I included only individuals for which there were at least three differences, so this LMM was based on 215 differences from 47 individuals in 20 groups. I then ran an additional model using only the subset of data involving head allogrooming bouts (108 differences from 27 individuals in 17 groups); that is, when allogrooming and self-grooming focused on different body parts, and thus any reduction in self-grooming is unlikely to be solely the consequence of a decrease in hygienic need. See the electronic supplementary material for more details.

3. RESULTS

Both donors (one-sample *t*-test: *t* = 4.86, *n* = 46, *p* < 0.001) and recipients (*t* = 6.47, *n* = 47, *p* < 0.001) spent a significantly smaller percentage of time self-grooming immediately following an allogrooming bout than in a control period. However, the reduction in self-grooming was significantly greater for recipients (LMM: Wald statistic = 10.98, d.f. = 1, *p* = 0.001; electronic supplementary material, table S1), and this difference was particularly pronounced after allogrooming bouts of longer duration (allogrooming role and duration interaction: Wald statistic = 5.13, d.f. = 1,

p = 0.025; electronic supplementary material, table S1 and figure 1*a*). Dominance status also had a significant effect, with subordinates exhibiting a greater reduction than dominants in the percentage of time spent self-grooming (Wald statistic = 8.12, d.f. = 1, *p* = 0.007; electronic supplementary material, table S1 and figure 1*b*). This status-dependent difference was apparent both when individuals were donors and when they were recipients (no significant interaction between allogrooming role and dominance status: Wald statistic = 0.85, d.f. = 1, *p* = 0.358). There was no significant effect of sex, group size, month or year on the difference between PAs and MCs in the percentage of time spent self-grooming (electronic supplementary material, table S1).

The same qualitative results were found when only considering PAs following head allogrooming bouts (allogrooming role: Wald statistic = 6.95, d.f. = 1, *p* = 0.010; role and duration of interaction: Wald statistic = 5.80, d.f. = 1, *p* = 0.018; dominance status: Wald statistic = 4.87, d.f. = 1, *p* = 0.037; electronic

supplementary material, table S2). That is, recipients exhibited lower subsequent levels of self-grooming than donors, as did subordinates compared with dominants, even when self-grooming and allogrooming involved different body parts.

4. DISCUSSION

The findings presented here provide, to my knowledge, the first evidence in an avian species that self-directed behaviour decreases following allogrooming. Previous studies of allogrooming receipt in mammals have not eliminated the possibility that any subsequent decrease in self-grooming simply results from a lessened hygienic need, but the reduction in woodhoopoe self-grooming after allogrooming bouts focused solely on the head indicates that a lower ectoparasite load is unlikely to be the only explanation. While my results support the recent finding in primates that allogrooming donors reduce self-directed behaviour in qualitatively the same way as recipients [11], and suggest this may be a widespread phenomenon across different taxa, they also demonstrate that the magnitude of such a reduction depends on the allogrooming role: recipients exhibited less subsequent self-directed behaviour than donors, particularly following longer allogrooming bouts. Moreover, subordinate group members reduced their self-grooming to a greater extent than the dominant pair.

In primates, self-directed behaviour has been shown to indicate the current distress/tension level of an individual [20,21]. If this is also true in birds—something requiring experimental confirmation—then the reduction in self-grooming by woodhoopoes that have recently participated in allogrooming would indicate decreased distress/tension, perhaps mediated by lowered levels of circulating glucocorticoids [24]. Such a short-term benefit could underpin the social functions of avian allogrooming [3,16–19] in the same way as suggested for various mammal species [4,13,14], and provide a proximate mechanism for the formation and maintenance of beneficial social networks (see [11]).

Allogrooming donation is costly because time is lost for activities such as foraging and vigilance [4,25]. A short-term benefit from reduced distress would mitigate this cost to some extent, but my results suggest that any such benefit might be less than that for recipients. Allogrooming donors could, however, receive other benefits from their behaviour. For example, they might be trading grooming for food [7], tolerance [8] or participation in later intragroup or intergroup conflicts [6,19]. There is also some evidence that allogrooming donors experience lower long-term stress levels than recipients [26], and grooming others might even be self-rewarding [27]. Clearly, assessment of the relative benefits to both allogrooming parties requires further research.

Most previous studies investigating the effects of allogrooming have focused on individuals of one sex, usually females, and have not considered dominance status (see [12]). My results suggest that group members do not respond equally to allogrooming participation, at least in terms of subsequent self-directed behaviour: subordinate woodhoopoes reduced their self-grooming more than dominants. In theory,

this might be because subordinates use allogrooming to alleviate potential aggression from dominants [8], although in woodhoopoes there is little intra-group aggression and conflicts tend to be resolved using vocalizations [28]. Future studies should consider whether characteristics of the allogrooming partner, such as dominance status and relatedness, influence the level of self-grooming that follows. Moreover, more subtle measures than simple participation, such as the identity of the bout initiator and the context, might shed valuable light on the relationship between allogrooming and subsequent behaviour.

In conclusion, my study provides a novel extension to the growing body of evidence that the likely tension-reducing properties of allogrooming are not simply restricted to the recipient [11,26], and also suggests that group members may not benefit equally from allogrooming participation. Such findings are important for our understanding of the costs and benefits of intragroup affiliative behaviour and, ultimately, the evolution of sociality.

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