

# Dual function of allopreening in the cooperatively breeding green woodhoopoe, *Phoeniculus purpureus*

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**Abstract** Allopreening is a widespread but little-studied phenomenon in birds and is particularly prevalent in species where individuals are forced into close proximity. Such a situation facilitates the transfer of ectoparasites between individuals and allopreening has therefore been proposed to serve a hygienic function. In addition, allopreening might theoretically play a role in social communication. Green woodhoopoes (*Phoeniculus purpureus*) are cooperatively breeding birds that roost communally every night in a tree cavity and are thus susceptible to high ectoparasite loads. Our results suggest that allopreening of the head and neck (“head”), which cannot be efficiently self-preened, serves a primarily hygienic function: all individuals, irrespective of sex, dominance status, and group size, donated and received similar rates of head allopreening and terminated a similar proportion of bouts in which they were involved. Furthermore, there was a high occurrence of reciprocation and head allopreening occurred at a constant rate throughout the year. In contrast, allopreening of the rest of the body, which is accessible to the recipient itself, is likely to serve a primarily social function: body allopreening rates were higher in larger groups; dominant individuals received more body allopreening and terminated a significantly

higher proportion of bouts than subordinates; and subordinates donated body allopreening at a higher rate than dominants. Moreover, bouts initiated by dominants were more likely to be reciprocated than those initiated by subordinates and body allopreening rates varied seasonally. Allopreening in the green woodhoopoe is therefore likely to serve a dual function, depending on the part of the body involved.

**Keywords** Allopreening · Ectoparasites · Hygienic function · Green woodhoopoes · Social communication · Reciprocation

## Introduction

Allogrooming, whereby one individual grooms another, is a widespread phenomenon among mammals and has been extensively studied in a variety of primates (e.g., Barrett et al. 1999; Manson et al. 2004), ungulates (e.g., Hart and Hart 1992; Feh and de Mazieres 1993), and rodents (e.g., Stopka and Macdonald 1999; Stopka and Graciasová 2001). Two general hypotheses have been proposed for the function of allogrooming:

### (1) Hygiene.

If self-grooming is effective in cleaning fur, removing ectoparasites, and preventing infection, allogrooming might be expected to be similarly useful (e.g., Freeland 1976; Barton 1985).

### (2) Social communication.

Allogrooming may, for example, be used by dominant individuals to reaffirm their status over subordinate group members (Sparks 1969; Eisenberg 1981) or to reconcile individuals after punishment (Call et al. 2002).

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It may also be used to divert aggressive attacks, reduce tensions (Schino et al. 1990; Baker and Aureli 2000), and/or maintain and improve affiliative relationships among group members (Seyfarth and Cheney 1984; O'Brien 1993).

These hypotheses are not mutually exclusive and some studies have demonstrated multiple functions of allogrooming within the same species (e.g., Sparks 1969; Perry 1996; Di Bitetti 1997).

Allopreening, the avian equivalent of allogrooming, is also widespread, but has received surprisingly little attention. This is perhaps because it was initially thought to serve a solely hygienic function (Brooke 1985), apparently being concentrated on areas of the body that are difficult or impossible for a bird to reach by itself (Harrison 1965). However, some bird species do allopreen accessible parts of their body and, furthermore, many avian species are found in complex, permanent groups in which social interactions are commonplace (Koenig and Dickinson 2004). Allopreening might therefore be expected to have similar social functions to those demonstrated for mammalian allogrooming, but this was not previously considered in any detail.

Green (also red-billed) woodhoopoes (*Phoeniculus purpureus*), a cooperatively breeding, group-territorial bird, offer an ideal opportunity to investigate the potential hygienic and social functions of allopreening. First, all group members spend the night in a communal roost hole, a behavior that is believed to minimize predation and/or thermoregulatory costs (Ligon and Ligon 1978; Du Plessis and Williams 1994). A particular group may use the same cavity for many consecutive months, forcing individuals into close proximity and facilitating a high level of ectoparasite transfer between group members. Second, as groups contain a single breeding pair and up to ten nonbreeding helpers (Ligon and Ligon 1978), social interactions, such as dominance assertions and tension amelioration, are likely to be commonplace. Third, the long bill of the green woodhoopoe prevents efficient self-preening of the head and neck region, perhaps necessitating allopreening for ectoparasite removal from these areas. However, in contrast to many bird species (Harrison 1965), allopreening is not confined to the head and neck, suggesting that it may serve an additional, social function.

In this study, we provide the first detailed consideration of the function of allopreening of different parts of the body and test a number of specific predictions. If allopreening serves a primarily hygienic function, individuals of different dominance status and in groups of different sizes might be expected to donate and receive allopreening at a similar rate to one another. In contrast, if allopreening plays a role in social communication, we predict that individual rates of allopreening donation and receipt will differ between

individuals of different dominance status and in groups of different sizes. Specifically, we predict that: (1) if allopreening is used by dominants to reaffirm their status over subordinates, dominants should donate more and subordinates should receive more allopreening; (2) if allopreening is used to divert aggressive attacks or reduce tensions, subordinates should donate more and dominants receive more allopreening; and (3) if allopreening is used to maintain or improve affiliative relationships among group members, there should be no difference in dominant and subordinate rates of allopreening donation and receipt. Furthermore, if allopreening is important for hygiene, bouts initiated by all group members should be equally likely to be reciprocated, whereas if social communication is critical, the likelihood of reciprocation should differ depending on the status of the donor and recipient. We therefore compare donation, receipt, and reciprocation of allopreening of different parts of the body among individuals in a woodhoopoe population. We also compare the ectoparasite loads of different individuals to consider the potential consequences of variation in allopreening rates.

## Materials and methods

### Data collection

Allopreening data were collected from six color-ringed groups of green woodhoopoes between February 1986 and February 1987 (M. A. Du Plessis) and from a further 12 color-ringed groups between November 2000 and May 2001 (A. N. Radford) near Morgan's Bay (32°43'S, 28°19'E), Eastern Cape Province, South Africa. Because juvenile woodhoopoes rarely allopreen (Du Plessis 1989), we only consider interactions between adult individuals (those older than 12 months). Because group members spent the majority of their time together, the absence of an individual on three consecutive observer visits to a group was assumed to reflect its death or dispersal to another territory. On the rare occasions (3 out of 18 groups) that a group permanently changed in size in this way, or it gained a new immigrant member, no further allopreening data were collected from that group. Thus, the adult size and composition of a particular group remained constant throughout the period of allopreening data collection. Groups ranged in size from two to seven adults (mean±SE 3.4±0.3). Adults could be sexed on the basis of sexual dimorphism in bill length (Radford and du Plessis 2003) and vocalizations (Radford 2004). Dominance status was established by watching displacement activity during group foraging, when "dominants" (the breeding pair) consistently displaced their nonbreeding "subordinate" helpers (Radford and du Plessis 2003). Within woodhoopoe groups, fixed linear dominance

hierarchies exist for each sex (Ligon and Ligon 1990). Because there was no change in the composition of each group during the period of allopreening data collection, an individual's dominance rank remained the same during this time.

Groups were watched through binoculars between 0500 and 1100 h and between 1500 and 1900 h because this was when the birds were most active (personal observation). Preening birds searched and stroked feathers with soft jabs of the bill and sometimes ran the feathers through their bill. "Allopreening" was defined as the behavior whereby one woodhoopoe brought its bill into firm contact with the feathers of another individual in a preening motion. Allopreening events were recorded ad libitum whenever the initiation of a bout was observed. Birds preening others were classified as "donors," while those being preened were the "recipients." An allopreening bout focused on either regions of the recipient's body that were "inaccessible" to itself (i.e., the head and neck, hereafter termed the "head") or regions that were theoretically "accessible" to itself (i.e., anywhere lower than the neck, hereafter termed the "body"). An allopreening bout was further defined as either "reciprocated," when two birds preened one another simultaneously or in succession, or "nonreciprocated," when one bird remained the recipient throughout the bout. In the case of reciprocated bouts, both individuals were classified as donors and recipients. An allopreening bout was considered finished whenever one or both individuals moved away from one another, or when no allopreening had occurred for 30 s. If one individual moved away from the other, which remained stationary, the former was considered to have "terminated" the interaction.

The following data were recorded for each observed allopreening bout: the body parts that were preened (either head or body), whether the interaction was reciprocated, the roles played by each participant (donor and/or recipient), the month, and the group size. Between November 2000 and May 2001, the identity of the individual (if any) that terminated the interaction was also noted.

To assess ectoparasite loads, birds were caught on 357 occasions (range 1–5 captures,  $n=242$  adult individuals) between 1981 and 2003. They were caught at dawn as they left a communal roost where they are likely to acquire most of their ectoparasites. Each bird was examined for mites, fleas, and lice by blowing the feathers under both wings, across the chest, neck and the top of the head, and down to the rump for 30 s (timed using a stopwatch) and was awarded a "parasite score" ranging from 0 (no ectoparasites visible) to 3 (severe ectoparasite infestation). Thirty birds were examined by two observers and were scored independently. The scores from the two observers were highly repeatable ( $P<0.01$ ; Lessells and Boag 1987) and so all subsequent parasite scores were assigned by one observer only. The

mass (in grams) of each bird was also determined using a 100-g Pesola balance. Birds were never caught between September and December to avoid disturbance of breeding attempts. Because birds were only caught once per season, individuals may have changed dominance status between captures.

Between February 1986 and February 1987, the composition of 29 groups was monitored every 3–7 days. Any loss (due to emigration or death) or gain (from immigration) of an adult group member constituted a "change" in the adult composition of that group, and the month in which it occurred was noted. We compared the proportion of groups that underwent a change in summer (January to April) and winter (May to August).

### Statistical analysis

Most analyses required the use of multivariate statistics and involved repeated measures of the same individual and/or group. Therefore, we first employed generalized linear mixed models (GLMMs), which enabled both fixed and random terms to be defined. Random terms allow the analysis to take account of repeated measures and were only included if the analysis indicated significant repeatability at that level (as per Pinheiro and Bates 2000). If no random terms were significant, we reverted to generalized linear models (GLMs). All fixed terms were initially entered into the model and then sequentially dropped until only terms whose elimination would have significantly reduced the explanatory power of the model remained. All two-way interactions were tested, but only those that were significant are presented in the "Results." The significance of a term was derived by dropping it from the final model (if it was part of the final model) or adding it to the final model and then dropping it (if it was not part of the final model). All statistical tests were conducted using GenStat (sixth edition, Lawes Agricultural Trust, Rothamsted, Harpenden, UK).

### *Donation and receipt of allopreening*

To investigate the factors affecting the rate of allopreening donation and receipt, we used two separate GLMMs with a normal error structure. For each individual, monthly rates of both head and body allopreening donation and receipt were calculated by dividing the number of bouts by the number of observation hours. A total of 2,409 cases of allopreening (1,542 involving the head and 867 involving the body) were recorded, which were collected from over 2,000 h of observations. Rates were log-transformed before analysis to normalize the data. In each case, there was significant repeatability of allopreening rate by individual identity ( $P<0.05$ ), so individual was included as a random factor.

There was no significant repeatability of group identity ( $P>0.05$ ) and so group was dropped from both models. The following fixed terms were included in both models: adult group size, individual sex and dominance status (dominant or subordinate), month, number of observation hours, and the body part being preened (head or body). Both models were based on 986 rates from 62 individuals in 18 groups.

#### Termination of allopreening

Individual rates of allopreening termination were calculated as the proportion of the number of allopreening bouts in which a particular individual had been involved (e.g., number of terminations by individual A relative to the number of allopreening bouts involving individual A). There were too few terminations to enable us to analyze the influence of month. Thus, data for each individual were combined from the entire period they were watched. A GLM with a binomial error structure and a logit link was used to assess the influence of adult group size, individual dominance status (dominant or subordinate) and sex, and the body part being preened (head or body) on termination rate. The analysis was based on a sample of 80 rates from 40 individuals in 12 groups. A similar mixed model confirmed no significant repeatability of either group or individual identity ( $P>0.05$ ).

#### Ectoparasite loads

To investigate the importance of month, group size and individual sex, dominance status (dominant or subordinate), and body mass on ectoparasite load, we conducted a GLM with a binomial error structure and logit link. The parasite score from the first time each individual was captured as an

adult was converted to 0 (no parasites) or 1 (some parasites). A similar mixed model confirmed no significant repeatability of parasite load by group identity ( $P>0.05$ ).

## Results

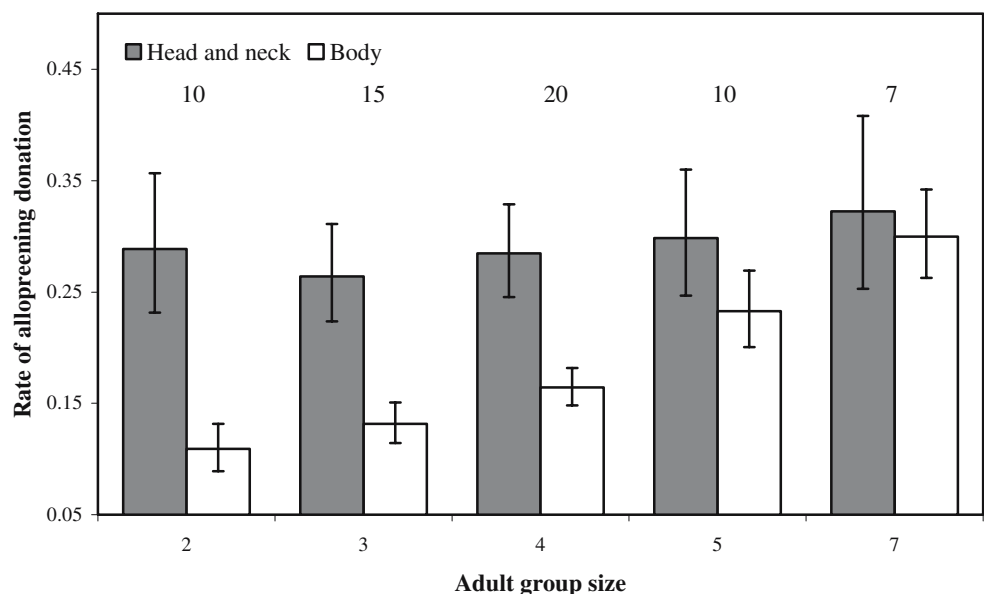
### Donation of allopreening

Head allopreening was donated at a significantly higher rate than body allopreening (GLMM  $\chi^2=36.14$ ,  $df=1$ ,  $P<0.001$ ) and body part interacted significantly with three other terms in the model. There was a significant interaction between body part and group size ( $\chi^2=129.27$ ,  $df=9$ ,  $P<0.001$ ): individuals in groups of all sizes donated approximately equal amounts of head allopreening, but there was an increase in the amount of body allopreening donated by individuals as group size increased (Fig. 1). There was also a significant interaction between body part and dominance status ( $\chi^2=42.64$ ,  $df=2$ ,  $P<0.001$ ): dominant and subordinate individuals donated allopreening of the head at a similar rate, but subordinates donated more body allopreening than dominants (Fig. 2a). Body part also interacted significantly with month ( $\chi^2=208.97$ ,  $df=22$ ,  $P<0.001$ ): head allopreening was donated at approximately equal rates throughout the year, whereas body allopreening peaked between the winter months of May and August (Fig. 3). There was no significant effect of either sex ( $\chi^2=0.07$ ,  $df=1$ ,  $P=0.791$ ) or the number of observation hours ( $\chi^2=0.12$ ,  $df=1$ ,  $P=0.738$ ) on the rate of allopreening donation.

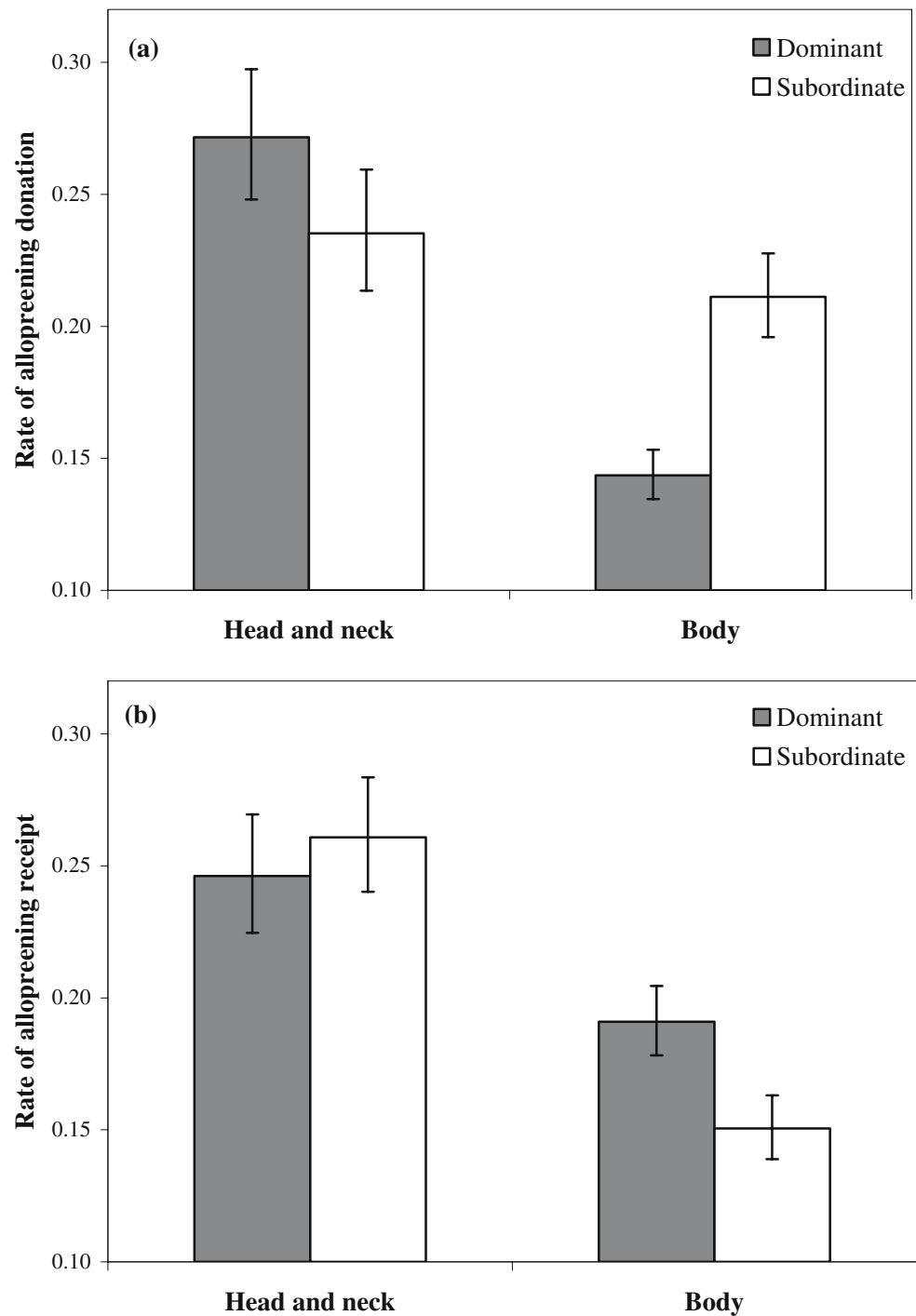
### Receipt of allopreening

As with donation, head allopreening was received at significantly higher rates than body allopreening (GLMM

**Fig. 1** The rate (occasions per observation hour) of allopreening donation by adult green woodhoopoes in 18 groups of different sizes. Shown are means  $\pm$  SE with number of individuals given above bars



**Fig. 2** The rates (occasions per observation hour) of allopreening **a** donation and **b** receipt by dominant ( $n=36$ ) and subordinate ( $n=26$ ) green woodhoopoe group members. Shown are means $\pm$ SE



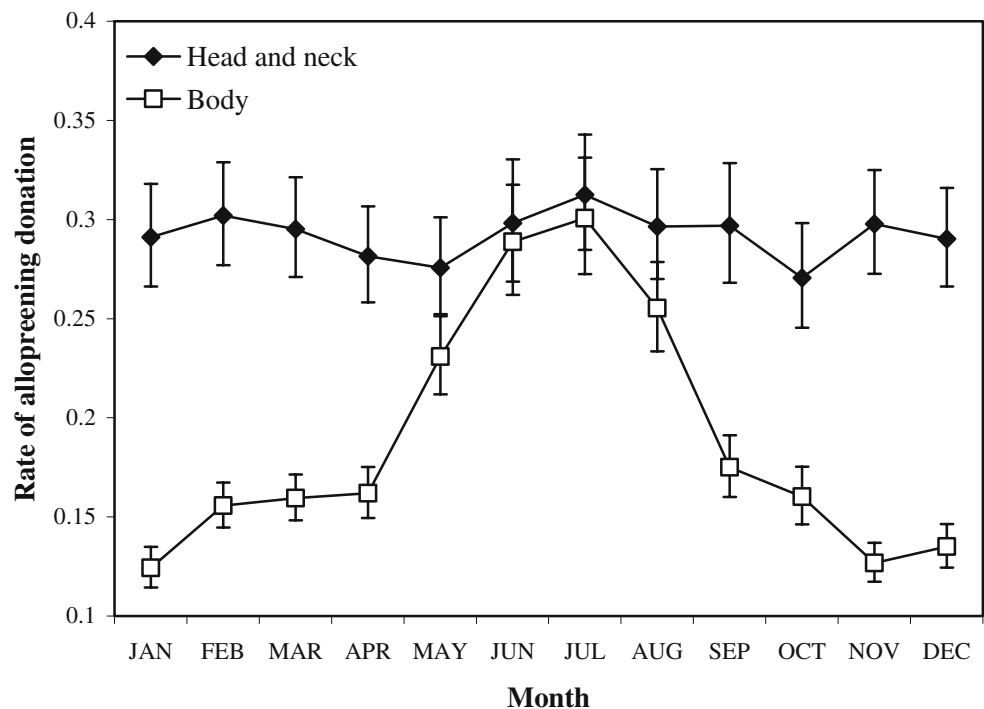
$\chi^2=17.76$ ,  $df=1$ ,  $P<0.001$ ) and body part interacted significantly with group size ( $\chi^2=175.73$ ,  $df=9$ ,  $P<0.001$ ), dominance status ( $\chi^2=16.32$ ,  $df=2$ ,  $P<0.001$ ), and month ( $\chi^2=185.26$ ,  $df=22$ ,  $P<0.001$ ). The relationships for group size and month were qualitatively the same as for allopreening donation. However, the dominance effect was different: dominants and subordinates received head allopreening at similar rates, but dominants received more body allopreening than subordinates (Fig. 2b). There was no

significant effect of either sex ( $\chi^2=0.19$ ,  $df=1$ ,  $P=0.664$ ) or the number of observation hours ( $\chi^2=0.06$ ,  $df=1$ ,  $P=0.813$ ) on the rate of allopreening receipt.

#### Termination of allopreening

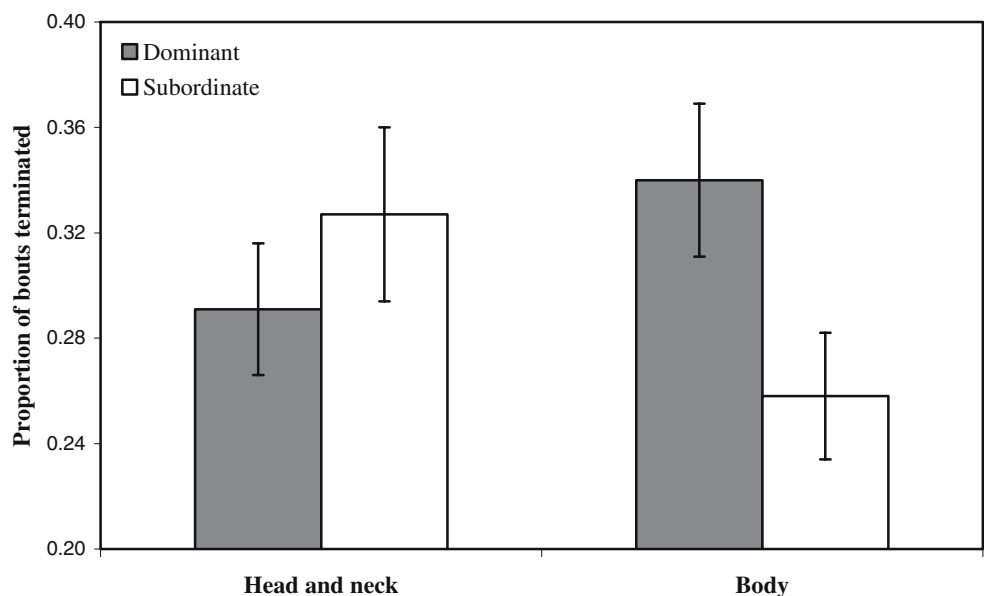
Although body part was not itself a significant predictor of the proportion of allopreening bouts that were terminated (GLM  $F_{1,69}=1.02$ ,  $P=0.314$ ), it did interact significantly

**Fig. 3** The rate (occasions per observation hour) of allopreening donation at different times of the year. Shown are means $\pm$ SE



with two other terms in the model. There was a significant interaction between body part and dominance status ( $F_{2,70}=5.62$ ,  $P=0.004$ ): although dominants and subordinates terminated a similar proportion of the head allopreening bouts in which they were involved, dominants terminated body allopreening bouts more often than subordinates (Fig. 4). There was also a significant interaction between body part and group size ( $F_{6,70}=2.90$ ,  $P=0.008$ ): there was no difference in the termination rates of head allopreening by individuals in groups of different sizes, but individuals in larger groups were more likely to terminate body allopreening bouts than those in smaller

**Fig. 4** The proportion of allopreening bouts terminated by dominant ( $n=36$ ) and subordinate ( $n=26$ ) green woodhoopoe group members. Shown are means $\pm$ SE

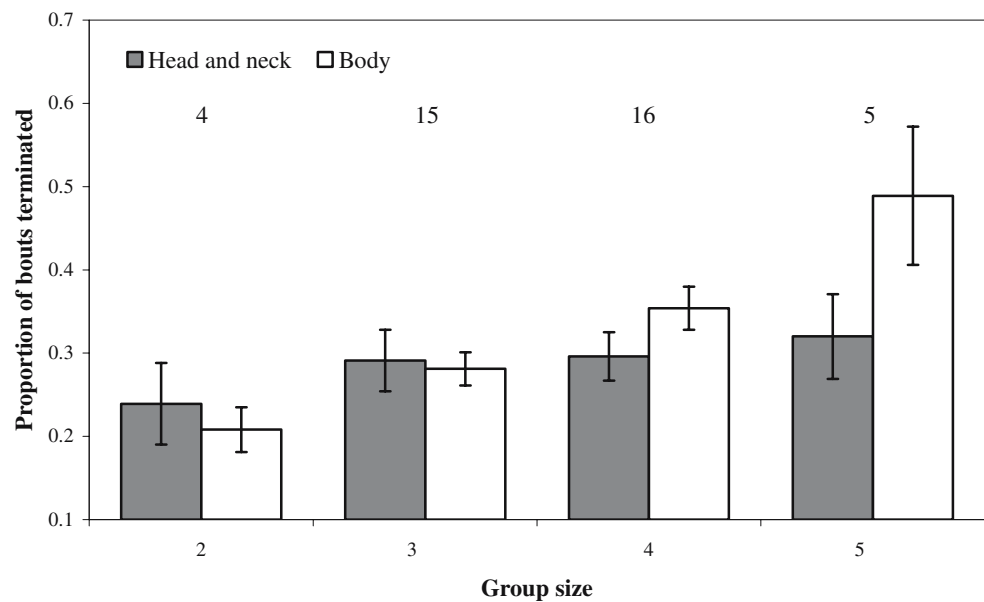


groups (Fig. 5). There was no significant influence of sex on the proportion of allopreening bouts terminated ( $F_{1,69}=1.11$ ,  $P=0.292$ ).

#### Reciprocation

Allopreening of the body was only rarely reciprocated (84 out of 867 bouts), in contrast to allopreening of the head, which was reciprocated at a significantly higher rate (1,148 out of 1,542 bouts; chi-square test  $\chi^2=931.5$ ,  $df=1$ ,  $P<0.001$ ). A similar percentage of all head allopreening bouts (54%) and those that were reciprocated (56%) were

**Fig. 5** The proportion of allopreening bouts terminated by adult green woodhoopoes in 12 groups of different sizes. Shown are means $\pm$ SE with number of individuals given above bars



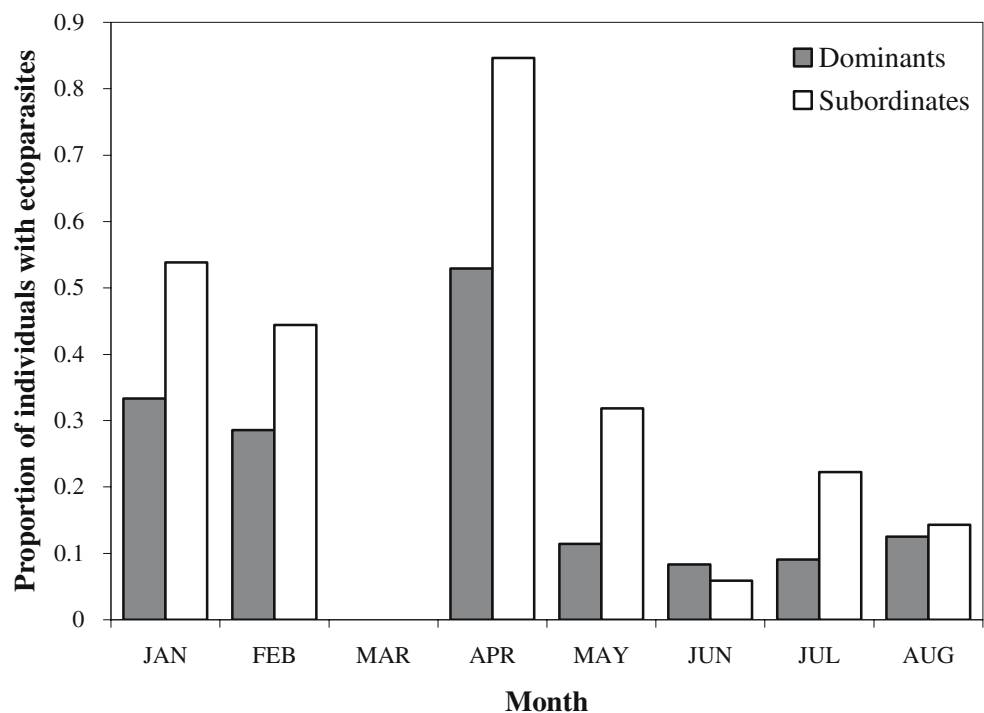
initiated by dominants; there was no significant difference between bouts initiated by dominants and subordinates in their likelihood of being reciprocated ( $\chi^2=0.89$ ,  $df=1$ ,  $P=0.346$ ). In contrast, although only 40% of all body allopreening bouts were initiated by dominants, 87% of those that were reciprocated had been initiated by dominant individuals; bouts initiated by dominants were significantly more likely to be reciprocated than bouts initiated by subordinates ( $\chi^2=83.18$ ,  $df=1$ ,  $P<0.001$ ). Furthermore, body allopreening bouts initiated by dominants were significantly more likely to be reciprocated if the recipient was a subordinate rather than another dominant ( $\chi^2=22.44$ ,  $df=1$ ,

$P<0.001$ ), whereas body allopreening bouts initiated by subordinates did not differ in their likelihood of being reciprocated depending on the dominance status of the recipient ( $\chi^2=0.38$ ,  $df=1$ ,  $P=0.537$ ).

#### Ectoparasite load

The likelihood that captured birds had any ectoparasites was significantly influenced by month (GLM  $F_{6,240}=8.80$ ,  $P<0.001$ ): birds caught in the winter (May to August) were less likely to have ectoparasites than those caught in the summer (January to April; Fig. 6). The effect of season was

**Fig. 6** The proportion of captured adult green woodhoopoes that possessed ectoparasites. No birds were caught in March or between September and December



confirmed by comparing the parasite scores (0–3) of the same individuals caught in both winter and summer and which had retained the same dominance status between captures: these individuals had significantly higher scores in summer than in winter (Wilcoxon test:  $Z=85.0$ ,  $n=35$ ,  $P=0.006$ ). There was also a significant effect of dominance status on the likelihood that captured birds had any ectoparasites (GLM  $F_{1,235}=15.82$ ,  $P<0.001$ ): dominant individuals were less likely to have ectoparasites than subordinates (Fig. 6). The importance of dominance status was confirmed by comparing the parasite scores (0–3) of individuals that were caught as both subordinates and dominants in the same season (i.e., summer or winter): when caught as dominants they had a significantly lower score (Wilcoxon test:  $Z=66.0$ ,  $n=19$ ,  $P=0.038$ ). There were no significant effects of sex (GLM  $F_{1,232}=1.16$ ,  $P=0.281$ ), body mass ( $F_{1,231}=0.27$ ,  $P=0.606$ ), or group size ( $F_{6,234}=1.07$ ,  $P=0.375$ ) on the likelihood that captured birds had any ectoparasites.

#### Changes in group composition

Groups were significantly more likely to experience a change in adult composition during the winter months of May to August (15/29 groups) than the summer months of January to April (6/29 groups; chi-square test  $\chi^2=6.05$ ,  $df=1$ ,  $P=0.014$ ).

## Discussion

#### Allopreening of inaccessible body parts

Green woodhoopoes of different dominance status and in groups of different sizes donated, received, and terminated head allopreening bouts with similar frequency. Furthermore, there was a high level of within-bout reciprocation with dominant- and subordinate-initiated bouts equally likely to be reciprocated, and head allopreening occurred at a constant rate throughout the year. Together, these results suggest a baseline frequency of head allopreening, similar for all individuals and perhaps most likely to be driven by hygienic needs.

A hygienic function for allopreening was suggested before. In Brünnich's guillemots (*Uria lomvia*), for example, the frequency of allopreening was greatly increased on days when mosquitoes affected the birds (Kober and Gaston 2003). Furthermore, Brooke (1985) demonstrated that allopreening reduces the number of ticks found on eudyptid penguins. Ectoparasites were experimentally shown to reduce the survivorship of adult birds (Brown et al. 1995), and they may do so in a number of different ways. First, ectoparasites may lower the bird's body mass (Senar et al. 1994). Second, hematophagous parasites, such

as fleas and amblyceran lice, cause blood loss that may result in anemia in their hosts (Lehmann 1993). Third, chewing lice can remove a substantial amount of feather mass, requiring the host to raise its metabolic rate if it is to compensate (Booth et al. 1993). Finally, ectoparasites may serve as vectors for a variety of endoparasitic cestodes, nematodes, and some bacteria and viruses (Lehmann 1993).

To minimize these potential costs, ectoparasites must be removed from the entire body, but the long bills of woodhoopoes prevent efficient preening of their own head and neck. In many avian species there are a variety of other maintenance behaviors, such as scratching with the feet, dusting, sunning, anting, and water bathing, which might play a crucial role (Simmons 1964); indeed, individuals with a deformed or missing foot often experience an increase in ectoparasite load restricted to the head and neck (Clayton 1991). However, these alternative maintenance behaviors are rarely seen in woodhoopoes (personal observation) and, moreover, they are likely to be less precise than preening. Consequently, woodhoopoes may be reliant on the allopreening of others to maintain head and neck ectoparasites at manageable levels.

#### Allopreening of accessible body parts

Body allopreening occurs at a significantly lower rate than head allopreening, presumably because birds can reach these areas themselves and remove ectoparasites by self-preening. Furthermore, our findings regarding the influences on body allopreening rates contrast strongly with those for head allopreening and suggest a primarily social function. First, whereas the time spent head allopreening by individual green woodhoopoes was constant in groups of different sizes, individual rates of body allopreening increased with increasing group size. Studies of some other species have demonstrated an increase in individual ectoparasite loads with increasing group size (Hoogland 1979; Brown and Brown 1986), which might theoretically explain this result, but our analysis of ectoparasite loads revealed no individual variation with group size. As in our study of woodhoopoes, Dunbar (1988, 1991) found a significant positive relationship between time spent grooming and group size in a number of catarrhine and platyrrhine primates. He suggested that this positive relationship may result from the reduced complexity of small groups and particularly from lessened competitive interactions between group members. In primates, for example, smaller groups normally have fewer matriline and a higher average relatedness than large groups (O'Brien 1991). In woodhoopoes, individuals in smaller groups may spend less time in close proximity while foraging and there is likely to be less competition for food resources than in larger groups (Radford and du Plessis 2003).



Second, whereas head allopreening bouts initiated by dominants and subordinates were equally likely to be reciprocated, body allopreening bouts initiated by dominants were much more likely to be reciprocated than those initiated by subordinates. Moreover, bouts initiated by dominants were more likely to be reciprocated if the recipient was a subordinate rather than another dominant. The difference between head and body allopreening is further emphasized by the variation in occurrence of within-bout reciprocation: whereas 74.4% of head allopreening bouts were reciprocated, this was the case for only 9.7% of body allopreening bouts. According to “biological markets” theory (Nöe and Hammerstein 1995), the intrinsic and hedonistic benefits of allopreening give it currency and mean that it may be exchanged for itself or in return for other goods depending on the supply and demand for a particular commodity. It appears that head allopreening is often traded for itself, which makes sense because both parties need ectoparasites to be removed from inaccessible parts of their body. However, this is not the case for body allopreening, which may therefore be traded for some other commodity, for example, tolerance at feeding sites and/or direct access to a resource such as food (De Waal 1997).

Third, individuals of different dominance status exhibited different levels of body allopreening donation and receipt, whereas there were no such interindividual differences in head allopreening. Subordinate woodhoopoes donated body allopreening at higher rates than dominants, while dominants received higher rates of body allopreening than subordinates, which was also found to be the case for overall allopreening rates in jackdaws (*Corvus monedula*; Katzir 1983). It seems unlikely, therefore, that body allopreening is being used either by dominants to reaffirm their status (because subordinates donate more) or by group members to maintain and improve affiliative relationships (because individuals of different dominance status donate and receive different amounts). Studies of a number of Old World monkeys and primates, in which allogrooming among females is directed up the hierarchy in a similar fashion to woodhoopoe allopreening, have suggested a variety of explanations for this pattern. First, subordinates might allopreen dominants to divert aggressive attacks (Baker and Aureli 2000). Although allopreening was considered to be a mechanism for reducing or sublimating aggression in some avian species (Harrison 1965; Birkhead 1978), overt intragroup aggression is rarely apparent in woodhoopoes (Ligon and Ligon 1978). Furthermore, if the diversion of attacks was important, subordinates would be expected to terminate the interaction once the threat of aggression was defused (O’Brien 1993). However, dominant woodhoopoes terminated a higher proportion of body allopreening bouts than subordinates. Second, subordinates might provide more allopreening to reinforce alliances,

particularly if coalitions are considered an important factor in determining individual status (Seyfarth and Cheney 1984). However, as green woodhoopoes at the study site disperse as individuals (Du Plessis 1989) and food items are not shared (Radford and du Plessis 2003); the formation of coalitions does not appear to be important here. Finally, subordinates might be using allopreening to reduce social tensions (Schino et al. 1990). This is the most likely explanation in woodhoopoes where group cohesion is important because territorial interactions involve extended contests in which the combined chorusing of all group members is vital to success (Radford 2003).

There was also a striking seasonal difference between head and body allopreening. Body allopreening was more prevalent among woodhoopoes in winter than in summer, but head allopreening occurred at a constant rate throughout the year. Seasonal variation in allogrooming is a common phenomenon in the New World monkeys, although in these species there is a reduction in allogrooming during the winter when food is scarcer (e.g., O’Brien 1993; Di Bitetti 1997). Because woodhoopoe food availability also decreases during winter (unpublished data), an alternative explanation for the seasonal pattern of body allopreening is required. Nights are longer in winter and so groups spend longer in their roost cavities at this time of year. Ectoparasite transfer might therefore be expected to be higher, necessitating an increase in allopreening. However, this would also predict an increase in head allopreening, which is not found. Alternatively, body allopreening may increase in the winter because this is when woodhoopoe mortality is highest and, hence, when changes in group composition are most apparent (this study; Du Plessis and Williams 1994). If body allopreening does play an important role in group cohesion, particularly the reduction of social tensions, it may increase at this time because social bonds are at their weakest and/or individuals are most likely to have changed position in the dominance hierarchy.

Although the primary function of body allopreening is likely to be a social one, two lines of evidence suggest that it may also have a hygienic benefit. First, dominant individuals receive more body allopreening than subordinates and have lower ectoparasite loads. Second, body allopreening is most prevalent during the winter (i.e., May to August) and, perhaps as a consequence, woodhoopoe ectoparasite loads were lowest at this time of the year. Alternatively, the seasonal change in ectoparasite loads may result from, for example, variation in rates of self-preening or an increase in parasite infection intensity during the host’s reproductive season (Christe et al. 2002). Several authors have previously suggested that allogrooming fulfills both a hygienic and a social role (e.g., Sparks 1969; Perry 1996; Di Bitetti 1997), but the present study is the first to consider avian allopreening in any detail. Allopreening in

green woodhoopoes appears to serve a dual function, depending on the part of the body that is being preened. This is the first consideration of the importance of body parts in such studies.

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