Manipulating grooming by decreasing ectoparasite load causes unpredicted changes in antagonism

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It is thought that allogrooming is practised strategically in order to establish, maintain and reinforce social bonds between group members, exchanging one altruistic behaviour for a different form of reciprocated benefit at a later date. Correlational evidence supports this, but evidence of causality is lacking. We reduced parasite loads in eight meerkat *Suricata suricatta* groups, generating a substantial decrease in grooming. Contrary to the predictions, overall antagonism did not increase. However, within group networks, grooming increased towards individuals who increased their antagonism. This was restricted to antagonism focused on social position, rather than access to physical resources. The treatment also increased an alternative placatory behaviour: unprompted submissions. Following treatment, individuals performed higher rates of guarding and marking behaviours, suggesting that they were stressed. A reduction in opportunity to mediate stress through grooming may explain local rises in antagonism and corresponding increases in placatory behaviours. We suggest that meerkats use allogrooming (and submissions) as a facultative response to antagonism, rather than a pre-emptive strategy to avert it by establishing a network of associations, as has been suggested for primates.

Keywords: antagonism; ectoparasites; grooming; meerkats; social networks; stress

1. INTRODUCTION

Patterns of allogrooming correspond to patterns of other social interactions in several species (Seyfarth & Cheney 1984; Wilkinson 1986; Hart & Hart 1992; Kutsukake & Clutton-Brock 2006a; Radford & Du Plessis 2006; Schino 2007). Individuals who groom each other subsequently reduce conflict with more dominant individuals (Silk 1982; Kutsukake & Clutton-Brock 2006a) and gain access to scarce resources (Cheney 1977; de Waal 1989). Removal of key group members disrupts both patterns of grooming and the social network (Flack *et al.* 2006). Therefore, it is suggested that individuals groom each other strategically and gain future benefits (Schino 2007). If so, a reduction in grooming levels is predicted to cause increased antagonism, removing potential benefits. However, no study has experimentally manipulated grooming levels and observed the resulting changes in antagonism.

Allogrooming can be manipulated by exploiting a second, more immediate, function of the behaviour: maintaining hygiene. Groomers target especially infected or inaccessible regions of their partner's bodies (Perez & Vea 2000; Zamma 2002; Radford & Du Plessis 2006) and, across populations, grooming rate correlated with ectoparasite load, suggesting a hygienic function (Sanchez-Villagra *et al.* 1998). Reducing ectoparasites' levels reduces the need for hygiene maintenance and could reduce grooming levels. A fall in grooming levels may

have additional physiological effects. Grooming decreases heart rate (Aureli *et al.* 1999) and alters beta-endorphin levels (Keverne *et al.* 1989). These effects could provide a mechanism for the relationship between grooming and antagonism. Habituated meerkats *Suricata suricatta* offer an unusual opportunity to conduct such a manipulation in which the levels of grooming can be experimentally altered, changes in individual behaviours can be observed and measures of stress can be obtained.

Meerkats live in groups headed by a dominant male and female who produce the majority of offspring (Griffin *et al.* 2003), cared for by other adults in the group (Clutton-Brock *et al.* 1998). Dominant individuals enforce their position through antagonistic interactions (Kutsukake & Clutton-Brock 2006b), while subordinates also compete for access to food resources and successful breeding opportunities. Antagonism over social status can range from actual fights to more chronic but subtle assertions of dominance, which subordinate individuals may immediately escape by submitting or avoiding contact with more dominant individuals (Kutsukake & Clutton-Brock 2006b, 2008). Antagonism is also common over access to food resources. Individuals groom frequently, typically in the morning or evening at their communal burrow (Kutsukake & Clutton-Brock 2006a), and subordinate individuals may groom more dominant individuals to avoid harassment (Kutsukake & Clutton-Brock 2006a, 2008). We anticipated that we could manipulate grooming levels in meerkats by altering their ectoparasite load (Sanchez-Villagra *et al.* 1998). As a consequence of this reduction in grooming, we expected to observe changes in antagonism between individuals over social status or access to resources and other corresponding changes in individual behaviours.

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2008.1661> or via <http://journals.royalsociety.org>.

2. MATERIAL AND METHODS

(a) *Data collection*

We studied a population of habituated meerkats in the south of the Kalahari desert. Further details of the site and population are given by Clutton-Brock *et al.* (1998). The behaviour of 136 individuals from 8 groups was observed for periods of 3 days prior to an application of a commercial treatment for ectoparasites and 3 days following treatment, with each group being observed one at a time, between April and July 2007. All members of the population were habituated to accept close observation from people within 1 m and could be individually identified via small marks of hair dye. Groups were watched by three to four observers ensuring that all occurrences of behaviour within the group were recorded, with observation periods lasting for at least 3 hours in the morning, after the meerkats emerged from their burrows, and for at least 1 hour before they re-entered their burrow in the evening. This gave us an average of 838 ± 77 min observation per group over the 3 days prior to treatment and 793 ± 41 min observation per group post-treatment. During the observation periods, we recorded a total of 2842 allogrooming events, 673 dominance interactions, 738 foraging competitions and 136 unprompted submissions across all eight groups. Rates of grooming were calculated as events per minute of observation at the group.

In addition to the all occurrence behavioural recording described above, focal animal watches were made on 48 individuals: 6 from each group, including both of the dominant pair, and four subordinate individuals. Each individual was followed by a trained observer for 30 min on each of the 3 days pre- and post-treatment, at a distance of 2–5 m, with observation periods starting 15 min after the group had left the vicinity of their sleeping burrow and started to forage. The order in which individuals were observed was randomized between days. The individual's behaviour was recorded at 30 s intervals, and the incidence of unusual events, such as marking (Jordan *et al.* 2007), was recorded as they occurred. The duration of each guarding bout was recorded (Clutton-Brock *et al.* 1998).

(b) *Definitions of interaction behaviours*

Allogrooming—when one individual groomed another (see also Kutsukake & Clutton Brock 2006a). When three or more animals were grooming together in a huddle, we recorded all interactions as dyads, entering only one record per dyad in the same huddle, regardless of how long the animals groomed or how many times each animal switched back and forth between partners. A separate grooming bout was considered to have started if the animals resumed grooming after a pause (during which there was no grooming at all) of more than 1 min.

Foraging competitions—when an individual approached a food item or hole owner to less than 50 cm, prompting a defensive action by the owner. These actions involve growling, moving of the owner's body to block approach, pushing of the owner's body against the other individual, charging at the other individual or biting the other individual.

Dominance interactions—aggressive interactions between individuals that are not caused by food or access to foraging holes or social foraging partners (see also Kutsukake & Clutton-Brock 2006b). Interactions include one individual physically attacking (biting, hitting, wrestling and chin marking) another and also instances of non-contact aggression between individuals (growling and assuming a dominant posture that provokes a submissive grovel).

Submissions—when initiated by an individual unprompted by the aggressive actions of another (see also Kutsukake & Clutton-Brock 2006b). Submissions include grovelling behaviours, submissive calls and interactions that began because two animals 'accidentally' bumped into each other provided that the submissive animal reacted first.

(c) *Ectoparasite reduction*

Ectoparasites were reduced at each group on the fourth day of the study. Half the individuals from each group were selected at random and treated with an anti-parasite spot-on solution, with the other half receiving a control. We used Advantix (Bayer Animal Health), a commercial anti-parasite treatment designed to protect dogs from ticks, fleas and mosquitoes, containing imidacloprid and permethrin. This is advertised as killing fleas and ticks within 1 day of application and preventing further infestations for 4 weeks. Meerkats were treated as they emerged from their sleeping burrow to sun themselves in the morning, after 3 days of pre-treatment observations at the group. The group were then weighed and no further data collected from them on that day. Treatment involved applying 0.1 ml per individual of Advantix to the nape of a meerkat's neck after the fur had been swept back to expose the skin. As a control, the other individuals had the same amount of water administered in an identical fashion. We confirmed the efficacy of the anti-parasite treatment (see the electronic supplementary material). Because treated and control individuals did not differ, we combined observations from both classes in our subsequent analyses.

(d) *Construction and analysis of interaction networks*

Most studies of social interactions between individuals analyse dyadic interactions between specific pairs, and previous studies typically look at the relationship between grooming and antagonism at a group level. However, for animals living in social groups, an individual's interactions are unlikely to be independent of the behaviours of others (Whitehead & Dufault 1999; Krause *et al.* 2007). Therefore, it is useful to consider the network of social interactions among the group, within which dyadic interactions occur. Construction and analysis of such networks is now well developed and applied to animal behaviour (Krause *et al.* 2007), and commercial software exists, that permits a range of analyses (Borgatti *et al.* 2002).

We analysed the relationship between changes in grooming and antagonistic behaviour at both the level of the group and in the context of the network of social interactions occurring within the group. We constructed networks of changes in grooming and antagonistic interactions between group members, and analysed the interaction matrices using the quadratic assignment procedure (QAP) correlation function in UCINET (Borgatti *et al.* 2002) to account for the non-independence of data within the matrices and to test how strongly related networks of one type were related to those of another, indicated by a Pearson correlation coefficient. For all analyses, 10 000 permutations were used to generate an associated *p*-value. Individuals were nodes, and the rate of interactions (analysis of pretreatment data), or the change in the rate of interactions (analysis of effect of treatment), were the edges between nodes.

When searching for general patterns of relationship between each of the three different network types across all eight groups, we had to calculate the relationships independently for each group, and we then used Fisher's method to

Figure 1. Mean (± 1 s.e.) rates of (a) grooming and (b) antagonistic interactions before (black bars) and after (white bars) a single application of Advantix anti-parasite treatment. Bars represent mean values from 136 individual meerkats in eight groups. Measures of antagonism are shown at 10 times their actual rates.

combine probabilities from each of the eight independent groups to calculate an overall level of significance (Sokal & Rohlf 1994). If the direction of relationship, or of differences, varied between groups, we calculated the strongest difference or relationship across all eight groups, and for those groups with an opposing relationship or difference we reversed the sign of their natural log-transformed p -value, effectively subtracting their contribution from the combined χ^2 statistic, and then calculated the final combined p -value.

When we considered overall changes in the levels of individuals' behaviour within groups, regardless of who they interacted with, we used mixed models, run in GENSTAT v. 8.1 (Lawes Agricultural Trust, Rothamstead, Harpenden, UK), with individual identity and group identity as random factors. Variance components of linear mixed models were estimated with the restricted maximum likelihood method. Residuals were checked for normality.

3. RESULTS

(a) Effect of treatment on allogrooming

Our treatment reduced ectoparasite levels by approximately 94 per cent (see the electronic supplementary material) and, correspondingly, rates of allogrooming fell by 64 per cent (linear mixed model (LMM): allogrooming, Wald $\chi^2=97.8$, $p<0.0001$; figure 1a). This could have been because the manipulation affected general associative behaviour, with individuals spending less time with each other, compensating for reduced allogrooming by increasing self-grooming. However, self-grooming also decreased significantly, falling by 31 per cent (LMM: Wald $\chi^2=75.2$, $p<0.0001$; figure 1a). The reduction in grooming of all types could have been due to a dislike of the taste of the treatment, with individuals trying to maintain hygiene by non-oral grooming methods. However, the rates of self-scratching, which did not involve the mouth, also declined by 19 per cent (LMM: Wald $\chi^2=22.83$, $p<0.0001$; figure 1a).

(b) Overall changes in levels of antagonistic interactions

When we considered the overall levels of interactions, we found that the reduction in grooming was not matched by a corresponding increase in the levels of antagonism (LMM: dominance interactions, Wald $\chi^2=0.50$, $p=0.48$; foraging competitions, Wald $\chi^2=0.03$, $p=0.87$; figure 1b). However, the rate of unprompted submissions increased by 57 per cent (generalized linear mixed model (GLMM): Wald $\chi^2=9.21$, $p=0.002$; figure 1b).

(c) Changes in networks of interactions

Contrary to the predictions derived from strategic grooming models, there was a positive relationship between the networks of changes in giving grooming and receiving dominance assertions (table 1). Dyads in which grooming levels decreased following treatment were also those in which the levels of dominance assertions decreased.

(d) Changes in non-social behaviours

Disrupting grooming behaviour had an effect on other, non-social behaviours. Focal individuals increased their time spent guarding by 34 per cent following treatment ($t_{48}=2.73$, $p=0.009$; figure 2a), despite there being no difference in the number of alarm calls that they experienced (Wilcoxon signed-rank test $Z=1.27$, $n=48$, $p=0.21$). Focal individuals increased their marking behaviour by 142 per cent following treatment ($Z=2.26$, $n=48$, $p=0.024$; figure 2b). Such increases could be explained by an increase in available time due to the reduction in time spent grooming. However, we recorded a total increase of 109 min in time spent guarding by focal individuals following treatment, whereas we recorded a total decrease of only 16 min in time spent grooming by the same individuals. Instead, these increases in guarding and marking appear to have occurred at the expense of

Table 1. QAP Pearson correlation coefficients (r) and associated probabilities (p) based on 10 000 permutations, between networks detailing the changes in the rates of interactions between individuals that initiate grooming and receive antagonistic interactions or initiate unprompted submissions, following treatment with Advantix. (The mean correlation coefficients (r -values) are given, as are the combined p -values, calculated from the two sets of eight independent analyses.)

group		dominance interactions	foraging competitions	unprompted submissions
CD	r	0.00	0.05	0.09
	p	0.39	0.12	0.03
D	r	0.26	-0.09	0.10
	p	0.01	0.15	0.13
E	r	0.10	-0.03	0.06
	p	0.07	0.35	0.13
F	r	0.01	-0.05	0.12
	p	0.47	0.31	0.14
L	r	0.09	-0.03	-0.06
	p	0.02	0.23	0.09
MM	r	0.01	0.06	0.02
	p	0.44	0.11	0.32
RR	r	0.05	-0.07	-0.03
	p	0.17	0.09	0.29
Y	r	0.23	0.04	0.02
	p	0.01	0.39	0.41
mean r		0.13	-0.02	0.04
combined p		<0.001	0.99	0.37

foraging, with individuals tending to decrease the time that they spent foraging following the treatment by approximately 5 per cent ($t_{48}=1.87$, $p=0.068$), representing a total decrease of approximately 163 min for all the focal individuals.

4. DISCUSSION

Our treatment of meerkats, which reduced their ectoparasite loads, also induced a suite of corresponding behavioural changes. Overall rates of allogrooming fell, and rates of unprompted submissions rose. Networks describing polyadic changes in the rates of allogrooming between group members were positively related to the networks describing changes in dominance assertions, but not those describing resource-focused antagonism. When overall levels of grooming within the group were decreased, focal individuals performed higher levels of guarding and marking behaviours, which suggest that they were stressed.

The reduction in allogrooming following a treatment for ectoparasites confirms the finding of previous correlational studies (e.g. Sanchez-Villagra *et al.* 1998; Perez & Vea 2000; Zamma 2002; Radford & Du Plessis 2006) that allogrooming serves, at least partially, a hygienic role specifically targeted at removing ectoparasites. Surprisingly, individuals experiencing our control treatment, receiving water instead of Advantix, also exhibited decreased parasite loads. This lack of difference between treated and control individuals is probably explained by the close association of meerkats, frequently rubbing against each other and sleeping in clusters, making for plentiful opportunities for the externally applied solution to be transferred between individuals. In addition, treating some group members may so reduce the numbers of ectoparasites in sleeping burrows that untreated individuals were less likely to acquire them. Regardless of the possible confounding explanations, our treatment caused an overall decrease in ectoparasite load and a corresponding overall decrease in the levels of

grooming within the group. The reduction may have two explanations: either there are reduced cues (visible ectoparasites) to stimulate the groomer or the potential groomer may be less likely to solicit or accept grooming because they too are experiencing reduced cues (ectoparasites attached to their body). The persistence of low levels of allogrooming, even after reducing ectoparasite load, can be explained without invoking social function: perhaps we failed to remove all ectoparasites, or allogrooming additionally serves to maintain fur quality and remove non-parasitic foreign bodies. Although these explanations may account for why individuals continue grooming after anti-parasite treatment has been applied, they do not account for the corresponding changes in social interactions that we observed.

Contrary to most previous correlational studies (e.g. Cheney 1977; Silk 1982; Wilkinson 1986; de Waal 1989; Hart & Hart 1992; but see Perry 1996; Schino *et al.* 2005), our experimental reduction of overall rates of grooming due to the removal of ectoparasites did not result in overall increases in the rates of antagonism. Instead, in dyadic interactions in which one individual increased dominance interactions towards another following treatment, we recorded a corresponding increase in grooming towards the antagonist that may have acted to placate them. This positive relationship with grooming was restricted to the forms of antagonism related to social status (dominance interactions), rather than antagonism determining access to resources (foraging competitions). Therefore, unlike some primates (Cheney 1977; de Waal 1989), grooming for meerkats did not mediate access to resources. Instead, changes in grooming prompted changes in non-resource-focused antagonism, which, as in primates (DiBitetti 1997; Schino 2001), relate to social status (Kutsukake & Clutton-Brock 2006a). These dominance interactions are crucial in shaping the social structure of meerkat groups (Clutton-Brock *et al.* 2001; Griffin *et al.* 2003; Kutsukake & Clutton-Brock 2006b; Young *et al.* 2006). If dominance interactions are so crucial to the structure

Figure 2. (a) Time spent guarding and (b) number of marking events by 48 individual meerkats before (pre) and after (post) the anti-parasite treatment had been applied. Bars show mean + 1 s.e.

and breeding success of meerkat groups, it seems unusual that their rate, distribution and mediation depend exclusively on ectoparasite load that may vary with environmental conditions. We were therefore not surprised to observe a second behaviour that covaried with the changes in grooming behaviour.

An overall decrease in grooming was matched by an overall increase in unprompted submissions. This suggests that meerkats may possess two (or more) mechanisms that mediate dominance interactions: grooming and unprompted submissions. Grooming is specific to dyadic interactions within the network of interactions within the group, and depends on the recipient accepting the approaches of the groomee. Unprompted submissions are a more general response of individuals, especially those encountering aggressive individuals that are reticent to accept grooming, perhaps because they are experiencing reduced cues in the form of ectoparasites on their body.

Why may a general decrease in grooming levels cause some individuals to increase rates of dominance interactions, which in turn provoke elevated grooming levels? Following treatment, individuals engaged in higher rates of behaviours that suggested that they were stressed. Individuals that guard at a high rate exhibit higher levels of circulating cortisol than matched control individuals within the same cohort (T. H. Clutton-Brock & M. Tatalovic 2007, unpublished data). Marking behaviour typically follows an encounter with another group, or their latrine (Jordan *et al.* 2007), and is accompanied by violent frenzied behaviour directed at other group members or inanimate objects. Individuals with high levels of circulating cortisol are typically those that assert dominance at high levels (Carlson *et al.* 2004). Grooming reduces stress (Keverne *et al.* 1989; Aureli *et al.* 1999), and meerkats engaged in allogrooming have lower heart rates than when at rest (J. R. Madden 2007, unpublished data). Lower levels of grooming mean that opportunities to lower heart rate and stress were reduced. This causes subsequent increases in the expression of behaviours typically performed by stressed individuals, including dominance assertions. Local increases in dominance interactions prompted elevated grooming by the recipients of the dominance assertions, explaining the positive relationship between networks of changes in grooming and dominance interactions. The alternative explanation for this positive relationship, which is that increases in grooming within a dyad prompts an increase in dominance assertions, seems unlikely, with costly allogrooming being rewarded with physical aggression.

Our experimental manipulation of grooming levels in meerkat groups, exploiting the hygienic role of grooming for the removal of ectoparasites, demonstrates a complex interplay between different types of social interaction. The primary result of our treatment was that a reduction in ectoparasites caused individuals to decrease their overall rates of grooming. This reduction in the rates of grooming was not matched by an overall increase in the rates of antagonism—specifically that relating to social dominance—contrasting with previous correlative studies of a range of mammal species (e.g. Cheney 1977; Silk 1982; Wilkinson 1986; de Waal 1989; Hart & Hart 1992). Indeed, pairs of individuals who most decreased their grooming rates also decreased their rates of dominance assertion. Conversely, for pairs of individuals who increased their rates of dominance assertion following treatment, levels of allogrooming also rose. This may have acted to placate the antagonist. However, the antagonist, carrying few ectoparasites, may have been less motivated to accept grooming because of their reduced hygienic need. This would explain the increase in an alternative placatory behaviour—unprompted submissions—that we observed being used when grooming levels decreased. The general reduction in grooming meant that its additional function of reducing stress was not fulfilled; hence, individuals became more stressed and performed behaviours indicative of this. Such behaviours included dominance assertions, which in turn were placated by local increases in grooming or a general increase in unprompted submissions. Thus, we support previous studies that observed a relationship between grooming and antagonism (e.g. Cheney 1977; Silk 1982; Wilkinson 1986; de Waal 1989; Hart & Hart 1992), and indeed reinforce the proposed relationship by demonstrating a causal link between the changes in grooming and the corresponding changes in antagonism. However, we suggest that, for meerkats, grooming primarily serves a hygienic function, and secondarily provides a facultative response to antagonism, functioning to halt persistence or escalation of antagonism. This contrasts with its proposed function suggested for primates as a pre-emptive strategy that inhibits the initiation of antagonism by establishing or reinforcing a social structure.

We thank Alison Geldhart, Tom Flower, Rob Sutcliffe, Dave Bell and the volunteers at Kuruman River Reserve for their help with the experiments and data collection. Two anonymous reviewers greatly improved the manuscript. We thank the Koetze family for allowing us to work on their land, and Northern Cape Conservation for allowing us to conduct

research in South Africa. J.R.M. was funded by a grant from BBSRC to T.H.C.-B. We operated under ethical permits from the University of Pretoria.

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