



Role of grooming in reducing tick load in wild baboons (*Papio cynocephalus*)

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Nonhuman primate species spend a conspicuous amount of time grooming during social interactions, a behaviour that probably serves both social and health-related functions. While the social implications of grooming have been relatively well studied, less attention has been paid to the health benefits, especially the removal of ectoparasites, which may act as vectors in disease transmission. In this study, we examined whether grooming behaviour reduced tick load (number of ticks) and haemoprotozoan infection status in a population of wild adult baboons (*Papio cynocephalus*). We found that younger and higher-ranking adults were groomed more often than older, low-ranking adults, and females were groomed more often than males. Animals that received more grooming, in turn, had lower tick loads. Baboons with lower tick loads had higher packed red cell volume (PCV or haematocrit), one general measure of health status. We detected a tick-borne haemoprotozoan, *Babesia microti*, but its low prevalence in the population precluded identifying sources of variance in infection.

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Grooming behaviour encompasses all forms of care and attention to the body surfaces (Saunders 1988). It constitutes a major social activity in many species of social mammals including ungulates (Mooring et al. 1996; Hart 2000; Heitor et al. 2006), rodents (Ferron & Lefebvre 1982), bats (Wilkinson 1986) and primates (Schino 2007) among others. Grooming is a frequent and conspicuous behaviour; indeed, some nonhuman primates invest at least one-fifth of their time engaged in grooming (Dunbar 1991; Shutt et al. 2007). This time investment in grooming suggests that it serves important functions. The social functions of grooming include the establishment and maintenance of affiliative relationships and the reduction of tension and aggression between individuals (Terry 1970; Saunders 1988; Kimura 1998; Kutsukake &

Clutton-Brock 2006). Grooming has also been used as a quantitative measure of the strength of dyadic social relationships (Lazaro-Perea et al. 2004).

Grooming varies with many factors. For example, in most primates, grooming patterns are highly kin biased, and kinship explains a large fraction of the variance in grooming patterns, as predicted by kin selection models of social evolution (Schino 2001; Chapais & Berman 2004). Grooming also has potential value in relationships among nonrelatives, and Seyfarth (1977) first suggested that grooming directed up a dominance hierarchy (i.e. preferential grooming of high-ranking animals) represents an exchange of grooming services for coalitional support (see also discussions in: Schino 2001; Lazaro-Perea et al. 2004). Other studies have documented increased grooming down the hierarchy (O'Brien 1993; Parr et al. 1997; Lazaro-Perea et al. 2004). These conflicting findings may result from differences in social and ecological contexts, which influence how resources are distributed in a social group. This in turn might affect the 'market' for grooming (Barrett et al. 1999; Henzi & Barrett 1999), although support for this idea is mixed (see e.g. discussions in Lazaro-Perea et al. 2004; Silk 2004; Silk et al. 2006a).

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In many primates, participation in grooming bouts differs between the sexes and with life history stage. In several studies on captive baboons, vervets and macaques, grooming was shown to be a female-biased behaviour established during the first year of life, with females grooming almost twice as often as males (Simonds 1974; Young et al. 1982). In these species, females are philopatric while males are the dispersing sex; as a correlate of female philopatry, females tend to form strong social bonds with other females (Wrangham 1980) and grooming is a major contributor to these social bonds (Silk et al. 2003, 2006a, b, 2010). Furthermore, Silk et al. (2006b) reported that female baboons that had the most equitable grooming relationships also had the strongest and most enduring social bonds. The strength, stability and quality of social bonds contribute, in turn, to offspring survival, enhanced longevity, and to the probability of receiving coalitionary support during within-group contests (Silk et al. 2003, 2006a, b, 2010). The age of an individual also plays a role in the amount of grooming received or given. Saunders (1988) showed that more than half of the grooming bouts between adult female and juvenile baboons were initiated by adult females. Adult male baboons groomed less often than adult females (Saunders 1988). Because males can provide important services, such as protection against infanticidal attacks and harassment (Smuts 1985; Saunders 1988; Silk et al. 2003; Nguyen et al. 2012), females may be motivated to groom males in return for these services.

Grooming may also have important indirect or direct health consequences. With respect to indirect consequences, previous work in rhesus macaques, *Macaca mulatta*, has shown that receiving grooming reduces heart rate and is thus presumed to improve physiological wellbeing (Boccia et al. 1989; Aureli et al. 1999). Additionally, a study on free-ranging Barbary macaques, *Macaca sylvanus*, has shown that grooming others is correlated with a reduction in the stress hormone cortisol in the groomer (Shutt et al. 2007). Finally, work in captive talapoin monkeys (*Miopithecus* spp.) has shown that participation in grooming (receiving or giving) increases the production of endorphins, a biomarker of increased psychological wellbeing (Keverne et al. 1989).

In most mammal species in which it has been investigated, grooming also has direct effects on wellbeing via removal of ectoparasites such as lice, fleas and ticks (e.g. Freeland 1981; Saunders & Hausfater 1988; Tanaka & Takefushi 1993; Eckstein & Hart 2000; Hart 2000; Zamma 2002; Kutsukake & Clutton-Brock 2006). Among ectoparasites, ticks are of particular medical and economic importance. They are prevalent in many environments, are

resistant to many environmental stressors, and have relatively long life cycles and high reproductive potential (Ginsberg & Stafford 2005). Ticks are vectors for transmission of infectious and toxic disease and are able to transmit pathogens to a wide range of hosts, including humans and nonhuman primates (Edlow 1999).

The tick family of greatest veterinary and medical importance is *Ixodidae*. Saunders (1988) found in the Amboseli basin of Kenya, several genera and multiple species of *Ixodidae* (hard) ticks (*Rhipicephalus*, *Ixodes*, *Hyalomma* and *Amblyomma* spp.), most of which were associated with domestic animals (e.g. cattle, sheep and goats) and with wild ungulates (e.g. wildebeests, zebras, gazelle). Direct detrimental effects of ticks to these hosts include inflammation and irritation from tick bites, itching, allergic reactions to protein in tick saliva, secondary anaemia (sometimes fatal) and paralysis. Ticks also transmit parasites such as bacteria, protozoa, viruses and nematodes, some of which cause diseases that generally affect the blood or the lymphatic system (Ginsberg & Stafford 2005). For example, ixodid ticks are known to carry *Babesia*, a haemoprotazoan parasite capable of infecting nonhuman primates in captivity and also present in nonhuman primate populations in the wild (Moore & Kuntz 1981; Maamun et al. 2011). Indeed, Maamun et al. (2011) found *Babesia microti* parasites, which present health risks to humans and nonhuman primates (Cogswell 2000; Ginsberg & Stafford 2005), in both free-ranging primates and in *Rhipicephalus simus* ticks. *Entopologyoides macaci*, a haemoparasite closely related to *Babesia*, is suspected of being transmitted by ectoparasites, although evidence of such transmission has yet to be demonstrated (Hawking 1972). *Entopologyoides macaci* has also been detected in wild primate populations (Jeneby et al. 2008).

Studies of the relationship between tick burden and grooming behaviour are relatively uncommon, and most have been done in wild ungulates (Hart 2000; Mooring et al. 2004). Observations of grooming in many different nonhuman primate species suggest its importance for ectoparasite removal (Freeland 1981; Sánchez-Villagra et al. 1988; Tanaka & Takefushi 1993; Zamma 2002; for similar discussions about wild ungulates, see: Norval et al. 1989; Hart 2000), but we are aware of only two studies that directly examined the relationship between tick burden and grooming in primates. Both cases provided only qualitative assessments of this relationship (Saunders & Hausfater 1988; Brain & Bohrmann 1992).

Here, we investigated the association between grooming behaviour and tick load in wild baboons in the Amboseli basin in southern Kenya. We also carried out a survey of tick-borne haemoparasite infection status in these baboons. Our study took advantage of three different data sets to examine these

Table 1
Summary of sample sizes of Amboseli baboons in models used for statistical analysis

Analysis	Total number of individuals	Number of adult males	Number of adult females	Missing individuals	Explanation for missing individuals
Grooming received					
Year 1	31	13	18		
Year 2	28	8	20		
Total	59	21	38	6 adult males	Three individuals in nonstudy groups lacked grooming and dominance rank data and three individuals in study groups lacked sufficient grooming data
Tick load (using total number of ticks)	59			6 adults males	Three individuals in nonstudy groups lacked grooming and dominance rank data and three individuals in study groups lacked sufficient grooming data
PCV (using total number of ticks)	61			4	Haematocrit was not measured for one individual and three individuals in nonstudy groups lacked dominance rank data
PCV (using number of adult ticks)	61			4	Haematocrit was not measured for one individual and three individuals in nonstudy groups lacked dominance rank data
Haemoparasite screening	63			2	Parasite screening was not completed for two individuals

associations. The first data set included demographic data on individual age, sex and group membership, as well as behavioural data on grooming and dominance rank. These data were used to investigate the factors that predict grooming and whether these factors had any association with tick presence. Both types of data were mined from the long-term database of the Amboseli Baboon Research Project, Babase. The second data set included tick identification and tick counts from baboons darted in Amboseli during darting and immobilization projects in 2007–2008. The third data set focused on health and haemoparasite screening data, which included packed cell volume (PCV) analysis and PCR screening of samples obtained during immobilization.

We used these three data sets to determine (1) whether the amount of grooming received varied by age, sex or dominance rank; (2) whether grooming received reduced tick load and (3) whether tick load was associated with any detrimental effects on health and whether these effects varied by sex, age and or rank. Based on previous studies, we predicted that older individuals, males and lower-ranked animals would receive less grooming (e.g. Simonds 1974; Seyfarth 1977; Young et al. 1982; Saunders 1988; Silk et al. 2006b). We also predicted that animals that received less grooming would carry more ticks, because of the role that grooming plays in reducing tick load (e.g. Freeland 1981; Saunders & Hausfater 1988; Brain & Bohrmann 1992). Lastly, we predicted that high tick loads would be associated with detrimental effects of tick parasitism, such as lower packed cell volume levels and increased presence of probable tick-borne haemoparasites, such as *Babesia* and *Entopolooides*.

METHODS

Study Subjects

Individuals in this study were adult members of a wild baboon population resident in the area immediately north and west of Mount Kilimanjaro in southern Kenya, part of the Amboseli region of East Africa. Individuals were considered adults based on the occurrence of menarche for females and the presence of testicular enlargement and rank attainment for males (for further description of determination of age at maturity, see Charpentier et al. 2008). This population has been studied by the Amboseli Baboon Research Project since 1971 (Altmann 1980; Alberts & Altmann 1995; Charpentier et al. 2008). The baboons in this area are yellow baboons, *Papio cynocephalus*, that experience some admixture with neighbouring populations of anubis baboons, *Papio anubis* (Alberts & Altmann 2001; Tung et al. 2008).

Darting: Collection of Blood and Tick Samples

Using an anaesthetic-bearing dart delivered from a hand-held blowgun (Altmann et al. 1996; Tung et al. 2011), we darted 32 individuals in June and July 2007 and an additional 33 individuals in June and July 2008. We darted no more than two animals on any day. These 65 dartings were done under the authority of the Kenya Wildlife Service, using the anaesthetic Telazol, a tiletamine–zolazepam combination (Altmann et al. 1996; Tung et al. 2011). From each individual, we collected blood samples from the saphenous vein and ticks as described below. Each study subject was placed singly into a covered holding cage until fully recovered from the effects of the anaesthetic (~3–4 h). Subjects were then released in the vicinity of their social group. All subjects rejoined their social groups quickly upon release and without incident.

Ticks were collected from each darted baboon using forceps and preserved in 70% ethanol for subsequent manual counting in a laboratory. Immature ticks were not plucked from the animal but

were counted on the baboon's body because they were too small to carefully retrieve. All aspects of tick collection and counting were supervised and validated by one person. For adult ticks, we identified species by microscopic morphological characterization using the International Livestock Research Institute (ILRI) *Tick Identification Training Manual* (ILRI 2004).

All protocols complied with regulations in Kenya (Republic of Kenya Research Permits NCST/5/002/R/776 to J.A. and NCST/5/002/

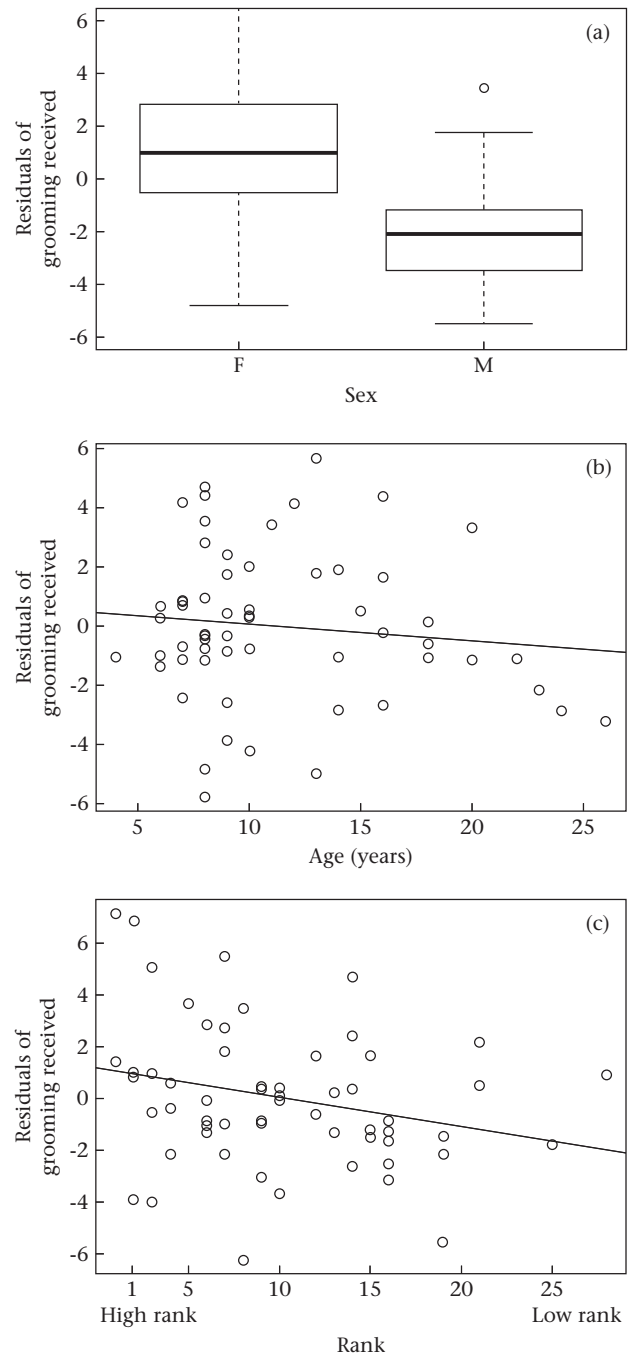


Figure 1. Results of mixed effects regression model of grooming received in Amboseli baboons. Residuals calculated from the multivariate model (Table 2) illustrate the effects of (a) sex, (b) age and (c) rank on the amount of grooming received. See Table 2 for parameter estimates for each independent variable.

Table 2Results of mixed model analysis of frequency of grooming received by Amboseli baboons (combined model: $N = 59$)

Predictor variable	Z	SE	β	P	Direction of observed effect
Sex	-12.78	0.049	-0.630	<0.0001	Adult females received more grooming than adult males
Age	-2.183	0.005	-0.011	<0.029	Younger adults received more grooming than older adults
Dominance rank	-6.59	0.004	-0.027	<0.0001	High-ranking adults received more grooming than low-ranking adults
Social group	–	–	–	–	Random variable
Intercept	28.38			<0.0001	

R/777 to S.C.A.) and in the United States (Duke University IACUC A028-12-02), and adhered to the ASAB/ABS Guidelines for the treatment of animals in behavioural research and teaching.

Grooming Data

Behavioural data on grooming were collected on all members of five different study groups, using both ad libitum and focal sampling methods (Altmann 1974). Ad libitum grooming data were collected throughout the day by observers who monitored the group members' behaviour; 1351 of the 1372 grooming records used in this analysis were collected as ad libitum grooming records. In collecting ad libitum data, we took great care to distribute our data collection effort evenly across group member; this effort was aided by the fact that the ad libitum data were collected while observers moved through the group searching for and sampling focal animals based on a randomly assigned rotation. In addition to the ad libitum data, we also collected grooming data during focal samples on adult females; all occurrences of grooming were recorded during 10 min focal samples on juveniles and on adult females, and 51 grooming events from focal samples contributed to the grooming data in this analysis (4% of the overall grooming data set). All grooming data were entered in the long-term relational database for the Amboseli Baboon Research Project, BABASE. We subsequently extracted grooming data (counts of grooming

received by each study animal in the 6 months prior to their darting date, which we refer to as the frequency of grooming received) from these data sets for 59 of the 65 individuals darted. Of the six remaining individuals, three individuals for whom we had darting samples were members of nonstudy groups, for which we lacked detailed observational data on grooming. Three others had recently joined the study groups in which they were darted, and we lacked complete grooming data for the 6 months prior to darting.

Social and Demographic Data

Data on age and dominance rank for individual study subjects were extracted from BABASE. The age of each individual was calculated based on a known birth date for individuals born within study groups (accurate within several days; $N = 54$), or estimated upon first entry into a study group based on external characteristics, such as body carriage, teeth and pelage condition in the case of immigrant males not born within study groups ($N = 11$). Dominance rank for each individual was determined based on field observations of dyadic agonistic interactions ($N = 62$). We calculated dominance ranks for adult females and adult males separately such that the highest-ranking female in the group was assigned a rank of 1, and the highest-ranking male in the group was also assigned a rank of 1. As with grooming data, we lacked dominance rank data for the three individuals that were darted in nonstudy

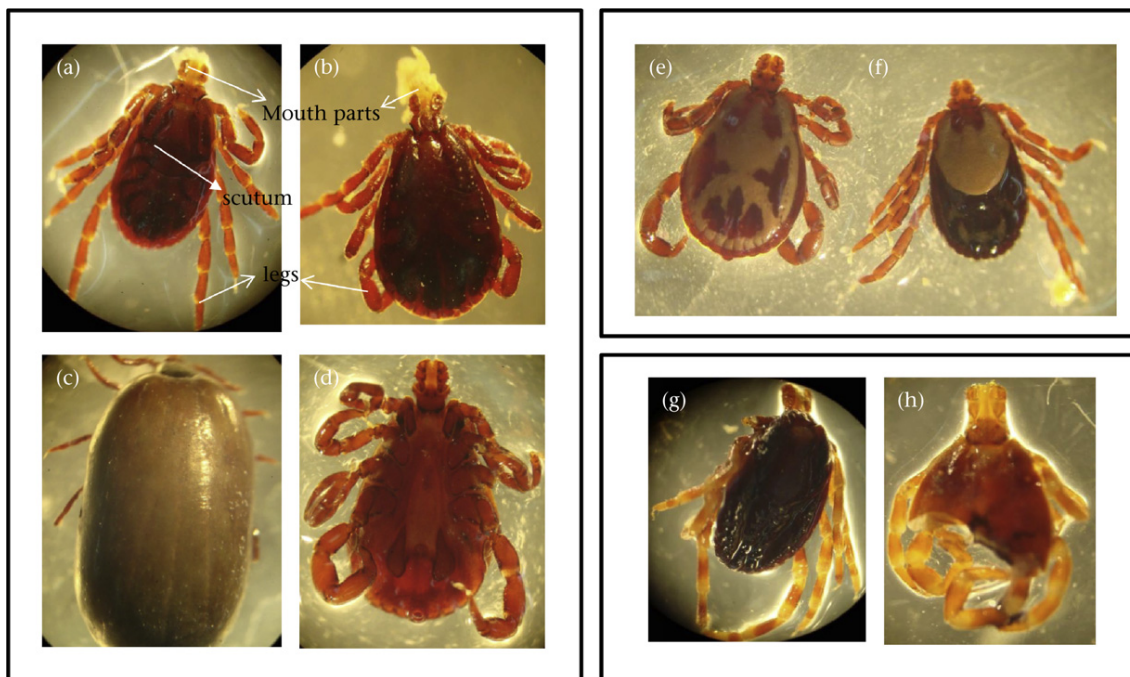


Figure 2. Representative tick specimens obtained from Amboseli baboons: (a) *Rhipicephalus simus simus* female, (b) *R. s. simus* male, (c) *R. s. simus*, engorged female, (d) *R. s. simus*, ventral view, (e) *R. pulchellus* male, (f) *R. pulchellus* female, (g) *Hyalomma truncatum* female and (h) *H. truncatum* of unknown sex.

Table 3Results of zero-inflated Poisson regression model of tick load in Amboseli baboons (using total number of ticks: adult ticks and larvae; $N = 59$ animals sampled)

	Predictor variable	Z	SE	β	P	Direction of observed effect
Effects of grooming on presence of ticks (Poisson part of the model)	Grooming received	-4.452	0.0013	-0.0058	<0.0001	More grooming was associated with fewer ticks
Effect of year on darting (logistic part of the model)	Year of darting	-2.084	0.533	-1.1477	0.0372	Animals darted in 2008 were more likely to have no ticks than animals darted in 2007

groups; [Table 1](#). These interactions were then used to compute social dominance rank for each animal on a monthly basis ([Hausfater 1975](#); [Alberts et al. 2003](#)). The dominance ranks used in this study represented the dominance rank for each animal in the month that it was darted. Dominance rank varies little over the lifetime of females. Although ranks in males are more dynamic ([Altmann et al. 1988](#); [Alberts et al. 2003](#)), during the 6 months prior to darting (the period for which grooming data were examined), male dominance ranks changed little ([Supplementary Material, Table S1](#)).

Packed Cell Volume (PCV)

Packed cell volume (PCV or haematocrit) is the volume percentage of red blood cells in a blood sample; it is a component of the total blood count and functions as an indicator of anaemia, which could arise from tick infestations either directly from ticks ingesting blood, or from haemoparasite infection. For field measurements of PCV, heparinized capillary tubes were filled with a sample of venous blood and spun for 5 min in a portable micro-haematocrit centrifuge (Zipocrit, model ZO-1, LW Scientific, Inc., Atlanta, GA, U.S.A.). PCV was measured with a standardized haematocrit card reader. Two to three replicate PCV measurements were obtained per animal, and the mean of the measurements was used in subsequent analyses.

Parasite Screening

Total genomic DNA was extracted from 200 μ l of each blood sample using a commercial Dneasy kit (Qiagen Blood and Tissue DNA extraction kit, Hilden, Germany).

We then used PCR-based screening to detect the presence or absence of haemoparasitic infections of two genera, *Babesia* and *Entopoloypoides*, which have been reported to cause infection in some nonhuman primates such as baboons (*Papio* spp.) and vervet monkeys, *Chlorocebus aethiops* ([Maamun et al. 2011](#)). As noted earlier, *Babesia* is transmitted by ticks, but such evidence is currently lacking for *Entopoloypoides*.

Parasite-specific DNA was amplified using four primer sets (see [Supplementary Table S2](#)). Primer set BmicF1/BmicR1 specifically targeted the 18s rRNA of *B. microti*, based on existing sequence in GenBank (accession number AB219802). Primer set EmacF1/EmacR1 specifically targeted the 18s rRNA of *E. macaci*. Two additional primer sets (F34/R323 and F79/R206, based on GenBank accession numbers AJ289244 to AJ289252) for nested PCR (n-PCR), were used to nonspecifically amplify a portion of the β -tubulin gene of tick-borne piroplasms of the genera *Babesia* and *Theileria* as described by [Caccio et al. \(2000\)](#). *Theileria* is a tick-borne parasite closely related to *Babesia* that has been identified in livestock that share the range of the baboons we studied.

PCR amplifications were done on a PTC-200 Peltier Thermocycler, and the resulting PCR products were visualized on a 1.5% agarose gel stained with ethidium bromide. Purification of PCR products was done using a Qiagen MinElute 96UF PCR purification kit and retrieved products were sequenced with an ABI 3730 DNA

Analyzer in the Duke's Genome Sequencing and Analysis Core Resource (see [Supplementary Table S3](#) for PCR amplification and sequencing preparation conditions). The resulting sequences were then compared to existing sequences in the GenBank sequence database by carrying out a BLAST search.

Statistical Analysis

Our statistical analyses focused on three main individual-level response variables: (1) the frequency of grooming received by an individual, (2) the individual's tick load (specifically the number of ticks present on an individual) and (3) the individual's PCV. In the analyses of grooming received and of PCV, we used multivariate analyses to control for the effects of multiple predictor variables, using the R statistical software package (R v.2.14.0, R Foundation for Statistical Computing, Vienna, Austria). The sample size varied slightly for different components of the analysis (see [Table 1](#) for explanations).

Because our grooming data were count data, we used a Poisson mixed effects regression model to determine the factors that influenced the frequency of grooming received. The fixed predictor variables in our model were the age, sex and dominance rank of each subject. The social group to which the individual belonged was treated as a random effect.

To determine whether the amount of grooming received influenced tick load, we carried out a zero-inflated Poisson regression. We used the zero-inflated Poisson regression because the distribution of the dependent variable (tick load) was highly skewed with many zero values. The predictor variable for the Poisson part of our model was the number of times we observed the individual receive grooming in the 6-month period prior to darting. We used the year of darting as a predictor variable for the logistic part of the model, as tick prevalence varied considerably across years (see [Supplementary Table S5](#)).

To assess the predictors of PCV, we used a multivariate general linear regression model. Our predictor variables were dominance

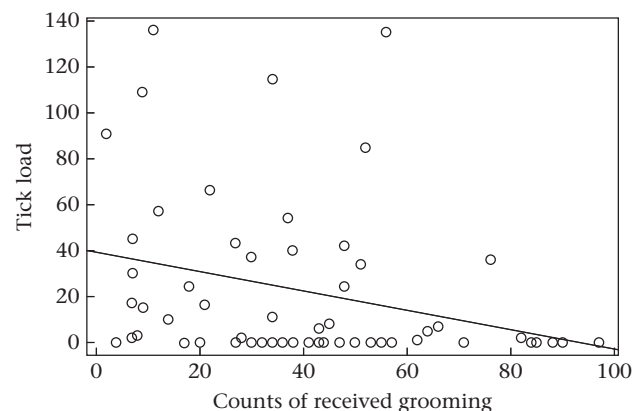


Figure 3. Relationship between tick load and counts of received grooming in Amboseli baboons.



Figure 4. Clustering of ticks on the (a) chest, (b) neck and (c) side of the body near the armpit of three Amboseli baboons.

rank, age, sex and the total number of ticks (adult ticks and larvae combined). We also modelled PCV in a multivariate analysis replacing the total number of ticks with only the number of adult ticks; the number of adult ticks was much greater in 2007 than in 2008 (Supplementary Table S5), and we reasoned that adult ticks (because of their size) were more likely than larvae to impact the host's PCV.

RESULTS

Factors Influencing Grooming Received

Our mixed effects Poisson regression model indicated that the frequency of grooming received was influenced by age ($\beta = -0.011$, $N = 59$, $P < 0.029$), dominance rank ($\beta = -0.0277$, $N = 59$, $P < 0.0001$), and sex ($\beta = -0.630$, $N = 59$, $P < 0.0001$). Younger and higher-ranking adults were groomed more often than older, low-ranking adults, and females were groomed more often than males (Fig. 1). The social group to which an individual belonged, which we included as a random variable in the model, was associated with 9% of the variance in the sample (Table 2).

Tick Species and the Effect of Grooming on Tick Load

The tick species identified in our samples were *Rhipicephalus simus*, *Rhipicephalus pulchellus* and *Hyalomma truncatum* (Fig. 2). The dominant tick species collected was *R. simus* (98% of 951 total ticks). *Rhipicephalus pulchellus* and *H. truncatum* were relatively rare, 1.8% (17 ticks) and 0.2% (2 ticks), respectively. See Supplementary Table S4 for a summary of the parasites collected and their relative abundance in the darted individuals. Baboons darted in 2007 had higher adult tick infestation than those darted in 2008 (see Supplementary Table S5).

We found that the frequency of grooming received by an individual significantly predicted tick load, such that individuals that had received more grooming in the 6 months prior to darting had fewer ticks ($\beta = -0.0058$, $N = 59$, $P < 0.0001$; Table 3, Fig. 3). The logistic part of our model strongly suggests that the year of darting contributed to the probability of an individual having no ticks ($\beta = -1.1477$, $N = 59$, $P < 0.0372$; Table 3), consistent with our field observations (Supplementary Table S5). We repeated the same

analysis using adult ticks only in the Poisson model and the results for the effect of grooming were similar ($\beta = -0.0038$, $N = 59$, $P < 0.0245$).

Direct Detrimental Effects of Ticks

Wounds

In a number of cases, especially in 2007 when adult ticks were quite abundant, we saw skin wounds caused by the clustering of ticks on various parts of the body (e.g. under the armpits, ears, neck and back region; Fig. 4). This clustering was observed somewhat more frequently in males, with 11 males and four females being extensively affected. These wounds were generally minor (Fig. 4c, d), and were often characterized by areas of scar formation indicating onset of healing. However, in some cases the wounds seemed severe enough that they could increase susceptibility to bacterial infection; such wounds were often characterized by signs of underlying inflammation such as redness (Fig. 4a).

Packed cell volume (PCV)

Average \pm SD packed cell volume among the study subjects was $41.91 \pm 4\%$ ($N = 64$). Individuals with fewer ticks had higher PCV than those with more ticks ($\beta = -0.037$, $N = 61$, $P = 0.010$), males had higher mean PCV than females ($\beta = 2.32$, $N = 61$, $P = 0.03$), and younger adults had higher PCV than older adults ($\beta = -0.29$, $N = 61$, $P < 0.003$). Dominance rank did not have a significant effect on PCV ($\beta = -0.095$, $P = 0.212$; Table 4, Fig. 5).

When only adult ticks were included in the model, the effect of number of ticks on PCV was larger than in the total tick count model (Table 5). Age and sex still contributed significantly to PCV. Bivariate comparisons of PCV by tick stages using *t* tests also showed that individuals with adult ticks had lower mean PCVs (38.73%) than those with immature ticks (43.83%) ($P = 0.004$, $N = 30$; the sample size reflects the number of animals that had ticks of only one kind or the other and excludes those that had no ticks). These results support our hypothesis that adult ticks had a larger effect on PCV than larvae.

Tick-borne haemoparasite screening

We screened blood samples from 63 of 65 individuals (refer to Table 1 for information on sample sizes) for various tick-borne

Table 4

Results of multivariate models of packed cell volume/haematocrit (PCV) in Amboseli baboons (using total number of ticks: adult ticks and larvae; $N = 61$ animals sampled)

Predictor variable	<i>t</i>	β	R_{adj}^2 (% variance explained)	<i>P</i>	Direction of observed effect
Age	-3.085	-0.29	–	<0.003	Younger animals had higher PCV than older ones
Sex	2.236	2.32	–	0.03	Females had lower PCV than males
Dominance rank	-1.262	-0.095	–	0.212	
Number of ticks	-2.655	-0.037	–	0.010	Individuals with fewer ticks had higher PCV than those with more ticks
Combined model			35		

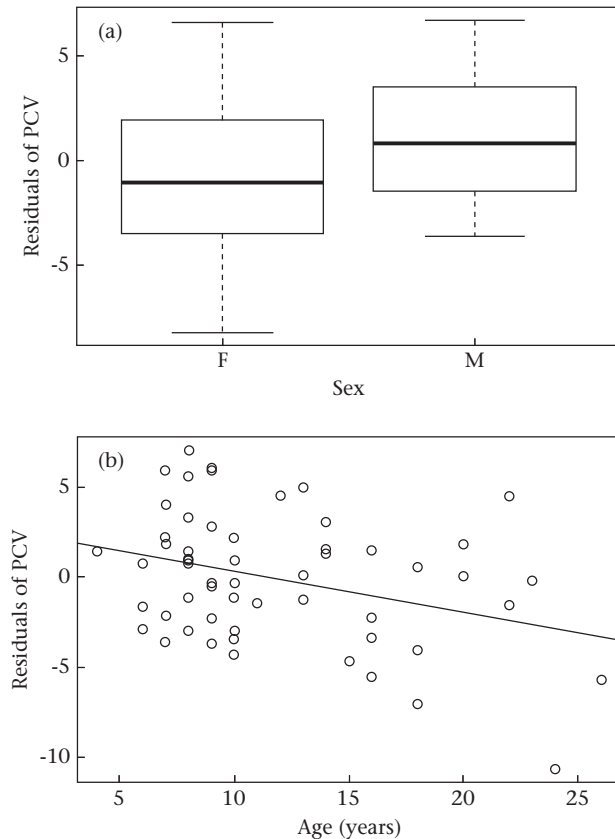


Figure 5. Results of multivariate general regression model. Residuals calculated from the model (Table 4) illustrate the effects of (a) sex and (b) age on packed cell volume/haematocrit (PCV) in Amboseli baboons.

parasitic infections using the primer sets described in the methods (Supplementary Table S2). None of the samples tested positive for *E. macaci* (i.e. no amplification occurred in the PCRs using *E. macaci* primers). However, amplification with *B. microti* primers produced bands at the expected size of 505 base pairs for two blood samples. Sequencing and BLAST search confirmed the presence *B. microti* in these two blood samples (BLAST *E* value of $5e-59$, with a maximum identity of 98%). These results provide strong evidence that *B. microti* occurs in this baboon population, although at a low frequency (3.2% of tested individuals). This low frequency of infection made it impossible to carry out a statistical analysis of the relationship between tick presence and probability of infection or to analyse the effect of grooming on the infection status of individuals.

Fifty-four of 63 samples were amplified by the two-stage nested PCR designed to detect the β -tubulin gene in any of two *Theileria* and six *Babesia* species (F34 and R323 primer set followed by the F79 and R206 primer set). However, the nested, nonspecific PCR product, when sequenced, BLASTed not only to multiple species of

Theileria and *Babesia*, but also to the *Papio hamadryas* β -tubulin gene; in other words, it was impossible to differentiate the source of the PCR product in any of our samples, suggesting that β -tubulin is too highly conserved between baboons and these parasites to be useful in determining parasite infections. This may be true for other nonhuman primates as well, and indicates caution in attempting to detect parasite infection via amplification of highly conserved genes alone.

DISCUSSION

Our study is unusual among primate studies of grooming in using quantitative measures of both tick burdens and grooming to evaluate the relationship between grooming and ectoparasite loads. We also examined the health consequences of tick infestations, specifically, the effects of ticks on blood composition (PCV), skin lesions and wounds, and tick-borne haemoparasite infections. Our results support a clear relationship between grooming and tick load, such that individuals that received more grooming had fewer ticks. Our results are consistent with other studies in ungulates (Norval et al 1989; Hart 2000) and primates (Brain 1992; Brain & Bohrman 1992) that have demonstrated health consequences of tick infestations.

Grooming and Ticks

Grooming can be directed to another individual (allogrooming), or to the groomer's own body (self-grooming.) Allogrooming has been suggested to play an important hygienic role. Several studies in primates have compared the sites targeted during self-grooming with those targeted during allogrooming. Self-grooming is generally directed to the legs, lower arms, genitals and the tail, all places that are readily accessible for an individual grooming itself. In contrast, allogrooming in several species has been reported to be directed mainly to the head, back, neck, shoulders and abdomen (see discussions in: Saunders 1988; Reichard & Sommer 1994; Franz 1999; Lazaro-Perea et al. 2004; Singh et al. 2006; Lewis 2010). Indeed, several authors have proposed that allogrooming is directed at inaccessible sites in several primate species and that self-grooming is directed to accessible parts, such that these two types of grooming are complementary (e.g. Barton 1985; Borries 1992; Pérez & Veà 2000). Zamma (2002) also showed that allogrooming in Japanese macaques, *Macaca fuscata*, is directed to sites that are more likely to be infested with louse eggs.

Several experimental studies of rodents and viverrids have demonstrated that when ectoparasites are experimentally removed, grooming rates decrease within social groups. These experiments provide several pieces of evidence supporting the ideas that the presence of ectoparasites stimulates grooming behaviour and that grooming functions to reduce ectoparasite load (Hawlena et al. 2008; Madden & Clutton-Brock 2009; Hillegass et al. 2010). Furthermore, experimental studies in several vertebrate species in which individuals were prevented from grooming themselves showed that grooming reduces ectoparasite loads

Table 5

Results of multivariate models of packed cell volume/haematocrit (PCV) in Amboseli baboons (using adult tick stages only; $N = 61$ animals sampled)

Predictor variable	<i>t</i>	β	R^2_{adj} (% variance explained)	<i>P</i>	Direction of observed effect
Age	-3.095	-0.27	—	<0.003	Younger animals had higher PCV than older ones
Sex	2.606	2.450	—	0.012	Females had lower PCV than males
Dominance rank	-1.353	-0.095	—	0.181	
Number of adult ticks	-4.058	-0.053	—	<0.0001	Individuals with fewer ticks had higher PCV than those with more ticks
Combined model			43		

(Mooring et al. 1996; Eckstein & Hart 2000). In our study, as predicted, we observed that individuals that received more grooming in the 6 months prior to darting had lower ectoparasite loads than those that received less grooming, suggesting that grooming reduced tick load.

Detrimental Effects of Ticks

The main beneficiaries of grooming in this study were younger individuals, females and high-ranking individuals. Because these individuals received higher rates of grooming, we predict that, all other things being equal, these classes of individuals will generally be in better health, at least with regard to the consequences of ectoparasite infection, than other classes of individuals. Specifically, our results indicate that individuals that received more grooming were less likely to suffer from the detrimental effects of tick infestation.

We found several detrimental health effects of ticks in this baboon population. First, we saw, in some cases, skin wounds caused by the clustering of the ticks on various parts of the body. An individual would have difficulty grooming itself in the areas where these clusters tended to occur (e.g. under the armpits, and on the ears, neck and back), unlike the legs and genitals, which are listed by Saunders (1988) as body parts that individuals can effectively self-groom. In these cases where the animals had clusters of embedded ticks, we speculate that the removal of ticks is challenging for the groomer and unpleasant for the groomee and thus grooming at this stage may not be as productive as grooming when fewer ticks are embedded. This suggests that frequent regular grooming is an essential part of baboon hygiene and that animals that are groomed rarely, after long intervals without grooming, are more likely to experience detrimental effects of tick clusters that are hard to remove. Previous studies in baboons in the Namib Desert showed that ticks caused direct harmful effects to the extent that some animals with heavier tick infestations died (Brain 1992; Brain & Bohrmann 1992). Similarly, ticks are implicated as a cause of detrimental effects in wild bovids, such as reduced weight gain, as well as blood loss and increased incidence of screwworms (Norval et al. 1989; Hart 2000).

Second, individuals with more ticks had lower PCV (an indicator of anaemia) perhaps because they lost blood to ticks. These PCV ranges were generally within the range observed in wild-caught captive *Papio anubis* baboons (33–57%; IPR 2011), except for two females that had PCV levels of 30%. Low PCV levels may contribute to reduced blood oxygen levels. However, we note that anaemia can only be completely evaluated by measuring not only PCV, but red blood cell counts and haemoglobin levels as well, neither of which we were able to measure in this study.

Our results also indicated a stronger effect of adult ticks than of larvae on PCV, which probably is a simple consequence of the size differences between adult and larval ticks. Compared to small larvae, adult ticks, especially adult female ixodid ticks, can undergo a 10- to 30-fold increase in size after ingesting blood (Fig. 2c). Our results suggest that grooming may be particularly important in maintaining a normal PCV during seasons of high tick infestation, as adult ticks are probably easier to remove than larvae, because of their size and visibility (Fig. 4). It is also well known that increased duration of tick attachment on a host is important in predicting tick-borne infection risks. For example, a study by Homer et al. (2000) on hamsters and white-footed mice has shown that the duration of tick attachment to the vertebrate host directly increases the efficacy of haemoparasite transmission from the tick to the host. Tick removal during grooming in nonhuman primates may reduce the time the tick is attached to the baboon, thus reducing downstream transmission of haemoparasitic infection.

As in other primates, sex and age influenced PCV (Harewood et al. 2000; Howell et al. 2003; Setchell et al. 2006). PCV was lower in older adults than in younger adults, and lower in adult females than in adult males. Consequently, older animals and females may be more vulnerable to tick-induced anaemia because of their higher tick loads.

Presence of Babesia microti

We observed a low prevalence (3.2%) of *B. microti* infections in this population of baboons. Our study complements a recent study carried out by Maamun et al. (2011), which reported the first case of *B. microti* parasites in free-ranging nonhuman primates (baboons and vervets). They detected the presence of *B. microti* and *Theileria* in *R. simus* ticks, suggesting the possibility of tick-borne transmission of these parasites to nonhuman primates. Our results suggest that factors affecting tick presence are likely to predispose individuals to downstream haemoparasite infection, such that older individuals, males and low-ranking individuals are more prone to infection. Unfortunately, the low prevalence of haemoparasite infection did not enable us to directly test our second hypothesis, which posited a link between increased tick presence and increased transmission of tick-borne haemoparasite infection.

Conclusion

Our study supports the idea that grooming, in addition to having social value, is a behavioural means by which baboons reduce tick loads, and thus grooming may protect baboons from the detrimental effects of ticks. These findings point to potentially important benefits of group living in primates. Having social partners confers multiple potential advantages including protection from detrimental effects of ticks through grooming. Freeland (1981) demonstrated the importance of social living as a means of tick removal by experimentally exposing a pet monkey to ticks; once exposed, the monkey was observed to present itself to be groomed, suggesting that primates may experience a need for partners to assist in ectoparasite removal. However, grooming also has disease-related costs in social animals such as nonhuman primates. Grooming requires that individuals are in close proximity and, thus, increases the probability of disease transmission, especially of airborne respiratory viruses or bacteria, by increasing contact rates between infected and noninfected individuals. Grooming may also influence transmission of infections or infestations that are also spread through contact, such as bacteria, haemorrhagic viruses or ectoparasites (for a discussion of parasite transmission in social living primates, see Nunn & Altizer 2006).

Our results provide clear evidence that individual differences in social behaviour, age and sex may result in differences in vulnerability to tick infestations. Whether grooming also reduces the transmission of tick-borne parasites remains unclear, and addressing this question will likely benefit from larger sample sizes.

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Supplementary Material

Supplementary material for this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2012.12.012>. In addition, data underlying the results have been deposited in the Dryad repository, at <http://dx.doi.org/10.5061/dryad.3r8n2>.

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