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Animal behaviour

Unconditional care from close maternal kin in the face of parasites

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Several species mitigate relationships according to their conspecifics' parasite status. Yet, this defence strategy comes with the costs of depriving individuals from valuable social bonds. Animals therefore face a trade-off between the costs of pathogen exposure and the benefits of social relationships. According to the models of social evolution, social bonds are highly kin-biased. However, whether kinship mitigates social avoidance of contagious individuals has never been tested so far. Here, we build on previous research to demonstrate that mandrills (*Mandrillus sphinx*) modulate social avoidance of contagious individuals according to kinship: individuals do not avoid grooming their close maternal kin when contagious (parasitized with oro-faecally transmitted protozoa), although they do for more distant or non-kin. While individuals' parasite status has seldom been considered as a trait impacting social relationships in animals, this study goes a step beyond by showing that kinship balances the effect of health status on social behaviour in a non-human primate.

1. Introduction

The evolution from a solitary lifestyle to life in permanent groups occurred independently in numerous taxa [1]. Living in groups entails, however, a major parasite cost [2] because sociality involves promiscuity between group-mates [3]. This transition has therefore driven the evolution of various defence mechanisms [4]. In particular, individuals able to detect the signs of infection and to behave accordingly should be favoured because one of the major sources of parasite transmission comes from contagious conspecifics [3]. As such, parasite-free bullfrog tadpoles (*Rana catesbeiana*) do not swim with parasitized conspecifics [5], social lobsters (*Panulirus argus*) do not share dens with conspecifics infected by a lethal virus [6], and olive baboons (*Papio anubis*) avoid mating with partners infected by a sexually transmitted virus [7]. In a recent study, we showed that wild mandrills avoid grooming conspecifics infected with gastro-intestinal protozoa but grooming rates return to normalcy following treatment of these infected groupmates [8]. Protozoa infecting mandrills are known to cause diverse symptoms in other primates; for instance, *Balantidium coli* and *Entamoeba histolytica* may cause fatal dysentery syndromes and amoebiasis [9–11]. This behavioural defence strategy may, however, incur costs because it deprives individuals from valuable social interactions. Decision to avoid contagious conspecifics results therefore from a cost–benefit trade-off depending on the probability of becoming infected, the fatality rate of the disease, the nature of social contact, the individual's current need for social interaction and the degree of genetic relatedness. Recent mathematical modelling showed that mildly virulent pathogens generate selection for flexible strategies of social avoidance depending on kinship. Under this scenario, the benefits of socializing with close kin would outweigh the costs of

exposure to pathogens and individuals should avoid only infected groupmates that are distantly related or non-kin [12]. Whether kinship modulates the social avoidance of contagious individuals remains, however, to be tested empirically.

In this study, we build on our previous research to test whether mandrills modulate the social avoidance of groupmates infected with gastro-intestinal protozoa as a function of kinship. We have recently demonstrated that mandrills avoid grooming, but not being groomed by, contagious groupmates infected with oro-faecally transmitted protozoa [8]. This strategy probably decreases parasite exposure because infected mandrills harbour transmissible stages of protozoa on their fur that could be ingested during grooming [8]. Grooming is, however, a fundamental and valuable component of primate sociality [13]: it serves several important social functions including the maintenance of group cohesion and it may also buffer within-group competition [14]. In addition, grooming has hygienic functions [15,16], destresses both groomers and groomees [14], decreases heart rate [17] and induces the release of pleasure hormones [18]. While grooming may increase parasite exposure, the social and physiological benefits of grooming may therefore decrease disease susceptibility under some circumstances [19]. Because of the benefits associated with grooming, kin selection models of social evolution predict individuals to groom their kin in preference to non-kin [20,21]. Consistent with this theory, in most mammal species, grooming patterns are highly kin-biased [22]. Here, we predict that individuals should avoid infected non-kin but still provide care (i.e. grooming) to contagious kin. Using long-term data collected on a wild group of mandrills from Gabon, we matched grooming time received and groomee's protozoa status to (i) test whether contagious groomees were similarly avoided by all kin and (ii) identify which kin took the risk of grooming highly contagious partners.

2. Material and methods

(a) Study population

In May 2019, the free-ranging population of mandrills comprised approximately 220 habituated individuals living in a private park (Lékédi Park, Bakoumba, Gabon). This population was founded in 2002 when 36 individuals were released from a captive population into the wild (see for details: [23]). Starting in 2003, wild males joined the group and reproduced with females born in captivity. In 2006, 29 other captive individuals were released into the initial group. In January 2012, a long-term field project was established to study this population of mandrills, consisting at that time of more than 80% of animals born in the wild ('Mandrillus Project': www.projetmandrillus.com). Because we conduct daily monitoring, more than 200 individuals are recognized and have been followed throughout the years. The present study includes 71 individuals, 57 of them were born in the wild.

(b) Behavioural observations

During 54 months (October 2012–March 2017), we collected 1557 h of behavioural observation from 71 individually recognized mandrills (29 males, 42 females). We did not consider sub-adult and adult males (greater than 7 years old) because female mandrills are philopatric and males are only temporary residents of the social group. They have therefore no kin in the group, except their own offspring that are generally still infants if co-residing with their father. We usually do not manage to collect faecal samples from infants. Trained observers, blind to the

protozoa status of the studied animals, performed behavioural observations using 5-min focal sampling [24]. All social interactions including grooming time were recorded. In this study, we matched an individual's rate of grooming received with groomee's parasitological status. Monthly dominance ranks were evaluated for each sex, using the outcomes of approach–avoidance interactions and calculated using normalized David's score. We divided adult females into three classes of rank of similar size across the entire study period (high-ranking, medium-ranking, low-ranking). We attributed their mother's rank to the males below 5 years of age. Males between 5 and 7 years of age were all classified as low-ranking.

(c) Parasitological analyses

We performed qualitative coprological analyses using a sedimentation protocol on faecal samples collected opportunistically since 2012 whenever a known animal was seen defaecating (see for details: [25]). The study group is known to be infected by seven different protozoa taxa: *Balantidium coli*, *Coccidian* sp., *Endolimax nana*, *Entamoeba coli*, *Entamoeba hartmanni*, *Entamoeba histolytica/dispar* complex and *Pseudolimax butschlii*. Over the study period, we collected 860 faecal samples from 60 groomees (39 females, 21 males; mean number per individual \pm s.d. = 23.0 ± 13.6). We evaluated monthly protozoa richness of groomees for 507 groomee.month, by calculating the average number of protozoa taxa retrieved from all samples collected from one groomee in a given month (mean number per individual.month \pm s.d. = 1.6 ± 1.3).

(d) Genetic analyses

Sixty-five individuals were trapped at least once using blowpipe intramuscular injections of anaesthetics [26,27] allowing the collection of blood samples. DNA extractions from the buffy coat were performed using QIAamp DNA Blood Mini Kits (Hilden, Germany) and microsatellite genotyping was carried out using 12–36 primer pairs [26–28]. Paternities were determined using Cervus 3.0 software using previously described procedures [28]. Among these 65 individuals, 14 of them were born in captivity and 51 were born in the wild. We reconstructed the full pedigree of individuals born in captivity going back as far as the generation of unrelated founder animals [28]. We genetically determined both parents for 43 individuals out of the 51 individuals born in the wild. For the remaining eight animals, we only knew the mother's identity because the genetic sample did not match any adult male of the genetic database. The study further included six young individuals, born in the wild but never captured, with an unambiguously known mother.

(e) Studied dyads

We considered groomee–groomer dyads meeting the following criteria for each studied month:

- (i) The groomer was observed at least once grooming the groomee the corresponding year. For example: A and B were not observed grooming each other in January 2015, we therefore considered this data point (as a zero) only if A and B were grooming partners this year (they groomed at least once in 2015). If they were never observed grooming each other in 2015, we did not consider them as grooming partners that year (no corresponding data point).
- (ii) At least one faecal sample was collected from the groomee.
- (iii) The total observation time of the groomee–groomer dyad reached at least 30 min. To calculate the observation time of the dyad, we summed-up the observation time of each partner when the other partner was co-resident (i.e. both individuals were present at the same time).

Table 1. Effect of groomee's protozoa richness on grooming received according to kinship. The reference dyad is indicated within parentheses. Significant test statistics are highlighted in bold ($p < 0.05$).

	estimate	s.e.	z	p-value
protozoa richness (non-kin)	-1.04	0.33	-3.19	0.001
protozoa richness (low-kin)	-1.63	0.40	-4.03	<0.001
protozoa richness (paternal half-siblings)	-1.43	0.45	-3.18	0.001
protozoa richness (offspring–mother)	-0.01	0.28	-0.02	0.99
protozoa richness (mother–offspring)	-0.20	0.27	-0.73	0.47
protozoa richness (maternal half-siblings)	0.15	0.29	0.50	0.62
protozoa richness*dyad category:				
protozoa richness*low-kin (non-kin)	-0.59	0.51	-1.15	0.25
protozoa richness*paternal half-siblings (non-kin)	-0.39	0.52	-0.76	0.45
protozoa richness*offspring–mother (non-kin)	1.04	0.43	2.44	0.015
protozoa richness*mother–offspring (non-kin)	0.94	0.41	2.29	0.022
protozoa richness*maternal half-siblings (non-kin)	1.18	0.43	2.73	0.006
age difference	-0.02	0.04	-0.47	0.64
groomee's sex (female): male	0.49	0.40	2.02	0.046
groomer's sex (female): male	-0.31	0.42	-0.73	0.47
groomee's dominance rank (high): middle	1.15	0.67	1.72	0.085
groomee's dominance rank (high): low	0.63	0.37	1.73	0.084
groomer's dominance rank (high): middle	-2.17	0.62	-3.53	<0.001
groomer's dominance rank (high): low	-0.81	0.36	-2.24	0.025

(iv) Kinship was unambiguously determined. Parents of both grooming partners were determined for 183 dyads. For 62 other dyads, the father of one grooming partner was undetermined because the genetic sample did not match any adult males from the genetic database. For six dyads, the father of one grooming partner was unknown because this grooming partner was not captured. However, in these six cases, grooming partners were not paternal half-siblings because they were too different in age (greater than 10 yr) to have the same father (mean age difference = 14.1 yr).

We considered six different kin categories of grooming partners: (i) 'offspring–mother' (i.e. the groomee is the offspring, the groomer is the mother), (ii) 'mother–offspring', (iii) 'maternal half-siblings', (iv) 'paternal half-siblings', (v) 'low-kin' and (vi) 'non-kin'. We considered as 'low-kin' dyads: offspring–grandmother and grandmother–offspring, offspring–aunt/uncle and aunt/uncle–offspring, and cousins. Low-kin dyads showed therefore a relatedness coefficient superior or equal to 0.0625. Following previously published procedure [29], the 'non-kin' category included all dyads for which the relatedness coefficient was less than 0.0625 (mean \pm SEM = 0.024 ± 0.001). The final dataset included 251 different dyads of co-resident grooming partners, including 34 'offspring–mother', 40 'mother–offspring', 36 'maternal half-siblings', 19 'paternal half-siblings', 56 'low-kin', and 66 'non-kin'. Full siblings ($N=3$ dyads) were classified as maternal half-siblings.

(f) Statistical analyses

All data were analysed in R v. 3.5.3 (R Core Team, 2016).

(i) Are contagious groomees similarly avoided by all kin?

We performed a generalized linear mixed model (negative binomial distribution for overdispersed count data, log link function, $N=1349$) to analyse grooming time each individual ($n=61$ groomees) received per grooming partner ($N=66$ groomers), per month, as a function of groomee's monthly protozoa richness (continuous variable), kin category ('offspring–mother': $N=194$, 'mother–offspring': $N=290$, 'maternal half-siblings': $N=263$, 'paternal half-siblings': $N=64$, 'low-kin': $N=218$, 'non-kin': $N=320$), and the interaction between these two variables. We compared the relative fits of the model with and without this interaction using a likelihood ratio test (LRT). We controlled for the absolute age difference between grooming partners, and the sex and dominance rank of both grooming partners. To adjust for variation in sampling effort, we included monthly log-transformed observation time of the dyad as an offset variable in the model. The dyad identity was further included as a random effect to control for pseudo-replication. The model was fitted using the package glmmADMB (R v. 3.5.0).

(ii) Which kin take the risk of grooming contagious partners?

We first split groomees into two categories according to their protozoa richness: 'low' corresponded to individuals infected by 0–3 protozoa taxa and 'high' corresponded to individuals infected by 5–6 protozoa taxa. For these two classes of groomees, we calculated the proportion of grooming time received from each of the six defined kin category. We investigated whether these proportions varied between 'low' and 'high' groomees' protozoa richness across kin categories using exact Fisher tests. These tests allowed analysis of the distribution of the proportions of grooming received across the six kin categories defined.

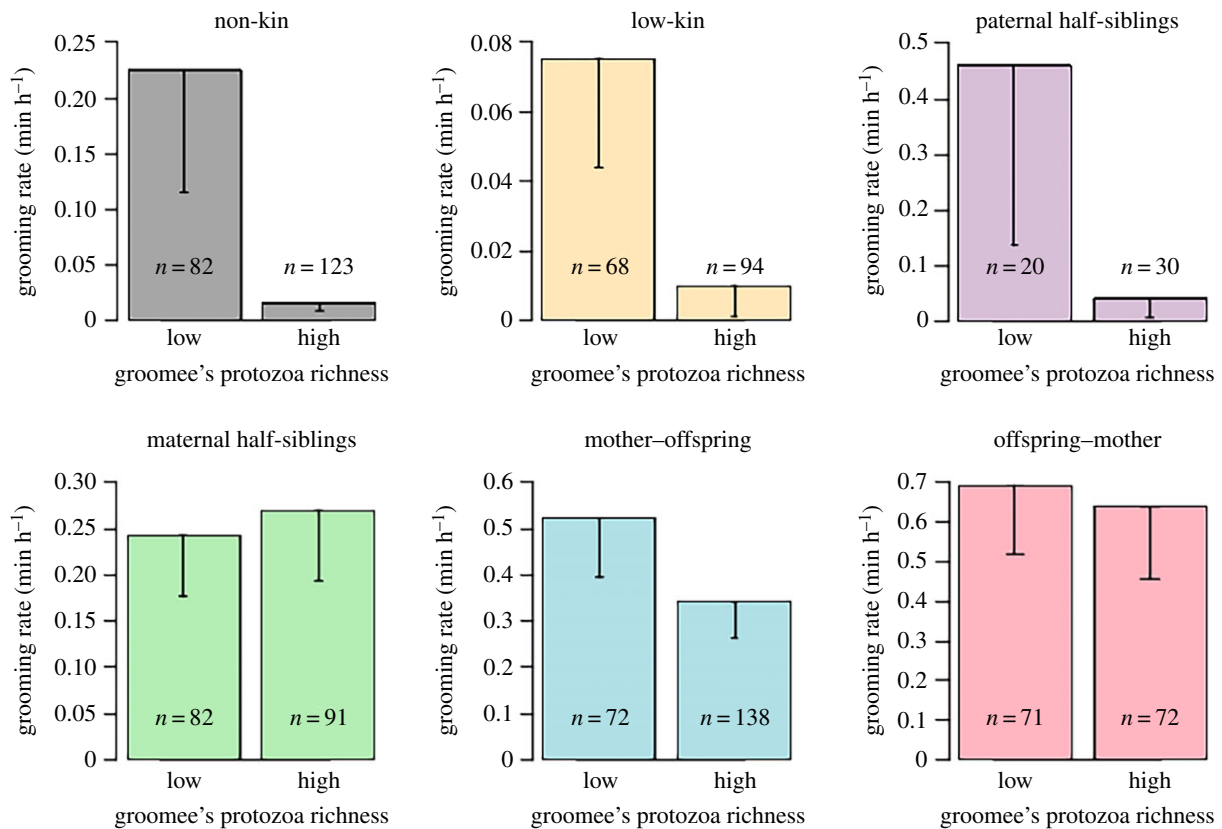


Figure 1. Effect of groomee's protozoa richness on grooming rate received. For the sake of clarity, we represented mean and standard error of the mean of grooming rate received from each kin category according to two levels of groomee's protozoa richness: 'low' corresponds to groomees infected by 0–3 protozoa taxa; 'high' corresponds to groomees infected by 5–6 protozoa taxa. Sample sizes are the number of dyad.month for each category. The corresponding statistical model on grooming time as a function of kinship and groomee's protozoa richness (expressed as a continuous variable), showed that only grooming received from non-kin, low-kin and paternal half-siblings decreased with groomee's protozoa richness.

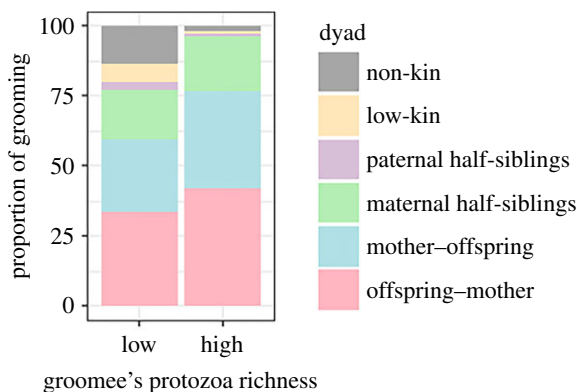


Figure 2. Effect of groomee's protozoa richness on the proportion of grooming received from each kin category. The figure is based on respectively 476 min 34 s and 316 min 45 s of grooming recorded when groomees showed 'low' versus 'high' protozoa richness. Fisher tests showed that 'high' groomees received almost only grooming from the three categories of maternal kin.

3. Results

(a) Are contagious groomees similarly avoided by all kin?

The interaction term between groomee's protozoa richness and kinship significantly contributed to variation in grooming time ($\Delta\text{LogLik}=12.1$, $Df=5$, $p<0.001$). In particular, the relationship between groomee's protozoa richness and grooming received from non-kin partners significantly differed from the relationship between groomee's protozoa

richness and grooming received from all maternal kin categories (non-kin versus mothers: $b=1.04$, $p=0.02$; non-kin versus offspring: $b=0.94$, $p=0.02$; non-kin versus maternal half-siblings: $b=1.18$, $p<0.01$; table 1). Grooming received from non-kin partners, low-kin partners and paternal half-siblings decreased with groomee's protozoa richness (non-kin partners: $b=-1.04$, $p=0.001$; low-kin: $b=-1.63$, $p<0.001$; paternal half-siblings: $b=-1.43$, $p=0.001$; figure 1 and table 1). By contrast, groomee's protozoa richness did not influence grooming received from mothers, offspring and maternal half-siblings (figure 1 and table 1). In other words, when infected, mandrills are less groomed by their groupmates except by their close maternal kin.

(b) Which kin take the risk of grooming contagious partners?

We found that the proportion of grooming received from non-kin partners, low-kin partners and paternal half-siblings decreased when groomees were highly parasitized (non-kin: 13.3 versus 2.0%, $p<0.001$, 95% confidence interval (CI)=0.12–0.14, odds ratio (OR)=0.13; low-kin: 6.6 versus 0.7%, $p<0.001$, CI=0.08–0.12, OR=0.10; paternal half-siblings: 3.3 versus 0.4%, $p<0.001$, CI=0.08–0.13, OR=0.10; figure 2). By contrast, the proportion of grooming received from mothers, offspring and maternal half-siblings increased in highly parasitized groomees (mothers: 42.0 versus 33.7%, $p<0.01$, CI=1.37–1.48, OR=1.42; offspring: 34.7 versus 25.8%, $p<0.001$, CI=1.47–1.59, OR=1.53; maternal half-siblings: 20.2 versus 17.3%, $p<0.001$, CI=1.16–1.28, OR=1.22).

Only close maternal kin continue to groom individuals that are highly parasitized, providing almost all grooming events (96.9%; figure 2).

4. Discussion

In this study, we showed that mandrills avoid grooming contagious groupmates except their close maternal kin, even when highly parasitized. Flexibility in social avoidance is expected to evolve if the social benefits of interacting with some individuals outweigh parasite costs. In matrilineal primate societies such as mandrills, highly differentiated social bonds usually occur among closely related groupmates [29,30]. These social bonds show adaptive values. More socially integrated female mandrills give their first birth on average a year before less socially integrated females [30]. Yellow baboon females (*Papio cynocephalus*) that are the most socially connected to their mothers, adult daughters and maternal siblings have highest offspring survival rates [29]. Additionally, because grooming close kin might alleviate physiological stress more efficiently, susceptibility to parasites might also be decreased when interacting with these partners, as shown in macaques (*Macaca mulatta*) [19,31]. Avoiding close maternal kin as grooming partners, even if highly contagious, may therefore have more detrimental social effects, for both the groomer and the groomee, than hygienic or physiological benefits.

Future research is required to understand the proximate mechanism allowing such flexibility. While we still have little understanding of the underlying cognitive processes involved in social avoidance, we know that disease recognition is based on the detection of multiple symptoms including behavioural modifications [32], appearance changes [33] or olfactory cues [8]. In mandrills, olfaction is at least one of the proximate mechanisms used to avoid contagious partners: during behavioural tests, individuals distinguished non-parasitized from parasitized conspecifics using faecal odorants [8]. We suggest that kinship may modulate this detection mechanism, decreasing sensitivity to pathogenic odour cues when associated with close

maternal kin. While body fluids are usually perceived as pathogenic cues parents feel little disgust towards their own baby's vomit, urine and faeces and experience less disgust towards their own baby's diaper than another diaper even when unaware of the diaper's origin [34].

Altogether, these findings shed light on a subtle behavioural defence strategy, allowing decreasing parasite risk related to frequent and close social interactions while maintaining social bonds with close maternal kin. The evolution of such behavioural flexibility towards diseased individuals has certainly had a broad impact on social evolution. In the human lineage, it has been suggested that caring for ill individuals likely emerged along kin networks and is possibly derived from grooming behaviours, because the costs of contact with pathogens may have been compensated by fitness benefits obtained through care-giving to close kin [12]. Further investigations on the role played by individual's health status and disease recognition in relation to kinship on the patterns of social interactions should improve our understanding of social evolution processes.

Ethics. This study was approved by an authorization from the CEN-AREST institute (permit no. AR0060/18/).

Data accessibility. Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.msbcc2ftf> [35].

Authors' contributions. C.P. and M.J.E.C. designed the study, performed the research and wrote the manuscript. All authors agree to be held accountable for the content therein and approve the final version of the manuscript.

Competing interests. We declare we have no competing interests.

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