

## Research



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# Mother-to-daughter transmission of hygienic anti-parasite behaviour in mandrills

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Social animals are particularly exposed to infectious diseases. Pathogen-driven selection pressures have thus favoured the evolution of behavioural adaptations to decrease transmission risk such as the avoidance of contagious individuals. Yet, such strategies deprive individuals of valuable social interactions, generating a cost–benefit trade-off between pathogen avoidance and social opportunities. Recent studies revealed that hosts differ in these behavioural defences, but the determinants driving such inter-individual variation remain understudied. Using 6 years of behavioural and parasite data on a large natural population of mandrills (*Mandrillus sphinx*), we showed that, when parasite prevalence was high in the population, females avoided grooming their conspecifics' peri-anal region (PAR), where contagious gastrointestinal parasites accumulate. Females varied, however, in their propensity to avoid this risky body region: across years, some females consistently avoided grooming it, while others did not. Interestingly, hygienic females (i.e. those avoiding the PAR) were less parasitized than non-hygienic females. Finally, age, dominance rank and grooming frequency did not influence a female's hygiene, but both mother–daughter and maternal half-sisters exhibited similar hygienic levels, whereas paternal half-sisters and non-kin dyads did not, suggesting a social transmission of this behaviour. Our study emphasizes that the social inheritance of hygiene may structure behavioural resistance to pathogens in host populations with potential consequences on the dynamics of infectious diseases.

## 1. Introduction

Hygiene can be defined as individual or collective practices that maintain individual health. In a narrower sense and in the context of parasite transmission risk, hygiene is a set of measures designed to prevent infections. Because parasites are ubiquitous organisms that largely impact host fitness [1,2], hygienic anti-parasite behaviours have evolved in a wide range of species, and include the avoidance of contaminated food [3–6] or habitats [5,7–9], selective defecation [5,10], waste management [11] and the use of plants with chemical properties that deter pathogen proliferation in the habitat [12]. However, most studies examining determinants of hygienic anti-parasite behaviours in animal species have mainly focused on food avoidance during feeding choice tests. These studies have revealed a widespread sex-bias across taxa, including in humans, with females being usually more hygienic than males [4–6,13,14]. Another common trend is that animals modulate feeding choices according to environmental conditions and their own internal state. For example, wild grey mouse lemurs (*Microcebus murinus*) in poor body condition or experiencing food scarcity fed more on contaminated food items than individuals in good physical shape or when food was not limiting [5]. The existence of

different ‘hygienic personalities’ was further uncovered in these lemurs because those individuals who avoided faecal contamination during feeding choice tests also consistently avoided contaminated water and nests. Interestingly, hygienic lemurs were less parasitized than non-hygienic individuals [5], emphasizing the efficacy of such behavioural strategies.

Yet, in social species, one major source of infection comes from infected conspecifics. Many infectious diseases, such as influenza or more recently COVID-19, are spreading rapidly because of frequent social contacts among social hosts, causing wildlife decline and significantly affecting human populations worldwide [15,16]. The avoidance of conspecifics with overt signs of infection may, therefore, constitute a behavioural adaptation to alleviate pathogen transmission risks due to group-living [17]. For example, social spiny lobsters (*Panulirus argus*) actively avoided conspecifics infected with a deadly virus (*Panulirus argus virus 1*) [18]. Spatial simulation models have further shown that this strategy could prevent large-scale epizootic outbreaks, again stressing the efficacy of hygienic practices [19]. However, and by contrast with experimental studies based on feeding choices, only a few studies have examined inter-individual variation in hygienic anti-parasite behaviours in social contexts. Yet, in humans, the level of disgust experienced towards contagious individuals varied with gender, age and personality traits [20] but poorly predicted social distancing behaviour during COVID-19 [21], possibly because the motivation to avoid people was influenced by the propensity to comply with governmental policies [22].

Here, we capitalized on 6 years of behavioural and parasite data collected on a natural population of mandrills (*Mandrillus sphinx*), a cercopithecine primate native to Central Africa, to study inter-individual variation in hygienic anti-parasite behaviours during social interactions. In non-human primates, grooming is a fundamental component of sociality [23–26] that allows, for example, social partners to access social resources such as support during agonistic interactions [27]. However, grooming also increases the risk of transmission of contagious parasites because of the close physical intimacy between partners [28]. In particular, mandrills are infested with several oro-faecally transmitted gastro-intestinal protozoa that accumulate around the perianal region (PAR) and can be transmitted during grooming interactions [29]. While some of these protozoa may provoke occasionally fatal dysenteries and amoebiasis in humans [30,31] and non-human primates [32], most of them are ubiquitous and generally non-pathogenic. However, even seemingly benign gastro-intestinal parasites can decrease host fitness [33], possibly leading to the evolution of hygienic anti-parasite behaviours. In line with this, we have recently shown that mandrills, probably thanks to an olfactory recognition system, avoided grooming those groupmates that were infected with contagious gastro-intestinal protozoa, especially around the PAR [29]. They further modulated this social avoidance with the perceived benefits of social interactions: while they avoided grooming contagious non-kin or distant kin, they did not do so with close maternal kin, possibly because maintaining strong social bonds with close family members was worth the risk of infection [34]. Hereafter, we reasoned that avoiding groupmates’ PAR during grooming interactions may represent a hygienic strategy in mandrills that would maximize chances of not getting contaminated without losing social opportunities. Grooming

this risky body region may, however, enable groomers to obtain crucial information on groomees’ health statuses [29] and individuals that take such a risk may be further perceived as highly valuable social partners because this body region is not easily accessible for self-grooming. Consequently, tendencies to groom (or not) the PAR of groupmates should result from a trade-off between the costs of infection and the benefits of socio-sexual relationships. Such a trade-off should thus generate inter-individual variation depending on individual needs, and on social and sanitary constraints.

In female mandrills from the study population, we first studied whether the probability to groom groupmates’ PAR during a grooming event varied with the level of protozoan infection in the population. We predicted females to be more hygienic (i.e. to groom PAR less frequently) when the risk of protozoan transmission was high. Second, to evaluate the risk taken when grooming such a body region, we studied whether the infection status of female groomers depended on their hygienic levels. We predicted a positive relationship between the probability to groom groupmates’ PAR and parasite richness in female groomers. Third, we determined whether different hygienic phenotypes occurred among female mandrills by analysing intra-female repeatability and inter-female variation in the probability to groom groupmates’ PAR. Here, we further studied the influence of female age, dominance rank and grooming frequency on inter-female variation in hygiene. We predicted both low-ranking and juvenile females to groom more frequently their groupmates’ PAR to improve social integration, compared to high-ranking and adult females, respectively. We did not exclude the possibility, however, that adult females might be less hygienic than juveniles because of their matured physiological immune system.

Finally, we evaluated the extent to which this trait was influenced by social and genetic relationships between females by studying this phenotype among mother–daughter dyads, paternal and maternal half-sisters and non-kin females. Indeed, if this hygienic trait had a genetic component, mother–daughter dyads should exhibit hygienic phenotypes more similar than maternal half-sisters or paternal half-sisters because the former dyads are more genetically related than the two latter kin categories. In addition, maternal and paternal half-sisters should also display some similarity in their hygienic phenotypes while non-kin dyads should differ in their hygienic propensity. Finally, if the social environment played a role in the expression of this behavioural trait, maternally related females (mother–daughter dyads and maternal half-sisters), sharing similar social (matrilineal) environments, should exhibit more similarity in their hygienic levels than paternal half-sisters or non-kin dyads, who lived in different social environments.

## 2. Material and methods

### (a) Study system

The study group of mandrills freely ranges in a private park (Lékédi Park) and its surroundings, near the village of Bakoumba (Southern Gabon). This population originated from two release events of captive mandrills that occurred in 2002 and 2006 [35]. In January 2012, a long-term field project was established to study this population (Mandrill Project). In 2021, the group was composed of ca 220–250 individuals of both sexes and all ages with wild-born individuals representing more than 95% of

the individuals from the study population. All of them are individually known and daily monitored.

We restricted our analyses to behavioural data collected on 297 mandrills with 102 female groomers (aged 6 months to 24 years old), and 152 female (including 92 of the female groomers) and 135 male groomees (aged 0–23 years old), during six study years from 2015 to 2021, when a protocol recording body location during grooming events was routinely performed. Each study year spanned from February to next January to follow ecological seasons [36]. Indeed, for the analyses below, we considered three ecological seasons: a long rainy season roughly corresponding to the birth season in mandrills and ranging from February to May, a long dry season roughly equating to the breeding season and ranging from June to September, and an intermediate season ranging from October to January.

## (b) Behavioural observations

Trained observers, blind to the study questions, performed daily behavioural observations using 5 min focal sampling [37], for a total of 4763 h of observation performed on the 297 studied individuals. During these focals, observers recorded, among others, all social interactions between the focal animal and its social partners. When a grooming event occurred, they further recorded, when visible (for a subset of approx. 50%), whether or not the event included groomees' PAR, regardless of the time spent grooming this body region. We excluded all grooming events that lasted less than 30 s to improve data quality. In addition, we excluded males as groomers, but not as groomees, because they groom their groupmates dramatically less often (about a 10th) and for shorter periods than females. With these constraints, we studied a total of 3429 grooming events that included the relevant information.

Using the outcomes of approach–avoidance interactions recorded during both focals and ad libitum sampling, we determined female dominance rank by calculating normalized David's score [38]. We considered three classes of dominance rank of similar size (low, middle and high-ranking individuals).

## (c) Coprological analyses

We performed qualitative coprological analyses using a sedimentation protocol on faecal samples collected opportunistically whenever a known individual was seen defecating (for details see [39]). Mandrills from the study population harbour seven different protozoan taxa [39]: *Balantidium coli*, Coccidian sp., *Endolimax nana*, *Entamoeba coli*, *Entamoeba hartmanni*, *Entamoeba histolytica/dispar* complex and *Pseudolimax butschlii*. Studied mandrills are also parasitized by several nematode taxa [39] but we did not focus on these parasites here because nematode eggs emitted in faecal material require a period of maturation to reach the infective larvae stage [13] and these larvae have never been retrieved from mandrills' body (M.J.E.C. & C.P. 2015, unpublished data). We collected a total of 1623 faecal samples from 204 individuals (101 females, 103 males), including 829 samples collected on the 102 female groomers. We specifically focused on protozoan richness because it is often considered a more robust measure of protozoan infection status than protozoan abundance, due to the intermittent shedding of protozoan cysts in faeces [40]. Over the study period, the average ( $\pm$ s.d.) population protozoan richness (i.e. number of different protozoan taxa per faecal sample averaged across all samples) was:  $4.47 \pm 1.27$  taxa.

## (d) Genetic analyses

Genetic relatedness in this population was determined using pedigree data obtained from paternity analyses (microsatellite genotyping) performed on most adult individuals and on a subset of immature individuals (for details see [41,42]). Among those females for whom at least one annual hygienic index was

determined ( $n=42$ , see below), 39 had their mother known, either from genetic analyses ( $n=37$ ) or based on sociality patterns ( $n=2$ ). Among these 42 females, 33 had their father genetically determined. Depending on the analysis, we used different subsets of these 42 females (see Results).

## (e) Statistical analyses

### (i) Grooming location and population protozoan richness

Using a generalized linear mixed-effects model (GLMM) with a binomial error structure and a logit link function, we first tested whether the probability that a grooming event included PAR (0/1) varied with the level of protozoan richness in the whole mandrill population. To obtain reliable parasite estimates at the time of each studied grooming event, we considered time windows ranging from two weeks before to two weeks after each grooming event (mean number of faecal samples considered per grooming event  $\pm$  s.d.:  $26.8 \pm 13.9$ ). For each four-week period associated with each grooming event, we then calculated the number of protozoan taxa averaged across all faecal samples collected per sampled individual during that period, and then considered the mean of all individuals' protozoan richnesses retrieved. We obtained a population protozoan richness for a total of 3402 grooming events performed by 102 female groomers. In this first analysis, we further considered the season when grooming events were recorded (three modalities) to control for possible environmental effects on grooming. Finally, we included the study year as a random factor to control for inter-annual variation in sociality.

### (ii) Evaluating parasite transmission risk

We evaluated the risk females took when grooming groupmates' PAR in a subset of 41 female groomers for whom parasitological data was also available. On a total of 357 female.months, we performed a linear mixed-effects model (LMM) to analyse females' monthly protozoan richness (number of protozoan taxa averaged across all faecal samples collected on each female, each month; mean number of faecal samples per female.month  $\pm$  s.d.:  $1.3 \pm 0.6$ ) as a function of females' probability to groom groupmates' PAR, retrieved as follows. For each female groomer and each study year, a 'proportion of risky grooming events' (PRG) was calculated as:  $\text{female.annual PRG} = (N \text{ risky grooming}) / (N \text{ grooming})$  with '*N risky grooming*' corresponding to the number of grooming events that included groupmates' PAR and '*N grooming*' representing the total number of grooming events given by that female that year. Due to a limited sample size, we were unable to analyse females' monthly PRG. To improve the accuracy of the dataset, however, we retrieved this annual PRG for each female who displayed at least 10 grooming events with a known body location that year (120 female.year, number of grooming events per female.year: range: 10–109, mean  $\pm$  s.d.:  $22.4 \pm 16.6$ ). We verified that for each female.year grooming events were evenly distributed throughout the year (for 109 out of 120 female.years, grooming events were recorded during the three seasons, representing, on average, eight different months of sampling per female.year). We also checked whether those female groomers for whom few grooming events were recorded ( $n=10$ –19 events) followed the same patterns found on the full dataset (see electronic supplementary material, appendix S1 and tables S1 and S2 for related results). In this model, we further considered the following predictors: female age and dominance rank to control for individual effects on parasitism, and the season as well as the monthly protozoan richness in the population (average number of protozoan taxa found in all faecal samples collected on each individual each month, averaged across all studied individuals sampled that month), to control for ecological and population effects. The study year and the female identity were considered as two random factors to control for inter-annual effects on parasitism and intra-individual repeated observations.

**Table 1.** Summary of the model investigating the effect of population protozoan richness and the season on the probability to groom groupmates' PAR during a grooming event. To test for significant differences between seasons, we changed the reference level sequentially. Significant test statistics are highlighted in italics ( $p < 0.05$ ).

parameters	estimates	s.e.m.	z-value	p-value
<i>population protozoan richness</i>	<i>-0.20</i>	<i>0.09</i>	<i>-2.19</i>	<i>0.029</i>
season:				
long dry versus long rainy	-0.10	0.12	-0.87	0.39
long dry versus intermediate	-0.03	0.13	-0.24	0.81
long rainy versus intermediate	0.07	0.12	0.63	0.53

We box-cox transformed the response variable using the package 'MASS' to normalize the distribution of the residuals.

### (iii) Intra-female repeatability and inter-female variation

To investigate intra-female repeatability and inter-female variation of hygienic levels, we calculated for each female groomer and each study year an 'hygienic index' (HI) as follows:  $\text{female.annual HI} = (\text{female.annual PRG}) / (\text{population.annual PRG})$  with '*female.annual PRG*' corresponding to the annual proportion of risky grooming events as described above, and '*population.annual PRG*' representing the annual proportion of risky grooming events averaged across all studied female groomers a given year. With this hygienic index, we thus controlled for yearly variation in the proportion of risky grooming events displayed by the studied females. Females with *female.annual HI* > 1 were those that groomed groupmates' PAR more often (i.e. were less hygienic) than an average female that year.

We first investigated the repeatability of *female.annual HI* across the study years by calculating adjusted repeatability estimates on a total of 120 female.years obtained from 42 females (mean number of study years per female  $\pm$  s.d.:  $2.9 \pm 1.6$ ), using the package 'rptR' that estimates 95% CIs based on parametric bootstrapping [43]. This procedure allowed the evaluation of individual consistency based on a LMM approach, considering the female identity as a random factor and controlling for female age (and its quadratic term), dominance rank and her frequency of grooming given (time spent grooming all groupmates, whether or not the information about the body location was available, divided by the total focal time performed on this female that year). With this latter variable, we, therefore, tested whether females that spent more time grooming others were those that groomed more often their groupmates' PAR. In preliminary analyses, we considered all possible interactions between female age, dominance rank and grooming frequency and found that models with interaction terms did not outperform models without these interactions using likelihood ratio tests. We, therefore, excluded all interactions from final models. We also investigated the repeatability of *female.annual HI* across years using different thresholds of the minimum number of grooming events considered per female.year (from 11 to 35, see electronic supplementary material, appendix S2 and figure S1 for corresponding results).

### (iv) Genetic and social inheritance of hygiene

For each female groomer with at least one *female.annual HI* available ( $n = 42$ ), we calculated a global hygienic index by averaging all her *female.annual HI* obtained across the study years. Among all possible dyads ( $n = 861$ ) involving these 42 studied females, 21 dyads were mother-daughter pairs and 22 were maternal half-sisters (for seven of them, the father of one female of the dyad was unknown but we excluded the possibility that they were full-sisters using demographic data). For those dyads

with both parents known, 29 were paternal half-sisters (for six of them, the mother of one female of the dyad was unknown but, again, we excluded the possibility that they were full-sisters using demographic data) and 209 were considered as unrelated pairs (i.e. with a relatedness coefficient inferior to 0.0625).

We studied the relationships between global hygienic indices of mothers and daughters, maternal half-sisters, paternal half-sisters and unrelated females using Pearson's correlations. Two dyads of mandrills were full siblings and were, therefore, considered both as maternal half-sisters and paternal half-sisters. Excluding them from the analyses did not change our results.

All statistical analyses were performed using R v.3.3.3. GLMM was fitted using the package 'lme4' and LMMs were fitted using the package 'nlme'. To validate these models, we visually inspected diagnostic plots to check for homoscedasticity and independence of error terms. In addition, we verified that the residuals of LMMs were normally distributed (Shapiro-Wilk normality tests:  $p > 0.05$  in all models). We further checked for the absence of collinearities and multicollinearities among the predictors by calculating variance inflation factors (VIFs) for each predictor in each model (VIFs close to 1 in all instances). Moreover, the stability of each model was assessed by excluding data points one by one and comparing the resulting estimates with estimates obtained with the full dataset (revealing stable models).

## 3. Results

### (a) Grooming location and population protozoan richness

The probability that grooming events included PAR decreased with an increased parasite risk in the population ( $p = 0.03$ ; table 1). For example, when protozoan richness in the population was below 3, on average 28.4% (s.d.:  $\pm 4.5$ ) of grooming events included PAR, while when protozoan richness was higher than 5, only 14% ( $\pm 1.4$ ) of grooming events included this region. The probability to groom PAR did not vary across seasons (all  $p > 0.10$ ; table 1).

### (b) Evaluating parasite transmission risk

*Female.annual PRG* varied from 0% to 60% across female.years (average *female.annual PRG*: 18%). Females allocating more grooming events to their groupmates' PAR were, on average, more parasitized than females avoiding this body region ( $p = 0.002$ ; table 2). Moreover, females' monthly protozoan richness was higher during the long dry than during the long rainy season ( $p = 0.001$ ; table 2) and also highly positively correlated with population monthly protozoan richness ( $p < 0.001$ ; table 2). Neither female age nor dominance rank

**Table 2.** Summary of the model investigating the effect of *female.annual PRG* on females' monthly protozoan richness. We further included in our model as potential confounding variables: female age and dominance rank, the season and monthly population protozoan richness. To test for significant differences between levels of female dominance rank and between seasons, we changed the reference level sequentially. Significant test statistics are highlighted in italics ( $p < 0.05$ ).

parameters	estimates	s.e.m.	d.f.	t-value	p-value
<i>female.annual PRG</i>	10.43	3.15	68	3.32	0.002
age	0.02	0.09	68	0.23	0.82
dominance rank:					
low versus high	0.36	0.81	38	0.44	0.66
middle versus high	0.33	1.38	38	0.24	0.82
low versus middle	0.04	1.37	38	0.03	0.97
season:					
<i>long dry versus long rainy</i>	2.72	0.83	243	3.28	0.001
long dry versus intermediate	1.36	0.90	243	1.52	0.13
long rainy versus intermediate	-1.36	0.84	243	-1.62	0.11
<i>population protozoan richness</i>	8.68	0.54	243	16.16	<0.001

**Table 3.** Summary of the model investigating the effects of female traits (age, dominance rank and grooming frequency) on *female.annual hygienic index*. To test for significant differences between levels of female dominance rank, we changed the reference level sequentially.

parameters	estimates	s.e.m.	d.f.	t-value	p-value
age	0.05	0.07	75	0.78	0.44
(age) <sup>2</sup>	-0.002	0.003	75	-0.84	0.41
grooming frequency	1.33	0.85	75	1.56	0.12
dominance rank:					
low versus high	0.20	0.25	39	0.78	0.44
middle versus high	0.18	0.31	39	0.58	0.56
low versus middle	0.02	0.31	39	0.06	0.96

significantly influenced females' monthly protozoan richness (both  $p > 0.10$ ; table 2). Our results did not change for those females for whom few grooming events [10–19] were recorded (electronic supplementary material, appendix S1 and table S1).

### (c) Intra-female repeatability and inter-female variation

*Female.annual HI* was highly consistent per female across years, with an adjusted repeatability estimate of 63% ( $R = 0.63$ , 95% CI = 0.50–0.80,  $p < 0.001$ ). Some female mandrills were, therefore, consistently hygienic across years while others were not. None of female age, dominance rank or grooming frequency influenced, however, *female.annual HI* (all  $p > 0.10$ ; table 3). Again, our results did not change for those females with few grooming events recorded (electronic supplementary material, appendix S1 and table S2). Finally, increasing thresholds of the minimal number of grooming events did not qualitatively change these results (electronic supplementary material, appendix S2 and figure S1).

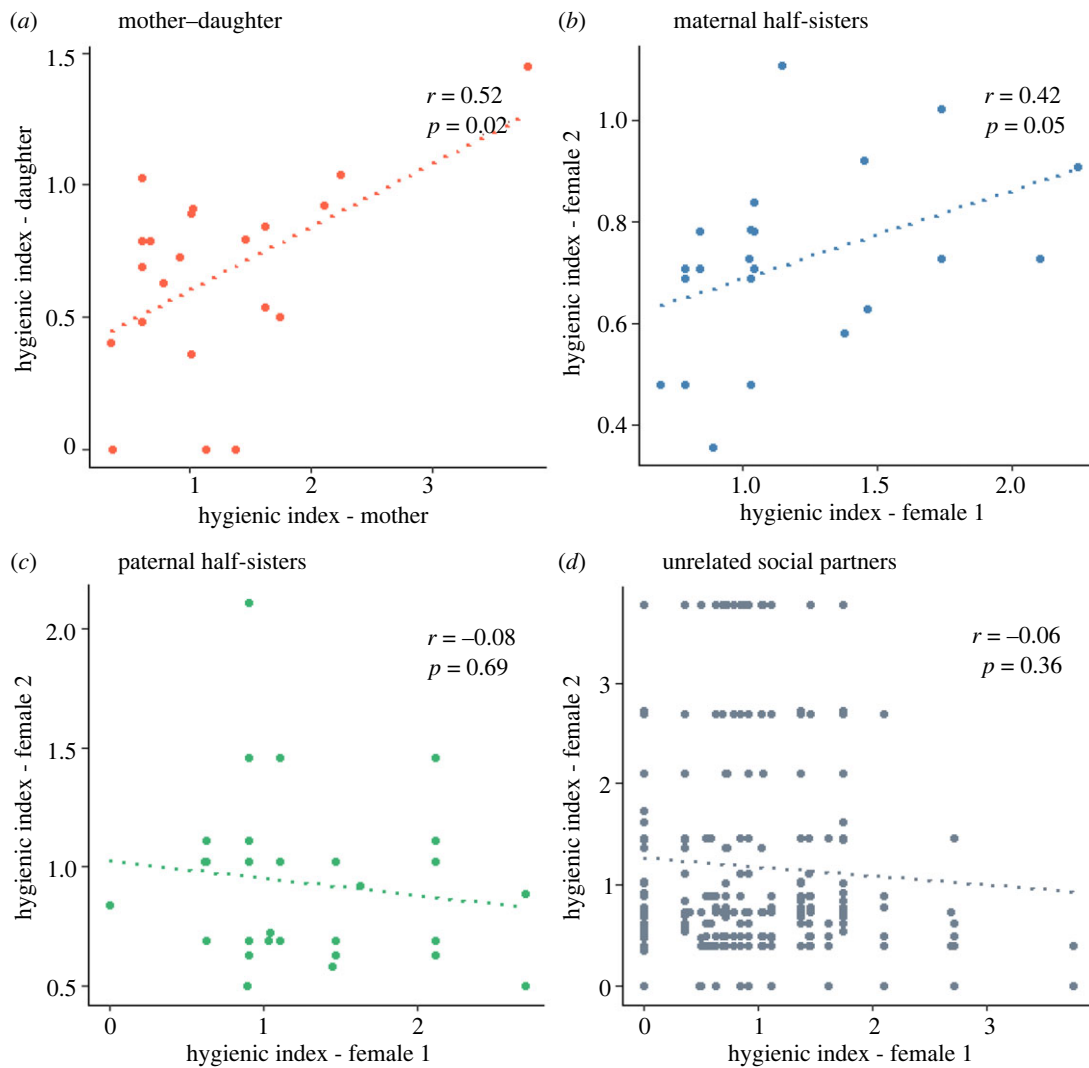
### (d) Genetic and social inheritance of hygiene

Mothers and their daughters showed highly correlated global hygienic indices ( $r_p = 0.52$ , 95% CI = 0.11–0.78,  $p = 0.02$ ; figure

1a) and we observed a similar trend for maternal half-sisters, although the test was at the limit of significance ( $r_p = 0.42$ , 95% CI = 0.00–0.72,  $p = 0.05$ ; figure 1b). By contrast, paternal half-sisters ( $r_p = -0.08$ , CI = -0.43 to 0.30,  $p = 0.69$ ; figure 1c) and unrelated females ( $r_p = -0.06$ , CI = -0.20 to 0.07,  $p = 0.36$ ; figure 1d) did not show similar hygienic indices. The similarity between global hygienic indices of mothers and daughters remained significant when considering females for whom few grooming events were recorded (electronic supplementary material, appendix S1).

## 4. Discussion

In this study, we showed that female mandrills avoided grooming the PAR of their groupmates when the risk of contamination was high. Similarly, when parasite pressure was elevated, chimpanzees (*Pan troglodytes*) increased their consumption of leaves and bitter pith to get rid of gastrointestinal parasites [44]. We suggest that the fine-tuned hygienic strategy observed in mandrills allows individuals to decrease contamination risk (by avoiding the PAR) without losing social opportunities (by continuing grooming). However, and given that the expression of this hygienic



**Figure 1.** Relationships between global hygienic indices retrieved from different kin categories: (a) mother–daughter dyads, (b) maternal half-sisters, (c) paternal half-sisters and (d) unrelated females. Pearson correlation coefficients and associated  $p$ -values are given for each pairwise comparison.

trait varied across females with clear consequences on their parasite status, we further suggest that this strategy is tuned by individual, social or environmental circumstances depending on a cost–benefit balance.

Although grooming may serve hygienic purposes, when used to remove dirt or ectoparasites [45–47], it can also act as a behavioural pathway for gastro-intestinal parasite transmission [28,48]. The PAR is particularly risky regarding contamination because parasites accumulate on this body area [29]. As such, the more female mandrills groomed their groupmates' PAR, the more they were parasitized. However, grooming the PAR could also bring some benefits to groomers. One advantage probably lies in the assessment of groupmates' health and sexual statuses. Indeed, mandrills are able to detect parasitized individuals from their faecal odours alone during olfactory tests [29]. Additionally, grooming groupmates' PAR, which almost always includes a close visual and olfactory investigation of the genitalia in our population, might allow to obtain cues on their reproductive state, as observed in several primate species [49–53]. Additionally, individuals willing to groom this area may be perceived as valuable social partners because self-grooming is hardly possible on this body region. This behaviour may, therefore, allow females who display it to improve social integration and gain social supports.

Interestingly, we further showed that some female mandrills consistently performed less grooming of the PAR across years than others, suggesting that individual characteristics might play a role in hygiene. Contrary to our predictions, however, none of female age, dominance rank or grooming frequency impacted hygiene. Other individual traits such as the quality of the immune system, may influence individual investment in hygiene. The 'pathogen defence optimization hypothesis' posits, indeed, that immuno-suppressed individuals should invest more into hygienic practices because both defence systems incur costs [54]. Less hygienic females could, therefore, be those that invest more in their physiological immune system, allowing them to groom risky, but valuable, body regions with a reduced risk of infection. In line with this, in Galapagos finches (*Geospiza fortis* and *G. fuliginosa*), individuals that showed risky social behaviours regarding parasite transmission were also those that invested more into their physiological immune system [54]. Additional data on mandrills' immune system are now required to fully address this hypothesis.

In this study, we have also evaluated the extent to which hygiene was influenced by social and genetic relationships between females. Mothers and their daughters showed similar hygienic levels, and we observed the same trend among maternal half-sisters, by contrast to paternal half-sisters and non-kin dyads. Contrasting these results with hygienic

similarity between full-sisters would help deciphering whether or not genetic influences the expression of this trait but our sample size (two dyads of full-sisters) did not allow to make such comparisons. However, we suggest that genetic inheritance, if at play, cannot explain alone this set of results because hygienic similarity between maternal half-sisters differed from the one observed among paternal half-sisters despite their similar genetic relatedness ( $r \sim 0.25$ ). Hygienic similarity among these close maternal kin, in particular between mothers and their daughters, point out the importance of the social environment where females live as an important determinant of hygiene in mandrills. This result could emerge because close maternal kin share similar sets of social partners and, therefore, face similar parasite risk when grooming their groupmates. We did not find, however, strong support for this mechanism. Indeed, when looking at each female's set of top-groomed partners each year (partners groomed for more than 10% of a female's total time of grooming; electronic supplementary material, table S3), we showed that maternal half-sisters shared, on average, more top grooming partners (7%) than mother–daughter pairs (3.8%).

Alternatively, we propose that hygienic behaviours could be socially transmitted from mothers to daughters through social learning. In mandrills, as in other non-human primates, infants stay in close contact with their mother for several years, and female maternal kin form stable and strong social bonds for their entire life [55], creating a familiar environment where females have repeated opportunities to learn from their maternal kin through observation. In humans, a recent study on monozygotic and dizygotic twins showed that within-family similarity in disgust sensitivity was partly due to genetic effects [56]. However, parents also played an active role in the development of their infants' disgust sensitivity: they exhibited more disgust towards contaminated items in the presence of their children who showed, in turn, similar disgust responses [57], a result echoing our own. While the role of social transmission on the expression of hygienic anti-parasite behaviours used in social contexts has never been investigated in animals, several studies reported vertical transmission (i.e. from mother to offspring) of socially learned behaviours [58–61]. In vervet monkeys, for example, a cleaning method used to process sandy food was socially transmitted from mothers to infants, although genetic inheritance could not be ruled out in this study [59]. In wild chimpanzees, mothers facilitated the acquisition of tool-using tasks [61], and self-medicative behaviours could be socially transmitted from mothers to infants through repeated observations starting at an early age [44]. In this great ape, individual frequencies of palm-to-palm claspings, a distinct style of high-arm grooming, were also highly consistent within matriline, indicating that

individuals adopted the grooming style of their mother [60]. Similarly, in mandrills, offspring could learn and copy the grooming style of their mother, including their tendency to avoid (or not) groupmates' PAR. Such social inheritance of hygienic behaviours could spatially structure behavioural resistance to pathogens, especially in those animal species forming well-differentiated social bonds with some of their groupmates (resulting in clusters of preferred social partners), as observed in typical matrilineal societies of primates or other large mammals. Inter-individual variation in hygienic behaviours could then drive the epidemiological structure of host populations, with some matriline being less hygienic and more parasitized than others, resulting in clusters of super-spreaders [62]. As such, specific disease control measures, targeting those non-hygienic, super-spreader clusters could limit pathogen spread more efficiently than conventional measures.

In this article, we provided evidence that mandrills can decrease the risk of contamination by exhibiting fine-tuned parasite avoidance behaviour during grooming interactions: they avoided grooming their groupmates' PAR when parasite pressure was high. However, females varied in their hygienic proclivity and this variation was consistent across years and within matriline. While a large number of studies have investigated the determinants of heterogeneous parasite distribution in natural populations, variation in hygienic behaviours have seldom been considered in epidemiological models despite their efficacy in reducing parasite transmission. Future studies measuring inter-individual variation in hygiene, including in social contexts, could help understanding how host behaviours might affect parasite dynamics, improving the scope and reliability of epidemiological models.

**Data accessibility.** Data are available at <https://orcid.org/0000-0001-5545-2985>.

The data are provided in electronic supplementary material [63].

**Authors' contributions.** C.P.: conceptualization, data curation, formal analysis, investigation, methodology; M.J.E.C.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

**Conflict of interest declaration.** We declare we have no competing interests.

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