## Research

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# Environmental, sex-specific and genetic determinants of infant social behaviour in a wild primate

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Affiliative social bonds are linked to fitness components in many social mammals. However, despite their importance, little is known about how the tendency to form social bonds develops in young animals, or if the timing of development is heritable and thus can evolve. Using four decades of longitudinal observational data from a wild baboon population, we assessed the environmental determinants of an important social developmental milestone in baboons—the age at which a young animal first grooms a conspecific—and we assessed how the rates at which offspring groom their mothers develops during the juvenile period. We found that grooming development differs between the sexes: female infants groom at an earlier age and reach equal rates of grooming with their mother earlier than males. We also found that age at first grooming for both sexes is weakly heritable ($h^2 = 0.043$, 95% CI: 0.002–0.110). These results show that sex differences in grooming emerge at a young age; that strong, equitable social relationships between mothers and daughters begin very early in life; and that age at first grooming is heritable and therefore can be shaped by natural selection.

## 1. Background

Observational studies of humans and other mammals indicate that individuals with more numerous or stronger social bonds in adulthood are healthier and live longer, suggesting that strong social relationships should be favoured via natural selection [1,2]. Social relationships in early life are also important, as they represent crucial opportunities to develop social skills and may have long-lasting consequences in their own right. For instance, in social mammals, positive social environments early in life have been linked to stronger or more numerous affiliative social relationships in adulthood [3–6], better health [3,7] and increased longevity [8–12].

In spite of the well-established importance of social bonds in mammals, very little is known about the ontogeny of affiliative social behaviours in natural populations—including the relative contributions of demography, environment and genetics during development. Sex differences are among the best-understood aspects of the development of social behaviour [13–17]. For example, in juvenile meerkats, females invest more in cooperative care of young, and in several species of primates, juvenile females invest more in grooming relationships,

while juvenile males invest more in play and agonistic behaviour [14,18–20]. Such sex differences may be caused by variation in mother–offspring relationships that influence the juvenile social environment or by sex-specific differences in future fitness benefits. For example, in species with sex-biased dispersal (e.g. yellow baboons and rhesus macaques), or where rank inheritance is nepotistic in one sex but based on physical competition in the other (e.g. spotted hyenas and many cercopithecine primates), early investment in affiliative behaviour may also have sex-biased benefits [13–15,21–23].

The importance of mothers for the development of social behaviour and fitness is also well-established in many species [3–5,24,25]. For example, in elephants, chimpanzees, and yellow baboons, early maternal loss, even after weaning, is associated with altered social relationships in adulthood [3–5,24,26] and reduced lifespan [8,10,12,24]. However, many gaps remain in our understanding of behavioural development in natural populations. Although laboratory studies long ago established that extreme maternal or social deprivation incurs major long-term costs (reviewed in [27]), studies of developmental trajectories in wild social mammals are relatively rare. Furthermore, most work focuses on mother–offspring relationships or play behaviour and many involve provisioned populations. In addition, very few studies consider potential genetic contributions to behavioural development in conjunction with environmental and demographic factors (e.g. [6,15,18,20,26,28–33]; but see [13,16,17,19,34,35]).

Considering the potential role of genetics in the development of social behaviour is important because of the strong links between affiliative social behaviour and fitness. Consequently, social behavioural traits should respond to natural selection if selection is sufficiently strong and if these traits are heritable. However, no study has assessed whether the onset of affiliative social behaviour is heritable in a wild animal population. Heritability is assessed by measuring the proportion of phenotypic variation explained by additive genetic effects (i.e. narrow-sense heritability [36]). In humans and non-human vertebrates, variation in affiliative social behaviour tends to be weakly, but measurably, heritable (e.g. in comparison to morphological or life-history traits [37–47]). However, in the absence of studies of the heritability of behavioural development in wild populations, the relative contributions of genes versus the environment, and the degree to which developmental features of social behaviour can respond to natural selection, remain unknown.

Here, we examined the development of grooming behaviour in infants living in the well-studied baboon population of the Amboseli basin [48]. We focused on grooming because social bonds are often developed and maintained through grooming, a primary affiliative behaviour in many social species, including baboons [49–52]. Furthermore, stronger grooming relationships and/or more frequent grooming have been linked to longer lifespans in both male and female baboons [24,49,53,54]. Investigating the development of grooming behaviour can therefore shed light on how environmental and genetic sources of variance contribute to the emergence of a social behaviour with clear links to fitness.

This study had four goals. In Analysis 1, we identified the socio-environmental determinants of the age at which a young animal first groomed a conspecific. In Analysis 2, we determined the identity of the recipient of each subject's first grooming efforts. Because infants are in frequent proximity to their mothers, who are important providers of nutrition and information, we predicted that subjects would groom their mother first. In Analysis 3, we assessed how grooming relationships develop by measuring 'grooming equivalence' with mothers, i.e. the proportion of mother–offspring grooming events that were initiated by the mother versus the offspring. Because young animals lack the coordination and skill to perform grooming behaviours, we predicted that when offspring are young, mothers would initiate grooming more, but that the mother–offspring grooming relationship would become more equitable over the course of development. We also predicted that mother–daughter relationships would have greater grooming equivalence than mother–son relationships because in the Amboseli baboons, as in many primates, mothers are an important social partner to females in adulthood [15,50,55]. By contrast, sons disperse from their natal social group around maturity, terminating mother–son relationships. Finally, in Analysis 4, we measured the heritability of age at first grooming.

## 2. Methods

### (a) Study population and study subjects

The Amboseli Baboon Research Project (ABRP) is a longitudinal study of wild yellow and yellow-anubis admixed baboons (*Papio cynocephalus* × *P. anubis*) living in and around Amboseli National Park, Kenya. Behavioural, environmental and demographic data have been collected on individually recognized baboons on a near-daily basis since 1971; blood and fecal samples for DNA analysis have been collected since 1989 and 2000, respectively [48]. Baboons in Amboseli live in stable social groups containing multiple adults and juveniles of both sexes, ranging in size from approximately 20–100 animals. The ABRP monitors multiple such groups (study groups) in the Amboseli ecosystem.

Our study subjects included 781 immature baboons (368 males and 413 females) who were born into unprovisioned study groups between 1983 and 2020 and for whom data were available for all our predictor variables. Ages of all subjects were known to within a few days' error. We included a small set of subjects whose mothers died before the subject began to groom conspecifics ($n = 11$ of 781 subjects), but excluded individuals who died before one year of age ($n = 28$). We excluded individuals whose first grooming was known to have occurred during a period of reduced data collection or during group fissions, as well as those whose first grooming was likely to have occurred during these gaps in data collection (i.e. animals between 0.58 and 2.6 years of age during these periods, the timespan during which most first grooming events occur, $n = 129$).

Study subjects were habituated to experienced observers who recognize individual baboons by sight. Age at first grooming was defined as a subject's age at the earliest interaction in which it was observed to perform coordinated and systematic picking through the fur of another animal. Data were collected using 'representative interaction sampling', which is designed to avoid biases from uneven sampling of study subjects [54]. Specifically, an observer moves systematically through the group while carrying out 10 min focal animal samples according to a predefined, randomized list of focal animals. They simultaneously record all grooming interactions in their line of sight, whether or not they involve the focal animal. While this approach is designed to mitigate bias, it cannot capture all grooming interactions (e.g. grooming may occur outside of an observer's line of sight). Consequently, the age at which we first observed a subject to groom (our

measurement of age at first grooming) should be considered the latest date by which this milestone was achieved. This ascertainment error is unlikely to be correlated with other predictors in our models except for group size, which affects the ratio of animals to observers in a group and hence per-animal observation effort. Because we are less likely to observe a given grooming interaction in a large group compared to a small group, we included a measure of observer effort in our models of age at first grooming (e.g. [24,54]).

## (b) Analysis 1: environmental predictors of age at first grooming

We assessed several maternal, social and physical environmental variables as potential predictors of age at first grooming; all are known or likely contributors to infant development and/or adult social behaviour (see 'Description of predictors used in our model selection analysis' in the electronic supplementary material). These variables included the subject's own sex (male or female) as well as: (i) maternal parity, (ii) maternal social isolation, (iii) maternal proportional dominance rank, (iv) maternal alpha rank status (whether or not the subject's mother was the highest-ranking female in the group at the subject's birth), (v) season of birth (wet or dry), (vi) drought in the first year of life, (vii) group size at birth and (viii) the presence of maternal siblings between birth and first grooming. In addition, because the Amboseli baboons are an admixed population between yellow baboons and anubis baboons [56,57], we conducted secondary analyses that included an estimate of genetic ancestry (e.g. the proportion of anubis ancestry across the genome) as a fixed effect. Because these secondary analyses included a smaller set of individuals (i.e. those for whom genetic ancestry estimates are available) and produced similar results to our main models, we present them in the electronic supplementary material (see 'Effects of genetic ancestry on age at first grooming behaviour').

We modelled age at first grooming—the dependent variable—as time-to-event data that were right-censored. When both sexes were combined in the same model, the analysis showed non-proportional hazards of age at first grooming (a violation of a key assumption of Cox proportional hazards models [58]). Consequently, we modelled the two sexes separately for all further analyses. For all subsequent analyses, we used a model selection approach that compared a set of mixed effects Cox proportional hazards models, run separately for each sex. We used a model selection approach because we did not have specific predictions about which combinations of our potential predictors would best explain variation in age at first grooming.

Because we were also interested in sex differences in the age of first grooming, but could not run both sexes together in our Cox proportional hazards model, we also fit a linear mixed model that included sex as the primary predictor of interest and random effects of social group identity, maternal identity and year of birth (using the Amboseli 'hydrological year', which begins in November with the annual rainy season and continues through October of the following year—e.g. hydrological year 2021 began in November 2020 and continued through October 2021). We fitted this model using the 'glmmTMB' R package using a Gaussian error distribution [59].

For model selection we used the 'coxme' function from the R package 'coxme' [60] with a Gaussian error distribution to evaluate a set of candidate models. These models included linear fixed effects of maternal parity, maternal social isolation, maternal proportional dominance rank, maternal alpha status, season of birth, drought, group size and the presence of maternal sibling. We also included a fixed effect of observer effort, which we calculated as the number of grooming events collected per group member per month for each group, averaged over the time period from birth to first grooming for each subject (see *Study*

*population and study subjects*). The fixed effects were largely uncorrelated and variance inflation values were less than 2.4 (electronic supplementary material, table S1). All models also included random effects of social group identity, maternal identity and hydrological year of birth, which were estimated via maximum likelihood.

To compare models, we calculated adjusted Akaike's information criterion ($AIC_c$) [61] for combinations of fixed effects using the 'dredge' function from the 'MuMIn' R package [62]. We calculated model-averaged parameter estimates for fixed effects using only 'top models' where $\Delta AIC_c$ values were within two units of the model with the lowest $AIC_c$ value [63]. Estimates were calculated from the full coefficient set using the 'model.avg' function from the 'MuMIn package', where terms that were not included were set to zero.

## (c) Analysis 2: recipients of first observed grooming effort (first grooming partner)

To gain insight into the social and demographic milieu associated with the development of grooming, we identified the recipients of all subjects' first observed grooming efforts (i.e. their 'first grooming partners'). First, we used a binomial test to test the prediction that mothers were disproportionately the recipients of subjects' first grooming efforts, compared to all other social group members. We expected that mothers would be groomed at a rate higher than their frequency in the social group (i.e. at a rate > 1/group size). Second, for individuals who did not groom their mother first, we used a binomial test to determine whether relatives ($r \geq 0.0625$ excluding mothers; see below) were disproportionally the subject's first grooming partner. For the kin analysis, we expected that relatives would be groomed at a rate higher than their frequency in the group (i.e. at a rate > n relatives/group size).

We categorized first grooming partners by relatedness using the 'kinship' function in the 'kinship2' R package [64], which estimates relatedness coefficients between dyads based on multi-generation pedigree information [44,65]. All 781 of our subjects had known mothers and 489 had known fathers. The number of fathers and paternal kin identified as first grooming partners is underestimated because 292 subjects lacked paternity assignments.

## (d) Analysis 3: mother–offspring grooming equivalence

To assess how offspring grooming relationships with their mother developed, we measured grooming equivalence. We defined grooming equivalence (the response variable for Analysis 3) as the number of grooming events per month initiated by the mother divided by the total number of grooming events per month between each mother–offspring dyad. Higher values of this metric correspond to cases where the mother initiated more grooming, while lower values correspond to cases where the offspring initiated more grooming; values of 0.5 represent perfect equivalence. We excluded several periods of reduced data collection and periods affected by group fissions.

Females in this population reach menarche—the onset of adulthood—in their 5th year of life; males typically reach puberty (testicular enlargement) in their 6th year of life, but usually do not attain full adult dominance rank and begin mating until their eighth year of life [66]. To account for these developmental differences, we split our analyses into two time periods. First, we assessed mother–offspring grooming equivalence from birth to the median age of female menarche (4.5 years), a time period when both males and females were immature. Second, we assessed mother–offspring grooming equivalence from the median age of menarche to the median

age of male rank attainment (7.7 years), a time period when females were fully adult but most males were not.

We modelled equivalence using binomial mixed effects models with a logit link using the 'glmmTMB' function in the 'glmmTMB' R package [59]. We assessed fixed effects of age (both linear and squared to account for nonlinear relationships), offspring sex and their interaction. To control for repeated measures and maternal effects, offspring identity was nested within maternal identity as a random effect. Social group and hydrological year of birth were also modelled as random effects. To assess which partner drove changes in mother–offspring equivalence over time, we built separate *post hoc* models of the number of grooming events initiated by the mother and the number of grooming events initiated by the offspring between each mother–offspring dyad. Here, we fitted the same fixed and random effects as used in the main equivalence model, using a mixed effects models with a zero inflated negative binomial error distribution. Our results were robust to the timing of dispersal by adult male offspring (a concern if males with stronger maternal bonds also delayed dispersal: see electronic supplementary material, 'Methods and analyses').

## (e) Analysis 4: genetic variance in age at first grooming

To estimate the heritability of age at first grooming, we combined males and females together ($n = 781$ subjects) and used the 'animal model', a linear mixed effects model that combines pedigree information with phenotypic values [67,68]. In the animal model, a vector of individual phenotypes is the response variable with estimates of each individual's breeding value included as a random effect. The covariance of breeding values among individuals is, in turn, affected by trait heritability and relatedness in the sample. Here, we derived relatedness values from the multigenerational Amboseli pedigree, subset to 1315 individuals and a maximum of six generations (i.e. the subset of the full pedigree necessary to estimate $r$ for animals in this dataset). Among these 1315 individuals, 871 had known mothers and 531 had known fathers; see electronic supplementary material, table S2 for full details on the pedigree.

In the animal model, environmental effects are important to include as fixed effects because, as with any linear model, correctly estimating the variance associated with the random effects (which, in the animal model, include genetic effects) depends upon accurately characterizing the fixed effects [69]. We created a nested set of models, a standard procedure for validating heritability estimates with the animal model: (1) a 'maternal effects' only model that included only the random effect of maternal identity, (2) an 'environmental random effects' model that included the random effects of maternal identity, social group and hydrological year of birth, and (3) a 'heritability' model that included a random effect of animal breeding value along with the random effects of maternal identity, social group and hydrological year of birth. Finally, because the fixed effects in an animal model can reduce residual variance and thus alter heritability estimates [69], we also report an 'intercept only' model that did not include fixed effects but did include all four random effects. In our calculations of heritability from models with fixed effects, we included the variance explained by fixed effects in our estimates of phenotypic variance [70,71].

Because our population is naturally admixed (*P. cynocephalus × P. anubis*), we also ran a secondary heritability analysis that included an estimate of the subject's genetic ancestry in addition to environmental fixed effects. However, the number of subjects with genetic ancestry estimates was small ($n = 237$ versus $n = 781$ for the full dataset), limiting our power (see electronic supplementary material, Methods and Analyses).

We implemented the animal model using the 'MCMCglmm' R package [72]. We used weakly informative priors ($V = 1$, nu =

0.002) and a total of 30 000 000 iterations with a burn-in period of 500 000 and a thinning interval of 10 000. Our effective sample sizes for fixed effects exceeded 2590 and those for random effects exceeded 2050 in all models. We compared model fit using deviance information criteria (DIC) scores, which is interpreted similarly to an AIC score [73]. Because variance component estimates are constrained to positive values, we used DIC comparisons of models with and without the random effect of animal breeding value to assess if heritability was significantly different than zero.

# 3. Results

## (a) Analysis 1: sex and environmental variables predict age at first grooming

Females were observed to groom earlier than males (electronic supplementary material, figure S1; GLMM: $b = 0.189 \pm 0.025$, $z = 7.60$; $p < 0.001$). Females first groomed other animals at an average age of 0.9 years (10.7 months; 95% CI: 10–11.5 months), whereas males did so at an average age of 1.1 years (13 months; 95% CI: 12.2–13.8 months). Our model selection using Cox proportional hazards models for females and males separately yielded 11 models with $\Delta AIC_c$ values less than 2 from the model with the lowest $AIC_c$ value. We refer to these models as the 'top models' (electronic supplementary material, table S3).

Social group size appeared as a fixed effect in all top models for both sexes (electronic supplementary material, table S3): males and females in smaller groups groomed earlier (electronic supplementary material, figure S2). Females in the smallest groups groomed a median of 0.2 years (2.4 months) earlier than those in the largest groups (HR = 0.989, 95% CI: 0.982–0.996; table 1a; electronic supplementary material, figure S2a). Males in the smallest groups groomed a median of 0.3 years (4 months) earlier than those in the largest groups (HR = 0.985, 95% CI: 0.975–0.995; table 1b; electronic supplementary material, figure S2b).

For females, drought in the first year of life also appeared in all top models (electronic supplementary material, table S3a): females who experienced drought in the first year of life groomed slightly earlier than those who did not (HR: 1.498, 95% CI: 1.041–2.155; table 1a; electronic supplementary material, figure S3). However, this small effect of drought is primarily evident in subjects who first groomed after the median age (i.e. 'late' groomers; electronic supplementary material, figure S3). Maternal social isolation, the presence of maternal sibling, maternal parity, season of birth and maternal proportional rank each appeared in only one of the top models for females, and model-averaged parameters showed hazard ratios that overlapped one (i.e. no effect; table 1a; electronic supplementary material, table S3a).

For males, maternal proportional rank and maternal alpha status were included in 4 of 5 top models (electronic supplementary material, table S3b). Males with alpha mothers were 1.47 times more likely to achieve first grooming at any age compared to males with non-alpha mothers (HR: 1.473, 95% CI: 1.048–2.410; table 1b). However, controlling for alpha status, males with high-ranking mothers were *less* likely to achieve first grooming at any age compared to males with low-ranking mothers (HR: 0.684, 95% CI: 0.416–0.970; table 1b). Drought in the first year of life, the presence of a maternal sibling, and maternal parity were each included in

**Table 1.** Model averaged parameter estimates for fixed effects that predict variance in age at first grooming. Estimates refer to change in the log hazard ratio and are calculated from the full coefficient set, but with terms not included in the top models set to zero. See electronic supplementary material, tables S6 and S9 for the results of a smaller, secondary analysis including genetic ancestry. Effects where 95% confidence intervals of the hazard ratio do not overlap one are italicized.

| sex | effect | estimate | s.e. | HR | 95% CI HR | interpretation |
|---|---|---|---|---|---|---|
| a) female | *group size* | *−0.011* | *0.004* | *0.989* | *0.982–0.996* | larger groups are associated with later age at first grooming: a one-member increase in group size = 0.99× the likelihood of a first grooming event at any age |
| | *observer effort* | *0.161* | *0.034* | *1.175* | *1.099–1.256* | more observer effort is associated with earlier detection of first grooming: for all ages, the likelihood of a first grooming is 1.18× greater for each one-unit[a] increase in observer effort |
| | sibling present | 0.016 | 0.060 | 1.017 | 0.879–1.379 | |
| | maternal social isolation | −0.021 | 0.068 | 0.979 | 0.709–1.131 | |
| | maternal proportional rank | 0.018 | 0.075 | 1.018 | 0.841–1.603 | |
| | maternal parity (primiparous) | −0.012 | 0.059 | 0.988 | 0.710–1.196 | |
| | *drought in first year of life* | *0.404* | *0.186* | *1.498* | *1.041–2.155* | drought in the first year of life is associated with earlier age at first grooming: drought in the first year of life corresponds to a 1.5× increase in the likelihood of a first grooming event at every age |
| | season of birth (wet) | -0.002 | 0.037 | 0.998 | 0.799–1.209 | |
| b) male | *group size* | *−0.015* | *0.005* | *0.985* | *0.975–0.995* | larger groups are associated with later age at first grooming: a one-member increase in group size = 0.99× the likelihood of a first grooming event at any age |
| | *observer effort* | *0.124* | *0.038* | *1.132* | *1.049–1.220* | more observer effort is associated with earlier detection of first grooming: for all ages, the likelihood of a first grooming is 1.13× greater for each one-unit[a] increase in observer effort |
| | sibling present | 0.021 | 0.069 | 1.021 | 0.881–1.432 | |
| | *maternal alpha rank* | *0.387* | *0.259* | *1.473* | *1.048–2.410* | sons of alpha females tended to groom earlier than other offspring: sons of alphas had a 1.47× increase in the likelihood of a first grooming event at every age |
| | *maternal proportional rank* | *−0.380* | *0.259* | *0.684* | *0.416–0.970* | sons of higher ranking females other than the alpha tended to first groom at later ages: the likelihood of first grooming is 0.68× greater for a one unit increase in mother's proportional rank (i.e. from the lowest to the highest ranking mother) |
| | maternal parity (primiparous) | −0.014 | 0.067 | 0.986 | 0.675–1.216 | |
| | drought in first year of life | −0.010 | 0.085 | 0.990 | 0.614–1.412 | |

[a]Observer effort is measured as average per capita grooms per month per group.
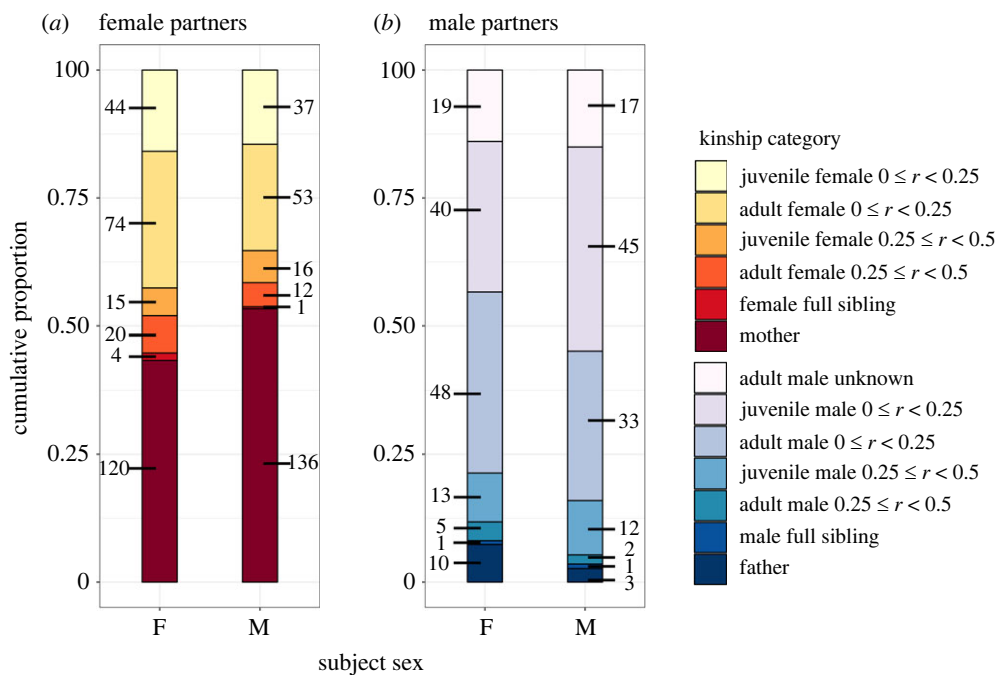
**Figure 1.** First observed grooming partners of study subjects. First observed partners were females (*a*) approximately twice as often as they were males (*b*), for both male and female subjects. Numbers next to each bar denote the number of first grooming partners in that category. (*a*) In total, 67% of first grooming partners were females among female subjects, and 69% were females for male subjects; stacked bars indicate the proportion of these partners that fell into different categories of female. (*b*) Only 33% of female subjects and 31% of male subjects first groomed a male partner; stacked bars indicate what proportion of these partners fell into different categories of male. Age categories were (i) juvenile males (aged < 7 years, includes subadults), (ii) juvenile females (age < 4 years), (iii) adult males and (iv) adult females. Kinship categories were $r = 0.5$ (e.g. parents, full siblings), $0.25 \leq r < 0.5$ (e.g. half-siblings, grandparents, full aunts and uncles), $r < 0.25$ (e.g. cousins, half aunts and uncles, half nieces and nephews, more distantly related kin and unrelated partners) and unknown (applies only to immigrant males with no known offspring or adult relative in the group). The number of fathers and paternal relatives as first grooming partners is underestimated, because 292 subjects lacked paternity assignments. More fine-grained kinship categories are presented in electronic supplementary material, figure S4.

only one top model for males, and model-averaged parameters for these effects showed hazard ratios that overlapped one (i.e. no effect; table 1*b*; electronic supplementary material, table S3*b*).

Observer effort—a technical rather than biological variable—appeared in all the top models for both sexes in the direction we expected: individuals were observed grooming at earlier ages when observer effort was greater (females: HR: 1.175, 95% CI: 1.099–1.256; males: HR: 1.132, 95% CI: 1.049–1.220; table 1; electronic supplementary material, table S3).

In our secondary analyses including the mother's or subject's genetic ancestry (electronic supplementary material, 'Methods and analyses', and tables S5–S10), the subject's genetic ancestry appeared in approximately half of the top models for both sexes. However, the confidence intervals for the model-averaged hazard ratio for subject's genetic ancestry were large and overlapped one for both sexes, indicating no statistically meaningful effect in either direction (electronic supplementary material, table S6; females: HR: 7.648, 95% CI: 0.680–85.983; males: HR: 7.716, 95% CI: 0.633–95.097).

## (b) Analysis 2: first grooming partners are often mothers or kin

Recipients of first observed grooming efforts (first grooming partners) were disproportionately female: 67% of female subjects ($n = 277$) and 69% of male subjects ($n = 255$) were first observed grooming a female, while 33% of female subjects ($n = 113$) and 31% of male subjects were first observed grooming a male ($n = 136$; figure 1). Mothers were 17 times and 21.7

times more likely to be the first grooming partner for daughters and sons, respectively, relative to chance (figure 1*a,b*; observed proportion for sexes combined = 0.328, expected = 0.017, binomial test of proportion grooming mother versus non-mother first, $p < 0.0001$).

Among the 67.2% of subjects who did not groom their mother first, 40% were first observed grooming close kin ($r > 0.0625$), compared to 24.2% expected (electronic supplementary material, figure S4, binomial test, $p < 0.0001$); 22% of subjects were first observed grooming their closest, non-mother kin ($r \geq 0.25$). However, fathers represented only approximately 1% to 6% of first grooming partners ($n = 13$ known fathers, $n = 49$ total fathers if all first grooming partners in the 'unknown adult male' category were fathers; figure 1*b*).

## (c) Analysis 3: mother–offspring grooming equivalence depends on subject age and sex

Mother–daughter dyads had significantly greater equivalence than mother–son dyads overall (figure 2, table 2). Furthermore, daughters reached full equivalence with mothers at 3.2 years, while males did not reach full equivalence with mothers until 5 years of age (figure 2). Relationships between mothers and daughters had greater equivalence than mother–son relationships during both the juvenile period for both sexes (birth to 4.5 years) and the period corresponding to subadulthood in males (4.5–7.7 years), but the sexes converged in mother–offspring equivalence by 8 years of age (figure 2).

Sex differences in mother–offspring grooming relationships were primarily driven by sex differences in the offspring's
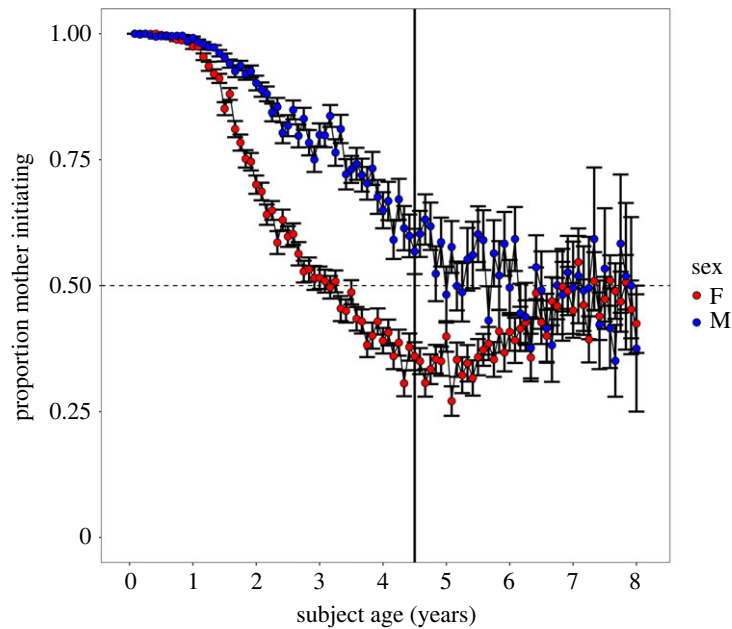
**Figure 2.** Proportion of mother–offspring grooming events where the mother initiated grooming events for sons (blue) and daughters (red). The dashed horizontal line indicates perfect grooming equivalence (i.e. 0.5). The solid vertical black line corresponds to 4.5 years (the median age at female menarche). Points are monthly averages and bars denote standard errors.

**Table 2.** Predictors of mother–offspring grooming equivalence: results of binomial generalized linear mixed models for two different time periods. Estimates represent change in grooming equivalence for 1 s.d. increase in age (age in years was centred and standardized). Significant effects are italicized.

| age range | effect | estimate | s.e. | Z value | p-value | interpretation |
|---|---|---|---|---|---|---|
| 0–4.5 years | sex (male) | 0.247 | 0.015 | 16.47 | <0.001 | on average, daughters initiate 4× more interactions with mothers than do sons at every age in this age range, leading to greater grooming equivalence with their mothers at every age |
| | age | -0.351 | 0.007 | -47.02 | <0.001 | on average, mothers initiate 94% of grooms with their 1-year-old offspring and 50% of grooms with their 4-year-old offspring |
| | $age^2$ | -0.031 | 0.008 | -3.81 | <0.001 | equivalence is approached more rapidly with increasing offspring age |
| | sex*age | 0.187 | 0.012 | 15.70 | <0.001 | equivalence is achieved earlier by daughters than by sons |
| | $sex*age^2$ | -0.015 | 0.012 | -1.25 | 0.213 | |
| 4.5–7.7 years | sex (male) | 0.162 | 0.059 | 2.75 | 0.006 | on average, daughters initiate 2× more interactions with mothers than do sons at every age in this age range, leading to greater grooming equivalence with their mothers; daughters exceed perfect equivalence with mothers in this age range while males achieve near-perfect equivalence (electronic supplementary material, figure S5) |
| | age | 0.101 | 0.020 | 5.13 | <0.001 | on average, mothers initiate more grooming events with 5-year-olds than with 7-year olds |
| | $age^2$ | 0.006 | 0.022 | 0.27 | 0.785 | |
| | sex*age | -0.160 | 0.041 | −3.86 | <0.001 | with increasing age, females return to equivalence with mothers after disproportionately being initiators; males maintain equivalence with mothers during this age range |
| | $sex*age^2$ | 0.026 | 0.044 | 0.60 | 0.548 | |

**Table 3.** Comparison of nested animal models. (i) Maternal effects model: random effects included only maternal identity (*m*); environmental fixed effects were sex (*s*), social group size (*gs*) and observer effort (*oe*). (ii) Environmental random effects model: random effects included maternal identity (*m*), social group identity (*g*) and hydrological year of birth (*hy*). Environmental fixed effects were as in (i). (iii) Heritability model: random effects include the breeding value, *a*, estimated in part based on the relatedness matrix as well as environmental random effects as in (ii) and environmental fixed effects as in (i) and (ii). (iv) Intercept-only model: random effects as in (iii); no environmental fixed effects other than an intercept were included. The best-fitting model was model (iii), the heritability model (italicized).

| model | fixed effects | random effects | DIC | Δ DIC | $h^2$ [95% CI] | residual variance [95% CI] |
|---|---|---|---|---|---|---|
| (i) maternal effects | $s + gs + oe$ | $m$ | 578.858 | 65.254 | — | 0.979 [0.946, 0.998] |
| (ii) environmental random effects | $s + gs + oe$ | $m + g + hy$ | 519.648 | 6.044 | — | 0.846 [0.765, 0.928] |
| (iii) *heritability* | $s + gs + oe$ | $a + m + g + hy$ | *513.604* | *0.000* | *0.043 [0.002–0.110]* | *0.801 [0.683, 0.897]* |
| (iv) heritability, intercept only | intercept only | $a + m + g + hy$ | 610.589 | 96.985 | 0.047 [0.002–0.122] | 0.773 [0.659–0.872] |

behaviour rather than the mother's behaviour (electronic supplementary material, figure S5 and table S12). During infancy, mothers groomed male and female offspring at similar relative frequencies, and although mothers groomed female offspring at a slightly higher frequency than male offspring starting around 2.1 years of age, these differences remained relatively small throughout the period of maturation (electronic supplementary material, figure S5a). By contrast, despite the fact that males were more likely to target their mothers for first grooming than females, female offspring directed grooming towards their mothers at a much greater relative frequency than male offspring. This pattern started early in life and persisted throughout the maturation period (electronic supplementary material, figure S5b).

## (d) Analysis 4: age at first grooming is weakly heritable

Heritability of age at first grooming was 0.043 in the best fitting model (95% credible interval: 0.002–0.110), which included genetic effects, environmental random effects and environmental fixed effects (electronic supplementary material, figure S6a; table 3). Nested models that did not include genetic effects (i.e. the 'maternal effects' and 'environmental random effects' models in table 3) had ΔDIC > 2 compared to models including additive genetic effects (i.e. models including genetic effects significantly improve fit over ones without them: table 3). In the 'intercept-only' model that included all random effects but no fixed effects, the heritability estimate was nearly identical to the 'heritability' model that included all random and fixed effects, and the credible intervals for heritability in the two models were very similar ($h^2 = 0.047$, 95% credible interval: 0.002–0.122; table 3). Thus, the inclusion of fixed effects does not appear to influence heritability estimates. In the model that included the subset of individuals with genetic ancestry estimates, the point estimate of heritability was higher ($h^2 = 0.125$, 95% credible interval: 0.001–0.307; electronic supplementary material, table S15 and figure S6), but the credible intervals of heritability estimates were larger and overlapped completely with those in the model without genetic ancestry.

## 4. Discussion

We report three major findings about the development of affiliative social behaviour in wild baboons. First, males and females differ in the age at which they first groom a conspecific, in their grooming relationships with their mothers, and in the environmental predictors of age at first grooming. Second, our results emphasize the important role of mothers in the development of their offspring's social behaviour: mothers were represented among first grooming partners 19-fold more than expected by chance (averaged across male and female subjects) and were the primary drivers of grooming relationships early in their offspring's lives. Finally, age at first grooming is weakly but detectably heritable, suggesting that evolution by natural selection has the potential to shape this early-life milestone [36].

## (a) Sex differences in the development of grooming and grooming equivalence

Females tended to groom for the first time about two months earlier than males (electronic supplementary material, figure S1). Females also reached grooming equivalence with mothers at an earlier age than males (figure 2, table 2). These sex differences in the development of social behaviour are driven primarily by offspring behaviour: mothers groomed sons and daughters at similar frequencies before 4.5 years of age, but daughters directed grooming towards their mothers at much higher relative frequencies than sons during this period. These patterns are consistent with the idea that strong bonds with mothers may be more important for the sex that associates more with the mother post-weaning, as has been suggested in species as diverse as red kangaroos, bottlenose dolphins and primates [14,16–18,20,30–32,34,74,75]. Interestingly, the number of daughter-initiated grooming events peaks around menarche and then declines into adulthood. This decline may occur both because daughters increase their investment in relationships with other adult females [76] and because they begin to invest in their own offspring (median age of first birth is 5.97 years in the study population [66]).

## (b) Environmental predictors of infant grooming patterns

Both males and females in larger social groups tended to begin grooming at later ages than those in small social groups. This could occur if adults in larger groups tend to

engage in less affiliative behaviour and more agonistic behaviour—as suggested for yellow-bellied marmots—potentially giving juveniles fewer opportunities to engage in grooming behaviour [77]. An alternative hypothesis is that larger groups contain more close-in-age juveniles who provide opportunities for non-grooming social interactions such as play. This possibility is supported by a larger effect of group size on age at first grooming in males, as males tend to play more than females in most mammals (reviewed in [78]). Because sex differences in play behaviour appear early in life, they likely lead to sex differences in the development of other social behaviours as well. Group size can also affect other aspects of a primate infant's behaviour that may explain differences in age of first grooming, including the resources available, the proportion of time it spends in proximity to its mother and other group members, and the strength of social ties to peers [28,29]. Finally, the group size effect we detected could also indicate that our measure of observer effort did not fully capture the limitations of our sampling scheme in large groups.

Beyond the consistent effect of group size in all our top models and in both sexes, we found modest evidence for other environmental effects on age at first grooming. For instance, maternal rank predicted male, but not female, age at first grooming, such that sons of alpha females tended to groom at earlier ages while sons of other high-ranking females tended to first groom at later ages (table 1). This result adds to a growing body of evidence suggesting that the highest-ranking individuals in baboon groups– the alpha individuals—experience social and physiological effects that are distinct and discontinuous from the effects experienced by other individuals in the hierarchy. Such 'alpha effects' have been documented for both alpha males and alpha females in Amboseli [79,80]. Their causes and consequences remain unclear, but are a particularly interesting topic of future study, especially in a plural-breeding species such as baboons. We also found some evidence that drought in the first year of life slightly accelerates age at first grooming for females (but not males), but only after the median age at first grooming (electronic supplementary material, figure S3). The small size of this effect and its restriction to a small age range (11–17 months) makes it difficult to interpret and will require a larger dataset to fully understand.

The presence of kin clearly shaped subjects' early grooming experiences: 59% of first grooming partners were kin with $r \geq 0.0625$, and most of these (48% of the total) were close kin ($r \geq 0.25$; figure 1; electronic supplementary material, figure S4). Mothers were the first grooming partners much more than expected by chance, by both male and female subjects. This result is unsurprising, as young baboons spend the majority of their time with their mothers, and mothers are key contributors to offspring development [81]. Together, our results are consistent with the extensively documented importance of mothers in particular, and kin in general, in affiliative relationships in mammals [5,25,82]. Whether this pattern reflects the development of true social preferences for mothers or is instead a passive by-product of spatial proximity patterns between infants and mothers remains an important open question for future work (e.g. [35]). In addition, future work identifying the factors that explain variation in the identity of the first grooming partner as well as how mothers influence other aspects of social development in baboons and other species is warranted.

## (c) Heritability of age at first grooming

Age at first grooming was heritable, albeit weakly, and thus has the potential to respond to natural selection if the strength of selection is substantial and directionally consistent [36]. In general, the heritability of behavioural traits is lower than that of morphological traits [40,83]. However, our value of $h^2 = 0.043$ is much lower than the average of $h^2$ approximately 0.30 reported in two meta-analyses of the heritability of social behaviour [39,47], and 4–6 times lower than the heritability of adult grooming behaviour ($h^2 = 0.16$–0.26) measured in our study population [44]. Part of this difference reflects measurement error: because first grooming events are relatively brief, one-time events in an individual's life, it is unlikely that we captured all first grooming events with high accuracy. Values for age at first grooming are therefore best treated as the *latest* date by which this milestone was achieved (see 'Methods'). Even treating our estimates as a lower bound, though, our results suggest that the environmental influences discussed above are very important for variation in age at first grooming. Given the major role of the environment, estimating the adaptive value of this trait—and therefore the likely strength of selection governing its evolution over time—is an interesting topic for future research.

In our best fitting model, 80% of the variance in age at first grooming was unexplained, a result that is likely a consequence of four contributing factors. First, the trait we measured is an integrated trait (i.e. one that emerges from the combination of a large number of component traits [47,84]). The variation in each component of an integrated trait—which, for a social developmental trait, may include multiple neurological, physiological and physical traits—contributes to compounded residual variation in the integrated trait [47,84–87]. Such compounded variation can be large, leading to large unexplained variation and to low heritability, even if the trait has relatively high additive genetic variance [47,85–87]. Second, the large amount of unexplained variation in our model points to unmeasured environmental effects, such as social proximity patterns, social network density and mothering style [14,15], which represent potential future targets of study. Third, unexplained variance may also be the result of measurement error: as noted above, it is unlikely that we captured all first grooming events with high accuracy. Finally, some of the unexplained variation in our model may be attributable to indirect genetic effects (IGEs) in which the genotypes of social partners affect focal phenotypes [88]. Given the demonstrated importance of IGEs in other studies of behaviour [44,89], the role of IGEs in the ontogeny of social interactions in the wild represents another important topic for future research.

Our work provides valuable fundamental information on the development of primate social relationships and their ability to evolve. We show that sex differences in affiliative behaviours arise early in life, and we provide new evidence of the crucial role of mothers in development even after weaning. Our results suggest that future work focused on the development of affiliative and non-affiliative social behaviours will yield valuable insights about how these phenotypes evolve.

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