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Investigating the relationship between sociality and reproductive success in wild female crested macaques,

Macaca nigra

Julie Duboscq^{1,2,3*}, Jérôme Micheletta^{1,4}, Dyah Perwitasari-Farajallah^{1,5,6}, Antje Engelhardt^{1,7}, Christof Neumann^{1,8,9}

¹ the Macaca Nigra Project, Tangkoko Reserve, Bitung, Indonesia

² Eco-Anthropologie (EA), UMR7206, CNRS-MNHN-Université Paris Cité, Paris, France

³ Department of Behavioral Ecology, University of Göttingen, Göttingen, Germany

⁴ Department of Psychology, Centre for Comparative and Evolutionary Psychology, University of Portsmouth, Portsmouth, UK

⁵ Primate Research Center (PSSP), IPB University, Bogor, Indonesia

⁶ Department of Biology, Faculty of Mathematics and Natural Sciences, IPB University, Bogor, Indonesia

⁷ Institute of Biology, Faculty of Life Science, University of Leipzig, Leipzig, Germany

⁸ Cognitive Ethology Lab, German Primate Center, Göttingen, Germany

⁹ Leibniz Science Campus Primate Cognition, Göttingen, Germany

* corresponding author: Julie Duboscq, Eco-Anthropologie (EA), UMR7206, CNRS-MNHN-Université

Paris Cité, Musée de l'Homme, 17 place du Trocadero, 75016 Paris, France, julie.duboscq@mnhn.fr

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Author Contributions

JD, CN, and JM originally formulated the idea; AE, JD, CN, and JM conducted fieldwork; JD and CN processed the data; CN performed statistical analyses; AE and DPF provided moral, administrative and logistic support in the field; and JD, CN, JM, AE and DPF discussed and wrote the manuscript.

Conflict of Interest

The authors declare that they have no conflict of interest.

Abstract

Studying the link between sociality and fitness is valuable to understand the costs and benefits of sociality. In many species, sociality is positively linked to fitness: having more, stronger, more equitable or predictable affiliative relationships leads to higher reproductive success, greater survival, or longevity, at least in females. We tested this sociality-fitness link in wild female crested macaques *Macaca nigra* in Tangkoko, North Sulawesi, Indonesia. Over 15 years, we studied six groups and collected behavioral, ecological, and demographic data on 140 females. We modeled the annual probability that females gave birth as a function of grooming rate with other females, adjusting for a number of control variables. We found no evidence for an overall association between grooming and the probability of giving birth. Further exploration of the results revealed large uncertainties in the model estimates and substantial idiosyncratic variation within and between females, and to a lesser extent, years and groups. This may have to do with constraints imposed on grooming, on reproduction, or on both. Further investigations into the significance and sources of this variation will help disentangle the pathways by which social interactions with other group members relate to fitness outcomes.

Keywords: social behavior; reproduction; grooming; birth rate; females; long-term data; Macaca Nigra Project; crested macaques

Introduction

Social relationships between group members are viewed as adaptive in a variety of contexts such as allyship against competition and danger, or for helping raise offspring. This social component of fitness - whereby sociality positively impacts reproduction, health, and survival - is indeed evident in many social vertebrates (Silk, 2007b, 2007a; Snyder-Mackler et al., 2020). Characteristics of social bonds (the positive or affiliative relationships between two individuals) such as their strength, consistency, or equitability, are frequently positively associated with fitness components such as increased longevity, higher offspring survival and greater fertility in a wide range of animals, from insects to humans (Silk, 2007b, 2007a; Snyder-Mackler et al., 2020). For instance, hunter-gatherer BaYaka (*Homo sapiens*) mothers with greater indirect network centrality (i.e., centrality determined by neighbors and neighbors of neighbors in the network) produced more living offspring (Page et al., 2017). Nevertheless, other studies highlight that this positive sociality-fitness link is not always present. For example, over multiple years and groups, blue monkey females (*Cercopithecus mitis stuhlmanni*) with strong bonds with other adult females had a higher risk of mortality when those bonds were not stable from year to year. This result was interpreted as a cost resulting from females' investment in strong social relationships that did not "pay off" in terms of future allyship (as they were not stable over time) (Thompson & Cords, 2018).

The conclusions drawn about the sociality-fitness links, whether positive, negative, or absent, can strongly depend on which variables are investigated (Ellis et al., 2019; Thompson, 2019). An analysis of the relationship between female survival and several categories of social connectedness in rhesus macaques (*Macaca mulatta*) showed that whereas the number of weak bonds was positively linked to survival under all chosen thresholds, the number of strong connections and the strength of bonds were only positively related to survival at the highest thresholds, i.e., when the authors considered 90% of bonds as strong, or when they took into account only the top one to three partners (Ellis et al., 2019). There is also some

evidence for within-species variation. For example, in two populations of chacma baboons (*Papio ursinus*), birth rate was positively linked to the number of strong bonds between females, whereas 12-month infant survival and infant longevity were positively linked to the number of weak bonds (McFarland et al., 2017). In contrast, in another population of chacma baboons, similar analyses revealed little to no evidence that the number of social bonds consistently affected female fertility, infant survival to one year and infant longevity, whereas having strong and well-differentiated social bonds had a positive impact on infant survival and female longevity (Silk et al., 2018).

The sociality-fitness link might also depend on breeding strategies (multiple vs. single breeders, communal vs. parental care) and ecological conditions (low vs. high competition, food abundance or availability) of the study species (Ebensperger et al., 2012). Because of a triangular relationship between feeding ecology, sociality, and fitness, at least for female primates, sociality could be most or least beneficial for reproduction depending on whether the ecological environment is mild or harsh (Ebensperger et al., 2012). Only a few primate studies have looked at this triangular relationship and mostly under harsh conditions, which are likely the most impactful (e.g., McFarland & Majolo, 2013; Young et al., 2014, 2019). One study in crested macaques (*Macaca nigra*) further investigated the combined impact of several social and ecological parameters on fetal and infant survival and showed that survival chances notably change with rainfall and adult female group size (Kerhoas et al., 2014), both markers of ecological and social competition.

When testing the hypothesis that sociality is related to fitness, it seems therefore necessary not only to define which variables we account for but more importantly, which predictions we make specifically with these variables as several mechanisms exist by which sociality can covary with fitness (Ostner & Schülke, 2018; Thompson, 2019). On the fitness side of the equation, variables often include female longevity or survival (e.g., Silk et al., 2010; Thompson & Cords, 2018), female birth rate (e.g., McFarland et al., 2017), or offspring survival (e.g., Silk et al., 2009). However, major components of fitness, namely

adult longevity and lifetime fecundity or offspring survival to reproduction, are rarely available to wildlife researchers, even in long-term studies spanning enough years to follow several generations. Fortunately, other fitness components are easier to measure and adequate (Ebensperger et al., 2012). The production of offspring or parturition is one such fitness component as reproductive success starts with being able to carry a pregnancy to term and to give birth to a live and healthy infant. Indeed, producing offspring is energetically costly for female mammals and carrying a pregnancy comes with a number of challenges (Emery Thompson, 2013; 2017; Touitou et al., 2021).

On the sociality side of the equation, sociality encompasses individual and dyadic, direct, and indirect aspects of social life, differently named as behavioral tendency, integration, or connectedness to give a few examples (Ellis et al., 2019; Silk et al., 2013). In many studies, sociality concerns forming and maintaining dyadic relationships. In these cases, indices of dyadic affiliative bond strength or individual derivatives thereof, such as cumulative strength of the strongest bonds or number of weak versus strong bonds, form the basis of sociality measures (e.g., McFarland et al., 2017; Silk et al., 2009, 2010). Sometimes, measures of sociality reflect individual behavioral tendency or social experience, in which case researchers use individual-based measures such as a network centrality index (e.g., degree or number of partners) or a basic rate of affiliation (e.g., Archie et al. 2014). In any case, grooming interactions and/or close spatial proximity always form the core of sociality measures (Silk et al. 2013). Grooming is indeed a widespread activity in many animals and plays a particularly important role in social bonding (Dunbar, 1991). The activity of grooming not only provides a way for individuals to be in close proximity and connect with each other intimately (Dunbar, 2010), it also has relaxing effects, both for the groomer and the groomee: actively grooming or being groomed triggers the release of endorphin hormones, which in turn are linked to relaxation and pleasure, and decrease the circulation of glucocorticoid hormones linked to stress (Aureli & Yates, 2010; Carter & Keverne, 2002; Dunbar, 2010; Keverne et al., 1989; Shutt et al., 2007). Crucially, bonding with others requires the ability and tendency to engage in the underlying bonding

behavior, e.g., grooming, in the first place. For example, in species that groom, an individual that does not engage in grooming cannot form and maintain relationships. At the same time, it is not because an individual engages in grooming that they are good at forming and maintaining relationships, for example if they groom others indiscriminately.

Putting this together, even under the best ecological conditions with abundant food and low levels of social competition which allow the female, and by extension the fetus, to be well nourished and relaxed, a pregnancy comes with great challenges and is a strain on her body (Emery Thompson, 2013). Therefore, being positively connected to other group members and engaging frequently in a relaxing activity through grooming could help a female carry a pregnancy to term and give birth to a healthy infant. In this way, grooming rates would link to increased reproductive success through the formation and maintenance of social relationships, whereby more sociable females would be able to form stronger, more numerous, more equitable, and/or more stable social relationships and ultimately, or consequently, gain reproductive benefits. In a sense then, although it might take a village to raise offspring and carefully choosing partners might be useful in this endeavor, fitness is intrinsically linked to an individual. Linking grooming rate, an individual measure of sociality, to the production of an offspring therefore allows us to investigate directly whether more social individuals have a reproductive advantage.

Crested macaques *Macaca nigra* are interesting for this line of inquiry because both males and females are socially tolerant and form extended social networks (Duboscq et al., 2013; Tyrrell et al., 2020); they also both face competition for resources, potentially greatly impacting their reproduction. For instance, in North Sulawesi where crested macaques are endemic, the climate is rather mild, food is relatively abundant and there is no felid predator (but reticulated pythons, *Malayopython reticulatus*, are abundant and a known predator of crested macaques) (Joly et al., this issue; Kinnaird & O'Brien, 2005; Micheletta et al., 2012; O'Brien & Kinnaird, 1997). Nevertheless, in terms of social behavior, males fight fiercely, presumably over access to mates, and intergroup encounters are frequent, often aggressive and involve both

adult females and males (Martínez-Íñigo et al., 2021, this issue; Marty et al., 2017). In the Tangkoko population, ecological factors linked to resource competition impacted fetal or infant survival probability analyzed over a period of five years: notably, survival probabilities increased with the number of adult females in the group (indicative of higher within-group competition but also higher chance of success in intergroup encounter), with rainfall (indicative of high food availability), and with rate of intergroup encounters (indicative of high home range quality) (Kerhoas et al., 2014). We do not know whether female social bonds are associated with improved fetal or infant survival under these conditions or indeed, whether any measure of sociality relates to any measure of fitness. As in most macaques, crested macaque groups are female-centered, females remain in their natal group their whole lives and form stable dominance hierarchies (Duboscq et al., 2013; Thierry et al., 2004). Wild female crested macaques in Tangkoko distribute their grooming fairly equitably (Duboscq et al. 2013), and form differentiated social bonds that seem to be of average strength, of moderate endurance and relatively balanced (Duboscq et al., 2017). Stronger bonds seem to be more equitable but less predictable than weaker bonds. Closely ranked females, but not kin or age peers, seem to have stronger, more predictable, and more equitable bonds than others (Duboscq et al., 2017). Furthermore, female crested macaques in Tangkoko responded more strongly to playbacks of alarm calls from strong affiliates compared to less strong affiliates (Micheletta et al., 2012). However, bond characteristics had little impact on the patterns of several other fitness-related behaviors, namely coalitionary support, feeding competition or reduced aggression (Duboscq et al., 2014, 2017), raising questions about the actual function(s) of social bonds in this population or species.

We thus investigated the relationship between a fundamental measure of sociality and of reproductive success over 15 years in wild female crested macaques living in the Tangkoko Reserve in North Sulawesi, Indonesia. More specifically, we tested the relationship between female grooming rate and offspring production, adjusting for female dominance rank, age, reproductive history, adult female group size, and rainfall. Under the hypothesis that sociality is positively related to reproductive success, we

predicted that, all else being equal, females with high grooming rates would be more likely to give birth than females with low grooming rates.

Methods

Ethical note

This research adheres to all legal requirements and guidelines of the German, French, British and Indonesian governments and institutions and to the “ASAB/ABS Guidelines for the treatment of animals in behavioral research and teaching” (ASAB/ASB, 2012). We did not trap or tag the animals. This is a wild population of Critically Endangered animals. We habituated the study animals to human observers before the start of data collection and could identify individuals based on physical characteristics alone (body size & shape, fur color, scars, scrotum, nipples or the color and shape of the ano-genital area). We used binoculars to ensure accuracy in identification and data collection.

Study area, species, subjects, and data collection

We have been studying wild crested macaques (*Macaca nigra*) in the Tangkoko Reserve, North Sulawesi, Indonesia, continuously since 2006 – notwithstanding two interruptions, between April and August 2017 and November 2017 and March 2018 – within the Macaca Nigra Project. The Macaca Nigra Project carries out research on the biology of crested macaques while supporting conservation and education programs dedicated to protecting the Critically Endangered crested macaque and its environment (Chanvin et al., 2023 (this issue)). We regularly observe two to four groups, well-habituated to human observers. We can identify all subadult and adult monkeys (and some infants and juveniles) by their natural physical features only. Over the 15 years of the study, focal groups split several times, and due to logistical considerations, we had to choose which subgroup to continue following, either the biggest subgroup or the one ranging closest to the research area.

We used data collected from 2006 to 2020 through focal observations on 140 adult females from six groups. We considered females as adults when they gave birth for the first time to a live infant. We allocated group membership on the last day of each month. For example, when group PB split into PB1 and PB2 on the 29th of September 2013, we assigned PB as a group identity for September 2013 but PB1 for October to females ending up in group PB1 on that day.

We observed adult females individually and collected data during standard focal observation protocols, lasting between 15 min to a whole day, depending on project and observer. We collected data with handheld computers using customized spreadsheets. At the signal of a stopwatch set at regular intervals (1, 2, or 5 min depending on project and observer), we wrote down the focal female's activity (feeding, foraging, resting, socializing, grooming, moving) and, if grooming, the identity of the grooming partner. We noted agonistic interactions involving the focal female and other group members continuously and supplemented with *ad libitum* data of agonistic interactions occurring around the focal female but not involving her. We focus here on adult female-female interactions.

We chose grooming as representative of the ability and tendency to engage in the behavior at the basis of building social relationships as a fundamental building block of a female's social life and birth occurrence as the basis of reproductive success. Using grooming rate and birth occurrence have not only the advantage of representing the female's overall level of affiliative involvement and reproductive success respectively, but are also easy to compute and, more importantly, readily comparable across females, years and groups.

Reproductive data

Females cycle and give birth throughout the year without any apparent seasonality (Figure 1). We recorded every instance where an adult female gave birth to a live infant. We defined a live birth as a female who gave birth to, carried, and cared for a live and healthy newborn. We then scored whether a female had

a live birth in a given calendar year (binary: yes or no). We also recorded whether a miscarriage occurred or whether the newborn infant survived their first year (to the extent that we could recognize the infants up to one year old). We defined a miscarriage as several situations: either the fetus was seen being expelled dead from the birth canal or found carried by the female dead and obviously in a fetal stage, or a female that had stopped cycling for at least two months (cycling is visible through showing red ano-genital swelling every month) unexpectedly resumed cycling (and sometimes, showed blood loss on the vulva/through the vagina) (Kerhoas et al., 2014).

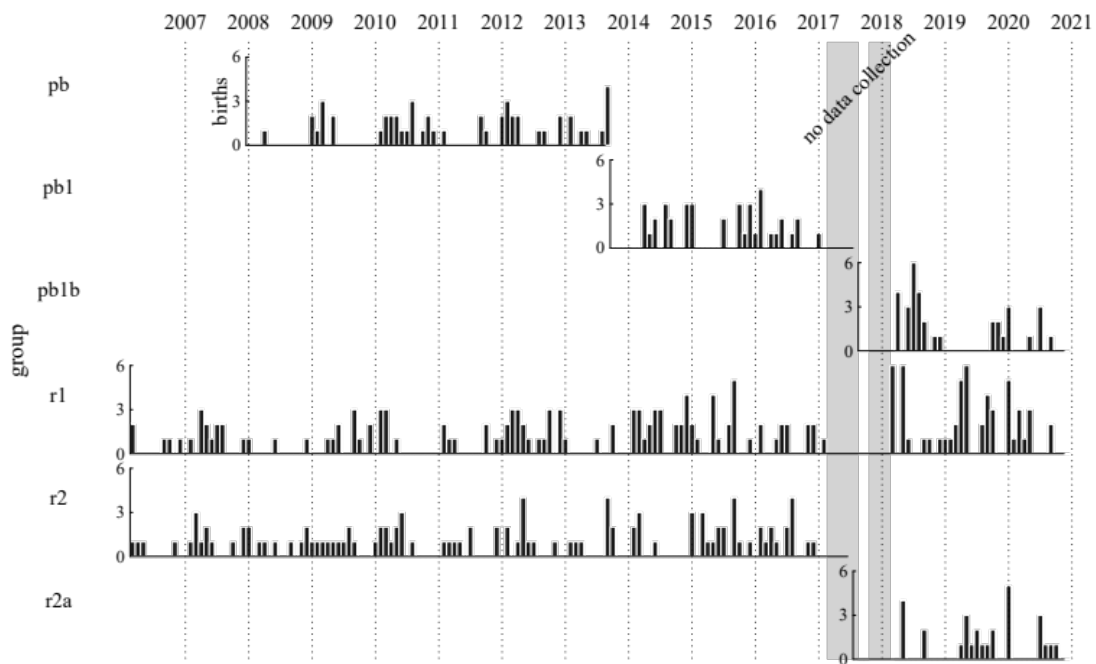


Figure 1. Monthly number of births across six groups of crested macaques, in Tangkoko, Indonesia, between 2006 and 2020. The vertical dashed lines represent the data for January of the respective year. The areas shaded in gray indicate two periods in which we did not collect behavioral data.

Sociality data

We quantified social behavioral tendency using grooming from point samples (see Figure S1 for raw data summary). For each female and calendar year, we counted the total number of point samples we

recorded for that female and all point samples in which the female groomed or received grooming by another adult female. Since the number of total point samples, i.e., observation effort, varied substantially between females and within females across multiple observation years, we first modeled grooming proportions with a binomial model. The goal of this model was to obtain grooming values with an associated measure of uncertainty due to varying observation effort for each data point (i.e., female year), which then could be used as a predictor in our final models. In this grooming model, the number of grooming samples of a female in a given year were the ‘successes’, and the total number of point samples in that year for that female were the ‘number of trials’. We fit this model with an overall intercept and an observation level (female-year) random effect with the package *brms* (Bürkner, 2017), using a logit link function and the default priors provided by *brms*. From this model, we extracted the posterior distribution for each observation on the linear predictor scale. We took the mean value of each distribution as the grooming value for that observation and the standard deviation of each observation as measurement error for that observation. We used each pair of values as a predictor in the final model: the mean as grooming predictor and the standard deviation as measurement error. In this way, less observation effort, i.e., less point samples, led to wider posterior distributions, i.e., higher measurement error (see Figure S2 and S3). For example, if we had 800 point samples for a female of which 100 were grooming samples, this led to the same grooming value as if we had 80 point samples with 10 grooming samples, i.e., 0.125. Importantly, we can be much more certain that this value reflects the true value for the former case compared to the latter because it is based on more observation effort. This uncertainty is reflected in the standard deviations of the two posterior distributions, which is larger in the latter compared to the former. For simplicity, we refer to this estimated variable as ‘grooming rate’.

Arguably, the presence of a dependent infant might affect the mother’s grooming activity (e.g., Frank & Silk, 2009; Jiang et al., 2019; Matsumura, 1997; Tiddi et al., 2010; Yu et al., 2013). If this pattern applied to our study system, it might compromise our analytic approach which is based on calendar years.

Therefore, we fit an additional model to assess how much a birth changes grooming rates of mothers. For this, we selected data collected either within the 155 days prior to giving birth or during the 155 days following a birth. We chose 155 days because it corresponds approximately to weaning age (Kerhoas et al., 2014). If an infant died before that cut-off, we only considered the post-birth data up to the infant's disappearance. We then compared grooming rates before and after a birth occurred. Specifically, we modeled the proportion of grooming in all point samples during these 155-day periods using a binomial error structure. As sole predictor of interest we included the type of period (binary: pre- or post-birth). We also fitted random intercepts for female identity and group, and uncorrelated random slopes for period type in both factors. The results of this model and the corresponding data are visualized in Figure S4 and indicate that there was no meaningful overall difference when comparing females' grooming behavior before and after giving birth. While the posterior means differ slightly with females grooming 3.9% of their time after birth compared to 3.7% before birth, this difference appears negligible. We conclude from this analysis that births per se did not modulate grooming behavior in an obvious way and that it is therefore justified to use yearly time windows to analyze the relationship between the probability of giving birth and grooming.

Control variables: individual and ecological data

As a measure of dominance, we computed Elo-ratings for each female for each year in each group at the end of the calendar year from the temporal sequences of all winner-loser interactions, displacements, and aggressions (threats, hits, and bites) (Duboscq et al., 2013; see Albers & de Vries, 2001; Neumann et al., 2011 for details on Elo-rating).

Because we did not know the exact age for the majority of females, we assessed to which broad age category a female belonged to (young, middle-aged, and old). This was based on females' reproductive history (e.g., number of dependent infants, age at first live birth) known since 2006, nipple shape (e.g., short or long) indicative of nursing history, the presence of physical injuries and general appearance (both linked

to age rather than rank due to mild level of aggression between females in this species) (Duboscq et al., 2017).

We read daily rainfall (in mm) from a rain gauge placed in the middle of the open courtyard of the field station and emptied every early morning. We included mean daily rainfall per year in our analyses as a proxy for food availability and abundance that year, especially figs, one of macaques' preferred food (Kinnaird and O'Brien, 2005).

As a measure of the degree of competition females may face within their group, be it ecological or social, we included mean yearly adult female group size, calculated from a matrix of monthly female co-presence in the group (a female was present / was not present that month).

Statistical analyses

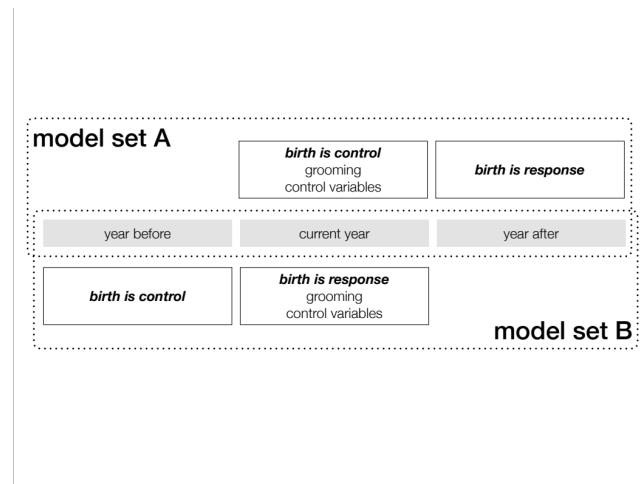


Figure 2. Schematic representation of our analytical approach for the study on crested macaques, in Tangkoko, Indonesia, between 2006 and 2020. In model set A, we modeled the probability that females gave birth in the year following our assessment of their grooming in the current year, including the occurrence of a birth in the current year as a control variable. In model set B, we modeled the probability that females gave birth in the same year as the assessment of their grooming. In this model set we included the occurrence of a birth in the year before as a control variable.

We fit two model sets that differed in the temporal offset between grooming behavior and births (Figure 2). In model set A, we modeled the probability of giving birth in the year after we assessed grooming and other control variables, to test the prediction that current social integration is related to future reproductive success. In these models, we also added whether females gave birth in the same year as the assessment of the predictor variables took place to control for the fact that females give birth every 18 months on average, and so are less likely to give birth again one year if they gave birth the year before, compared to females who did not give birth one year. In model set B, we shifted the two birth variables such that we modeled the birth probability during the same year as the assessment of grooming, while controlling for the occurrence of births in the year preceding the current year. In this way, we tested the prediction that current social integration and current reproductive success are linked.

In each model set, we fit four models to explain variation in whether a female gave birth in the year after we assessed her grooming rate (model set A) or in the same year as we assessed her grooming (model set B). In the following, we describe the structure of the models in set A (the models in set B only differed with respect to shifting the two yearly birth variables and are not explicitly described here, see Figure 2). We fit all four models to the same data set but let the models differ in their structural complexity (see Table S1 for details of model structures). We first describe the most complex model (*model A1*), before outlining simplifications.

The main predictor variable was grooming rate as estimated above with associated measurement errors. In addition, we also adjusted for several variables that we thought to be relevant for explaining birth occurrence. On the female level, we included the female's dominance rank (continuous: Elo-rating at the end of the year), the female's age (categorical: young, middle, old) and whether the female gave birth in the current year (binary: yes or no). On the study group level, we included yearly mean group size (continuous: mean of number of adult females present each month). On the population level, we included yearly mean daily rainfall (continuous).

In addition, we fit three two-way interactions. First, we included the interaction between grooming and rank. Lower-ranking females may experience more challenges (aggression, feeding competition) more frequently, potentially compromising their reproductive success (Pusey, 2012). Having a good grooming network might be more important for them compared to higher-ranking females. Therefore, we thought it plausible that the effect of sociality on reproduction depends on a female's Elo-rating, this relationship being more pronounced for lower-ranking females than higher-ranking females.

Second, we included the interaction between grooming and female group size. Adult female group size can be considered a proxy for competition. When female group size is bigger, competition for food and social partners might be higher therefore the impact of sociality on fitness might be more pronounced.

Third, we included the interaction between grooming and rainfall. Rainfall is positively related to food availability in Sulawesi (Joly et al., this issue; Kinnaird and O'Brien, 2005), thus the impact of sociality on reproductive success might be less pronounced when rainfall is high because females might find enough energy to sustain their biological needs and might need less social support (Kerhoas et al., 2014).

We specified random effects in the following way. For female ID, we fit uncorrelated random slopes for grooming, rank, group size and rain to account for between-female variation in the relationships between these predictors and the response. Ideally, we would have also fit random slopes for age, the occurrence of a birth in the current year and the interaction terms. However, these random slopes were unidentifiable, and therefore, we could not fit them. For example, to identify a random slope for a binary predictor (like birth occurrence in the current year), an absolute minimum of two observations are required for each of the two levels for the majority of subjects. In the case of birth occurrence in the current year, we only had 38 females (out of 107) for which this was the case.

For the variable study group, we fit uncorrelated random slopes for grooming, rank, group size, rainfall, female age, and birth occurrence in the current year, and in addition the interactions between grooming and rank, grooming and group size, and grooming and rainfall.

Finally, for the variable study year, we fit uncorrelated random slopes for grooming, rank, group size, female age, and birth occurrence in the current year, but not rainfall. Here we fit the two-way interactions between grooming and rank, and grooming and group size.

Our second model represented a simplified version of model A1 where we removed the interaction terms with grooming from the random effects structure (*model A2*). Our third model simplified this even further by also removing the interaction terms with grooming from the fixed effects, thus leaving only the main effect of grooming rate (*model A3*). In our final model, we also removed the main effect of grooming. This final model therefore can be considered as our null model.

We fit models using a binomial error structure with the brms package (Bürkner, 2017). Prior to fitting, we standardized all numeric predictors to mean = 0 and SD = 1. We used Leave-One-Out Cross-Validation for model ranking (Vehtari et al., 2017). Data and code to reproduce the results presented in this study are available in Neumann (2023).

Results

From 2006 to 2020, in total, we collected data on 140 adult females present in their group for a median of 52 months (range = 6 - 187). In these 15 years, we recorded 440 live infant births (Figure 1), 46 miscarriages and 52 disappearances (unsuccessful reproductive events) of infants before reaching one year of age. Excluding intervals when groups split or when females had an unsuccessful reproductive event, females gave birth on average every 19 months (median = 592 days, N = 287 births, minimum = 174 days, maximum = 1730 days). Young, mid-aged and old females accounted for 191 (43%), 202 (46%) and 47 (11%) live births and for 49 (50%), 37 (38%) and 12 (12%) unsuccessful reproductive events respectively. Lower-ranking females (i.e., those with an Elo-rating below the mean of their group for a given year) accounted for 199 live births out of 373 (53%) and 44 unsuccessful reproductive events out of 77 (57%)

(the number of live births and unsuccessful reproductive events considered here are lower than the total because there were sometimes little to no behavioral data collected on adult females).

Overall, the analysis included 107 females, representing 457 female-years, for which we had both social and reproductive data in model set A (models in set B comprised 99 females, representing 392 female-years). In model set A, where we modeled the probability of giving birth in the subsequent year, the null model, i.e., without grooming included as fixed effect, had by far the highest weight among the models we fit (model weight = 0.97), which indicates that grooming rates with other females did not play a major overall role in explaining the variation in whether females gave birth or not in the subsequent year. All parameter estimates in this model were associated with large uncertainties (Figure 3). We found a substantially lower model weight for the simplest model that contained grooming as fixed effect (model A3, weight = 0.03), while the more complex models carried almost no weight (models A1 and A2, both weights = 0.00). The results for model set B were qualitatively similar, including the highest model weight for the null model (see Tables S2-S9 for detailed model results of all eight models and Figures S5-S6 for equivalent figures for model set B as Figures 3-4).

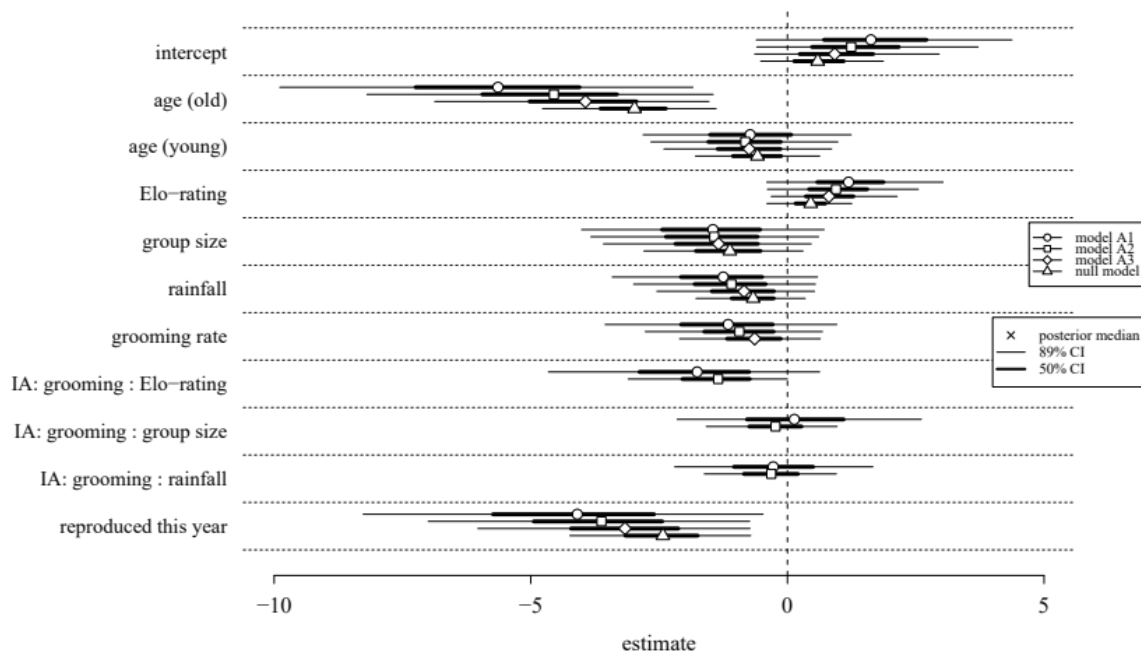


Figure 3. Summary of estimates for the fixed effects of the four fit models in model set A, in crested macaques, in Tangkoko, Indonesia, between 2006 and 2020. Models are ordered by decreasing complexity within each predictor variable (matched through different symbols). The upper-most model is the most complex model (A1), while the bottom-most model is the null model. Symbols represent posterior medians, thick lines correspond to 50% credible intervals and thin lines to 89% credible intervals.

In addition to this overall result, we explored our models further. This revealed variation in the estimated relationship between grooming and birth probability across females, study groups and years. We illustrate this with model A3, i.e., the simplest model that included grooming as fixed effect (Figure 4). At the female level, variation in the grooming slope was greatest, ranging from strongly negative (e.g., individual *md*), over slightly negative (e.g., individual *is*) to strongly positive (e.g., individual *cp*). Variation was smaller at the level of study group and year. While for study group all slopes were similarly negative, slopes for year ranged from strongly to only slightly negative. However, all these estimates were associated with very large uncertainties.

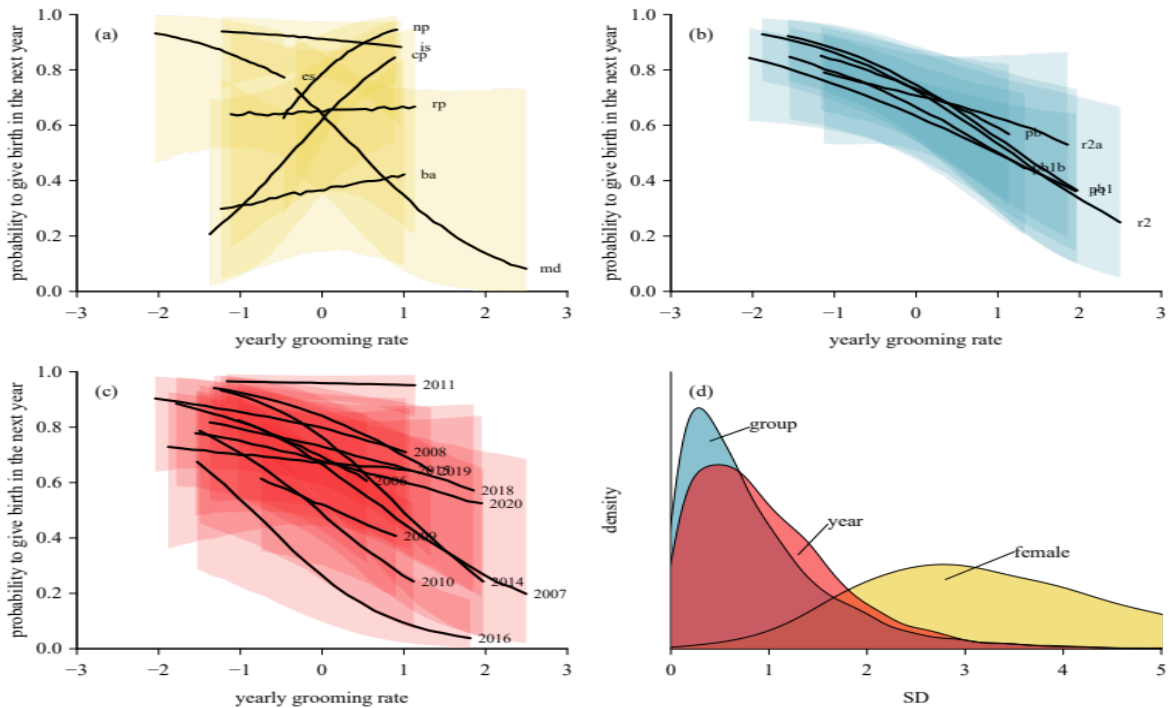


Figure 4: Variation in the relationship between grooming and birth probability across all modeled measurement levels (female, study group, year) in crested macaques, in Tangkoko, Indonesia between 2006 and 2020 (the visualized model received almost no support compared to the null model). (a) Predicted birth probability for females alongside their 50% credible interval for a subset of seven females. For the sake of display, we considered all females as middle aged, having not reproduced in the current year and average in all other covariates. (b) Predicted birth probabilities for each study group. (c) Predicted birth probabilities for each study year. (d) Posterior distributions for the estimated standard deviations of the random slopes for grooming separated by measurement level.

Discussion

In this study we found no overall evidence for grooming being associated with birth probability. The results of the models suggested, however, the presence of a substantial amount of variation in the relationship between grooming and reproduction on different levels: individual females, years, and groups.

Since the seminal studies conducted by Silk and colleagues on chacma baboons (Cheney et al., 2016; Silk et al., 2006a, 2006b, 2009, 2010), many other non-human primate studies have shown that being highly social, that is, having above-average strong affiliative bonds, results in having better health, greater well-being, and higher fitness (Snyder-Mackler et al., 2020; Silk, 2007a; Silk, 2007b). These are general patterns, but the picture is, in fact, more nuanced. In some animal populations, the strength of social bonds between individuals has no link - or a negative one - to reproduction; rather, how equitable or durable social bonds are is important (e.g., Thompson & Cords, 2018; Wey et al., 2013; Barocas et al., 2011). In some other cases, having many weak or average bonds trumps having strong but fewer bonds (McFarland et al., 2017). Studies integrating a direct individual (instead of dyadic) measure of sociality, like we did, also report contrasting findings. For instance, in female rhesus macaques, grooming rate was overall not related to yearly adult survival (Ellis et al., 2019). However, in chacma baboons, infant survival to one year was linked to grooming received by the mother but not grooming given by the mother (Silk et al., 2003), which might indicate that survival of the infant to one year is linked to the care and attention their mothers (and themselves) might get. Our long-term study of wild female crested macaques contributes to this body of research by highlighting that in absence of any systematic overall relationship between grooming and reproduction, substantial idiosyncratic variation in this relationship within and between females, years and groups occurred. This may have to do with constraints imposed on grooming, on reproduction or on both, which we discuss in turn here.

In our study, we investigated grooming rate, an individual component of sociality. Grooming is the key component of social bonding (at least in primates but in other mammals and birds too) (Dunbar, 1991). Grooming, as any daily activity, is under constraints of time and of partner availability (Dunbar, 1991; Lehmann et al., 2007). The social time budget of an individual is indeed limited given the importance of feeding and reproducing (Dunbar et al., 2009). Partner availability or choice itself might be dependent on social status (high-ranking versus low-ranking, with young infants versus without) or ecological conditions

(high predation, harsh environment), meaning individuals might have more or less freedom to interact or might be more or less attractive as social partners or might have to more or less submit to life contingencies (Barrett & Henzi, 2001). These social and ecological contingencies in turn influence the capacity of individuals to form bonds, hence bond characteristics such as strength, number, equitability, and stability. That being said, how this relates to explaining the relationship between grooming and birth is complex. The link between sociality and fitness is often related to predation risk, such as a more social individual might occupy more central position and be less vulnerable or in better health or have many more defense partners. It could also be related to wounding risk such as a more social individual might experience less dangerous attacks from others. It could be related to access to food and allies, such as a more social individual might have more cooperation partners or less worthy competition (Snyder-Mackler et al., 2020; Thompson, 2019; Ostner and Schülke, 2018; Silk, 2007b). These benefits as well as the tendency to be social are also all linked to individual characteristics such as age, rank, or matriline membership. A young or high-ranking individual or member of a larger matriline therefore might also experience lower predation risk and wounding risk and greater access to food and allies. These individual effects alone might explain why some females showed a negative relationship between sociality and fitness while others show a positive or a flat one, like in our study.

In our study, births occurred throughout the year without any apparent seasonality. The models we ran did not test specifically the effect of particular individual (e.g., dominance rank, age) or ecological (e.g., food abundance proxy) variables on reproduction so we are limited in the conclusions we can draw regarding these variables being able to explain the probability of giving birth. We recorded fewer live births from older females than from mid-aged or young females, but this is hardly surprising because old age is associated with deteriorating physical condition, and, obviously, young and mid-aged females live longer so have more births recorded, or it may be an artifact of observation effort. Dominance rank, mostly stable and maternally inherited in female macaques (Chapais, 1992), did not seem to be related to reproduction

either, so we would have difficulties relating it to higher access to resources translating into higher reproductive success, but this also remains to be investigated properly. The ecological environment itself did not show strong seasonality overall: temperatures were quite stable within the year and between years, rainfall was seasonal within a year but stable between years (Joly et al., this issue), and, analyses of data between 2012 and 2020 showed that there was no obvious seasonal flowering or fruiting pattern with tree species showing great inter- and intraspecific variation in their fruiting cycles (Joly et al., this issue). Moreover, in Tangkoko, crested macaques' preferred food, figs, are present year-round too (Joly et al., this issue; Kinnaird and O'Brien, 2005) and are found in large trees that can accommodate an entire group most of the time (Kinnaird and O'Brien, 2005; O'Brien and Kinnaird, 1997). This suggests that the ecological environment can sustain reproduction year-round. As such, within a group, competition for food seems quite low, access to food does not seem very constrained and would thus not be expected to strongly impact the reproduction of females (or males) in Tangkoko. These patterns might also explain the relatively low variation in the relationship between grooming and reproduction across years and groups compared to the individual level.

Nevertheless, inter-group encounters are frequent, and presumably, inter-group competition is high, often aggressive and linked to both female resource and male mate access defense (Martínez-Íñigo et al., 2021, this issue). A previous study also found that rainfall (linked to higher fruit availability within the next three months) and adult female group size (linked to higher food competition but also higher cooperation within- and between-group settings), but not the rate of intergroup encounters per se most impacted infant survival to one year (Kerhoas et al., 2014). Although the focus of our study was on grooming, our results seem to mirror these findings about the potential importance of ecological factors for the reproduction of female crested macaques at Tangkoko. Females were more likely to give birth while living in smaller groups and in years with more rainfall, although the uncertainty around these estimates was also very large. We might thus speculate that the link between sociality and reproduction is ecological in nature, i.e., ecological

conditions affect both sociality and reproduction but independently: according to environmental conditions in that year for that group, some females reproduced well, some others less so, and some females exchanged more grooming than others, but with little to no link between the two. There is contradictory evidence in other primates that grooming is more or less affected by variations in ambient temperature or relative humidity (Ventura et al. 2004; Hill 2005) or by differences in habitat and feeding conditions (Hanya et al. 2008; Henzi et al. 2009). But, as much as variation in reproductive patterns, whether climate or food has a strong impact on grooming - and hence relationships - remains to be properly investigated as well.

Altogether, in our study, we are unable to pinpoint by which exact mechanisms grooming and birth would be linked. It is notably difficult to predict what motivates social relationships between wild female crested macques in Tangkoko in the first place (Duboscq et al., 2014, 2017). Social bonds when quantified through the calculation of a dyadic sociality index, are moderately differentiated, moderately stable and moderately enduring (Duboscq et al. 2017). Bond strength, symmetry and equitability are not influenced by age difference nor by kinship but mostly by differences in dominance rank, the smaller the rank difference the stronger, more equitable, more enduring the social bond (Duboscq et al., 2017). Although having strong bonds potentially enhances predator defense, indicating their possible adaptive value in this situation (although kinship between dyads was unknown so firmer conclusions are awaiting) (Micheletta et al., 2012), in contrast to other social mammal species (Silk, 2007b), the benefits of forming strong social bonds in other fitness-related behavior, such as coalitionary support, feeding in proximity, or reduced aggression, are either absent or limited (Duboscq et al., 2017). Given how diverse and dense female grooming networks are, all females seem to produce great efforts at being social (i.e., grooming is quite equitably distributed among adult females, Duboscq et al., 2013). These diverse dense networks do not mean there is no individual variation, only that this variation does not percolate into meaningful downstream effects and that these great degrees of freedom in many aspects of the females' social life do not seem to translate into fitness benefits (nor costs; see also Duboscq et al., 2014, 2017). That being said,

we stayed here at the individual level and can therefore not conclude that dyadic relationships are not related to reproductive success.

We highlight some methodological considerations. First, our models allowed for variation in the relationship between our measures of sociality and fitness across females, groups, and years. The general absence of evidence for an important role of grooming notwithstanding, our results suggested that any relationship between grooming and reproduction can vary on multiple levels, most notably across females and to a lesser degree across years and groups. Previous studies, including ours, appear to have overlooked this potentially important aspect either by pooling data for individuals over time or not allowing effects to vary across time periods or groups (e.g., Silk et al., 2003, Ellis et al., 2019, Archie et al., 2014, Duboscq et al., 2017). Second, we considered our measurement of yearly grooming rate as uncertain in itself, i.e., we modeled grooming rate in its own right and carried over the uncertainty associated with it into our final models. The primary reason for doing so was highly variable observation effort over females and years. It seems intuitive, especially with low observation effort, that measuring behavior rates as point estimates will be noisy. It therefore seems worthwhile for future studies to take these idiosyncrasies into account. Both fitness and sociality have many facets and have direct and indirect components. Mechanisms underlying the relationship between the two may be different according to which components are taken into consideration. The adaptive function of the individual versus dyadic components of sociality might be different, e.g., a high individual behavioral tendency might allow them to easily build bonds whereas their dyadic synergy with others might allow them to maintain those bonds in predictable and durable ways. Therefore, we think we should embrace the variation found herein in the absence/presence or strength of the social component(s) of fitness. Although studies might not be directly comparable because they use different proxies of sociality and fitness, they are all part of the same discussion about the costs and benefits of being social.

In sum, our study suggested that grooming did not play an important role overall in explaining annual birth probabilities. At the same time, all our model estimates were very uncertain and varied substantially across females, groups and over years. This variation and the uncertainty surrounding the relationship investigated is rarely reported in the literature, but for now constitutes our main finding for female crested macaques in Tangkoko. We suggest further investigations in this area to dig deeper into the value and intricacies of social bonds in primates and other social species. We do not claim that social relationships between wild female crested macaques in Tangkoko are not valuable, only that it is not yet clear which components of sociality are valuable and what fitness benefits (e.g., survival instead of reproduction), if any, sociality might be linked to.

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Supplements to Investigating the relationship between sociality
and reproductive success in wild female crested macaques, *Macaca*
nigra

Julie Duboscq^{1,2,3}, Jérôme Micheletta^{1,4}, Dyah Perwitasari-Farajallah^{1,5,6}, Antje
Engelhardt^{1,7}, and Christof Neumann^{1,8,9}

¹Macaca Nigra Project, Tangkoko Reserve, Bitung, Indonesia

²Eco-Anthropologie (EA), UMR7206, CNRS-MNHN-Université Paris Cité, Paris, France

³Department of Behavioral Ecology, University of Göttingen, Göttingen, Germany

⁴Department of Psychology, Centre for Comparative and Evolutionary Psychology, University of
Portsmouth, Portsmouth, UK

⁵Primate Research Center (PSSP), IPB University, Bogor, Indonesia

⁶Department of Biology, Faculty of Mathematics and Natural Sciences, IPB University, Bogor, Indonesia

⁷Institute of Biology, Faculty of Life Science, University of Leipzig, Leipzig, Germany

⁸Cognitive Ethology Laboratory, German Primate Center Göttingen, Germany

⁹Leibniz Science Campus Primate Cognition, Göttingen, Germany

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Table S1: Structure of fitted models. Level refers to either population level effects ('fixed effects') or random slopes (for levels female, group and year). Intercepts are not included in table for clarity. Note that 'previous reproduction' is relative to the year that we used in the response variable. yes = term included in model, no = term not included, - = not identifiable.

| term | level | model 1 | model 2 | model 3 | null |
|---|--------|---------|---------|---------|------|
| grooming | fixed | yes | yes | yes | no |
| | female | yes | yes | yes | yes |
| | group | yes | yes | yes | yes |
| | year | yes | yes | yes | yes |
| Elo-rating | fixed | yes | yes | yes | yes |
| | female | yes | yes | yes | yes |
| | group | yes | yes | yes | yes |
| | year | yes | yes | yes | yes |
| age | fixed | yes | yes | yes | yes |
| | female | - | - | - | - |
| | group | yes | yes | yes | yes |
| | year | yes | yes | yes | yes |
| reproduced this year ¹ | fixed | yes | yes | yes | yes |
| | female | - | - | - | - |
| | group | yes | yes | yes | yes |
| | year | yes | yes | yes | yes |
| reproduced the year before ² | fixed | yes | yes | yes | yes |
| | female | - | - | - | - |
| | group | yes | yes | yes | yes |
| | year | yes | yes | yes | yes |
| group size | fixed | yes | yes | yes | yes |
| | female | yes | yes | yes | yes |
| | group | yes | yes | yes | yes |
| | year | yes | yes | yes | yes |
| rainfall | fixed | yes | yes | yes | yes |
| | female | yes | yes | yes | yes |
| | group | yes | yes | yes | yes |
| | year | - | - | - | - |
| grooming : Elo-rating | fixed | yes | yes | no | no |
| | female | - | - | - | - |
| | group | yes | no | no | no |
| | year | yes | no | no | no |
| grooming : group size | fixed | yes | yes | no | no |
| | female | - | - | - | - |
| | group | yes | no | no | no |
| | year | yes | no | no | no |
| grooming : rainfall | fixed | yes | yes | no | no |
| | female | - | - | - | - |
| | group | yes | no | no | no |
| | year | - | - | - | - |

¹: only applies to model set A

²: only applies to model set B

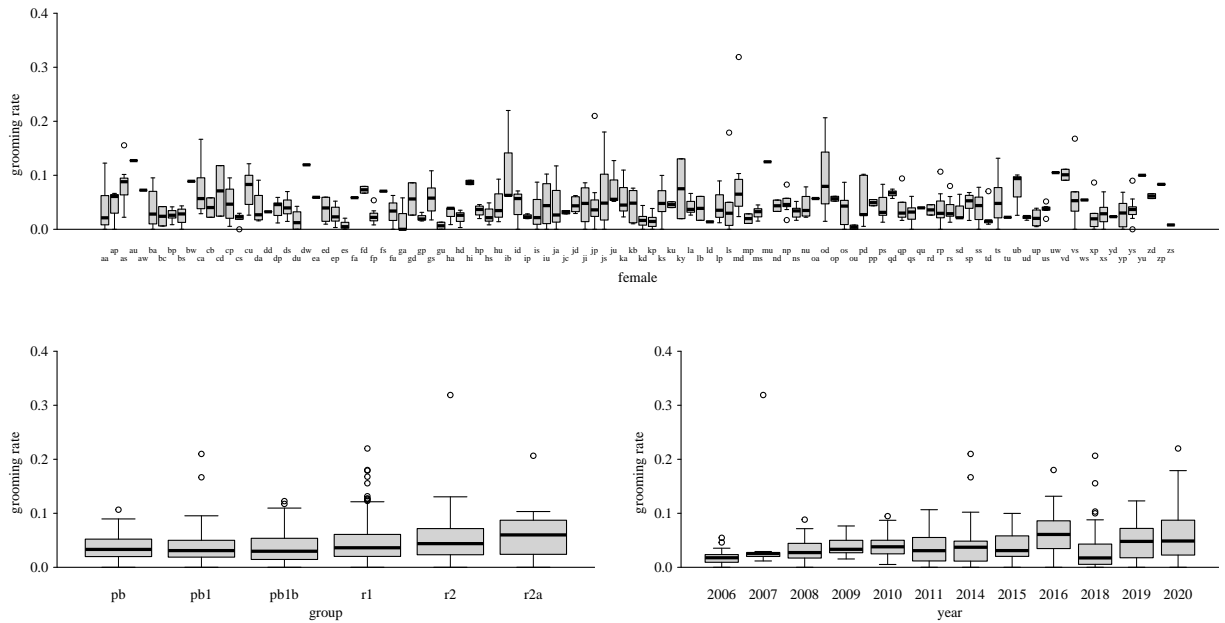


Figure S1: Variation in raw grooming data across females, groups and years. The number of individual data points per boxplot ranged between 1 and 11 for females, 12 and 241 for groups, and 13 and 78 for years. Boxplots show medians and interquartile ranges. Whiskers extend to maximally 1.5 times the interquartile range. Observations outside that range are depicted as individual circles.

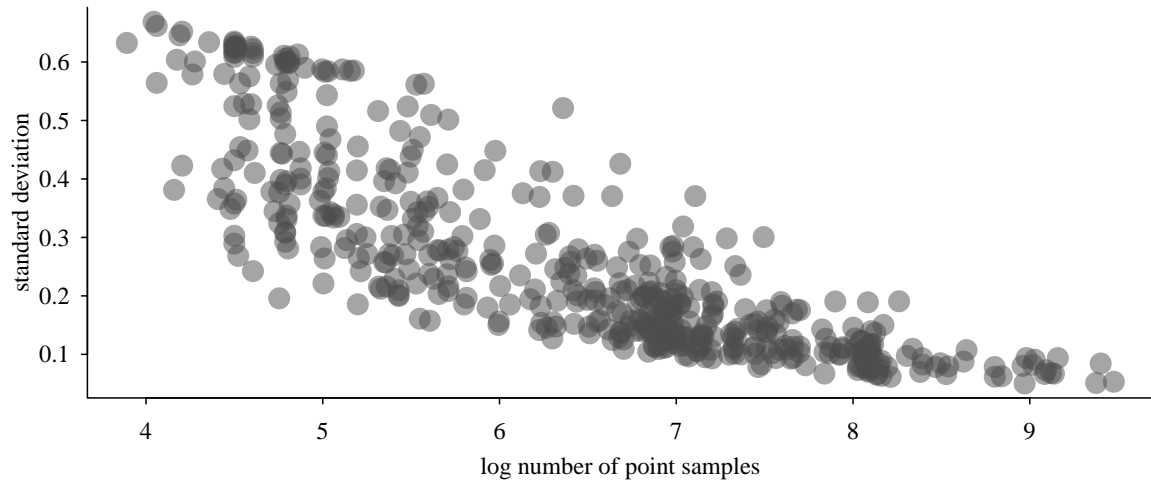


Figure S2: Observation effort as measurement error. Larger observation effort leads to smaller standard deviations in posterior distributions.

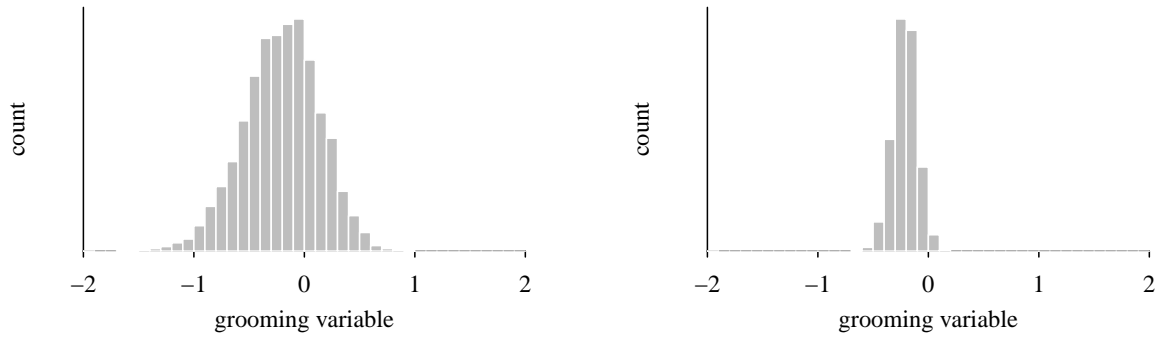


Figure S3: Two examples of grooming rates. In both cases, mean grooming values are approximately identical (-0.2). The example on the left is based on substantially less observation effort than the right (254 versus 3189 point samples). This difference in observation effort translates into different standard deviations of these two posterior distributions (0.34 versus 0.11), which we consider to reflect measurement error of grooming rate.

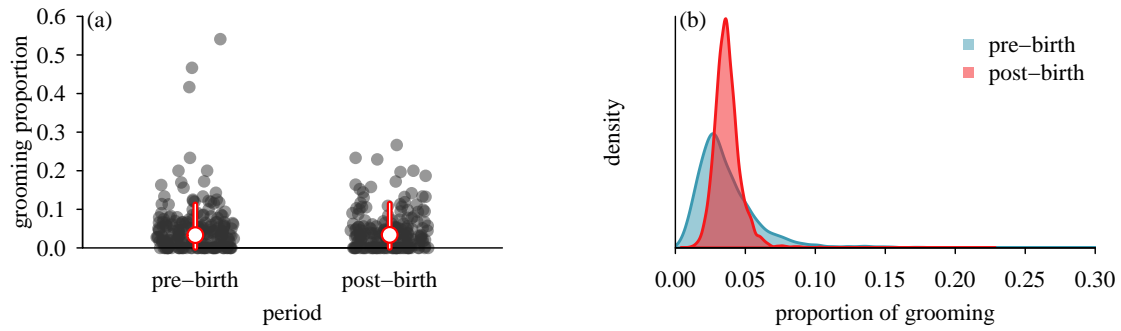


Figure S4: (a) Raw data for grooming proportions in the 155 days prior and after a female gave birth. Each circle reflects the pooled data for one period per female (186 periods prior to birth, and 203 periods after births, from 94 females). Red circles indicate medians and whiskers are 10% and 90% quantiles. (b) Posterior distributions of predicted grooming proportions for pre- and post-birth periods of 155 days. Expected grooming proportions were slightly higher during the post-birth periods (posterior mean: 0.038) compared to pre-birth periods (posterior mean: 0.037), but the two posteriors overlap to a very large extent.

Model set A: reproduction in the next year

Table S2: Full results for model A1. Provided are estimates for slopes (fixed effects) and standard deviations (random slopes for levels: female, group and year). Alongside these estimates are estimated errors and the limits of 89% credible intervals. For age the reference category was ‘middle’. Interaction terms are indicated by ‘IA’.

| source | term | estimate | est. error | lower 89% CrI | upper 89% CrI | \hat{R} |
|--------|-------------------------------------|----------|------------|---------------|---------------|-----------|
| fixed | intercept | 1.74 | 1.57 | -0.61 | 4.37 | 1.00 |
| fixed | age (old) | -5.72 | 2.55 | -9.89 | -1.84 | 1.00 |
| fixed | age (young) | -0.74 | 1.30 | -2.81 | 1.24 | 1.00 |
| fixed | reproduced this year | -4.21 | 2.45 | -8.27 | -0.48 | 1.00 |
| fixed | Elo-rating | 1.25 | 1.12 | -0.40 | 3.03 | 1.00 |
| fixed | group size | -1.53 | 1.49 | -4.01 | 0.72 | 1.00 |
| fixed | rainfall | -1.31 | 1.26 | -3.41 | 0.59 | 1.00 |
| fixed | grooming rate | -1.20 | 1.42 | -3.55 | 0.96 | 1.00 |
| fixed | IA: grooming rate : Elo-rating | -1.86 | 1.69 | -4.66 | 0.63 | 1.00 |
| fixed | IA: grooming rate : group size | 0.17 | 1.54 | -2.15 | 2.61 | 1.00 |
| fixed | IA: grooming rate : rainfall | -0.27 | 1.23 | -2.20 | 1.67 | 1.00 |
| female | intercept (SD) | 2.80 | 1.01 | 1.37 | 4.58 | 1.00 |
| female | Elo-rating (SD) | 1.47 | 1.07 | 0.14 | 3.46 | 1.00 |
| female | group size (SD) | 0.70 | 0.58 | 0.06 | 1.77 | 1.00 |
| female | rainfall (SD) | 2.76 | 1.19 | 1.05 | 4.82 | 1.00 |
| female | grooming rate (SD) | 5.49 | 2.02 | 2.68 | 8.99 | 1.00 |
| group | intercept (SD) | 1.30 | 1.08 | 0.10 | 3.25 | 1.00 |
| group | Elo-rating (SD) | 1.47 | 1.17 | 0.13 | 3.60 | 1.00 |
| group | group size (SD) | 1.75 | 1.33 | 0.17 | 4.16 | 1.00 |
| group | rainfall (SD) | 1.12 | 0.96 | 0.10 | 2.86 | 1.00 |
| group | age (old) (SD) | 2.58 | 2.29 | 0.22 | 6.76 | 1.00 |
| group | age (young) (SD) | 1.81 | 1.47 | 0.15 | 4.48 | 1.00 |
| group | reproduced this year (SD) | 2.50 | 1.76 | 0.34 | 5.59 | 1.00 |
| group | grooming rate (SD) | 1.42 | 1.18 | 0.11 | 3.61 | 1.00 |
| group | IA: grooming rate : Elo-rating (SD) | 1.78 | 1.41 | 0.15 | 4.28 | 1.00 |
| group | IA: grooming rate : group size (SD) | 1.55 | 1.32 | 0.12 | 3.97 | 1.00 |
| group | IA: grooming rate : rainfall (SD) | 1.16 | 1.03 | 0.10 | 2.98 | 1.00 |
| year | intercept (SD) | 2.49 | 1.06 | 1.09 | 4.36 | 1.00 |
| year | Elo-rating (SD) | 1.35 | 0.80 | 0.27 | 2.79 | 1.00 |
| year | group size (SD) | 2.04 | 1.12 | 0.51 | 4.04 | 1.00 |
| year | age (old) (SD) | 2.76 | 2.06 | 0.31 | 6.30 | 1.00 |
| year | age (young) (SD) | 1.59 | 1.23 | 0.14 | 3.86 | 1.00 |
| year | reproduced this year (SD) | 6.41 | 2.91 | 2.99 | 11.60 | 1.00 |
| year | grooming rate (SD) | 1.66 | 1.21 | 0.16 | 3.83 | 1.00 |
| year | IA: grooming rate : Elo-rating (SD) | 3.62 | 2.01 | 0.77 | 7.17 | 1.00 |
| year | IA: grooming rate : group size (SD) | 2.12 | 1.27 | 0.40 | 4.38 | 1.00 |

Table S3: Full results for model A2. See table S2 for details.

| source | term | estimate | est. error | lower 89% CrI | upper 89% CrI | \hat{R} |
|--------|--------------------------------|----------|------------|---------------|---------------|-----------|
| fixed | intercept | 1.37 | 1.37 | -0.60 | 3.72 | 1.00 |
| fixed | age (old) | -4.68 | 2.14 | -8.19 | -1.45 | 1.00 |
| fixed | age (young) | -0.83 | 1.16 | -2.66 | 0.98 | 1.00 |
| fixed | reproduced this year | -3.73 | 1.97 | -7.00 | -0.74 | 1.00 |
| fixed | Elo-rating | 1.01 | 0.95 | -0.39 | 2.55 | 1.00 |
| fixed | group size | -1.51 | 1.42 | -3.83 | 0.61 | 1.00 |
| fixed | rainfall | -1.14 | 1.13 | -3.00 | 0.55 | 1.00 |
| fixed | grooming rate | -0.97 | 1.11 | -2.77 | 0.68 | 1.00 |
| fixed | IA: grooming rate : Elo-rating | -1.43 | 0.99 | -3.10 | 0.00 | 1.00 |
| fixed | IA: grooming rate : group size | -0.26 | 0.81 | -1.58 | 0.97 | 1.00 |
| fixed | IA: grooming rate : rainfall | -0.32 | 0.84 | -1.62 | 0.95 | 1.00 |
| female | intercept (SD) | 2.17 | 0.85 | 0.97 | 3.63 | 1.00 |
| female | Elo-rating (SD) | 1.10 | 0.82 | 0.10 | 2.59 | 1.01 |
| female | group size (SD) | 0.61 | 0.50 | 0.05 | 1.56 | 1.00 |
| female | rainfall (SD) | 2.31 | 1.03 | 0.84 | 4.10 | 1.00 |
| female | grooming rate (SD) | 4.61 | 1.81 | 2.15 | 7.87 | 1.00 |
| group | intercept (SD) | 1.14 | 0.97 | 0.09 | 2.89 | 1.00 |
| group | Elo-rating (SD) | 1.30 | 1.07 | 0.11 | 3.23 | 1.00 |
| group | group size (SD) | 1.73 | 1.28 | 0.19 | 4.03 | 1.00 |
| group | rainfall (SD) | 0.98 | 0.86 | 0.07 | 2.61 | 1.00 |
| group | age (old) (SD) | 2.32 | 2.03 | 0.19 | 5.91 | 1.00 |
| group | age (young) (SD) | 1.77 | 1.44 | 0.16 | 4.36 | 1.00 |
| group | reproduced this year (SD) | 1.96 | 1.40 | 0.24 | 4.44 | 1.00 |
| group | grooming rate (SD) | 1.11 | 0.96 | 0.09 | 2.87 | 1.00 |
| year | intercept (SD) | 2.06 | 0.91 | 0.87 | 3.65 | 1.00 |
| year | Elo-rating (SD) | 1.19 | 0.69 | 0.26 | 2.42 | 1.00 |
| year | group size (SD) | 2.13 | 1.00 | 0.83 | 3.89 | 1.00 |
| year | age (old) (SD) | 2.44 | 1.75 | 0.25 | 5.48 | 1.00 |
| year | age (young) (SD) | 1.23 | 1.00 | 0.10 | 3.09 | 1.00 |
| year | reproduced this year (SD) | 4.98 | 2.31 | 2.28 | 8.98 | 1.00 |
| year | grooming rate (SD) | 1.32 | 1.01 | 0.13 | 3.13 | 1.00 |

Table S4: Full results for model A3. See table S2 for details.

| source | term | estimate | est. error | lower 89% CrI | upper 89% CrI | \hat{R} |
|--------|---------------------------|----------|------------|---------------|---------------|-----------|
| fixed | intercept | 1.01 | 1.14 | -0.64 | 2.96 | 1.00 |
| fixed | age (old) | -4.04 | 1.73 | -6.87 | -1.53 | 1.00 |
| fixed | age (young) | -0.75 | 1.04 | -2.41 | 0.86 | 1.00 |
| fixed | reproduced this year | -3.23 | 1.68 | -6.03 | -0.73 | 1.00 |
| fixed | Elo-rating | 0.84 | 0.80 | -0.32 | 2.14 | 1.00 |
| fixed | group size | -1.43 | 1.29 | -3.59 | 0.46 | 1.00 |
| fixed | rainfall | -0.90 | 0.98 | -2.54 | 0.53 | 1.00 |
| fixed | grooming rate | -0.67 | 0.89 | -2.10 | 0.64 | 1.00 |
| female | intercept (SD) | 1.72 | 0.71 | 0.74 | 2.95 | 1.00 |
| female | Elo-rating (SD) | 0.85 | 0.67 | 0.07 | 2.08 | 1.00 |
| female | group size (SD) | 0.51 | 0.42 | 0.04 | 1.29 | 1.00 |
| female | rainfall (SD) | 1.69 | 0.94 | 0.33 | 3.27 | 1.01 |
| female | grooming rate (SD) | 3.47 | 1.60 | 1.41 | 6.32 | 1.01 |
| group | intercept (SD) | 0.98 | 0.84 | 0.08 | 2.53 | 1.00 |
| group | Elo-rating (SD) | 1.08 | 0.89 | 0.09 | 2.73 | 1.00 |
| group | group size (SD) | 1.66 | 1.16 | 0.21 | 3.70 | 1.00 |
| group | rainfall (SD) | 0.88 | 0.77 | 0.07 | 2.29 | 1.00 |
| group | age (old) (SD) | 1.97 | 1.73 | 0.14 | 4.99 | 1.00 |
| group | age (young) (SD) | 1.60 | 1.26 | 0.15 | 3.91 | 1.00 |
| group | reproduced this year (SD) | 1.71 | 1.23 | 0.23 | 3.89 | 1.00 |
| group | grooming rate (SD) | 0.85 | 0.77 | 0.06 | 2.27 | 1.00 |
| year | intercept (SD) | 1.76 | 0.81 | 0.73 | 3.16 | 1.00 |
| year | Elo-rating (SD) | 0.85 | 0.60 | 0.12 | 1.90 | 1.00 |
| year | group size (SD) | 1.80 | 0.88 | 0.65 | 3.37 | 1.00 |
| year | age (old) (SD) | 2.00 | 1.47 | 0.21 | 4.65 | 1.00 |
| year | age (young) (SD) | 0.98 | 0.84 | 0.08 | 2.51 | 1.00 |
| year | reproduced this year (SD) | 4.06 | 1.88 | 1.83 | 7.41 | 1.00 |
| year | grooming rate (SD) | 0.98 | 0.76 | 0.10 | 2.36 | 1.00 |

Table S5: Full results of null model in model set A. See table S2 for details.

| source | term | estimate | est. error | lower 89% CrI | upper 89% CrI | \hat{R} |
|--------|---------------------------|----------|------------|---------------|---------------|-----------|
| fixed | intercept | 0.62 | 0.78 | -0.52 | 1.87 | 1.00 |
| fixed | age (old) | -3.02 | 1.09 | -4.77 | -1.39 | 1.00 |
| fixed | age (young) | -0.58 | 0.79 | -1.79 | 0.63 | 1.00 |
| fixed | reproduced this year | -2.45 | 1.13 | -4.24 | -0.72 | 1.00 |
| fixed | Elo-rating | 0.44 | 0.53 | -0.40 | 1.25 | 1.00 |
| fixed | group size | -1.17 | 0.99 | -2.80 | 0.30 | 1.00 |
| fixed | rainfall | -0.68 | 0.68 | -1.78 | 0.35 | 1.00 |
| female | intercept (SD) | 1.13 | 0.40 | 0.51 | 1.76 | 1.00 |
| female | Elo-rating (SD) | 0.60 | 0.44 | 0.05 | 1.39 | 1.00 |
| female | group size (SD) | 0.31 | 0.25 | 0.03 | 0.78 | 1.00 |
| female | rainfall (SD) | 0.84 | 0.50 | 0.13 | 1.69 | 1.00 |
| female | grooming rate (SD) | 2.81 | 3.67 | 0.19 | 7.62 | 1.00 |
| group | intercept (SD) | 0.69 | 0.62 | 0.05 | 1.81 | 1.00 |
| group | Elo-rating (SD) | 0.81 | 0.68 | 0.07 | 2.03 | 1.00 |
| group | group size (SD) | 1.32 | 0.89 | 0.20 | 2.91 | 1.00 |
| group | rainfall (SD) | 0.67 | 0.60 | 0.05 | 1.77 | 1.00 |
| group | age (old) (SD) | 1.41 | 1.21 | 0.12 | 3.54 | 1.00 |
| group | age (young) (SD) | 1.29 | 0.97 | 0.14 | 3.04 | 1.00 |
| group | reproduced this year (SD) | 1.22 | 0.84 | 0.15 | 2.72 | 1.00 |
| group | grooming rate (SD) | 2.74 | 2.93 | 0.21 | 7.56 | 1.00 |
| year | intercept (SD) | 1.12 | 0.51 | 0.42 | 1.99 | 1.00 |
| year | Elo-rating (SD) | 0.46 | 0.36 | 0.04 | 1.10 | 1.00 |
| year | group size (SD) | 1.20 | 0.58 | 0.41 | 2.20 | 1.00 |
| year | age (old) (SD) | 1.12 | 0.89 | 0.10 | 2.76 | 1.00 |
| year | age (young) (SD) | 0.62 | 0.50 | 0.05 | 1.55 | 1.00 |
| year | reproduced this year (SD) | 2.72 | 1.07 | 1.33 | 4.62 | 1.00 |
| year | grooming rate (SD) | 2.75 | 3.86 | 0.19 | 7.57 | 1.00 |

Model set B: reproduction in the current year

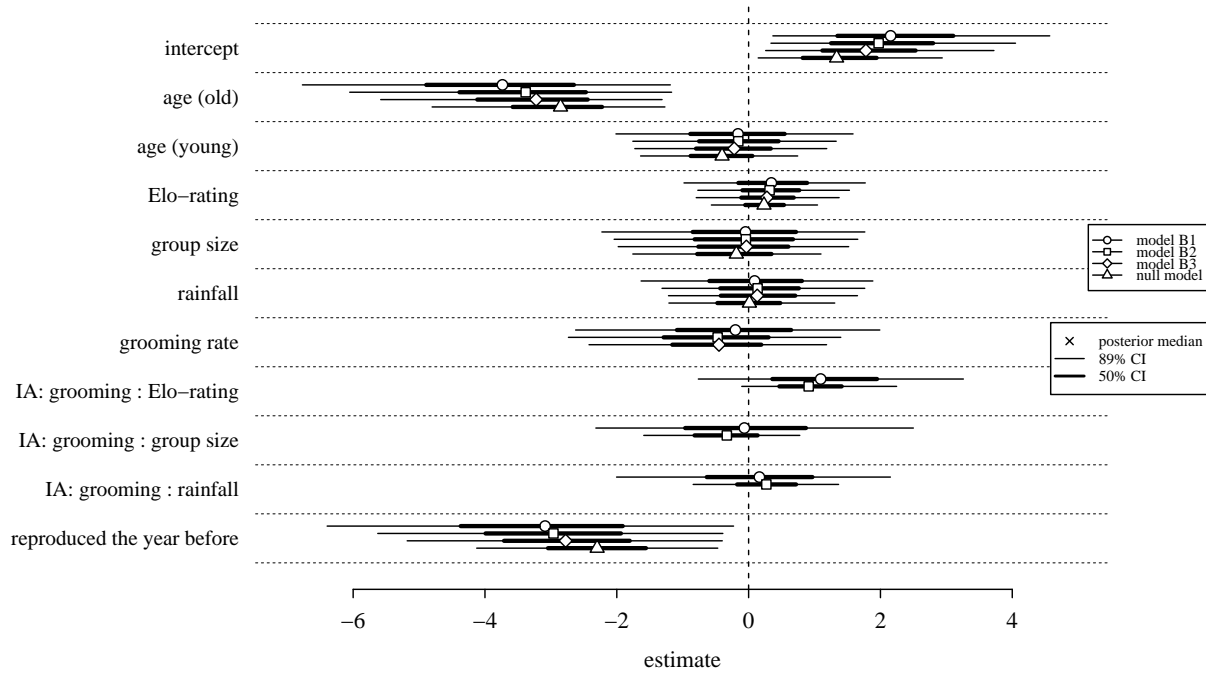


Figure S5: Summary of estimates for the fixed effects of the four fit models in model set B. Models are ordered by decreasing complexity within each predictor variable (matched through different symbols). The upper-most model is the most complex model (B1), while the bottom-most model is the null model. Symbols represent posterior medians, thick lines correspond to 50% credible intervals and thin lines to 89% credible intervals.

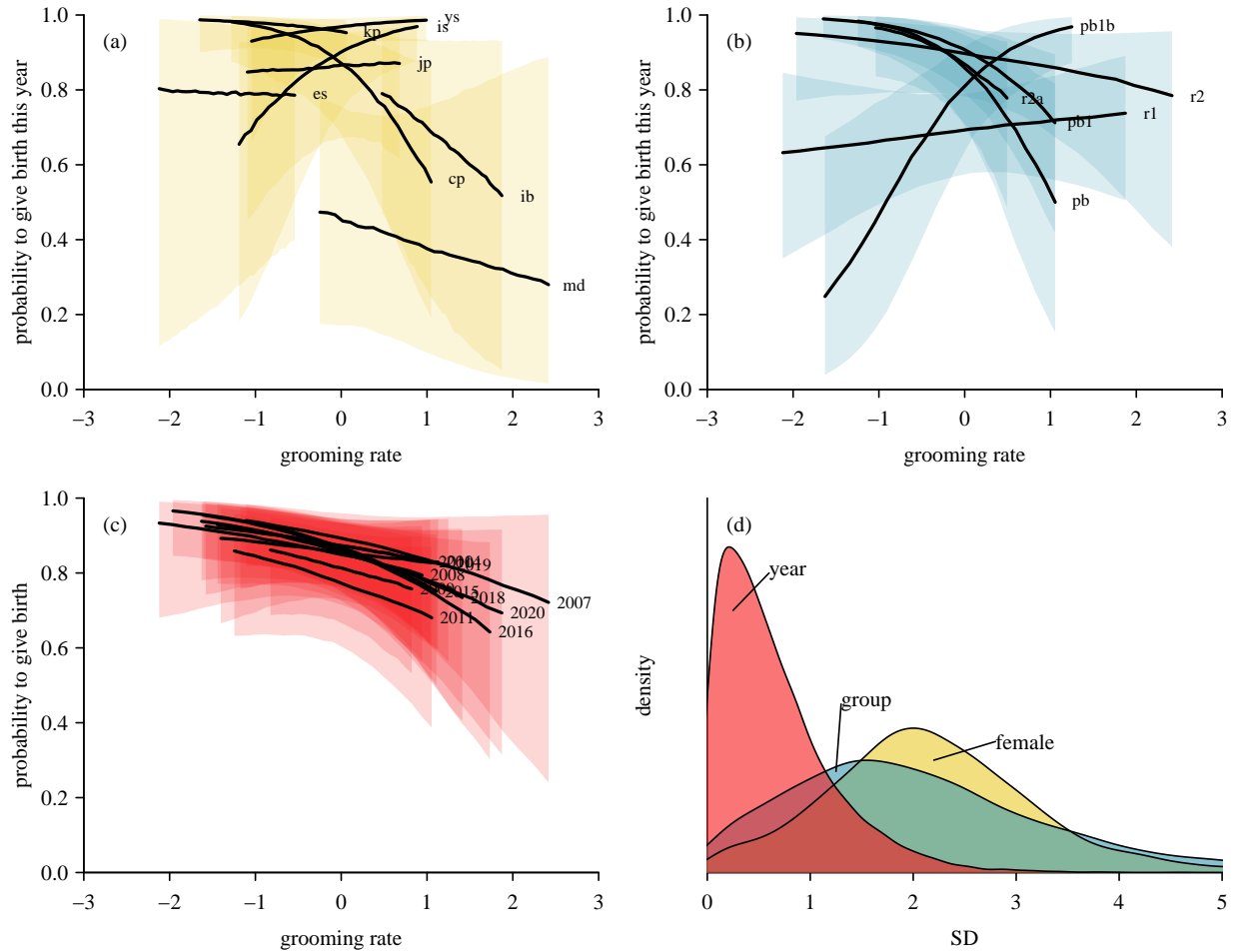


Figure S6: Variation in the relationship between grooming and birth probability across all modeled measurement levels (female, study group, year) in the four fit models in model set B. (a) This panel shows a subset of seven females. Each line represents the predicted birth probability for a female alongside its 50% credible interval. For the sake of this display, all females are considered to be of middle age, did not reproduce the year before and are average in all other covariates. (b) This panel shows the predicted birth probabilities for each study group. (c) This panel shows the predicted birth probabilities for each study year. Panel (d) shows the posterior distributions for the estimated standard deviations of the random slopes for grooming separated by measurement level. It also shows that variation is largest for individual females compared to study group and study year.

Table S6: Full results for model B1. Provided are estimates for slopes (fixed effects) and standard deviations (random slopes for levels: female, group and year). Alongside these estimates are estimated errors and the limits of 89% credible intervals. For age the reference category was ‘middle’. Interaction terms are indicated by ‘IA’.

| source | term | estimate | est. error | lower 89% CrI | upper 89% CrI | \hat{R} |
|--------|-------------------------------------|----------|------------|---------------|---------------|-----------|
| fixed | intercept | 2.28 | 1.35 | 0.37 | 4.57 | 1.00 |
| fixed | age (old) | -3.83 | 1.80 | -6.77 | -1.19 | 1.00 |
| fixed | age (young) | -0.18 | 1.15 | -2.01 | 1.58 | 1.00 |
| fixed | reproduced the year before | -3.19 | 1.97 | -6.39 | -0.23 | 1.00 |
| fixed | Elo-rating | 0.37 | 0.89 | -0.98 | 1.77 | 1.00 |
| fixed | group size | -0.11 | 1.26 | -2.23 | 1.76 | 1.00 |
| fixed | rainfall | 0.12 | 1.12 | -1.63 | 1.88 | 1.00 |
| fixed | grooming rate | -0.26 | 1.47 | -2.62 | 1.99 | 1.00 |
| fixed | IA: grooming rate : Elo-rating | 1.17 | 1.30 | -0.76 | 3.26 | 1.00 |
| fixed | IA: grooming rate : group size | -0.01 | 1.53 | -2.32 | 2.50 | 1.00 |
| fixed | IA: grooming rate : rainfall | 0.14 | 1.35 | -2.00 | 2.15 | 1.00 |
| female | intercept (SD) | 2.95 | 0.89 | 1.75 | 4.51 | 1.00 |
| female | Elo-rating (SD) | 0.83 | 0.69 | 0.07 | 2.14 | 1.00 |
| female | group size (SD) | 0.65 | 0.54 | 0.05 | 1.64 | 1.00 |
| female | rainfall (SD) | 1.30 | 0.80 | 0.17 | 2.69 | 1.00 |
| female | grooming rate (SD) | 3.96 | 1.65 | 1.81 | 6.78 | 1.00 |
| group | intercept (SD) | 1.54 | 1.09 | 0.17 | 3.47 | 1.00 |
| group | Elo-rating (SD) | 1.28 | 1.03 | 0.11 | 3.12 | 1.00 |
| group | group size (SD) | 1.63 | 1.24 | 0.17 | 3.89 | 1.00 |
| group | rainfall (SD) | 1.73 | 1.12 | 0.33 | 3.72 | 1.00 |
| group | age (old) (SD) | 2.12 | 1.79 | 0.19 | 5.31 | 1.00 |
| group | age (young) (SD) | 1.25 | 1.05 | 0.10 | 3.23 | 1.00 |
| group | reproduced the year before (SD) | 2.71 | 1.51 | 0.71 | 5.31 | 1.00 |
| group | grooming rate (SD) | 2.07 | 1.66 | 0.19 | 5.08 | 1.00 |
| group | IA: grooming rate : Elo-rating (SD) | 1.59 | 1.37 | 0.13 | 4.13 | 1.00 |
| group | IA: grooming rate : group size (SD) | 2.33 | 1.98 | 0.20 | 5.82 | 1.00 |
| group | IA: grooming rate : rainfall (SD) | 2.02 | 1.64 | 0.20 | 4.96 | 1.00 |
| year | intercept (SD) | 0.98 | 0.73 | 0.09 | 2.32 | 1.00 |
| year | Elo-rating (SD) | 0.60 | 0.49 | 0.05 | 1.46 | 1.00 |
| year | group size (SD) | 0.81 | 0.72 | 0.06 | 2.14 | 1.00 |
| year | age (old) (SD) | 1.74 | 1.42 | 0.13 | 4.38 | 1.01 |
| year | age (young) (SD) | 1.63 | 1.06 | 0.21 | 3.52 | 1.00 |
| year | reproduced the year before (SD) | 4.38 | 2.13 | 1.69 | 8.12 | 1.00 |
| year | grooming rate (SD) | 1.10 | 0.92 | 0.09 | 2.83 | 1.00 |
| year | IA: grooming rate : Elo-rating (SD) | 1.23 | 0.98 | 0.11 | 3.00 | 1.00 |
| year | IA: grooming rate : group size (SD) | 1.06 | 0.93 | 0.09 | 2.75 | 1.00 |

Table S7: Full results for model B2. See table S6 for details.

| source | term | estimate | est. error | lower 89% CrI | upper 89% CrI | \hat{R} |
|--------|---------------------------------|----------|------------|---------------|---------------|-----------|
| fixed | intercept | 2.07 | 1.19 | 0.34 | 4.05 | 1.00 |
| fixed | age (old) | -3.47 | 1.56 | -6.05 | -1.17 | 1.00 |
| fixed | age (young) | -0.17 | 0.98 | -1.76 | 1.33 | 1.00 |
| fixed | reproduced the year before | -2.97 | 1.65 | -5.63 | -0.39 | 1.00 |
| fixed | Elo-rating | 0.34 | 0.74 | -0.77 | 1.53 | 1.00 |
| fixed | group size | -0.09 | 1.19 | -2.04 | 1.66 | 1.00 |
| fixed | rainfall | 0.18 | 0.99 | -1.31 | 1.76 | 1.00 |
| fixed | grooming rate | -0.54 | 1.32 | -2.73 | 1.40 | 1.00 |
| fixed | IA: grooming rate : Elo-rating | 0.97 | 0.75 | -0.10 | 2.25 | 1.00 |
| fixed | IA: grooming rate : group size | -0.36 | 0.75 | -1.59 | 0.78 | 1.00 |
| fixed | IA: grooming rate : rainfall | 0.27 | 0.72 | -0.84 | 1.36 | 1.00 |
| female | intercept (SD) | 2.46 | 0.70 | 1.51 | 3.72 | 1.00 |
| female | Elo-rating (SD) | 0.69 | 0.57 | 0.05 | 1.74 | 1.01 |
| female | group size (SD) | 0.56 | 0.45 | 0.04 | 1.41 | 1.00 |
| female | rainfall (SD) | 0.90 | 0.59 | 0.12 | 1.92 | 1.00 |
| female | grooming rate (SD) | 2.95 | 1.23 | 1.25 | 5.11 | 1.00 |
| group | intercept (SD) | 1.44 | 0.97 | 0.18 | 3.13 | 1.00 |
| group | Elo-rating (SD) | 1.12 | 0.89 | 0.11 | 2.78 | 1.00 |
| group | group size (SD) | 1.55 | 1.15 | 0.15 | 3.60 | 1.00 |
| group | rainfall (SD) | 1.49 | 1.01 | 0.27 | 3.29 | 1.00 |
| group | age (old) (SD) | 2.00 | 1.67 | 0.19 | 5.00 | 1.00 |
| group | age (young) (SD) | 1.09 | 0.95 | 0.07 | 2.85 | 1.00 |
| group | reproduced the year before (SD) | 2.27 | 1.32 | 0.55 | 4.54 | 1.00 |
| group | grooming rate (SD) | 2.59 | 1.67 | 0.52 | 5.42 | 1.00 |
| year | intercept (SD) | 0.81 | 0.62 | 0.08 | 1.95 | 1.00 |
| year | Elo-rating (SD) | 0.49 | 0.39 | 0.05 | 1.20 | 1.00 |
| year | group size (SD) | 0.68 | 0.61 | 0.05 | 1.82 | 1.00 |
| year | age (old) (SD) | 1.41 | 1.15 | 0.12 | 3.53 | 1.00 |
| year | age (young) (SD) | 1.33 | 0.92 | 0.15 | 3.01 | 1.00 |
| year | reproduced the year before (SD) | 3.69 | 1.80 | 1.38 | 6.87 | 1.00 |
| year | grooming rate (SD) | 0.88 | 0.75 | 0.07 | 2.25 | 1.00 |

Table S8: Full results for model B3. See table S6 for details.

| source | term | estimate | est. error | lower 89% CrI | upper 89% CrI | \hat{R} |
|--------|---------------------------------|----------|------------|---------------|---------------|-----------|
| fixed | intercept | 1.86 | 1.10 | 0.26 | 3.72 | 1.00 |
| fixed | age (old) | -3.32 | 1.37 | -5.58 | -1.31 | 1.00 |
| fixed | age (young) | -0.23 | 0.92 | -1.73 | 1.19 | 1.00 |
| fixed | reproduced the year before | -2.78 | 1.52 | -5.18 | -0.40 | 1.00 |
| fixed | Elo-rating | 0.29 | 0.70 | -0.79 | 1.37 | 1.00 |
| fixed | group size | -0.12 | 1.11 | -1.98 | 1.52 | 1.00 |
| fixed | rainfall | 0.16 | 0.92 | -1.22 | 1.65 | 1.00 |
| fixed | grooming rate | -0.52 | 1.16 | -2.42 | 1.18 | 1.00 |
| female | intercept (SD) | 2.18 | 0.59 | 1.36 | 3.22 | 1.00 |
| female | Elo-rating (SD) | 0.58 | 0.47 | 0.04 | 1.44 | 1.00 |
| female | group size (SD) | 0.48 | 0.38 | 0.04 | 1.19 | 1.00 |
| female | rainfall (SD) | 0.72 | 0.48 | 0.08 | 1.57 | 1.00 |
| female | grooming rate (SD) | 2.19 | 1.04 | 0.63 | 3.95 | 1.00 |
| group | intercept (SD) | 1.33 | 0.93 | 0.17 | 2.96 | 1.00 |
| group | Elo-rating (SD) | 1.00 | 0.81 | 0.09 | 2.46 | 1.00 |
| group | group size (SD) | 1.46 | 1.08 | 0.14 | 3.41 | 1.00 |
| group | rainfall (SD) | 1.44 | 0.96 | 0.25 | 3.14 | 1.00 |
| group | age (old) (SD) | 1.87 | 1.51 | 0.17 | 4.65 | 1.00 |
| group | age (young) (SD) | 1.07 | 0.91 | 0.09 | 2.72 | 1.00 |
| group | reproduced the year before (SD) | 2.08 | 1.19 | 0.54 | 4.23 | 1.00 |
| group | grooming rate (SD) | 2.13 | 1.40 | 0.33 | 4.61 | 1.00 |
| year | intercept (SD) | 0.69 | 0.53 | 0.07 | 1.64 | 1.00 |
| year | Elo-rating (SD) | 0.41 | 0.33 | 0.04 | 1.02 | 1.00 |
| year | group size (SD) | 0.60 | 0.55 | 0.04 | 1.62 | 1.00 |
| year | age (old) (SD) | 1.24 | 1.01 | 0.11 | 3.04 | 1.00 |
| year | age (young) (SD) | 1.20 | 0.83 | 0.13 | 2.68 | 1.00 |
| year | reproduced the year before (SD) | 3.27 | 1.64 | 1.21 | 6.17 | 1.00 |
| year | grooming rate (SD) | 0.65 | 0.55 | 0.05 | 1.69 | 1.00 |

Table S9: Full results of null model in model set B. See table S6 for details.

| source | term | estimate | est. error | lower 89% CrI | upper 89% CrI | \hat{R} |
|--------|---------------------------------|----------|------------|---------------|---------------|-----------|
| fixed | intercept | 1.42 | 0.89 | 0.15 | 2.94 | 1.00 |
| fixed | age (old) | -2.94 | 1.13 | -4.80 | -1.27 | 1.00 |
| fixed | age (young) | -0.42 | 0.77 | -1.64 | 0.74 | 1.00 |
| fixed | reproduced the year before | -2.30 | 1.16 | -4.13 | -0.47 | 1.00 |
| fixed | Elo-rating | 0.24 | 0.53 | -0.57 | 1.05 | 1.00 |
| fixed | group size | -0.24 | 0.90 | -1.76 | 1.10 | 1.00 |
| fixed | rainfall | 0.01 | 0.81 | -1.21 | 1.31 | 1.00 |
| female | intercept (SD) | 1.72 | 0.42 | 1.11 | 2.45 | 1.00 |
| female | Elo-rating (SD) | 0.48 | 0.38 | 0.04 | 1.20 | 1.00 |
| female | group size (SD) | 0.41 | 0.31 | 0.03 | 0.98 | 1.00 |
| female | rainfall (SD) | 0.48 | 0.34 | 0.04 | 1.10 | 1.00 |
| female | grooming rate (SD) | 2.72 | 3.15 | 0.19 | 7.48 | 1.00 |
| group | intercept (SD) | 1.04 | 0.78 | 0.12 | 2.40 | 1.00 |
| group | Elo-rating (SD) | 0.73 | 0.64 | 0.06 | 1.88 | 1.00 |
| group | group size (SD) | 1.25 | 0.88 | 0.16 | 2.84 | 1.00 |
| group | rainfall (SD) | 1.27 | 0.85 | 0.22 | 2.76 | 1.00 |
| group | age (old) (SD) | 1.56 | 1.33 | 0.13 | 3.98 | 1.00 |
| group | age (young) (SD) | 0.99 | 0.82 | 0.08 | 2.48 | 1.00 |
| group | reproduced the year before (SD) | 1.60 | 0.95 | 0.34 | 3.27 | 1.00 |
| group | grooming rate (SD) | 2.74 | 3.08 | 0.16 | 7.75 | 1.00 |
| year | intercept (SD) | 0.54 | 0.42 | 0.04 | 1.31 | 1.00 |
| year | Elo-rating (SD) | 0.31 | 0.26 | 0.03 | 0.77 | 1.00 |
| year | group size (SD) | 0.51 | 0.47 | 0.03 | 1.40 | 1.00 |
| year | age (old) (SD) | 1.00 | 0.78 | 0.08 | 2.42 | 1.00 |
| year | age (young) (SD) | 0.91 | 0.66 | 0.10 | 2.12 | 1.00 |
| year | reproduced the year before (SD) | 2.35 | 1.17 | 0.76 | 4.45 | 1.00 |
| year | grooming rate (SD) | 2.76 | 3.31 | 0.22 | 7.58 | 1.00 |