Sumatran orangutan mothers differ in the extent and trajectory of their expression of maternal behaviour

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Abstract

Mothers arguably play a crucial role in the early development and survival of mammalian offspring, and differences in maternal care may affect offspring's physical and cognitive development. Whereas biological and socioecological factors contribute to differences among mothers, the individual as a source of variation remains understudied. We investigated between-individual variation in the average expression of and plasticity in six maternal behaviours in Sumatran orangutans, using 15 years of mother-offspring behavioural data. We found that mothers differed substantially in the average expression of four maternal behaviours, even after controlling for known predictors of these behaviours, and that not controlling for these confounding effects erroneously leads to larger estimated between-individual behavioural variation. Furthermore, orangutan mothers substantially differed in how they adjusted two maternal behaviours as their offspring aged – i.e., they showed variation in behavioural plasticity. Our study suggests that Sumatran orangutan mothers are constrained in the average expression of maternal behaviours and their plastic responses, potentially resulting in consistent differences among mothers, otherwise called maternal personality. Our findings highlight that individual variation around the population mean in maternal behaviour is more than noise but also that controlling for confounding effects is crucial to avoid the overestimation of individual variation.

Keywords: Between-individual variation, Within-individual variation, Plasticity, Behavioural reaction norm, Maternal behaviour, Great apes

1. Introduction

In all mammals, mothers are crucial for offspring's healthy development, enabling its survival into adulthood, and, eventually, successful reproduction [1–5]. Mothers achieve this by nursing, provisioning food, grooming, and defending their offspring, through imparting knowledge on their offspring, and through providing coalitionary and reproductive support to their offspring [6–11]. Ultimately, maternal behaviour is an adaptive trait affecting the fitness of both the mother and the offspring [9].

Maternal behaviour towards offspring is particularly varied in long-lived species – such as primates [7] – in which mothers support their offspring through a lengthy period of development, and the mother-offspring relationship often extends far beyond weaning [9]. In several primate species, the extent of expression of a maternal behaviour does not always completely overlap among all individuals in a population, i.e., there may be behavioural variation among mothers [12] (henceforth, between-individual variation in the average expression of a maternal behaviour). Though such between-individual variation among mothers can arise from the differences in mother-offspring characteristics and the immediate socioecological conditions under which they are observed, previous research suggests that there may be fundamental differences among mothers, which may remain consistent across different conditions, including across different offspring and different social and ecological environments [13,14].

Consistent differences among females in their maternal behaviour can emerge through differences in social and environmental conditions they faced during their own early developmental period or can be intrinsic [15,16]. In humans, consistent behavioural differences among individuals are often termed personality, and this term is applied more and more to nonhuman species as well [17–20]. Although maternal behaviours are rarely included in the traits used to assign personality, they are interesting candidates to investigate consistent behavioural differences. Differences among mothers may lead to differences in the quantity and quality of offspring-directed maternal behaviours. In human and non-human primates, the quantity and quality of offspring-directed maternal behaviours may influence offspring's pace of development, exploration tendencies, cognitive abilities, learning, skill acquisition, social behaviour, and ultimately survival [21–25], (but see [26]). Therefore, beyond the immediate presence of the mother [3–5], the nature of her investment plays an important role in the successful rearing of her offspring.

Consistent differences between individuals in maternal behaviour over time does not mean that mothers will not exhibit short-term variation in their behaviour within their limits. Indeed, maternal behaviour is usually flexible in nature, in that individuals alter the expression of their behaviour in response to changes in their ecological and social environment [12]. Maternal behavioural expression is, therefore, seldom constant, even within one offspring's developmental period. Flexibility in the expression of maternal behaviour is expected to be especially pronounced in long-lived, large-brained (relative to body size) species, as they are more likely to face fluctuating socio-ecological conditions during their lifetime and have a greater cognitive potential to exhibit behavioural flexibility [27–29]. Long-lived, large-brained species were thus hypothesised to achieve adaptation to prevailing conditions through being behaviourally flexible (i.e., show behavioural plasticity) [27]. Primate mothers, for example, flexibly vary the expression of maternal behaviours in response to experienced ecological conditions such as food availability or predation risk [30,31] and social conditions such as social unit size, dominance structure, and presence of kin or a male in the social unit [32–34]. Primate mothers also vary their maternal behaviours as a function of their biological and social characteristics such as body condition, parity, age, and dominance status [35–37], and to those of their offspring – most importantly offspring age [35,37–40]. In other words, there is within-individual variation or behavioural plasticity in maternal behaviour measured over the ranges of different predictors.

Behavioural plasticity in maternal behaviour is hypothesized to positively affect female lifetime reproductive success [6]. Two recent studies found that not all primate mothers exhibit the same degree of plasticity in maternal behaviours such as offspring-directed communication, time spent in proximity to their offspring, retrieving and restraining their offspring, and mother leaving their offspring [26,41]. Though behavioural plasticity and between-individual variation in maternal behavioural plasticity remain largely understudied in primates, a study on at least one non-primate species has revealed that females who exhibited higher phenotypic behavioural plasticity were also found to have a higher reproductive success [41].

Though behavioural traits from an individual's perspective can be viewed through the above two contrasting ideas of consistency and flexibility, most behaviours are neither fully intrinsic nor unlimitedly plastic, i.e., they are shaped by both the flexible and consistent nature of individuals [12]. Estimating between-individual variation in the average expression of a behaviour is often complicated by the fact that between-individual variation is confounded by the factors influencing within-individual variation (i.e., confounding effects of maternal

behaviour). Therefore, only through the simultaneous investigation of between- and within-individual variation can we fully understand the role of individuals in the expression of maternal behaviour.

To understand the adaptive value of between- and within-individual variation, it is important to investigate these in wild animals. However, estimating between- and within-individual variation in maternal behaviour using field data is challenging, as data on wild individuals are rarely complete due to the practical challenges associated with uniformly sampling the individuals through an extended period of offspring development, such as in primates. For example, individuals cannot always be found in the study area or only a limited number of individuals can be observed simultaneously due to logistic constraints. This introduces sampling discrepancies among individuals, resulting in a significant risk of wrongly inferring the presence of between-individual variation in maternal behaviour when there is none (i.e., false-positive difference); or a failure to detect the presence of between-individual variation when it is actually present (i.e., false-negative similarity), further discussed in [26,43]. These constraints raise the question of whether studies actually measure consistent, fundamental between-individual variation when they do not control for the confounding effects (i.e., offspring age, offspring sex, mother's parity, sample size, etc., as discussed above). This question is important, as consistent, heritable individual variation in fitness-related traits forms the raw material upon which selection can act.

The behavioural reaction norm approach [42,44–47] offers a way to reliably estimate between- and within-individual variation in maternal behaviour simultaneously, especially when faced with sampling discrepancies and/or confounding effects. The approach entails controlling for confounding effects and estimating between- and within-individual behavioural variation – without isolating them, using a mixed model approach, (Box 1), which allows one to estimate between-individual variation relative to within-individual variation. The approach has been successfully applied to several behavioural traits, including maternal behaviours, movement behaviour, calving date, egg laying date, chick provisioning behaviour and male territorial aggressive behaviour, in different species [42,47–52]. Studies on mammalian maternal behavioural variation using behavioural reaction norms are sparse and are conducted mainly on terrestrial primates [26], but see [41]. As long-term data on individually identified animals and large sample sizes are necessary to identify individual variation, such studies are challenging in species with slow life-histories and prolonged maternal care – i.e., the species

in which we would expect variation in maternal behaviour to most likely occur, example primates.

In this study, we aimed to shed light on the extent to which maternal behaviour in wild Sumatran orangutans (*Pongo abelii*) is shaped by individual variation by integrating both consistent individual differences and variation in individuals' plasticity. We investigated between-individual variation in the average behavioural expression and between-individual variation in plasticity in six maternal behaviours while controlling for previously established confounding effects, using longitudinal and cross-sectional behavioural data. Since previous studies on individual variation in maternal behaviour in primates did not control for all known confounding effects before quantifying individual variation [13,26,39,53,54, but see 41], one of the aims of this study was to identify whether not controlling for the confounding effects (i.e., the biological characteristics of the offspring, the prevailing socioecological conditions experienced by the mother-offspring pair, sample size, and sampling scheme; see Methods for further details) would influence the estimation of between-individual variation in the average expression of maternal behaviour.

Sumatran orangutans are large-brained and long-lived arboreal apes, living up to at least 50-60 years in the wild [55,56]. Sumatran orangutan females start reproducing from around 15 years of age and with a duration of about 8 years, their inter-birth interval is the longest among all the non-human primates [57]. Sumatran orangutans are an excellent study system to investigate individual maternal behavioural variation, as mothers provide care to each of their offspring for about 6-9 years without help from other individuals [58], through extensive caretaking behaviours such as carrying, bridging, nest-sharing, and maintaining proximity to offspring, while serving as role models for the offspring's acquisition of learning-intense subsistence skills such as feeding and nest building [59–62].

In line with the hypothesis that individuals may be constrained in their behavioural expression due to their genetic and/or developmental background [15,16], a previous study on wild and captive orangutans found that orangutans show between-individual variation in communicative behaviours, including offspring-directed maternal communication and responsiveness [41]. Based on this result and the results from studies on other primates [26,32,39,63], we predicted that:

- Sumatran orangutan mothers will differ in the average expression of maternal behaviours even after controlling for the known confounding effects.

In a previous work on the study population [40], we found that offspring's biological characteristics (i.e., offspring age, offspring sex) and experienced socioecological factors (i.e., food availability, association size, and presence of a male) had significant effects on several maternal behaviours. We thus hypothesised that the estimation of between-individual variation in the average expression of maternal behaviour is influenced by whether these known confounding effects are controlled for in the analysis. We predicted that

- Estimated between-individual variation in the average expression of maternal behaviour will be exaggerated and will have a higher uncertainty associated with it when confounding effects are not controlled for than when they are appropriately controlled for in the analysis.

The extent of behavioural plasticity is hypothesised to be positively correlated with brain size [27]. Accordingly, orangutans have been found to show considerable plasticity in maternal behaviours and maternal gestural communication [40,41]. Since behavioural plasticity is expected to balance the costs and benefits of maternal behaviour, and as it is unlikely that all mothers face similar pressures during the long offspring developmental period, it is likely that the plastic responses are different among the mothers in Sumatran orangutans. In fact, a recent study found that mothers differed in how they altered their responsiveness towards offspring depending on the context of interaction [41]. Thus, we predicted that

- Sumatran orangutan mothers will differ in their plasticity in maternal behaviours – i.e., mothers will differ in their maternal behavioural trajectories over offspring age.

To carry out this study, we focused on maternal behaviours related to proximity maintenance, skill acquisition, and locomotory support [40] in 15 wild Sumatran orangutans at the Suaq Balimbing monitoring station in South Aceh, Indonesia.

Box 1: Behavioural Reaction Norms

With the behavioural reaction norm approach [40,42–45], repeated observations of individuals over time are analysed to divide the observed behavioural variance into fixed effects and random effects (including within- and between- individual variation) components using a regression method. The intercept of the model represents the population average expression of a behaviour. Behavioural plasticity is inferred via the slope of the regression, which represents behavioural variation over a predictor's range at the population level. Between-individual variation in the average expression of a behaviour is measured as the difference between the population-level and the individual-level intercepts. Between-individual variation in behavioural plasticity is measured as the difference between the population-level and individual-level slopes.

2. Methods

(a) Study site and data collection

To study individual variation in maternal behaviour, we used long-term data on six maternal behaviours, namely *carrying*, *initiation* and *termination of body contact* and *close proximity*, and *feeding in close proximity* (described in Supplementary Material 1, Table S1), collected on wild Sumatran orangutan mother-offspring pairs (*Pongo abelii*). The data were collected between 2007 and 2022 in the Suaq Balimbing research area, which is a coastal peat swamp forest in the Gunung Leuser National Park in South Aceh, Indonesia. These behaviours are commonly expressed by primate mothers and are used to measure the dynamics of the mother-offspring relationship in many primate and non-primate species [26,40,53,64–67]. Though nursing is an important maternal behaviour, it often occurs inconspicuously in orangutans due to their arboreal lifestyle. Thus, our sample size did not allow to us to analyse this behaviour in our study. Maternal behaviours common to most primates such as grooming, social play, food sharing, and agonistic protection were only rarely observed in the study population (field data).

Behavioural data were collected during focal follows, conducted continuously from morning nest to night nest when possible, based on an established protocol for orangutan data collection (https://www.ab.mpg.de/571325/standarddatacollectionrules_suaq_detailed_jan204.pdf).

During the focal follows, scan sampling [68] was conducted every two minutes during which the activity of the focal individual (i.e., a mother with a dependent offspring) and distances (measured in classes of 0 m (contact), <2 m, 2-5 m, 5-10 m, and 10-50 m) between the focal and all the association partners (of any age) were noted down. A party was defined as two or more individuals who were within 50 m of one another. For further details about the study site and data collection see [58,61,69]. When the distance class changed between two scans, the observers noted down the identity of the individual initiating the change.

(b) Sample size

We had behavioural data on 15 mothers, for nine of whom we had data on one dependent offspring (between birth and eight years of age), and for six others we had data on more than one offspring. Though data on multiple offspring (of both the sexes) per mother are ideal for detecting differences among mothers that are independent of offspring characteristics (e.g., offspring sex), such data sets are difficult to obtain in species with long interbirth intervals. Including data about multiple offspring for some mothers and data about only a single offspring for others partially conflates between-mother differences and between-offspring differences, which makes it harder to tease their effects apart. Since we had data on multiple offspring for only less than half the number of focal mothers (*carrying*: 6/13 mothers, *feeding in close proximity*: 6/15 mothers, *body contact initiation* and *termination*: 3/11 mothers; *close proximity initiation*: 2/11 mothers; *close proximity termination*: 4/12 mothers), we included data on only one offspring per mother per behaviour to get reliable random effects estimates of mother identity. For each behaviour, when there were mothers with data on multiple offspring, we chose the offspring with the highest number of focal follows available for that behaviour. As a result, for two of the mothers the identity of the offspring whose data was included in the analyses differed across behaviours (Supplementary Material 1, Table S2).

We operationalised maternal behaviour as the proportion of scans in which the mother showed a behaviour, where the denominator controls for the opportunities available to the mother to show that behaviour (Supplementary Material 1, Table S1). As a result of opportunistic sampling, the number of focal follows and total observation duration differed among the mothers and across behaviours (Supplementary Material 1, Figure S1). The number of focal follows per behaviour ranged between 568 and 710 (i.e., the number of days during which focal individuals were followed and the behaviour could be assessed; see Table 1 for sample sizes), which equalled between 5311.9 *h* and 6482.5 *h of* observation time (see

supplementary material 1, Figure S1 for details on individual sample sizes and number of mother-offspring pairs for each behaviour). To get reliable results, we used a cut-off of at least five follows per mother per behaviour. Therefore, not all mothers could be included in all the behavioural analyses. Despite these constraints, we had data on most behaviours for most mothers (for ten mothers six behaviours, for one mother five behaviours, for one mother four behaviours, and for three mothers one behaviour). However, the range of offspring age during which maternal behaviour could be recorded (i.e., sampling scheme) varied substantially among the mothers (Supplementary Material 1, Figure S2).

(c) Statistical analysis

Estimating between-individual variation in average maternal behavioural expression and plasticity

We used a generalized linear mixed effects model (GLMM) to quantify between-individual variation in the average expression of a behaviour and between-individual variation in behavioural plasticity. In a recent study on the Suaq orangutan population, we found that certain offspring characteristics (offspring age [continuous], offspring sex [binary; male/female] and socioecological factors (prevailing food availability [henceforth, FAI; continuous], average association size during a follow [continuous], and male presence during a follow [binary; presence/absence]) were significant predictors of different maternal behaviours, but not mother's parity [40; Supplementary Material 2, Table S1]. Therefore, as detailed in the introduction, any variation among mothers in their maternal behaviour is likely to be at least partly caused by the variation introduced by these predictors. Hence, we modelled each maternal behaviour as function of the respective known significant predictors of that behaviour. Further details about these predictors are available in [40]. The sampling scheme discrepancies in our study (Supplementary Material 1, Table S2), additionally underscore the importance of including offspring age as a predictor [43]. We z-standardized the continuous predictors to a mean of zero and a standard deviation of one to ease model convergence and interpretation [70]. We dummy coded binary predictors (as 0 and 1) and mean centered them, such that the intercept corresponds to the expected average maternal behavioural expression without being dependent on any one level of the categorical predictors. We included a random intercept of mother identity (15 levels). The estimated standard deviation of random intercepts gives us the extent of between-individual variation in the average expression of maternal behaviour. We further included random slopes of offspring age within mother identity. The

estimated standard deviation of random slopes gives us the extent of between-individual variation in behavioural plasticity. Such a model allowed us to partition the phenotypic variance in maternal behaviour into between-individual variance in the average expression of maternal behaviour and behavioural plasticity. Since our models were already too complex given the dataset and as slope estimates were 0 for FAI, average association size, and male presence during a follow for most of the behaviours when analysed with a similar dataset [40], we did not include these variables in the random slopes part. We could not calculate repeatability (calculated as variance among individuals/variance within individuals over time; [50,71]) to get population-level estimates of the fraction of maternal behavioural variation that is due to between-individual variation, as we did not have repeated measures on maternal behaviour across multiple offspring for all the focal mothers – i.e., we did not have information on within-individual variation over multiple reproductive events.

Modelling procedure

We fitted the GLMMs explained above (henceforth, full model) using a Bayesian framework in R, version 4.2.2 [72], using Stan, version 2.32.5 [73,74], via the brms package [75], which retrieves posterior distributions of estimated parameters. We fitted the models using a beta-binomial error distribution for *initiation* and *termination of body contact* and *close proximity* (events), and with a beta error distribution for *carrying* and *feeding in close proximity* (which are both states rather than events), both with a logit link function. We used brms' default (un-informative) priors. We ran one chain for each model with 5000 iterations, with a warm-up period of 2000 iterations. This resulted in an effective sample size (*ESS*) of >400 and an Rhat of 1 for each estimated parameter across all the models. To prevent divergent transitions, adapt-delta was set to 0.99. To examine the goodness-of-fit of the models, we computed Bayesian R^2 [76] using the *bayes_R2* function as implemented in the brms package.

Statistical support for random effects

In addition to each of the full models, we fitted a model excluding the random intercept and random slope of mother identity (henceforth, fixed effects model) and one including the random intercept of mother identity but excluding the random slope of offspring age within mother identity (henceforth, random intercept model). We then compared these models using the leave-one-out cross-validation (LOO-CV) [77] as implemented in the loo package (version 2.7.0) using the *loo* function. LOO-CV allowed us to examine whether the out-of-sample predictive performance of a model is improved by the addition of model terms (here, the

random intercepts and slopes). It does so by estimating the difference in the expected log predictive density (*ELPD*), which is analogous to the Akaike information criterion [78]. We considered two models to be similar in their predictive performance if their $\Delta ELPD \pm 2 \times SE$ overlapped zero, where $\Delta ELPD$ indicates the *ELPD* difference of both models and *SE* the corresponding standard error.

If $\Delta ELPD \pm 2 \times SE$ between the full model and the fixed effects model overlapped zero, we inferred that adding the random effects of mother identity did not improve the predictive performance of the model (i.e., that our data does not provide convincing evidence that there was variation across mothers or across mothers over offspring age). Similarly, if $\Delta ELPD \pm 2 \times SE$ between the full model and the random intercept model overlapped zero, we inferred that adding the random slope of offspring age within mother identity did not improve the predictive performance of the model (i.e., our data does not provide convincing evidence that there was variation across mothers over offspring age). We chose the more parsimonious model whose $\Delta ELPD \pm 2 \times SE$ did not overlap zero to draw inferences about interindividual differences in maternal behaviour.

Influence of confounding effects

To understand whether and how not controlling for known confounding effects affect the estimation of between-individual variation in the average expression of maternal behaviour, we fitted another model to each of the maternal behaviours without any fixed effects (i.e., not controlling for the known confounding effects) and with only a random intercept of mother identity. We then compared the estimated between-individual variation in the average expression of maternal behaviour and the uncertainty associated with it between the full model and the above model. We assessed these results via visual inspection.

We report the population-level effects in the supplementary material (Supplementary material 3, Table S1), along with the highest density interval (HDI) of posterior distributions of the estimated parameters (Supplementary material 3, Figure S1) obtained from the more parsimonious model for each behaviour.

3. Results

Between-individual variation in the average expression of maternal behaviour

After having controlled for mother-offspring characteristics and socioecological conditions, we found that in four of the behaviours, namely *contact termination*, *close proximity termination*, *carrying*, and *feeding in close proximity*, there was substantial between-individual variation among mothers in the expression of these behaviours, as indicated by the credible intervals obtained from the full model-random intercept model comparison or the full model-fixed effects model comparison not overlapping zero (Supplementary Material 4, Table S1) and the posterior distributions of standard deviation of the random intercept of mother identity being away from zero (Supplementary Material 5, Figure S1). Between-individual standard deviations ranged between 0.6 and 1.09 across these models (Table 1). A value of 0 indicates no measurable difference among mothers; the higher the estimate of the standard deviation, the higher is the extent of difference among mothers. For two other behaviours, *contact initiation* and *close proximity initiation*, the model's predictive performance did not improve with the addition of random effects of mother identity, as indicated by the credible intervals obtained from both the full model-random intercept model comparison and the full model-fixed effects model overlapping zero (Supplementary Material 4, Table S1).

Table 1. Estimated between-individual variation in the average expression of a behaviour and between-individual variation in behavioural plasticity. Means and standard deviations of the posterior distribution of parameters, their 95% credible intervals (CI), along with ESS for the random effects for four of the maternal behaviours are shown.

Random effect	Estimate	Estimated Error	95% CI	Rhat	Bulk ESS	Tail ESS
Contact termination: Random intercept model; *N*: 666 focal follows						
$SD_{Intercept}$	1.09	0.38	[0.53, 2.03]	1	586	1114
Close proximity termination: Full model; *N*: 640 focal follows						
$SD_{Intercept}$	0.6	0.21	[0.32, 1.14]	1	935	1757
$SD_{Offspring\ Age}$	0.45	0.22	[0.16, 1.01]	1	965	1710
$COR_{(Intercept,Offspring\ Age)}$	-0.09	0.39	[-0.77, 0.69]	1	889	1601
Carrying: Full model; *N*: 692 focal follows						
$SD_{Intercept}$	0.98	0.32	[0.49, 1.71]	1	709	1146
$SD_{Offspring\ Age}$	0.77	0.26	[0.38, 1.37]	1	812	1287
$COR_{(Intercept,Offspring\ Age)}$	0.70	0.23	[0.08, 0.96]	1	1126	1558
Feeding in close proximity: Random intercept model; *N*: 710 focal follows						
$SD_{Intercept}$	0.77	0.22	[0.46, 1.28]	1	753	1357

* In these models, the inclusion of either the random intercept of mother identity or the random intercept of mother identity and the random slope of offspring age within mother identity substantially improved the predictive performance of the models. Offspring age was z-transformed.

We found the largest estimated between-individual variation among mothers for the behaviours *contact termination* and *carrying* (Table 1, Figure 1a,c), while *close proximity termination* and *feeding in close proximity* had lower estimated between-individual variation among mothers (Table 1, Figure 1b,d). Furthermore, the estimated average expression of a behaviour for each mother varied across the behaviours (Figure 1a-d).

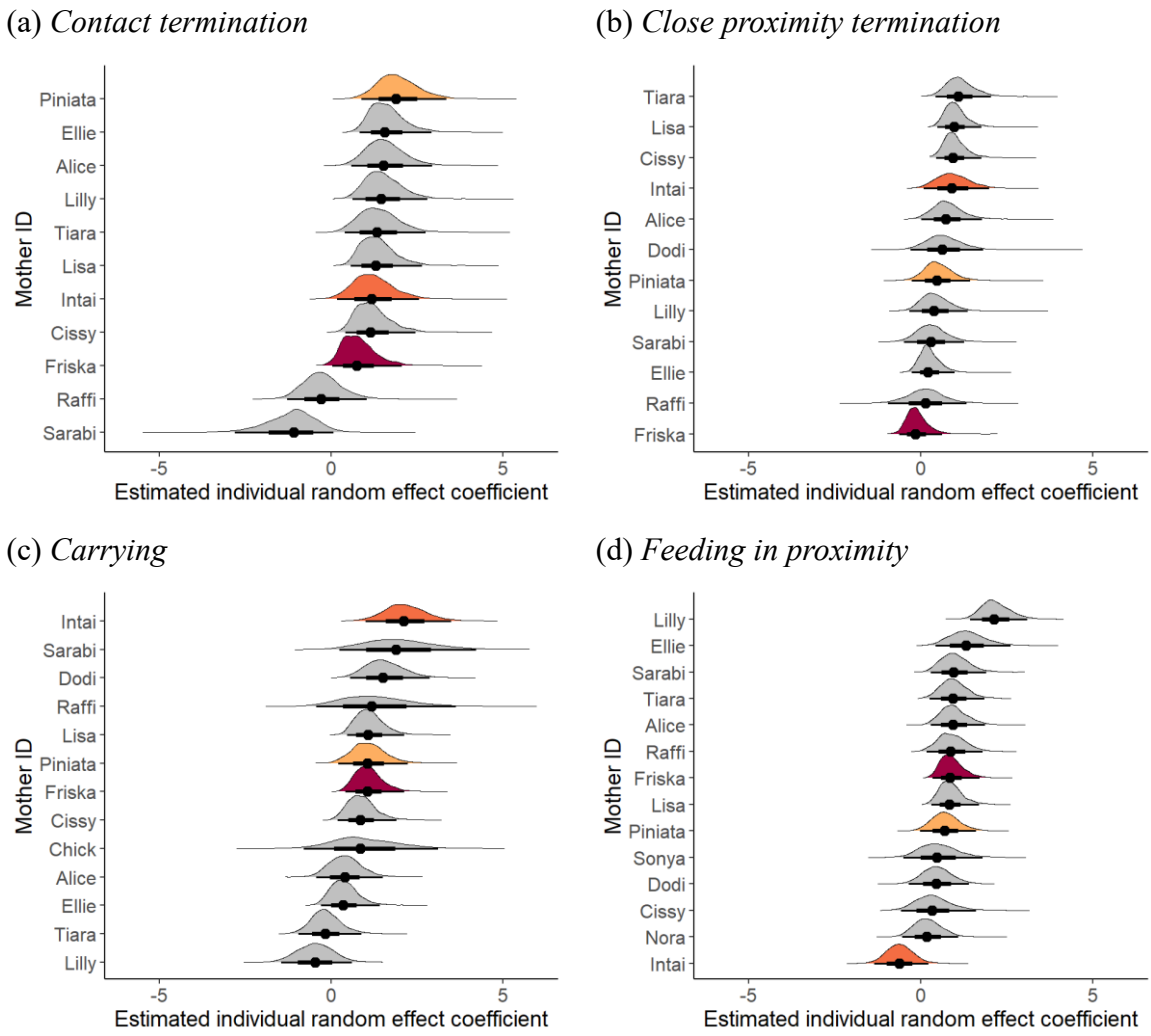

Figure 1. Between-individual variation in the expression of four maternal behaviours. Posterior distributions (on the logit scale) are shown for (a) *body contact termination* (random intercept model), (b) *close proximity termination* (full model), (c) *carrying* (full model), and (d) *feeding in close proximity* (random intercept model) for the individual mothers relative to the estimated between-individual variation at the population-level. Friska, Intai, and Piniata are coloured maroon, orange, and yellow in the graphs to visualize differences in the pattern of average expression across the different behaviours for individual mothers. Filled dots show the posterior median for each mother. Thick black horizontal lines show 66% credible intervals,

and thin horizontal lines show 95% credible intervals of the posterior draws. Positive estimates indicate higher than average behavioural expression, while negative estimates indicate lower than average behavioural expression.

Influence of confounding effects

When we compared the estimated between-individual variation in the average expression of maternal behaviour obtained from models in which we did and did not control for the known confounding effects, we found that for all but one analysed maternal behaviour, not controlling for the confounding effects resulted in a higher estimated between-individual variation than controlling for these effects (Figure 2). This difference was most pronounced for *body contact initiation* and *termination*, where the models that did not control for the known confounding effects (Supplementary Material 2, Table S1) estimated the between-individual variation to be more than twice as high as the models that did control for the confounding effects (Figure 2). The differences between the estimated between-individual variations were moderate for *close proximity termination* and negligible for *close proximity initiation* and *carrying*. Additionally, for three of the behaviours (i.e., *body contact initiation* and *termination*, and *close proximity termination*), the 95% credible intervals associated with the estimates were wider when the confounding effects were not controlled than when they were controlled for in the analysis (Figure 2). On the contrary, for the rest of the behaviours (i.e., *carrying*, *close proximity initiation*, and *feeding in close proximity*), the 95% credible intervals associated with the estimates were wider when the confounding effects were controlled than when they were not controlled for in the analysis (Figure 2).

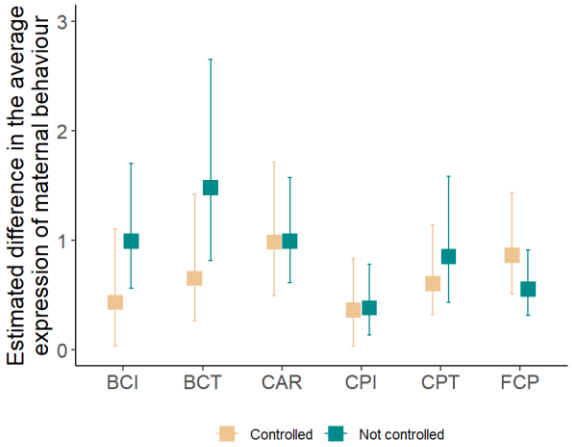

Figure 2. Comparison of the estimated differences among mothers in maternal behaviour. Estimated between-individual variation in the average expression of maternal behaviour (i.e.,

the estimated standard deviation of mother identity intercepts) is shown for each of the six maternal behaviours when the respective confounding effects were (full model) and were not controlled for in the analysis. The vertical lines represent 95% CI associated with the estimates. BCI: *Body contact initiation*; BCT: *Body contact termination*; CAR: *Carrying*; CPI: *Close proximity initiation*; CPT: *Close proximity termination*; FCP: *Feeding in close proximity*.

Between-individual variation in maternal behavioural plasticity

For two of the behaviours – *close proximity termination* and *carrying*, there was evidence of between-individual variation in behavioural plasticity over offspring age, as indicated by the credible intervals obtained from both the full model-random intercept model comparison and the full model-fixed effects model comparison not overlapping zero (Supplementary Material 4, Table S1) for these behaviours. *Carrying* had larger between-individual variation in behavioural plasticity (Table 1, Figure 3a) than *close proximity termination* (Table 1, Figure 3b, Supplementary Material 5, Figure S2). The individual trajectories of maternal behaviour over offspring age suggest that mothers varied in how they adjusted their behaviour as their offspring developed (Figure 3a,b).

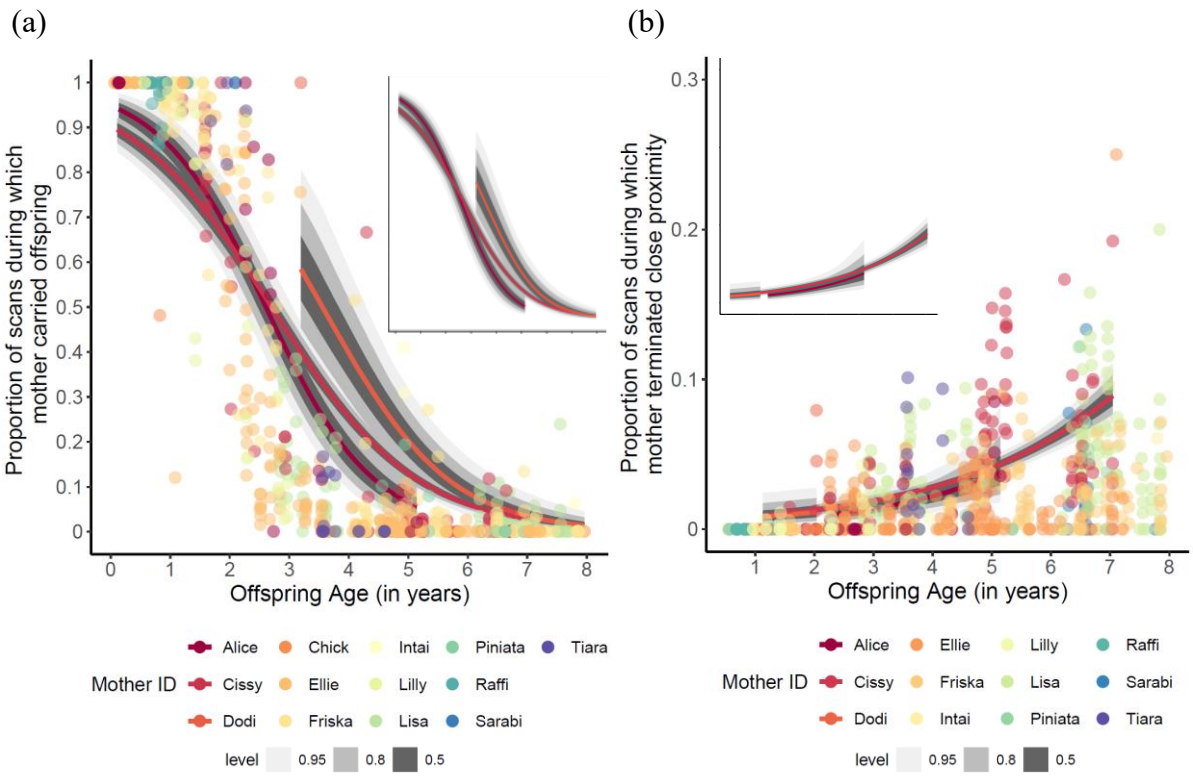

Figure 3. Between-individual variation in behavioural plasticity. Fitted lines and their (95%, 80%, and 50%) credible intervals are shown for (a) *carrying* and (b) *close proximity*

termination for three mothers from the respective full models to visualize the distinct trajectories of maternal behaviour over offspring age. Plots without the datapoints of all the focal mothers are shown in the insets for clearer visualization of the trajectories. Note that y-axis scale is different between (a) and (b).

4. Discussion

Much research to date on primate maternal behaviour has focused on the effect of biological characteristics of the mother and offspring, social factors, and ecological conditions on maternal behaviour [40,79–81], but little attention has been paid to individuals as a source of variation. Here we used a behavioural reaction norm approach to investigate between-individual variation in the average expression of maternal behaviour and between-individual variation in behavioural plasticity during offspring development in Sumatran orangutans. We found that mothers substantially differed in their average expression of maternal behaviour even after controlling for known confounding effects. Furthermore, we found that not controlling for the confounding effects resulted in exaggerated estimated between-individual variation in most behaviours. We further found that mothers differed in how they modified their behaviour in response to their offspring's increasing age – i.e., mothers showed individual-specific trajectories of maternal behaviour during offspring development and thus between-individual variation in behavioural plasticity.

As predicted, our analyses revealed substantial between-individual differences in the average expression of *carrying*, *feeding in close proximity*, *body contact termination*, and *close proximity termination* when controlling for confounding effects. This suggests that Sumatran orangutan mothers likely differ in the expression of these maternal behaviours regardless of their offspring's age and experienced socioecological conditions. Differences among mothers in maternal behaviours such as carrying, rejection, restraint, and ventral contact have been previously found in Guinea baboons, rhesus macaques, and vervet monkeys [13,26,39] – though these studies did control for all the confounding effects – as well as in offspring-directed maternal communication in orangutans [41]. Our results indicate that the differences are likely to be consistent differences among the mothers, or at least among mother-offspring dyads, strengthening the notion that there is personality – specifically maternal personality – in nonhuman primates as well [15]. Maternal personality could be the result of genetic differences among the mothers or differences in developmental effects experienced by the mother and/or

offspring [15,16]. In species with large brains, developmental effects that lead to consistent individual differences are likely to occur [82]. This is because the larger the brain (relative to body size) the more important developmental effects become, as large-brained species are more prone to developmental inputs [83], and a large share of the brain development happens after birth [84]. In Sumatran orangutans (i.e., also in our data set), *body contact initiation* and *close proximity initiation* with offspring are both rarely shown by mothers [40]. Accordingly, most of the data points for these behaviours in our data set were zero, which makes it difficult to discern variation with the currently available analysis techniques.

In our study, the magnitude of variation among mothers was higher for *body contact termination* and *carrying* than that for *close proximity termination* and *feeding in close proximity*. In orangutans, *carrying* is a form of locomotory support [40,62] and close range feeding can provide social learning opportunities for offspring [61], whereas body contact and proximity maintenance are often associated with protection/thermoregulation in primates [85]. *Carrying* is energy intensive [86] and close range feeding may increase feeding competition and thus also have negative energetic effects for the mothers. Individual differences in the expression of a maternal behaviour could be the consequence of differences in the maximum investment that individual mothers can show (based on her genetic foundation or irreversible effects of early developmental experience). A mother's genetically or developmentally determined body condition may thus constrain her investment in energetically critical maternal behaviour. However, since mother-offspring interactions are always dyadic in nature, it is possible that the differences we observed among mother may be partly driven by differences among their offspring. Unfortunately, our sample sizes did not allow us to further partition the variance to investigate the effect of differences among offspring on maternal behaviour. Future studies could investigate between-individual maternal behavioural variation using multiple offspring per mother – ideally including offspring of both sexes – to understand how much of the observed variation is due to the mother *versus* the offspring.

Interestingly, mothers differed in their average expression across different behaviours: whereas a mother showed higher than the population average expression in one behaviour, she also could show lower than the population average expression in other behaviours. In primates, variation in maternal behaviours usually falls along two dimensions, namely protection and rejection [32,79]. A mother's behaviour in one dimension cannot predict her behaviour in another dimension – a protective mother who, for example, spends a higher proportion of time in body contact with her offspring than an average mother need not necessarily be less rejecting

by, for example, showing a smaller proportion of rejections to food solicitation by offspring than an average mother. The dissimilarity of individuals' patterns of maternal behavioural variation across the different behaviours suggests that the maternal behaviours that we analysed fall on different dimensions in Sumatran orangutans, as those seen in captive chimpanzees and bonobos and many other primates [22,32,79].

As predicted, we found that failing to appropriately control for the known confounding effects while estimating between-individual variation in the average expression of maternal behaviours can result in exaggerated estimation of differences among individuals. When differences in the biological characteristics and the socioecological environment under which the different mother-offspring pairs were observed [40] cause differences among individual behaviour, then by not deliberately adding these factors as predictors in their models, researchers risk wrongly assigning these differences to individual effects (i.e., false-positive between-individual difference) – i.e., overestimation of such differences [26,43]. Failure to control for the confounding effects not only affects the estimated variation between mothers but also the uncertainty associated with it. Credible intervals were wider when confounding effects were not controlled for than when they were controlled for in half of our models. As the values of the different predictors, such as offspring age, association size, etc., change over time and as females are responding to the changes in these variables [40], differences in the effects of these variables among individuals further add on to the inherent differences among individuals, resulting in increased uncertainty around the estimates. In general, this result highlights the importance of controlling for the confounding effects in animal personality studies, as most behaviours have various confounding factors associated with them.

Though variation in behavioural plasticity is usually studied along an environmental or a social gradient [41,42,45,51], we investigated whether mothers differ in how they adjust their behaviour over offspring development. As predicted, our analyses revealed substantial between-individual variation in maternal behavioural plasticity in response to increasing offspring age (and thus competence and independence), however in only two of the behaviours – *close proximity termination* and *carrying*. That orangutans showed variation in plasticity in maternal behaviour across offspring age means that not all individuals adjusted their behaviour to the same extent during offspring development. This may be a result of mothers being limited in their individual behavioural expression range. As with between-individual difference in the average expression of these behaviours, because *body contact* and *close proximity initiation* are rarely shown by mothers, it is difficult to discern between-individual variation in plasticity

in these two behaviours. Interestingly, our analyses did not detect substantial between-individual variation in plasticity in the behaviours *contact termination* and *feeding in close proximity*, despite these behaviours having similar sample sizes and sampling schemes as the behaviours *close proximity termination* and *carrying*, respectively. On the one hand, it may be that the range of behavioural expression for *body contact termination* and *feeding in close proximity* is indeed similar across mothers, despite the significant variation in the average expression of these behaviours across the mothers. On the other hand, it may be that offspring affect their mothers' *close proximity termination* and *carrying* more than *contact termination* and *feeding in close proximity*. This may mask the difference among mothers in their plasticity in *contact termination* and *feeding in close proximity*. Studies looking into the effects of the offspring on maternal behavioural plasticity are needed to disentangle these two scenarios.

Differences in mothers' physiological conditions can lead to differences in their ability or willingness to respond to their offspring's needs, which may be a source of individual differences in plasticity in maternal behaviour. In line with this reasoning, we found the most pronounced between-individual variation in plasticity for the most energetically costly behaviour, namely *carrying*. Maternal condition was also found to influence between-individual differences in time spent in and out of contact with offspring and frequency of rejection in other primates [81]. However, as evidence suggests that orangutan mothers are capable of adjusting their behaviour in response to their offspring's growing age, i.e., competence [40,60], it is possible that variation in the development of the offspring's locomotor skill levels lead to differences in the mothers' readiness to carry them. In other words, differences in offspring's pace of development and, especially, variation in the magnitude of these differences can bring about individual differences in maternal behavioural plasticity. Our results on behavioural plasticity in maternal behaviour in Sumatran orangutans are in line with the hypothesis that large-brained species with a long dependency period use behavioural flexibility to adapt to prevailing conditions [27].

Overall, our results support that there is consistent, fundamental between-individual behavioural variation in maternal behaviour in Sumatran orangutans in terms of the average expression of maternal behaviours and the extent of plasticity in their expression. However, as with any field-based study, individual mothers differed in the conditions under which they were observed, which may affect both individual differences in the average expression and plasticity of the maternal behaviours. Even though we controlled for previously established confounding effects [40], there may be other socioecological variables that affect variation in maternal

behaviour that we currently cannot quantify or are not even aware of. Furthermore, the complexity of these effects may exceed the way we quantified them. For example, we took into account the current presence or absence of males because of their known effects on maternal behaviours, which likely arise from the risk they may pose to immature individuals [40,87]. However, individual males likely differ in the risk they pose to the offspring [88] and thus also in the effects they have on maternal behaviour. Controlling for more accurately quantified prevailing social risk faced by offspring would thus be a better approach, even though not feasible with the current data set. Despite our study making use of around 6000 hours of behavioural observation conducted over the span of 15 years, it is constrained by the limited number of focal individuals, the offspring's lengthy developmental periods, and long inter-birth intervals. Accordingly, sample size and sampling scheme substantially varied among the mothers, which inevitably limits the inferences possible with our study. For a more accurate quantification of between-individual differences in maternal behaviour, we need data on mother-offspring pairs spanning the entire range of offspring developmental period and, ideally, data on multiple offspring of the same mother.

Our study aimed to disentangle actual pattern from noise through partitioning observed variation in maternal behaviour. Our results suggest that Sumatran orangutan maternal behaviour is shaped by individuality, apart from mother-offspring social and biological state characteristics and socioecological conditions [40]. Our study adds to previous research on maternal personality in primates and other species in showing that there are fundamental differences among mothers in their behaviour towards offspring [13,26,32,39,48,66]. Our study signifies the importance of expanding research focus from average behaviour to individual behaviour such that variation around the mean is not considered as pure noise. Consistent between-individual variation in the average expression of a behaviour and plasticity can have important consequences and present novel opportunities for studies of the evolutionary processes that shape the behaviour.

We hope our work lays the foundation for future studies to test the effects of differences in maternal behaviour on offspring development, behaviour, and personality. For consistent, heritable variation to undergo natural selection, there should also be fitness consequences associated with such variation. Investigating whether differences in maternal behaviour are associated with differences in the speed at which offspring reach developmental milestones and the offspring's future reproductive success will shed light on the adaptive value of maternal behavioural variation for both the mother and the offspring. Future studies may also be able to

test whether differences among mothers are consistent through time and/or context – i.e., whether mothers behave similarly towards each of their offspring, or whether they are consistent for a few years or in a few behaviours only. The scale or the period of consistency can have different ecological and evolutionary consequences. Our study also sets the stage to address whether daughters inherit maternal personality – socially and/or biologically – potentially giving rise to matrilineal differences in maternal behaviour [13,63]. Ultimately, studies on individual variation in maternal behaviour can help shed light on the causes, maintenance, and consequences of such variation.

Ethics

To minimise the effect of observer presence on the natural behaviour of the individuals, we collected data from a distance of at least 7 m in the field. As orangutans are arboreal and as observers are on the ground, this minimum observation distance is quite different from that used in studies on primarily terrestrial apes. Data collection was purely observational in nature, and it was non-invasive. The research followed the recommendations of the Animals (Scientific Procedures) Act 1986, as published by the UK government, and the principles of Ethical Treatment of Non-Human Primates as stated by the American Society of Primatologists. Approval for this study was obtained from the Indonesian State Ministry for Research and Technology (RISTEK).

Data accessibility

Data and original code are deposited at Dryad data repository.

Authors' contributions

Conceptualization: TR, MvN, MF, CS; Data collection: TUN, CS; Data curation: TR, CS; Methodology: TR, RM, PB, CS; Formal analysis: TR; Funding acquisition: CS; Investigation: TR; Field project administration: SSUA, CS; Supervision: CS; Visualization: TR; Writing—original draft: TR; Writing—review & editing: TR, RM, SSUA, TUN, MvN, MF, PB, CS.

Conflict of interest declaration

We declare that we have no competing interests.

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