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Cite this article: Linossier J, Casey C, Charrier I, Mathevon N, Reichmuth C. 2021 Maternal responses to pup calls in a high-cost lactation species. *Biol. Lett.* **17**: 20210469.
https://doi.org/10.1098/rsbl.2021.0469

Received: 31 August 2021
Accepted: 15 November 2021

Subject Areas:
behaviour

Keywords:
acoustic communication, mother–offspring bonding, maternal investment, vocalizations

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Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.5744036.

THE ROYAL SOCIETY PUBLISHING

Animal behaviour

Maternal responses to pup calls in a high-cost lactation species

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Bonding between mothers and their young is fundamental to mammalian reproductive behaviour and individual fitness. In social systems where the risk of confusing filial and non-filial offspring is high, mothers should demonstrate early, strong and consistent responses to their kin throughout the period of offspring dependence, irrespective of maternal traits. We tested this hypothesis through playback experiments in the northern elephant seal *Mirounga angustirostris*, a phocid species that breeds in high-density colonies. We found that mothers recognized their offspring throughout lactation and as early as 1–2 days after parturition. Measures of experience (age) and temperament (aggressivity) did not predict their response strength to filial playback treatments, nor did pup age or sex. Some mothers showed great consistency in behavioural responses throughout the lactation period, while others were less predictable. The strength of a female's response did not influence her pup's weaning weight; however, more consistent females weaned pups of higher mass. This is a rare demonstration of individual recognition among phocid mothers and their offspring, and suggests that consistency in maternal responsiveness may be an important social factor influencing the pup's growth and survival.

1. Introduction

In mammals, most newborns call promptly after birth to solicit maternal care, and the young of many species produce vocalizations when hungry, cold, scared, threatened or separated from their mothers (e.g. cries of babies and bleats of lambs). Mothers preferentially respond to the calls of their own offspring in comparison to those from non-filial young, and this process is supported by individuality in vocal cues that females learn to recognize [1–4]. The onset and efficiency of individual recognition appear to be strongest in social systems where the risks of misdirecting maternal care are great. These include colonial species where density is high, when young are mobile and mothers do not maintain continuous contact with their offspring, or when lactation extends over a long period [5–8].

Northern elephant seals form large coastal colonies during the annual breeding season [9,10]. Each mother gives birth to a single pup within a crowded harem, and females and their offspring remain together until weaning while females fast (approximately 25 days; [11]). Depending on location, harem density can range from a few dispersed individuals to more than 1000 females in close contact. During lactation, mothers lose 40–60% of their mass [12], while pups undergo a sevenfold increase in body weight [13] due to the exceptional fat content of their mother's milk [14]. A combination of intrinsic (e.g. age, experience and individual behaviour) and extrinsic (e.g. environmental conditions, harem density and social interactions) factors influence the risk of pup separation during this intensive period of maternal investment [11,15,16]. Orphaned or lost pups usually die on the colony, although some steal milk from other mothers in crowded harem conditions [16]. Despite high costs of maternal care [17], allonursing behaviour (i.e. females feeding a non-filial pup) has been reported in this species with adoption rates of 18% [16,18]. Among mammals, allonursing tends to occur in systems where group-living females breed cooperatively or produce litters of multiple offspring [19,20]. As these conditions do not occur in northern elephant seals, recognition abilities become a key consideration, as a mother's ability to successfully nurse her own offspring dramatically influences pup survivorship [21].

We conducted field playback experiments to explore the onset and stability of vocal recognition by female elephant seals during the rapid period of pup growth prior to weaning. Although visual and olfactory cues support pup identification, acoustic signals were emphasized as mothers and their pups regularly exchange contact calls from birth to weaning [22,23]. Further, we sought to evaluate how female responsiveness relates to individual maternal traits and predicts pup weaning mass within this high-cost lactation system.

2. Methods

(a) Identification of individuals and acoustic recordings

Research was conducted at Año Nuevo State Park (San Mateo County, California, USA) over two successive breeding seasons (electronic supplementary material, supplement 1a). We dye marked seals with alphanumeric codes to identify and monitor 30 mothers, their confirmed filial pups, and other pups from birth through weaning (electronic supplementary material, supplement 1b). Long-term population monitoring and tagging efforts [24] provided a subset of 14 known-age females.

Pups frequently emit vocalizations to elicit attention from their mothers. We recorded pup calls using a digital recorder linked to a dynamic microphone on an extension pole placed 0.7 to 4.5 m away at pup level; this system was capable of capturing complete, undistorted calls (electronic supplementary material, supplement 1c). Voice annotations were recorded to a separate channel.

(b) Playback experiments

We tested 22 mothers during early, mid and late lactation (weeks 1, 2 and 3) when filial pups were 7.5 ± 1.2 days, 14 ± 1.8 days and 20.4 ± 3.2 days old, respectively. During the first season, playbacks were conducted with six untagged adult females. To avoid possible replication the following season, we selected 16 tagged individuals for participation in playback trials. Focal females were exposed to two successive treatments on each trial: one call series from her own pup that had been recorded 1 to 3 days prior, and one call series from a non-filial but similar-aged pup. The presentation order of filial and non-filial call treatments was changed between trials and balanced weekly and by individual. The non-filial pup on each trial was unfamiliar (i.e. from a distant harem) and selected from our call bank.

Playback treatments were created from recordings using signal processing software and projected from a wireless speaker system configured to replicate the source characteristics of pup calls (electronic supplementary material, supplement 1d). Each call series contained six call exemplars from the same pup played at the same natural rate and amplitude. The speaker was positioned 2–4 m from the target female on the opposite side of her pup. After an acclimation period of at least 2 min, the first treatment was played when the female was calm and awake, not interacting with surrounding animals, and ignoring the speaker. The second series was played when the female had returned to a relaxed state for at least 2 min after the end of the first treatment. Field experiments were videotaped from 20+ m away.

Based on findings from weekly playback trials, we tested eight additional mothers just 1–2 days post-parturition (1.3 ± 0.5 days) using the same methods. These females were not tagged or of known age. We recorded filial and non-filial pups within 4 h of observed birth to establish the treatment series for each female.

(c) Behavioural response analysis

Two observers blind to the treatment sequence later scored six behaviour variables from each playback: latency to look towards the speaker (s), latency to move towards the speaker (s), latency to vocalize (s), latency to touch (sniff) the speaker (s) and number of vocalizations produced during the first minute following the playback onset. Inter-observer reliability of behavioural scoring was 96% (Spearman rank correlation).

To evaluate the response strength of each mother to each treatment, behavioural variables were pooled into a principal component analysis (PCA) with a composite score (PC1, the first principal component; [25]). We conducted separate PCAs for the longitudinal (weekly) playbacks and the playbacks conducted 1–2 days postpartum as the latter experiments involved different individuals. We used linear mixed models to determine which factors influenced behavioural responses. For the longitudinal playbacks, playback treatment, timing (week) and interaction between treatment and timing were fixed factors, while treatment presentation order and mother's identity were considered random factors. No model selection took place and residuals were inspected to ensure normality of error. For the playbacks conducted 1–2 days postpartum, we used playback treatment as the fixed factor and treatment presentation order and mother's identity as random factors.

(d) Correlation between maternal traits, responsiveness to playbacks and pup weaning weight

Age and aggressiveness were considered as maternal traits. We used age as a measurable factor that is highly correlated with experience (number of pups) in this species [16]. We used a simple metric of 'aggressiveness' to characterize a mother's tendency to control or displace other females. During 60 min focal sampling intervals, interactions were observed between the target mother and other females in the harem. Her wins and losses (see [26]) were determined, with 3–13 interactions sampled per female during the lactation period. Mothers who won more interactions (i.e. displacing another female with threatening behaviour) than lost (i.e. retreating from another female) were considered aggressive (score of 2), and those that lost more fights than won were considered to be less aggressive (score of 1). No interactions were observed for four focal females and these individuals were not assigned an aggressivity score. This measure was not an ideal indicator of aggressive temperament, as it does not consider contextual variables and was limited by low sample size. However, this score provides a useful gross metric of individual behaviour.

After abrupt weaning, elephant seal pups remain at natal sites while fasting for 8–12 weeks [27]. We weighed the 22 pups born to focal females within 10 days of separating from their mother; mass at weaning was determined using known rates of mass loss per day (as in [28]) and confirmed separation dates.

We used a linear mixed model to assess whether the behavioural responses of mothers to filial pups were influenced by female age, aggressiveness level, playback timing (week) or pup sex. These variables were considered fixed factors, with female

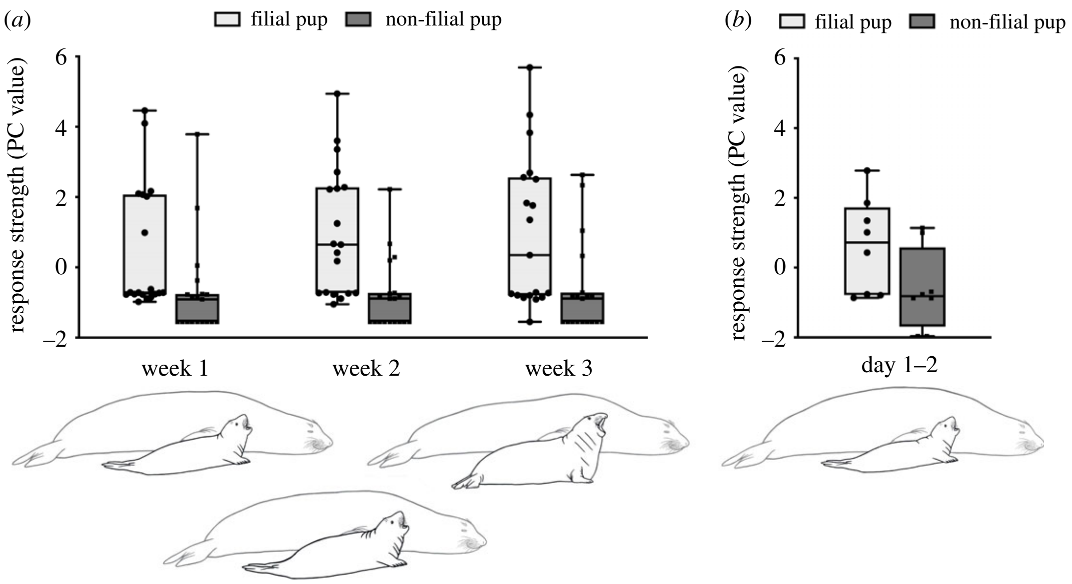

Figure 1. Mothers recognize the vocalizations of their own pups. (*a*) Females ($n = 22$) respond more strongly to the calls of their own pup than to same-age, non-filial pups during early (week 1), mid (week 2) and late (week 3) lactation (*b*) Similar results were obtained for females ($n = 8$) tested just 1–2 days after parturition ($n = 8$ other females). PCA results are provided in the electronic supplementary material, supplement 2a. Responsivity (*y*-axis) corresponds to composite (PC1) behavioural scores; boxes show 25%, median and 75% distribution data, whiskers depict range. Line drawings courtesy of E. Levy.

identity as a random factor. We further assessed whether pup weaning weight was related to either the strength or consistency of each mother's response to the filial playback treatment. To evaluate the response consistency of mothers, we used a nonparametric bootstrap to obtain an interval estimate of correlations.

3. Results

(a) Maternal response to pup calls

Mothers responded more strongly to the vocalizations of their own pups than to calls of similar-aged, non-filial pups during early, mid and late lactation ($F_{1,105} = 52.95$, $p < 0.001$, figure 1*a*; electronic supplementary material, 2a and b). This differential response was present as soon as 1–2 days after parturition (Wilcoxon paired test: PC1, $V = 33$, $p = 0.04$; PC2, $V = 17$, $p = 0.95$, figure 1*b*; electronic supplementary material, figure S2a).

Overall, mothers moved faster towards the speaker and called more quickly and more often when hearing calls produced by their own offspring (electronic supplementary material, supplement 3). However, maternal responsiveness varied among individuals. Some mothers (8/22) displayed consistent responses to their pup's calls during the longitudinal playbacks, being either highly or weakly responsive; other females (7/22) were less predictable in their response strength over time (figure 2*a*).

(b) Factors modulating maternal response and pup weaning mass

Age ($F_{1,10} = 0.69$, $p = 0.43$) and aggressiveness level of mothers ($F_{1,10} = 0.54$, $p = 0.48$) did not predict their response strength to filial playbacks, nor did pup age ($F_{2,26} = 1.1$, $p = 0.35$) or sex ($F_{2,26} = 0.15$, $p = 0.71$) (electronic supplementary material, supplement 2c).

Pup weaning weight was not linked to maternal response strength (bootstrapped Pearson's correlation $t = 0.91$, $p = 0.69$; figure 2*b*). However, females that exhibited more variable responses to filial treatments throughout lactation (unpredictable females) weaned pups with lower weights (bootstrapped Pearson's correlation $t = -0.44$, $p = 0.02$). Conversely, females showing greater consistency in responses to their pups' calls (predictable females) produced larger pups (figure 2*c*).

4. Discussion

The ability of mammals to identify their young leads to increased survivorship of offspring and enhanced reproductive success among females [29]. In dense harems where the chances of confusion are high, female northern elephant seals recognize their pups throughout the period of dependence and can do so within a few days of birth. Reliable acoustic identification occurs despite pup calls being complex, with features that vary with motivational context ([23]; J. Linossier 2019, unpublished data). The acoustic features that enable females to identify their pups are as yet unresolved. While rapid and accurate vocal recognition of offspring occurs in other group-living mammals (e.g. bats, sea lions and sheep), it has rarely been demonstrated among phocids [6,30,31].

These experimental findings suggest that the paradox of costly allonursing in this species cannot be explained by misdirected maternal care resulting from deficient vocal recognition. Furthermore, observations of maternal behaviour confirm that while some mothers foster or adopt pups within days of giving birth, this behaviour may also commence later in the lactation period [16,18] after recognition has presumably emerged. It is possible that this allonursing behaviour could be driven by inclusive fitness benefits given high observed levels of philopatry [32] and extraordinary genetic similarity among northern elephant seals [33], although it is notable that kin selection does not influence fostering behaviour in grey and harbour seals with more typical genetic variation [34,35]. Alternative hypotheses related to reciprocity, increased maternal experience, or physiological influences may further explain the relatively high occurrence of nursing non-filial young in this species [36]. Parental behaviour is modulated by an array of hormonal, neurochemical, epigenetic and genetic factors [37–42], as well as body condition and experience [43,44]. For example, oxytocin and prolactin influence maternal

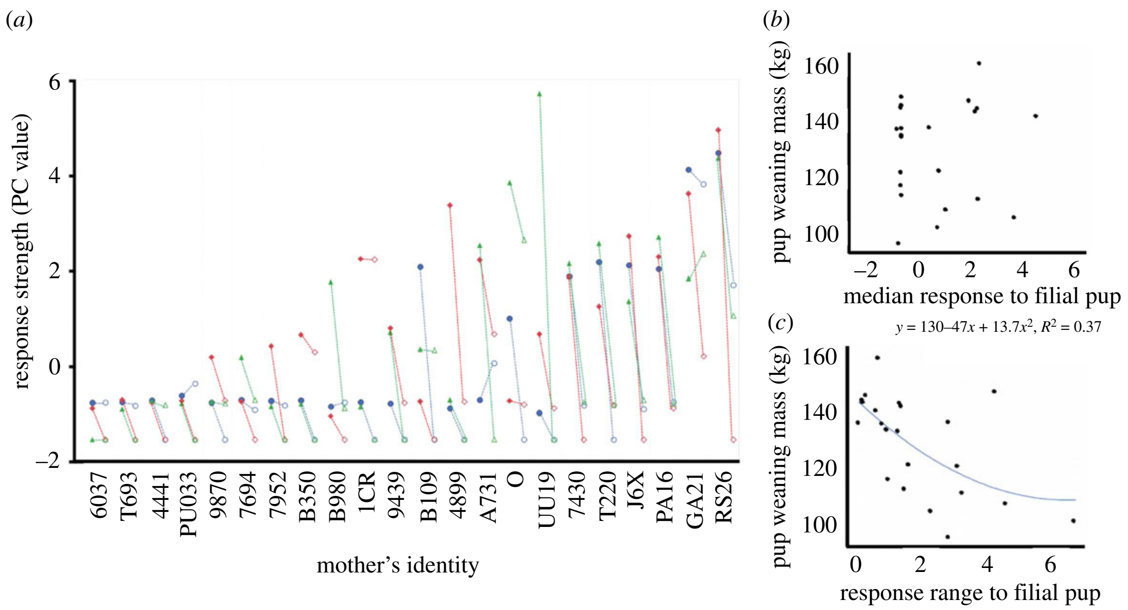

Figure 2. Mothers differ in their responsivity to playback treatments. (*a*) Twenty-two females (*x*-axis) are ordered by their behavioural response strength to filial pup calls (filled forms), with some females consistently responding more strongly than others (right portion of plot); responses to non-filial pup calls were usually weak (open forms). Response strength indicates PC1 scores with blue circles corresponding to early lactation (week 1), red diamonds to mid lactation (week 2) and green triangles to late lactation (week 3). Pup weaning weight shows (*b*) no relationship to mother's typical response strength to filial pup calls (median value of PC1), but does show (*c*) correlation to mothers' response range to filial pup calls (maximum PC1 value – minimum PC1 value), with more consistent females weaning pups of higher mass (bootstrapped Pearson's correlation $t = -0.44$, $p = 0.02$; residual standard error of the polynomial regression = 14.5).

behaviour and weaning success in seals [45,46]; oxytocin also enables social recognition in some mammals [47] and warrants further investigation in the focal species.

Given high expected costs of misdirected parental care [48], we had predicted that northern elephant seal mothers would consistently exhibit strong responses to the calls of their own offspring. While mothers recognized their filial pups, we found significant variability in maternal responses. Some mothers were extremely reactive to their filial pup's calls, while others were more variable during the tripartite testing period. A mother's experience or aggressiveness was not linked to her responsivity. However, females that exhibited consistent responses (either reliably reactive or passive) weaned heavier pups than females showing more variable responses to the calls of their young. It seems contradictory that both behavioural tendencies were associated with pups of greater mass at weaning. Perhaps predictability in maternal responses enables offspring to rapidly learn to alter their behaviour relative to their mother's disposition to maximize feeding efficiency. We suggest that stability in maternal responsiveness may be an important social factor influencing pup well-being and growth, ultimately influencing survivorship after weaning.

Ethics. Research was conducted without harm under authorization of US National Marine Fisheries Service marine mammal permit no. 19801 with approval from the Institutional Animal Care and Use Committee at UC Santa Cruz.

Data accessibility. Data used in this study as well as a description of the data can be found in the external Dryad Dryad Repository: https://doi.org/10.5061/dryad.hmgqnk9h7 [49].

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

Competing interests. We declare we have no competing interests.

Funding. Funding was provided to J.L. by the Fyssen Foundation.

Acknowledgements. The UC Natural Reserve System and Año Nuevo State Park facilitated fieldwork. We thank D. Costa, D. Crocker and P. Robinson for coordinating research activities and E. Levy, G. Faggio, I. Agosto and S. Weindorf for essential support. Several anonymous reviewers provided insightful comments that improved the manuscript.

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Supplement 1. Details of study methods

(a) Population. The study site was located at Año Nuevo State Park, San Mateo County, California, USA (37.121 N, -122.340 W), which includes a 2.7 km^2 shoreline area with ~ 2000 northern elephant seals during the winter breeding season. Data were collected from January – March 2018 and 2019. The image illustrates typical harem density during the breeding season.

(b) Individual identification. Pregnant female elephant seals were marked with alphanumeric codes upon their arrival at the breeding colony by applying black hair dye to their brown coats. Births were directly observed during daytime hours, and the thick black coat of the newborn pups was marked with blonde hair dye following observation of successful nursing. To minimize disturbance, females were marked either while at rest by a hand-held squeeze bottle or with a 1 m pole stamp, while pups were marked with a stencil applied to a 4 m extension pole that was deployed while their mothers were asleep. Image shows marked female with newborn pup.

(c) Acoustic recording. To obtain recordings of spontaneous vocalizations without disturbing mothers or pups we used a Marantz PMD 670 or a PMD 661 digital recorder (sampling rate 44.1 kHz) linked to a Beyerdynamic M69TG microphone that was mounted on a 4 m extension pole; the microphone was gradually positioned 0.7 to 4.5 m from the target pup at a height of 20 cm. A lapel microphone was used to record annotations to a second channel; comments included pup identity, pup age in days, distance and orientation of pup relative to microphone, and behavioural context. Vocalizations were screened for quality and catalogued to create a bank of call for each pup. The image shows a typical pup recording session.

(d) Field experiments. Playback treatments were created with Avisoft SASLab Pro v5.2.12 software and projected from a portable self-powered speaker (JBL Charge3, +/- 5 dB from 0.1-15 kHz) linked to a Bluetooth digital player (iPhone SE). Each treatment included a call series for the filial pup and the non-filial pup such that pups were close in age (+/- 3 days), the behavioural context of the recordings was similar, and the pups were recorded at > 85 m apart. Each call series contained six call examples from the same pup played at a natural rate (~3 s between calls) and amplitude (90 dB SPL @ 5 m). Field experiments were audio/video recorded from a location out of view of the target seals with a Nikon D700 or D800 camera. The image shows the configuration of a typical playback trial, with the speaker position, the target female, and her filial pup indicated by arrows. Corresponding video data of the playback trial is provided in Supplement 3.

Supplement 2. Details of statistical analyses

(a) Principal component analysis of mothers' behavioural responses to longitudinal (weekly) playbacks and early (day 1 or 2) playbacks. Behavioural measures that were the most correlated to PC values are indicated in bold.

Behavioural response measures	**Weekly playbacks**		**1-2 days postpartum playback**	
	PC1	**PC2**	**PC1**	**PC2**
Latency to look towards the speaker (s)	0.33	-0.17	**0.55**	0.14
Latency to move towards the speaker (s)	**0.50**	0.27	0.40	**0.82**
Latency to vocalize (s)	**0.51**	-0.36	**0.83**	-0.40
Latency to sniff the speaker (s)	0.37	**0.79**	0.19	**0.91**
Number of vocalizations	**-0.49**	0.39	**-0.85**	0.29
Eigenvalue	**2.73**	0.85	1.92	1.77
Percentage of variance explained	54.7	17.0	38.4	35.4

(b) Linear mixed model results show that mothers reliably discern the calls of their own pups during lactation but show individual differences in behavioural responses. Model conducted with PC1 score as the response variable; treatment (calls from filial or non-filial pup), timing (week 1, 2, or 3), and interaction between treatment and timing as fixed factors, and treatment presentation order and mother's identity as random factors. The significant outcomes of playback treatment ($F_{1,105}$=52.95) and mother's identity are indicated in bold; * denotes use of Wald *p*-value, n=22 females.

Effect	**Parameter**	**β (Estimate)**	**Std. Error**	**95% Confidence Interval**	***p*-value**
Fixed	Intercept	0.00	0.22	-0.46 – 0.46	1.00
	Timing [Week 1]	0.18	0.15	-0.12 – 0.48	0.24
	Timing [Week 2]	-0.03	0.15	-0.34 – 0.27	0.83
	Treatment [Filial]	-0.78	0.11	-1.00 – -0.57	**<.0001**
	Timing [Week 1] * Treatment [Filial]	0.19	0.15	-0.11 – 0.50	0.20
	Timing [Week 2] * Treatment [Filial]	-0.13	0.15	-0.43 – 0.18	0.41
Random	**Mother's identity**	0.82	0.33	0.17 – 1.48	**0.0139***
	Residual	1.53	0.21	1.19 – 2.05	
	Total	2.36	0.38	1.76 – 3.31	

(c) Linear mixed model showing that female age and aggressivity, as well as pup sex and age, do not influence a mother's responsivity. Model conducted with PC1 score as the response variable and playback treatment, female age, aggressiveness score, pup sex, and playback timing (week) as fixed effects and mother's identity as a random effect. No significant outcomes were identified.

Effect	**Parameter**	**β (Estimate)**	**Std. Error**	**95% Confidence Interval**	***p*-value**
Fixed	Female age	0.08	0.09	-0.1 – 0.3	0.43
	Aggressivity score	-0.53	0.73	-2.0 – 0.9	0.48
	Pup sex	0.12	0.32	-0.5 – 0.7	0.71
	Timing	-0.34	0.24	-0.8 – 0.1	0.35
Random	Mother's identity	0.72	0.51	-0.3 – 1.7	0.16
	Residual	1.18	0.33	0.7 – 2.2	
	Total	1.90	0.54	1.2 – 3.6	