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Original Article

Early-life behavior, survival, and maternal personality in a wild marsupial

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Individual behavior varies for many reasons, but how early in life are such differences apparent, and are they under selection? We investigated variation in early-life behavior in a wild eastern gray kangaroo (*Macropus giganteus*) population, and quantified associations of behavior with early survival. Behavior of young was measured while still in the pouch and as subadults, and survival to weaning was monitored. We found consistent variation between offspring of different mothers in levels of activity at the pouch stage, in flight initiation distance (FID) as subadults, and in subadult survival, indicating similarity between siblings. There was no evidence of covariance between the measures of behavior at the pouch young versus subadult stages, nor of covariance of the early-life behavioral traits with subadult survival. However, there was a strong covariance between FIDs of mothers and those of their offspring tested at different times. Further, of the total repeatability of subadult FID (51.5%), more than half could be attributed to differences between offspring of different mothers. Our results indicate that 1) behavioral variation is apparent at a very early stage of development (still in the pouch in the case of this marsupial); 2) between-mother differences can explain much of the repeatability (or “personality”) of juvenile behavior; and 3) mothers and offspring exhibit similar behavioral responses to stimuli. However, 4) we found no evidence of selection via covariance between early-life or maternal behavioral traits and juvenile survival in this wild marsupial.

Key words: animal personality, early-life behavior and survival, macropods, maternal variance, multivariate Bayesian statistics.

INTRODUCTION

Behavior varies both within and between individuals. Interest in consistent behavioral differences between individuals has generated the field of animal “personality,” and with it substantial research on the causes and consequences of individual behavioral variation (Laskowski et al. 2022). These differences may be family-specific: for any trait, behavioral, or otherwise, offspring of different mothers (referred to here as “non-siblings”) are likely to differ in phenotype due both to differences in the genes they have inherited, and to maternal effects, which may be genetic or environmental (Mousseau and Fox 1998; Räsänen and Kruuk 2007). For behavioral traits, differences between offspring of different mothers may contribute to repeatable individual variation and,

hence, to measures of individual personality. The extent of this maternal-level variation can be estimated using the same variance-component approach used to estimate individual repeatability of behavioral traits from between-individual variance in behavior (Dingemanse and Dochtermann 2013). If heritable genetic or maternal effects are important sources of individual differences (Taylor et al. 2012; White and Wilson 2019; Zabolocki-Thomas et al. 2019), they will play an important role in determining offspring behavioral repeatability. In mammals, maternal effects are especially important for early-life traits but typically decline as offspring age (e.g. Wilson and Réale 2006; Gauzere et al. 2020), thus maternal effects on offspring behavior may play an especially important role early in offspring life. Understanding the causes of variation in behavior is particularly relevant when behavioral differences have fitness consequences (Smith and Blumstein 2008). If variation in behavior is associated with differences in survival or reproduction,

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pouch. We then extracted the young from the pouch for measurement and tagging, and while we weighed the mother. We returned the young to the pouch after an average of 8 min. As described below, we scored the behavior of each young during its short removal from the pouch. We also did not measure behavior of the mother within a few days following capture.

Definitions of traits

We recorded data on four traits: 1) movement of PY during handling at capture; 2) FID, of subadults aged 13–35 months; 3) FID of adult females; and 4) survival of subadults to weaning at 21 months. We describe these in turn below; summary statistics and sample sizes for each trait are given in Table 1.

1) PY movement

We assessed PY behavior by scoring body movements across eight stages of handling at the point of capture of the mother: extraction from the mother's pouch, placement of the offspring inside a cloth bag, weighing, collection of three body measurements (foot, hind leg, and head length), tagging, and being held briefly inside an observer's jacket (for warmth) while the mother was weighed. We recorded 1/0 for any presence/absence of movement at each stage, summed these values across all points to a maximum of 8, then divided by 8 to estimate an individual score ranging from 0 to 1. For practicality, in 2019, we combined responses for foot and hind-leg length measurements and for extraction from the pouch and placement inside a cloth bag, to give a total of only six stages of handling, but again deriving a 0–1 score. The mean total duration of the handling process across all years was 7.9 (± 1.9 SD) minutes. The PY data (PY movement) were assessed for the 2017, 2018, and 2019 cohorts, at 6.4–10.8 months of age. The average score of PY Movement was 0.47 (± 0.24 SD, range 0–1). All analyses of PY Movement included age at capture (mean 8.0 ± 0.8 SD months) as a covariate in the model, to account for any changes in behaviour with age.

2) Subadult FID and (3) Adult Female FID

We measured FID of subadult offspring (age range 13–35 months) and of adult females, as the distance to the nearest metre at which a kangaroo moved away when approached by a human (Strong et al. 2017). High values of FID indicated a response

to the approaching human at a greater distance, whereas low values indicated that the individual allowed the human to come closer before it moved, implying a “bolder” response. The observer started at 30 m from a target kangaroo that was positioned alone or in the periphery of a group, walked directly toward that individual at a constant pace, and stopped when the individual took flight. The terrain was flat and there were no obstructions that could limit the view of the approach. We tested one individual per group per approach, in group sizes of 1 to 6. In groups, the target individual was always the closest to the observer. We always tested mothers and their offspring on different dates, and we also always avoided tests when they were within 3 m of each other. FID measures were made in 2017, 2018, and 2019. Juveniles from the 2016 and 2017 cohorts thus had their responses measured at ages 1 and 2 years, whereas juveniles from the 2018 cohort were measured at age 1 year only. The 2019 cohort was not tested for FID. We measured the FID of 156 adult females between 2017 and 2019; of these 156 females, we also had measures of PY Movement or Subadult FID measures of 87 (Table 1).

For all measures of FID, we also noted the date, time, geographic position, group size, and the presence of the mother or an offspring in the same group when applicable. Geographic positions were recorded with a Garmin® GPSMAP 64 device, as an east–west coordinate in meters. To determine membership of groups, we followed a “10-m chain rule” (Jarman 1987; King et al. 2015), so individuals were considered to be in the same group if they were within 10 m of at least one other group member. “Group size” was the number of individuals aged 1+ years in a group. For each individual being tested for FID, we also classified the presence of its mother or an offspring within the group as a factor: alone, that is, neither a mother nor an offspring present; mother present (for 1-year-olds and 2-year-olds); small PY present (for adult females); medium PY present (for adult females); large PY present (for adult females); and 1-year-old offspring (for adult females). To avoid an extra parameter in the models, the rare cases of a female with both a PY and a yearling were considered within the class of their PY if carrying a large PY, but within the class of 1-year-old offspring if carrying a small or medium-stage PY. Subadults were tested with their mother in the same group in 31.4% of tests, but never at the same time. For adult females, 20.9% of the tests were with a small PY, 6.6% with a medium PY, 18.7% with a large PY, 9.4% were with a

Table 1.
Means, standard deviations, and sample sizes for all traits.

Trait	Number of observations	Number of individuals	Mean # of observations per individual	Number of mothers	Mean # of young per mother	Trait mean
Pouch Young (PY) Movement (score 0–1)	126	126	1	87	1.4 (± 0.6)	0.47 (± 0.24)
Subadult Flight Initiation Distance (meters)	490	107	4.6 (± 2.2)	86	1.2 (± 0.5)	6.6 (± 4.4)
Adult Female Flight Initiation Distance (meters)	875	156	5.6 (± 3.2)	–	–	6.6 (± 3.7)
Subadult Survival (binary)	181	181	1	111	1.6 (± 0.8)	0.67 (± 0.47)

Pouch Young Movement is a score from 0 to 1 (see “Methods” section); FID is in meters (m); Subadults consists of individuals aged 13–35 months. Subadult Survival scores survival from 6 to 21 months (0 died, 1 survived). Subadult Survival data includes but is not limited to individuals in the PY Movement and Subadult FID datasets. The mean difference in age between siblings of the same mother was 1.7 (± 0.7) years (range 1–3 years).

where “var_Residual” = 1, and “var_Binomial sampling” is the variance related to binomial sampling (Nakagawa and Schielzeth 2010; de Villemereuil et al. 2016).

We used Model I (the four-trait model) to estimate the covariances between the four traits. In particular, we estimated maternal-level covariance between the Mother ID effects, for all behavioral responses, to test for maternal-level associations across offspring traits (e.g. do mothers whose offspring have high PY Movement also have offspring with high FID?), and for associations between maternal FID and offspring average behavior and Subadult Survival (e.g. do mothers with a high FID have offspring with high PY Movement, and do they have offspring with high survival rates?). We also fitted residual covariances for offspring traits to test for within-mother-offspring-level associations (e.g. for an individual offspring is high PY Movement associated with high FID?). For the random effect Mother ID, a covariance matrix between traits was set using an unstructured covariance structure in MCMCglmm (Hadfield 2017). We also fitted the covariance for the residual variance-covariance of the three offspring traits. We could not estimate residual covariance with the Adult Female FID because this was the only trait measured on adults, so we fixed this covariance to zero.

Model II was a bivariate model for Subadult FID and Adult Female FID, and was used to estimate the contribution of between-mother variation to the repeatability of juvenile behavior, and also the covariance between mother and offspring FID. This model included multiple measures on each offspring for Subadult FID (average 4.6 observations per individual, range 1–10; Table 1). For the response variable Subadult FID, we fitted random effects of Mother ID and Offspring ID, and for the response variable Adult Female FID, we fitted a random effect of Mother ID. For both traits, we fitted the fixed effects of GPS location along the east–west axis, group size, presence of the mother or offspring, test number, the number of days from the previous test, and year. Further, for Subadult FID, we fitted fixed effects of age at observation (in months, as a covariate) and sex, and for Adult Female FID, a two-level effect of observer.

As in Model I, we fitted the covariance between the Mother ID effects across the behavioral responses. We fixed the covariance to zero for the residual effects, as there could be no covariance across the two traits in within-individual effects.

Both Models I and II were run for 1300×10^3 iterations, with a burn-in of 300×10^3 , a thinning interval of 1×10^3 and an inverse-Wishart prior distribution. We report the posterior distribution mode and 95% CIs for each parameter, considering there to be statistical support for the covariance of random effects if the 95% CIs did not overlap 0 and, for fixed effects, if p MCMC (Probability of Markov Chain Monte Carlo) was <0.05 .

For Subadult FID in Model II, we estimated *maternal repeatability* by dividing the variance between mothers (Mother ID variance) by the total variance, and *individual repeatability* by dividing the variance between offspring (Offspring ID variance) by the total variance as above. For Adult Female FID, we estimated *individual repeatability* by dividing the variance between individuals (Mother ID variance) by the total variance. Model II only had Gaussian-family traits, so unlike Model I, we did not need to convert repeatability to the data scale in Model II.

In the Subadult FID response, we then estimated *total repeatable* variance between individuals from the variance between mothers plus the additional variance between offspring, and hence a *total repeatability* by dividing this sum by the total variance:

$$\begin{aligned} &\text{Total repeatability in subadult FID} \\ &= \frac{\text{var_Mother} + \text{var_Offspring}}{\text{var_Mother} + \text{var_Offspring} + \text{var_Residual}} \end{aligned} \quad (3)$$

Finally, we estimated the proportion of total repeatability (offspring plus maternal variance, as in a model without Mother ID between-mother variance would be attributed to between-offspring variance) that could be ascribed to maternal-level effects as:

$$\begin{aligned} &\text{Maternal proportion of total repeatability} \\ &= \frac{\text{var_Mother}}{\text{var_Mother} + \text{var_Offspring}} \end{aligned} \quad (4)$$

Mother-offspring regression for FID

We did not have a sufficiently informative multi-generational pedigree to estimate heritability of FID from a quantitative genetic “animal model” (Kruuk 2004). Instead, we used the estimates of the phenotypic covariance between mothers’ and offspring’s FID to calculate the mother-offspring regression slope, and hence (having doubled the estimate; Falconer and Mackay 1996) to provide an upper limit on the heritability upper h^2 (Falconer and Mackay 1996), noting that this is very likely to be inflated by maternal or shared environmental effects (Lande and Price 1989; Kruuk and Hadfield 2007):

$$\text{upper_}h^2 = 2 \times \frac{\text{cov}(\text{Mother}, \text{Offspring})}{\text{var_Mother}} \quad (5)$$

Note that both Models I and II provided estimates of the covariance between mothers and offspring in FID and the variance between mothers, and hence an estimate of the regression slope. We opted to use the estimates from Model II only to calculate upper h^2 , as it was a more detailed FID model, using the repeated measures for both mothers and offspring. We estimated the upper h^2 , as described above, for each sample of the posterior distribution, and report the resulting posterior mode and 95% CI.

Finally, we made use of the (rare) occurrence of adoption in kangaroos (King et al. 2015) and examined the association between mothers and offspring in six cases of adoption in 2016 and 2017: 4 involving reciprocal switches and 2 involving mothers whose biological young disappeared. All adoptions occurred when PYs were aged 8–10 months. The adoptive mother was responsible for all subsequent maternal care until weaning, about 6–9 months later (King et al. 2015). We repeated the analysis of the association between Adult Female FID and Subadult FID using observations on adopted individuals for which we had measured FID for the young and both the biological and adoptive mothers. Despite the very small sample size, this analysis could potentially indicate the relative importance of genetic and non-genetic causes of similarity in behavior.

RESULTS

We present below the results from the two models addressing our four questions. The main results for Model I (the four-trait model) are in Table 2 and Figure 1, and the main results for Model II, focusing on FID, are in Table 3 and Figure 2; further details for both models are available in Supplementary Tables S1 and S2.

Table 2.**Summary of the four-trait Model I, analyzing repeatability in the behavior of eastern gray kangaroos, with response variables**

	PY Movement		Subadult FID		Subadult Survival		Adult Female FID	
(a) Fixed effects	Estimate	<i>p</i> -MCMC	Estimate	<i>p</i> -MCMC	Estimate	<i>p</i> -MCMC	Estimate	<i>p</i> -MCMC
Intercept	0.16 (−0.62, 0.88)	0.662	5.56 (4.47, 6.67)	<0.001	1.02 (0.08, 1.85)	0.022	−1.10 (−8.56, 7.65)	0.778
Sex (Female)	0.09 (−0.04, 0.22)	0.200	0.50 (−0.87, 1.74)	0.418	−0.41 (−1.30, 0.43)	0.360	–	–
Year (base 2017)								
–2018	−0.15 (−0.29, 0.02)	0.076	1.58 (0.28, 3.08)	0.026	−0.40 (−1.42, 0.86)	0.478	0.10 (−0.64, 0.85)	0.746
–2019	0.08 (−0.05, 0.23)	0.240	2.51 (1.14, 3.99)	0.004	2.62 (0.56, 4.79)	0.004	0.98 (−0.43, 2.52)	0.164
–2020	–	–	–	–	0.28 (−0.67, 1.38)	0.592	–	–
(b) Random effects	Variance–covariance matrices							
	PY movement		Subadult FID		Subadult Survival		Adult female FID	
Mother ID								
PY Movement	0.10 (0.07, 0.14)							
Subadult FID	−0.04 (−0.34, 0.23)		7.89 (2.90, 13.54)					
Subadult Survival	−0.01 (−0.13, 0.11)		1.25 (−0.84, 3.38)		1.54 (0.30, 3.33)			
Adult Female FID	−0.03 (−0.25, 0.21)		5.11 (2.40, 7.66)		0.76 (−0.58, 2.06)		4.94 (3.37, 6.67)	
Residual								
PY Movement	0.08 (0.05, 0.10)							
Subadult FID	0.00 (−0.23, 0.23)		7.56 (4.57, 11.61)					
Subadult Survival	0.00 (−0.08, 0.09)		0.05 (−2.16, 2.25)		Fixed to 1			
Adult Female FID	–		–				8.54 (7.74, 9.47)	
(c) Variance proportions	PY Movement		Subadult FID		Subadult Survival (latent scale)		Adult Female FID	
Maternal repeatability	58.5% (46.7%, 68.1%)		59.2% (26.4%, 75.7%)		64.1% (34.3%, 82.9%)		4.1% (1.6%, 11.4%)	
Residual (latent scale = overdispersion on data scale)	–		–		36.0% (17.1%, 65.7%)		–	
Residual (data scale)	41.5% (31.9%, 53.3%)		40.8% (24.3%, 73.6%)		–		92.1% (88.1%, 98.8%)	

PY Movement ($n = 126$), Subadult FID (one average value per individual, $n = 107$), Subadult Survival ($n = 181$), and Adult Female FID ($n = 156$). We show only the fixed effects of sex and year as they were more important for our questions in this study; see Supplementary Table S1 for estimates of all variables included in the model. (a) fixed effects of sex and year for each response variable. The “base” level for sex is male, and for year is 2017. (b) random effects: (co) variance estimates from posterior distribution mode and respective 95% CI in parentheses; variances are on the diagonal and covariances below diagonal. (c) Estimates of individual and maternal repeatability (posterior mode) followed by the 95% CI in parentheses. “–” indicates that the variable was not fitted in the model. Bold indicates p MCMC (Markov Chain Monte Carlo) < 0.05 for fixed effects or that the CIs were separated from zero for random effects and repeatability estimates. In (c), the “maternal repeatability” means “individual repeatability” for the Adult Female FID traits (see main text), and we included data on all adult females, not only mothers of subadults in the sample.

1) Do siblings behave similarly to each other and differently from non-siblings?

We found support for maternal repeatability in both PY Movement and Subadult FID (Table 2b, Supplementary Table S1, and Figure 1). PY Movement and Subadult FID had maternal repeatability of 58.5% and 59.2%, respectively (Table 2c), with CIs clearly separated from zero, so the majority of variance in these offspring traits could be ascribed to different mothers. For Subadult Survival, maternal repeatability accounted for a large part of the total variation on the latent scale (64.1%, Table 2c). When we back-transformed the GLMM latent-scale estimates for Subadult Survival to proportions on the data-scale, adding the stochastic variation associated with moving from the expected to observed data scale (Nakagawa and Schielzeth 2010; de Villemereuil et al. 2016), the overall maternal repeatability estimates decreased to 4.1%, but with CIs still separated from zero (Table 2c). The back-transformation thus illustrates the dramatic change in estimates of proportions depending on whether estimates are considered on latent versus data scales.

2) Is either offspring early-life behavior or maternal behavior associated with offspring survival to weaning?

Considering the covariances estimated in Model I, there was no support for any association of either offspring or maternal behavioral traits with Subadult Survival. This was the case both across mothers (Table 2b, “Mother ID” covariance), in that there was no indication that groups of siblings with higher average levels of PY Movement or Subadult FID had higher (or lower) average Subadult Survival, nor within mothers (Table 2b, “Residual” covariance), as there were no associations at the level of individual offspring.

From the estimates of the other covariances in Table 2b, there was also no support for any association between offspring behavior at the different life stages, namely between PY Movement and Subadult FID (Table 2b). The covariance between Subadult FID and Maternal FID was large, however, and we consider this association in more detail with Model II below.

3) Do maternal effects contribute to the repeatability of offspring behavior?

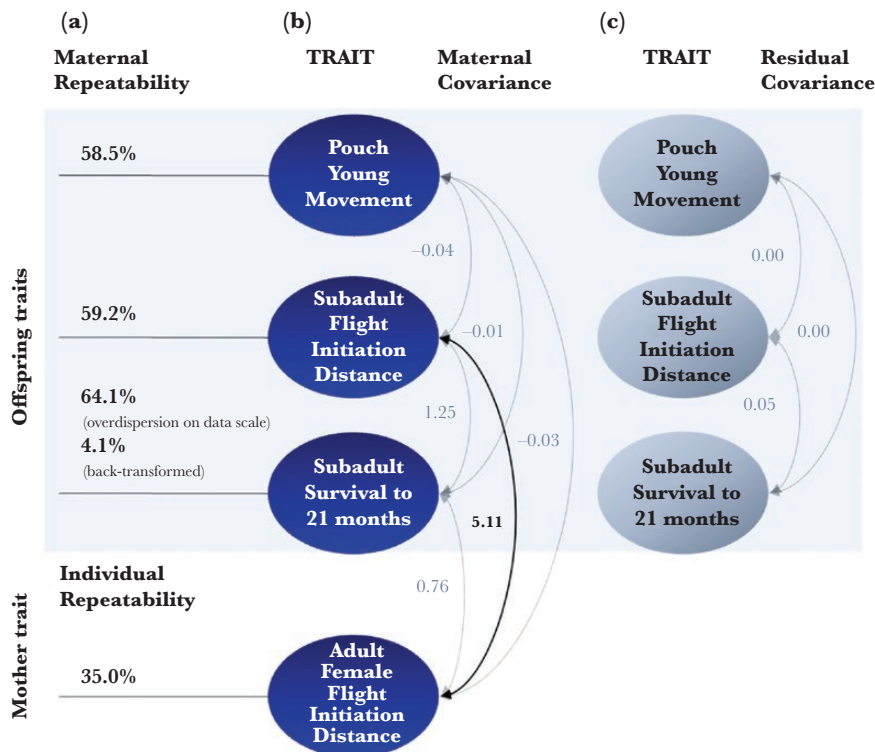


Figure 1. Mother and offspring (co)variances estimated from Model I (Table 2) for eastern gray kangaroos. (a) *maternal repeatability* estimates for offspring traits, and *individual repeatability* for Adult Female FID (Table 2c), (b) maternal-level covariances across offspring and mother traits (Table 2b), (c) residual (offspring-within-mother) covariances across offspring traits (Table 2b). Bold indicates statistical support for non-zero estimates of the parameter. Arrows link pairs of traits for which covariance estimates are shown.

Table 3. Random effect results from the bivariate Model II, using repeated measures of FID for each juvenile ($n = 107$) and adult female kangaroo ($n = 156$).

	Subadult FID	Adult female FID
(a) Random effects (variance and covariance estimates)		
Offspring ID variance	3.61 (1.55, 6.37)	–
Mother ID: variance–covariance matrix		
Trait: Subadult FID	4.97 (1.45, 8.63)	
Trait: Adult Female FID	4.14 (1.98, 6.11)	4.78 (3.07, 6.44)
Residual variance	8.11 (7.08, 9.45)	8.50 (7.70, 9.45)
(b) Variance proportions		
Maternal repeatability	27.5% (12.4%, 45.7%)	–
Individual repeatability	21.6% (9.3%, 37.1%)	38.9% (27.5%, 45.1%)
Residual	48.5% (37.7%, 60.3%)	61.1% (54.9%, 72.5%)
Total repeatability	51.5% (39.7%, 62.3%)	
Maternal proportion of total repeatability	55.3% (26.6%, 80.4%)	–

Fixed effect parameters are in Supplementary Table S2. (a) Random effect variance–covariance estimates. (b) Proportions of total variance contributed by maternal, individual, and residual variances. Total repeatability is defined as the sum of between-mother (maternal repeatability) and between-individual (individual repeatability) proportions. Estimates are followed by the 95% CIs in parenthesis.

Model II focused on the repeated measures of FID in both offspring and mothers (Table 3). Maternal repeatability was 27.5% for Subadult FID in this model (Table 3b), lower than the value estimated in Model I, possibly due to the averaging within offspring for Model I. A further 21.6% of the variance was due to differences between individuals (“individual repeatability” over and above maternal repeatability, Table 3b), so the “total repeatability” of Subadult FID was 51.5%. Variation between mothers, therefore,

accounted for 55.3% (95% CI: 26.6%, 80.4%) of the total repeatability of Subadult FID. The individual repeatability of Adult Female FID was 38.9% (Table 3b).

4) Are maternal and offspring behaviors correlated, and do these associations differ for biological vs adoptive mothers?

We found a strong association between measures of FID of mothers and their offspring (Figure 2; FIDs were always estimated at different

(Onyango et al. 2008). Maternal sociality is linked with offspring mortality via infanticide in white-faced capuchin monkeys (*Cebus capucinus*; Kalbitzer et al. 2017).

In subadult FID, we found that 55% of the total repeatability was explained by differences in the mothers of the juveniles (maternal repeatability) compared to less than half being explained by differences between juveniles themselves (individual repeatability). To our knowledge, only a few studies to date have tried to isolate such effects during repeatability estimation (Taylor et al. 2012; White and Wilson 2019; Zablocki-Thomas et al. 2019). This separation is important because genetically and/or environmentally induced effects can contribute to differences between individuals. Some researchers recommend not to “correct” for intrinsic or extrinsic sources of individual heterogeneity when analyzing personality, as these may be relevant to the individual differences observed in the population (Wilson 2018). However, it is still valid to ask how much of the total repeatability is actually due to maternal influences, in the same way as analyses may consider how much of repeatability is due to sex, age, or environmental effects (Bell et al. 2009).

Furthermore, in subadult FID, we found support for covariance with mothers' FID (arguably a measure of personality; Figure 2). Despite the rapid expansion of the animal personality field (Beekman and Jordan 2017), the investigation of how maternal personality contributes to offspring trait variation has received less attention (Reddon 2012; Schuett et al. 2013). In mammals, most investigations into heritability of personality have been restricted to primates and ungulates (Dochtermann et al. 2019). Our analyses estimate an upper limit on the heritability of FID based on the regression of offspring values on maternal values. We only had information on the resemblance between mothers and offspring, though ideally, we would have fitted a model estimating both additive genetic variance and maternal effects variance separately, to separate the shared-genes effects from maternal environmental effects (Kruuk and Hadfield 2007). Some studies of personality using this approach have found support for heritability of behavioral traits (Taylor et al. 2012; Dochtermann et al. 2015; Zablocki-Thomas et al. 2019). Given the definition of heritability as the proportion of total phenotypic variance due to additive genetic variance (Falconer and Mackay 1996), the value of heritability should lie between 0 and 1. Our results show an unrealistically large upper-limit heritability estimate (substantially >1), presumably because environmental effects inflated similarities between mothers and offspring. Our regression has also not been age-standardized, with the maternal and offspring phenotypes being measured at different ages, which may affect the upper-limit estimates (Chevin 2015). A study on zebra finches (*Taeniopygia guttata*) cross-fostered offspring and found that “personality” variation arose primarily as a maternal effect derived from the foster mother, indicating that shared environmental effects may be more important than genes in shaping personality variation in that system (Schuett et al. 2013). For the few cases of adoption in our population, the covariance of offspring with the foster mother was nearly twice as large as that with the biological mother, indicating a similar trend to that found in zebra finches, but high uncertainty precluded meaningful conclusions. If we ignore the uncertainty due to small sample sizes and consider the biological mother association as the better estimate of heritability, the upper-limit heritability estimate is around 70% for FID; however, this estimate may still be confounded by environmental and maternal effects prior to the adoption. Future analyses with genomic data for the

study population will allow us to separate the different environmental and genetic factors contributing to phenotypic variance in eastern gray kangaroos.

Several aspects of the environment could cause mothers and offspring to have similar personalities. Mother and offspring share physical and social environments, particularly when the juvenile is 10–18 months old, as they are closely associated before weaning (King and Goldizen 2016). As we did not find any correlation between mother's FID and offspring behavior when the young were in the pouch (PY movement, measured at ~8 months old), it is possible that the offspring learn a level of responsiveness to threats from their mother during the first days after pouch exit (~10-month-old), a critical life stage (Breed and Sanchez 2010). After that stage, the offspring behavior does not seem to change with age or conditions. We always tested mother and offspring FID responses at different times and in most cases when they were not grouped together. Subadult FID did not change with age (across the period 1–2 years old, changing from dependent to independent of maternal care) and the presence of the mother in the group did not affect the subadult FID (Supplementary Table S2). In the minority of cases when they were in the same group, both did not always take flight, and when both did, sometimes the young fled first, other times the mother did. Therefore, the similarities in FID are likely not the result of the offspring copying their mother's immediate behavior during the test (or vice versa), but possibly suggest that offspring FIDs are learned early in life and/or inherited. A laboratory study on a lizard, *Liopholis whitii* (Munch et al. 2018), housed offspring either with their mother or alone during the first 8 weeks of life and found that maternal presence affected juvenile expression of three key behaviors (latency in time until offspring emerged after a threat, time spent moving in the familiar environment, and time spent moving in a novel environment) compared to individuals housed alone. The lizard study did not quantify the similarities in behavior between mother and offspring in either treatment but provided evidence that even relatively simple forms of mother–offspring association early in life can significantly impact offspring behavioral phenotypes.

In conclusion, our study revealed that variation in behavior and early survival of juveniles is influenced by differences between offspring of different mothers and that these maternal differences also explained a large part of individual differences in the personalities of a wild marsupial. Juvenile behavior covaried with maternal behavior, with the similarity potentially driven by both genetic and shared environmental effects. Mothers are an important source of variation in behavior and survival of juveniles, and more studies using multivariate approaches will contribute to our understanding of the causes and consequences of variance and covariance between individuals in their behavior at different stages of life.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

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CONFLICT OF INTEREST:

The authors affirm that they possess no identifiable financial conflicts of interest or personal affiliations that could be perceived as exerting influence over the research presented in this paper.

DATA AVAILABILITY:

Analyses reported in this article can be reproduced using the data provided by Menário Costa et al. (2023). Statistical code is provided in the Supplementary Material.

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