

## Article

# Nonlinear maternal effects on personality in a rodent species with fluctuating densities

Bram VANDEN BROECKE<sup>a\*</sup>, Aurelia BONGERS<sup>a</sup>, Ladslaus MNYONE<sup>b</sup>, Erik MATTHYSEN<sup>a</sup>, and Herwig LEIRS<sup>a</sup>

<sup>a</sup>Evolutionary Ecology Group, Department of Biology, University of Antwerp, Antwerp, Belgium and

<sup>b</sup>Pest Management Centre, Sokoine University of Agriculture, P.O.Box 3110 Chuo Kikuu, Morogoro, Tanzania

\*Address correspondence to Bram Vanden Broecke. E-mail: bram.vdbroecke@gmail.com.

Handling editor: Claudio Carere

Received on 2 May 2020; accepted on 16 June 2020

## Abstract

Consistent among-individual variation in behavior, or animal personality, is present in a wide variety of species. This behavioral variation is maintained by both genetic and environmental factors. Parental effects are a special case of environmental variation and are expected to evolve in populations experiencing large fluctuations in their environment. They represent a non-genetic pathway by which parents can transmit information to their offspring, by modulating their personality. While it is expected that parental effects contribute to the observed personality variation, this has rarely been studied in wild populations. We used the multimammate mouse *Mastomys natalensis* as a model system to investigate the potential effects of maternal personality on offspring behavior. We did this by repeatedly recording the behavior of individually housed juveniles which were born and raised in the lab from wild caught females. A linear correlation, between mother and offspring in behavior, would be expected when the personality is only affected by additive genetic variation, while a more complex relationship would suggest the presence of maternal effects. We found that the personality of the mother predicted the behavior of their offspring in a non-linear pattern. Exploration behavior of mother and offspring was positively correlated, but only for slow and average exploring mothers, while this correlation became negative for fast exploring mothers. This may suggest that early maternal effects could affect personality in juvenile *M. natalensis*, potentially due to density-dependent and negative frequency-dependent mechanisms, and therefore contribute to the maintenance of personality variation.

**Key words:** animal personality, exploration, *Mastomys natalensis*, maternal effects, multimammate mice

Consistent among-individual variation in behavior through time and/or across context, or animal personality, has been observed in a wide variety of species (Gosling 2001; Réale et al. 2007; Carere and Maestripieri 2013). Indeed, several studies have shown that this behavioral variation within species is adaptive (Dingemans and Wolf 2010) with potential fitness costs and benefits (Smith and Blumstein 2008). Fluctuating and negative frequency-dependent selection are being considered as the main evolutionary mechanisms responsible for the existence of personality variation (Dall et al. 2004; Boon et al. 2007; Wolf et al. 2007, 2008; Dingemans and Wolf 2010;

Wolf and Weissing 2010, 2012; Bergeron et al. 2013). Meta-analyses have shown that the average heritability of personality traits is relatively high, where 20–50% of the behavioral variation between individuals is due to additive genetic variation (Dochtermann et al. 2015, 2019).

However, this means that 50–80% of the behavioral variation within a species stems from a combination of measurement error, behavioral plasticity, and permanent environmental effects which have long-term impacts on the individuals' phenotype, such as their habitat (Dochtermann et al. 2015). Urban populations of the

European blackbirds *Turdus merula*, for instance, are more neophobic than individuals from rural areas (Miranda et al. 2013), while urban great tits *Parus major* are more explorative and bolder compared with individuals living in forests (Riyahi et al. 2017). Another important environmental effect, which may influence behavioral variation, is conspecific density (Wright et al. 2019). Red squirrels *Sciurus vulgaris*, for example, living in low-density areas are more active and aggressive compared with individuals from high-density areas (Haigh et al. 2017). Indeed, conspecific density has been argued to have a large influence on personality variation among as well as within populations (Le Galliard et al. 2015; Nicolaus et al. 2016; Araya-Ajoy et al. 2018; Wright et al. 2019). The multimammate mice *Mastomys natalensis*, for instance, experiences strong fluctuations in density over a short period of time (Leirs et al. 1994, 1997; Sluydts et al. 2007) which has been shown to affect the composition of the population with respect to personality as density changes (Vanden Broecke et al. 2019).

A special case of permanent environmental factors are parental effects which have been shown to affect the observed phenotypic variation as well, especially for behavioral traits (Groothuis and Carere 2005; Groothuis et al. 2008; Taylor et al. 2012; Groothuis and Dario 2013). For instance, body size of cross-fostered zebra finches *Taeniopygia guttata* was predicted by their genetic parents, indicating genetic inheritance, while this was not the case for their exploration behavior. Instead, this was predicted by the behavior of their non-genetically related foster parent (Schuett et al. 2013). Another example is that risk taking in juvenile Trinidadian guppies *Poecilia reticulata* was strongly influenced by maternal traits, while this effect diminished in adults (White and Wilson 2019). Parental effects are expected to evolve in species living in variable environments, where parents modulate the personality of their offspring in order to increase their fitness (Marshall and Uller 2007; Reddon 2012; Groothuis and Dario 2013). However, the type of modulation depends on the predictability of the environmental conditions in the future (Proulx and Teotónio 2017). When there is either little or no information available about future environmental conditions, parents may use a bet-hedging strategy whereby they produce offspring with a variety of personalities ensuring that some individuals are suited for their environment. Alternatively, when there is information available, parents could predict the future environmental conditions and bias the personality of their offspring in order to make them more suited for that specific environment (Marshall and Uller 2007; Reddon 2012; Proulx and Teotónio 2017; Langenhof and Komdeur 2018). The is commonly referred to as anticipatory parental effects and are expected when, for instance, changes in predation pressure (Storm and Lima 2010; Bestion et al. 2014; Bell et al. 2016), resource availability (Warner and Lovern 2014), or population density (Dantzer et al. 2013) are good predictors of future environmental conditions which allow parent to anticipate on these changes (Marshall and Uller 2007; Reddon 2012; Langenhof and Komdeur 2018). It is therefore expected that parental effects should contribute to the observed personality variation within species experiencing different, yet predictable, environmental conditions between parent and offspring, but this has rarely been studied.

In this study, we used the multimammate mice *M. natalensis* as a model system to investigate the potential effects of the parental personality on the behavior of their offspring. Two personality axes have been described for this species using a hole-board test. The first one is an exploration-activity axis (referred to as exploration) where highly explorative individuals were more active and explored the blind holes more frequently compared with less explorative

individuals. The second personality axis is a grooming–jumping axis (referred to as stress-sensitivity) where high stress sensitive individuals jumped more frequently, but spent less time grooming themselves compared with less stress sensitive individuals (Vanden Broecke et al. 2019). We focused on maternal effects since mothers provide most of the parental care; moreover, multiple paternity has been found in more than 47% of the litters (Kennis et al. 2008). Their reproductive cycle is strongly correlated with seasonal rainfall patterns and starts when food becomes abundantly available (Leirs et al. 1989, 1994, 1997; Sluydts et al. 2007). This leads to strong seasonal and annual fluctuations in density, where the population size changes from 20 to 500 individuals per hectare in just a couple of months (Leirs et al. 1994; Sluydts et al. 2007; Borremans et al. 2017). During this period of increasing density, home range sizes decrease (except for adult females) while home range overlap increases resulting in an increase of foraging contacts and competition among individuals (Borremans et al. 2014, 2017). We therefore expect that mothers can predict these environmental changes and hence adjust the behavior of their offspring in order to increase their fitness in the future environment.

However, these mothers should only alter the personality of their offspring if it increases their fitness (Marshall and Uller 2007). While it is currently unknown if there are potential fitness consequences of personality in *M. natalensis*, more explorative and stress sensitive individuals have been found more frequently at higher densities (Vanden Broecke et al. 2019). This may suggest that increased exploration behavior may be beneficial at higher densities, since it could provide the individual with information about the environment such as the availability of food resources (Tebbich et al. 2009). This information might be crucial for juveniles, since they have been found to be more explorative than adults and even increase their exploration behavior when density increases (Vanden Broecke et al. 2018, 2019). However, it is currently unknown if these differences in exploration behavior between adults and juveniles are purely driven by environmental cues or due to early maternal effects.

In order to test the hypothesis that maternal effects affect variation in juvenile behavior, we raised juveniles in a controlled laboratory setting from wild mothers. These mothers were caught during different time-points in the breeding season, when densities change rapidly, and therefore experienced different levels of population densities. We used this data to test three predictions. 1) If the personality scores are only affected by additive genetic variation, we would expect a linear correlation between maternal personality and that of her offspring, resembling a parent–offspring regression (Falconer and MacKay 1996). 2) A more complex relationship between maternal personality and her offspring is expected when maternal effects, in combination with genetic variation, contribute to the variation in juvenile behavior. On the one hand, we expect that slow exploring mothers, occurring more frequently at low densities (Vanden Broecke et al. 2019), should produce offspring with a fast exploring personality. These fast exploring juveniles should have a competitive advantage in the predicted future environment of increased density and competition for food resources, since food becomes more scarcely available at higher densities (Leirs et al. 1997; Myers 2018). On the other hand, fast exploring mothers are expected to produce less explorative offspring allowing them to invest more resources into survival in order to survive until the next breeding season (Leirs et al. 1993; Réale et al. 2010). 3) Finally, it is possible that exploration behavior in juveniles is not affected by genetic or maternal effects. If this would be the case, we would expect to find no effect of maternal behavior on their offspring and current

environmental conditions will be the main driver of the personality differences between adults and juveniles in *M. natalensis*.

## Material and Methods

### Study species

*Mastomys natalensis* is the most common indigenous rodent in sub-Saharan Africa, an agricultural pest species (Leirs et al. 1994) and host for several diseases such as Lassa virus (Frame et al. 1970), plague (Ziwa et al. 2013), and Morogoro virus (Günther et al. 2009). Two personality traits have been found in this species: exploration and stress sensitivity of which the former has been found to influence viral infection probability (Vanden Broecke et al. 2018, 2019). The analysis of movement patterns during a long-term field study has shown that during periods of high resource availability, home ranges overlap greatly with each other indicating a low level of territoriality and reduced spatial activity (Borremans et al. 2014). The absence of territoriality is in line with the scramble mate competition, where males roam around to find as many females as possible (Kennis et al. 2008). While males are polygynous, females are polyandrous and multiple paternity occurs in more than 47% of the litters (Kennis et al. 2008). The mean gestation period is 23 days and *M. natalensis* is able to produce large litters, with a mean litter size in utero between 11.3 and 12.4 young (Leirs 1995).

### Experimental setup

Pregnant females were trapped from May until July 2017 on three different areas on the main campus of the Sokoine University of Agriculture (SUA) in Morogoro, Tanzania. Due to technical and logistical problems, we were not able to trap for three consecutive nights in a row at a certain location, which is needed to accurately estimate the population density size within a trapping grid. However, the period in which we trapped the pregnant females coincided with the start of the breeding season when the population density is expected to increase rapidly, with a peak in October (Leirs 1995). We therefore believe that females that were captured later in the breeding season would have experienced a larger density compared with those that were captured earlier in the breeding season. In order to avoid spatial dependence, we spaced the three trapping areas at least 2 km from each other (Borremans et al. 2014). Sherman LFA live traps (Sherman Live Trap Co., Tallahassee, FL) were set in the evening in both fallow land and maize fields within each area using a mix of peanut butter and maize flour as bait. Traps were checked in the early morning and captured individuals were transported to the animal facilities of the SUA Pest Management Centre. We recorded the weight, sex, and reproductive status of the trapped rodents following Leirs et al. (1994). Pregnant females were kept solitary in cages (28 × 11.5 × 12 cm, food and water *ad libitum*) in the laboratory for no longer than 80 days after they gave birth. The young were kept together with their mother until they were independent (15–29 days old; Coetzee 1975), after which they were marked, weighed, sexed, and housed in individual cages. Due to variation in litter size and neonate survival, we selected at least two and maximal five individuals of each nest.

Behavioral trials were conducted using a hole-board test, which is based on the open field test with holes in the floor to measure exploration independently of activity (File and Wardill 1975; Martin and Réale 2008b). The box (75 × 55 × 90 cm;  $L \times W \times H$ , respectively) was constructed out of strong white plastic with six blind holes in the bottom ( $\varnothing$ : 3.5 cm; depth: 6 cm) each spaced 19 cm

apart from each other. The box was closed with a lid containing an infrared camera. Behavioral recordings lasted for 10 min and started when the individual was inside the box, and the lid was closed. All behavioral recordings were made during the evening, which coincides with the active period of *M. natalensis* (Coetzee 1975; Borremans et al. 2017), in a completely dark room within the SUA Pest Management Centre. Juveniles were recorded for the first time when they were, on average 26.47 days old (range = 17–52), after which they were housed in individual cages. The box was cleaned with 70% ethanol after each trial to remove scent and dirt. Each individual was tested up to four times (one individual died during the experiment and was observed only three times) and each consecutive test was separated by 2 weeks. The juveniles were released in the area where we captured their mother after the experiment.

### Video analysis

We measured five different behaviors during the hole-board test: activity, hole sniffing, head dips, time spent grooming, and number of jumps using MTrackJ (Meijering et al. 2012), a plugin for ImageJ (Schneider et al. 2012) and JWatcher 1.0 (Blumstein and Daniel 2007). See Vanden Broecke et al. (2019) for a more detailed description of the different behaviors.

All experimental procedures were approved by the University of Antwerp Ethical Committee for Animal Experimentation (LA1100135) and adhered to the EEC Council Directive 2010/63/EU and followed the Animal Ethics guidelines of the Research Policy of SUA.

### Statistical analysis

#### Maternal effects

The fieldwork of this study was performed during the same period, and in collaboration with Vanden Broecke et al. (2019). Therefore, all behavioral measurements in this study were performed using the same hole-board test as described in Vanden Broecke et al. (2019), with animals that were trapped at the same location during the same period. We therefore decided to pool all behavioral measurements from this study with those previously published in Vanden Broecke et al. (2019) which allowed us to compare our results with the previous research. This led to the construction of a dataset of 1001 behavioral recordings of 295 unique individuals. All individuals were recorded on average 3.5 times (range = 2–8 observations) with an average of 17 days between recordings (range = 11–71). In order to reduce the number of variables, we ran a principal component analysis (PCA) on the pooled dataset using the Kaiser–Guttman criterion (eigenvalue > 1; Kaiser 1991; Peres-Neto et al. 2005) to decide on the number of components to retain. After the PCA, we removed all datapoints from Vanden Broecke et al. (2019) and used the original dataset for further analysis.

During this experiment, we conducted a total of 255 behavioral observations involving 65 unique juvenile individuals from 18 different mothers. Individuals were recorded four times, except one individual who was recorded three times, with on average 13.4 days between subsequent recordings (range = 11–15). However, one nest was identified as an outlier and had a disproportional large influence on the results and was therefore removed from the analysis.

We used generalized additive mixed models (GAMMs; Zuur et al. 2009; Wood 2017) to study the effects of maternal personality on their offspring's behavior. This was done because an exploratory data analysis suggested a non-linear relationship between the response and explanatory variables. GAMMs are a combination of

linear mixed models (LMMs) and generalized additive models allowing to estimate random effects as well as linear and non-linear covariates within one model (Zuur et al. 2009; Wood 2017).

We ran two models using either exploration or stress sensitivity as dependent variables. For both variables we started first with a full model where we included the individual's sex (male or female) and age in days (which was within-individual centered: deviation of one observation from the individuals' mean; van de Pol and Wright 2009) as fixed effects. The former was included to look for potential differences in behavior due to sex, while the latter allowed us to look at group-level plasticity. However, it is unclear if this group-level plasticity is due to increasing age or habituation to the hole-board test since the individuals became older the more they were recorded and it is therefore impossible to distinguish these two effects from each other. In order to test for potential maternal effects, we included the personality of the mother (average exploration behavior or average stress-sensitivity in the model with, respectively, exploration or stress-sensitivity as response variables) as additional fixed effect with a smoother function to look for a potential non-linear relationship between the personality of the mother and the behavior of her offspring. Finally, we added the date when we captured the mother as an additional fixed effect. This would allow us to test if only the density that the mother experienced before being brought to the laboratory would affect the behavior of her offspring. We included the field of origin of the mother as a random effect in order to test if it was the mother's environment rather than maternal personality per se that affected the phenotypical variation between individuals. Additionally, we included *M. natalensis* identity (ID) as a random effect to account for pseudo replication, because we repeatedly sampled each individual. Finally, individual variation in plasticity was estimated by including age (within-individual centered) as a random slope (Dingemans and Dochtermann 2013). Significance of the random effects was tested using a likelihood ratio test (LRT) comparing the model with and without the random effect, a  $P$ -value  $< 0.05$  indicates that it explained a significant amount of the variance, non-significant random effects were removed from the final model.

#### Personality–density

The main assumption in our study is that more explorative and stress sensitive mothers would occur more frequently at higher densities, as has been found in Vanden Broecke et al. (2019), resulting in a positive correlation between density and the mean exploration and mean stress-sensitivity of the mother. In order to test this, we created two LMMs with either average exploration or average stress-sensitivity of the mother as response variables. We included the date that the mother was captured as a fixed effect which we used as an alternative for density, since we assumed that individuals that were captured later in the breeding season experienced higher population densities. Indeed, all the individuals were captured during the breeding season in which the population density increases rapidly through time (Leirs 1995). The area where the mother originated from was included as a random effect. However, our analysis showed no correlation between date of capture and mean exploration or stress-sensitivity behavior of the mother (see the “Results” section) due to a low sample size ( $N = 17$ , one mother was removed as it had been identified as an outlier). We therefore created a larger dataset including all animals that were captured on the same three locations and whose behavior was first recorded in the laboratory. This led to a dataset of 50 unique individuals ( $N_{\text{males}} = 11$ ,  $N_{\text{females}} = 39$ ). We reran the LMMs as described above, with sex as an

additional fixed effect. All continuous covariates were centered around their grand mean before analysis and all statistical analyses were executed using R software 3.6.0 (R Core Team 2013) with the R packages “gamm4” (version 0.2-5; Wood and Scheipl 2017) and “lmer4” (version 1.1-21; Bates et al. 2015).

## Results

### Principal component analysis

The PCA reduced the number of behavioral variables to two components, explaining 66.45% of the total variance (Table 1). The loadings of both components were very similar as previously found in Vanden Broecke et al. (2019) except for the directions, which were reversed. We therefore multiplied both components with  $-1$  allowing us to compare our results with those from Vanden Broecke et al. (2019). The first component was positively correlated with activity, hole sniffing, and head dipping and can be seen as an activity-exploration axis and will further be referred to as “exploration” (Table 1). The second component was negatively correlated with auto-grooming and positively with jumping. We named this second component “stress-sensitivity” (Table 1), in line with Vanden Broecke et al. (2019).

### Exploration

The GAMM with exploration as dependent variable revealed that there was a significant non-linear correlation between the exploration personality score of the mother and of her offspring (Table 2 and Figure 1). The model showed a positive correlation between offspring and maternal exploration behavior, but only for slow and average exploring mothers. Fast exploring mothers, on the other hand, produced offspring with a lower exploration score compared with their mother (Figure 1). Additionally, we found evidence for group-level plasticity, where individuals became less explorative when they became older (Table 2 and Figure 2). However, it remains unclear if this is an age effect or if they habituated to the test. Interesting is that this effect differed between individuals since the random slope was significant (Table 2) with a positive intercept-slope correlation. This suggests that there is individual variation in plasticity based on the individuals' personality, where slow exploring individuals decreased their exploration behavior inside the hole-board test faster than average when they became older compared with fast exploring juveniles (Figure 2). We found no statistical difference between males and females in exploration behavior (Table 2). Maternal origin did not explain a significant amount of

**Table 1.** Correlation of each behavior observed during the hole-board test with the components of the PCA (all the values were multiplied with  $-1$ )

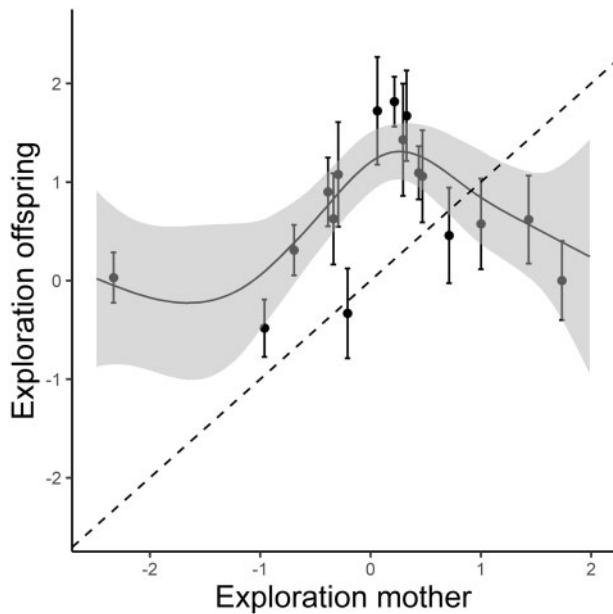
Component	PC1 (exploration)	PC2 (stress-sensitivity)
Activity	0.552	-0.111
Head dip	0.454	-0.069
Sniffing	0.584	-0.321
Grooming	-0.336	-0.517
Jumping	0.116	0.783
Total variance (%)	42.35	24.10
Eigenvalue	2.117	1.205

Notes: The two components were named, respectively, exploration and stress-sensitivity. Bold type indicated the behaviors that have a major contribution to the component.

**Table 2.** Results from the two GAMMs with either exploration (PC1) or stress sensitivity (PC2) as dependent variables

Fixed (linear) effects	PC1 (exploration)			PC2 (stress-sensitivity)		
	Est±SE	t-Value	P-value	Est±SE	t-Value	P-value
Intercept	0.796±0.178	4.478	<b>&lt;0.001</b>	-0.544±0.068	-7.998	<b>&lt;0.001</b>
Sex (male)	-0.137±0.252	-0.547	0.585	-0.053±0.106	-0.503	0.616
Age (mean centered)	-0.299±0.093	-3.206	<b>0.002</b>	0.008±0.034	0.226	0.822
Capture date mother	0.159±0.136	1.167	0.245	0.048±0.055	0.871	0.385
Fixed (non-linear) effects	Smooth	F-value	P-value	Smooth	F-value	P-value
Exploration mother	3.536	3.449	<b>0.007</b>	-	-	-
Stress sensitivity mother	-	-	-	2.514	1.938	0.080
Random effect	Variance	Corr.	P-value	Variance	Corr.	P-value
Individual	0.960	-	<b>&lt;0.001</b>	0.078	-	<b>0.001</b>
Age (mean centered)	0.199	1	<b>&lt;0.001</b>	0.016	-0.15	0.618
Origin mother	<0.001	-	1	0.037	-	0.103
Residual	1.346	-	-	0.264	-	-
Repeatability	0.416	-	-	0.205	-	-

Note: Statistical significant results ( $P < 0.05$ ) are marked in bold.

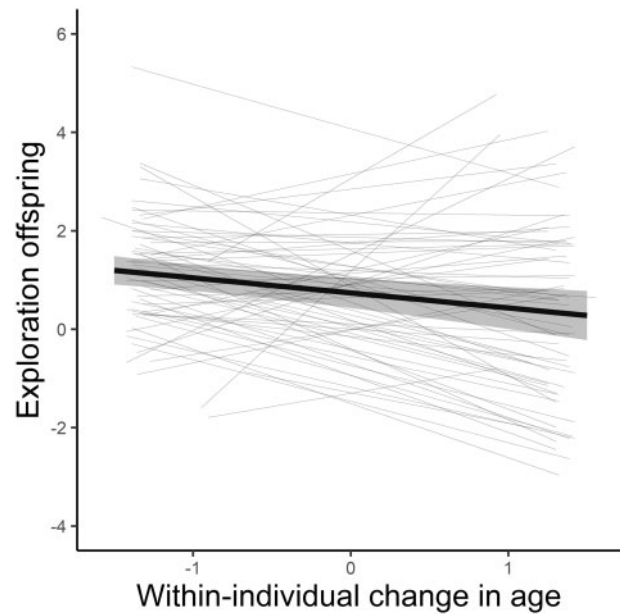


**Figure 1.** Fit of the GAMM of average exploration score of the mother against exploration behavior of their offspring. Exploration behavior is averaged within each nest and represented as dots with the standard error of the mean.

variance (Table 2) but there were repeatable differences between individuals, with a repeatability of  $R = 0.416$  (Table 2). The final model had an  $R^2$  of 0.096 which is low and suggest that other, unaccounted factors (e.g., *in utero* variations in maternal care or multiple paternity) affected juvenile behavior as well.

### Stress-sensitivity

The GAMM with stress-sensitivity as dependent variable revealed that none of the fixed effects explained a significant proportion of the variation in stress-sensitivity (Table 2). There were no differences between males and females and their stress-sensitivity did not change when they became older, suggesting that they did not habituate to the test regarding stress-sensitivity (Table 2). The personality



**Figure 2.** Linear correlation between the individuals exploration behavior and their within-individual changes in age. The solid black line represents the population effect, while the smaller black lines are the individuals' reaction norms.

score of the mother, regarding stress-sensitivity, did not correlate that of her offspring (Table 2). Additionally, we found no indication for individual variation in plasticity nor for an effect of maternal origin (Table 2). However, individual identity was significant (Table 2) suggesting that there are consistent differences between individuals in stress-sensitivity, with a repeatability of  $R = 0.205$ .

### Personality-density

The LMM with mean exploration behavior as response variable, using only the mothers from the experiments, revealed no correlation between the date that the mother was captured (used as an alternative for density size) and mean exploration behavior



(estimate  $\pm$  SE =  $-0.249 \pm 0.436$ ,  $t_{15} = -0.572$ ,  $P = 0.576$ ). This effect was also absent for the LMM with mean stress-sensitivity as response variable ( $-0.113 \pm 0.153$ ,  $t_{15} = -0.739$ ,  $P = 0.472$ ). The area where the mother was captured had no effect on either mean exploration behavior (LRT = 0,  $P = 1$ ) nor on mean stress sensitivity (LRT = 0.005,  $P = 0.944$ ).

However, the lack of a correlation between personality and capture date might be due to low sample size. We therefore created a larger dataset including all animals that were captured on the same three locations and whose behavior was first recorded in the laboratory and reran the LMMs. The LMM with exploration as response variable revealed, as predicted, a positive correlation between the date that the mother was captured and mean exploration behavior ( $0.317 \pm 0.116$ ,  $t_{47} = 2.728$ ,  $P = 0.009$ , Figure 3). This suggests that we caught more explorative individuals later in the breeding season, when population densities are expected to be higher (Leirs 1995), which is in line with the results from Vanden Broecke et al. (2019). We found no difference between males and females ( $-0.119 \pm 0.277$ ,  $t_{47} = -0.428$ ,  $P = 0.671$ ) and no differences among the areas in which the individuals were trapped in (LRT = 0,  $P = 1$ ). We found, however, no effect of capture date on mean stress-sensitivity ( $-0.040 \pm 0.055$ ,  $t_{47} = -0.730$ ,  $P = 0.469$ ) and no differences between males and females ( $-0.189 \pm 0.132$ ,  $t_{47} = -1.430$ ,  $P = 0.159$ ). Additionally, there were no differences between the three areas in mean stress-sensitivity in which the individuals were trapped (LRT = 0,  $P = 1$ ).

## Discussion

Parental effects are expected to evolve in species that experience fast and large changes in environmental conditions such as *M. natalensis* (Marshall and Uller 2007; Reddon 2012; Taylor et al. 2012; Proulx and Teotónio 2017). Indeed, reproduction of *M. natalensis* is strongly correlated with seasonal rainfall which leads to large density fluctuations (Leirs et al. 1994, 1997; Sluydts et al. 2007). In turn, this

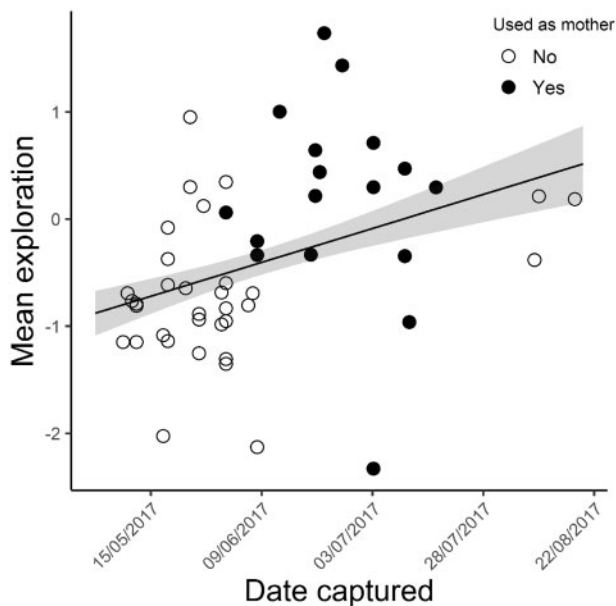
results in large changes in their environment on a very short temporal scale, due to density-dependent changes in foraging contacts (Borremans et al. 2017), home range size, and overlap (Borremans et al. 2014). Parental effects are expected to influence behavioral variation within these populations, allowing fast adaptation to these rapid changing environments (Mousseau 1998; Kuijper and Hoyle 2015; Proulx and Teotónio 2017). We found a non-linear relationship between mother and offspring behavior, with respect to exploration, even though they were born and raised individually in a controlled laboratory setting. This may suggest that personality in young *M. natalensis* is at least partly determined by maternal effects.

Nonetheless, our findings cannot be assigned solely to maternal effects. Since we had only one generation, we were not able to disentangle between genetic and non-genetic effects (Wolf and Wade 2009). It has been argued that genetic variation influences personality in a wide variety of species (Dochtermann et al. 2015). Indeed, 23% of the behavioral variation within populations, across species, is due to the effects of additive genetic variation (Dochtermann et al. 2019). Nevertheless, a non-linear pattern would not be possible if our results were only determined by additive genetic effects. We are therefore confident that personality in *M. natalensis* is at least partly determined by maternal effects for which we have two explanations: either due to a combination of density dependence and negative-frequency-dependent mechanisms or due to differences in maternal stress.

Density dependence and negative-frequency-dependent mechanisms, where the fitness payoff of a certain phenotype (or personality) is expected to increase as it becomes rarer, are being considered to be among the main mechanisms responsible for the existence and maintenance of personality variation within populations (Dall et al. 2004; Wolf et al. 2007, 2008; Dingemans and Wolf 2010; Wolf and Weissing 2010; Wolf and McNamara 2012). We argue that these processes might also be responsible for the non-linear pattern that we have observed in exploration behavior between the mother and offspring. While exploration behavior provides an individual with information about the environment (Schwagmeyer 1995; Tebbich et al. 2009; Rojas-Ferrer et al. 2020), the competitive advantage and benefits of expressing high levels of exploration behavior is expected to change with density and the frequency of certain personalities in the population.

We found that slow and average exploring mothers produced offspring which were slightly more explorative than themselves. These mothers were caught early in the breeding season, when densities are expected to be low (Leirs 1995) and corresponds with Vanden Broecke et al. (2019), who found that the population contains more slow and average exploring individuals at lower densities. During these periods, food is abundantly available (Leirs et al. 1989, 1994) and together with a lack of territoriality (Borremans et al. 2014) and a generalist diet (Mulungu et al. 2011) results in low competition for food resources. However, densities are expected to increase rapidly throughout the breeding season and food becomes more scarce (Leirs et al. 1989). During this period, fast exploring individuals are expected to have a competitive advantage over slower exploring individuals. Indeed, fast exploring great tits, for instance, outcompete slower individuals at clumped food resources in winter and obtain higher quality territories (Dingemans and de Goede 2004; Both et al. 2005; Cole and Quinn 2012).

This competitive advantage of fast exploring individuals would result in a positive correlation between density and exploration, leading to an increase of fast exploring individuals entering the population when density increases, which has been observed for



**Figure 3.** Linear correlation between the mean exploration behavior of the wild caught individuals with their capture date. Black dots represent the females that gave birth in the laboratory and who were used in the experiment.

*M. natalensis* (Vanden Broecke et al. 2019). However, this proportional increase of fast exploring individuals at higher densities may result in an increase of intra-specific competition and a reduced fitness payoff for fast exploring individuals compared with slower individuals (Wright et al. 2019). Indeed, food becomes extremely scarce at high densities which eventually leads to a population crash due to food depletion (Leirs et al. 1997). Wright et al. (2019) suggested that fast exploring individuals are less resistant to the increased intra-specific competition at high densities potentially affecting their survival. Indeed, fast exploring and active individuals are found to have a lower survival probability at high densities in great tits (Nicolaus et al. 2016) and in the common lizard (*Zootoca vivipara*; Le Galliard et al. 2015). Fast exploring mothers should, in order to increase their fitness during these conditions, produce offspring which are on average less explorative than themselves. These juveniles will be more resistant to the high levels of intra-specific competition resulting in an increased survival probability, which is important for young *M. natalensis* since juveniles breed in the next breeding season after the one in which they were born (Leirs et al. 1993). This may result in the observed negative correlation in exploration behavior between fast exploring mothers and her offspring.

Previous studies have found maternal effects on behavior in, for example, yellow-bellied marmots (*Marmota flaviventris*; Petelle et al. 2013), North American red squirrels (*Tamiasciurus hudsonicus*; Taylor et al. 2012), zebrafish (*Danio rerio*; Ariyomo et al. 2013), and Trinidadian guppies (*P. reticulata*; White and Wilson 2019). However, mothers can only alter the behavior of their offspring toward a better suited personality for future environments if they can predict those environmental conditions (Marshall and Uller 2007; Reddon 2012; Proulx and Teotónio 2017; Langenhof and Komdeur 2018). It is possible that the density increase in *M. natalensis* could be predicted by the mother via changes in the social environment (Borremans et al. 2014; Borremans et al. 2017). Indeed, variation in the perceived social environment, rather than resource availability itself, have been found to affect maternal hormones in North American red squirrels (*T. hudsonicus*; Dantzer et al. 2013) and prenatal social conditions, experienced by the mother, has been found to affect the behavior of their offspring in guinea pigs (Guenther et al. 2014). An alternative is predation pressure, which increases with density as well (Leirs et al. 1997; Vibe-Petersen et al. 2006) and has been found to affect maternal effects in field crickets (*Gryllus pennsylvanicus*; Storm and Lima 2010) and in common lizards (Bestion et al. 2014).

Nonetheless, we found no significant relationship between the date that the mother was captured (which was used as a proxy for density) and exploration behavior of her offspring. While this could be due to a low sample size, it may also indicate that the density, experienced by the mother, may not fully explain the observed variation in exploration behavior among the nests. This may result from differences in maternal stress or due to unaccounted environmental differences between the three areas from which the mothers originated. However, the latter seems unlikely since the area of origin from the mother was not significant in any of our models, suggesting that there were similar environmental conditions between the different areas during our experiment. Maternal stress may provide an alternative explanation for our results, which would be more prominent in fast exploring mothers. Indeed, prenatal stress has been found to affect exploration behavior in rodents and other mammals, where juveniles that were exposed to stress prenatally were less explorative compared with juveniles from non-stressed mothers (Polyrev et al. 1996; Braastad 1998; Curley et al. 2008;

Groothuis and Dario 2013). This could potentially explain the negative correlation in exploration behavior between fast exploring mothers and her offspring, while the observed positive correlation may reflect the heritability of this trait (Dingemans et al. 2002; Drent et al. 2005; Dochtermann et al. 2015, 2019). However, this is not always the case (Groothuis and Dario 2013) and contradicts with studies on stress and personality, where shy and slow exploring individuals are commonly found to be more stressed in both rodents (Montiglio et al. 2012; Clary et al. 2014) and birds (Carere et al. 2003; Cockrem 2007; Baugh et al. 2013).

Our analysis revealed an effect of group-level plasticity, where all the individuals decreased their exploration behavior during subsequent recordings. These results reflect either an age effect or habituation to the test. The latter contradicts previous findings of Vanden Broecke et al. (2018, 2019) who found no effects of habituation in juveniles to the same experimental setup. These different results are probably due to variations in days between consecutive recordings. In this study, we were able to control the time between recordings, which was not possible in the previous studies since it was performed on wild caught individuals. Those individuals were released back in the wild after being recorded, resulting in large variation between consecutive recordings within and among individuals (Vanden Broecke et al. 2018, 2019). Indeed, Dingemans et al. (2012) found that the level of habituation in great tits was generally more pronounced when the time interval between subsequent tests was short compared with long intervals. Nonetheless, this suggests that exploration behavior is flexible in juveniles and correspond to previous results, where juveniles changed their exploration behavior with changes in the environment (Vanden Broecke et al. 2019). However, the level of habituation to the hole-board test differed among individuals and depended on the individual personality. Our results suggested that slow exploring individuals habituated faster compared with fast exploring juveniles, which fits within the general idea that fast exploring individuals are less flexible compared with slow individuals (Coppens et al. 2010).

We found no correlation between mother and offspring for the second personality trait, which we referred to as stress-sensitivity (Vanden Broecke et al. 2019). This suggests that stress-sensitivity in juveniles is not affected by potential maternal effects and/or that the heritability is low and therefore largely determined by environmental effects. Vanden Broecke et al. (2019) found that this trait was highly repeatable in wild *M. natalensis* and suggested that these repeatable behavioral differences between individuals are probably the consequence of environmental effects which the juvenile itself experiences rather than being the result of maternal and genetic effects. An alternative explanation is that mothers use a bet-hedging strategy, where they increase the variety of personalities within their offspring ensuring that some individuals are suited for their environment (Marshall and Uller 2007; Reddon 2012).

To summarize, our results suggest that pregnant females can anticipate on the considerable environmental changes experienced by *M. natalensis* and potentially modulate the behavior of their offspring in order to increase their fitness. These early maternal effects may therefore contribute significantly to the maintenance of personality variation in the multimammate mice.

## Acknowledgments

The authors would like to thank the staff at the Pest Management Center (SUA) for their excellence assistance during the fieldwork and experiments, specifically Shabani Lutea, Goefrey Sabuni, Omary Kibwana, Baraka Edson,

Bert Thys, Maddy Wheatley, Aurelia Bongers, and Steven Van den Panhuysen. They also thank three anonymous reviewers for their constructive comments which greatly improved the manuscript.

## Funding

B.V.B. was funded by the Ph.D. fellowship from the Research Foundation Flanders (FWO) (grant ID: 11A0817N).

## References

- Araya-Ajoy YG, Bolstad GH, Brommer J, Careau V, Dingemans NJ, Wright J, 2018. Demographic measures of an individual's "pace of life": fecundity rate, lifespan, generation time or a composite variable? *Behav Ecol Sociobiol* 72: 75.
- Ariyomo TO, Carter M, Watt PJ, 2013. Heritability of boldness and aggressiveness in the zebrafish. *Behav Genet* 43: 161–167.
- Bates D, Mächler M, Bolker B, Walker S, 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw* 67: 1–48.
- Baugh AT, van Oers K, Naguib M, Hau M, 2013. Initial reactivity and magnitude of the acute stress response associated with personality in wild great tits *Parus major*. *Gen Comp Endocrinol* 189: 96–104.
- Bell AM, McGhee KE, Stein LR, 2016. Effects of mothers' and fathers' experience with predation risk on the behavioral development of their offspring in threespined sticklebacks. *Curr Opin Behav Sci* 7: 28–32.
- Bergeron P, Montiglio P-O, Réale D, Humphries MM, Gimenez O et al., 2013. Disruptive viability selection on adult exploratory behaviour in eastern chipmunks. *J Evol Biol* 26: 766–774.
- Bestion E, Teyssier A, Aubret F, Clobert J, Cote J, 2014. Maternal exposure to predator scents: offspring phenotypic adjustment and dispersal. *Proc R Soc B Biol Sci* 281: 20140701.
- Blumstein DT, Daniel JC, 2007. *Quantifying Behavior the JWatcher Way*. Sunderland (MA): Sinauer Associates.
- Boon AK, Réale D, Boutin S, 2007. The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecol Lett* 10: 1094–1104.
- Borremans B, Hughes NK, Reijnders J, Sluydts V, Katakweba AAS et al., 2014. Happily together forever: temporal variation in spatial patterns and complete lack of territoriality in a promiscuous rodent. *Popul Ecol* 56: 109–118.
- Borremans B, Reijnders J, Hughes NK, Godfrey SS, Gryseels S et al., 2017. Nonlinear scaling of foraging contacts with rodent population density. *Oikos* 126: 792–800.
- Both C, Dingemans NJ, Drent PJ, Tinbergen JM, 2005. Pairs of extreme avian personalities have highest reproductive success. *J Anim Ecol* 74: 667–674.
- Braastad BO, 1998. Effects of prenatal stress on behaviour of offspring of laboratory and farmed mammals. *Appl Anim Behav Sci* 61: 159–180.
- Carere C, Groothuis TGG, Möstl E, Daan S, Koolhaas JM, 2003. Fecal corticosteroids in a territorial bird selected for different personalities: daily rhythm and the response to social stress. *Horm Behav* 43: 540–548.
- Carere C, Maestripietri D, 2013. *Animal Personalities: Behavior, Physiology, and Evolution*. Chicago (IL): University of Chicago Press.
- Clary D, Skyner LJ, Ryan CP, Gardiner LE, Anderson WG et al., 2014. Shyness–Boldness, but not exploration, predicts glucocorticoid stress response in Richardson's ground squirrels *Urocyon richardsonii*. *Ethology* 120: 1101–1109.
- Cockrem JF, 2007. Stress, corticosterone responses and avian personalities. *J Ornithol* 148: 169–178.
- Coetzee CG, 1975. The biology, behaviour, and ecology of *Mastomys natalensis* in southern Africa. *Bull World Health Organ* 52: 637–644.
- Cole EF, Quinn JL, 2012. Personality and problem-solving performance explain competitive ability in the wild. *Proc R Soc B Biol Sci* 279: 1168–1175.
- Coppens CM, de Boer SF, Koolhaas JM, 2010. Coping styles and behavioural flexibility: towards underlying mechanisms. *Philos Trans R Soc B Biol Sci* 365: 4021–4028.
- Curley JP, Champagne FA, Bateson P, Keverne EB, 2008. Transgenerational effects of impaired maternal care on behaviour of offspring and grandoffspring. *Anim Behav* 75: 1551–1561.
- Dall SRX, Houston AI, McNamara JM, 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol Lett* 7: 734–739.
- Dantzer B, Newman AEM, Boonstra R, Palme R, Boutin S et al., 2013. Density triggers maternal hormones that increase adaptive offspring growth in a wild mammal. *Science* 340: 1215–1217.
- Dingemans NJ, Both C, Drent PJ, van Oers K, van Noordwijk AJ, 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Anim Behav* 64: 929–938.
- Dingemans NJ, Bouwman KM, van de Pol M, van Overveld T, Patrick SC et al., 2012. Variation in personality and behavioural plasticity across four populations of the great tit *Parus major*. *J Anim Ecol* 81: 116–126.
- Dingemans NJ, Dochtermann NA, 2013. Quantifying individual variation in behaviour: mixed-effect modelling approaches. *J Anim Ecol* 82: 39–54.
- Dingemans NJ, de Goede P, 2004. The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behav Ecol* 15: 1023–1030.
- Dingemans NJ, Wolf M, 2010. Recent models for adaptive personality differences: a review. *Philos Trans R Soc B Biol Sci* 365: 3947–3958.
- Dochtermann NA, Schwab T, Anderson Berdal M, Dalos J, Royauté R, 2019. The heritability of behavior: a meta-analysis. *J Hered* 110: 403–410.
- Dochtermann NA, Schwab T, Sih A, 2015. The contribution of additive genetic variation to personality variation: heritability of personality. *Proc R Soc B Biol Sci* 282: 20142201.
- Drent PJ, van Noordwijk AJ, van Oers K, de Jong G, Kempenaers B, 2005. Contribution of genetics to the study of animal personalities: a review of case studies. *Behaviour* 142: 1191–1212.
- Falconer DS, MacKay FC, 1996. *Introduction to Quantitative Genetics*. 4th edn. Harlow (UK): Introduction to Quantitative Genetics.
- File SE, Wardill AG, 1975. Validity of head-dipping as a measure of exploration in a modified hole-board. *Psychopharmacologia* 44: 53–59.
- Frame JD, Baldwin JM, Gocke DJ, Troup JM, 1970. Lassa fever, a new virus disease of man from West Africa. I. Clinical description and pathological findings. *Am J Trop Med Hyg* 19: 670–676.
- Gosling SD, 2001. From mice to men: what can we learn about personality from animal research? *Psychol Bull* 127: 45–86.
- Groothuis TGG, Carere C, 2005. Avian personalities: characterization and epigenesis. *Neurosci Biobehav Rev* 29: 137–150.
- Groothuis TGG, Carere C, Lipar J, Drent PJ, Schwabl H, 2008. Selection on personality in a songbird affects maternal hormone levels tuned to its effect on timing of reproduction. *Biol Lett* 4: 465–467.
- Groothuis TGG, Dario M, 2013. Parental influences on offspring personality traits in oviparous and placental vertebrates. In: Carere C, Maestripietri D, editors. *Animal Personalities, Behaviour Physiology and Evolution*. United States of America: University of Chicago Press. 317–352.
- Guenther A, Kowalski G, von Engelhardt N, 2014. Prenatal social conditions shape offspring adult phenotype and reproductive success. *Behav Ecol Sociobiol* 68: 1661–1667.
- Günther S, Hoofd G, Charrel R, Röser C, Becker-Ziaja B et al., 2009. Mopeia virus-related arenavirus in natal multimammate mice, Morogoro, Tanzania. *Emerg Infect Dis* 15: 2008–2012.
- Haigh A, O'Riordan R, Butler F, 2017. Variations in aggression and activity levels amongst squirrels inhabiting low and high density areas. *Ecol Res* 32: 931–941.
- Kaiser H, 1991. Coefficient alpha for a principal component and the Kaiser–Guttman rule. *Psychol Rep* 68: 855–858.
- Kennis J, Sluydts V, Leirs H, van Hooft WFP, 2008. Polyandry and polygyny in an African rodent pest species, *Mastomys natalensis*. *Mammalia* 72: 150–160.
- Kuijper B, Hoyle RB, 2015. When to rely on maternal effects and when on phenotypic plasticity? *Evolution* 69: 950–968.
- Langenhof MR, Komdeur J, 2018. Why and how the early-life environment affects development of coping behaviours. *Behav Ecol Sociobiol* 72: 34.



- Le Galliard J-F, Paquet M, Mugabo M, 2015. An experimental test of density-dependent selection on temperament traits of activity, boldness and sociability. *J Evol Biol* 28: 1144–1155.
- Leirs H, 1995. Population ecology of *Mastomys natalensis* (Smith, 1834): implications for rodent control in Africa. A report from the Tanzania–Belgium Joint Rodent Research Project (1986–1989). Publ Agric.
- Leirs H, Stenseth NC, Nichols JD, Hines JE, Verhagen R et al., 1997. Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent. *Nature* 389: 176–180.
- Leirs H, Verhagen R, Verheyen W, 1993. Productivity of different generations in a population of *Mastomys natalensis* rats in Tanzania. *Oikos* 68: 53–60.
- Leirs H, Verhagen R, Verheyen W, 1994. The basis of reproductive seasonality in *Mastomys* rats (Rodentia: muridae) in Tanzania. *J Trop Ecol* 10: 55–66.
- Leirs H, Verheyen W, Michiels M, Verhagen R, Stuyck J, 1989. The relation between rainfall and the breeding season of *Mastomys natalensis* (Smith, 1834) in Morogoro, Tanzania. *Ann Soc Zool Belgique* 119: 59–64.
- Marshall DJ, Uller T, 2007. When is a maternal effect adaptive? *Oikos* 116: 1957–1963.
- Martin JGA, Réale D, 2008. Temperament, risk assessment and habituation to novelty in eastern chipmunks *Tamias striatus*. *Anim Behav* 75: 309–318.
- Meijering E, Dzyubachyk O, Smaï I, 2012. Methods for cell and particle tracking. *Methods Enzymol* 504: 183–200.
- Miranda AC, Schielzeth H, Sonntag T, Partecke J, 2013. Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? *Glob Chang Biol* 19: 2634–2644.
- Montiglio P-O, Garant D, Pelletier F, Réale D, 2012. Personality differences are related to long-term stress reactivity in a population of wild eastern chipmunks, *Tamias striatus*. *Anim Behav* 84: 1071–1079.
- Mousseau T, 1998. The adaptive significance of maternal effects. *Trends Ecol Evol* 13: 403–407.
- Mulungu LS, Mahlaba TA, Massawe AW, Kennis J, Crauwels D et al., 2011. Dietary differences of the multimammate mouse, *Mastomys natalensis* (Smith, 1834), across different habitats and seasons in Tanzania and Swaziland. *Wildl Res* 38: 640–646.
- Myers JH, 2018. Population cycles: generalities, exceptions and remaining mysteries. *Proc R Soc B Biol Sci* 285: 20172841.
- Nicolaus M, Tinbergen JM, Ubels R, Both C, Dingemanse NJ, 2016. Density fluctuations represent a key process maintaining personality variation in a wild passerine bird. *Ecol Lett* 19: 478–486.
- Peres-Neto PR, Jackson DA, Somers KM, 2005. How many principal components? Stopping rules for determining the number of non-trivial axes revisited. *Comput Stat Data Anal* 49: 974–997.
- Petelle MB, McCoy DE, Alejandro V, Martin JGA, Blumstein DT, 2013. Development of boldness and docility in yellow-bellied marmosets. *Anim Behav* 86: 1147–1154.
- van de Pol M, Wright J, 2009. A simple method for distinguishing within- versus between-subject effects using mixed models. *Anim Behav* 77: 753–758.
- Polytsev T, Keshet GI, Kay G, Weinstock M, 1996. Role of experimental conditions in determining differences in exploratory behavior of prenatally stressed rats. *Dev Psychobiol* 29: 453–462.
- Proulx SR, Teotónio H, 2017. What kind of maternal effects can be selected for in fluctuating environments?. *Am Nat* 189: E118–E137.
- R Core Team 2013. *R: A Language and Environment for Statistical Computing*. Vienna (Austria): R Foundation for Statistical Computing.
- Réale D, Garant D, Humphries MM, Bergeron P, Careau V et al., 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philos Trans R Soc B Biol Sci* 365: 4051–4063.
- Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ, 2007. Integrating animal temperament within ecology and evolution. *Biol Rev* 82: 291–318.
- Reddon AR, 2012. Parental effects on animal personality. *Behav Ecol* 23: 242–245.
- Riyahi S, Björklund M, Mateos-Gonzalez F, Senar JC, 2017. Personality and urbanization: behavioural traits and DRD4 SNP830 polymorphisms in great tits in Barcelona city. *J Ethol* 35: 101–108.
- Rojas-Ferrer I, Thompson MJ, Morand-Ferron J, 2020. Is exploration a metric for information gathering? Attraction to novelty and plasticity in black-capped chickadees. *Ethology* 126: 383–392.
- Schneider CA, Rasband WS, Eliceiri KW, 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat Methods* 9: 671–675.
- Schuett W, Dall SRX, Wilson AJ, Royle NJ, 2013. Environmental transmission of a personality trait: foster parent exploration behaviour predicts offspring exploration behaviour in zebra finches. *Biol Lett* 9: 20130120.
- Schwagmeyer PL, 1995. Searching today for tomorrow's mates. *Anim Behav* 50: 759–767.
- Sluydts V, Crespin L, Davis S, Lima M, Leirs H, 2007. Survival and maturation rates of the African rodent *Mastomys natalensis*: density-dependence and rainfall. *Integr Zool* 2: 220–232.
- Smith BR, Blumstein DT, 2008. Fitness consequences of personality: a meta-analysis. *Behav Ecol* 19: 448–455.
- Storm JJ, Lima SL, 2010. Mothers forewarn offspring about predators: a transgenerational maternal effect on behavior. *Am Nat* 175: 382–390.
- Taylor RW, Boon AK, Dantzer B, Réale D, Humphries MM et al., 2012. Low heritabilities, but genetic and maternal correlations between red squirrel behaviours. *J Evol Biol* 25: 614–624.
- Tebbich S, Fessl B, Blomqvist D, 2009. Exploration and ecology in Darwin's finches. *Evol Ecol* 23: 591–605.
- Vanden Broecke B, Borremans B, Mariën J, Makundi RH, Massawe AW et al., 2018. Does exploratory behavior or activity in a wild mouse explain susceptibility to virus infection?. *Curr Zool* 64: 585–592.
- Vanden Broecke B, Mariën J, Sabuni CA, Mnyone L, Massawe AW et al., 2019. Relationship between population density and viral infection: a role for personality? *Ecol Evol* 9: 10213–10224.
- Vibe-Petersen S, Leirs H, De Bruyn L, 2006. Effects of predation and dispersal on *Mastomys natalensis* population dynamics in Tanzanian maize fields. *J Anim Ecol* 75: 213–220.
- Warner DA, Lovern MB, 2014. The maternal environment affects offspring viability via an indirect effect of yolk investment on offspring size. *Physiol Biochem Zool* 87: 276–287.
- White SJ, Wilson AJ, 2019. Evolutionary genetics of personality in the Trinidadian guppy I: maternal and additive genetic effects across ontogeny. *Heredity* 122: 1–14.
- Wolf JB, Wade MJ, 2009. What are maternal effects (and what are they not)?. *Philos Trans R Soc B Biol Sci* 364: 1107–1115.
- Wolf M, van Doorn GS, Leimar O, Weissing FJ, 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature* 447: 581–584.
- Wolf M, van Doorn GS, Weissing FJ, 2008. Evolutionary emergence of responsive and unresponsive personalities. *Proc Natl Acad Sci U S A* 105: 15825–15830.
- Wolf M, McNamara JM, 2012. On the evolution of personalities via frequency-dependent selection. *Am Nat* 179: 679–692.
- Wolf M, Weissing FJ, 2010. An explanatory framework for adaptive personality differences. *Philos Trans R Soc B Biol Sci* 365: 3959–3968.
- Wolf M, Weissing FJ, 2012. Animal personalities: consequences for ecology and evolution. *Trends Ecol Evol* 27: 452–461.
- Wood S, Scheipl F, 2017. Estimate generalized additive mixed models via a version of function gamm() from “mgcv”, using “lme4” for estimation. R package version 0.2-5. Available at <https://CRAN.R-project.org/package=gamm4>.
- Wood SN, 2017. *Generalized Additive Models*. 2nd edn. New York (NY): Chapman and Hall/CRC.
- Wright J, Bolstad GH, Araya-Ajoy YG, Dingemanse NJ, 2019. Life-history evolution under fluctuating density-dependent selection and the adaptive alignment of pace-of-life syndromes. *Biol Rev* 94: 230–247.
- Ziwa MH, Matee MI, Kilonzo BS, Hang'ombe BM, 2013. Evidence of *Yersinia pestis* DNA in rodents in plague outbreak foci in Mbulu and Karatu Districts, northern Tanzania. *Tanzan J Health Res* 15: 1–8.
- Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM, 2009. *Mixed Effects Models and Extensions in Ecology with R*. New York (NY): Springer (Statistics for Biology and Health).

