

# Exploration Behavior and Morphology are Correlated in Captive Gray Mouse Lemurs (*Microcebus murinus*)

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**Abstract** Behavior varies among individuals and is flexible within individuals. However, studies of behavioral syndromes and animal personality have demonstrated that animals can show consistency in their behavior and as such may be restricted in their behavioral responses. Like any other trait, including morphology, performance, or physiology, personality is now considered an important component of ecology and may have fitness consequences. Moreover, in some species personality correlates with other traits, as predicted in the context of a recent theoretical framework postulating that individual differences in growth and body size can affect behavior through effects on growth–mortality tradeoffs. This “pace of life” hypothesis predicts that animals that explore more should be larger and have higher growth rates than those that explore less. We tested for associations between morphology and a behavioral trait in a captive colony of gray mouse lemurs (*Microcebus murinus*). We used open-field tests to evaluate exploration behavior and measured a series of morphological traits in 72 individuals (32 males and 40 females). Our results show that the latency to start exploring correlates positively with adult body size and body weight at birth. These data provide evidence for a link between morphology and behavior in this species, thus supporting predictions of dispersal models but diverging from the predictions of the “pace of life” model.

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## Introduction

Behavior varies both among and within individuals. This flexibility allows individuals to respond to environmental variation in food availability (Dingemanse *et al.* 2004), predation pressure (Dammhahn and Almeling 2012; Réale and Festa-Bianchet 2003), and changes in social context (Both *et al.* 2005). In other words, behavioral plasticity can improve individual fitness. However, the flexibility of animal behavior may be limited, resulting in consistent and repeatable behavioral responses at the individual level across different behavioral contexts. The concepts of personality (Réale *et al.* 2007), behavioral syndromes (Sih *et al.* 2004), and temperament (Réale *et al.* 2007) were introduced to describe this stability in behavior. Personality and temperament are often described by means of a set of five axes (Réale *et al.* 2007): shyness/boldness, sociability, aggression, activity, and exploration. The last two dimensions of personality (activity and exploration) can have a strong effect on individual fitness because they are related to dispersal and thus the ability of animals to move to a new territory (Réale *et al.* 2007).

Research on personality is moving toward an integrative approach, with researchers testing links between behavior and physiology (Albert *et al.* 2008; Careau and Garland 2012; Guenther and Trillmich 2015), morphology, and performance (Le Galliard *et al.* 2013; Videlier *et al.* 2014, 2015). Such an approach can improve our understanding of the proximate and ultimate drivers of personality (Careau and Garland 2012; Réale *et al.* 2007, 2010). This view has been conceptualized in the pace-of-life syndrome hypothesis (Réale *et al.* 2010). According to this hypothesis, many different traits, including physiology and behavior, coevolve with life-history traits. Moreover, studies on the heritability of personality and the genetic basis of behavior show that behavior, e.g., foraging behavior, can be transmitted from one generation to the next. Examples include explorative personality in great tits (*Parus major*: Dingemanse 2002), behavior in an antipredator context in squid (*Euprymna tasmanica*: Sinn *et al.* 2006), personality disorders in humans (Jang *et al.* 1996), and dominance in chimpanzees (*Pan paniscus*: Weiss *et al.* 2000).

A link between growth, fecundity, and life-history traits may result in correlations between morphology and behavior (Biro and Stamps 2008; Stamps 2007). As shown recently for exploration behavior and locomotor performance in lizards (*Zootoca vivipara*: Le Galliard *et al.* 2013), performance and morphological traits can also correlate with behavioral traits. Moreover, body condition, weight, and personality correlate in spiders (*Stegodyphus dumicola*: Wright *et al.* 2015). Personality traits can be selected for when they lead to variation in fitness (Biro and Stamps 2008; Careau and Garland 2012; Réale *et al.* 2007). In addition, the development of personality in animals may be influenced by their hormonal status and early life development (Stamps and Groothuis 2010). Moreover, dispersal models propose that dispersers should benefit from lower costs than resident individuals in addition to avoiding competition (Clobert *et al.* 2009), suggesting that younger and smaller individuals may benefit from early dispersal.

The gray mouse lemur (*Microcebus murinus*) is among the smallest primates in the world and is a nocturnal solitary forager that feeds on fruits, leaves, arthropods, and gum (Dammhahn and Kappeler 2008). This species is of particular interest in the context of studies on the relationship between morphology and behavior because body condition is a major component of its survival, even in captivity (Terrien *et al.* 2008). Moreover, it has a seasonal activity pattern that may favor behavioral flexibility. Finally, it is particularly suitable for manipulation and large sample sizes are feasible because of its small size.

We used an open-field test to quantify exploration behavior and its repeatability in a large group of captive gray mouse lemurs and investigated whether exploration behavior is associated with variation in morphology. We focus on overall size, age, sex, adult body weight, weight at birth, and growth rate during the first 3 mo of life to test the hypothesis that behavior correlates with morphology, as predicted in the context of the pace-of-life hypothesis. Specifically, we predict individuals that explore their environment sooner and more should be bigger and have higher growth rates than those that have a longer delay to exploration and explore less. Moreover, we predict that animals with longer limbs, and thus better locomotor capacity, will explore their environment sooner and more than those with shorter limbs and lower locomotor capacity. Given that dispersal models predict that dispersers should benefit from lower costs than resident individuals we hypothesize that smaller individuals that are at a competitive disadvantage may explore their environment more than bigger individuals with a competitive advantage.

## Methods

### Subjects

We studied 72 individuals (32 males, 40 females, aged 1–7 yr) from a captive mouse lemur colony in Brunoy (UMR7179 CNRS/MNHN, France). Mouse lemurs live in large cages with two to seven individuals housed together. The rooms were maintained at around 25°C with 50% humidity. Food (including fresh fruits, a milk porridge mixture, and mealworms) was provided daily and water was available *ad libitum*. Seasonal variations in photoperiod are simulated by alternating 6 mo of a summer-like period with 14 h of light per day and a winter-like period with 10 h of light per day. Except during the reproductive season, which occurs at the beginning of the summer-like period, males and females are housed separately. Eleven of the study individuals had performed a 20-min open-field test 1 yr earlier. All other study individuals were naïve for this experiment.

### Open-Field Test

We measured the exploration behavior of the gray mouse lemurs in an open-field test and recorded behavior with Video-Track (View-Point; Némoz-Bertholet and Aujard 2003). We conducted the open-field test during the artificial summer after the reproductive period. We observed subjects under red light conditions while they explored a 25 cm high 95 × 95 cm square Plexiglas box. We tested individuals between 13:00 h

and 17:00 h, a period of the day when the activity level of the individuals is high enough to show exploration behavior but low enough to facilitate handling, thus reducing stress (Giroud *et al.* 2008). All of the subjects were used to being handled because they are weighed monthly and showed minimal signs of stress due to handling. We placed each individual in the box by hand and waited 10 s before starting recording. The test lasted 30 min. This duration gave the mouse lemurs time to calm down after handling and provided enough time for them to start exploring their environment. From the videos we extracted 1) latency to first move 10 cm, 2) distance traveled, and 3) time spent moving. After the test, we gently chased the individual from the box into its nest box. Between each test we cleaned the box with 70% ethanol. If the subject did not move, we set the latency to first move to 1800 s (the end of the test), as in other studies of this species (Dammhahn 2012; Némoz-Bertholet and Aujard 2003). We tested the 72 individuals twice, with at least 2 wk between the two sessions to test for repeatability of behavior. To avoid a bias in repeatability due to the experimental conditions, e.g. hour of testing, we tested individuals randomly.

### Morphological Measures

We measured hind limb (tarsus and tibia), forelimb (ulna), and head (length, width, and depth) dimensions using digital calipers ( $\pm 0.01$  mm, Mitutoyo, Kanagawa Japan) immediately after the behavioral experiments. We obtained the weight at testing and the weights during the first months of life for each individual from the colony database. We calculated an individual's growth rate by calculating the body weight increase per day for the first 3 mo of life by taking the weight at birth and the weight at 3 mo and dividing this by the number of days, assuming linear growth. The first 3 mo of life correspond to the summer-like period and reflect the period during which most of the growth occurs. Sexual dimorphism in body size and weight has been reported for this species (wild animals: Kappeler 1991; captive animals: Thomas *et al.* 2015). The mean age of males and females included in our tests did not differ (female =  $3.72 \pm 1.68$  yr; male =  $3.31 \pm 1.62$  yr;  $t = 1.05$ ,  $df = 67.1$ ,  $P = 0.30$ ), but body mass differed between the two sexes (female =  $96.7 \pm 16.51$  g; male =  $83.6 \pm 17.14$  g;  $t = 3.29$ ;  $P < 0.01$ ). A MANOVA showed that females were significantly bigger than males in body size and mass (Wilks'  $\lambda = 0.76$ ,  $F_{6,66} = 3.5$ ;  $P = 0.004$ ). The two head dimensions, head width ( $F_{1,71} = 13.61$ ;  $P = 0.0004$ ) and head depth ( $F_{1,71} = 4.55$ ;  $P = 0.036$ ), principally accounted for this difference, as documented previously (Chazeau *et al.* 2013). Limb dimensions were not significantly different between the two sexes (tarsus:  $F_{1,71} = 1.45$ ;  $P = 0.23$ ; tibia:  $F_{1,71} = 0.30$ ;  $P = 0.61$ ; ulna:  $F_{1,71} = 0.33$ ;  $P = 0.57$ ) as previously shown in Thomas *et al.* 2016.

### Statistical Analysis

We  $\log_{10}$ -transformed all data before analysis to comply with assumptions of normality and homoscedascity. We calculated repeatability as an intraclass correlation coefficient, which is the ratio of the interindividual variance to the sum of inter- and intraindividual variances. We used the `rpt` function in the `rptR` package (Nakagawa and Schielzeth 2010), which estimates these variances directly via linear mixed-effects models (LMMs) using restricted maximum likelihood (REML).

We conducted a principal component analysis on the morphometric measurements and body mass, and extracted the first component as an indicator of body size.

We used an LMM (nlme package; Pinheiro *et al.* 2016) and the  $\log_{10}$ -transformed behavioral variable as the response variable. We added the experimental conditions (Giroud *et al.* 2008) as fixed effects: the number of individuals in the home cage, day of the week, hour of testing, and number of days after the beginning of the summer period. We also included biological parameters including age, sex, and the age by sex interaction (Dammhahn 2012), and the quadratic effect of age as fixed effects. The final fixed factor was the first component of the principal component analysis (body size). We added the identity of the individuals as a random factor.

We conducted model selection using a multimodel inference procedure using the AIC criterion on all possible models using MuMIn v. 1.15.1 (Bartoń 2015) in R v. 3.2.2 (R Core Team 2015). This allowed us to select a simplified model that best explains variability in the behavioral variable. We considered the model when the difference in AIC from the null model was  $>2$ .

## Ethical Note

All subjects were born and reared in captivity (European Institution Agreement No. D-91-114-1) in a colony that descends from wild animals caught on the southwestern coast of Madagascar 40 yr ago.

## Results

### Behavioral Variation

Of the three behavioral components we measured, only “latency to first move” showed significant and moderate repeatability ( $r=0.25\pm 0.10$ ,  $P=0.04$ ; Table I) and could thus be considered as a personality trait. We retained this variable for further analyses as our indicator of exploration behavior and discarded the variables that were not repeatable. Of the 72 subjects we tested, 28 individuals never moved during the two sessions. Males and females did not differ in the latency to start exploring (mean female =  $1227\pm 540$  s; mean male =  $1339\pm 544$  s;  $t=-0.87$ ,  $df=66.4$ ,  $P=0.38$ ,  $CI_{95}=[-368; 145]$ ), so we pooled the sexes in subsequent analyses.

**Table I** Summary of repeatability for three behavioral variables for captive gray mouse lemurs in an open-field test

Parameter	Latency to first move	Distance traveled	Duration in movement
Regression slope ( $r$ ) $\pm$ SE	0.25 $\pm$ 0.10	0.035 $\pm$ 0.081	0 $\pm$ 0.072
CI (95%)	0.029–0.045	0–0.27	0–0.24
$P$	<b>0.04</b>	0.37	0.65

Bold results are significant results with  $\alpha = 0.05$

The hour of testing had a small but significant effect on the latency to start exploring, with subjects starting to explore more quickly later in the afternoon than in the beginning of the afternoon (Table II).

## Relationships Between Morphology and Behavior

The best model explaining variability in exploration behavior model included body dimensions and the hour of testing (AIC weight=0.10; Table II). Smaller individuals started exploration before larger individuals (Fig. 1). We also found that the latency to start exploring correlated with tibia length, radius length, and tarsus length (Table III).

We found a positive relationship between body weight at birth and exploration behavior (Table IV), meaning that individuals that were lighter at birth started exploring earlier than adults when the hour of the test was taken into account. There was, however, no relationship between growth rate during the first 3 mo of life and exploration behavior (Table IV).

## Discussion

### Behavioral Variation

Our study showed that some aspects of personality can be estimated using an open-field test in captive gray mouse lemurs (Freeman and Gosling 2010). Our results showed that the latency to first move in an open-field test was repeatable and variable, so we could consider it a personality trait. The other two variables, time spent moving and distance traveled, were

**Table II** Results of linear mixed models testing the effects of different environmental and biological factors on latency to start exploring by captive gray mouse lemurs in an open-field test

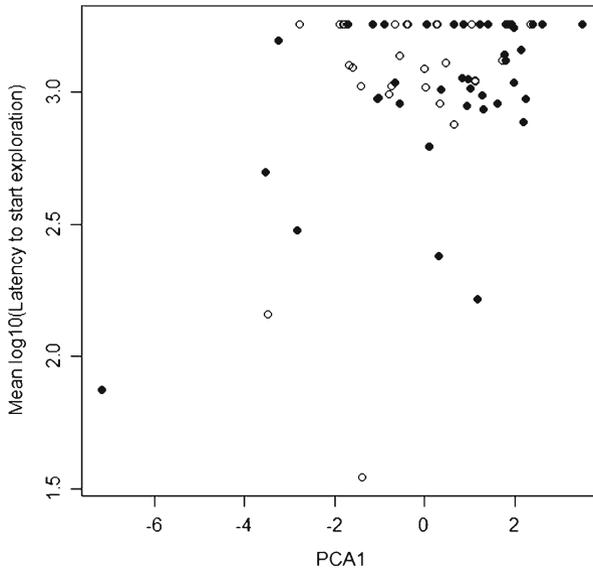
Response variable	AIC	Predictor variable	Estimate $\pm$ SE	df	<i>P</i>
$\log_{10}$ (latency to start exploring)	353.4	—			
$\log_{10}$ (latency to start exploring)	351.7	PCA1 (body size)	0.15 $\pm$ 0.04	68	<b>&lt;0.01</b>
		Day of the week	0.07 $\pm$ 0.12	64	0.56
		Hour	-0.73 $\pm$ 0.32	64	<b>0.02</b>
		Social context	-0.02 $\pm$ 0.064	64	0.72
		Days of summer	-0.17 $\pm$ 0.34	64	0.60
		Age	-0.16 $\pm$ 0.26	65	0.52
		Sex M	-0.47 $\pm$ 0.26	68	0.24
		Age:sex M <sup>a</sup>	0.18 $\pm$ 0.1	64	0.09
		<i>I</i> (age <sup>2</sup> ) <sup>b</sup>	0.013 $\pm$ 0.04	64	0.70
$\log_{10}$ (latency to start exploring)	344.1	PCA1 (body size)	0.13 $\pm$ 0.04	69	<b>&lt;0.01</b>
		Hour	-0.72 $\pm$ 0.31	70	<b>0.02</b>

We included individual identity as a random effect in all models.

Bold results are significant results with  $\alpha = 0.05$

<sup>a</sup> Interaction between age and sex

<sup>b</sup> *I* represents quadratic effect of age



**Fig. 1** Mean latency to start exploring the open field arena vs. a measure of body size (PCA1: body size) over two sessions in captive gray mouse lemurs. Females are in black; males are in white.

not repeatable, suggesting that these variables do not reflect personality in this species. These variables may be influenced by the current state of the individual or may be subject to rapid habituation between sessions (Réale *et al.* 2007).

### Relationship Between Morphology and Behavior

Our results showed that behavior correlated with morphology in a small nocturnal primate, when controlling for hour of testing. This suggests that selection may act on morphology and behavior in a concerted way. This is supported by the fact that individuals that started exploring a novel environment more quickly were born with a lower body weight than those born with a higher body weight. However, the relationship between morphology and behavior is not very strong. Adult body size is strongly influenced by body weight at birth and the growth rate during the first months of life (Electronic Supplementary Material Table SI). It has been suggested previously (Stamps 2007) that bolder individuals should grow more and faster than shy individuals because their bold behavior and increased exploration provide them with greater access

**Table III** Correlations between limb dimensions and latency to start exploring in an open-field test in captive gray mouse lemurs

	<i>r</i>	<i>P</i>
log10 (tarsus length)	0.29	<b>0.01</b>
log10 (tibia length)	0.38	<b>&lt;0.01</b>
log10 (ulna length)	0.34	<b>&lt;0.01</b>

Bold results are significant results with  $\alpha = 0.05$

**Table IV** Results of linear mixed models testing the effect of early life parameters on adult behavior in captive gray mouse lemurs

Response variable	Predictor variable	Estimate $\pm$ SE	df	<i>P</i>
$\log_{10}$ (latency to start exploring)	Birth weight	1.98 $\pm$ 0.93	68	<b>0.04</b>
	Growth rate	1.3 $\pm$ 1.05	68	0.22
	Hour	-0.7 $\pm$ 0.31	70	<b>0.03</b>

Latency to start exploring is the time in seconds that the individual waits to start moving in the open field. We included individual identity as a random effect in all models.

Bold results are significant results with  $\alpha = 0.05$

to food. Moreover, other researchers have suggested that costly behaviors such as exploration and boldness should relate to individual traits such as size or strength (Wolf and Weissing 2010). Larger individuals can likely afford to be bolder, resulting in adaptive feedback of body condition on behavior. In the context of the pace-of-life syndrome, higher growth rate should also typify bolder individuals (Réale *et al.* 2010). Although we found that higher growth rates and higher weight at birth resulted in larger adults, lighter newborns explored new environments more quickly than heavier newborns. Thus, our results do not support predictions that growth rates should correlate positively with more explorative behavior (Biro and Stamps 2008), at least for our captive population of mouse lemurs. We found that small individuals and individuals with shorter limbs started to explore the new environment sooner. This observation is at first sight rather surprising, as we predicted that animals with longer limbs, and thus better locomotor capacity, would explore their environment sooner and more than animals with shorter limbs and lower locomotor capacity. However, performance and behavior may be decoupled, as observed in other studies (Videliér *et al.* 2014), and the observed effect may simply be due to a strong overall effect of body size on the latency of exploration.

Correlations between personality and other traits have also been observed in spiders (Wright *et al.* 2015) and lizards (Careau and Garland 2012; Le Galliard *et al.* 2013). In social spiders (*Stegodyphus dumicola*), boldness depends on body condition and body mass, with individuals with a lower body condition being more bold than individuals with a better body condition. As in our study, smaller individuals were bolder than larger individuals (Wright *et al.* 2015). In lizards, activity and foraging behavior were associated with differences in locomotor performance and metabolic rate (Le Galliard *et al.* 2013). Positive correlations between exploration behavior, resting metabolic rate, growth rate, but also body mass and weight at birth were observed in lizards, suggesting that this kind of relationship may occur in a large range of taxa. In primates, personality traits of assertiveness and neuroticism are associated with facial dimensions (Wilson *et al.* 2014), suggesting that facial features may act as “biomarkers of personality.”

In our study, body weight at birth correlated positively with the latency to start exploring. Although we have no direct evidence, smaller individuals may have a disadvantage in a competitive environment and may benefit more from early dispersal than bigger individuals with a competitive advantage. As suggested by Wolf and Weissing (2010), positive feedback of even small differences at the beginning of an animal’s life could result in an adaptive personality. Dispersal models commonly propose that dispersers should benefit from lower costs than resident individuals in addition to avoiding competition (Clobert *et al.* 2009). In

addition, in primates, disadvantaged individuals, e.g., low-ranking animals (Konečná *et al.* 2012), may be forced to explore more than others with advantages (Pouydebat *et al.* 2006). In great tits, fast explorers had lower dominance ranks (Dingemanse and de Goede 2004) and smaller mouse lemurs may also be at disadvantage if they have to contest a resource. In contrast, in lizards earlier dispersers typically have a higher body mass and a better body condition than resident animals (Clobert *et al.* 2009).

### Comparison with Wild Animals

In wild gray mouse lemurs, body mass correlates positively with dispersal distance, but the relationship between body mass and personality traits *per se* has not been investigated (Schliehe-Diecks *et al.* 2012). Dammhahn and Almeling (2012), however, found no correlation between body condition and the boldness axis of personality in gray mouse lemurs based on novel object tests. In our study, we considered only the body mass at testing because body mass shows large variation within a single season (Vuarin *et al.* 2013) and we were interested in the influence of current body mass on behavior. Interestingly, Dammhahn (2012) found that wild male gray mouse lemurs become bolder after 3 yr, suggesting a link between personality (particularly boldness and exploration) and potential reproductive success. She suggested, moreover, that older males are bolder and more risk prone than younger males that have not yet reproduced because they have already reproduced.

Wild and captive individuals face very different selection pressures and may thus adopt different life-history strategies to optimize their fitness. For example, captive hyenas (*Crocuta crocuta*) are often less neophobic and more explorative than wild animals (Benson-Amram *et al.* 2013). Captivity may also explain the low latency of exploration in our young male mouse lemurs. Wild individuals are smaller than captive animals and should thus start exploration earlier if our results hold for wild populations. The size and color of the open field arena and the duration of the test also differ from those used to study wild gray mouse lemurs (Dammhahn 2012), which may explain the difference in behavioral response between wild and captive individuals. However, in blue tits personality traits in captivity correlated positively with analogous personality traits in wild populations in novel environment experiments: for the same individual a higher exploratory rate in captivity correlated with a higher probability to find new sites for feeding (Herborn *et al.* 2010). Along the same lines, wild caught starlings (*Sturnus vulgaris*) started to explore a new environment earlier than captive individuals, and this was interpreted as a higher motivation to escape (Feenders *et al.* 2011). Comparable tests in the field and in the laboratory are needed to help understand how captivity influences behavior in gray mouse lemurs.

Additional experiments quantifying exploration behavior in more realistic settings than the open-field test and with wild individuals are needed to address the hypothesis that morphology influences behavior or to understand why they are correlated. We recorded a large number of individuals (29) that did not move during the 30 min of testing and included these “meaningful zeros” in our analysis. Wild mouse lemurs actively explore their environment even after handling (P. Thomas *pers. obs.*), suggesting that the lack of exploration may simply be due to a lack of motivation. More complex test environments than the open-field test may be more suitable for the study of personality traits such as exploration or boldness in small primates such as the gray mouse lemur.

## Conclusion

Our study shows that a personality trait is linked to body size and the body weight at birth in a small captive primate (*Microcebus murinus*). The link between personality and life history is, however, not translated into a significant link between growth rate and exploration behavior, in contrast to predictions of the pace-of-life hypothesis. Rather, smaller individuals and individuals that had lower birth weights explored their environment sooner, in accordance with predictions of dispersal models.

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