Are personality differences in a small iteroparous mammal maintained by a life-history trade-off?

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Despite increasing interest, animal personality is still a puzzling phenomenon. Several theoretical models have been proposed to explain intraindividual consistency and interindividual variation in behaviour, which have been primarily supported by qualitative data and simulations. Using an empirical approach, I tested predictions of one main life-history hypothesis, which posits that consistent individual differences in behaviour are favoured by a trade-off between current and future reproduction. Data on life-history were collected for individuals of a natural population of grey mouse lemurs (Microcebus murinus). Using open-field and novel-object tests, I quantified variation in activity, exploration and boldness for 117 individuals over 3 years. I found systematic variation in boldness between individuals of different residual reproductive value. Young males with low current but high expected future fitness were less bold than older males with high current fecundity, and males might increase in boldness with age. Females have low variation in assets and in boldness with age. Body condition was not related to boldness and only explained marginal variation in exploration. Overall, these data indicate that a trade-off between current and future reproduction might maintain personality variation in mouse lemurs, and thus provide empirical support of this life-history trade-off hypothesis.

Keywords: behavioural types; boldness; exploration; sex differences; Microcebus murinus; asset protection

1. INTRODUCTION

Understanding the determinants and consequences of individual behavioural variation is a central topic in behavioural ecology. Recently, the ecological and evolutionary significance of intraindividual consistency and interindividual variation in behaviour (i.e. animal personality) has been widely recognized [1–4], because personality traits are ubiquitous, moderately heritable [5,6] and have fitness consequences [7,8]. Several theoretical models have been proposed to explain the evolution and maintenance of animal personality either in a constraint or an adaptive framework (reviewed in [9,10]), which are mainly supported qualitatively [11–13] or by simulations and game-theoretical approaches [14–17].

Empirical attempts to test contrasting predictions of the major models are still scarce, leaving a gap between theoretical and empirical personality research [10]. The aim of this study is to test one current theoretical model with long-term data from a natural population of a small Malagasy primate.

I will focus on one state-dependent personality model because it has potential general explanatory power for a variety of species and allows predictions for both sexes in contrast to other life-history hypotheses [11,12]. This hypothesis [16] posits that interindividual variation in personality traits is maintained by a life-history trade-off between current and future reproduction, resulting in populations in which some individuals invest in current and others more in future reproduction. The differences in fitness expectations (i.e. assets) associated with these strategies should result in differences in risk-taking between the two types of individuals. Using an evolutionary model, Wolf et al. [16] demonstrated that asset protection can indeed explain the evolution and maintenance of consistent individual differences in behaviour and the emergence of correlations between personality traits (i.e. behavioural syndromes).

Iteroparous species with discrete reproductive seasons separated by long non-reproductive phases are particularly suited to test the life-history trade-off hypothesis. This pattern is common in seasonally breeding species such as the grey mouse lemur (Microcebus murinus, Cheirogaleidae), a small (60 g), nocturnal, omnivorous Malagasy primate. Mouse lemurs tune their reproductive schedule to the seasonality of their habitat and have only one reproductive cycle per year in the centre of their geographical distribution [18]; in more productive habitats two to three cycles occur [19]. Mouse lemurs have a fast life history and enter their first reproductive cycle at approximately 10 months of age. During the short annual mating period, males roam extensively in search of receptive females, and also guard and aggressively defend access to them [20]. Whereas females reproduce in their first year, the chances of not yet fully grown yearling males fathering offspring are low because male reproductive success is determined by body mass [20]. Annual survival rate is low, resulting in an average life span of 2–3 years, and only a few individuals reach 10 years of age in natural populations [21]. Hence,
individuals of different sex and age classes vary in current and future fitness expectations, which, according to the life-history hypothesis, should lead to predictable patterns of stable individual differences in behavioural traits.

Specific predictions of the life-history model were based on three assumptions. (i) Heavier males have higher reproductive success [20]. (ii) Male size and body mass increase with age in the first 3 years of life (M. Dammhahn 2002–2011, unpublished data). (iii) Boldness negatively affects survival [8]. Based on these assumptions and the life-history trade-off hypothesis I made the following predictions. (i) Since body mass is a predictor of reproductive success for males, and older individuals are heavier than younger ones, young males should be less active, explorative and bold than old males. (ii) This age difference in personality traits is not expected for females because in females assets vary less with age. Because future fitness varies with age, I predicted (iii) higher within-year consistency than between-year consistency in males, and (iv) an increase of activity, exploration and boldness with age (individual plasticity) in males. Finally, (v) I expected a positive correlation between boldness and exploration, forming a behavioural syndrome.

2. METHODS

(a) Study area and field methodology

The study was conducted in the Forêt de Kirindy/CNFREF, a dry deciduous forest in central western Madagascar (44°39′E, 20°03′S). Beginning in August 2002, I and Malagasy field assistants had regularly (re)captured and marked individuals of a population of 50–150 individuals of M. murinus at a time (for details, see [22,23]). Capture was performed with Sherman live traps in three consecutive nights about once per month during the non-wet season, and five to nine times per year in a study area of 25 ha. During capture, monthly body weight data were taken for each individual, and about once per year a set of standard morphometric measurements including body length were taken. Since capture probabilities of M. murinus in the Kirindy are high, juveniles are captured in their first year. Age estimates for all individuals dispersing into the study area as adults are based on body size and tooth wear (M. Dammhahn 2002–2011, unpublished data).

(b) Measuring activity, exploration and boldness

Subjects were trapped between 18:00 and 22:00, and tested subsequently in their home range area. An open-field test was used to quantify behaviours related to activity and exploration in a novel environment. The test was performed in a white wooden box (80 × 60 × 60 cm) with a mesh lid and four blind holes. I superimposed a grid of eight cells (20 × 15 cm) on the area of the box to record the location of the animal. Subjects were released into the box from the trap and their behaviour was video-taped from above using infrared flashlight. The open-field test started when the full body of the mouse lemur was inside the box and ended after 5 min. A novel-object test was performed subsequently in the box and started when a novel object was fully introduced into the box, while the animal was at the opposite side of the box. The novel-object test was used to quantify behaviours related to exploration and boldness. I used two different types of novel objects: a plastic toy car (10 cm) and a plastic duck (5 cm). The behaviour of the subject was video-recorded for 5 min using infrared flashlight. Subsequently, the animal was released and the box was cleaned with 70 per cent ethanol before a new animal was placed inside. I used a blind video analysis to score behaviours expressed in both tests. For the open-field test, I recorded the proportion of time spent climbing, walking, rearing, resting, scanning, sniffing and showing other behaviour (e.g. autogrooming), the rates of inspecting blind holes and jumping, and the number of grid cells covered (table 1). For the novel-object test, I recorded the latency to approach the novel object, the latency to contact with the novel object, the latency to enter the same grid cell, the frequency of approaches, the frequency of entering the same grid cell and the proportion of time spent in contact with the novel object. If the animal did not approach the novel object, the latencies were set at 5 min. In total, 185 tests were performed with 117 individuals (50 females and 67 males) between end of August and end of October 2008–2010.

(c) Statistical analyses

I used principal component analysis (PCA) to reduce the number of dependent variables prior to statistical analyses and to illustrate relationships between behavioural variables. PCA was performed with untransformed variables for open-field and novel-object tests, respectively. I retained principal components with eigenvalue greater than 1 (Kaiser–Guttman criterion [26]) and based on screen plots, which were used as composite behaviour variables for further analyses.

I assessed temporal individual consistency of behaviours for n = 53 individuals, for which I obtained multiple measurements (n = 121). As suggested by Lessells & Boag [24], I calculated repeatability as an intraclass correlation coefficient (r) based on variance components derived from a one-way analysis of variation (ANOVA) with individual as a factor. Standard errors for ANOVA-based repeatability were calculated as suggested by Nakagawa & Schielzeth [25]. Additionally, I compared within-year repeatability (repeated testing within four to six weeks, n = 21) and between-year repeatability (repeated testing after 1–2 years, n = 18) for males. The existence of a behavioural syndrome was assessed by Spearman rank correlations between composite behaviour variables.

I used restricted maximum-likelihood linear mixed modeling (LMM) with normal errors to evaluate the relationship between composite behavioural variables from PCA and sex, age class, test year, total number of test trials, and the interaction of sex and age class as fixed effects. I defined three age classes: yearlings (class 1, ≤ 1 yr; nmales = 25, n females = 18), individuals of average age (class 2, >1 yr and <3 yr; nmales = 42, n females = 29) and individuals older than the average life expectancy (class 3, ≥3 yr; nmales = 9, n females = 10). Individual identity (ID) and the total number of trials performed were added as correlated random effects in each model, forming a random slope model [27]. This model structure included between-individual variation in slope of the within-individual relationship between composite behavioural variables and the number of trials performed, as well as between-individual variation in intercepts. I tested the additional explanatory power of adding the random effect ID and total number of trials by comparing models with and without the random effects using a log-likelihood ratio test [28]. The interaction of sex and age class showed no significant effect and was therefore excluded from subsequent analyses.

The composite behaviour variable NO1 (boldness) was not normally distributed and showed an inflation of minimum
Table 1. PCA loadings of behaviours in open-field test (OF1 and OF2, activity; OF3, threat response; OF4, exploration) and novel-object test (NO1, boldness; NO2, exploration thoroughness) in 117 grey mouse lemurs. Bold type indicates behaviours that contributed importantly to a component.

<table>
<thead>
<tr>
<th>behaviour</th>
<th>OF1</th>
<th>OF2</th>
<th>OF3</th>
<th>OF4</th>
<th>behaviour</th>
</tr>
</thead>
<tbody>
<tr>
<td>climbing</td>
<td>-0.12</td>
<td>-0.61</td>
<td>0.02</td>
<td>-0.05</td>
<td>contact</td>
</tr>
<tr>
<td>walking</td>
<td>-0.40</td>
<td>0.14</td>
<td>-0.07</td>
<td>-0.31</td>
<td>latency approach</td>
</tr>
<tr>
<td>rearing</td>
<td>-0.32</td>
<td>0.24</td>
<td>-0.24</td>
<td>-0.33</td>
<td>latency same grid cell</td>
</tr>
<tr>
<td>scanning</td>
<td>-0.05</td>
<td>0.29</td>
<td>0.82</td>
<td>0.05</td>
<td>latency contact</td>
</tr>
<tr>
<td>sniffi</td>
<td>-0.32</td>
<td>0.17</td>
<td>-0.19</td>
<td>-0.23</td>
<td>approach rate</td>
</tr>
<tr>
<td>stilli</td>
<td>0.38</td>
<td>0.15</td>
<td>-0.42</td>
<td>0.16</td>
<td>same grid cell rate</td>
</tr>
<tr>
<td>otheri</td>
<td>-0.11</td>
<td>0.20</td>
<td>0.14</td>
<td>-0.20</td>
<td></td>
</tr>
<tr>
<td>head dipping ratei</td>
<td>-0.36</td>
<td>0.15</td>
<td>-0.11</td>
<td>0.57</td>
<td></td>
</tr>
<tr>
<td>head dipping locationi</td>
<td>-0.36</td>
<td>0.11</td>
<td>-0.07</td>
<td>0.58</td>
<td></td>
</tr>
<tr>
<td>square rate</td>
<td>-0.42</td>
<td>-0.23</td>
<td>0.03</td>
<td>-0.09</td>
<td></td>
</tr>
<tr>
<td>jump ratei</td>
<td>-0.17</td>
<td>-0.54</td>
<td>0.13</td>
<td>0.07</td>
<td></td>
</tr>
</tbody>
</table>

| eigenvalue                               | 2.09 | 1.38 | 1.08 | 1.00 |           |
| variance explained (%)                   | 39.5 | 17.3 | 10.7 | 9.2  |           |
| repeatabilityi                           | 0.45 | 0.22 | 0.28 | 0.16 |           |
| (mean ± s.e.)                            | ±0.10| ±0.12| ±0.12| ±0.12|           |
| LRT (d.f. = 3)i                          | 17.22| 13.10| 6.00 | 3.40 |           |
| p2                                       | <0.001| <0.01| n.s. | n.s. |           |

*pProportion of time spent climbing on walls and lid.
*Proportion of time spent walking or running.
*Proportion of time spent rising up on hind legs.
*Proportion of time spent moving the head by greater than 45°, while the rest of the body is immobile.
*Proportion of time spent sniffing the floor or walls.
*Proportion of time spent non-moving.
*Proportion of time spent auto-grooming, hunting and feeding insects.
*Number of times the head was inserted into one of the blind holes.
*Number of different holes in which the head was inserted.
*Number of grid cell changes.
*Number of jumps.
*Proportion of time spent in body contact with the novel object.
*Latency to approach novel object by one grid cell.
*Latency to enter the same grid cell as the novel object.
*Latency to body contact with the novel object.
*Number of approaches.
*Number of times entering same grid cell as novel object.
*Repeatability was calculated after Lessells & Boag [24] as an intraclass correlation coefficient from a one-way ANOVA with individual as a factor, standard errors (s.e.) were calculated after Nakagawa & Schielzeth [25].
*The significance of repeatability was tested by comparing mixed models including the correlated random effects individual identity and number of test trials performed to linear models without it, using a likelihood ratio test (LRT).

values (zero inflation). These values correspond to animals not showing any behaviour towards the novel object, and were therefore treated as ‘true zeros’ [28]. An inflation of zeros in the response variable—more zeros than expected based on underlying model distributions—can cause biased parameter and error estimates or overdispersion. As suggested by Zuur et al. [29], I used a two-step modelling approach to analyse the zero-inflated data. First, all minimum values were set at 0 and all non-minimum data at 1, and a generalized linear mixed model (GLMM) with binomial distribution was used. Second, all non-zero observations were modelled with an LMM. The full model contained sex, age class, test year, total number of test trials, novel object, and the interaction of sex and age class as fixed effects. Individual ID and the total number of trials performed were added as correlated random effects in each model, forming a random slope, random intercept model structure. Since novel object and the interaction of sex and age class showed no significant effects, they were excluded from subsequent analyses.

To estimate individual variation in plasticity of behaviour with age, I used within-subject centring [30,31], and first calculated the mean age for each individual and second the mean-centred age as the deviation from the individual mean age for all observations of each individual. Then I extracted individual slopes from random slope models for individual plasticity in the first PCA component fitted for the mean-centred age for a subset of individuals that were tested repeatedly in different ages (males: n = 18 individuals, n = 48 cases; females: n = 16, n = 33 cases). Finally, I used linear models to test the relationship between individual slopes (i.e. individual plasticity) and age change for males and females, respectively.

Finally, I tested whether between-individual differences in behaviour are simply condition-dependent. Body condition was calculated using the scaled mass index (WSMA) [32] as the mass of an individual standardized to the mean body size of all individuals in the population retaining the population-specific allometric relationship. I included in this analysis only individuals for which recent measurements of body mass (less than one month) and body length (less than three month) in relation to the behavioural tests were available, yielding 70 individuals. To evaluate the relationship between composite behaviour variables and body condition, WSMA was included as an additional fixed effect in the final models for all composite behaviour variables. An improvement of model fit of the extended model was judged based on ANOVA and Akaike information criterion (AIC) comparison with the model without WSMA. All data were analysed by using R v. 2.13 [33]. Values of p
were two-tailed throughout and the accepted significance level was \( p < 0.05 \).

### 3. RESULTS

(a) **Open-field test**

Following PCA, I retained four components with eigenvalue greater than 1, which explained 77 per cent of the total variance (table 1). The first component of the open-field test OF1 was characterized by behaviours of locomotion and exploration, and will be referred to as activity hereafter. OF2 was primarily characterized by climbing and jumping, and thus also represents activity. OF3 was characterized by threat response of the animal, such as freezing and scanning behaviour. OF4 was composed of two exploration behaviours related to the blind enclosures and will be referred to as exploration hereafter.

Overall, repeatability for behaviours expressed in the open-field test ranged between 0.16 and 0.45 for all PCA components (table 1). In males, individual behaviour was repeatable within years, such that repeatability differed from 0 for activity (OF1: \( r = 0.41 \pm 0.19, F_{20,21} = 2.19, p = 0.036 \)) and showed a trend for a difference for climbing activity (OF2: \( r = 0.30 \pm 0.21, F_{20,21} = 1.75, p < 0.099 \)) and exploration (OF4: \( r = 0.30 \pm 0.21, F_{20,21} = 1.75, p < 0.098 \)), but not for threat response (OF3: \( r = 0.22 \pm 0.23, F_{20,21} = 1.49, p = 0.18 \)). Individual behaviour was not repeatable between years for activity (OF1: \( p = 0.18 \); OF2: \( p = 0.63 \)) and exploration (OF4: \( p = 0.16 \)), but showed a trend for repeatability for threat response (OF3: \( r = 0.37 \pm 0.22, F_{17,18} = 1.97, p = 0.078 \)). In females, activity was repeatable within years (OF1: \( r = 0.49 \pm 0.26, F_{8,9} = 2.94, p = 0.064 \); OF2: \( r = 0.56 \pm 0.24, F_{8,9} = 3.57, p = 0.038 \)) and between years (OF1: \( r = 0.69 \pm 0.13, F_{14,15} = 5.64, p < 0.001 \)). Threat response and exploration were only repeatable between years (OF3: \( r = 0.41 \pm 0.21, F_{14,15} = 2.47, p = 0.039 \); OF4: \( r = 0.35, F_{14,15} = 2.16, p = 0.067 \)).

Activity and exploration varied between test years (OF1: \( t = 2.70, p < 0.01 \); OF2: \( t = -6.66, p < 0.001 \); OF4: \( t = 3.53, p < 0.01 \); electronic supplementary material, table S1). Sex did not explain variance for activity, threat response behaviour nor exploration. There was a marginal trend for an age-class effect for activity (OF1: \( t = -1.84, p = 0.1 \)). Exploration varied with the number of trials experienced (OF4: \( t = -1.88, p < 0.05 \)). Including the correlated random effects ID and total number of trials experienced improved model fit for activity (OF1: \( LRT = 17.22, d.f. = 3, p < 0.001 \); OF2: \( LRT = 13.10, d.f. = 3, p < 0.01 \)), but not for the threat response (OF3: \( LRT = 6.00, d.f. = 3, p > 0.05 \)) nor exploration (OF4: \( LRT = 3.40, d.f. = 3, p > 0.05 \)). Mouse lemur ID explained significant proportions of variance for all composite behaviour variables (OF1: 66.0%; OF2: 6.5%; OF3: 19.8%; OF4: 42.0%). Finally, there was no individual variation in plasticity of activity (OF1) with age in males (\( R^2 = 0.08, F_{1,16} = 1.45, p = 0.25 \)) nor in females (\( R^2 = 0.02, F_{1,13} = 0.20, p = 0.66 \)).

(b) **Novel-object test**

Following PCA of all behaviours related to the novel object, I retained two principal components, which explained 79 per cent of the total variance (table 1). All latencies and approach behaviours loaded on NO1, which will be referred to as boldness hereafter. Although the eigenvalue was less than 1, I further retained NO2 because it was characterized by the time spent in contact with the novel object indicating exploration thoroughness.

Overall, novel-object-related behaviours were repeatable (NO1: \( r = 0.31 \pm 0.11 \); NO2: \( r = 0.34 \pm 0.11 \); table 1). In males, within-year repeatability in boldness and exploration thoroughness was high and significantly different from 0 (NO1: \( r = 0.68 \pm 0.12, F_{20,21} = 4.66, p < 0.001 \); NO2: \( r = 0.65 \pm 0.13, F_{20,21} = 4.17, p < 0.001 \)), whereas between-year repeatability was low and not different from 0 for both behaviours (NO1: \( r = 0.12 \pm 0.26, F_{17,18} = 1.24, p = 0.32 \); NO2: \( r = 0.02 \pm 0.27, F_{17,18} = 0.97, p = 0.52 \)). In females, boldness and exploration thoroughness were repeatable neither within nor between years (all \( p > 0.1 \)).

Boldness varied between the sexes (NO1: binomial GLMM, \( z = 2.04, p = 0.041 \)) and age classes (NO1: LMM for non-zero observations, \( t = 2.15, p = 0.040 \); electronic supplementary material, table S2; figure 1). Including the correlated random effects improved model fit for the binomial GLMM (LRT = 14.40, d.f. = 3, \( p < 0.01 \)) but not for the LMM for non-zero observations (LRT = 3.60, d.f. = 3, \( p > 0.05 \)). Mouse lemur ID explained 72.7 per cent of the variance in the GLMM and 38.1 per cent in the LMM. For exploration thoroughness (NO2), none of the fixed effects explained variation. Including the correlated random effects improved model fit (NO2: \( LRT = 16.40, d.f. = 3, p < 0.001 \)) and mouse

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**Figure 1.** Boldness scores (NO1) for males and females of different age classes. Males and females differ in boldness only for individuals older than the population average life expectancy of 3 years (left: \( \leq 1 \) yr, middle: \( 2–3 \) yr, right: \( > 3 \) yr). Males older than 3 years are bolder than younger males. Shown are median, interquartile range, min–max range and outliers; box width corresponds to sample size.
lemur ID explained 67.0 per cent of the variance of exploration thoroughness. Finally, there was a trend for individual variation in plasticity of boldness (NO1) with age in males ($R^2 = 0.21$, $F_{1,16} = 4.29$, $p = 0.055$) but not in females ($R^2 = 0.02$, $F_{1,15} = 0.27$, $p = 0.61$), suggesting that males might get slightly bolder with age.

(c) Behavioural syndrome

Boldness (NO1) was positively correlated with activity (OF1: $r = -0.48$, $p < 0.001$; OF2: $r = -0.24$, $p < 0.001$) and exploration (OF4: $r = -0.21$, $p = 0.004$), but not with threat response (OF3: $r = 0.03$, $p = 0.64$). Exploration thoroughness (NO2) correlated with activity (OF1: $r = 0.26$, $p < 0.001$) but not with climbing activity (OF2: $r = 0.12$, $p = 0.11$), threat response (OF3: $r = 0.04$, $p = 0.60$) nor exploration (OF4: $r = 0.01$, $p = 0.96$).

(d) Condition-dependency of personality traits

Including body condition (WSMA) in the final LMMs did not improve model fit for activity (OF1: $\chi^2 = 0.35$, d.f. = 1, $p = 0.56$; OF2: $\chi^2 = 0.10$, d.f. = 1, $p = 0.76$) and threat response behaviour (OF3: $\chi^2 = 1.14$, d.f. = 1, $p = 0.29$). For exploration only (OF4), model fit was increased ($\chi^2 = 8.69$, d.f. = 1, $p = 0.003$) and WSMA explained a significant part of the variance of exploration ($r = 2.92$, $p = 0.006$). For boldness (NO1), including WSMA in the final model did not improve model fit for the binomial GLMM ($\chi^2 = 0.23$, d.f. = 1, $p = 0.63$) nor for the LMM with non-ZERO values only ($\chi^2 = 2.61$, d.f. = 1, $p = 0.11$). For exploration thoroughness also (NO2), model fit did not improve by including WSMA ($\chi^2 = 0.10$, d.f. = 1, $p = 0.76$).

4. DISCUSSION

(a) Individual consistency and behavioural syndromes

Three major dimensions of behavioural variation in mouse lemurs emerged: activity, exploration and boldness. Individual variation in these behavioural traits was repeatable and was lower than interindividual variation in the population. Hence, activity, exploration and boldness are personality traits in mouse lemurs (as defined by Sih et al. [2] and Réale et al. [4]). Overall, repeatability was well within the ranges described for other species [34]. Interestingly, males and females differed in repeatability of boldness, which is discussed in detail below. In accordance with the life-history hypothesis, differences between individuals in activity, exploration and boldness were positively correlated, forming a behavioural syndrome.

(b) Asset protection and boldness in males

As predicted by the life-history trade-off hypothesis [16], I found systematic variation in boldness behaviour between individuals of different residual reproductive value. In males, younger individuals expressed lower boldness than older individuals. Yearling males have much to lose because their chances of fathering offspring in their first reproductive season are low [20], but they have high future reproductive value, once they survive to the next breeding season and grow larger. In contrast, older males have much to gain. Males that reach an age of 3 years are the heaviest and acquire the highest reproductive share of up to five offspring per reproductive season [20]. Given low annual survival probabilities of only 0.49 in the natural population [21], the future reproductive value of these males in their prime is low. Hence, these males may increase investment in reproductive effort and express risk-taking behaviour [35,36]. Similarly, in bighorn sheep (Ovis canadensis), older rams are bolder, and boldness had a positive effect on reproductive success later in life, but decreased reproductive success early in life [37]. Although older mouse lemur males are heavier than young males, there is no difference in body condition between yearlings (WSMA = 62.9 ± 9.0 g) and older males (WSMA = 59.0 ± 3.6 g). Hence, between-individual variation in behaviour was not simply condition-dependent.

As predicted, there are first indications that individual males systematically increased in boldness once they reached physical prime status. These findings imply that personality traits are not set for life [27,38]. Indeed, consistency in boldness was high over one mating season, but low when tested between years. Hence, males express plasticity in response to changing conditions (i.e. an individual × age interaction [31]). Prior experience could increase boldness [39], leading to higher risk-taking behaviour in older males. Variation in individual male plasticity with age was high in all age classes, however, suggesting a cautious interpretation of the individual × age interaction. Since we know so little about the ontogeny of personality traits in mouse lemurs and other species, only future studies can reveal patterns and mechanisms of individual personality development [27,38].

(c) Sex differences in trade-offs and personality traits

Male and female mouse lemurs differed in boldness. In particular, at older ages, males were consistently bolder than females (figure 1) and boldness was more repeatable in males than in females. Sex differences in personality traits are common (summarized in Schuett et al. [13]), and several mechanisms could lead to this pattern. First, personality-dependent dispersal might facilitate interindividual variation in activity, exploration and boldness [40], resulting in phenotypic differences between dispersing and resident individuals (e.g. Parus major [41], Microtus oeconomus [42], Gambusia affinis [43]). Male-biased dispersal is the general mammalian pattern and has been described for mouse lemurs [44], with most males dispersing before entering their first reproductive season. Sex differences in personality traits would be expected particularly for yearlings, but are evident only at older ages, long after dispersal has occurred. Therefore, sex-biased dispersal is unlikely to explain sex differences in boldness in mouse lemurs. Second, different androgen levels of males and females could lead to differences in behavioural tendencies [45]. In this study, behavioural tests were performed before the short annual mating season, when testes size is maximal [46] and testosterone production in males peaks [47]. However, plasma testosterone levels in male mouse lemurs were not related to body weight and age before and during the mating season in a captive study [47], and hence are unlikely to explain the age-related sex differences in boldness. Further, despite potential tremendous changes in hormone levels between first and
second behavioural tests, males expressed very high short-term repeatability in personality traits.

Third, sexual selection might lead to sex differences in personality traits and consistency [13]. Mouse lemurs have a promiscuous mating system, with some indirect indications for post-copulatory female choice [48] and heavier males siring most offspring [18,20]. Hence, higher levels and consistency in boldness are expected for males as the chosen sex [13]. Indeed, male mouse lemurs have higher absolute values and repeatability in this personality trait than females. If boldness could indicate male quality, this pattern should be consistent over all age stages, however.

Finally, owing to different male and female reproductive potential, the life-history trade-off model [16] predicts age-related difference in boldness. Female mouse lemurs can reproduce until late ages in captivity and can have at least one litter per year in the field until the age of 10 years [18] (M. Dammhahn 2002–2011, unpublished data), indicating low asset variation with age. Given this low variation in fitness expectations in females, stable individual differences in boldness cannot emerge based on a life-history trade-off between current and future reproduction [16]; instead females might plastically adapt their risk-taking behaviour to current environmental conditions. Whether high repeatability of female activity and exploration behaviour could be maintained by consistent individual differences in life-history productivity [12] needs to be addressed in future research. In contrast to females, male future reproductive value is strongly age-dependent, which might facilitate high boldness as a potential terminal investment strategy. Increased ‘risky male behaviour’, particularly during the short annual mating season, is costly, however, because it reduces male survival probability by up to 25 per cent compared with females [21].

(d) Conclusion: life-history trade-offs and the maintenance of animal personality traits

Empirical data on personality traits and life history of mouse lemurs demonstrated that the life-history trade-off between current and future reproduction [16] can ultimately maintain personality variation in natural populations of iteroparous mammals. Owing to sex differences in reproductive potential and reproductive skew, this trade-off is stronger in males, leading to systematic variation in boldness between the sexes, and between males of varying current and residual reproductive value. Since sex differences and age-related variation in personality traits are common [13,37], the link between differential asset-protection strategies and personality offers great potential for further empirical and experimental studies. What need to be addressed in future research are: (i) the mechanisms facilitating long-living individuals systematically switching behavioural tendencies, associated with asset accumulation or at certain life-history stages; and (ii) the adaptive nature of the interplay of plasticity and personality offers great indications for post-copulatory female choice [48] and can have a promiscuous mating system, with some indirect indications for post-copulatory female choice [48] and heavier males siring most offspring [18,20]. Hence, higher levels and consistency in boldness are expected for males as the chosen sex [13]. Indeed, male mouse lemurs have higher absolute values and repeatability in this personality trait than females. If boldness could indicate male quality, this pattern should be consistent over all age stages, however.

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