

# Is risk taking during foraging a personality trait? A field test for cross-context consistency in boldness

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During foraging, animals have to balance the risk of predation with the energy gain. The amount of risk animals take for a given resource depends on their energy budget but is expected also to vary between individuals of different personality types. We tested whether individuals of free-ranging grey mouse lemurs, *Microcebus murinus*, forage risk-sensitively and are consistent in their risk-taking behaviour. Furthermore, we tested whether boldness towards a novel object predicts risk taking in a foraging task. In a field experiment, we simulated low and high predation risk at artificial feeding sites. During focal platform observations, we quantified behaviours related to exploration and feeding for 36 individuals. Furthermore, we used a novel object test to quantify variation in boldness for 22 of these individuals. As predicted, grey mouse lemurs foraged risk-sensitively indicated by longer latencies to enter a feeding platform and to start feeding as well as by relatively longer feeding time compared to nonfeeding in high-risk situations. Individual differences in risk taking were repeatable and repeatability increased with increasing risk. Individual plasticity was higher for low-risk individuals providing field evidence for coping styles. There was no relationship between individual body condition and risk-taking behaviour. Finally, boldness measured in a novel object test was correlated with risk taking in a foraging task, providing a rare ecological validation for this personality trait. These results suggest that intrinsic individual differences in boldness need to be considered as an important source of variation when testing predictions of risk-sensitive foraging using optimality approaches.

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One of the most fundamental problems governing animal behaviour is finding food while avoiding being food for others. Based on this trade-off, an individual has to weigh the benefit of energy gain with the risk of predation according to its current energy balance (McNamara & Houston 1987; Lima & Dill 1990; Lima 1998). Recent research has provided convincing experimental proof for the existence of this relationship. These studies have focused on two main contexts: (1) risk taking concerning the unpredictability of resource availability (risk-sensitive foraging theory: Caraco 1980; Stephens & Krebs 1986) and (2) feeding under conditions with varying predation risk (e.g. Brown 1992, 1999; Verdolin 2006). In both contexts, individuals in a poor energetic state take generally higher risks during feeding than conspecifics in good condition (e.g. Verdolin 2006). Although many studies provide evidence for the existence of a trade-off between energy gain and risk avoidance, there are also numerous attempts that have failed to demonstrate

optimal foraging under these conditions. For example, Verdolin (2006) reported that 20% of the studies included in a meta-analysis of terrestrial species did not find the expected positive relationship between risk taking and energy gain. The real number of negative results is likely to be even higher because of general publication bias against negative findings (e.g. Fanelli 2010). Furthermore, the remaining unexplained variation has been generally large (e.g. Blumstein 2006). Hence, when facing the fundamental problem between foraging and risk avoidance, individuals do not necessarily behave optimally.

Intrinsic individual differences in behavioural tendencies may represent an explanation for suboptimal risk-taking behaviour. Such intraindividual consistency and interindividual variation in behavioural traits has been defined as animal personality or temperament (Sih et al. 2004; Réale et al. 2007). Interindividual differences in behavioural phenotypes have been widely ignored in optimal foraging and antipredator behavioural research (e.g. Brown & Kotler 2004; Verdolin 2006) and were only recently acknowledged as an important source of variation, which might constrain flexibility in behavioural responses (Sih et al. 2004). Indeed, the emerging field of animal personality research has provided many examples of intrinsic individual differences in behavioural

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phenotypes, which challenge the optimality approach to behavioural problems (reviewed e.g. in Sih et al. 2004; Réale et al. 2007). Classic examples were provided by Huntingford (1976, 1982), who found that bold and active stickleback, *Gasterosteus aculeatus*, individuals take greater risks in the presence of predator dummies. Here, we define risk taking as the behaviour expressed in a risky or novel situation and boldness as consistent individual differences in risk-taking behaviour (Réale et al. 2007). Such consistent individual differences in risk taking have been demonstrated in a variety of species, including invertebrates (e.g. Wilson et al. 2010), fish (e.g. Wilson et al. 1994; Godin & Dugatkin 1996; Sih et al. 2003; Ward et al. 2004; Bell 2005; Jones & Godin 2010), birds (e.g. van Oers et al. 2004) and mammals (e.g. Réale et al. 2009; Dammhahn 2012). It is well established that boldness has fitness consequences (Smith & Blumstein 2008) and influences important life history decisions such as dispersal (Grand 1999). Exposure to predators might even generate personality as has been shown experimentally and empirically for sticklebacks (Bell & Sih 2007; Dingemanse et al. 2009) and via game-theoretical modelling (Dall et al. 2004) owing to differential predation risk among personality types (Sih et al. 2003; Dingemanse et al. 2004; Quinn & Cresswell 2005). Furthermore, unpredictability in resource availability during development increased boldness and exploration in guppies, *Poecilia reticulata* (Chapman et al. 2010) and sticklebacks (Brydges et al. 2008). Hence, risk-taking behaviour has an important intrinsic component leading to consistent individual differences in response level, that is, average behavioural expression, and in response plasticity, that is, a change in behaviour when environmental conditions change (behavioural reaction norm approach, cf. Dingemanse et al. 2010). Furthermore, the large fitness consequences of risk taking qualify it as an important evolutionary trait.

In animal personality research, boldness is typically quantified via novel object tests or exposure to predator dummies (Réale et al. 2007); both situations involve only artificial risk. Only a few studies have tested whether exploration and boldness quantified in artificial experimental settings, for example a closed room, test box or tank, indeed reflect natural behaviour in new or risky situations. For example, Wilson & McLaughlin (2007) tested brook charr, *Salvelinus fontinalis*, individuals both in the field and in the laboratory and found very similar behavioural tendencies. Furthermore, many studies involve trapping of free-ranging individuals (e.g. Dingemanse et al. 2003; Martin & Réale 2008; Dammhahn 2012), which might cause a sampling bias towards individuals with higher risk-taking tendencies and thereby affect results on population variation, fitness consequences and heritability (Biro & Dingemanse 2009; Carter et al. 2012). Only a few studies have quantified personality traits in the wild, for example Garamszegi et al. (2009) assessing exploration, boldness and aggressiveness in collared flycatchers, *Ficedula hypoleuca*. Hence, animal personality studies in general rarely involve a 'reality check' and might be affected by a sampling bias. The aim of this study was to test for the first time experimentally in the field whether individual differences in boldness towards novel objects indeed predict individual differences in risk taking during foraging of free-ranging, small, arboreal primates. Combining the classic experimental approaches to quantify risk taking under varying predation risk and boldness when exposed to a novel object, this study contributes a rare ecological validation of personality traits, which are often studied in isolation from 'real-life behaviour' (Réale et al. 2007; Archard & Braithwaite 2010).

We studied personality and risk taking in a foraging context in free-ranging grey mouse lemurs, *Microcebus murinus* (Cheirogaleidae), small (60 g), nocturnal Malagasy primates that are widely distributed over various forest habitats in western and

southern Madagascar (Kappeler & Rasoloarison 2003; Radespiel 2006). The species is ecologically very tolerant and an omnivorous generalist, which feeds on arthropods, small vertebrates, fruit, gum and homopteran secretions (e.g. Dammhahn & Kappeler 2008a). Interindividual variation and intraindividual consistency in activity, exploration and boldness have been demonstrated recently (Dammhahn 2012). Mouse lemurs face high predation risk by carnivores (*Cryptoprocta ferox*, *Mungotictis decemlineata*), snakes (*Ithycyphus miniatius*, *Sanzinia madagascariensis*), raptors (*Accipiter henstii*), owls (*Tyto alba*, *Asio madagascariensis*) and occasionally even by the larger giant mouse lemur, *Mirza coquereli* (Goodman et al. 1993; Rasoloarison et al. 1995; Schliehe-Diecks et al. 2010; M. Dammhahn, unpublished data). As a result, annual survival rate is only 0.52 for males and 0.67 for females and the average life span is only 2–3 years (Kraus et al. 2008).

To test whether individual differences in boldness towards a novel object predict individual differences in risk taking during foraging we conducted a field experiment. In detail we asked the following questions. (1) Do grey mouse lemurs forage risk-sensitively? If they discriminate between low-risk (LR) and high-risk (HR) feeding situations, we expected longer latencies to enter HR than LR platforms, as well as shorter total time on platforms and higher relative feeding times on HR than LR platforms. Furthermore, we expected a negative relationship between individual body condition and risk-taking behaviour. (2) Do individuals consistently differ in risk-taking behaviour? Since boldness is a personality trait in mouse lemurs (Dammhahn 2012), we expected repeatability in risk-taking behaviour. Furthermore, we expected older males to take higher risks than females and young males as has been shown for boldness (Dammhahn 2012). (3) Is there a relationship between personality and plasticity expressed in a risk-sensitive foraging test? Based on other studies (e.g. Quinn & Cresswell 2005), we expected individuals to differ not only in average boldness, that is, the intercepts of behavioural reaction norms, but also in how fast they habituate to a new (or risky) situation, that is, in the slopes of behavioural reaction norms, which describe the behavioural response of an individual over a gradient of environmental variation (Dingemanse et al. 2010). We expected shyer individuals to express higher plasticity in boldness (coping styles sensu Koolhaas et al. 1999). (4) To validate boldness measures ecologically, we asked whether individual behaviours expressed in a novel object test and in a risk-sensitive foraging test are correlated. If these behaviours reflect the same personality dimension, that is, boldness, we expected a positive correlation between the latencies to enter HR feeding platforms and the latencies to make contact with an unfamiliar object in a novel object test (e.g. Huntingford 1976).

## METHODS

### Study Area and Field Methodology

We conducted the study in the Forêt de Kirindy/CNFEREF, a dry deciduous forest in central western Madagascar (44°39'E, 20°03'S). Individuals of a free-ranging population of 50–150 grey mouse lemurs have been regularly (re)captured and marked with subdermally implanted microtransponders (Trovan, Usling, Germany) by M. D. and Malagasy field assistants beginning in 2002 (for details see Dammhahn & Kappeler 2008a, b). Capture was performed with Sherman live traps on three consecutive nights about once per month mainly during the dry season, and five to nine times per year in a study area of 25 ha. During capture, monthly body mass data were taken for each individual and, about once per year, various standard morphometric measurements were taken. Capture probabilities of *M. murinus* in Kirindy are very high

(Kraus et al. 2008), leading to low capture-based sampling bias and allowing us to capture most juveniles in their first year of age. Age estimates for all individuals dispersing into the study area as adults are based on body size and tooth wear (M. Dammhahn, unpublished data).

#### *Risk-sensitive Foraging Test*

In a field experiment, we simulated low (LR) and high (HR) predation risk at artificial feeding sites. Feeding sites consisted of wooden platforms (30 cm × 30 cm), which were fixed on piles and were provisioned with the same amount of mashed banana as bait (for details see Dammhahn & Kappeler 2009; Lührs et al. 2009). Mouse lemurs usually forage at a height of 1–6 m and come down to the ground only occasionally for short periods of time to forage on highly preferred food such as insects or insect secretions (Dammhahn & Kappeler 2008a; M. Dammhahn, unpublished data). Foraging and feeding on the ground exposes mouse lemurs to additional predators such as ground-dwelling snakes and carnivores and often increases conspicuousness because of the rustling sounds made when moving in dry leaf litter. Therefore, in the LR design a platform was installed at a height of 1.5 m and in the HR design at a height of 0 m. During experiments, each platform was equipped with an automatic RFID reading device (custom made EURO ID, Germany) to determine individual identity of visiting mouse lemurs. In a repeated measurement design, each LR platform was transformed into an HR platform and vice versa without any change in location. This design allowed us to control for potential site effects (e.g. canopy cover, accessibility, adjacent food sources or sleeping places). We set up HR and LR platforms ca. 50 m apart at  $N = 10$  (2008) and  $N = 6$  (2010) different locations. One or two platforms were used at the same time and platforms remained in place for 3–4 nights. On average each platform location was visited by one to seven individuals and each individual visited one to three different platforms. First, each platform was prebaited as LR for 1–2 nights to familiarize subjects with the artificial food source. Subsequently, we performed platform focal observations (two to three per platform), in which we videotaped the behaviour of visiting individuals using infrared flash light. Based on video analysis, we recorded the following behavioural variables for each visit: (1) latency of the individual to access the feeding platform after arriving within 3 m of it, (2) latency of the individual to start feeding after entering the platform, (3) total duration of an individual's feeding bouts while remaining within 3 m of the platform, (4) relative feeding time in relation to the total time on the platform and (5) total time spent on the platform. All visits that were interrupted by either other mouse lemur approaching the feeding stations to within 3 m or other disturbances (e.g. noisy movements of larger arboreal lemurs, predators passing on the ground) were discarded from the analyses. The platform experiments were performed between September and November in 2008 and between August and October in 2010. In total, we collected data for 98 undisturbed visits of 36 individuals (26 males, 10 females). Individuals visited the platforms on average twice (range 1–4) in the HR experiment and on average twice (range 1–6) in the LR experiment.

#### *Novel Object Test*

As described in detail in Dammhahn (2012), we trapped subjects at the beginning of their nocturnal activity period, between 1800 and 2200 hours, and tested them subsequently in their home range area. All novel object tests were performed between September and October when food availability is minimal (Dammhahn & Kappeler 2008a) and capture probability for grey mouse lemurs is very high

(Kraus et al. 2008). We performed a novel object test to quantify behaviours related to boldness. The test was performed in a white wooden box (80 × 60 cm and 60 cm high) with a mesh lid. Individual behaviour during the test was videotaped from above using infrared-flash light. Subjects were released into the box from a trap and were left to habituate to the box for 5 min, in which all but one subjects started to move. Subsequently, a novel object represented by a plastic toy car 10 cm long was fully introduced into the box. All individuals first maximized the distance to the novel object by moving to the opposite side of the box and scanned the object. Only then did some individuals start to approach the object. After the test, the animal was released and the box was cleaned with 70% ethanol before a new subject was placed inside. Using blind video analysis, one of us (M. D.) measured the latency to make contact with the novel object, which strongly reflects all behaviours towards a novel object as described previously (Dammhahn 2012). If the animal did not approach the novel object, the latency was set at 5 min. In total we performed novel object tests with 22 individuals, which also participated in the risk-sensitive foraging test. We have shown previously (Dammhahn 2012) that behaviour towards novel objects, that is, boldness, was repeatable for 117 individuals with particularly high repeatability if tests were performed within a few weeks. We therefore considered the latency to make contact with a novel object as reflecting consistent individual differences in boldness. To account for potential temporal changes in personality scores (e.g. Dammhahn 2012), we used only test scores obtained in the same year as the risk-sensitive foraging test was performed.

#### *Statistical Analyses*

First, we used principal component analysis (PCA) to reduce the number of dependent variables in the platform observations prior to statistical analyses and to illustrate relationships between behavioural variables. PCA was performed with log-transformed and mean-centred variables (see Table 1 for behavioural variables). We retained principal components with eigenvalue > 1 (Kaiser–Guttman criterion: Kaiser 1991) and based on scree plots, which were used as composite behaviour variables for further analyses.

Second, we assessed temporal individual consistency of behaviours expressed during the platform tests based on the PCA components. Since we expected an effect of experiment, we calculated repeatability separately for HR and LR experiments (HR:  $N = 43$  tests,  $N = 29$  individuals; LR:  $N = 58$  tests,  $N = 30$  individuals). As suggested by Lessells & Boag (1987), we calculated repeatability as an intraclass correlation coefficient ( $r$ ) based on variance components derived from a one-way ANOVA with individual as a factor and each composite behavioural variable as the dependent variable. We included individuals tested only once because they contribute to the population-level variation in behavioural traits. Standard errors for ANOVA-based repeatability were calculated as suggested by Nakagawa & Schielzeth (2010).

**Table 1**

PCA loadings of behaviours expressed during feeding platform tests (P1: exploration time; P2: boldness; P3: relative feeding time) of composite behavioural variables of 36 free-ranging grey mouse lemurs in 98 test trials

Behaviour	P1	P2	P3
Latency to enter platform		0.70	0.26
Latency to start feeding	0.14	0.69	
Time spent on platform	−0.58	0.15	−0.54
Time spent feeding	−0.69		
Proportion of time spent feeding	−0.41	−0.12	0.80
Eigenvalue	1.44	1.16	0.96
Variance explained (%)	41.5	26.9	18.4



Third, we applied restricted maximum likelihood linear mixed modelling (LMM) with normal errors to reveal differences in behaviour between LR and HR experimental tests using PCA components as dependent variables. We included sex and age as fixed effects because a previous study revealed differences between these classes of individuals (Dammhahn 2012). Furthermore, we included the test year and the location of the feeding platform as fixed effects to account for potential temporal or spatial variation. To differentiate within- and between-subject effects in plasticity caused by experience with the experimental set-up, we followed the approach suggested by van de Pol & Wright (2009) and used the mean number of trials (HR and LR combined) that an individual experienced (TM) and the within-subject centred number of trials experienced ( $TMC_i = T_i - TM$ , with  $i$  = all observations) as further fixed effects. We added individual ID as a random effect (specified as a random intercept) and TMC as a random effect (specified as a random slope; Pinheiro & Bates 2000). This model structure allowed us to assess between-individual variation in intercepts (i.e. individual differences in the average behavioural response) and between-individual variation in slope of the within-individual relationship between composite behavioural variables and the number of trials performed (i.e. individual differences in plasticity over several trials). To test whether individual variation in plasticity of behaviour correlates with individual differences in average behavioural response, we extracted individual slopes and intercepts from random slope models and calculated Pearson correlations for individuals that were tested repeatedly ( $N = 22$ ). Interactions between fixed effects were not significant in any model and were therefore excluded from subsequent analyses.

Fourth, we used linear models to test whether individual body condition explained variation in individual composite behavioural variables, that is, in predicted individual intercepts of the mixed models. Body condition was calculated using the scaled mass index (WSMA) proposed by Peig & Green (2009) as the mass of an individual standardized to the mean body size of all individuals in the population retaining the population-specific allometric relationship. Head width ( $\pm 0.1$  mm) was the morphometric measure that correlated most tightly with body mass and was therefore taken as the parameter for body size (Peig & Green 2009) for 217 adult individuals (97 females and 120 males caught and measured in 2002–2010 in Kirindy forest, M. Dammhahn, unpublished data). We included in this analysis only individuals for which recent measurements of body mass ( $< 1$  month) and body size ( $< 3$  month) in relation to the behavioural tests were available, yielding 22 individuals.

Finally, we assessed whether risk taking expressed in the risk-sensitive foraging test and boldness expressed in the novel object tests were correlated. We used the latency to enter the HR platform at the first trial and the latencies to make contact with the novel object in the first trial for this correlation. This relationship was assessed for 22 individuals (18 males, four females) using Spearman rank correlations. All data were analysed using R 2.13 (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>). Values of  $P$  were two tailed throughout and the accepted significance level was  $P < 0.05$ .

#### Ethical Note

All aspects of this study are in compliance with animal care regulations and applicable national laws of Germany and Madagascar and all research protocols were approved by the Bundesministerium für Naturschutz, BfN (Germany), the Commission Tripartite CAFF and the Ministère de l'Environnement et des Eaux et Forêts, MINEEF (Madagascar) No.213 08/MEFT/SG/DGEF/DSAP/SSE. During capture sessions, traps were set between 1800 and

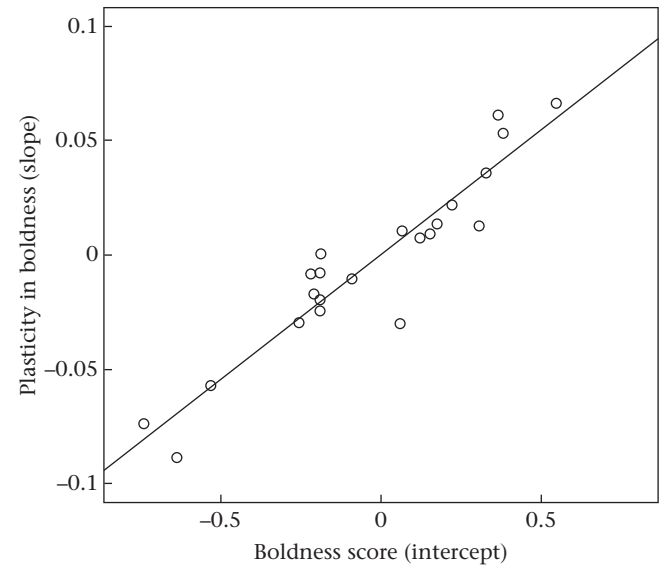
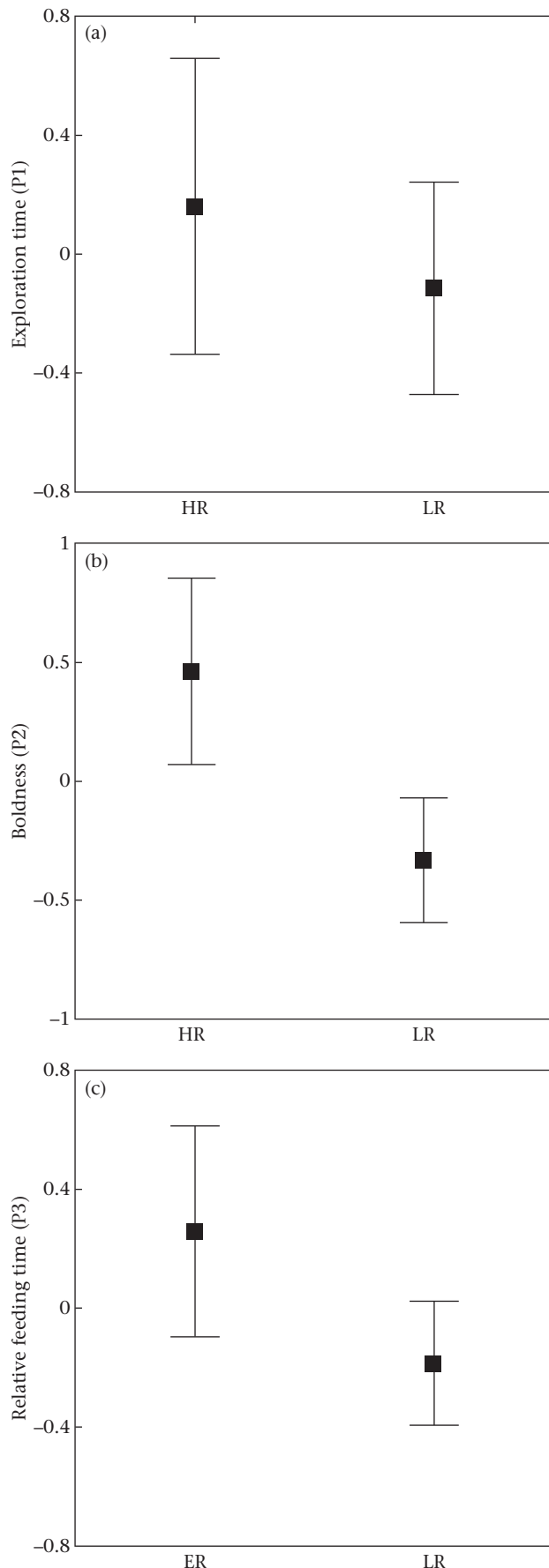
2300 hours and were checked hourly. Animals were provided with moist food in the traps and released directly after the behavioural test. Trapping was performed only in dry weather conditions. All trapping was performed before the highly synchronized short annual gestation period (November–December). Overall, these measures minimize the impact of trapping on the animals' regular activities. At the population level, trapping had no effect on survival and body condition for individuals (M. Dammhahn, unpublished data).

#### RESULTS

Following PCA, we retained three components, which explained 86% of the total variance (Table 1). The first component, P1, was characterized by the time spent on the platform and the time spent feeding and is referred to as 'exploration time' hereafter. The second component, P2, was characterized by the latency to enter the platform and the latency to start feeding after entering the platform and is referred to as 'boldness' hereafter. We also retained the third component, P3, although the eigenvalue slightly missed the Kaiser–Guttman criterion (Kaiser 1991) because it represents the 'relative feeding time', that is, the proportion of time on the platform spent feeding, which did not load significantly on the other two components. In the HR experiment, individuals visited the platform on average twice (range 1–4) and individual behavioural responses were significantly repeatable for exploration time (P1:  $r = 0.73 \pm 0.12$ ,  $F_{26,14} = 4.97$ ,  $P = 0.002$ ) and boldness (P2:  $r = 0.61 \pm 0.17$ ,  $F_{26,14} = 3.27$ ,  $P = 0.012$ ) but not for relative feeding time (P3:  $r = 0.31 \pm 0.26$ ,  $F_{26,14} = 1.47$ ,  $P = 0.16$ ). In the LR experiment, individuals visited the platform on average twice (range 1–6) and only boldness was significantly repeatable (P2:  $r = 0.39 \pm 0.16$ ,  $F_{28,28} = 2.20$ ,  $P = 0.021$ ); exploration time and relative feeding time were not repeatable (P1:  $r = 0.18 \pm 0.19$ ,  $F_{28,28} = 1.41$ ,  $P = 0.19$ ; P3:  $r = 0.02 \pm 0.20$ ,  $F_{28,28} = 1.04$ ,  $P = 0.46$ ).

Grey mouse lemurs foraged risk-sensitively. Although there was no difference between experimental designs in exploration time (P1:  $t = 0.70$ ,  $P = 0.49$ ; Fig. 1a), the lemurs entered LR platforms faster than HR platforms and commenced feeding faster on LR platforms (P2: experiment:  $t = 3.77$ ,  $P = 0.0004$ ; Fig. 1b). The relative feeding time was higher in HR situations (P3:  $t = 2.25$ ,  $P = 0.026$ ; Fig. 1c). None of the composite behavioural variables differed between males and females or between individuals of different age (all  $P > 0.3$ ; Appendix Table A1). The mean number of trials experienced (between-subject variation component) and the within-subject centred number of trials experienced (within-subject component) did not explain significant parts of the variation for any composite behavioural variable (all  $P > 0.4$ ; Table A1). Relative feeding time tended to differ between feeding platform locations (P3:  $t = -1.99$ ,  $P = 0.061$ ). The random effects did not explain significant parts of the variance for exploration time (P1) and relative feeding time (P3). For boldness (P2) the random intercept ID explained 25% and the random slope 0.5% of variance, respectively. Predicted individual intercepts, that is, individual differences in boldness scores, were positively correlated with predicted individual slopes, that is, individual plasticity in response over the trials experienced (P2: Pearson correlation:  $r_{20} = 0.93$ ,  $P = 0.0001$ ; Fig. 2). Thus, shy individuals, which took long latencies to enter feeding platforms and to start feeding (positive boldness scores in Fig. 2), shortened their latencies with increasing experience (positive boldness plasticity slope in Fig. 2), whereas bold individuals (negative boldness scores in Fig. 2) either slightly prolonged latencies or remained constant in their behaviour.

There was no relationship between individual body condition and predicted individual intercepts in boldness (P2:  $R^2 = 0.05$ ,  $F_{1,20} = 1.14$ ,  $P = 0.30$ ). Finally, the latency to enter an HR feeding



**Figure 2.** Correlation between predicted individual intercepts, that is, consistent individual differences in boldness, and predicted individual slopes, that is, individual plasticity in boldness as a result of increased experience, for  $N = 22$  individuals that were tested repeatedly.

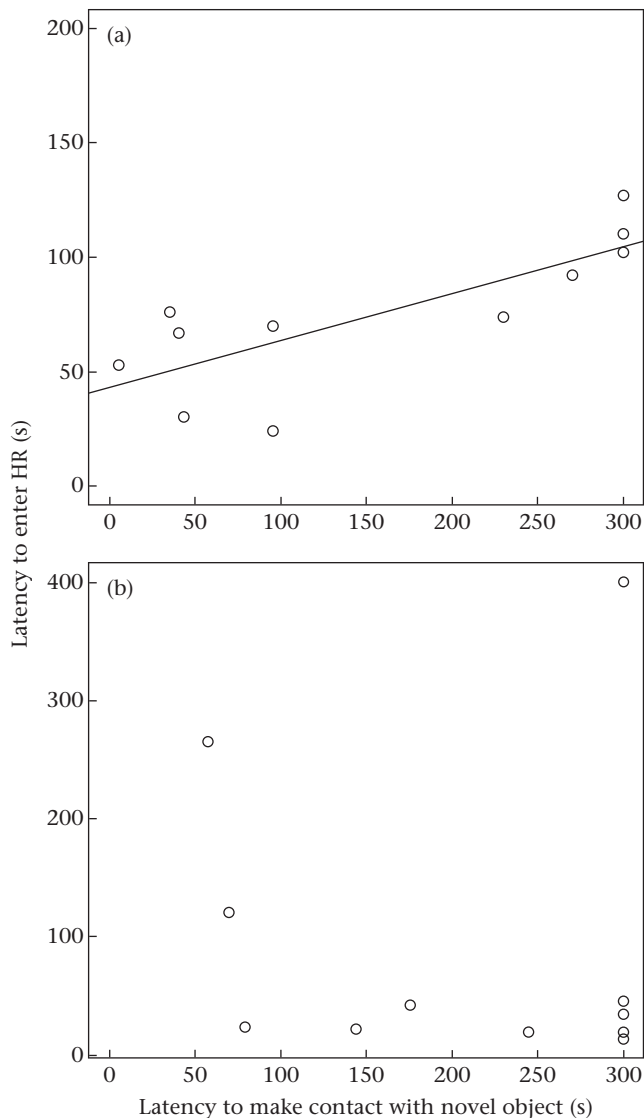
platform in the first trial was positively correlated with the latency to make contact with a novel object in the first trial in 2008 (Spearman rank correlation:  $r_s = 0.72$ ,  $N = 11$ ,  $P = 0.013$ ; Fig. 3a) but not in 2010 ( $r_s = -0.29$ ,  $N = 11$ ,  $P = 0.38$ ; Fig. 3b). This result was robust when excluding females (2008:  $N = 1$ ; 2010:  $N = 3$ ).

## DISCUSSION

### *Risk-sensitive Foraging in Grey Mouse Lemurs*

As predicted by the general trade-off between energy gain and predation avoidance (McNamara & Houston 1987; Lima & Dill 1990; Lima 1998), we found that grey mouse lemurs foraged risk-sensitively. When exposed to an artificial food source on the ground, individuals intensively scanned the surroundings before entering the platform and took longer to start feeding. Furthermore, they only remained on the platform for feeding and often the food was not finished. In contrast, feeding platforms at normal foraging height were entered directly and often explored intensively even after the food was finished (see also Dammhahn & Kappeler 2009; Lühns et al. 2009). As described above, ground foraging is more risky. Although mouse lemurs occasionally forage on the ground, they do so for only short periods and only after long bouts of scanning for potential predators (M. Dammhahn, personal observation). Similarly, small terrestrial mammals balance predation risk and energy gain when foraging under different levels of cover (e.g. Brown et al. 1988; Cassini 1991). Grey mouse lemur risk-taking behaviour did not covary with body condition in our study. Body condition fluctuates markedly between seasons in this species and reaches a minimum at the end of the dry season (Schmid 1999) when we performed our study. Thus, between-individual differences in energetic state should be reflected in body condition. Since we could only weigh animals once per month, actual body

**Figure 1.** (a) Exploration time, (b) latency to enter the platform and start feeding and (c) time spent feeding by grey mouse lemurs. Means are shown  $\pm 95\%$  confidence intervals of composite behavioural variables for high-risk (HR) and low-risk (LR) platforms based on  $N = 98$  tests of  $N = 36$  individuals.



**Figure 3.** The latency to enter a high-risk (HR) platform in the first trial in relation to the latency to make contact with the novel object in the first trial in (a) 2008 and (b) 2010; note different scales.

condition during the test was unknown, however. Thus, grey mouse lemurs adjust their behaviour flexibly to the level of perceived predation risk during foraging but appear not to adjust risk taking to their energetic state.

#### Repeatability and Plasticity in Risk-taking Behaviour

Mouse lemur risk-taking behaviour not only varied between situations posing different levels of risk but also had an intrinsic individual component. We found that individual differences in behaviour were consistent over time, in particular in the high-risk situation. Repeatability in boldness is common in a variety of taxa (e.g. meta-analysis: Bell et al. 2009) rendering this behaviour one of the major animal personality dimensions (Réale et al. 2007). For example, startled great tits, *Parus major*, were repeatable in the latencies to resume feeding and individual differences in response to a startling stimulus were moderately heritable (van Oers et al. 2004). Furthermore, many experiments have demonstrated intra-individual consistency in boldness towards predator dummies in

fish (e.g. Wilson et al. 1994; Godin & Dugatkin 1996; Sih et al. 2003; Farwell & McLaughlin 2009). Since the majority of these studies have been performed in the laboratory, it remains unclear whether individual consistency in boldness persists under real-life conditions. Answering this question is particularly crucial because boldness emerged as the most fitness relevant personality trait in a meta-analysis (Smith & Blumstein 2008). In accordance with our findings, vigilance of flock-feeding redshanks, *Tringa totanus*, was flexibly modified according to perceived risk but was also repeatable (Couchoux & Cresswell 2012). Here, we could demonstrate for the first time that repeatability even increases with increasing risk indicating that personality differences are expressed particularly in fitness-relevant situations.

One of the major questions in animal personality research is why individual behaviour is repeatable if flexible responses would be optimal (e.g. Sih et al. 2004). This question is particularly intriguing for risk taking under predation because the fitness consequences are likely to be severe. First, besides intrinsic differences in behavioural types, individual consistency in risk taking might be the result of spatial or temporal environmental effects. Although we made an effort to choose comparable locations for the feeding platforms, there might still be subtle differences, for example in canopy cover, vegetation density, proximity to tree holes, which could influence the level of perceived risk for foraging individuals. At the population level, the platform location tended to influence the relative time spent feeding but boldness and exploration behaviour did not differ systematically between platforms. At the individual level, spatial environmental effects are unlikely to explain consistency in risk taking because on average each individual was tested at two different platform locations. Since we tested individuals over several days and weeks, temporal environmental effects are also unlikely to explain repeatability in individual behaviour (as for example in Garamszegi et al. 2009).

Second, hormonal differences might proximately explain individual differences in risk taking (e.g. Koolhaas et al. 1999). Most of our tests were performed before and after the short annual mating season, when testosterone peaks in male grey mouse lemurs (Perret 1992). Thus, individual levels of testosterone are expected to vary between males and might proximately cause consistent risk-taking behaviour. However, males tested once before and once after the mating season were consistent in their risk-taking behaviour despite a decrease in testosterone towards the end of the mating season (Perret 1992). Similarly, studies that directly measured testosterone did not find any effect on aggressiveness/boldness in greylag geese, *Anser anser* (Kralj-Fiser et al. 2010), aggressiveness in western bluebirds, *Sialia mexicana* (Duckworth & Sockan 2012), or on exploration in house sparrows, *Passer domesticus* (Mutzel et al. 2011). Although no study has assessed the influence of testosterone on risk taking directly, these results render an androgen-related explanation for high repeatability unlikely. Whether individual differences in stress hormones proximately lead to consistent individual differences in risk taking, as has been demonstrated for the proactive–reactive personality dimension in several rodent species (Koolhaas et al. 1999; Costantini et al. 2012), remains to be explored for free-ranging grey mouse lemurs and other mammals (for a review on birds see Cockrem 2007).

Third, at the ultimate level, several theoretical models have been put forward to explain consistent individual differences in personality in an adaptive framework (reviewed in Dingemanse & Wolf 2010). Potential benefits of being consistent include reduced conflict and competition, increased effectiveness of specialists over generalists and reliable signalling of individual quality (reviewed in Bergmüller 2010). For grey mouse lemurs, it was demonstrated recently that variation in residual reproductive potential best

explains interindividual variation and intraindividual consistency in personality; individuals with low current but high expected future fitness were less bold than those with high current fecundity (Dammhahn 2012).

Thus, our findings are in concordance with other mainly laboratory-based studies and reveal that risk taking is a personality trait. These results suggest that there is potential for conflicting selection for consistency, that is, the personality type, and for flexibility in antipredator behaviour (see also Couchoux & Cresswell 2012). Notably, individual differences in risk taking were more consistent in HR situations than LR situations and individuals with high boldness scores habituated less than individuals with low boldness scores. Similarly, Quinn & Cresswell (2005) found that less active individuals showed higher plasticity in response to predator dummies in chaffinches, *Fringilla coelebs*. These and our results suggest that plasticity and consistency might not vary independently, that is, there may be an interaction between individual and environment (Dingemanse et al. 2010). Disentangling the selective forces acting on consistency and plasticity in risk taking using a behavioural reaction norm approach would be a fascinating area of future research.

#### *Ecological Validation of Boldness*

Boldness measured in a novel object test predicted individual risk taking of free-ranging grey mouse lemurs in a foraging task. Our results add a rare case of ecological validation to laboratory-biased animal personality research (Archard & Braithwaite 2010). Only a few other studies, mainly on fish and birds, have revealed similar cross-context and cross-approach consistency in individual behaviour. For example, Pellegrini et al. (2010) found that fathead minnows, *Pimephales promelas*, were consistent in their predator inspection behaviour when measured in the field and in the laboratory. Also, activity of brook charr in the laboratory was predicted by activity in the field (Wilson & McLaughlin 2007). In blue tits, *Cyanistes caeruleus*, exploration and boldness measured in captivity reflected individual differences in exploration of artificial feeders and reaction towards novel objects in the wild (Herborn et al. 2010). Notably, exploration thoroughness but not the commonly measured exploration speed of a novel environment predicted habitat use in the wild for juvenile starlings, *Sturnus vulgaris* (Minderman et al. 2010). Overall, these direct phenotypic correlations between individual behaviour in standardized tests and under natural conditions suggest that artificial tests indeed quantify ecologically relevant aspects of behaviour.

Although boldness towards a novel object predicted risk-taking behaviour in one of our study years, we did not find this relationship in the second year. Interannual variation in personality traits has been described in several other species. For example, in great tits selection pressures on exploration behaviour fluctuate between low and high food years, which might even ultimately maintain personality variation in the population (Dingemanse et al. 2003). Similarly, food availability for mouse lemurs in the dry deciduous forest is highly seasonal (Dammhahn & Kappeler 2008a) and varies unpredictably between years (Dewar & Richard 2007). Since we performed our experiments at the end of the 7-month dry season, when food availability is minimal, variation in natural food availability is likely to have a pronounced impact on risk-taking behaviour during foraging. In fact, there was an overall difference in body condition of animals between the two study years; individuals tested in 2008 were in better body condition (WSMA = 61.2 g,  $N = 7$ ) than those tested in 2010 (WSMA = 55.5 g,  $N = 15$ ), which is representative of the whole population (2008: WSMA = 64.2 g, 2010: WSMA = 51.4 g). Furthermore, individual differences in risk taking might be modified by population density

(but see Korpela et al. 2011), which increased by 20% over the course of the study. On the one hand, crowding effects might have increased competition over high-quality rewards while, on the other, dilution effects might have decreased antipredator behaviour. Hence, interannual variation in intraspecific food competition might have changed the trade-off between energy gain and predation risk in our experiment.

Ecological validation of animal personality traits is important because of methodological issues. In particular, testing individual differences of free-ranging individuals will help overcoming problems with personality-based sampling bias (Biro & Dingemanse 2009). Shy and bold individuals are likely to differ in their individual capture probabilities, which might influence the results of personality studies (e.g. Boon et al. 2008; Carter et al. 2012). This is a common methodological problem, because many studies rely on capturing animals in the wild to assess personality in the laboratory (e.g. Dingemanse et al. 2003; Bell 2005) or in test chambers in the wild (e.g. Martin & Réale 2008). Here, we combined a capture-based method with assessing personality of free-ranging individuals in a species with very high capture probabilities (i.e. they show 'trap happiness', Kraus et al. 2008) and found concordance in individual differences in boldness. Furthermore, the subsample of animals that participated in the foraging test was representative of the population and included individuals at both ends of the shy–bold continuum (Dammhahn 2012). However, assessing behavioural differences in free-ranging animals might also involve a sampling bias owing to differential reaction towards the presence of an observer. Since mouse lemurs are naturally habituated and observation from a few metres away is possible, such an observer effect is unlikely to bias the results of our study. During the experiments the observer was stationary and motionless at a distance of about 7 m from the platform. In addition, remote ID-reading at the feeding platforms revealed that all individuals visited the platform with and without a human observer present.

Furthermore, ecological validations are crucial to understand how personality traits can impact fitness components (Réale et al. 2007). Only if individual differences assessed in an artificial test indeed translate into differential fitness under real-life conditions can the evolution and maintenance of personality be illuminated. For example, Dingemanse et al. (2003) linked consistent individual differences in exploration behaviour assessed in the laboratory to natal dispersal in the field in great tits. Also, habitat use of free-ranging individual North American red squirrels, *Tamiasciurus hudsonicus*, could be predicted by exploration behaviour expressed in a controlled behavioural test (Boon et al. 2008). In mouse lemurs, risk taking during foraging is likely to be relevant for fitness. In most of their geographical range, grey mouse lemurs experience pronounced seasonal fluctuations in food resource availability, with long periods of fruit and arthropod scarcity during the austral winter (e.g. Dammhahn & Kappeler 2008a). As a result, reproduction is highly seasonal in the study population with only one short mating season per year coinciding with minimal food availability. During 4 weeks of mating activities males compete over promiscuously mating females (Eberle & Kappeler 2002, 2004a). Paternity analyses revealed that male reproductive success is determined by size and body condition (Eberle & Kappeler 2004a). Similarly, females in good condition have more surviving offspring (Eberle & Kappeler 2004b). Thus, risk taking during foraging should translate into higher body condition and ultimately reproductive success in males and females.

It has been argued recently that risk avoidance has shaped the cognitive abilities of lemurs (MacLean et al. 2012), which are thought to be inferior to other primates (but see Fichtel & Kappeler 2010 for an updated lemur baseline). According to this risk



avoidance hypothesis, lemurs evolved strategies to minimize energetic demands as adaptations to the harsh and unpredictable environmental conditions in Madagascar and, thus, are predicted to be risk averse (MacLean et al. 2012). Here, we found pronounced intrinsic individual differences in risk taking that were stable in time and across context. Given the fact that environmental variation in Madagascar is very seasonal, that is, is predictable annually, and only unpredictable between years, such environmental heterogeneity should rather select for different types of risk-seekers in a population, which are favoured under either good or bad environmental conditions (see also Dingemanse et al. 2004).

## Conclusions

Risk taking during foraging of free-ranging animals could provide a general experimental test for assessing the boldness personality dimension in the wild. Since behaviour under predation risk is a key determinant of both components of fitness (Sih et al. 2004), it is likely to be an ecologically relevant personality trait. Intrinsic individual differences in risk taking need to be considered as an important source of variation when testing predictions of risk-sensitive foraging using optimality approaches. Indeed, the results of this and other studies question the optimality approach and rather support a paradigm shift towards behavioural reaction norms to assess both the adaptive individual consistency and flexibility in behaviour (Dingemanse et al. 2010).

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## Appendix

**Table A1**

Estimates of the fixed effects of linear mixed models of composite behavioural components with mouse lemur identity and within-subject centred number of trials experienced as correlated random effects ( $N = 98$  tests,  $N = 36$  individuals)

	Coefficient	Error	<i>t</i>	<i>P</i>
<b>P1: exploration time</b>				
Intercept	107.30	340.68	0.32	0.754
Sex	−0.25	0.37	−0.67	0.511
Age	0.04	0.15	0.30	0.766
Test year	−0.05	0.17	−0.32	0.754
Location	0.02	0.03	0.84	0.406
Experiment	0.22	0.32	0.70	0.488
TM	−0.06	0.08	−0.82	0.419
TMC	−0.04	0.07	−0.58	0.567
<b>P2: boldness</b>				
Intercept	111.36	308.20	0.36	0.719
Sex	−0.02	0.35	−0.07	0.946
Age	0.03	0.14	0.20	0.843
Test year	−0.06	0.15	−0.36	0.717
Location	−0.01	0.02	−0.40	0.693
Experiment	<b>0.88</b>	<b>0.23</b>	<b>3.77</b>	<b>0.0004</b>
TM	−0.03	0.07	−0.38	0.704
TMC	−0.02	0.06	−0.45	0.656
<b>P3: feeding time</b>				
Intercept	−73.73	217.10	−0.34	0.810
Sex	−0.10	0.02	−0.46	0.588
Age	0.11	0.10	1.13	0.368
Test year	0.04	0.11	0.34	0.811
Location	−0.04	0.02	−1.99	0.061
Experiment	<b>0.46</b>	<b>0.05</b>	<b>2.25</b>	<b>0.026</b>
TM	0.00	0.05	0.02	0.958
TMC	0.02	0.04	0.55	0.597

TM: the mean number of trials that an individual experienced; TMC: the within-subject centred number of trials experienced. Significant effects are marked in bold.