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# Personality does not constrain social and behavioural flexibility in African striped mice

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**Abstract** The development and persistence of personality in nature are counterintuitive because, in heterogeneous environments, personality is expected to limit the degree of behavioural flexibility. Recent work has shown that personality and behavioural flexibility might be linked, but their interaction is not well understood and could be elucidated by studying a socially flexible species. Using well-established tests, we measured the personality traits of activity, boldness, exploration and aggressiveness in free-living striped mice (*Rhabdomys pumilio*) in South Africa. Specifically, we tested whether personality changes when individuals change their reproductive tactic, either from group-living philopatrics to solitary-living females and roaming males or from non-breeding philopatrics to breeders. Our results showed that striped mice have personalities: Individuals behaved consistently for all the behavioural traits measured both over time and contexts (breeding to non-breeding season). While most of the personality traits measured remained consistent among tactics, they did not predict which tactic an individual would adopt next, suggesting that environmental conditions rather than personality influence tactic switching. Additionally, we found important differences in the consistency of the behaviours measured between males and females, indicating that sexual selection might play a prominent role in the maintenance of personality in this species. Our study demonstrates that some personality traits can be stable over an entire lifetime even in socially flexible species and that personality does not constrain social flexibility.

**Keywords** Dyadic encounter · Intra-specific variation in social organisation · Novel object · Open-field · Social flexibility · Alternative reproductive tactics

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## Introduction

Phenotypic plasticity occurs when the phenotype expressed by a given genotype changes with prevailing environmental conditions (Pigliucci 2005; Nussey et al. 2007). Behavioural flexibility is a form of reversible phenotypic plasticity where individuals change their behaviour to cope adaptively with environmental changes (Piersma and Drent 2003; Dingemanse et al. 2010). Behavioural flexibility enables individuals to respond quickly to adverse environmental challenges (Hazlett 1995). The ability to produce an appropriate behavioural response in the face of a challenge is expected to be beneficial for an individual, yet such responses may be costly to produce (Hazlett 1995; DeWitt et al. 1998; Dall et al. 2004). The costs of producing a flexible behavioural response may therefore vary in magnitude depending on the life-history of the individual in question.

Variation between individuals that is consistent over time and across contexts is referred to as personality (Sih et al. 2004a; Bell 2007). Personality has been reported in hundreds of species as diverse as non-human primates, birds, reptiles, fish and invertebrates (Gosling and John 1999; Sih et al.

2004b; Dingemanse et al. 2010; Réale et al. 2010; Stamps and Groothuis 2010; Schuett et al. 2011). While the study of animal personalities is still in its infancy, the field is rapidly expanding (Réale et al. 2010) with studies focussing on both the proximate (Koolhaas et al. 1999; Biro and Stamps 2008; Careau et al. 2008) and ultimate questions (Komdeur 2006; Bell and Sih 2007; Cote and Clobert 2007; Wolf et al. 2007).

From an adaptive perspective, it would be disadvantageous for an individual to show limited flexibility (DeWitt et al. 1998; Dall et al. 2004), particularly in heterogeneous environments where the evolution of broad behavioural flexibility rather than behavioural consistency should be favoured (Via and Lande 1985; Via et al. 1995; Dingemanse et al. 2009). In this respect, the existence and persistence of individual personality traits might seem counterintuitive. Yet, behavioural flexibility alone cannot explain the behavioural variation observed in natural populations (Nussey et al. 2007), and it is becoming evident that individual behavioural flexibility and personality may in fact be functionally linked (Koolhaas et al. 1999; Sih et al. 2004a, b; Schjolden and Winberg 2007; Sih and Bell 2008; Briffa et al. 2008; Dingemanse et al. 2010).

Both behavioural flexibility and personality may be adaptive (Briffa et al. 2008), and recent theoretical work has attempted to provide a better understanding of why consistent individual differences in behaviour across contexts might be adaptive (Wolf et al. 2007, 2008; McNamara et al. 2009). For example, specific life-history trade-offs can generate variation in animal personality (Wolf et al. 2007; Dingemanse et al. 2009). Indeed, an individual may adjust its behaviour in response to different situations but still show a consistent level of response relative to the responses of other individuals (Johnson and Sih 2007; Dingemanse et al. 2010). In addition, the existence of personality does not necessarily imply that each individual is completely consistent in its behaviour (Sih et al. 2004b), and individuals might exhibit considerable flexibility (Martin and Réale 2008; Dingemanse et al. 2010). While personality and behavioural flexibility can be viewed as complementary aspects of the same individual phenotype (Dingemanse et al. 2009), the two must be investigated concurrently to understand their link (Briffa et al. 2008; Dingemanse et al. 2009, 2010). Studying personality or individual flexibility in isolation can lead to erroneous conclusions about their fitness consequences (Dingemanse et al. 2009). To elucidate the link between individual flexibility and personality would require studying species that are well-known for their behavioural flexibility, such as socially flexible species. Yet, only few species known for high flexibility in social behaviour have been studied for the relationship between personality and behavioural flexibility, notably *Homo sapiens* (Dudycha 1936; Mischel 2004) and cooperatively breeding cichlids (Arnold and Taborsky 2010; Le Vin et al. 2011). However, the results have been inconsistent, as for example, under natural conditions (in school, at home),

humans show low consistency in their behavioural traits (Zimbardo 1995).

An ideal species to investigate the interaction between personality and behavioural flexibility is the African striped mouse (*Rhabdomys pumilio*), a socially flexible muroid rodent (Schradin et al. 2012). Depending on prevailing ecological conditions, especially food availability, duration of the breeding season and population density, striped mice can either live solitarily or form extended family groups with communal breeding, helpers at the nest and paternal care (Schradin 2005; Schradin and Pillay 2004, 2005; Schradin et al. 2006; Schoepf and Schradin 2012a). Adult individuals can follow three different alternative reproductive tactics (Schradin et al. 2009a, 2010a) and are able to switch between them during their life (Schradin et al. 2012). Specifically, males can (1) remain in their natal nest as non-breeding group-living philopatrics, (2) disperse and become solitary-living roaming males with some chance of breeding, or (3) immigrate into a group of communally breeding females and become group-living territorial breeders (Schradin et al. 2009a, 2010a). Females can (1) remain in their natal nest as non-breeding group-living philopatrics, (2) disperse and become solitary-living breeding females, or (3) breed communally (Schradin et al. 2010b). Dispersal and tactic switching typically occur during the breeding season, which normally lasts from August to November (Schradin et al. 2010a; Schoepf and Schradin 2012b). Outside of the breeding season, individuals typically remain group-living (Schradin et al. 2010a; Schoepf and Schradin 2012b). Thus, striped mice show high flexibility in the social behaviour, which could also indicate greater flexibility in personality traits and thus absence or reduced stability of personality, especially over longer periods that include changes of reproductive tactics. In the present study, we used well-established tests to study personality traits in free-ranging striped mice. Specifically we aimed to (1) establish and validate a method that would allow for the reliable collection of data on personality traits from wild striped mice, (2) examine whether individual striped mice showed consistency in their behavioural traits over time and context, (3) test whether the personality of an individual remained consistent across different reproductive tactics and would predict the tactic that an individual would adopt later in its life, and (4) investigate the interplay between behavioural flexibility and personality.

Personality research has recently been criticised, as some of the results obtained are constrained in their strength by a lack of validation (Carter et al. 2012a). Researchers studying personality in wild animals have to decide whether to test several traits with one test (e.g. Boon et al. 2007) or to test one trait per day (e.g. Dingemanse et al. 2007). However, it is not clear whether the two approaches would yield the same result. In the present study, we investigated whether testing free-living striped mice sequentially for the three different personality traits on 1 day (i.e. (1) activity and boldness, (2) exploration,

and (3) aggressiveness) gave the same results as testing them on different days. We predicted striped mice that were the most active, the boldest, the most explorative and the most aggressive when tested sequentially on 1 day, to be still the most active, the boldest, the most explorative and the most aggressive when tested on separate days. To establish whether striped mice had personality, we examined whether individuals showed consistency in their behavioural traits over context and time, by testing striped mice in the three personality tests twice, 2 weeks apart, within the same season. To test whether personality remained stable over context, we tested individuals during the breeding season and repeated the tests 5 months later in the non-breeding season. We predicted that the boldest, the most explorative and the most aggressive striped mouse would still be boldest, the most explorative and the most aggressive when tested (1) 2 weeks later within the same breeding season and (2) 5 months later in the non-breeding season. To investigate the interplay between personality and behavioural flexibility, we used the 'behavioural reaction norms' approach (Dingemanse et al. 2009) as this method allows for assessing the link between personality and behavioural flexibility concurrently and for investigating whether personality traits were consistent across different reproductive tactics or occurred independently of tactics. We predicted that the most active, the boldest, the most explorative and the most aggressive philopatrics were also the most active, the boldest, the most explorative and the most aggressive once becoming a breeder or a solitary-living individual. In addition, to establish whether personality can predict the tactic that an individual will adopt later in its life, we measured personality traits of philopatric males and then assessed whether males that became solitary roamers in the next breeding season differed from males that became group-living territorial breeders. Group-living striped mice differ in their behavioural traits from solitary-living ones (Schoepf and Schradin 2012a), yet it is unclear whether these differences are already present in philopatric individuals before they change their reproductive tactics. If such differences are already present, we expected individuals which were the most active, the boldest, the most explorative and the most aggressive to be more likely to become solitary-living individuals, while philopatrics were less active, less bold, less explorative and less aggressive to be more likely to become group-living breeders.

## Methods

### Study area and field techniques

Data were collected during the breeding and the non-breeding seasons of 2008–2012 on a field site located in the Goegap Nature Reserve, near the town of Springbok, in South Africa

(41.56 S, 1.60 E). Striped mice were trapped with Sherman-like metal traps ($26 \times 9 \times 9$ cm) baited with a mixture of bran flakes, currants, sea salt and salad oil (Schradin 2005). Traps were set twice a day, once in the early morning and once in the early evening directly at striped mouse nests, and were checked 45 min later (Schradin 2005). Each trapped mouse was weighed, sexed and received a permanent ear-tag (National Band and Tag Co., Newport, KY, USA). Additionally, individuals were marked with a non-toxic hair dye (Inecto Rapido, Pinetown, South Africa), which aided with individual recognition during behavioural observations. The fur dyeing procedure has not been observed to cause adverse effects in striped mice (CS unpublished data). Striped mice at our field site are habituated to our presence and readily enter traps once they are set. While bolder individuals might be more likely to enter traps than less bold individuals, we know from cross-checking data of trapping, behavioural observations and radio-tracking that we are typically able to capture all individuals within the study population, even the less bold ones, repeatedly. As such, we were easily able to recapture individuals for a second test. Trapping and behavioural tests did not have any adverse effect on individuals' behaviour (CHY unpublished data). Behavioural observations were performed at each group's nest in the morning and in the evening and were used to determine individual affiliation to specific groups. In addition, at least one breeding female from each group was fitted with a PD-2C transmitter (Holohil, Carp, Ontario, Canada; 2.5–4.4 g) and radio-tracked to ascertain the nesting site location of the group (Schradin and Pillay 2005). Radio-tracking was achieved using an AOR 8000 wide range receiver (Tokyo, Japan), an H-antenna (Africa Wildlife Tracking, Pretoria, South Africa) and a global positioning system (GPS) navigation device (eTrex Venture, GARMIN International, USA) with accuracy of ±5 m. All striped mice fitted with a transmitter were radio-tracked twice a day every day to determine ranging areas and sleeping sites.

### Measuring personality traits in striped mice

We measured activity, boldness, exploration and aggressiveness under standardised conditions in a laboratory at the research station, 200 m from the field site. Striped mice are typically active in the early morning and evening (Schradin and Pillay 2004), when all individuals were tested. All individuals used in tests were trapped directly at their nests in the early morning, within 30 min after sunrise, when they first emerged to bask. Trapped mice were transported to the research station and transferred to a type III Perspex cage ($38 \times 22 \times 15$ cm) in the test room where they were allowed to settle down for 10 min. Each cage was provided with bedding (sand) and food (10 sunflower seeds). After the initial settling down period, the focal mouse was placed in a neutral presentation arena where it was tested. The test arena was

made of white chipboard (80×65×94 cm) with a partition in the middle, similar to the one previously used by Schradin et al. (2010b) and Schoepf and Schradin (2012b). The presentation arena was cleaned with a solution of diluted odourless disinfectant (Dis-Chem Pharmacies, Northriding, South Africa) and water at the conclusion of each test. A maximum of three individuals were tested in a day. All personality data were collected in the neutral presentation arena by direct observations. We studied only adult individuals that had a body weight of at least 30 g and were more than 6 weeks of age at the time of testing. The age (in weeks) of each individual tested was determined using previously calculated growth curves based on the trapping history and body mass of individuals (Schradin et al. 2009b).

Activity and boldness were measured using an open field test (Wilson et al. 1976; Réale et al. 2007) and were recorded over 5 min. Activity was recorded every 15 s using instantaneous focal sampling (1/0 sampling; Martin and Bateson 1993). Boldness was measured using continuous focal sampling techniques (Martin and Bateson 1993) as the total time (in seconds) an individual spent in the open field (at least half-a-mouse length away from the wall of the arena).

Exploration was measured using a novel object test (Birke and Archer 1983; Greenberg 1984; Verbeek et al. 1994) which lasted 5 min. A fixed and a mobile object were set at the far side of the arena, in the opposite corner to where the focal individual was located. The fixed object consisted of a small plastic toy, which was secured to the floor of the arena and could not be moved by a mouse. The mobile object was a white table tennis ball that could be easily moved by a mouse when touched. Originally, we expected mice to behave differently towards the fixed and the mobile object, but this was not the case. Thus, exploration was measured as the latency (in seconds) it took the focal mouse to physically come into contact with either the fixed or the mobile object.

Aggressiveness was tested using dyadic encounters with a novel conspecific (Verbeek et al. 1994; Benus and Rondigs 1996). We presented the focal mouse with an individual of the same sex (the stimulus) taken from a captive colony, which is permanently maintained at the research station. Stimulus animals were always at least 3 g (but never more than 7 g) lighter than the focal animal. Because body mass is known to have a positive influence on the outcome of aggressive encounters (Schradin 2004), we wanted the focal mouse to initiate interactions. Aggressiveness tests were performed using standard procedures previously used for striped mice (Schradin et al. 2010b; Schoepf and Schradin 2012b; Schradin and Pillay 2014). Focal and stimulus mice were placed on different sides of the arena with the partition lowered and were allowed to settle in their own side of the arena for 3 min. At the end of the settling down period, the partition was removed and interactions were recorded for a period of 5 min. The following behaviours were considered as aggressive: chasing, standing on hind legs and boxing. Aggressiveness was measured as the total number of aggressive encounters initiated by the focal individual. To remain consistent with data previously collected on aggressiveness in striped mice (Schradin et al. 2010b; Schoepf and Schradin 2012b; Schradin and Pillay 2014) and to prevent individuals from being injured, we immediately terminated tests when individuals started to wrestle (before any biting occurred). Less than 1 % of all tests had to be prematurely terminated due to enhanced aggressiveness. To correct for this, all data were calculated as relative frequencies. In addition to aggressiveness, we also recorded sniffing, body contact, grooming and activity, but these behaviours occurred too infrequently for statistical analysis and were not considered any further. All mice remained in the laboratory for a maximum period of 1 h, after which they were immediately returned to their nests in the field. All individuals were released in good conditions.

## Method validation for the study of personality in striped mice

We first investigated whether testing free-living striped mice sequentially for the three different personality tests on 1 day would yield the same results as testing them on three consecutive days. A total of 21 individuals were used for this validation. Of these, 11 were initially tested on three consecutive days and then for all three tests in 1 day, while 10 individuals were tested first for all three tests on 1 day and then for three separate days. For focal individuals tested separately for the different behavioural traits over 3 days, we tested them on (1) day 1 for boldness and activity only, (2) day 2 for exploration only and (3) day 3 for aggressiveness only. The same individuals were later also tested in a single day for all three behaviours, one after another ((1) boldness and activity, (2) exploration and (3) aggressiveness).

## Consistency in behavioural traits across time and context

As our validation tests showed that there was no significant difference between performing all three tests in 1 day or on three separate days (see results), we performed personality tests thereafter on 1 day, with all individuals sequentially tested for (1) boldness and activity, (2) exploration and (3) aggressiveness. Each focal mouse remained in the arena for the duration of all three tests before being removed and returned to its nest. To assess whether personality traits were consistent over time, we tested 29 individuals (15 males and 14 females) twice during the breeding season, 2 weeks apart. To investigate whether personality remained consistent over the long-term and over context (in the presence or absence of reproduction), we tested 37 individuals (18 males and 19 females) during the breeding season and repeated the tests 5 months later during the non-breeding season.

## Personality and tactic switching in striped mice

To test whether females were consistent in their personality traits when they adopted a new reproductive tactic, we tested 16 females when they were philopatrics in the non-breeding season and repeated the tests 5 months later once they became breeders in the following breeding season. Similarly, to test whether males differed in their personality traits when they adopted a new reproductive tactic, we tested 18 males when they were philopatrics in the non-breeding season and repeated the tests 5 months later once they became breeders or roamers in the following breeding season. All individuals had reached adulthood at the time of testing.

In addition, to assess whether personality could predict the tactic that an individual would later adopt, we compared the personality traits of 13 philopatric males that became solitary roaming males and 12 philopatric males that became group-living breeding males.

## Data analysis

Data analysis was performed using R version 3.0.2 (The R Foundation for Statistical Computing, Vienna, Austria). We used Wilcoxon Sign-Rank tests to measure differences in the behavioural traits of individuals when tested on 1 day and on three separate days. We calculated Kendall's $W$ coefficient of concordance (Package irr; Gamer et al. 2012) to assess whether behavioural traits of individuals remained consistent: (1) when measured on 1 day and on 3 days. We chose to calculate the more conservative Kendall's $W$ rather than Spearman's $r_s$ as a Kendall's $W$ value significantly differing from random expectation means that individuals' rankings based on a given behavioural variable are in agreement with the different times when measurements were made (Legendre 2005), i.e. individuals behave consistently over time (Briffa et al. 2008; Gyuris et al. 2011; Hoset et al. 2011). In addition, to assess the proportion of phenotypic variation attributable to between-individual variation, we calculated the coefficient of repeatability $R$ and estimated the 95 % confidence intervals (CI) around the repeatability estimates (Nakagawa and Schielzeth 2010). For count data, we calculated repeatability using rpt.poisGLMM.multi function, while for proportion data, we used the rpt.binomGLMM function (Package rptR; Nakagawa and Schielzeth 2010).

To assess the effect of personality (between individual differences in behaviour), we used random intercept models to determine consistency of behavioural traits (1) in the short-term (2 weeks apart), (2) in the long-term (5 months apart) and over context (in the presence or absence of reproduction), and (3) for different tactics (philopatric females→breeding females; philopatric males→roaming or breeding males). Random intercept models were fitted using GLMMs (glmer; Package lme4; Bates et al. 2014). Each GLMM had one of the

behaviours as the response variable, while test (week 1, week 3), experience (breeding season, non-breeding season) or tactic (philopatric, breeder, roamer/solitary-breeding female) was the fixed factors in the different models. The interactions between sex and test, and sex and experience were entered as covariates in those models to test for short- and long-term consistency, because we wanted to control for potential differences in behaviour between males and females. As males and females significantly differed in their behavioural traits (see results), we subsequently ran separate models for each sex. Individual ID was entered as the random factor in each model. We verified our models by (1) plotting the model residuals versus the fitted values, (2) checking the normal distribution of the model residuals using normal probability plots, (3) checking for heteroscedasticity and (4) checking leverage (Crawley 2007). Count data (activity, aggressiveness) were analysed using Poisson GLMMs, whereas proportion data (boldness, exploration) were analysed using binomial GLMMs.

As the calculation of models with random slopes is a suitable method for testing plasticity (Dingemanse et al. 2009, 2010; Martin et al. 2011), we compared random intercept models with random slope (tactic) and intercept models (individual ID) with a correlated random slope and intercept structure to assess how strong the added effect of between-individual difference in flexibility was for individuals that changed tactics. In order to compare the relative strength of the personality and the behavioural flexibility results, we compared the effect sizes and the $R^2$ values of GLMMs calculated without random slopes (test for personality) with the effect sizes and $R^2$ of GLMMs calculated with random slopes (test for flexibility). $R^2$ (adjusted) was calculated following Nakagawa and Schielzeth (2010) (Package rptR; Nakagawa and Schielzeth 2010). We selected the model that best fitted our data by selecting the model that yielded the lowest Akaike's information criterion (AIC) and using likelihood ratio tests (Zuur et al. 2009). When random slopes significantly improved model fit, this suggested that there were between-individual differences in behavioural flexibility between reproductive tactics. Only individuals that changed tactics were considered. We excluded individuals from the analysis that changed their reproductive tactic from roamer to breeder as the switch occurred over a different timescale (typically a few weeks) to the one measured from philopatric to roamer/breeder (5 months apart). A total of 16 females and 18 males were measured before and after switching tactics and were included in the analysis to compare effects sizes of behavioural flexibility and personality.

We used generalised linear models (GLM) to assess whether behavioural traits of philopatric males that later adopted a roaming tactic already differed from behavioural traits of philopatric males that would later become breeders before adopting the new tactic (either roaming or breeding). We used a GLM with a quasi-Poisson family to assess differences in

activity levels of philopatric individuals that would go on to become roamers against activity levels of philopatric individuals that would go on to become breeders. We used GLMs with a quasi-binomial family to assess differences in boldness and exploration levels of philopatric individuals that would later become roamers against boldness and exploration levels of philopatric individuals that would later become breeders. We used GLMs with a zero-inflated negative binomial family (zeroinfl; Package pscl; Jackman 2008) to assess differences in aggressiveness levels of philopatric individuals that would go on to become roamers against aggressiveness levels of philopatric individuals that would go on to become breeders. A total of nine philopatric males that would later adopt a roaming tactic were measured against nine philopatric males that would later adopt a breeding tactic.

## Results

### Method validation for the study of personality in striped mice

Individuals displayed significant rank-order consistency in all four behaviours when their scores taken on 1 day were compared with their scores taken on three separate days, meaning that the measurements done on 1 day did not differ significantly from the measurements taken on 3 days (activity, Wilcoxon test $n=21$, $W=225.5$, $P=0.91$; boldness, Wilcoxon test $n=21$, $W=253.0$, $P=0.42$; exploration, Wilcoxon test $n=21$, $W=229.0$, $P=0.84$; aggressiveness, Wilcoxon test $n=21$, $W=257.5$, $P=0.34$). Specifically, individuals that were active, bold, explorative and aggressive when tested on three different days were also the most active (Kendall test for concordance $W=0.85$, $\chi^2=34.0$, $P=0.03$), the boldest (Kendall test for concordance $W=0.87$, $\chi^2=34.7$, $P=0.02$), the most explorative (Kendall test for concordance $W=0.80$, $\chi^2=32.1$, $P=0.04$) and the most aggressive (Kendall test for concordance $W=0.87$, $\chi^2=34.8$, $P=0.02$) when tested for all four behaviours on a single day. Individuals displayed significant repeatability in all four behaviours when their scores were taken on 1 day and on three separate days (activity $R=0.78\pm0.10$, 95 % CI 0.53–0.90, $P=0.001$; boldness $R=0.71\pm0.13$, 95 % CI 0.39–0.87, $P=0.001$; exploration $R=0.64\pm0.14$, 95 % CI 0.28–0.83, $P=0.001$; aggressiveness $R=0.80\pm0.09$, 95 % CI 0.60–0.92, $P=0.001$). Figure 1 shows the observed regression lines and predicted ones arising from the expectation that individuals would have shown exactly the same scores in both tests.

### Consistency in behavioural traits across time and context

The behaviour of individuals was highly consistent over short- and long-time and in the presence or absence of

reproduction. Specifically, individuals which were initially active, bold, explorative and aggressive were still the most active (Poisson-GLMM $z=2.64$, $P=0.01$; Fig. 2a), the boldest (binomial-GLMM $z=4.91$, $P<0.0001$; Fig. 2b), the most explorative (binomial-GLMM $z=-24.10$, $P<0.0001$; Fig. 2c) and the most aggressive (Poisson-GLM $z=2.36$, $P=0.02$; Fig. 2d) when tested 2 weeks later within the same season. Including the interaction between test and sex improved model fit only for exploration ($\chi^2=293.04$, $P<0.0001$) and aggressiveness ($\chi^2=9.17$, $P=0.01$), but not for activity ($\chi^2=0.81$, $P=0.67$) and boldness ($\chi^2=0.40$, $P=0.82$), meaning that only the personality traits of exploration and aggressiveness were significantly different between males and females (exploration, binomial-GLMM $z=16.97$, $P<0.0001$; aggressiveness, Poisson-GLMM $z=-3.12$, $P=0.002$). Individuals also displayed significant repeatability in all four behaviours over time (activity $R=0.48\pm0.14$, 95 % CI 0.17–0.72, $P=0.03$; boldness, $R=0.013\pm0.009$, 95 % CI 0.003–0.04, $P=0.008$; exploration $R=0.007\pm0.005$, 95 % CI 0.001–0.021, $P=0.001$; aggressiveness $R=0.75\pm0.09$, 95 % CI 0.56–0.90, $P=0.001$).

The most active, the boldest, the most explorative and the most aggressive individuals during the breeding season were also the most active (Poisson-GLMM $z=-2.61$, $P=0.02$; Fig. 3a), the boldest (binomial-GLMM $z=3.55$, $P=0.0004$; Fig. 3b), the most explorative (binomial-GLMM $z=-5.45$, $P<0.0001$; Fig. 3c) and the most aggressive individuals (Poisson-GLMM $z=2.80$, $P=0.006$; Fig. 3d) when they were tested 5 months later in the non-breeding season. Including the interaction between test and sex improved model fit for boldness ($\chi^2=27.77$, $P<0.0001$) and exploration ($\chi^2=487.05$, $P<0.0001$), but not for activity ($\chi^2=4.45$, $P=0.11$) and aggressiveness ($\chi^2=0.47$, $P=0.79$). Individuals also displayed significant repeatability in all four behaviours when tested 5 months apart (activity $R=0.46\pm0.13$, 95 % CI 0.17–0.69, $P=0.001$; boldness $R=0.014\pm0.011$, 95 % CI 0.005–0.041, $P=0.007$; exploration $R=0.002\pm0.002$, 95 % CI 0.001–0.008, $P=0.02$; aggressiveness $R=0.61\pm0.10$, 95 % CI 0.44–0.83, $P=0.001$).

### Personality of individuals before and after switching tactics

Females that changed their tactic from philopatric to breeder remained consistent for activity (Poisson-GLMM $z=-2.17$, $P=0.03$; Fig. 4a), boldness (binomial-GLMM $z=-7.47$, $P<0.0001$; Fig. 4b) and exploration (binomial-GLMM $z=-7.15$, $P<0.0001$) but were not consistent for aggressiveness (Poisson-GLMM $z=-1.41$, $P=0.16$). Males that changed their reproductive tactic remained consistent for exploration (binomial-GLMM $z=12.81$,

**Fig. 1** Results of the personality tests performed on 1 day were consistent with the results obtained from the personality tests performed over separate days for all the behavioural traits measured: **a** activity (*P*=0.03), **b** boldness (*P*=0.02), **c** exploration (*P*=0.04) and **d** aggressiveness (*P*=0.02). Predicted line (*dotted line*), from the expectation that individuals would show exactly the same score in both methods; observed line (*solid line*)
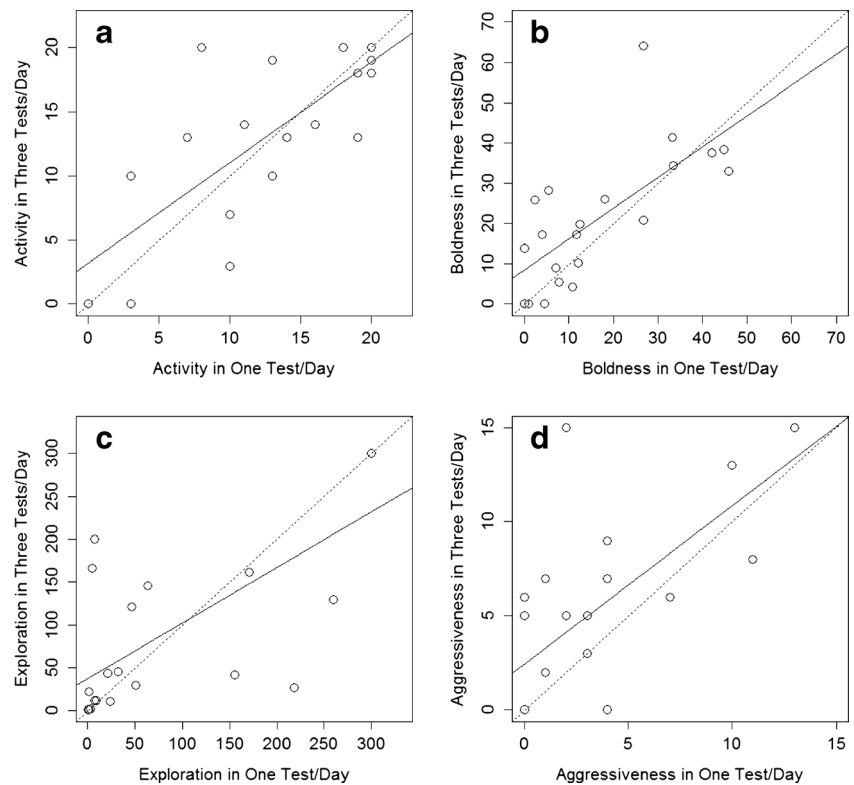


$P<0.0001$; Fig. 4c) and aggressiveness (Poisson-GLMM $z=-3.34$, $P=0.0008$; Fig. 4d), but not for activity (Poisson-GLMM $z=0.21$, $P=0.83$; Fig. 4a) or boldness (binomial-GLMM $z=1.64$, $P=0.10$; Fig. 4b).

**Fig. 2** Striped mice showed consistency in all the personality traits when measured across time (2 weeks apart, on week 0 and on week 2). **a** Activity (*P*=0.01), **b** boldness (*P*<0.0001), **c** exploration (*P*<0.0001) and **d** aggressiveness (*P*=0.021). Observed female line (*dotted line*); observed male line (*solid line*). Females (*white circles*) and males (*black circle*)
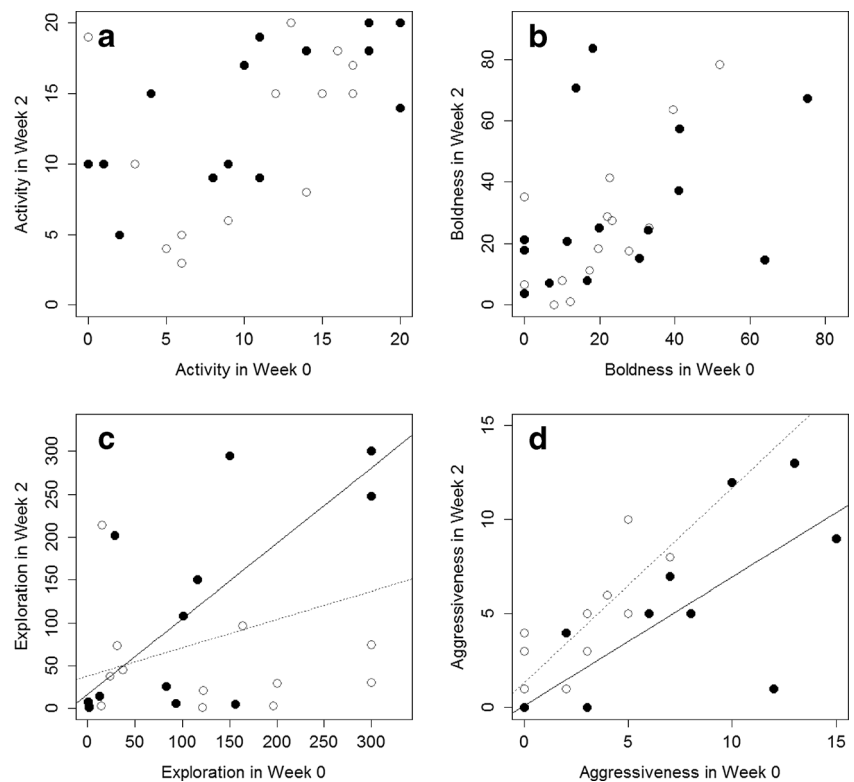
**Fig. 3** Striped mice showed
long-term consistency (5 months
apart) and consistency across
context (presence of
reproduction=breeding season,
absence of reproduction=non-
breeding season) in the personal-
ity traits of **a** activity
(*P*=0.02), **b** boldness (*P*=
0.0004), **c** exploration
(*P*<0.0001) and **d** aggressiveness
(*P*=0.006). Observed female line
(*dotted line*); observed male line
(*solid line*). Females (*white
circles*) and males (*black circle*)
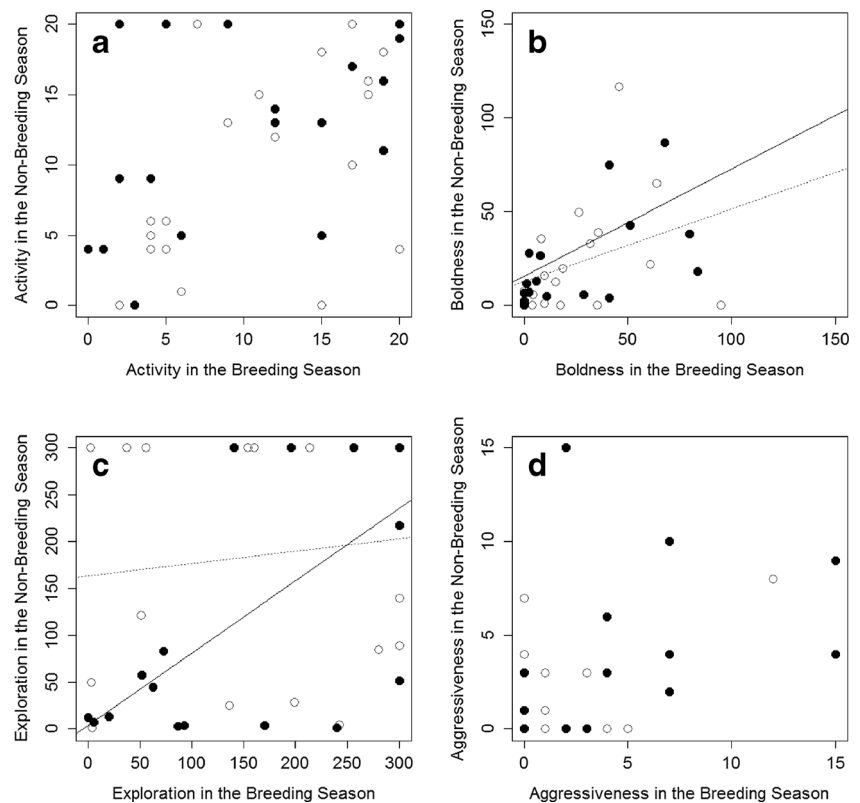


## Behavioural flexibility of individuals before and after switching tactics

Females were significantly more active (Poisson-GLMM
*z*=−2.34, *P*=0.02) and bolder (binomial-GLMM *z*=−2.05,

*P*=0.04) after changing their reproductive tactic from
philopatric to breeder but did not differ in their explora-
tion (binomial-GLMM *z*=−0.94, *P*=0.35) or aggressive-
ness when they became breeders (Poisson-GLMM *z*=
−0.43, *P*=0.67). Males were significantly more

**Fig. 4** Female striped mice that
switched from philopatric (before,
in *white*) to breeder (after, in *grey*)
showed consistency in the
personality traits for **a** activity
(*P*=0.03), **b** boldness (*P*<0.0001)
and **c** exploration (*P*<0.0001) but
were not consistent for **d**
aggressiveness (*P*=0.16). Male
striped mice that switched tactics
showed consistency in the
personality traits for **c** exploration
(*P*<0.0001) and **d** aggressiveness
(*P*=0.0008), but not for **a** activity
(*P*=0.83) and **b** boldness (*P*=
0.10). *Boxes* drawn proportional
to sample size. + indicate the
population mean. *Notches*
indicate CI of the median. *Dots*
indicate outliers
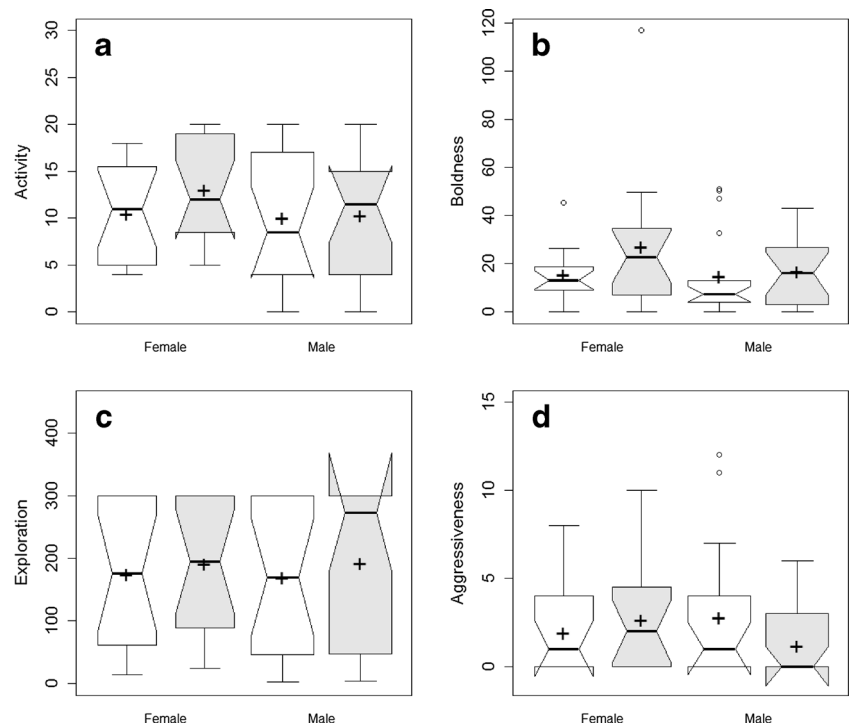
explorative (binomial-GLMM $z=2.10$, $P=0.04$) and less aggressive (Poisson-GLMM $z=-1.92$, $P=0.05$) after changing their reproductive tactics but were not more active (Poisson-GLMM $z=-0.24$, $P=0.81$) nor bolder (binomial-GLMM $z=0.59$, $P=0.56$).

Philopatric males that became roamers did not differ from philopatric males that became breeders in any of the personality traits investigated (activity $10.58\pm1.90$ versus $7.46\pm1.70$; quasi-Poisson-GLM $F_{1,23}=1.48$, $P=0.24$; boldness $20.25\pm5.25$ versus $11.76\pm4.14$; quasi-binomial-GLM $F_{1,23}=1.61$, $P=0.22$; exploration $185.49\pm40$ versus $199.77\pm36.09$; quasi-binomial-GLM $F_{1,23}=0.07$, $P=0.79$; and aggressiveness $1.33\pm0.74$ versus $1.69\pm0.96$; zero-inflated negative binomial-GLM $z_{1,23}=-0.32$, $P=0.75$).

## Comparison between personality and behavioural flexibility in individuals that switched tactics

For females, including a random slope improved model fit for boldness ($\chi^2=27.28$, $P<0.0001$; Table 1), exploration ($\chi^2=2323.8$, $P<0.0001$; Table 1) and aggressiveness ($\chi^2=27.77$, $P<0.0001$; Table 1), but not for activity ($\chi^2=1.60$, $P=0.45$; Table 1), suggesting that there were between-individual differences in behavioural flexibility between reproductive tactics for boldness, exploration and aggressiveness in females. For males, including a random slope improved model fit for activity ($\chi^2=6.51$, $P=0.04$; Table 2), boldness ($\chi^2=39.16$, $P<0.0001$; Table 2) and exploration ($\chi^2=535.16$, $P<0.0001$; Table 2), but not for aggressiveness ($\chi^2=1.71$, $P=0.42$; Table 2), suggesting that there were between-individual differences in behavioural flexibility between reproductive tactics for activity, boldness and exploration in males.

## Discussion

Individual striped mice behaved consistently over time and across context in all the tests conducted, indicating personality. Specifically, personality traits were consistent when tested 2 weeks apart within the same season and when tested 4–5 months apart in the breeding and non-breeding seasons. Male striped mice that changed their reproductive tactics maintained consistent personality traits for exploration and aggressiveness, while females remained consistent for activity, boldness and exploration, indicating that there are important sex-related differences in the way personality is maintained in striped mice. Furthermore, personality traits of philopatric males that later became roamers did not differ from those of philopatric males that became breeders, indicating that the personality of an individual does not predict the reproductive tactic that it will adopt later. In sum, we demonstrated that personality, a form of individually constrained behaviour, exists in a species characterised by high behavioural flexibility.

However, personality did not predict which tactic an individual would adopt next, suggesting that environmental conditions rather than personality influence tactic switching in this species.

In a recent paper, Carter et al. (2012b) highlighted the importance of validation for personality studies. Typically, personality studies focus on several different traits, which might be measured either sequentially on the same day or on different days. However, it is unknown whether testing individuals for several behavioural traits consecutively in 1 day yields the same results as testing them over several days. Additionally, to sample an individual repeatedly over several days is unfeasible for most wild species. It is therefore important to test whether conducting measurements of several behavioural traits consecutively in 1 day is as reliable as having intervals between tests. Assuming that there is concordance, testing less frequently could save time and would reduce stress to the animals. Yet, in spite of their importance, validation methods are seldom employed in personality research. In striped mice, performing multiple tests on 1 day or performing a single test per day yielded similar results for all the behavioural traits measured. This may be important also for other species as it is easier to trap wild individuals twice to test for consistency of four personality traits rather than to capture them eight times. While our validation method could serve as a framework for future studies that investigate personality in species with low capture rates, we share the concerns of Carter et al. (2013) and recommend validation to be routinely incorporated as part of any personality studies.

Several studies have shown that personality traits such as activity, boldness, exploration and aggressiveness can be consistent across time and context (Gosling and John 1999; Réale et al. 2010). Consistent individual differences may explain up to 30 % of the behavioural phenotypic variance within populations (Bell et al. 2009; Chapman et al. 2013). While most studies have measured the consistency of personality traits within a relatively short period of time of a few weeks (Chapman et al. 2013), few long-term studies about personality have been conducted (Dammhan 2012; Herde and Eccard 2013; Montiglio et al. 2014). Here, we showed that behavioural traits of individuals were consistent in the short (2 weeks) and long term (4–5 months), after one third of the lifespan of a striped mouse. Additionally, striped mice behavioural traits were consistent under different environmental conditions (during the moist breeding season with high food availability and the hot non-breeding seasons with very low food availability) and in the presence and in the absence of reproduction, indicating that personality in this species is also consistent over context. In sum, our study demonstrates that personality can be stable in the long term over drastically changing environmental conditions.

Both males and females that changed their reproductive tactics remained consistent in their behavioural traits.

**Table 1** Effect size estimates (fixed and random) and $R^2_{(adj)}$ for personality (random intercept) and behavioural flexibility (random intercept and slope) models before and after female striped mice adopted a new tactic

|  |  | Activity | Boldness | Exploration | Aggression |
|---|---|---|---|---|---|
| Random intercept model | AIC | 197.1 | 273.6 | 2631.3 | 151.5 |
|  | BIC | 201.5 | 278.0 | 2635.7 | 155.9 |
|  | Random effects |  |  |  |  |
|  | 1\|MouseID variance | 0.14 | 0.79 | 6.63 | 0.82 |
|  | 1\|MouseID sd | 0.37 | 0.89 | 2.57 | 0.90 |
|  | Fixed effects |  |  |  |  |
|  | Intercept | 2.50 | −2.61 | 1.33 | 0.62 |
|  | Tactic | −0.22 | −0.63 | −0.38 | −0.34 |
|  | $R^2_{(adj)}$ | 0.57 | 0.31 | 0.49 | 0.08 |
| Random slope and intercept model | AIC | 199.5 | 255.4 | 311.6 | 140 |
|  | BIC | 206.8 | 262.7 | 318.9 | 147.4 |
|  | Random effects |  |  |  |  |
|  | 1\|MouseID variance | 0.09 | 1.18 | 31.61 | 1.70 |
|  | 1\|MouseID sd | 0.30 | 1.08 | 5.62 | 1.30 |
|  | 1+Tactic\|MouseID variance | 0.03 | 0.30 | 43.65 | 2.92 |
|  | 1+Tactic\|MouseID sd | 0.17 | 0.54 | 6.61 | 1.71 |
|  | Correlation of random effects | 1.00 | −0.86 | −0.76 | −0.71 |
|  | Fixed effects |  |  |  |  |
|  | Intercept | 2.53 | −2.74 | 4.14 | 0.29 |
|  | Tactic | −0.28 | −0.36 | −1.95 | −0.28 |
|  | $R^2_{(adj)}$ | 0.48 | 0.30 | 0.97 | 0.29 |

Females that changed from the philopatric non-breeding to the breeding tactic were consistent for activity, boldness and exploration, but not for aggressiveness. Males that changed their reproductive tactic from philopatric to either roamer or

**Table 2** Effect size estimates (fixed and random) and $R^2_{(adj)}$ for personality (random intercept) and behavioural flexibility (random intercept and slope) models before and after male l striped mice adopted a new tactic

|  |  | Activity | Boldness | Exploration | Aggression |
|---|---|---|---|---|---|
| Random intercept model | AIC | 252.2 | 314.3 | 835.3 | 119.2 |
|  | BIC | 257.0 | 319.0 | 840.1 | 124.0 |
|  | Random effects |  |  |  |  |
|  | 1\|MouseID variance | 0.45 | 1.52 | 23.27 | 3.19 |
|  | 1\|MouseID sd | 0.67 | 1.23 | 4.82 | 1.79 |
|  | Fixed effects |  |  |  |  |
|  | Intercept | 2.11 | −3.49 | 1.82 | −0.19 |
|  | Tactic | 0.02 | 0.14 | 0.84 | −0.87 |
|  | $R^2_{(adj)}$ | 0.58 | 0.31 | 0.29 | 0.45 |
| Random slope and intercept model | AIC | 249.7 | 279.1 | 304.2 | 121.5 |
|  | BIC | 257.6 | 287.0 | 312.1 | 129.4 |
|  | Random effects |  |  |  |  |
|  | 1\|MouseID variance | 0.46 | 1.76 | 23.51 | 2.64 |
|  | 1\|MouseID sd | 0.68 | 1.33 | 4.85 | 1.62 |
|  | 1+Tactic\|MouseID variance | 0.38 | 1.10 | 18.43 | 0.70 |
|  | 1+Tactic\|MouseID sd | 0.61 | 1.05 | 4.29 | 0.84 |
|  | Correlation of random effects | −0.15 | −0.25 | 0.24 | 1.00 |
|  | Fixed effects |  |  |  |  |
|  | Intercept | 2.10 | −3.64 | 2.14 | −0.01 |
|  | Tactic | −0.05 | 0.18 | 2.93 | −1.84 |
|  | $R^2_{(adj)}$ | 0.70 | 0.33 | 0.78 | 0.71 |

breeder remained consistent for exploration and aggressiveness, but not for activity or boldness. Sexual selection has been proposed as one mechanism for the evolution and maintenance of personality (Schuett et al. 2010). In female mammals, reproductive success often depends on body condition, and it is thus critical that females, especially during lactation and pregnancy, are able to access food efficiently. Activity, boldness and exploration might be therefore particularly important in female mice striped mice as these personality traits might allow gestating and nursing individuals to be able to locate food resources more effectively. Additionally, personality has been proposed as a way for an individual to assess the quality of a competitor or a potential mate (Schuett et al. 2010). In striped mice, both sexes participate in territorial defence (Schradin 2006), yet males spend considerably more time than females patrolling territory boundaries (Schradin 2006) and can be especially aggressive towards neighbouring and unfamiliar males (Schradin 2004; Schradin et al. 2010b). As females are the choosing sex in striped mice (Pillay 2000; Schradin et al. 2012), females might be assessing the quality of their mate based on their aggressiveness, which could signal a male's capacity to successfully defend a territory from intruders. Further, females typically remain within the family group, whereas males are the dispersing sex (Schradin 2004). Exploration and aggressiveness might thus be more important in males than in females as these personality traits might allow for the successful dispersal of an individual into a new territory. Aggressiveness has been linked to dispersal tendencies previously, with several studies showing that more aggressive individuals are more likely to disperse (Myers and Krebs 1971; Kaplan et al. 1995; Howell et al. 2007; for striped mice, see Schoepf and Schradin 2012b). Several studies have also found a positive correlation between exploration and dispersal (Holekamp 1986; Belthoff and Dufty 1998; Dingemanse et al. 2003), with individuals that are more explorative to be able to assess risks more rapidly (Crusio 2001; Tebbich et al. 2009). Our results corroborate previous finding by Schoepf and Schradin (2012b) that showed male striped mice to be more socially investigative than females, which they interpreted as a willingness of males to more rapidly assess whether a stranger was a potential competitor or a mate. Taken together, our results indicate that there are important differences in the way personality is maintained within the sexes in striped mice, which could be related to differences between males and females in the costs and benefits of expressing a particular behaviour (Chapman et al. 2013). Our findings that the personality of striped mice does not affect their social and reproductive tactics suggest that personality is unlikely to influence tactic switching and social systems, at least in species in which tactic switching follows a single strategy.

Comparing random intercept models (test for personality) with random intercept and slope models (test for flexibility) in our study showed that in females, there was a strong added effect of between-individual differences in flexibility for boldness, exploration and aggressiveness, and in males, for activity, boldness and exploration. While the ability to appropriately adjust behaviours between different contexts would be advantageous, several studies have now shown that consistent individual differences in behaviour are often distributed in a non-random way (Gosling 2001; Boon et al. 2008; Dingemanse et al. 2009), leading to the conclusion that this variation is adaptive (Dall et al. 2004; Dingemanse et al. 2009). Such adaptability of personality traits could allow individuals to mount the appropriate response to the environmental challenge while at the same time reducing investment in costly behavioural plasticity (Briffa et al. 2008; Dingemanse et al. 2010), especially in continuously changing environments (Dall et al. 2004; Sih et al. 2004a). While this is true for most of the behavioural traits we measured, activity in females and aggressiveness in males were only consistent but not flexible. In a recent paper, Kluen and Brommer (2013) observed that blue tits (*Cyanistes caeruleus*) showed more inconsistent behaviour during the breeding season and attributed the lack of between-individual variation observed to individuals having different priorities at such time. It could therefore be that striped mice females and males are somehow constrained in expressing behavioural flexibility in activity and aggressiveness during the breeding season (when tactic switching takes place), which causes the loss of between-individual variation observed for these traits. Taken together, our results suggest that in striped mice, personality can be adaptive and does not constrain the evolution of behavioural flexibility.

Several studies have demonstrated personality to be widespread in nature, and here, we focused on a non-human species well known for its social flexibility. Striped mice show high social flexibility, which is not constrained by personality. Philopatric males that became roamers did not differ from philopatric males that became breeders in any of the personality traits investigated. Our results thus indicate that tactic change is primarily driven by environment change. We found that even in such a flexible species, personalities are well developed and highly stable over an individual's lifetime, independent of changes in season but do not predict the change in tactic, which seems to be environmentally determined. In conclusion, while personality may constrain behavioural flexibility, it does not hinder social flexibility and the evolution of alternative reproductive tactics.

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