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PERSONALITY OF A SOCIALLY FLEXIBLE MAMMAL

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A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Doctor of Philosophy

Johannesburg 2017

DECLARATION

I declare that this thesis is my own unaided work. It is being submitted for the Degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.



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Chi Hang Yuen

2nd day of May 2017

ABSTRACT

The study of personality has received much attention in recent years, because it might explain why individuals are constrained in their ability to respond to changes in their environment. Recent publications have shown that behavioural flexibility and personality might be linked; however, their interaction is not well understood and could be elucidated by studying a socially flexible species, such as the African striped mouse (*Rhabdomys pumilio*). Striped mice are an ideal species to address this topic because individuals of both sexes can follow different alternative reproductive tactics, which are reversible.

Firstly, I investigated personality in striped mice by examining whether individuals showed consistency in their behavioural traits across time and context. Secondly, I addressed the interplay between personality, behavioural flexibility and social flexibility, by performing personality tests before and after individuals adopted a new reproductive tactic. Thirdly, I examined whether personality and behavioural syndromes measured under standardised laboratory conditions correlated with personality measures obtained from the striped mice in nature. Finally, I assessed whether the open field test and the startle test, two assays typically used to measure boldness, were correlated.

The results of my research showed that personalities are well developed and highly stable over an individual's entire lifespan even in this very flexible species. I found that some personality traits measured remained stable even after individuals adopted new tactics, and comparisons between individuals before and after tactic change indicated that personality traits were unable to successfully predict which tactic an individual would choose in the future. This is important as it shows that personality does not constrain behavioural flexibility. Further, I demonstrated that sexual selection can have a strong influence on personality, with males and females differing quite remarkably in their personality traits. By using a carefully validated methodology, my research additionally provides validation and support that personality measures obtained from standardised laboratory conditions are representative of individuals' natural behaviours. Interestingly, I found that two separate latent variables (one for the field and one for the lab) underpinned all the behaviour measured indicating that there is a context-specific behavioural syndrome in this species. In sum, my

study demonstrated that lifelong stable personality traits are well established in a socially flexible mammal.

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CHAPTER 1

INTRODUCTION

1. PERSONALITY: DEFINITION, MECHANISMS, FUNCTION AND EVOLUTION

Individuals often exhibit consistent differences in their behavioural responses when faced with the same environmental challenge (Bell et al. 2009). For example, juvenile fishing spiders (*Dolomedes triton*) that show a long latency to re-emerge after being frightened will show the same shy behaviour as adults, while others will show a short latency at both ages (Johnson and Sih 2007). Great tits (*Parus major*) that show a high level of exploratory behaviour in one test will do so in another (Verbeek et al. 1994). Such consistent behavioural responses over time and across contexts have been termed "personalities" (Sih et al. 2004a; Bell 2007). Consistent differences have been reported for a large number of behavioural traits, including aggression, boldness, activity, sociability and exploration (Gosling 2001; Sih et al. 2004b; Réale et al. 2007; Bell et al. 2009). Personality has been shown to be a widespread phenomenon, and has now been reported in several vertebrates and invertebrates species (Gosling and John 1999; Conrad et al. 2001; Dingemanse et al. 2003; Réale et al. 2007; Schuett et al. 2011; Chapman et al. 2013). Consistency for a given behaviour often correlates with other behavioural responses in "behavioural syndromes" (Clark and Ehlinger1987; Sih et al. 2004b; Bell 2007). For instance, studies in three-spined sticklebacks (*Gasterosteus aculeatus*; Dingemanse et al. 2007) and red squirrels (*Tamiasciurus budsonicus*; Boon et al. 2008) have shown aggressive individuals to also be highly active. This has led to the discovery that some syndromes (e.g. the dispersal syndrome; Duckworth 2008; Cote et al. 2010; Chapple et al. 2012) are found in a wide range of taxa. For example, a positive correlation between boldness and aggression, indicating that the boldest individuals are also the most aggressive (aggression-boldness syndrome; Sih et al. 2004b) has been found in species as diverse as zebrafish (*Danio rerio*; Norton et al. 2011) and rock ants (*Temnothorax rugatulus*; Bengston and Dornhaus 2014). Another example of across-species syndrome is the pace-of-life syndrome, which suggests that consistent individual behavioural

differences co-vary with a suite of physiological (e.g. metabolic, hormonal, immunological) and life-history traits at the population and species levels (Biro and Stamps 2008; Réale et al. 2010). This has been documented in damselflies (*Coenagrion hastulatum*; Brodin and Johansson 2004), field crickets (*Gryllus integer*; Niemela et al. 2012) and crayfish (*Cherax destructor;* Biro et al. 2014).

Much of the personality research carried out in recent years has aimed to address both the ultimate reasons (Komdeur 2006; Bell and Sih 2007; Cote and Clobert 2007; Wolf et al. 2007) and the proximate mechanisms underpinning personality (Koolhaas et al. 1999; Biro and Stamps 2008; Careau et al. 2008). At the ultimate level researchers have attempted to integrate the study of animal personalities and behavioural syndromes into an ecological and evolutionary framework (Bell 2007; Réale et al. 2007; Burns 2008) and have proposed some ground-breaking theories to explain the apparently suboptimal behavioural tendencies associated with animal personalities (Dingemanse and Wolf 2010; Wolf and Weissing, 2010). For example, theories based on cost-benefit trade-offs predict that a bolder individual may receive a benefit by outcompeting conspecifics to gain greater access to resources (Pruitt et al. 2008; Short and Petren 2008), but bolder animals may also take more risks making them more susceptible to predation (Carter et al. 2010). An increasing number of studies have shown that natural selection, gene flow, and dispersal favour the maintenance of personality (Dingemanse et al. 2004; Dingemanse and Réale 2005; Smith and Blumstein 2008; Cote et al. 2010; Réale et al. 2010). For example, ecological studies of personality have shown that natural selection acts on inter-individual behavioural variation (Dingemanse and Réale 2005, Smith and Blumstein 2008). Further, individuals' differences in behaviour are stable over time and across contexts, even among those of the same age and sex (Verbeek et al. 1994; Koolhaas et al. 2010). Moreover, males and females of several species have also been shown to differ remarkably and consistently in some of their personality traits, suggesting that sexual selection has an important role in maintaining individuals' personalities in certain species (Van Oers et al. 2008; Schuett et al. 2010).

At the proximate level, personality differences have been studied in the context of the genetic and physiological mechanisms underpinning consistent behavioural differences. Several studies have shown that between-individual personality differences are reflected in

differences, for example, in their metabolism (Careau et al. 2008; Biro and Stamps 2010) and stress physiology (Koolhaas et al. 1999). Further, differences between individuals' personalities have been shown to relate to genetic differences, which may help to explain co-adaptation between personality and other traits (Kölliker et al. 2005; Harris et al. 2007; Roulin et al. 2010). Moreover, personality has been demonstrated to have a heritable component (Van Oers et al. 2005; Réale et al. 2007; Dotcherman et al. 2014). Finally, a few studies have recently also confirmed personality over long-term developmental phases, showing that at any given age or life-stage, an individual's personality is contingent upon a wide range of experiential factors that occur early in life, and even can be formed at conception and exist all the way through to adulthood (Sinn et al. 2008; Stamps and Groothuis 2010a, b).

2. PROBLEM IDENTIFICATION

Sub-optimal behaviour and personality

The study of animal personalities aims to understand how behavioural traits co-vary within individuals and which evolutionary processes might generate such trait variability (Sih et al. 2004a; Réale et al. 2007), yet it still remains puzzling why behaviour, probably the most flexible phenotypic trait in animals, is not flexible enough to reach optimality. The persistence of sub-optimal behaviour within wild populations has been linked to the existence of differences in personalities among individuals (Careau et al. 2008; Dingemanse and Wolf 2010; Wolf and Weissing 2010). For example, in a study in streamside salamanders (*Ambystoma barbouri*), Sih et al. (2003) expected to find the larvae of this species to be more active and spend more time foraging when no predators were around, and, instead, to show very little activity during the day when their main predator, the sunfish (*Lepomys canellus*), was present. Indeed, their results showed that salamander larvae reduced their activity by about 50% when sunfish were present. However, highly active larvae that grew well in the absence of a predator remained considerably more active even when sunfish were present, and, as a consequence, suffered higher predation risk. Further, Sih and colleagues found that no salamander larvae showed optimal behaviour (i.e. being active when predators were

absent and inactive when predators were present) indicating that their behavioural plasticity was lower than the optimum (Sih et al. 2004a, b).

Behavioural plasticity is defined as the ability of an individual to alter its phenotype in response to changing environmental conditions so to maximise its fitness (e.g. enhanced survival probabilities, increased mating probability, etc.; Schlichting and Pigliucci 1998; West-Eberhard 2003). Behavioural flexibility is a similar term, and in the literature the two terms have been used interchangeably (e.g. Holekamp et al. 2013), yet behavioural flexibility differs from behavioural plasticity in the fact that behavioural flexibility specifically refers to the ability of individuals to facultatively and reversibly change their phenotype in response to changes in their environment. The key aspect here is the ability of individuals to switch back and forth between phenotypes. Behavioural plasticity is a more general term, which in addition to the above, also includes examples of individuals with developmental plasticity, arising during ontogeny when one of several alternative tactics are developed and maintained into adulthood (Piersma and van Gils 2010). Here, I treat the two terms as being separate and distinguish behavioural flexibility from behavioural plasticity in the fact that behavioural flexibility allows for behavioural adaptation that are reversible. Behavioural flexibility allows individuals to respond quickly and adaptively to challenges in the environment, and as such it should be favoured by selection. Yet, individuals show great variability in their ability to mount behavioural responses, even when confronted with same environmental challenge (e.g., individuals facing a decline in resources availability within the same habitat). This is because producing a flexible phenotype is costly and, thus, different individuals may be constrained in their ability to be flexible depending on their life-history (Hazlett 1995; DeWitt et al. 1998; Dall et al. 2004).

Several studies have now shown that there is not only a between-individuals difference in behavioural responses to challenges, but also that this behavioural differences are consistent (i.e. individuals have different personalities). In other words, an individual may be able to adjust its behaviour when conditions in its environment change, but still show a consistent level of response relative to those of other individuals in the population (Johnson and Sih 2007; Dingemanse et al. 2010). Thus studying the link between behavioural flexibility and personality may elucidate why individuals show such a variability of responses to changes in

environmental conditions. Personality research has seen a surge in publications, particularly in recent years (Chapman et al. 2013), but the field is still mired by a lack of empirical studies (DiRienzo and Montiglio 2015) and is laden with terminological inconsistencies (Réale et al. 2007), including methodological discrepancies between which assays best measure particular personality traits (e.g. boldness; Carter et al. 2013). Perhaps part of the problem stems from the fact that animal personality research is mostly theory-driven and does not have a strong conceptual framework (David and Dall 2016) or that the vast majority of studies have investigated personality and behavioural flexibility in species that are not especially well known for having either. Yet, if we are to understand the contribution of both to produce variable individual responses, they need to be studied concurrently. To understand the link between behavioural flexibility and personality would therefore be better if this topic were addressed using a species where personality was well-developed, but also that show high degree of flexibility in its behavioural responses. Socially flexible species are great candidates to study the link between personality and behavioural flexibility because individuals of these species show alternative phenotypes that are highly flexible and adapted to the environmental conditions to which they are exposed. Most importantly, individuals of socially flexible species are able to respond to changes in their environment by facultatively switching back and forth between alternative phenotype when conditions change (Schradin et al. 2012). As a result of adaptations arising in response to changes in the environment, the entire social system of these species can change. While socially flexible species may provide great model organisms to study behavioural flexibility and personality, to date, they have been used rarely to address this topic (Zimbardo 1995; Arnold and Taborsky 2010; Le Vin et al. 2011), with different studies producing conflicting results.

Studying personality and validation

Even though the study of animal personality has been regarded as one of the most exciting fields of research in animal behaviour in recent years (Sih et al. 2004b; Bell and Sih 2007; Wolf et al. 2007), it is mostly restricted to artificial conditions in field arenas or experimental rooms, while personality measures are rarely taken under natural conditions. In addition, with a few noticeable exceptions, such as great tits (Dingemanse et al. 2004; Carere et al. 2005)

and red squirrels (Boon et al. 2008), few field studies have been able to gather long-term data collected over several years. In fact, the vast majority of studies have been conducted either in captivity or under semi-natural conditions (e.g. Bell and Sih 2007; Cote and Clobert 2007; Johnson and Sih 2007). One problem field scientists face is how to reliably collect data from their study animals which is representative of the behaviour they are trying to measure (Réale et al. 2007).

Researchers also have to tackle the problem of having to decide whether to perform one or several tests in a day, and, if so, how long they should wait between tests. Many approaches have been followed, such as testing several traits with one test (Boon et al. 2008) or testing one trait per day (Dingemanse et al. 2007). There are two intrinsic problems: 1. little to no validation is provided for the approach used; and 2. testing only one trait per day is often not achievable for most field studies. In the first case, it is not known whether similar or different results can be obtained when testing individuals for several behavioural traits consecutively, with half a day, one day or several days in between tests. In the second case, field researchers need to be able to catch individuals repeatedly to test for consistency, but this can be very difficult to achieve over a period of several days and is unlikely to be a feasible method for many species. It would be important therefore to test whether conducting measurements of several behavioural traits in quick succession is as reliable as having intervals between tests. Assuming there is concordance, testing less frequently could save time in field studies and reduce stress to individuals by trapping and testing them only a few times instead of many times.

3. STUDY SPECIES

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). The genus *Rhabdomys* comprises of 3-4 species, which inhabits the southern parts of the African Continent (Du Toit et al. 2012). *R. pumilio* is mostly found in the arid and semi-arid regions of western southern Africa. Within South Africa, *R. pumilio* is mostly found within the semi-desert Succulent Karoo area. The University of the

Witwatersrand, in collaboration with the University of Strasbourg in France, has established a long-term monitoring program of a wild population of African striped mice in the Succulent Karoo, in the Goegap Nature Reserve, near the town of Springbok (29.6830° S, 17.9640° E).

In the Succulent Karoo, the dry season typically lasts from December to April and is characterised by low food abundance and low precipitation (Schradin and Pillay 2005, 2006). The long dry season is followed by a moist season in winter (May-July) and by a spring with displays of wildflowers (August-November). As such, the habitat of striped mice in the area is open and characterised by the presence of ephemeral wildflowers and dwarf succulent shrubs, typical of the Succulent Karoo semi-desert (Cowling et al. 1999). Striped mice living in this environment usually nest in shrubs, such as *Zygophyllum retrofractum*, which also provide food during the dry season (Schradin et al. 2015). Temperatures are also consistent with semi-arid regions, with significant thermal differences between day and night and striped mice spend considerable time in the morning in front of their nests thermoregulating through basking in the sun (Schradin et al. 2007). Sitting in front of the nest in the morning also affords individuals an opportunity to socialise with other group members before leaving to forage alone (Schradin and Pillay 2004). Both the topography of the environment and the behaviour of the striped mouse, a diurnal species that can be easily observed during the day, make it an excellent study organism to be directly observed in the field.

In the Succulent Karoo, mice live in extended families consisting of 1 breeding male, 2-4 breeding females and their adult philopatric offspring (both males and females) that remain in the natal group and act as helpers at the nest (Schradin 2005). Consequently, by the end of the breeding season, groups may consist of up to 30 adult individuals (Schradin 2005). In African striped mice, breeders of both sexes participate in costly parental care (Schradin and Pillay 2005), and females also show allo-parental care including allo-nursing towards offspring of other females (births are typically synchronised; Schradin and Pillay 2004; Schradin et al. 2009c). Females typically give birth to litters of 2-5 pups, after a gestation period of 20 days and have an inter-litter interval of approximately 23-30 days (Pillay 2000; Krug 2002). Striped mice reach sexual maturity at around 4-6 weeks of age when they weigh more than 30 g (Schradin et al. 2009a, b).

In the Succulent Karoo, population density of striped mice is typically high (Schradin 2005) and they typically live in groups (and always do so outside of the breeding season; Schradin and Pillay 2005; Schoepf and Schradin 2012a). However, it has been shown that under certain ecological conditions (particularly when population density is low) they can change from group-living to solitary living during the breeding season (Schradin et al. 2010; Schoepf and Schradin 2012a). As such, both males and females can follow three alternative reproductive tactics (Schradin et al. 2009, 2010a): 1. young adult philopatrics living in their natal group, 2. solitary-living or 3. communally-living breeders. Single individuals can switch their tactic repeatedly during their life, for example from group-living philopatric to solitary breeder to communal breeder, while other individuals are group-living for their entire life (Schradin et al. 2012). Different tactics are associated with differences in the degree of reproductive success, with communally-living breeders typically having the highest reproductive success, solitary-living individuals having intermediate reproductive success and group-living philopatrics having very low reproductive success (Schradin et al. 2012). Interestingly, however, when population density decreases, communally breeding and solitary individuals have similar reproductive success (Schradin and Lindholm 2011). Interestingly, even typically non-breeding philopatrics have been shown to have some degree of reproductive success (Schradin and Lindholm 2011), highlighting the fact that remaining as a philaptric in the natal group can be considered a true alternative reproductive tactic.

Individuals following different social and reproductive tactics differ considerably in their hormone levels. Corticosterone levels of non-breeding philopatric striped mice are higher than breeding individuals during the breeding season, but these levels drop in the non-breeding season (Schradin 2008), or when they disperse and adopt a solitary tactic (Schoepf and Schradin 2013). Further, testosterone levels of males following the subordinate tactic (i.e. living in their natal group) are typically lower than those of males following the dominant bourgeois tactic (breeding males in a social group; Schradin et al. 2009) and can change according to the tactic adopted (Schradin and Yuen 2011).

Most interestingly, striped mice following different social tactics also differ considerably in their behaviour. For example, individuals that follow a solitary tactic are also more aggressive than individuals that follow a group-living tactic (Schoepf and Schradin 2012b). Remarkably,

however, individuals are able to change their behaviour according to the tactic they adopt. During a field experiment where population density was manipulated, Schoepf and Schradin (2012a, b) found that group-living individuals that dispersed from their natal nests and became solitary also changed their behaviour. Specifically, striped mice became more aggressive towards same-sex conspecifics, were more socially investigative and were more amicable to opposite-sex conspecifics when they changed from group-living to solitary-living. Further, individuals that would go onto become solitary were more aggressive than their siblings that remained group-living even before the former became solitary, with this difference becoming more prominent after the adoption of a solitary tactic (Schoepf and Schradin 2012b).

These findings demonstrate high flexibility in the social behaviour of striped mice, which could also indicate higher flexibility in personality traits, and thus absence or reduced stability of personality, especially over longer periods that include changes of reproductive tactics.

4. RESEARCH AIMS, OBJECTIVES AND PREDICTIONS

The aims of my study were to:

1. Establish and validate a method to collect data on personality traits from a wild population of striped mice.

2. Examine whether individual striped mice show consistency in their behavioural traits across time and context.

3. Test whether personality predicts which reproductive tactic is adopted by an individual later in its life.

4. Establish whether personality traits measured in the field are consistent over time and correlate with measures obtained under standardised condition.

5. Investigate whether behavioural syndromes found in individuals tested under laboratory conditions are stable and can predict behavioural syndromes found in the same individuals in nature.

6. Clarify whether the different assays currently employed to measure boldness are in fact assessing the same behavioural axis.

The objectives/questions and predictions of each aim are listed below.

Aim 1. *Establish and validate a method to collect data on personality traits from a wild population of striped mice*.

I investigated whether testing free-living striped mice sequentially for the four different personality traits on one day would yield the same results as testing them on different days. The personality traits investigated were: activity, boldness, exploration and aggression.

Objective 1: Does testing striped mice sequentially for four different personality traits in one day yield the same results as testing individuals on different days?

Predictions: I predicted striped mice that were the most active, the boldest, the most explorative and the most aggressive when tested sequentially on one day, to be still the most active, the boldest, the most explorative and the most aggressive when tested on separate days.

Aim 2. *Examine whether individual striped mice show consistency in their behavioural traits across time and context*.

To assess whether personalities are consistent over time, I tested individuals twice within the same season, with each series of tests being two weeks apart. To determine whether personalities were consistent across context, I captured the same individuals previously tested in the breeding season and repeated the tests on them in the non-breeding season.

Objective 2: Is striped mice behaviour consistent over time and across context?

Predictions: If striped mice have different personalities, their behaviour should be consistent over time and across contexts. Thus, I predicted to find the boldest, the most explorative and the most aggressive striped mouse to be still the boldest, the most explorative and the most aggressive when tested: 1) two weeks after within the same breeding season; 2) five months after in the non-breeding season. In addition, I predicted to find the most active, the boldest, the most explorative and the most aggressive philopatric mice to be also the most active the boldest, the most explorative and the most aggressive once he/she had become a breeder or a solitary-living individual subsequently.

Aim 3. *Test whether personality predicts which tactic is adopted by an individual later in its life.*

To assess whether personality predicts the tactic that an individual would later adopt, I compared the personality traits of philopatric males that became solitary roaming males with philopatric males that became group-living breeding males. In doing so, I presented data collected over the entire adult lifespan of an individual.

Objective 3: Can an individual's specific personality predict which tactic he will adopt later in life?

Predictions: Group-living striped mice are known to differ in their behavioural traits from solitary-living ones (Schoepf and Schradin 2012b). For example, solitary-living striped mice have been shown to be more aggressive and more socially investigative (expressed as lower sniffing rates) than their conspecifics that remain group living (Schoepf and Schradin 2012b). Yet, it remains unclear whether these differences are already present in philopatric individuals before they change their reproductive tactics. If such differences were already present, I 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 that were less active, less bold, less explorative and less aggressive to be more likely to become group-living breeders. As tactic switching in males is more common than in females, I will specifically focused this part of the study on males, as I expect to be able to find very few females becoming solitary-living compared to males.

Aim 4. *Establish whether personality traits measured from the field correlate with measures obtained under standardised laboratory condition*.

In order to establish whether personality traits measured in the laboratory reflect personality traits of individuals in the wild, I compared measures of activity, boldness, exploration and aggression obtained from the neutral arena with measures of activity, boldness, exploration and aggression collected from striped mice when at their nest during their peak activity times. To ensure that the personality traits measured under the two different conditions were comparable, I employed the same tests used in the arena and adapted them to the field conditions.

Objective 4: Were personality traits measured in the laboratory consistent with personality measured in the field?

Predictions: If the personality measures obtained from the laboratory reflected "genuine" personality traits of individuals (rather than laboratory artefacts), I expected to find individuals that were the most active, the boldest, the most explorative and the most aggressive in the laboratory to still be the most active, the boldest, the most explorative and the most aggressive when tested under natural conditions in the field.

Aim 5. *Investigate whether behavioural syndromes found in individuals tested under laboratory conditions were able to predict behavioural syndromes found in the same individuals in nature.*

Personality traits of individuals can be correlated in behavioural syndromes. However it is unclear whether behavioural syndromes can be stable in different contexts and whether behavioural syndromes measured in captivity can be used to predict behavioural syndromes measured in the nature.

Objective 5: Were behavioural syndromes measured in the lab good predictors for behavioural syndromes measured in nature?

Predictions: If behavioural syndromes are stable across contexts, I expected to find the same correlation between the different behavioural traits when these were measured in the laboratory under standardised conditions and in nature. For example, if a positive correlation existed between activity and boldness in the laboratory, I expected to find the same positive correlation between activity and boldness when measures were taken in the field.

Aim 6. *Clarify whether the different assays currently employed to measure boldness are in fact assessing the same behavioural axis*.

Boldness, defined as the willingness of an individual to engage in risk-taking behaviour (Réale et al. 2007), is one of the most studied personality traits in animal behaviour research. Yet, there is disagreement regarding the way boldness should be measured and currently there are several assays, which are used interchangeably to measure boldness. I tested whether measures of boldness obtained from two of the most popularly used assays (the open field and a startle test) were comparable. This is important, because if the two tests are not measuring the same personality trait, there is a risk to fall in a 'jingle' fallacy (Block 1995).

Objective 6: Did behavioural measures obtained from a startle test correlate with behavioural measures obtained from an open field test?

Predictions: If the open field and the startle test were both measuring boldness, I expected the two assays to be positively correlated, with individuals that showed the most risk-prone behaviour in an open field also showing the most risk taking behaviour when confronted with a simulated predator.

5. THESIS OUTLINE

The thesis follows an integrative approach to study personality, combing ecological, life-history and behavioural aspects. My thesis comprises of five chapters. Apart from a general introduction (**chapter 1**) and final discussion chapter (**chapter 5**), I have three experimental chapters that address the aims of my research, two of which have been published with the third being submitted for publication. Because of this approach, there is inevitable overlap of

information across the chapters. Each chapter has its own reference list. Figures and tables are numbered sequentially per experimental chapter. Page numbers run consecutively.

Aims 1, 2 and 3 were tested in **chapter 2**. As such, this chapter covered the validation methodology to study personality in striped mice, examined whether the traits measured showed consistency over time and across context and analysed the link between personality, behavioural flexibility and social flexibility.

In **chapter 3**, I addressed aims 4 and 5. It includes all comparisons between personality traits of striped mice when tested under standardised conditions in a neutral presentation arena in the laboratory and directly in their natural habitat. This chapter examines correlations between and among personality traits.

In **chapter 4**, I assessed whether boldness measured with an open field test yields the same results if boldness were measured using a startle test, addressing aim 6.

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CHAPTER 2

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 aggression 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.

Key-words

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

1. 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; Briffa et al. 2008; Sih and Bell 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 and Pillay 2004, 2005; Schradin 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. 2008) 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) aggression) 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.

2. MATERIAL AND METHODS

(a) 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 (29.6830° S, 17.9640° E). Striped mice were trapped with Sherman-like metal traps (26×9×9 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 (AfricaWildlife 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.

(b) Measuring personality traits in striped mice

We measured activity, boldness, exploration and aggression 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 (38×22×15 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.

Aggression 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. Aggression 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 minutes. 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. Aggression was measured as the total number of aggressive encounters initiated by the focal individual. To remain consistent with data previously collected on aggression 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 aggression. To correct for this, all data were calculated as relative frequencies. In addition to aggression, 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.

(c) 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 aggression 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) aggression).

(d) 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) aggression. 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 (15males 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.

(e) 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.

(f) 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 *rs* 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* 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 (2weeks apart), (2) in the long-term (5months 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, aggression) 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 flexibility (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 R2 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 aggression levels of philopatric individuals that would go on to become roamers against aggression 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.

3. RESULTS

(a) 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; aggression, 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 ± 0.10, 95 % CI 0.53 – 0.90, P = 0.001; boldness R = 0.71 ± 0.13, 95 % CI 0.39 – 0.87, P = 0.001; exploration R = 0.64 ± 0.14, 95 % CI 0.28 – 0.83, P = 0.001; aggression R = 0.80 ± 0.09, 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.

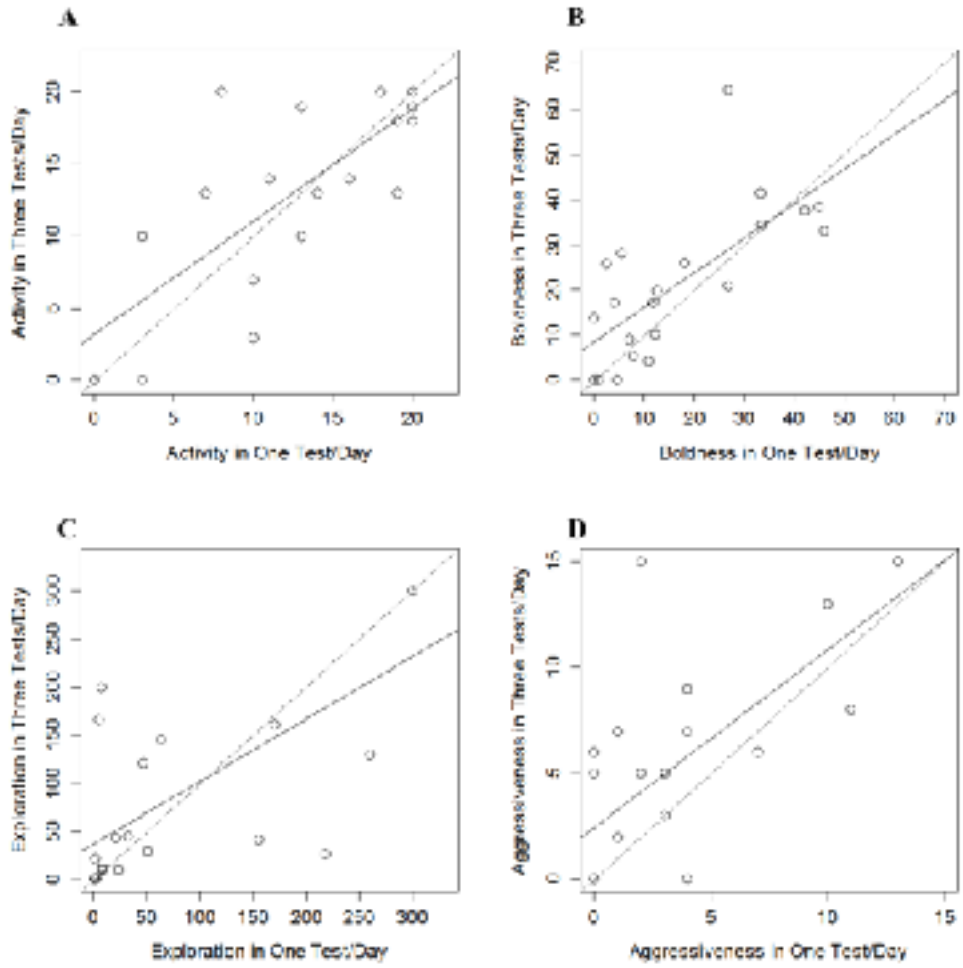


Figure 1

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. aggression (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).

(b) 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 ($\chi2 = 293.04$, $P < 0.0001$) and aggression ($\chi2 = 9.17$, $P = 0.01$), but not for activity ($\chi2 = 0.81$, $P = 0.67$) and boldness ($\chi2 = 0.40$, $P = 0.82$), meaning that only the personality traits of exploration and aggression were significantly different between males and females (exploration, binomial-GLMM $z = 16.97$, $P < 0.0001$; aggression, Poisson-GLMM $z = -3.12$, $P = 0.002$). Individuals also displayed significant repeatability in all four behaviours over time (activity $R = 0.48 \pm 0.14$, 95 % CI 0.17 – 0.72, $P = 0.03$; boldness, $R = 0.013 \pm 0.009$, 95 % CI 0.003 – 0.04, $P = 0.008$; exploration $R = 0.007 \pm 0.005$, 95 % CI 0.001 – 0.021, $P = 0.001$; aggression $R = 0.75 \pm 0.09$, 95 % CI 0.56 – 0.90, $P = 0.001$).

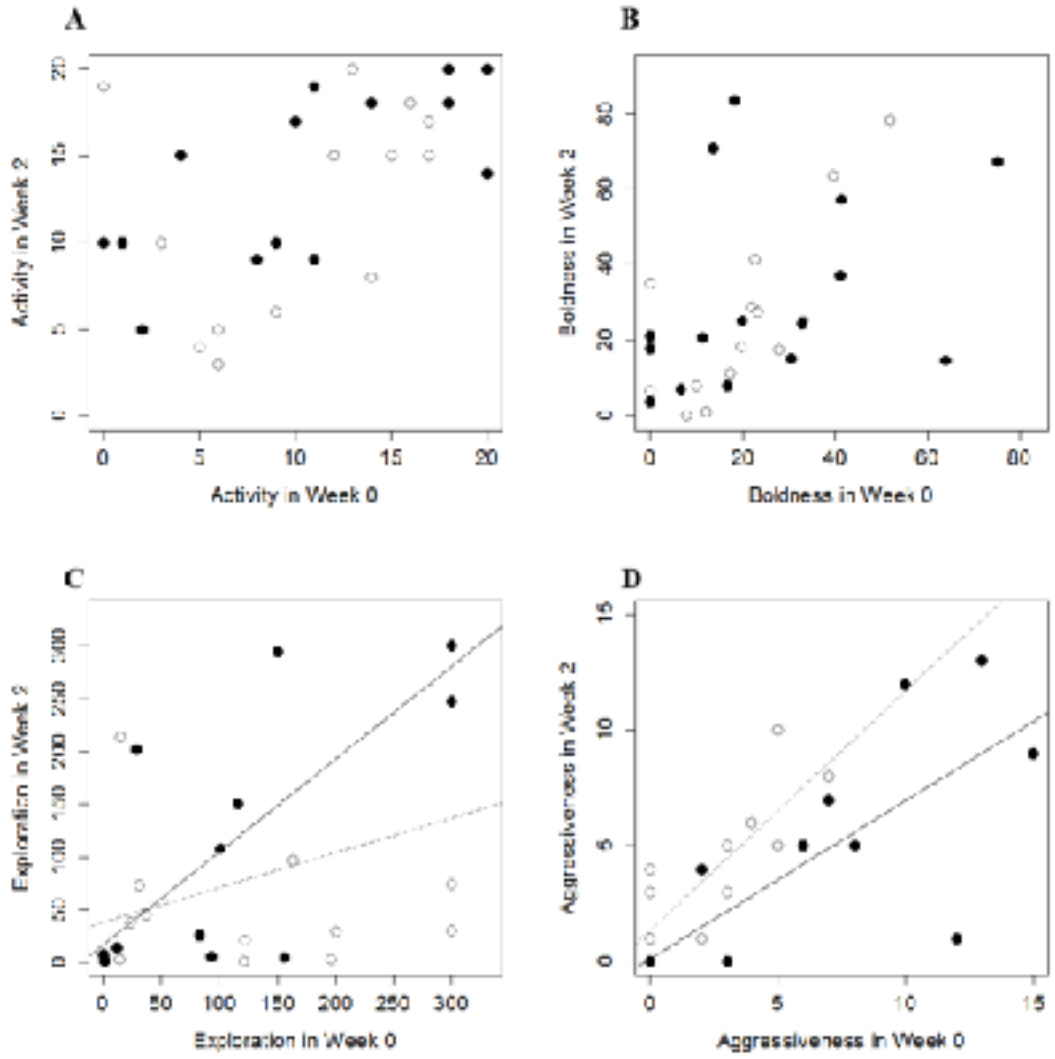


Figure 2

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. aggression ($P = 0.021$). Observed female line (dotted line); observed male line (solid line). Females (white circles) and males (black circle).

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 ($\chi2 = 27.77$, $P < 0.0001$) and exploration ($\chi2 = 487.05$, $P < 0.0001$), but not for activity ($\chi2 = 4.45$, $P = 0.11$) and aggression ($\chi2 = 0.47$, $P = 0.79$). Individuals also displayed significant repeatability in all four behaviours when tested 5 months apart (activity $R = 0.46 \pm 0.13$, 95 % CI 0.17 – 0.69, $P = 0.001$; boldness $R = 0.014 \pm 0.011$, 95 % CI 0.005 – 0.041, $P = 0.007$; exploration $R = 0.002 \pm 0.002$, 95 % CI 0.001 – 0.008, $P = 0.02$; aggression $R = 0.61 \pm 0.10$, 95 % CI 0.44 – 0.83, $P = 0.001$).

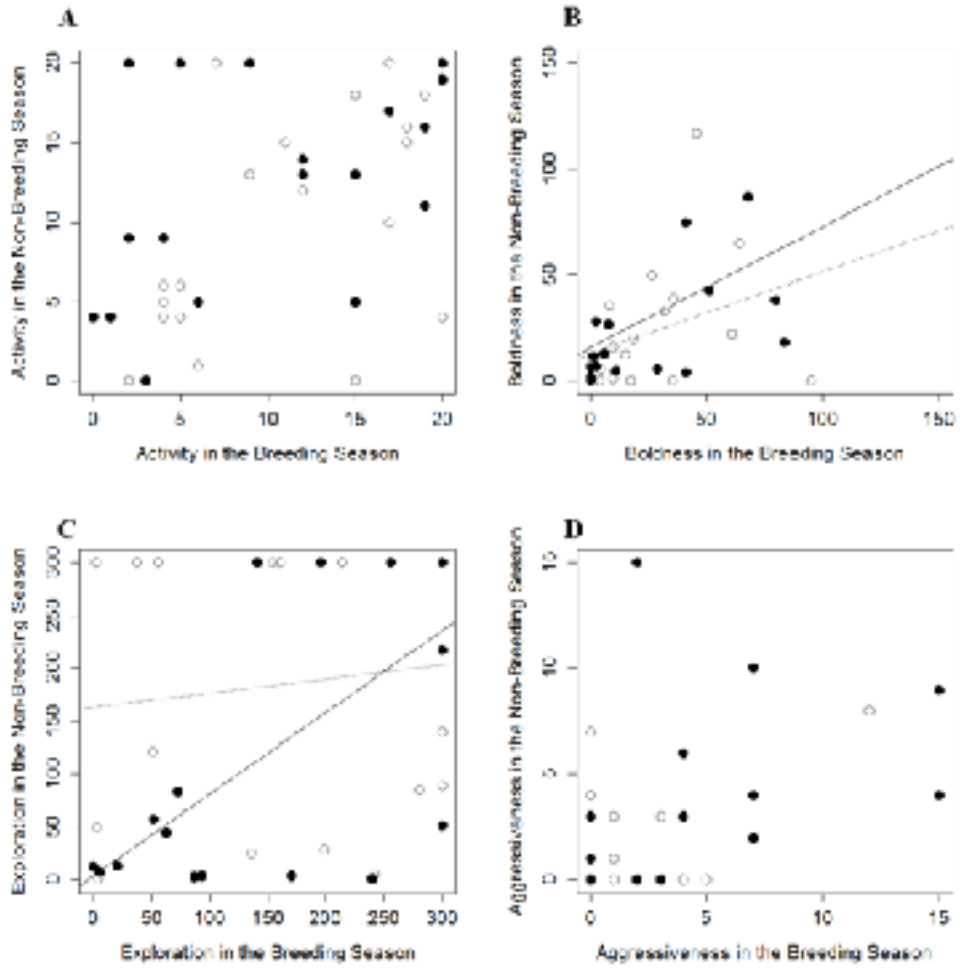


Figure 3

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 personality traits of a. activity ($P = 0.02$), b. boldness ($P = 0.0004$), c. exploration ($P < 0.0001$) and d. aggression ($P = 0.006$). Observed female line (dotted line); observed male line (solid line). Females (white circles) and males (black circle).

(c) 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 aggression (Poisson-GLMM $z = -1.41$, $P = 0.16$). Males that changed their reproductive tactic remained consistent for exploration (binomial-GLMM $z = 12.81$, $P < 0.0001$; Fig. 4c) and aggression (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).

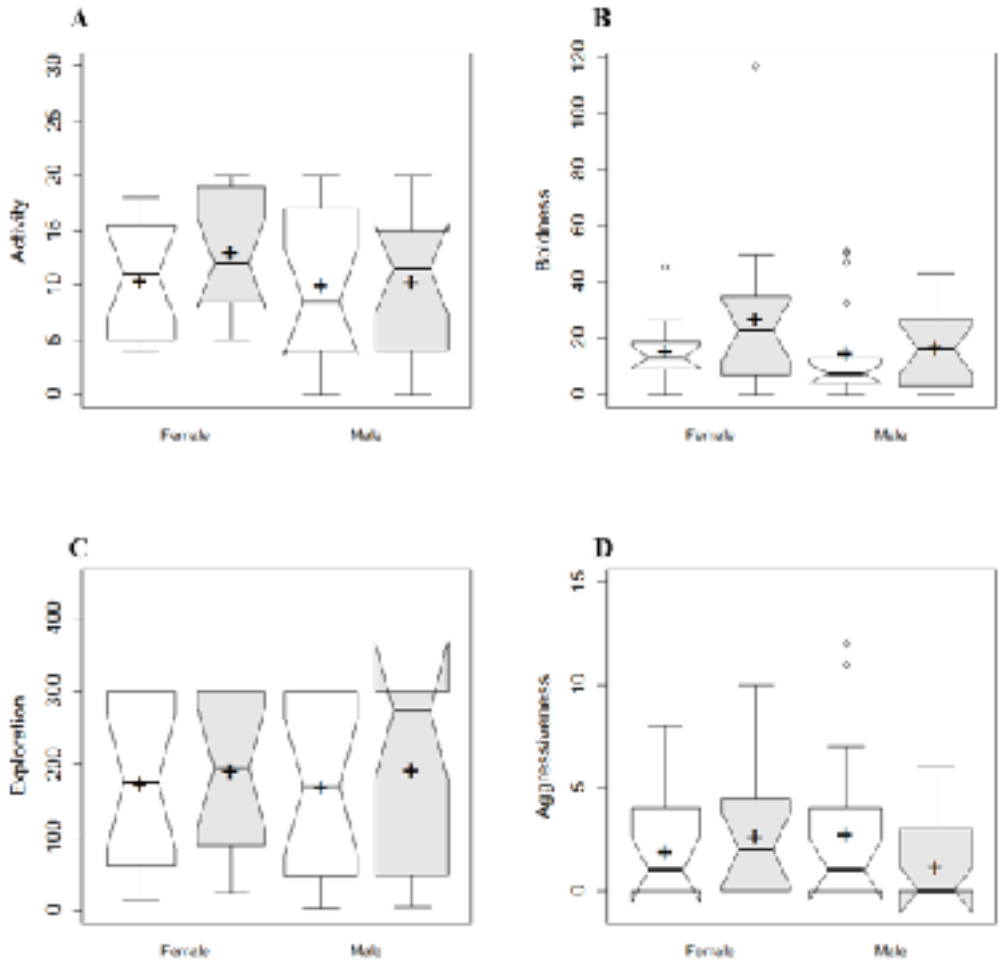


Figure 4

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. aggression ($P = 0.16$). Male striped mice that switched tactics showed consistency in the personality traits for c exploration ($P < 0.0001$) and d aggression ($P = 0.0008$), 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.

(d) 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 exploration (binomial-GLMM $z = -0.94$, $P = 0.35$) or aggression when they became breeders (Poisson-GLMM $z = -0.43$, $P = 0.67$). Males were significantly more 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 ± 1.90 versus 7.46 ± 1.70; quasi-Poisson-GLM $F_{1, 23} = 1.48$, $P = 0.24$; boldness 20.25 ± 5.25 versus 11.76 ± 4.14; quasi-binomial-GLM $F_{1, 23} = 1.61$, $P = 0.22$; exploration 185.49 ± 40 versus 199.77 ± 36.09; quasi-binomial-GLM $F_{1, 23} = 0.07$, $P = 0.79$; and aggression 1.33 ± 0.74 versus 1.69 ± 0.96; zero-inflated negative binomial-GLM $z_{1, 23} = -0.32$, $P = 0.75$).

(e) Comparison between personality and behavioural flexibility in individuals that switched tactics

For females, including a random slope improved model fit for boldness ($\chi2 = 27.28$, $P < 0.0001$; Table 1), exploration ($\chi2 = 2323.8$, $P < 0.0001$; Table 1) and aggression ($\chi2 = 27.77$, $P < 0.0001$; Table 1), but not for activity ($\chi2 = 1.60$, $P = 0.45$; Table 1), suggesting that there were between-individual differences in behavioural flexibility between reproductive tactics for boldness, exploration and aggression in females.

For males, including a random slope improved model fit for activity ($\chi2 = 6.51$, $P = 0.04$; Table 2), boldness ($\chi2 = 39.16$, $P < 0.0001$; Table 2) and exploration ($\chi2 = 535.16$, $P < 0.0001$; Table 2), but not for aggression ($\chi2 = 1.71$, $P = 0.42$; Table 2), suggesting that there were between-individual differences in behavioural flexibility between reproductive tactics for activity, boldness and exploration in males.

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 | Mouse ID variance	0.03	0.30	43.65	2.92
	1 + Tactic | Mouse ID 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

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 | Mouse ID variance	0.38	1.10	18.43	0.70
	1 + Tactic | Mouse ID 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

4. 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 aggression, 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 aggression 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. Females that changed from the philopatric non-breeding to the breeding tactic were consistent for activity, boldness and exploration, but not for aggression. Males that changed their reproductive tactic from philopatric to either roamer or breeder remained consistent for exploration and aggression, 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 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 aggression, 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 aggression 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. Aggression 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 stripedmice, 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 aggression, 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 flexibility (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 aggression 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 aggression 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.

5. ACKNOWLEDGEMENTS

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6. ETHICAL NOTE

Fieldwork for this study was carried out under the necessary licenses and was in accordance with the relevant animal welfare regulations. We received ethical clearance from the Animal Ethics Committee and the University of the Witwatersrand (AESC: 2007/38/04).

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CHAPTER 3

Personality traits are consistent when measured in the field and in the laboratory in African striped mice (*Rhabdomys pumilio*)

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Chapter 3 – Consistency in Personality traits between the laboratory and nature

Abstract

Personality in free-living individuals has predominantly been measured under standardised laboratory conditions. Such measurements have been then linked to life-history traits, fitness and survival. Yet, it remains unclear how such personality measurements reflect the variation shown by free-living individuals, if the same measurements were taken directly in their natural environment. Here, we used free-living African striped mice to test whether the personality traits of activity, boldness, exploration and aggression are consistent when measured in the laboratory and in the field contexts. First, we established whether personality traits were repeatable and consistent within one context. Next, we compared measurements across the two different contexts. Additionally, we established whether personality traits were correlated with one another in behavioural syndromes and assessed whether the resulting syndromes were consistent across the two contexts. All personality traits in the laboratory were measured using classical personality tests. The same tests were then modified and used to measure personality of the same individuals in the field. All personality traits were highly repeatable and consistent within the same context. In addition, individuals behaved consistently for all the behaviours measured both in the laboratory and in the field. Further, we found that the presence of two correlated context-specific separate latent variables (one for the field and one for the laboratory) underpinned all the behaviours measured, indicating that there is a context-specific syndrome in this species. Overall, our results confirm that measurements of personality traits of wild striped mouse individuals recorded in the laboratory environment are consistent with the traits that the same individuals show under natural conditions.

Key-words

Context-dependent behavioural syndrome, Dyadic encounter, Novel object, Open field, *Rhabdomys pumilio*

Chapter 3 – Consistency in Personality traits between the laboratory and nature

1. INTRODUCTION

Understanding how and why individual variation in behaviour is maintained in a population is an important area of research in animal behaviour. Variation among individuals that is consistent over time and across contexts is defined as personality (Sih et al. 2004; Bell 2007). Personality studies have described the predictable manner in which individuals maintain consistent differences in the face of environmental challenges (van Overveld and Matthysen 2013). Such research has often involved capturing free-living individuals and measuring their behaviour under standardised conditions in the laboratory, and then relating personality measurements to varying life-history and fitness parameters (Dingemanse et al. 2004; Bell 2005). These studies have been extremely valuable for demonstrating that individual variation in one behaviour is often linked with variation in other behaviours, creating behavioural syndromes (Sih et al. 2004), which are ecologically relevant, such as dispersal (Cote et al. 2010), foraging (Quinn et al. 2012), predator-avoidance (Jones et al. 2009) and space-use (Kurvers et al. 2010). While testing individuals under standardised conditions eliminates several extrinsic influences on the data (Campbell et al. 2009), it is unclear whether the personality of free-living individuals measured in a laboratory environment is truly representative of the behaviour that the same individuals would show if the measurements were taken directly in their natural environment (Herborn et al. 2010; Niemela and Dingemanse 2014).

Behaviour measured under laboratory conditions can be adversely affected by stress brought about by the artificial environment, which may result in a modification to their gene expression and behaviour (individual × environment and genes × environment; Hodgins-Davis and Townsend 2009; Niemela and Dingemanse 2014). Biro (2012) demonstrated that initial tests in a novel laboratory setting did not relate to later tests within the same settings, and that individuals tested in a familiar environment display different behaviour when tested in a novel but also artificial environment, leading him to question whether personality measured from a single assay under artificial conditions can be reliably used to infer personality in nature. Similarly, Carter et al. (2012) showed that multiple assays meant to measure a single trait may not always relate to each other.

Consequently, laboratory tests may produce behavioural differences between behavioural types that are not present in nature and vice versa (Herborn et al. 2010), especially in studies where wild individuals are particularly sensitive to being handled and housed in captivity. Studies of great tits (*Parus major*) performed in the laboratory have, for example, found an overall negative correlation between dominance rank and exploratory tendency (Verbeek et al. 1999), but when the relationship between dominance and exploration was investigated in the wild, it was only negative in non-territorial juvenile males (Dingemanse and De Goede 2004). Psychologists have shown that humans show low consistency in their behavioural traits when these are measured in different contexts. For example, an early study found that honesty of school children was not consistent across different situations (e.g. at home or at school; Hartshorne and May 1928). In another study of 300 college students, there was no consistency for the personality trait punctuality across different situations (Dudycha 1936). These studies show that measuring personality in the laboratory only may be misleading and limit the ability to predict the ecological significance of personality traits in captivity (Herborn et al. 2010). It would therefore be timely and necessary to test whether wild behavioural types can extend to the laboratory, particularly in the light of how environmental sensitivity can affect gene expression and behaviour (Niemela and Dingemanse 2014).

While the importance of measuring personality of individuals directly in their natural environment is widely recognized (Bell 2012; Niemela and Dingemanse 2014), this often remains difficult to achieve practically because obtaining reliable measures necessitates individuals being captured and handled multiple times. To date, a few studies have successfully compared results obtained from individuals tested in their natural environment with results obtained from the same individuals under captive conditions (Coleman and Wilson 1998; Brown et al. 2005; Wilson and McLaughlin 2007; Briffa et al. 2008; Hollander et al. 2008; Herborn et al. 2010; Cole and Quinn 2014). While these studies underline the importance of comparing laboratory with field tests, their strength is often constrained by a lack of validation or biased by the use of different types of tests in the field and in captivity to measure the same trait. For example, Herborn et al. (2010) investigated personality in free-living blue tits (*Cyanistes caeruleus*) by cleverly adapting the exploration test of Verbeek et al. (1994) and the novel object test of Greenberg (1984) developed in the laboratory to measure individual variation in exploratory tendency and neophobia in nature. Their results

showed that personality measures obtained in captivity can uncover differences among individuals in their natural behaviour and demonstrated that the personality of individuals can be consistent over different contexts even in nature (Herborn et al. 2010). While their results provide important validation for captive versus free-living personality measures, each bird was tested in a non-random way (first in captivity and then in nature) which could have affected the findings. Further, there seems to be a general discrepancy and a lack of consistency between findings from the laboratory and the field by different authors. For example, Herborn et al. (2010) found positive relationships for two behaviours they measured, and Boon et al. (2008) have also confirmed that assays in the laboratory relate to similar behaviours in the field. However, recent work by Fisher et al. (2015) found relationships for activity and exploration, but not for boldness in field crickets. Similarly, Boyer et al. (2010) and van Overveld and Matthysen (2010) found relationships between different behaviours between the laboratory and the field. Thus, it still remains unclear whether individual-level correlations measured in captivity remain consistent when measured in nature across a range of taxa.

In the present study, we investigated whether personality and behavioural syndromes observed in African striped mice (*Rhabdomys pumilio*) in the field also occurred in the laboratory. Striped mice are socially flexible, with individuals of both sexes following alternative reproductive tactics (Schradin et al. 2012). In a previous study, we showed that wild-caught African striped mice show consistency in personality traits when measured under standardised conditions in a field laboratory (Yuen et al. 2015), using a battery of classical personality tests (i.e. open field, novel object and novel conspecific tests; Verbeek et al. 1996; van Oers et al. 2004; Réale et al. 2007). However, we do not know whether striped mice show consistency in personality traits under natural conditions, and whether this is correlated to personality traits measured under standardised laboratory conditions.

Here, we examined whether the personality traits of activity, boldness, exploration and aggression were consistent across the laboratory-field context. To ensure that we measured the same behaviour in both the laboratory and the field, we used classical personality tests previously employed to study personality in striped mice in the laboratory (Yuen et al. 2015) and adapted them to the field. First, we tested whether personality was present within

contexts, i.e. in the laboratory and in the field (within context comparisons) by repeatedly measuring individuals within the same context. Second, we correlated personality measures from the laboratory with the same measures from the same individuals tested in the field (across context comparisons). Finally, we tested whether the different personality traits were correlated with each other in behavioural syndromes and whether the laboratory and the field setting resulted in similar behavioural syndromes. To do so, we follow procedures outlined in Araya-Ajoy and Dingemanse (2014) and tested four a priori hypotheses: (a) was each behavioural type underpinned by a separate factor (the null model; Fig. 1a); (b) was a single latent variable affecting all behaviours in both the field and the laboratory environment (Fig. 1b); (c) were two context-specific separate latent variables underpinning all the behaviours (Fig. 1c); and (d) were two correlated context-specific separate latent variables underpinning all the behaviours (Fig. 1d)?

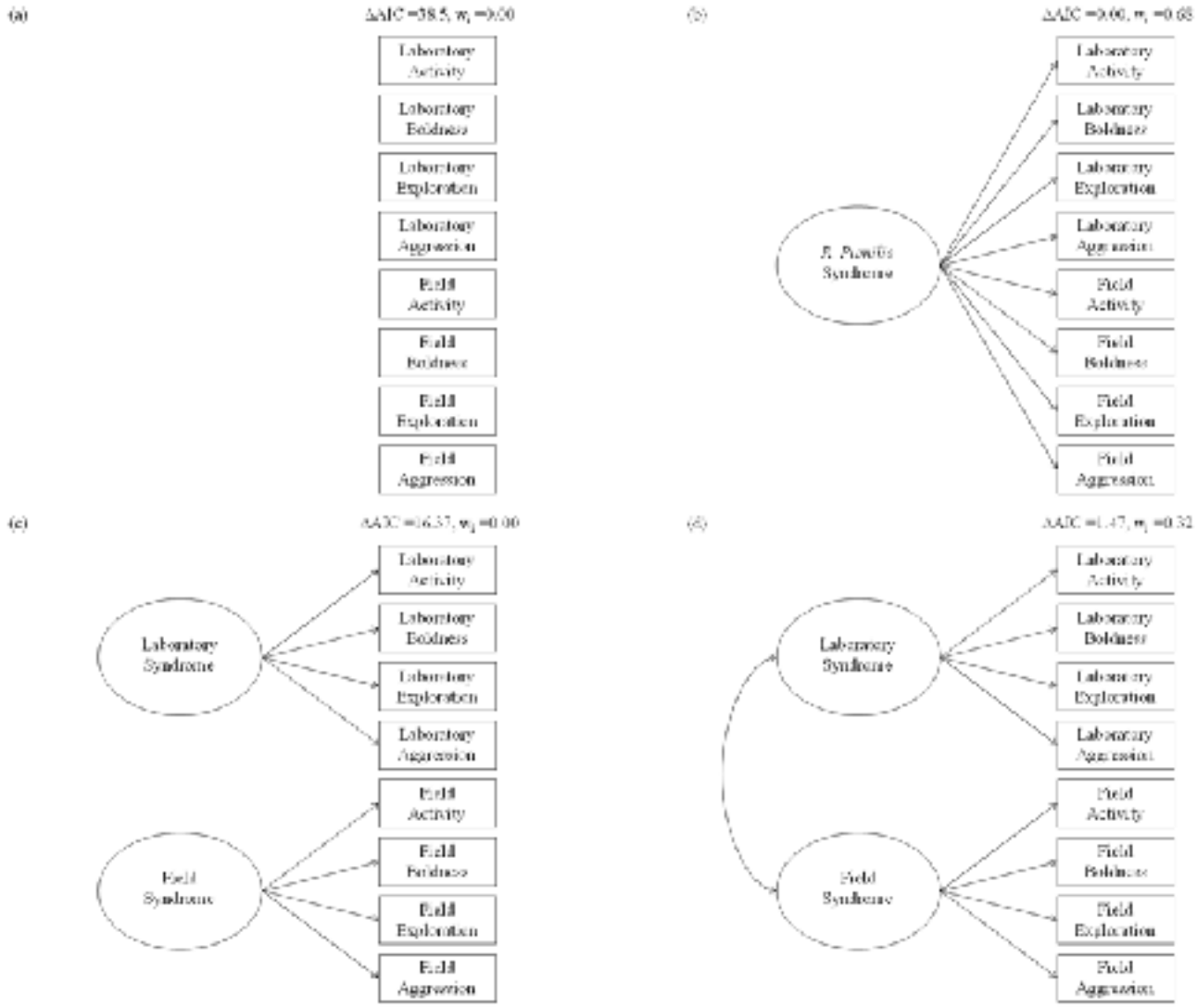


Figure 1

Four models (hypotheses) explaining syndrome structure among the different behavioural types (activity, boldness, exploration and aggression) assayed in free-living striped mice in the laboratory and in the field. Model (a) predicted that each behavioural type was underpinned by a separate factor (the null model). Model (b) predicted that a single latent variable (referred to as *BR. pumilio syndrome*) affected all behavioural types.Model (c) predicted that two context-specific separate latent variables underpinned all the behavioural types.Model (d) predicted that two correlated context-specific separate latent variables underpinned all the behaviours types. For each model, we provide the ΔAIC as well as its associated Akaike weight (wi).

2. MATERIAL AND METHODS

(a) Study area and field techniques

Data were collected in the non-breeding seasons (December–April) between 2008 and 2012 on a field site located in the Goegap Nature Reserve, in the Succulent Karoo biome, South Africa (29.6830° S, 17.9640° E). In the semi-arid Succulent Karoo, striped mice are typically group-living, with each group consisting of one breeding male, two to four breeding females and their philopatric offspring (Schradin and Pillay 2004). However, if population density is low during the breeding season, philopatrics leave their natal group and start to breed solitarily (Schradin et al. 2010; Schoepf and Schradin 2012a). Trapping, behavioural observations and radio-tracking were used to identify striped mice within the study site and to determine social tactics and group composition (Schradin and Pillay 2004, 2005; Schradin et al. 2010).

Striped mice were trapped with Sherman-like metal traps (26×9×9 cm) baited with a mixture of bran flakes, currants, sea salt, and salad oil (Schradin 2005). Traps were set directly at striped mouse nests in the early morning and were checked 45min later (Schradin 2005). Each trapped mouse was weighed, sexed and received a permanent ear-tag (National Band and Tag Co., Newport, KY, U.S.A.). Additionally, individuals were marked with a non-toxic hair dye (Inecto Rapido, Pinetown, South Africa), which aided with individual recognition during behavioural observations and field personality tests. Striped mice at our field site are habituated to our presence and readily enter traps once they are set. This allowed us to easily capture individuals that were observed during field tests for testing in the laboratory.

Trapping and behavioural tests did not have any adverse effects on individuals' behaviour (Yuen et al. 2015). Behavioural observations were made at each group nest in the morning and evening to determine individual affiliation to specific groups. In addition, at least one breeding female from each group was fitted with a radio-collar (Holohil, Carp, Ontario, Canada; 2.5–4.4g) and was radio-tracked to determine the nesting site location of the group (Schradin and Pillay 2005). Radio-tracking was carried out using an AOR8000 wide range receiver (Tokyo, Japan), an H-antenna (AfricaWildlife Tracking, Pretoria, South Africa) and a

global positioning system (GPS) navigation device (eTrex Venture, GARMIN International, USA) with an accuracy of ±5 m. All striped mice fitted with a transmitter were radio-tracked twice a day to determine ranging areas and sleeping sites.

(b) Personality tests under standardised laboratory conditions

Test subjects were all adult. Captive and field tests were randomised so that half of the individuals were first tested in the laboratory while the other half were first tested in the field. All laboratory tests were performed within 2 weeks of the tests in the field and vice versa so that all individuals were measured under the same conditions (e.g. age, reproductive status, season). Multiple-samples per individuals were obtained by selecting specific individuals so that each individual was tested within a week of one another. Striped mice are diurnal, with peak activity in the early morning and evening (Schradin and Pillay 2004). Therefore, all individuals were tested in the early morning. Mice were trapped directly at their nests as they emerged to bask and were taken to the research station, where they were transferred to a type III Perspex cage (38 × 22 × 15 cm). Each cage was provided with bedding (sand) and food (10 sunflower seeds) to account for hunger during tests. Mice were left to settle for a period of 10 min in the test room before being transferred individually to a neutral presentation arena made of wood chip (80×65 cm and 94 cm high, with a partition in the middle), similar to the one used in previous personality studies in striped mice (Schoepf and Schradin 2012b; Yuen et al. 2015). The presentation arena was cleaned with a mixture of odourless disinfectant (Dis-Chem Pharmacies, Northriding, South Africa) and water after each mouse had been tested. For all tests in the laboratory, we followed the same procedure that we validated previously (Yuen et al. 2015). Specifically, each focal mouse was sequentially tested for (a) activity and boldness, (b) exploration, and (c) aggression.

Activity was measured using an open field test (Wilson et al. 1976; Réale et al. 2007). During this test, a focal individual was placed in a corner of the arena for a period of 5 min. Activity was recorded every 15 s using instantaneous focal sampling (Martin and Bateson 1993) as the number of times an individual spent being active. In the same open field test, boldness was recorded using continuous focal sampling (Martin and Bateson 1993) as the total time (in

seconds) an individual spent at least half-a-mouse length away from the wall of the arena (estimated by sight).

Exploration was tested using a novel object test (Birke and Archer 1983; Greenberg 1984; Verbeek et al. 1994) which lasted for 5 min. A fixed object, consisting of a small plastic animal toy (115×20×44mm),which was secured to the floor of the arena and could not be moved by the test subject, was set at the far side of the arena, in the opposite corner to where the focal individual was located. Exploration was measured as the latency (in seconds) it took the focal mouse to physically come into contact with the fixed object.

Aggression was tested in dyadic encounters with a novel conspecific test (Verbeek et al. 1994; Benus and Rondigs 1996), during which we tested the focal mouse against a stimulus individual of the same sex (the stimulus) from our captive colony, which was permanently maintained at the research station. Stimulus individuals were always at least 3 g (but never more than 7 g) lighter than the focal animal. Because body mass has a positive influence on the outcome of aggressive encounters (Schradin 2004), we expected the focal mouse to initiate interactions. Aggression tests were performed using standard procedures previously used for striped mice (Schoepf and Schradin 2012b). Aggression was measured as the total number of aggressive encounters initiated by the focal individual during a period of 5 min. In addition to aggression, we also recorded sniffing the stimulus mouse, body contact between the dyad, allo-grooming and activity, but these behaviours occurred too infrequently for statistical analysis and were not considered any further.

To minimise the effect that the captive environment could have on personality, we kept mice in the laboratory for a maximum of 2 h before release (Yuen et al. 2015). A maximum of three individuals were tested in a day. Once tests ended, all mice were returned in good condition to the field and released in the same place where they were captured. To minimise observer bias, a blind protocol was adopted when all behavioural data were recorded and/or analysed. A total of 41 individuals were measured for activity and boldness, 48 for exploration and 20 for aggression in the laboratory.

(c) Personality tests in the field

To assess activity in the field, we used a modified version of the "whole-day follow" (Schradin 2006). All focal mice were fitted with radio-collars and followed for a period of 3 h during their peak activity times in the early morning and for another 3 h in the early evening (6 h total observation time per mouse). Activity was recorded as the frequency of all the "active" behaviours displayed by the focal individual (e.g. travelling, foraging, self-grooming). We recorded whether the mouse had been active or inactive in the past minute, and then calculated the percentage of the 180 recordings from the 6-h observation that the individual had been active. From the same observations, boldness was recorded as the time an individual spent in the open at least one mouse length away from the nearest shrub.

To assess exploration, we presented a novel object in front of individual nests (Fig. 2).



Figure 2

African striped mouse during an exploration test in the field, showing a striped mouse mounting a novel plastic toy (photograph by CHY).

The novel object was a plastic animal toy (115×20×44mm), which was fixed to the ground and was the same as the one used in the neutral presentation arena tests in captivity. To be consistent with data collected under captive conditions, the novel object was placed at a distance of 70 cm away from the entrance of the nest. Exploration was recorded as the latency (in seconds) it took focal individuals to approach the novel object. Recording started as soon as an individual was seen outside of its nest. The novel object was cleaned between tests. As exploration in both the laboratory and the field was measured during a 5-min trial, the maximum value for exploration was always 300 s. Measures of exploration obtained in this way indicated that individuals with high values were the least explorative. To facilitate interpretation of the results, we subtracted all exploration data from a value of 300 so that individuals with the highest score were the most explorative.

To assess aggression, we placed a food-scented box (the same as the one used for boldness tests) at the boundaries between two different group territories. Individual striped mice from two different groups were attracted by the scent from the box at the territory boundary. Aggression was measured as the total number of aggressive encounters between individuals belonging to different groups and the same aggressive behaviour patterns as in the laboratory were recorded.

To correct for difference in test length between the field and the laboratory and thus enable comparisons of data between the two contexts, all data were converted into behaviour/minute prior to analysis. The same individuals were scored in both captive and field studies (i.e. a total of 41 individuals were measured for activity and boldness, 48 for exploration and 20 for aggression in the field). As such, each individual was assayed four times: twice in the laboratory and twice in the field. Among all individuals sampled, 18 individuals were measured in all tests and were used to determine the existence of potential behavioural syndromes among the different personality traits. Two individuals that were measured for aggression were not sampled for measurements of activity and boldness in the field and were thus excluded from the behavioural syndrome analysis.

(d) Data analysis

Data analysis was performed using R version 3.0.2 (The R Foundation for Statistical Computing, Vienna, Austria). We checked for the normal distribution of the data using the Shapiro-Wilk test. To reach normality, activity, boldness and exploration were log-transformed whereas aggression was square-rooted. We used random intercept models to evaluate the degree of among-individual variation. Random intercept models were fitted using linear mixed effects models (LMMs, *lmer*; Package *lme4*; Bates et al. 2014). Each LMM was a univariate model consisting of one of the behavioural traits (activity, boldness, exploration or aggression) as the response variable, while testing sequence (first, second) was the fixed factor. Individual ID was entered as a random factor in each model. Univariate models were calculated separately for each behaviour within each context. To check whether the degree of among-individual variance was significant at the 95% level, we compared models that included the random effect of individual ID with simpler models without it, while maintaining the same fixed factors structure using likelihood ratio tests (Crawley 2007; Zuur et al. 2009). We used the package *RLRsim* (Scheipl 2010) using the exactLRT function to calculate accurate P values when comparing models with a single random effect to models with no random effect (P values were based on 10 000 simulated values; Crainiceanu and Ruppert 2004). For all our models, we report the R^2 (adjusted), as calculated following Nakagawa and Schielzeth (2013). We verified our model selection 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) leverage (Crawley 2007). 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 for each behaviour in each context (laboratory, field) separately (Nakagawa and Schielzeth 2010). Repeatabilities (adjusted) were calculated for each model as the between-individual variance divided by the sum of the between-individual and the residual variance (Nakagawa and Schielzeth 2010).

Additional linear models were used to assess whether personality measured under standardised conditions in the laboratory were good predictors of personality measured in the field. Each of these models were constructed following Herborn et al. (2010) and Fisher et al. (2015) and had one of the behavioural scores measured in the nature (e.g. activity in the field) as the response variable, and the corresponding measured score for that individual's

behaviour in the arena (e.g. activity in the laboratory) as the fixed factor. Individual ID was included in each model as the random factor to control for possible bias arising when repeated measures were taken from the same individual.

We used structural equation models (SEM; Package *lavaan*; Rosseel 2012) to investigate whether the different personality traits resulted in behavioural syndromes (Dochtermann and Jenkins 2007). To do so, we followed procedures outlined in Araya-Ajoy and Dingemanse (2014) and tested the four above-mentioned a priori hypotheses. Support for each model was determined by calculating Akaike information criteria (AIC). We selected the model that best fitted our data by selecting the model that yielded the lowest AIC (Dochtermann and Jenkins 2007). Repeated measures taken from individuals within each context were averaged prior to all SEM analysis. Pair-wise Spearman rank correlations (rs) were additionally calculated between the different behavioural characteristics to further elucidate syndrome structure. Because we conducted multiple comparisons, all the P values were adjusted using the Benjamini-Hochberg method (Benjamini and Hochberg 1995). All tests were two-tailed. For all tests, a significance level (α) of 0.05 was selected. Data are presented as mean and confidence intervals. Data were z transformed prior to analysis.

3. RESULTS

(a) Consistency and repeatability of personality traits in the laboratory

Including the random effect of mouse ID in our LMMs improved model fit for activity (ExactLRT: L.Ratio = 60.13, P < 0.0001; R^2adj. = 0.88; Tables 1 and 2), boldness (ExactLRT: L.Ratio = 30.81, P < 0.0001; R^2adj. = 0.73; Tables 1 and 2), exploration (ExactLRT: L.Ratio = 17.15, P < 0.0001; R^2adj. = 0.56; Tables 1 and 2) and aggression (ExactLRT: L.Ratio = 7.01, P = 0.006; R^2adj.= 0.54; Tables 1 and 2), suggesting that there was an inter-individual difference in the level of activity, boldness, exploration and aggression within the laboratory environment. Individuals displayed significant repeatability in all four behaviours when they were measured in the arena (activity: P < 0.0001; boldness: P < 0.0001; exploration: P = 0.0005; aggression: P = 0.03; Fig. 3).

Table 1

Mean and confidence interval for activity, boldness, exploration and aggression observed in each of the two contexts (laboratory, field) in free-living striped mice in the Succulent Karoo (South Africa).

Behavioural Trait	Laboratory		Field	
	First	Second	First	Second
Activity	2.29 (1.88, 2.71)	2.52 (2.16, 2.89)	0.40 (0.32, 0.47)	0.48 (0.40, 0.59)
Boldness	4.49 (3.13, 5.85)	5.60 (3.96, 7.23)	0.18 (0.12, 0.23)	0.15 (0.11, 0.19)
Exploration	14.69 (8.22, 21.15)	21.60 (14.81, 28.39)	17.99 (10.77, 25.22)	19.04 (11.96, 26.11)
Aggression	0.54 (0.25, 0.83)	0.64 (0.20, 1.08)	0.05 (0.02, 0.07)	0.03 (0.01, 0.05)

Table 2

Summary of the results obtained from univariate mixed-effect models on each behavioural type within each context.

		Activity	Boldness	Exploration	Aggression
	Fixed effects				
	Intercept	1.61 (1.55, 1.67)	0.54 (0.40, 0.68)	-0.76 (-1.07, -0.46)	0.91 (0.71, 1.10)
Laboratory	Test	-0.03 (-0.06, 0.00)	0.10 (0.00, 0.20)	0.37 (0.08, 0.67)	-0.01 (-0.20, 0.18)

	Random effects				
	Mouse ID	0.18 (0.15,0.23)	0.38 (0.29, 0.49)	0.81 (0.57, 1.06)	0.33 (0.17, 0.50)
	Residual	0.07 (0.06,0.09)	0.23 (0.19, 0.29)	0.73 (0.60, 0.90)	0.30 (0.22, 0.41)
Field	**Fixed effects**				
	Intercept	0.49 (0.31,0.67)	0.24 (0.06, 0.43)	0.47 (0.44, 0.52)	0.93 (0.72, 1.13)
	Test	0.11 (-0.04,0.26)	-0.03 (-0.23, 0.16)	-0.01 (-0.05, 0.11)	-0.07 (-0.23, 0.08)
	Random effects				
	Mouse ID	0.47 (0.35,0.62)	0.40 (0.24, 0.56)	0.42 (0.33, 0.52)	0.40 (0.26, 0.57)
	Residual	0.34 (0.28,0.43)	0.44 (0.36, 0.55)	0.20 (0.16, 0.25)	0.24 (0.18, 0.34)

Estimates were derived separately for each behaviour. Each model included mouse ID as the random factor, while test (first or second) was the fixed effect. For each model, we report point estimates for the fixed (mean) and the random parameters (variance) along with their 95%confidence intervals.

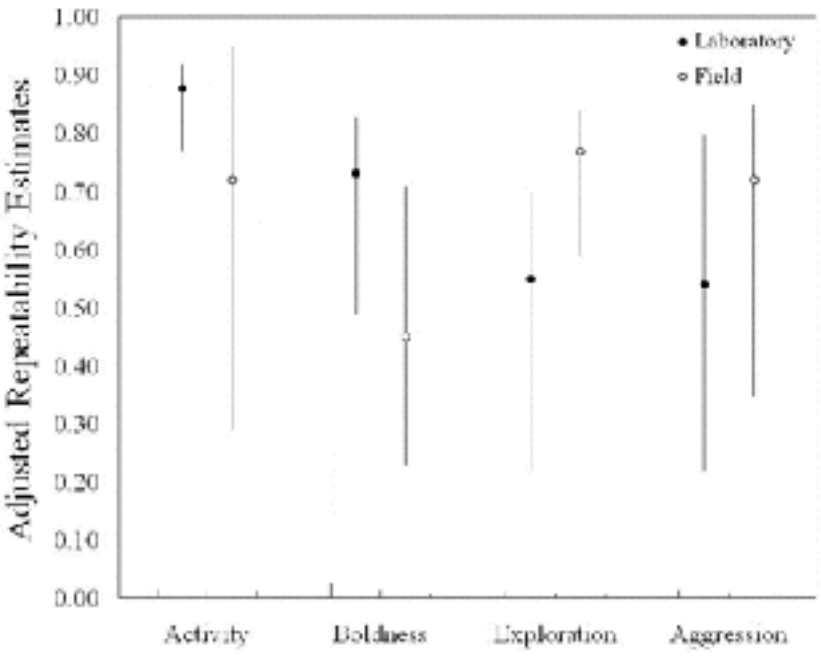


Figure 3

Estimates of the repeatability measures obtained when running repeated tests within the laboratory and the field context. Black circles represent adjusted repeatability measures from the arena. White circles represent adjusted repeatability measures from the field. Adjusted repeatability measures are reported together with their 95 % confidence intervals.

(b) Consistency and repeatability of personality traits in the field

We found that the random effect of mouse ID in our LMMs was significant for activity (ExactLRT: L.Ratio = 22.76, P < 0.0001; R^2adj. = 0.66; Tables 1 and 2), boldness (ExactLRT: L.Ratio = 9.35, P=0.002; R^2adj.= 0.45; Tables 1 and 2), exploration (ExactLRT: L.Ratio = 49.20, P < 0.0001; R^2adj.= 0.77; Tables 1 and 2) and aggression (ExactLRT: L.Ratio =14.60, P = 0.0001; R^2adj.= 0.72; Tables 1 and 2), suggesting that there was an inter-individual difference in the level of activity, boldness, exploration and aggression within the field environment. Individuals displayed significant repeatability in all four behaviours when they were measured in the field (activity: P = 0.004; boldness: P = 0.01; exploration: P < 0.0001; aggression P = 0.04; Fig. 3).

(c) Comparisons of personality traits between the laboratory and the field

Personality measured in captivity was a good predictor for personality measured in the field for all the behavioural characteristics measured. Specifically, models, which included the fixed effect of captivity better explained our data than models without them (activity: $\chi2$ = 9.64, P = 0.002; R^2adj.= 0.65; boldness: $\chi2$ = 6.21, P = 0.01; R^2adj. = 0.45; exploration: $\chi2$ = 25.99, P < 0.0001; R^2adj.= 0.81; aggression: $\chi2$ = 24.17, P < 0.0001; R^2adj.= 0.72; Table 3).

Table 3

Summary of the results obtained from univariate mixed-effect models to test whether personality measured under standardised conditions in the laboratory were good predictors of personality measured in the field.

	Activity	Boldness	Exploration	Aggression
Fixed effects				
Intercept	2.34 (1.18, 3.53)	0.03 (-0.21, 0.27)	0.69 (0.57, 0.81)	1.10 (0.97, 1.24)
Test	0.08 (-0.07, 0.22)	-0.07 (-0.27, 0.12)	-0.03 (-0.11, 0.04)	-0.09 (-0.27, 0.08)
Laboratory Score	-1.15 (-1.88, -0.44)	0.40 (0.09, 0.70)	0.17 (0.10, 0.23)	0.36 (0.29, 0.49)
Random effects				
Mouse ID	0.45 (0.33, 0.59)	0.36 (0.17, 0.50)	0.35 (0.27, 0.44)	0.05 (0.00, 0.24)
Residual	0.32 (0.26, 0.40)	0.44 (0.36, 0.55)	0.18 (0.15, 0.22)	0.28 (0.20, 0.35)

Each of these models had one of the behavioural scores measured in the wild (e.g. activity) as the response variable and the corresponding measured score for that individual's behaviour in the arena (e.g. activity in the laboratory) as the fixed factor. Individual ID was entered as the random factor in each model. For each model, we report point estimates for the fixed (mean) and the random parameters (variance) along with their 95%confidence intervals.

(d) Behavioural syndromes in the laboratory and in the field

The comparison of our four a priori hypotheses using structural equation modelling (SEM) resulted in two models with similar AICs, which could have potentially explained our data: model 2 (AIC=393.93) and model 4 (AIC=395.39). However, the cross-context correlation

between the latent variables of field and laboratory was rather strong ($z = 5.16$, $P < 0.0001$), suggesting that model 4 was a better fit for our data (Fig. 1). This model predicted that two correlated context-specific separate latent variables underpinned all the behaviours (Fig. 4).

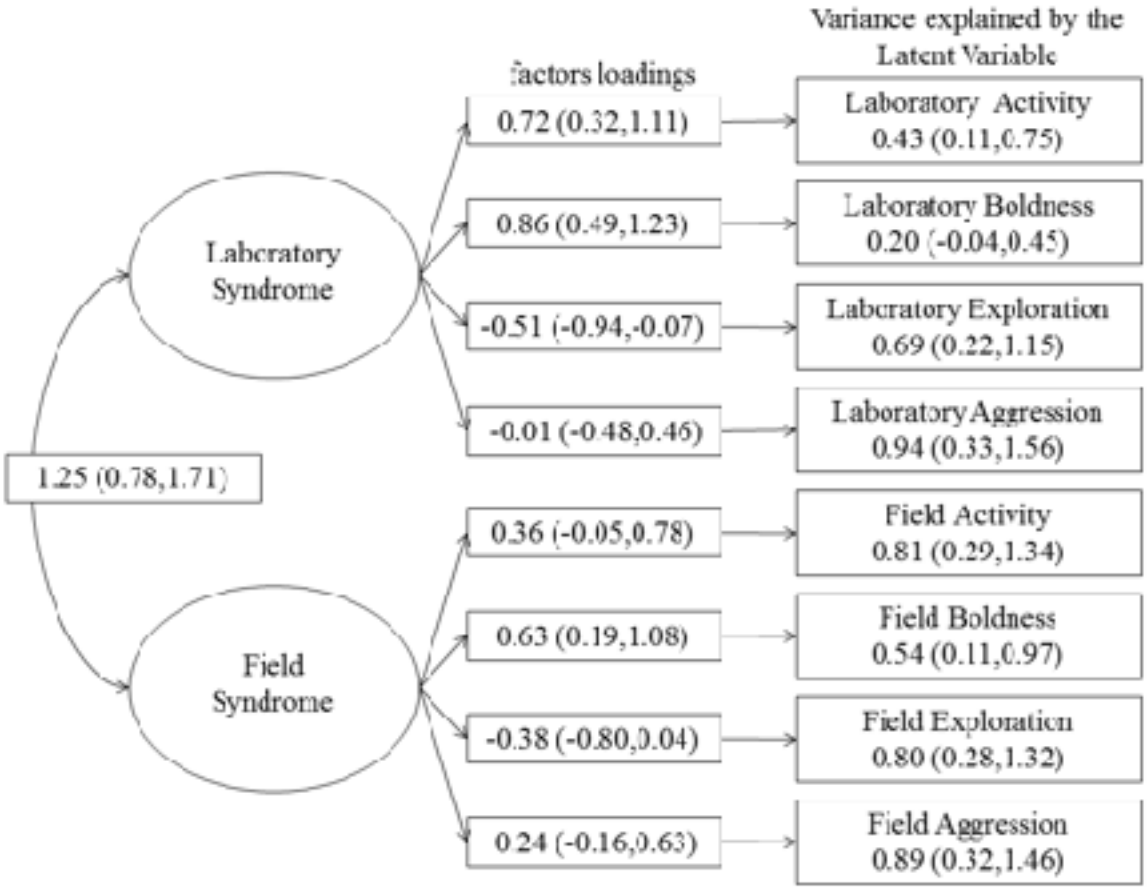


Figure 4

Parameter estimates of the structural equation model that best fitted our data and thus considered to be representative of the behavioural syndrome structure for *R. pumilio*. Factors loadings together with their 95 % confidence intervals as well as variance estimates explained by the latent variables are reported.

Pair-wise correlations of the different personality traits showed the existence of a negative behavioural syndrome between boldness and exploration in both the laboratory and in the field (Table 4), indicating that the boldest individuals took the least amount of time to approach the novel object in both environments. Two further behavioural syndromes were found in the laboratory: a behavioural syndrome between (1) activity and boldness, indicating that the most active individuals were also the boldest, and (2) activity and exploration, indicating that the most active individuals took the least amount of time to approach the novel object (Table 4). No evidence of behavioural syndromes was found when any of the other personality traits were correlated using either field or laboratory data (Table 4).

Table 4

Correlations between different personality traits of striped mice tested in a neutral arena in captivity and in the field, indicating behavioural syndromes. Only individuals that were tested twice in the arena and twice in the field were included in the analysis. Numbers in italics indicate significant differences

	Laboratory			Field		
Behavioural Syndrome	**n**	**rho**	**P**	**n**	**rho**	**P**
Activity-Boldness	18	0.62	0.01	18	0.23	0.36
Activity-Exploration	18	-0.78	0.0001	18	-0.07	0.76
Activity-Aggression	18	0.14	0.58	18	-0.19	0.44
Boldness-Exploration	18	-0.65	0.004	18	-0.55	0.02
Boldness-Aggression	18	-0.04	0.87	18	-0.18	0.46
Exploration-Aggression	18	0.21	0.41	18	-0.09	0.73

Chapter 3 – Consistency in Personality traits between the laboratory and nature

4. DISCUSSION

We showed that personality traits of individual African striped mice tested under standardised conditions in the laboratory were consistent with measurements of personality traits from the same individuals in their natural habitat. We showed that all personality traits were consistent and repeatable both within and between the laboratory and the field, thereby demonstrating that personality measures collected under artificial laboratory conditions did reflect natural behavioural tendencies, regardless of the sequence of the testing. Moreover, we found that the presence of two correlated context-specific separate latent variables (one for the field and one for the laboratory) explained all the behaviours measured, indicating that there is a context-specific syndrome in this species.

Several studies have described personality variation in wild animals tested under standardised laboratory conditions (Bell and Sih 2007; Cote and Clobert 2007; Johnson and Sih 2007). Most recently, however, the urgency of establishing whether the behaviour observed in the laboratory are reliably representing the behaviour of individuals under natural conditions have been highlighted (Bell 2012), especially in the light of the fact that the environment in which an individual is tested may end up modifying its behaviour (Hodgins-Davis and Townsend 2009; Niemela and Dingemanse 2014). As a consequence, several authors have started to investigate whether wild behavioural types can also spill over to the laboratory, resulting in conflicting reports regarding the degree of consistency between the two contexts. For example, Boon et al. (2008) and Herborn et al. (2010) found consistency in all the behavioural traits measured between the laboratory and the wild, whereas Boyer et al. (2010), van Overveld and Matthysen (2010) and Fisher et al. (2015) only found consistency for some measures but not others. Our results support the former, as we found that in striped mice all the behaviours we measured (activity, boldness, exploration and aggression) were consistent across the field-laboratory context. From a methodological point of view, our results are important because they show that (1) the tests we employed to measure the different behaviour were representative of the target behaviour we measured in both contexts, and (2) classical personality tests, such as open field, novel object and dyadic encounters with a novel conspecific, typically used to measure individuals in a neutral presentation arena can be successfully transposed to the field, at least for striped mice.

Our results are also significant as they show that the laboratory environment in which striped mice were tested did not adversely affect them, as was expected in the literature (Hodgins-Davis and Townsend 2009; Niemela and Dingemanse 2014). This might have been the direct result of either our sampling protocol, which restricted the time each individual spent in the laboratory, or could have been due to the fact that striped mice at our field site are habituated to our presence because each individual is trapped and handled several times per month (Yuen et al. 2015). This is further supported by the fact that corticosterone levels, which are typically elevated in individuals experiencing a stressful event, remained similar before and after individuals were tested for personality in the laboratory (CHY, unpublished data).

We found repeatability to be higher in certain behaviours more than others. Activity and boldness were found to be highly repeatable in the laboratory, but less so in the field and the relationship of both behaviours between the field and the arena was the weakest. The lower repeatability observed for activity and boldness in the field compared to the laboratory suggests that these behaviours might be more easily affected by external stimuli, such as weather conditions or temperature or by the type of environment in which they are assayed (novel versus unfamiliar).Though significant, aggression was found to be the least repeatable trait within both the field and the laboratory, but the relationship between field and laboratory measures was among the strongest. Aggression, in contrast to activity and boldness, was always performed in a neutral setting whether it be in the wild (at the border between territories) or in the laboratory (in the neutral presentation arena), which could have accounted for the high strength in the relationship between aggression measured between the two contexts. However, aggression was also most likely affected by the type of stimulus presented, with individuals always being presented with different stimulus mice whether in the field or in the laboratory. Aggressive encounters may be affected by within contest decision-making and information gathering, and are also highly energetically demanding, resulting in post-contest changes in behaviour (Briffa et al. 2015). Further, as individuals will engage in more than one contest over their life, their behaviour will be affected both by the opponent's identity and behaviour (Briffa et al. 2015) as well as by their own previous experience and familiarity with that opponent. As all of these factors will bear on aggression by varying degrees, different individuals will elicit different aggressive responses, which might explain why repeatability for this behaviour was not as high as for the other

behaviours. In this respect, our results are consistent with other studies that have shown aggression to have a low repeatability overall (Briffa et al. 2015).

On the other hand, exploration was highly repeatable in both contexts and had the strongest relationship between the field and the laboratory; exploring a novel environment is particularly important for dispersing individuals (Schoepf and Schradin 2012b). Further, of all the behaviours measured, exploration was tested in the most similar way in both the field and the laboratory, further highlighting the need of carefully designing tests that are as similar as possible when doing across context comparisons.

Different personality traits are often correlated with each other, creating behavioural syndromes (Sih et al. 2004), which can be present both in the captive environment and in nature (Dochtermann and Jenkins 2007; Adriaenssens and Johnsson 2013).While some studies have shown that syndromes can be stable over time (Chapman et al. 2013) and across different ecological conditions (Mowles et al. 2012), some authors have found syndromes to differ among conditions, populations or over time (Bell and Stamps 2004; Dingemanse et al. 2007; Clobert et al. 2009). In our study, we found that two separate, but correlated; latent variables affected all the behaviours, pointing to the presence of a context-specific syndrome structure in this species, although the support for this model was rather weak. Closer inspection of the estimates obtained from the SEM model revealed that the two latent variables loaded most heavily on activity, boldness and exploration in the laboratory context and on boldness in the field context respectively. Further analysis using pair-wise correlations revealed that boldness-exploration behavioural syndrome was consistent in both contexts. Specifically, we found that the boldest individuals, which approached the novel object fastest in the arena, were also the boldest and approached the novel object fastest in the field, indicating that the boldest individuals were the most exploratory in both the laboratory and in the field.

Surprisingly, however, we found no consistency between the other behavioural syndromes in the two different contexts. This is intriguing because it would be expected that if all the personality traits measured in isolation are present between the captive and the natural environment, the correlations between such personality traits should also be present. Herborn et al. (2010) suggested that boldness and exploration might be perceived as two measures of a

single approach–avoidance trait, with risk-prone, fast-exploring individuals at the one extreme and risk-averse, slow-exploring individuals at the other, thus indicating that the open field test developed by Wilson et al. (1976) and the novel object test developed by Greenberg (1984) to be regarded as approach–avoidance in a novel and a familiar environment, respectively (Clark and Ehlinger 1987;Wilson et al. 1994; Johnson and Sih 2007).

Another equally plausible explanation for why we did not find a relationship between activity and boldness in the field is that in the laboratory activity assays were conducted within a very short time of each other. In contrast, activity and exploration in the field were tested separately with a greater time interval between them. This temporal separation might have weakened the correlation between activity and exploration in the field. Similarly, the lack of a boldness-activity correlation in the field might have been the result of a time discrepancy between the measures of boldness, because in the laboratory, boldness was measured during a period of 5 min whereas in the field it was measured during a period of 6 h. Another possibility could be that our results reflect the small sample number of individuals at our disposal. In a previous study, we showed that male and female striped mice differ in their personality traits (Yuen et al. 2015), with females being consistent for activity, boldness and exploration and males being consistent for exploration and aggression, even after adopting a new alternative reproductive tactic. In the present study, 18 individuals were available to test for behavioural syndromes, which included both males (nine) and females (nine). If the two sexes display different behavioural syndromes, the low number of samples might have constrained detecting sex differences. This could also explain why some of the behavioural syndromes did not match between the field and the arena.

Several studies have measured personality of wild-caught individuals in captivity and used these measures to explain individual differences in fitness observed in nature (e.g. Dingemanse et al.2004).Most recently, however, several authors have started to investigate whether wild behavioural types can also spill over to the laboratory because concerns have been raised regarding the effect of the environment on behaviour. This has resulted in a surge of studies testing for consistency across contexts, with different authors often reporting different levels of consistency between the field and the captive environment (Boon et al. 2008; Boyer et al. 2010; Herborn et al. 2010; van Overveld and Matthysen 2010; Cole and

Quinn 2014; Fisher et al. 2015). Ours is the first study that has measured four of the most common behaviours (activity, boldness, exploration and aggression) typically researched in personality by using similar protocols both in the laboratory and in the field. We showed that personality measures from standardised laboratory conditions can reflect field measurements, at least in striped mice. Furthermore, to our knowledge, ours is one of the few studies that have investigated whether behavioural syndromes measured in captivity can be related to behavioural syndromes measured in nature. Our methodological approach validates previous field studies and confirms that personality traits of free-living individuals measured under standardised laboratory conditions reflect the natural variation related to important life-history parameters, such as reproductive fitness and survival.

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6. ETHICAL NOTE

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Fieldwork for this study was carried out under the necessary licences and was in accordance with the relevant animal welfare regulations. Research permits were obtained from the Department of Tourism, Environment and Conservation of the Northern Cape. We received ethical clearance from the Animal Ethics Committee and the University of the Witwatersrand (AESC: 2007/38/04).

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CHAPTER 4

Boldness: Are open field and startle test measuring the same personality trait?

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Abstract

Boldness, the willingness of an individual to engage in risky behaviour, is one of the most studied personality traits. To date, boldness has been measured using a variety of tests. For instance, some studies have assessed boldness in a novel environment, while others have used risk-taking behaviour as a measure of boldness. Few studies have attempted to breach this gap by comparing the different boldness assays with mixed results. The limitations of these approaches mostly stems from a lack of repeatability or/and corroboration with measures of boldness obtained from the same individuals in their natural settings. Here, we tested free living African striped mice under standardised laboratory conditions and compared measures of boldness obtained from two assays: an open field test and a startle test. These measures were then compared to boldness measures obtained from equivalent open field and startle tests performed on the same individuals under natural conditions. During open field tests, we assessed the time (in seconds) an individual spent at least half-a-mouse length away from the wall of the arena (in the laboratory) or from its nest (in nature). During startle tests, we measured the latency to re-emerge from either a protective box (laboratory) or a nest (nature) after a predation simulation. Our results show that boldness using both the open field and the startle test were repeatable within the same context (tested twice per assay) and across-contexts (laboratory vs nature). However, measures obtained using open field tests were not correlated with measures from startle tests, supporting the idea that the two tests may not assess boldness. In our study species, the startle test was more likely measuring anxiety. Thus, while both might represent risk-taking behaviour, their measures are obtained by presenting individuals with different stimuli, and as such might not be measuring the same personality trait.

Key-words

Fear, ‘Jingle’ fallacy, Novelty, Learning, *Rhabdomys pumilio*, Shyness

1. INTRODUCTION

Why and how personality (i.e. consistent individual variation in behaviour over time and across context; Sih et al. 2004a; Bell 2007) is maintained in natural populations is one of the most discussed topics in the recent animal behaviour literature (Gosling and John 1999; Sih et al. 2004b; Dingemanse et al. 2009; Réale et al. 2010; Schuett et al. 2010; Stamps and Groothuis 2010). Réale et al. (2007) defined five 'main' axes of personality traits: (1) shyness-boldness; (2) exploration-avoidance; (3) activity, (4) aggressiveness; and (5) sociability. Of the five, the shyness-boldness axis has received significant attention, being the focus of a variety of vertebrate (Carere et al. 2005; López et al. 2005; Wilson and Stevens 2005) and invertebrate (Sinn et al. 2008; Gyuris et al. 2016) studies. The popularity of boldness as a topic of research can be traced back to its far-reaching implications, being associated with antipredator behaviour (Brown et al. 2005), mate choice (Godin and Dugatkin 1996), dispersal (Fraser et al. 2001), and survival (Réale et al. 2000). Furthermore, boldness has been correlated with fitness (Dall et al. 2004; Dingemanse et al. 2004; Bell 2007), is heritable (Drent et al. 2003; Brown et al. 2007), and is influenced by environmental variables during ontogeny (Brown et al. 2005; Chapman et al. 2010). Finally, extrinsic factors (e.g. environmental conditions, food availability and predation; Lopez et al. 2005; Nelson et al. 2008) and intrinsic factors (e.g. age, experience, hormone levels and sex; Boissy 1995; Sinn and Moltschaniwskyj 2005; Frost et al. 2007) affect boldness at the phenotypic level.

Boldness has been defined as the willingness of an individual to engage in risk-taking behaviour (Réale et al. 2007). The shyness-boldness axis represents a continuum (Cockrem 2007). Bold individuals typically show risk-prone behaviour, such as predator inspection (Huntingford et al. 1994); whereas shy individuals show risk-adverse behaviour, such as becoming more vigilant in the presence of a predator (Ward et al. 2004). Boldness has been measured using a variety of methods, e.g. open field, novel object, predator inspection and startle tests. As a consequence, there is much debate over which assay best represents boldness (Carter et al. 2012; Magnhagen et al. 2014). Réale et al. (2007) defined boldness as "an individual's reaction to any risky situation" (p 295) and were careful in stating that their definition of boldness deliberately avoided including any aspect of novelty, which they described as being a feature of the exploration-avoidance axis instead. Following this

definition, boldness would therefore optimally be assayed experimentally by measuring the reactions of individuals to a predatory event (Bell and Stamps 2004; Magnhagen and Borcherding 2008; Bell et al. 2010). However, other researchers have argued that boldness can be defined as the willingness of an individual to take risks in return for potentially higher foraging or reproductive gains (Ward et al. 2004). According to the latter definition, individuals could be categorised as "being bold" when they are willing to move beyond the safety of their refuge into unfamiliar surroundings (Wilson et al. 1993) or when inspecting a novel feature in their home environment (Wilson 1998). Interestingly, from a psychological perspective, in humans, the boldness-shyness axis has been typically characterised by an individual's initial reaction to unfamiliar events (Kagan et al. 1988), highlighting ''novelty'' as a key component for investigating boldness. Nonetheless, the two definitions of boldness are not mutually exclusive, and, consequently, the type of tests used to measure them may necessarily produce the same results (Burns 2008; Toms et al. 2010; Conrad et al. 2011).

Given the importance of boldness in personality research, it is surprising that only a handful of studies have addressed this issue, producing mixed results. Burns (2008) measured boldness using a novel object and two different kinds of novel environment tests (emergence and open-field) in guppies (*Poecilia reticulata*) in the laboratory and did not find significant correlations between these three measures, which led him to conclude that the emergence and novel-object test were not valid protocols for their species. Carter et al. (2012) measured boldness in free-living Chacma baboons (*Papio ursinus*) by presenting individuals either with a threatening stimulus or a novel object, and found that the two measures did not correlate significantly, suggesting that threat-directed behaviours describe anxiety rather than boldness. Furthermore, Andersson et al. (2014) used factor analysis to analyse boldness in domestic rabbits in the laboratory and found that of the four different tests they employed (novel object, novel environment, social, and predator interactions) the novel object and predator interaction test were not representative of boldness, but rather explained exploration and anxiety respectively. In another study, Magnhagen et al. (2014) used four different tests (emergence, open field, trappability and time spent remaining immobile after disturbance) to investigate boldness in two-spotted gobies (*Gobiusculus flavescens*) in the laboratory and found consistent ranking among the four different assays. While these studies are commendable in their approach, they lack validation, repeatability and corroboration with

boldness measures obtained from the same individuals, particularly in their natural settings. Thus, it still remains unclear whether boldness assayed experimentally by measuring predator related behaviours is comparable to boldness measured using a test that incorporates an aspect of novelty.

In the present study, we investigated whether boldness measured following one definition (risk-taking in novel environments) was comparable to boldness measured following another definition (risk-taking during a simulated predatory event) in African striped mice (*Rhabdomys pumilio*). To do so, we chose two assays that were behaviourally and ecologically relevant for our study species: the open field and the startle tests. The open field test is one of the most common assays used to measure boldness in unfamiliar environments (Brown and Braithwaite 2004; Dingemanse et al. 2004; Carere et al. 2005) and is considered by some authors to be the most reliable way to assay boldness (Burns 2008; Boulton et al. 2014). The startle test is reputed to provide an unambiguous measure of boldness in the predatory context (Wilson et al. 1993; Brown et al. 2005; Johnson and Sih 2007). In this test, risk-taking is typically measured as the latency it takes an individual to re-emerge from a shelter after a simulated predatory event. Because, as pointed out by Beckmann and Biro (2013) and Carter et al. (2013), one assay may not be sufficient to be able to interpret the test results as indicators of a specific personality, we first tested whether our boldness measures were repeatable within the same assay within the same context (e.g. boldness in the open field in the laboratory conducted twice). Second, we correlated boldness measures from the laboratory with the same measures from the same individuals tested in nature, thus assessing across context comparisons. These comparisons were important because they could provide support for the ecological relevance of the two assays to accurately reflect boldness in the wild (i.e. whether the willingness to venture in an exposed area in the arena was a good predictor of risk-taking behaviour as shown by individuals in nature when venturing out in the open). Finally, we compared whether measures of boldness obtained using one assay (e.g. open field) were comparable with measures of boldness obtained using a different assay (e.g. startle test) in the same individuals within and across contexts (laboratory and nature).

2. MATERIAL AND METHODS

(a) Study period and field techniques

Data were collected in 2012 on a field site located in the Goegap Nature Reserve, South Africa (29.6830° S, 17.9640° E). Striped mice were trapped with Sherman-like metal traps (26 x 9 x 9 cm) baited with a mixture of bran flakes, currants, sea salt, and salad oil. Traps were set directly at striped mouse nests and were checked 45 minutes later. Each trapped mouse was weighed, sexed and received a permanent ear-tag (National Band and Tag Co., Newport, KY, U.S.A.). Additionally, individuals were marked with a non-toxic hair dye (Inecto Rapido, Pinetown, South Africa), which aided with individual recognition during personality tests in nature. None of the individuals used in the personality tests were first-time captures. Striped mice at our field site are habituated to our presence and readily enter traps once they are set so that we did not experience a sampling bias for boldness (Yuen et al. 2015). This allowed us to easily capture individuals that were observed during tests in nature for testing in the laboratory. Trapping and behavioural tests did not have any adverse effects on the behaviour of individuals (Yuen et al. 2015).

(b) Measuring boldness using the open field test

Test subjects were all adult. Captive and field tests were randomised so that half of the individuals were first tested in the laboratory while the other half was first tested in nature. All laboratory tests were performed within two weeks of the tests in nature and vice versa so that all individuals were measured under the same conditions (e.g. age, reproductive status, season). Multiple-samples per individuals were obtained by selecting specific individuals so that each individual was tested within a week. Striped mice are diurnal, with peak activity in the early morning and evening (Schradin and Pillay 2004). Therefore, all individuals were tested in the early morning. Mice were trapped directly at their nests as they emerged to bask and were taken to the research station, where they were transferred into a type III Perspex cage (38 x 22 x 15cm). Each cage was provided with bedding (sand) and food (10 sun flower seeds) to account for hunger during tests. Mice were left to settle for a period of 10 minutes in the test room before being transferred individually to a neutral presentation arena made of wood chip (80 x 65 cm and 94 cm high, with a partition in the middle), similar to the one

used in previous personality studies in striped mice (Yuen et al. 2015; 2016). The presentation arena was cleaned with a mixture of odourless disinfectant (Dis-Chem Pharmacies, Northriding, South Africa) and water after each mouse had been tested.

In the laboratory, boldness measures in open field tests were obtained by placing a focal individual in a corner of the arena for a period of 5 minutes. Boldness was recorded using continuous focal sampling (Martin and Bateson 1993) as the total time (in seconds) an individual spent at least half-a-mouse length away from the wall of the arena (estimated by sight).

Open field measures of boldness in nature were obtained using a modified version of the "whole-day follow" (Schradin 2006). Each individual was fitted with a radio-collar (Holohil, Carp, Ontario, Canada; 2.5-4.4g) and was 'followed' for a period of three hours during their peak activity times in the early morning and for another 3 hours in the early evening (six hours total observation time per mouse). Boldness was recorded as the amount of time an individual spent in the open at least one mouse length away from the nearest shrub. Because assays were carried out within a short time span, we were able to always test individuals under the same conditions (i.e. individuals fitted with radio-tags before the start of the studies, carried collars throughout all their tests, and individuals without tags at the start of the study, did not wear collars during any of the assays).

To minimise the effect that the captive environment could have on personality, we kept mice in the laboratory for a maximum of two hours before release (Yuen et al. 2015; 2016). A maximum of three individuals were tested on a day. Once tests ended, all mice were returned in good condition to the field and released in the same place where they were captured. To minimise observer bias, a blind protocol was adopted for all behavioural data recorded and analysed. A total of 34 individuals (13 females and 21 males) were measured for boldness using an open field test in the laboratory and in nature.

(c) Measuring boldness using the startle test

In the laboratory, boldness measures using startle tests were obtained by recording the latency (in seconds) it took a focal individual to re-emerge from a shelter and approach a food-scented box after a predator-simulation event. The food-scented box consisted of a hollow yellow plastic container (115 x 80 x 40 mm) with holes (3 mm) drilled at random on all sides. Food (a mixture of peanut butter and bran flakes) was placed enclosed inside the box, so that focal individuals could smell the food but could not reach it. The shelter consisted of a black box (25 x 25 cm and 24 cm high), which provided the focal individual with a hiding place and served to mimic a nest in the field. The shelter was placed against the wall at one side of the arena, 70 cm away from the food-scented box. When an individual approached the food-scented box, we scared it away by dropping a plastic animal toy (115 x 20 x 44 mm), which was kept suspended 150 cm above the test mouse out of sight and served to mimic a predator attack.

Startle measures of boldness in nature were obtained by placing a food-scented box (the same as the one used for startle tests in the laboratory) and recording the latency (in seconds) it took a focal individual to re-emerge from its nest and approach the food-scented box after a predator-simulation event. The food-scented box was placed 70 cm away from the focal individual's nest (the same distance as the startle test in the laboratory). When an individual approached the food-scented box, we scared it away by steering a remote-controlled car towards the focal individual. The remote-controlled car was kept out of sight 150 cm away from the nest.

The same 34 individuals measured for the open field test were tested in both captivity and nature for the startle test. Each individual was assayed a total of eight times: twice in the laboratory in open field tests; twice in the laboratory in startle tests; twice in nature in open field tests; and twice in nature in startle tests. To correct for differences in length of tests between natural and laboratory tests and thus enable comparisons of data between the two contexts, all data were converted into behaviour/minute prior to analysis. Test subjects were all adult. Captive and field tests were randomised, following procedures described in Yuen et al. (2016).

(d) Data analysis

Data analysis was performed using R version 3.2.4 (R Core Team 2016). Data were log transformed to reach normality. We used random intercept models to evaluate the degree of among-individual variation. Random intercept models were fitted using linear mixed effects models (LMMs, *lmer*; Package *lme4*; Bates et al. 2015). Each LMM was a univariate model consisting of one measurement of boldness as the response variable, while testing sequence within the same assay in the same context (first, second) was the fixed factor. Individual ID was entered as a random factor in each model. Univariate models were calculated separately for each measure of boldness obtained from the open field or the startle test within each context (laboratory, nature). To check whether the degree of among-individual variance was significant at the 95% level, we compared models that included the random effect of individual ID with simpler models without it, while maintaining the same fixed factors structure using likelihood ratio tests (Crawley 2007; Zuur et al. 2009). We used the package *RLRsim* (Scheipl 2008) using the exactLRT function to calculate accurate P values when comparing models with a single random effect to models with no random effect. For all our models, we report the R^2 (adjusted), as calculated following Nakagawa and Schielzeth (2013). 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 for each measure of boldness obtained from the open field or the startle test within each context (laboratory, nature) separately (*rpt*; Package *rptR*; Nakagawa and Schielzeth 2010).

Additional linear models were used to assess whether boldness measured in the open field were correlated with boldness measured obtained from startle tests. Each of these models had one of the boldness scores measured in the open field as the response variable, and the corresponding boldness score measured for that individual during a startle test as the fixed factor. Individual ID was included in each model as the random factor to control for possible bias arising when repeated measures were taken from the same individual. For all tests, a significance level (α) of 0.05 was selected. Data are presented as mean and confidence intervals. Data were z transformed prior to analysis.

3. RESULTS

(a) Consistency and repeatability of boldness measured using an open field test

Including the random effect of mouse ID in our LMMs improved model fit for boldness measured in the open field in the laboratory (ExactLRT: L.Ratio = 11.01, P = 0.0004; R^2adj. = 0.54; Fig. 1a) and boldness measured in the open field in nature (ExactLRT: L.Ratio = 11.42, P = 0.0001; R^2adj. = 0.54; Fig. 1b), indicating that there was an inter-individual difference in the level of boldness measured in the two contexts (Table 1 and 2). Repeatability measures (i.e. individuals tested twice per assay per context) in the laboratory and nature during open field tests indicated that data were repeatable (laboratory: R + 95% CI = 0.62 + 0.35 - 0.79, P = 0.0002; wild: R + 95% CI = 0.51 + 0.21 - 0.73, P = 0.005).

Table 1

Mean and confidence intervals for boldness measured using open field and startle tests in each of the two contexts (laboratory, nature) in free-living striped mice in the Succulent Karoo (South Africa). Each measure of boldness was converted into behaviour/minute.

Test	Laboratory		Wild	
	First	Second	First	Second
Open Field	2.15 (1.00; 3.30)	2.23 (1.43; 3.03)	0.09 (0.05; 0.13)	0.10 (0.06; 0.13)
Startle	6.96 (2.86; 11.06)	9.99 (4.69; 11.66)	5.37 (1.53; 7.35)	7.35 (2.82; 11.87)

Table 2

Summary of the results obtained from univariate mixed-effect models for each test for boldness within each context (laboratory, nature). Estimates were derived separately for each measure of boldness Each model included mouse ID as the random factor, while sequence (first or second) was the fixed effect. For each model, we report point estimates for the fixed (mean) and the random parameters (variance) along with their 95% confidence intervals.

		Laboratory	**Wild**
Open Field	**Fixed effects**		
	Intercept	-1.11 (-1.54; -0.67)	0.42 (0.25; 0.60)
	Experience	0.42 (-0.01; 0.85)	0.06 (-0.10; 0.23)
	Random effects		
	Mouse ID	0.94 (0.59; 1.30)	0.37 (0.23; 0.51)
	Residual	0.89 (0.70; 1.13)	0.35 (0.27; 0.44)
Startle	**Fixed effects**		
	Intercept	-1.31 (-1.79; -0.85)	-2.12 (-2.72; -1.53)
	Sequence	0.21 (-0.11; 0.53)	0.17 (-0.42; 0.75)
	Random effects		
	Mouse ID	1.25 (0.94; 1.64)	1.28 (0.80; 1.78)
	Residual	0.67 (0.53; 0.85)	1.22 (0.96; 1.55)

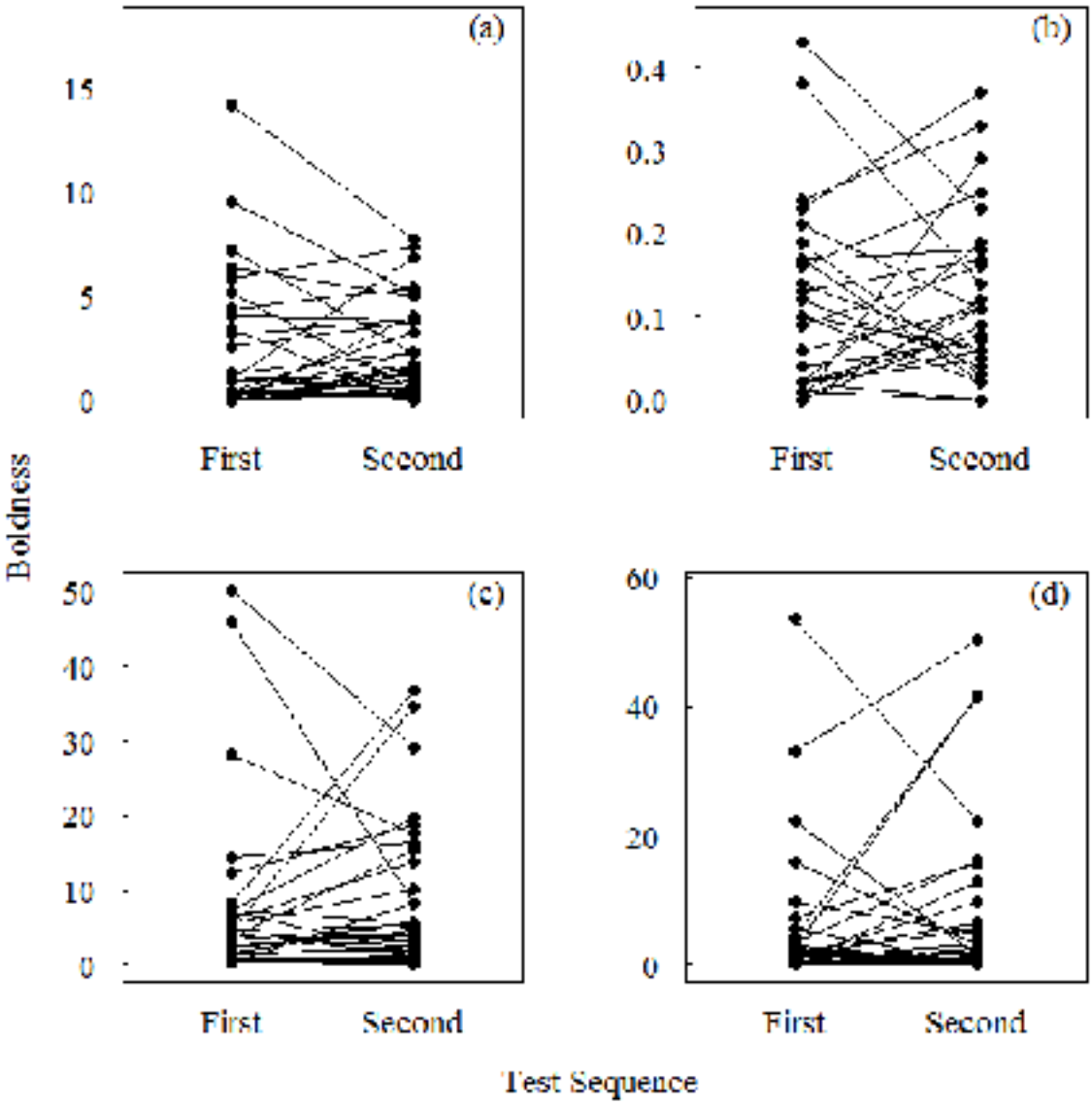


Figure 1

Consistency of the personality trait boldness (behaviour/minute) measured repeatedly in the same individuals within the same context. (a) Measures of risk-taking behaviour obtained from open field tests in the laboratory; (b) measures of risk-taking behaviour obtained from open field tests in nature; (c) measures of risk-taking behaviour obtained from startle tests in the laboratory; and (d) measures of risk-taking behaviour obtained from startle tests in nature.

(b) Consistency and repeatability of boldness measured using a startle test

Including the random effect of mouse ID in our LMMs improved model fit for boldness measured in the startle test in the laboratory (ExactLRT: L.Ratio = 31.64, P < 0.0001; R^2adj. = 0.78; Fig. 1c) and boldness measured in the startle test in nature (ExactLRT: L.Ratio = 10.95, P = 0.001; R^2adj. = 0.53; Fig. 1d), indicating that there was an inter-individual difference in the level of boldness measured in the two contexts (Table 1 and 2). Repeatability measures obtained in the laboratory and nature in the startle tests were repeatable (laboratory: R + 95% CI = 0.47 + 0.19 - 0.69, P = 0.01; wild: R + 95% CI = 0.45 + 0.16 - 0.68, P = 0.02).

(c) Comparisons of boldness measured in the laboratory and nature in open field and startle tests

Models, which included the fixed effect of laboratory better explained our data than models without them for both the open field and startle tests (open field: $\chi 2$ = 10.25, P = 0.001; R2adj.= 0.54; startle: $\chi 2$ = 15.70, P = 0.0001; R^2adj.= 0.52), indicating that boldness measured using the open field test in the laboratory was a good predictor of boldness measured in the open field test in nature, and boldness measured using the startle test in the laboratory was a good predictor of boldness measured using the startle test in nature (Table 3).

Table 3

Summary of the results obtained from univariate mixed-effect models to test whether boldness measured under standardised conditions in the laboratory were good predictors of boldness measured in nature in the open field or the startle test. Each of these models had one of the scores of boldness measured in the nature (e.g. open field) as the response variable and the corresponding score for boldness measured for the same individual in the laboratory (e.g. open field boldness in the laboratory) as the fixed factor. Mouse ID was entered as the random factor in each model. For each model, we report point estimates for the fixed (mean) and the random parameters (variance) along with their 95%confidence intervals.

	Open Field	**Startle**
Fixed effects		
Intercept	0.59 (0.40; 0.77)	-1.07 (-1.53; -0.58)
Sequence	-0.01 (-0.16; 0.16)	0.06 (-0.50; 0.63)
Laboratory Score	0.15 (0.06; 0.24)	0.52 (-0.50; 0.63)
Random effects		
Mouse ID	0.32 (0.19; 0.46)	0.21 (0.00; 0.79)
Residual	0.33 (0.26; 0.42)	1.17 (0.91; 1.39)

(d) Comparisons of open field and startle tests for boldness

The model which included the fixed effect of open field did not better explain our data than the model without it ($\chi 2 = 0.92$, $P = 0.33$; R^2adj. = 0.65), indicating that boldness measured using the open field test was not a good predictor for boldness measured using the startle test (Table 4).

Table 4

Summary of the results obtained from univariate mixed-effect model to test whether boldness measured using an open field test was a good predictor of boldness measured using a startle test. Boldness measured with a startle test was entered as the response variable, while the corresponding score for boldness obtained for the same individual from the open field was the fixed factor. Sequence (first, second) and location (laboratory, nature) were entered as additional fixed factors, while Mouse ID was entered as the random factor. We report point estimates for the fixed (mean) and the random parameters (variance) along with their 95%confidence intervals.

	Boldness (Startle)
Fixed effects	
Intercept	0.53 (0.06; 1.01)
Sequence	0.19 (-0.11; 0.50)
Location	0.63 (0.26; 1.00)
Open Field Score	-0.05 (-0.15; 0.05)
Random effects	
Mouse ID	1.17 (0.88; 1.54)
Residual	0.91 (0.79; 1.04)

4. DISCUSSION

Measures obtained from open field and startle tests were highly repeatable within the same context (laboratory or nature) and across contexts (laboratory and nature). This is important because it shows that both tests were accurately measuring a behavioural response repeatedly, and both tests conducted in the laboratory were representative of the behaviour that individuals would typically show under natural conditions. However, measures obtained from the open field and the startle tests were not correlated, indicating that the two assays were not measuring the same personality trait in striped mice.

Boldness measured in the open field was not correlated with boldness measured with a startle test. These results cannot simply be explained by the fact that the open field test incorporated an element of novelty; particularly as boldness measured with similar methodology in the field did not feature any aspect of novelty (i.e. data were obtained from individuals in their natal territories).

The startle and open field assays had one fundamental difference: in the startle test, risk-taking was measured after the individual had already been exposed to an imminent threat. In the open field test, there was no-prior exposure to an imminent threat. Predator-inspection is costly as it takes time and energy away from other competing activities (e.g. foraging, basking), but at the same time it provides individuals with vital information that may help them reduce the risk of mortality in future (Dugatkin and Godin 1992; Pitcher 1992; Walling et al. 2004). In prey species, such as striped mice, mounting an anti-predator response (e.g. remaining vigilant or escape in the presence of a threat) may also be costly, resulting, for example, in missed feeding opportunities. Striped mice live in a highly seasonal environment, and in the dry season when resources are scare, individuals need to maximise feeding opportunities if they are to remain in good health and survive the dry season (Schoepf et al. 2016). Studies have shown that physical condition may also promote boldness, because individuals in better health are better able to escape risky situations (Caro 1995; Pellegrini et al. 2010). It would be therefore advantageous if individuals were able to quickly assess whether a stimulus represented a potential threat and adjust their behaviour accordingly.

Stamps (2007) suggested that correlations between behaviour patterns that are assumed to reflect the same underlying behavioural tendency (in this case boldness) may depend upon the potential effects of those behaviour patterns on growth and mortality. Several studies support the idea that indices of boldness with different potential effects on growth and mortality are not necessarily correlated with one another (Sinn and Moltschaniwskyj 2005; Wilson and Stevens 2005). Boldness measures in our study were collected during the dry season, when resources are most limited for striped mice (Schradin and Pillay 2005). Delayed foraging impacts on an individual's nutritional state (van der Veen and Sivars 2000) and increases the probability of starvation (Sih 1997). A change in an individual's internal state, such as that caused by hunger, may thus lead it to reassess the costs and benefits associated with hiding and risk-taking (Damsgard and Dill 1998). For example, the potential cost of exposure to a threat might be offset by a need to forage. Therefore, it can be expected that even usually shy individuals might become risk-takers when their nutritional state is low and will begin to forage under risky situations (Höjesjö et al. 1999; Dall et al. 2004; Thomson et al. 2012). For example, Braithwaite and Salvanes (2005) found that juvenile cod (*Gadus morhua*) reared on an unpredictable food supply left a refuge significantly faster in a novel environment than those reared with a predictable food supply. This finding could explain the lack of correlation between the startle and the open field test.

Boldness can be driven by differences in underlying physiology or life history, but also by prior experience (Huntingford et al. 1994; Frost et al. 2007), including learning (Dugatkin and Alfieri 2003; Sneddon 2003; Guillette et al. 2009). In the open field test, striped mice had no prior knowledge of the risk potentially awaiting them when entering an open area. Thus, they might have relied more on other indirect cues from the environment to make a risk-assessment. Emergence into an open habitat carries a certain level of risk (Sih 1997). For a prey species, such as the striped mouse, one of the main risks associated with entering an open habitat is predation. The absence of cues from a predator might have thus indicated that the environment was potentially safe (Welton et al. 2003; Stamps et al. 2009). Several studies have now shown that experience influences the behavioural response to predation risk (Wilson et al. 1993; Riesch et al 2009; Hellstrom and Magnhagen 2011), which may lead an individual to reconsider the costs and the benefits of its responses (Cote et al. 2008). Further, Sneddon (2003) found that bolder animals learned to associate a visual cue and food delivery

faster than less bold animals. They attributed the difference to the fact that bolder animals more readily acquire information about novel situations and as a result learn the requirements of novel task more quickly than shyer animals. It is therefore plausible to assume that individuals quickly learnt that the remote-control car used in nature and the toy used in the laboratory were not a threat and adjusted their response levels accordingly.

While we cannot rule out that differences in boldness shown during the startle and the open field assays are attributable to learning or experience, we can suggest that boldness in striped mice is not context-specific (see also Yuen et al. 2015; 2016), because boldness measured in the laboratory was a good predictor for boldness measured with the same assay in nature. Our results support previous findings that tests predicted a priori to reflect boldness were shown to be uncorrelated with one another (Coleman and Wilson 1998; Sinn and Moltschaniwskyj 2005; Sinn et al. 2008). Réale et al. (2007) has suggested that context-specific traits can be usefully considered as two traits. Further, Stamps and Groothuis (2010) mentioned that it may be erroneous to assume that behavioural patterns that appear similar are in fact reflective of the same dimension. Our results support these ideas and point to the fact that the startle and the open field test may not be measuring the same personality trait. While both tests might be considered as measuring risk-taking behaviour, in our study, the results obtained from the startle test were more representative of another behavioural axis: fear-anxiety.

Anxiety has been found to be part of a behavioural syndrome (Sih et al. 2004a) because it correlates with many personality traits (e.g. exploration, Liebsch et al. 1998; aggression, Nyberg et al. 2003). A basic aspect of anxiety is uncertainty and a sense of uncontrollability rising from anticipated potentially aversive events, such as a response to an unknown threat (Barlow 2000; Steimer 2002), and it is thus heavily influenced by prior experience. In humans, people who are more vigilant when confronted with threatening stimuli are also more anxious (Mogg et al. 2004). Generally, anxiety is considered an emotion, which would be less consistent than a personality trait. But our and other research suggests that considering anxiety as a personality trait separate, though related, to boldness might be useful and suggest future studies look into this more closely. Our study supports previous findings that suggested that current boldness assays may not be interchangeable, and in some cases may not measuring boldness at all, potentially leading to a ‘jingle’ fallacy (Block 1995).

Several previous studies have attempted to quantify which assay best measures boldness (Burns 2008; Carter et al. 2012; Andersson et al. 2014; Magnhagen et al. 2014). However, we are the first to: a) provide a comparison between two assays by measuring each individual repeatedly within- and across-contexts; b) show that laboratory measures are representative of the natural behaviour of striped mice; and c) use tests that were ecologically relevant for our target species. We found that measures using an open field test were not correlated with measures using a startle test, supporting the idea that the two tests are not measuring the same personality trait (Toms et al. 2010). While both tests might assess measures of risk-taking behaviour, they are exposing individuals to different stimuli, eliciting different types of reactions from individuals based on their prior experience and internal state. We therefore suggest that the startle test in our study was in fact measuring anxiety because individuals during this assay were exposed to a threatening stimulus, which could have generated an anxious response rather than a bold one. We thus conclude that at least in our study system, the open field test is the more accurate assay to measure boldness, because it does not include the presentation of a threatening component as part of the assay.

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6. ETHICAL NOTE

All data were collected under the necessary licenses, were in accordance with the relevant animal welfare regulations and received ethical clearance from the Animal Ethics Committee of the University of the Witwatersrand (AESC: 2007/38/04). Mice handling time was kept to

a minimum and always performed with care. Trapping was performed only when conditions were optimal for the animals, avoiding heat and cold weather. Research permits were obtained from the Department of Tourism, Environment and Conservation of the Northern Cape.

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CHAPTER 5

GENERAL DISCUSSION

In the research presented here, I focused on the role of personality in a socially flexible mammal, the African striped mouse (*Rhabdomys pumilio*). First, I showed that personality is well-developed even in a socially flexible species that shows high flexibility in its behavioural response to environmental change. Then, I demonstrated that the personality of an individual remains stable over its life-span, even when it adopts an alternative reproductive tactic. Moreover, I presented evidence that personality traits collected under standardised laboratory settings can successfully predict personality traits that the same individuals show when data are collected directly in their natural environment. I showed how two separate latent variables (one in nature and one in the laboratory) underpinned all the behaviour measured in the two contexts, indicating that there is a context-specific behavioural syndrome in this species. Finally, I provided data indicating that different assays used to test a single personality trait (i.e. boldness) do not necessarily provide similar results and suggested that the different tests may in fact be measuring different personality axes. In this concluding chapter, I will bring all these different findings together. First, I will emphasise the importance of using well-designed and validated methods to study personality. Second, I will highlight the need to make a careful choice when deciding which test to use to measure personality in a target species. Third, I will address the role of personality in influencing individuals from reaching an *optimum*. Fourth, I will discuss the importance of sex in determining stability of personality traits. Lastly, I will provide suggestions for future directions for personality research in general and particularly in striped mice.

1. THE IMPORTANCE OF VALIDATION IN PERSONALITY STUDIES

Validation is a methodology used to justify the findings of a study. In personality research, it can be argued that validation is of particular importance because it establishes the accuracy of the behaviour under scrutiny. The need to present validated methodologies has recently been highlighted by Carter and colleagues (2012; 2013). Yet, to date, the vast majority of studies

rarely employ validated methods or report them in publications. This is peculiar and raises the question of whether the results reported in the literature are representative of the behaviour being measured (Réale et al. 2007). In personality research, scientists are presented with the conundrum of how to validate a study in the first place. Should one or several tests be performed in a day? What should the interval between tests be?

Some researchers have opted to either assess several traits with one test (Boon et al. 2007) or testing one trait per day (Dingemanse et al. 2007). The problem with the first approach is that it is difficult to ascertain whether similar or different results can be obtained when testing individuals for several behavioural traits consecutively, with half a day, one day or several days in between tests. The problem with the second methodology is that it is difficult to capture individuals repeatedly over several days, particularly when working with free-living, cryptic species. In **chapter 2,** I presented the results of my validation procedure. I focused on the validation of four of the most studied traits in the personality literature (activity, boldness, exploration and aggression) and employed classical assays only (open field, novel object and dyadic encounters with a novel conspecific). Taking advantage of the very trap-happy nature of striped mice at our field site in the Goegap Nature Reserve, I was able to trap and test striped mice either sequentially on different days for three different personality traits, or on one day for all three traits. Most importantly all my tests were randomised, so that half of the individuals were tested first for all the behavioural traits on one day and the other half of the individuals were tested for a behaviour/day.

My results showed that testing striped with either of the approaches led to similar results. This is a significant finding, because it shows that: 1. testing less frequently can yield similar outcomes as testing several times – this can save the researcher time and decreases stress to the animal; 2. testing less frequently might minimise the bias emerging from the habituation of individuals to multiple tests; and 3. the procedure presented here can be used as a framework for future studies that investigate personality in free-living species, where capturing individuals many times may be unfeasible.

The environment has a significant effect on behaviour (Coppens et al. 2010; Koolhaas et al. 2010; van Overveld and Matthysen 2013), so that it can be expected that free-living individuals might change their behaviour as they “adapt” to test conditions under a

standardised laboratory setting (Butler et al. 2006). This may result in the laboratory tests indicating different personality types that are not present in nature (Herborn et al. 2010). This is important to examine, particularly as several studies have linked personality traits of wild-caught individuals measured in captivity and made inferences about how these traits will have important effects on individuals` life-histories in nature, such as dispersal and survival. It is therefore surprising to find that, to date, only a few studies have compared results obtained from individuals tested in their natural environment with results obtained from the same individuals under captive conditions (Coleman and Wilson 1998; Brown et al. 2005; Wilson and McLaughlin 2007; Briffa et al. 2008; Hollander et al. 2008; Herborn et al. 2010; Cole and Quinn 2014), and these studies have produced mixed results. In **chapter 3**, I therefore aimed to investigate whether the personality traits of striped mice tested under natural and laboratory conditions remained consistent.

I examined whether the personality traits of activity, boldness, exploration and aggression were consistent between the laboratory-field contexts by using a battery of classical personality tests previously employed to study personality in striped mice in the laboratory (Yuen et al. 2015) and used the very same tests and adapted them to the field. First, I tested consistency and repeatability of personality traits within one context (e.g. the laboratory). Then, I correlated personality measures from the laboratory with measures from the same individuals tested in the field. I showed that personality traits of individual striped mice tested under standardised conditions in the laboratory were consistent with measurements of personality traits from the same individuals taken from their natural habitat. This is important as it demonstrates that personality measures collected under artificial laboratory conditions reflect natural behavioural tendencies. My results therefore not only validate previous studies in striped mice, but also indicate that personality measurements done in the laboratory are a valid representation of personality in nature.

2. CHOOSING THE CORRECT TEST TO STUDY A SPECIFIC PERSONALITY TRAIT

Personality is one of the most studied topics in the animal behaviour literature in recent years (Gosling and John 1999; Conrad et al. 2001; Dingemanse et al. 2003; Réale et al. 2007; Schuett et al. 2011; Chapman et al. 2013) and as a result of this rapidly expanding field, several alternative methods have been proposed to research its constituent behavioural traits. For example, several assays have been proposed to measure boldness, such as the open field, novel object, predator inspection, and the startle test. As a result, there is much disagreement over which assay gives the most accurate measurements for boldness (Carter et al. 2012; Magnhagen et al. 2014). For example, some researchers have suggested that boldness is optimally assayed experimentally by measuring an individual's reactions to a predatory event, such as a startle test (Bell and Stamps 2004; Magnhagen and Borcherding 2008; Bell et al. 2010), whereas others have argued that it is best measured using an open field or even a novel object test (Wilson et al. 1994; Ward et al. 2004).

In **chapter 4,** I compared measures of boldness obtained from two of the most popular assays used: the open field and the startle tests. To show that the behavioural measures obtained with either assays were valid, I first investigated their repeatability within a standardised laboratory settings. Then, I compared these measures with repeatabilities shown by the same individuals when they were tested in nature. Finally, I compared the results obtained from the two different assays to assess whether they yielded the same results. While the results of each test were highly repeatable using the same assay both within and across contexts, the comparison between assays did not yield similar outcomes. This indicates that the two tests might not be actually measuring the same behavioural trait. I argued that the different stimuli presented during the two tests are key in understanding such different results. In particular, the predictability of the risk awaiting individuals during the startle test may have enabled individuals to "learn from experience" and influenced their decisions when emerging from the protection of a shelter. Similarly, the unpredictability of the open field and the "not knowing what to expect" scenario may have encouraged the decision by individuals to venture out in an open habitat based on individuals prior experiences and internal state (e.g. hunger conditions). I therefore propose that future studies investigating boldness, or any

personality trait for that matter, might want to consider and individual's motivational state and experience when choosing an assay to measure the behaviour intended.

3. THE UBIQUITNESS OF PERSONALITY IN NATURE

Behavioural flexibility enables individuals to change their behaviour adaptively in response to altering and potentially adverse environmental conditions (Hazlett 1995; Piersma and Drent 2003; Dingemanse et al. 2010). Flexible behavioural responses are beneficial (Briffa et al. 2008), but also costly to produce (Hazlett 1995; DeWitt et al. 1998; Dall et al. 2004), and might be dependent on an individual's life-history. Increasing evidence suggests that much of the behavioural variation observed in natural populations cannot be attributed to behavioural flexibility of individuals alone (Wilson 1998; Nussey et al. 2007), but maybe also linked to individual differences in personality (Dall et al. 2004, Sih et al. 2004a,b; Sih and Bell 2008). From an evolutionary point of view, behavioural flexibility rather than personality should be favoured (Via and Lande 1985; Via et al. 1995), yet personality is ubiquitous in nature (Gosling and John 1999; Dingemanse et al. 2003; Bell and Sih 2007; Réale et al. 2007; Biro and Stamps 2008; Schuett et al. 2011) and it has been shown to explain >30% of the phenotypic variance within populations (Bell et al. 2009). It has been argued that personality results in sub-optimal behaviour (Careau et al. 2008; Dingemanse and Wolf 2010; Wolf and Weissing 2010).

Recent studies have suggested that behavioural flexibility and personality may be in fact functionally linked (Koolhaas et al. 1999; Sih et al. 2004a,b; Schjolden and Winberg 2007; Briffa et al. 2008; Sih and Bell 2008; Dingemanse et al. 2010) and that the strength of the flexibility-consistency axis is the result of evolutionary trade-offs (Dall et al. 2004). Theoretically, an individual may modulate its behaviour to generate appropriate responses to different situations, but still show consistency in the level of its response compared to other individuals in the population (Johnson and Sih 2007). This also implies that different individuals may display different levels of consistency in their behavioural traits compared with others (Sih et al. 2004b; Martin and Réale 2008). While great strides have been made, the link between behavioural flexibility and individual's personality remains unclear.

In **chapter 2,** I set out to investigate the link between behavioural flexibility and personality using the African striped mouse, a species well-known for its high social flexibility. African striped mice proved to be an excellent study system to investigate this topic, because individuals of this species are able to switch between different alternative reproductive tactics according to changes in environmental conditions. For example, individuals can switch from the group-living to the solitary tactic when population density declines (Schoepf and Schradin 2012a). As a consequence of this switch, the entire social system of the population can change. Striped mice following different reproductive tactics also differ considerably in their behavioural traits, but interestingly, these behavioural differences can become more or less apparent depending on which tactic is adopted (Schoepf and Schradin 2012b). Thus, striped mice show high flexibility in their behavioural traits, but most remarkably, this flexibility is also linked to their personality, with individuals showing consistent behavioural shifts (e.g. being always the most aggressive) when compared with other individuals within the population. I used the behavioural reaction norm approach (Dingemanse et al. 2009) to examine the link between behavioural flexibility and personality in striped mice before and after individuals adopted a new reproductive tactic. I found that striped mice had very well developed personalities, which remained stable independent of changes in season. Interestingly, the personality of individual striped mice did not predict the change in tactic. Rather tactic change seemed to be environmentally determined. My results indicate that, in striped mice, personality does not influence behavioural flexibility, social flexibility or the evolution of alternative reproductive tactics.

4. THE POTENTIAL ROLE OF SEX IN MAINTAINING STABILITY IN PERSONALITY TRAITS

While my results show that striped mice behaved consistently for all the behaviours measured both in the laboratory and in the field, I found no such consistency when I compared behavioural syndrome (**chapter 3**). In fact, my results show that there are two correlated context-specific separate latent variables (one for the field and one for the laboratory), which explained the behavioural traits measured. This is remarkable because one would expect that if all the behavioural traits measured within one context are consistent when measured in

another context, the correlation arising between them (i.e. their behavioural syndromes) should also be similarly correlated. This because individuals' personalities can be expected to fall along the so-called reactive-proactive behavioural syndrome continuum, where proactive individuals are able to control their environments, while reactive individuals respond more passively to their environments (Sih et al. 2004a, b). Consistency in personality traits and stability in syndrome structures has been shown in several species, such as the brown trout (*Salmo trutta*; Adriaenssens and Johnsson 2012), hermit crabs (*Pagurus bernhardus*; Mowles et al. 2012) and rock pool prawn (*Palaemon elegans;* Chapman et al. 2013).

However, other factors, putatively the role of genes as opposed to previous experiences, as well as the degree of behavioural flexibility may affect the way an individual responds in different environments (Briffa et al. 2015). Further, physiological constraints, such as those imposed by metabolic ceilings may constrain behaviours in one environment versus the other (for example, temperature fluctuations in the natural environment versus constant temperature experienced in the captive environment) and may cause the correlations between the different behavioural traits to disappear as individuals are measured in two different contexts (Careau et al. 2008). It is therefore plausible that syndromes themselves can be variable and can change across situations.

One other aspect that we need to consider is the role of sexual selection in shaping and maintaining behavioural syndromes stability. Sexual selection has been proposed as one mechanism for the evolution and maintenance of personality (Schuett et al. 2010). My research (**chapter 2**) revealed that male and female striped mice differed considerably in their personality traits when they adopted a new reproductive tactic. Males were found to be both consistent and flexible for exploration, whereas females showed both consistency and flexibility for both activity and boldness. A study in Namibian rock agama, *Agama planiceps* ,found that males show fitness trade-offs between boldness and time budgets, feeding rates, territory size and predation risk (Carter et al. 2012). Specifically, the study found that bolder males basked and moved more, fed more and had larger territories but had more predator-related injuries than shyer males (Carter et al. 2012), but also that personality differences in their risk-taking behaviour varied according to whether individuals were measured during or outside the reproductive season (Carter et al. 2012). Further, studies in

rock pool prawns have also revealed that while syndromes can be stable over different contexts, males and females display sex-specific syndromes (Chapman et al. 2013). My results in striped mice suggest that sexual selection may be responsible for producing differences between males and females in investing in the same behaviour (e.g. exploration) and that there might be costs and benefits associated to said behaviour according to which sex is expressing them. For example, being overtly explorative may be too costly in terms of predation risks for females particularly during the reproductive season, when they have to raise dependent pups. This indicates that sexual selection may be an important factor shaping personality in this species, though further research is needed to confirm this hypothesis.

5. FUTURE DIRECTIONS FOR STRIPED MICE PERSONALITY RESEARCH

Two relevant topics that can be tackled in future personality research are summarised below.

1. What are the underlying physiological mechanisms underpinning personality in striped mice?

Hormone levels act directly in the brain and on the peripheral organs, play a prominent role in affecting an individual's behaviour (Buntin 1996) and may play a key role in maintaining and regulating the personality of an individual. Glucocorticoids, such as corticosterone, are, for example, important modulators during the stress responses as they allow individuals to react to energetically demanding situations, such as those encountered during social interactions or when exploring novel environments (Belthoff and Dufty 1998; Creel 2001; Young and Monfort 2009), while androgens (e.g. testosterone) are strong modulators of reproduction, dominance and aggression (Moore et al. 1998; Evans et al. 2000). Striped mice following different reproductive tactics are known to differ in both their corticosterone and testosterone levels, but it is yet unclear how these hormones affect the personality of an individual. This could be elucidated by examining the endocrine mechanisms underlining personality in striped mice.

If corticosterone and testosterone underpin striped mice personalities, I would expect their levels to be tightly linked to specific behavioural traits. A potential explanation for the occurrence of personality is that suites of behavioural traits may co-vary with stable

differences in individuals' physiological profiles (Biro and Stamps 2010; Coppens et al. 2010; Dingemanse and Wolf 2010). The stress-coping style hypothesis suggests that differences in personalities, particularly along the reactive-proactive continuum, may be linked to an individual's physiological stress responses (Koolhaas et al. 1999; Øverli et al. 2007; Coppens et al. 2010). Reactive and proactive behavioural types are considered adaptations to unstable and stable environments, respectively. Therefore, shy, reactive individuals are expected to have higher levels of physiological stress responses than bold, proactive individuals (Cockrem 2007). Thus, I predict to find the more active, the bolder, the more explorative and the more aggressive striped mice to have lower corticosterone levels. Further, research on sex steroids and personality has found a positive link between testosterone levels and aggression, coping and exploration in both humans and non-human animals (Wingfield et al. 1990; Caramaschi et al. 2013). Testosterone, in addition to corticosterone, has been suggested to be an important factor in determining risk-taking and antipredator behaviour (Fürtbauer et al. 2015). Therefore, I predict to find more active, bolder, more explorative and more aggressive striped mice to have higher testosterone levels.

2. Do personality traits of individuals have fitness-consequences and are they linked to differing ecological conditions?

Personality influences reproductive success under varying ecological conditions. The variance in personality traits could be explained if under certain ecological conditions one personality extreme has the highest fitness (e.g. bold individuals in dry years with low food abundance), while under different environmental conditions another personality extreme would have the highest fitness (e.g. shy individuals in wet years with high food abundance). Therefore it would be important to establish whether the fitness consequences of personality traits differ between years differing in ecological conditions (e.g. between years with low and high food availability). For example, personality traits of individuals may have long-term fitness consequences that could affect their survival and reproductive success, depending on ecological conditions. If this were true, personality traits could be shown to vary according to differing environmental conditions, which could make certain traits more favourable under specific conditions. This may help explain why personality is maintained in a population.

If personality traits of individuals have fitness consequences, which are dependent on environmental conditions, I predict to find individuals which are more active, bolder, more explorative and more aggressive to have better survival probabilities in years when food is less abundant as they will be better competitors than individuals, which are less active, less bold, less explorative and less aggressive.

6. CONCLUSIONS

My PhD research aimed to understand the relationship between personality and behavioural flexibility and how the link between the two determines individual persistence in a heterogeneous environment. To do so, I investigated personality using the socially flexible African striped mouse (*Rhabdomys pumilio*) as a model. My study was conducted on free-living striped mice in nature using a field laboratory in Goegap Nature Reserve, Springbok, South Africa. Overall, my findings show that even in a very flexible species, like the striped mouse, personalities are well developed and highly stable over an individual's lifespan. This shows that personality does not constrain behavioural flexibility or hinders the evolution of alternative reproductive tactics. By using a carefully validated methodology, my research additionally provides validation for future studies of personality in striped mice, and personality research in general, by providing support that personality measures obtained from standardised laboratory conditions are representative of individuals' behaviours in nature.

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