

**DOTTORATO DI RICERCA IN ETOLOGIA ED  
ECOLOGIA ANIMALE  
(XXX CICLO)**

**Individual differences in personality and cognition in bank  
voles (*Myodes glareolus*)**

Tesi di  
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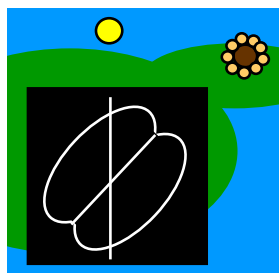
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DOTTORATO DI RICERCA IN  
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COORDINATORE Prof. Ugolini Alberto

Individual differences in personality and cognition in bank voles (*Myodes glareolus*)

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*To stubbornness, hope, and the animals that made this work possible.*

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## ABSTRACT

Consistent among-individual differences are found in most areas of biological research, and appear to constrain animals' plasticity and thus the possibility to adapt optimally to the environment. Recent years have seen increased interest in individual variation in behaviour, cognition and physiology, the proximate causes and the evolutionary mechanisms maintaining this variation. Not only there is reason to believe that individual differences in these domains affect fitness, it is likely that they are inter-related, forming a complex net of interactions regulated by different trade-offs. Empirical testing of recent theoretical framework – suggesting possible mechanisms linking behaviour, cognition and physiology – provided mixed findings. The aim of this thesis was to investigate whether individual differences in behaviour (animal personality), cognition and physiology are linked, and whether individuals that present different profiles display ecologically-relevant differences that might affect their fitness. To achieve this goal I assessed 86 bank voles (*Myodes glareolus*) for personality (i.e. activity and boldness), associative learning and reversal learning, as well as foraging and anti-predator strategies. I also evaluated their response to challenges, through measurement of faecal corticosterone metabolites. Main results support the predictions made by authors Carere and Locurto (2011) and Sih and Del Giudice (2012). Voles' personality and cognitive style were indeed connected, and constrained by a speed-flexibility/accuracy trade-off. Proactive (i.e. bolder and more active) individuals were faster but more rigid learners, whereas reactive individuals (i.e. shyer and less active) proved slower but more flexible.

Personality and cognitive style predicted the individual bias in a risk-reward trade-off. Proactive individuals tended to maximise reward at the cost of running higher risks, and reactive individuals favoured safety in spite of increased searching effort. However, body weight changes did not differ between the two groups. The response to a moderate challenge was not correlated with either personality or cognitive style. However, individual profiles predicted individual endocrine state in two relatively undisturbed conditions. Taken together, these results show consistent individual differences in personality, cognition and physiology. Such differences appear inter-related and extend to fitness-relevant traits. These results might help future research in the investigation of the evolutionary maintenance of among-individual variation.

## GENERAL INTRODUCTION

It is a truth universally acknowledged that individuals of the same species differ from each other. Or is it? Aristotle pondered over the different types of men in the fourth century B.C., and the first scientific study of individual differences in *Homo sapiens*, or human personality, is about a century old (Galton, 1883). Animal research instead has long considered the differences among individuals as random noise, meaningless variation around a tyrannical ‘golden mean’ (Bennett, 1987; Dall *et al.*, 2004; Wilson *et al.*, 1994). The 3R principle (Replacement, Reduction and Refinement; Russell and Burch, 1959) indeed advised to reduce this variation in the sample size as much as possible. Still, even controlling for sex and age and providing standardized rearing conditions, individuals greatly differ from each other. Recently, this random noise started to be considered as a potential source of valuable information, being in fact non-random at all. When taken into account, differences between individuals can promote rather than cloud the understanding of the processes under investigation.

Stable long-term behavioural, emotional, and physiological differences in suites of traits among individuals of the same species are termed ‘animal personality’ in its broadest sense (Carere and Locurto, 2011; Réale *et al.*, 2010). Their study has outlined recognisable and repeatable patterns in more than 100 vertebrate and invertebrate species (e.g. Gosling, 2001). In their seminal work, Réale *et al.* (2007) have identified five main axes along which personality is supposed to vary, called the ‘big five’: aggression, exploration, activity, sociality and boldness. Personality in its narrow sense is now defined as ‘among-individuals differences consistent across time and context’ relative to these five dimensions or axes. Thus, measuring an individual’s personality traits means describing its relative position on one of these axes, and assessing its consistency, at different moments in time and in different contexts (e.g. foraging vs mating). Associations between different behavioural traits, such as a correlation between aggressiveness and exploratory behaviour, are referred to as behavioural syndromes (Bell 2007; Sih *et al.* 2004 a-b). Behavioural syndromes are an attribute of populations and cover rank-order differences between individuals (Herde & Eccard, 2013). Stable traits forming “packages” can lead to behaviour that seems suboptimal or even maladaptive (Bell *et al.* 2013; Stamps, 2007; Sih *et al.* 2003; Sih *et al.* 2004b). For example, being overly-aggressive during courtship might translate into reduced reproductive success for a male, and being too bold and explorative might lead to increased risk of predation. Similarly, being cautious will certainly increase chances of survival, but might lead to a high number of lost confrontations, lower social rank and diminished chances to reproduce. This consistency is puzzling, because individuals are generally expected to behave optimally under any circumstance, minimising variation in behaviour between individuals and maximising behavioural plasticity (Bell, 2007; Dall *et al.*, 2004; Sih *et al.*, 2004a). The existence of animal personality therefore implies that individuals are limited in their behavioural plasticity (Bell *et al.* 2013), at least to some extent. The field of animal personality thus fills an important role in aiming to understand the possible

evolutionary mechanisms that maintain among-individual variation and allow such constraints on behavioural plasticity (e.g. Dall *et al.*, 2004).

A syndrome involving exploratory behaviour, fearfulness, aggression, and response to environmental change has been identified in a number of species and termed the 'proactive-reactive axis' (Sih *et al.*, 2004). Traits describing a proactive individual include boldness, risk-taking, fast exploration and aggressiveness (e.g. Benus and Røndigs 1997; Hessing *et al.* 1994; Koolhaas *et al.* 1999; 2007; 2010). Reactive individuals on the other hand, are described as cautious, shy, slow-explorers and unaggressive (e.g. Benus and Røndigs 1997; Hessing *et al.* 1994; Koolhaas *et al.* 1999; 2007; 2010). Proactive and reactive individuals also show different response patterns to novel or challenging situations. These alternative patterns are termed 'coping styles', and sometimes used a synonym of personality, although they describe traits that, albeit related, do not necessarily completely overlap (e.g. Zidar *et al.*, 2017). The coping style model predicts a more active fight-flight response to challenges in proactive individuals, and a withdrawal-conservation strategy for reactive ones. The model extends to physiological traits (e.g. Koolhaas *et al.* 1999; 2007; 2010). Compared to more reactive individuals, proactive individuals show higher sympathetic activity and reactivity, lower hypothalamic-pituitary-adrenal (HPA) axis activity and reactivity, and lower heart and breathing rates (e.g. Koolhaas *et al.*, 1999).

Furthermore, proactive and reactive individuals are found to be differently flexible in their responses as well as sensitive to environmental cues and changes. They acquire, process, store, and use environmental information in a specific and distinctive way. Proactive individuals have been shown to quickly establish routines, to be relatively superficial in information-acquisition and insensitive to environmental cues; they would be therefore more challenged when it comes to producing a new response to altered circumstances. Conversely, reactive individuals have been shown to be more accurate in their information-gathering, more sensitive to environmental cues and more flexible in their responses (e.g. Benus *et al.*, 1990; Sih *et al.*, 2004b; Sih and Del Giudice, 2012). The acquisition, processing, storage and use of information from the environment is one of the most widely used definitions of cognition (Shettleworth, 2010). Different personalities might therefore show differences in cognition, and a reciprocal influence was proposed (Locurto, 2007; Carere and Locurto, 2011). The connection between personality and cognition is highly relevant for both fields. Cognition encompasses perception, learning and decision-making, that will in turn affect ecologically relevant decisions and behaviours regarding for example risk-taking, foraging and mate-choice (Shettleworth, 2010). Personality, on the other hand, may prove helpful in accounting for unexplained variation in cognitive performance, and the maintenance of slow-learning individuals in a population. Such an understanding could be crucial from a methodological point of view, as fearful or shy individuals are often discarded simply because of their reluctance or inhibition to perform, not because of their actual inability (Carere and Locurto, 2011; Coleman *et al.*, 2005). Furthermore, with the exclusion of neurobiology, behavioural

observations are our only way to infer cognitive processes. Challenging events may also differentially impact on cognitive performance depending on personality.

It was already suggested by Pavlov (1941) that behavioural traits - currently considered as personality, reaction to challenges and cognitive abilities - could be inter-related. However, for about a century, research focused mainly on topics strictly related to each domain. It is only very recently, with the flourishing of studies on among-individual differences, that the suggestion of the inter-relatedness of behaviour, cognition, and physiology was revived (e.g. Carere and Locurto, 2011; Koolhaas *et al.*, 2010; Sih and Del Giudice, 2012). Although the theoretical framework connecting the three domains is convincing, studies addressing the inter-relation between personality, cognition, and physiology are relatively scarce and present mixed findings.

### *Personality and cognition*

If one personality type had better overall cognitive abilities compared to others, we would expect selection to favour this specific combination of traits. There is in fact support for the idea that cognitive abilities are heritable and selected for (Boogert *et al.*, 2011). Instead, individuals greatly vary in their cognitive performance, and different conclusions can be drawn depending on how cognitive performance is assessed. Some individuals master novel skills or learn new tasks faster than others (e.g. Coleman *et al.*, 2005). Others make fewer mistakes, showing higher accuracy (e.g. Ducatez *et al.*, 2014). Others still quickly update their information and easily master reversal learning tasks (e.g. Brust *et al.*, 2013). Furthermore, different personality types seem to do better in different cognitive tasks. For instance, there is ample evidence that active explorers excel in activity-based cognitive tasks (e.g. Chang *et al.*, 2017; DePasquale *et al.*, 2014; Guenther *et al.*, 2013; Griffin *et al.*, 2014; Mamuneas *et al.*, 2015; Trompf and Brown, 2014) and fearful individuals perform better in avoidance-learning tasks (e.g. Budaev and Zhuikov, 1998). However, results cannot be easily generalised, being sometimes sex- and context- dependent (e.g. Titulaer *et al.*, 2012). Sih and Del Giudice (2012) suggested that individual differences in personality and cognitive types might be functionally related because both share the same speed–accuracy/flexibility and risk–reward trade-offs. This theory was tested by numerous studies, but results are mixed, even within the same species tested in standard conditions (e.g. Guillette *et al.*, 2009, 2011, 2015).

Researchers have also tried to establish whether personality plays a role in problem solving and innovation propensities. While some studies found that innovation-prone individuals were more explorative and neophilic (e.g. Overington *et al.*, 2011), others reported that reactive, less competitive individuals were better problem-solvers than proactive conspecifics (Cole and Quinn, 2011). It is therefore clear that we are still far from ascertaining whether there is a common pattern of co-variation connecting personality and cognition, and which proximate and ultimate mechanisms might underlie this connection.



### *Cognition and stress*

Depending on intensity and congruence, challenging, unexpected and uncontrolled events (commonly referred to as stressors in the broadest sense, but see Koolhaas *et al.*, 2011) can have either a beneficial or a detrimental effect on cognition. The U-shaped model (Kim and Diamond, 2002) posits that stressors that are either too bland or too strong will fail to motivate the subject to learn or remember, whereas an intermediate amount of stress will facilitate information retrieval. Other studies suggest that stressors that are convergent in time and space with the learning experience, induce focused attention and improve memory of relevant information, whereas an unrelated stressor, possibly occurring before the cognitive effort is required, might impair the performance (reviewed in Joëls *et al.*, 2005). Furthermore, there is evidence that cognitive performance might be affected by a combination of personality and the kind of reinforcement (positive or negative) used in the learning contingency (e.g. Valenchon *et al.*, 2017).

### *Personality and stress*

Although numerous studies support the coping style model as it was originally proposed (Koolhaas *et al.*, 1999) and demonstrated a connection between personality and physiological profiles, recent studies found no evidence of direct co-variation. Some reported that endocrine state is positively correlated with proactive traits such as boldness and aggressiveness (Boulton *et al.*, 2015; Martins *et al.*, 2007). Others found no correlation between endocrine response and activity, which is an extremely common measure of personality (e.g. Van Reenen *et al.*, 2005). Others still reported no correlation between different physiological variables such as heart rate, breathing rate and cortisol production (Ferrari *et al.*, 2013). Methodological issues were recently raised, that might impair the comparison of different studies, because only a few used a repeated-measure design (but see Boulton *et al.*, 2015; Ellis *et al.* 2004; Ferrari *et al.* 2013; Sebire *et al.* 2007). Lastly, most studies measure differences in endocrine response in populations that were artificially selected for their personality traits. Those that considered wild or unselected populations, suggest a more complex relationship between behaviour and physiology (e.g. Boulton *et al.*, 2015; Ferrari *et al.*, 2013; Rangassamy *et al.*, 2016).

Taken together, all these findings seem to agree on only one point: behaviour (in its broadest sense) is constrained by trade-offs, which have a role in maintaining individual variation. Therefore, few recent studies explicitly addressing the relationship between these domains (e.g. Bebus *et al.*, 2016; Benus *et al.*, 1990; Christensen *et al.*, 2012) suggest that further investigation is needed to understand which mechanisms underlie these constraints, and how these are relevant in terms of fitness.

Hence, the aim of this thesis is to investigate the relationship between animal personality, animal cognition and endocrine state, and their implications for fitness. This overall goal was achieved through: 1) evaluating the potential relationship between cognitive style and personality, 2) assessing

possible ecological effects and fitness consequences of the different personality/cognitive styles in a semi-natural environment, and 3) measuring the corticosterone levels under three different conditions in relation to the coping style model.

As a study species I used the bank vole (*Myodes glareolus*), a common small rodent that has been widely used in behavioural ecology research. Bank voles live in a relatively unstable environment that is presumed to favour behavioural and cognitive flexibility and variation (e.g. Niemelä *et al.*, 2013). Bank voles inhabit mainly woodland areas in central and northern Europe (e.g. Mazurkiewicz 1983; Sptizenberger, 1999) where reproduction and eruptive population dynamics largely depend on food pulses such as seed mast (e.g. Abt and Bock, 1998; Hansson 1979, 1985; Imholt *et al.*, 2016; Reil *et al.*, 2015). They are subject to intense predatory pressure by avian and terrestrial predators alike (e.g. Jędrzejewski *et al.*, 1993; Sundell *et al.*, 2003). Bank voles have a promiscuous and non-resource-based mating system (e.g. Klemme *et al.*, 2007, 2008), with females preferring dominant over subordinate males (e.g. Horne and Ylönen 1996; Klemme *et al.* 2006). Small social aggregations as well as large breeding groups were observed in the wild; the great variability in breeding systems reported so far seems to depend mainly on density as well as season (Bujalska and Grüm, 1989; Eccard *et al.* 2011; Eccard and Ylönen 2001; Ylönen *et al.* 1988; Ylönen and Viitala 1991). Males and females differ in their space use: females are territorial; males have large overlapping home ranges (e.g. Bujalska 1973; Mazurkiewicz 1971). When possible, individuals in natural conditions seem to avoid direct encounters (e.g. Lopucki, 2007). Bank voles have been shown to display repeatable personality (e.g. Korpela *et al.*, 2011) and physiological traits (i.e. metabolic rate: Labocha *et al.*, 2004), and some indication of covariation between the two were recently reported (e.g. Šíchová *et al.*, 2014). They also have well-developed spatial reference abilities and working memory (e.g. Haupt *et al.*, 2010), and can flexibly adjust their anti-predatory responses to the perceived predator cues (e.g. Jędrzejewski *et al.*, 1993; Liesenjohann and Eccard, 2008). Working with a small rodent species presents indubitable advantages concerning relatively easy management as well as large sample size. Bank voles thus make a suitable study species to investigate the interplay between the domains of behaviour, cognition and physiology and its fitness consequences.

## Chapters overview

In chapter 1 I empirically tested Carere and Locurto (2011) hypothesis regarding personality types being markers for different cognitive styles, and Sih and Del Giudice (2012) hypothesis that this connection is mediated by a speed-accuracy/flexibility trade-off. The study describes the relationship between personality traits boldness and activity, and cognitive traits such as associative learning speed, flexibility, accuracy and persistence, along with motivation to initiate the test. Results are consistent with the presence of a speed-flexibility and accuracy trade-off in relation to personality.

In chapter 2 I tested whether the relationship we found was relevant in terms of fitness. For this I used two fitness proxies, foraging and anti-predator strategies, measured in enclosed landscapes of varying risks and resources. Different personality and cognitive styles affected individuals' decision making and risk-reward bias. I discussed the potential fitness consequences of the different strategies, both in terms of survival and missed-opportunity costs.

In chapter 3 I assessed the voles' endocrine response to three conditions with different challenging potential. Based on recent studies that re-evaluate the original coping style model, and the need of further data regarding unselected population, I investigated whether the proactive and reactive traits previously measured in the voles aligned with their physiological conditions. Results showed only partial support for the original model, suggesting that that its updated version – that differentiates between the quantitative and qualitative response to stress – requires further attention and formal testing. I finally discussed the differential vulnerability to change and challenges, artificial housing conditions and their implications for animal husbandry and welfare.



**Fig. 1** – A bank vole exploring the testing arena.

*“The power of doing anything with quickness is always prized much by the possessor, and often without any attention to the imperfection of the performance.”*

J. Austen, 1813

*“Courage and timidity are extremely variable qualities in the individuals of the same species.”*

C. Darwin, 1871

## Chapter 1

### THE FAST AND THE FLEXIBLE: COGNITIVE STYLE DRIVES INDIVIDUAL VARIATION IN COGNITION IN A SMALL MAMMAL

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#### **Abstract**

Patterns of individual differences in cognition have been studied empirically and systematically in the last decade, but causes and consequences of this variation are still largely unclear. A recent hypothesis suggests that one predictor of individual variation in cognition is personality, and specifically that personality types are linked to cognitive styles through a speed–accuracy trade-off. We tested specific predictions of this hypothesis, measuring individual differences in associative learning speed and flexibility, quantified via reversal learning, of 86 bank voles, *Myodes glareolus*, along with their activity and boldness. We found that bolder and more active individuals were fast, inflexible and persistent in the associative learning tasks, whereas shy and less active individuals were slow and flexible. We also found evidence for a speed–accuracy trade-off: correct choices in the cognitive tasks required more time for all individuals compared to incorrect choices, but bolder, more active voles always made their decisions faster than reactive ones. The difference between the time required for a correct and an incorrect choice was most pronounced in initial learning for shy and less active individuals, but for bolder, more active individuals it was most pronounced in the reversal learning task. We also found differences related to sex and age: females were faster than males to update information or correct incorrect choices and older animals took longer to initiate the test. Our results confirm the hypothesis

that individual differences in behaviour are reflected in different ‘cognitive styles’, differentially trading off speed for flexibility and accuracy in cognitive tasks. Moreover, we provide the first evidence for the mechanisms of such a trade-off in a small mammal.

**Keywords:** animal personality; associative learning; behavioural syndrome; fast and slow learner; individual differences; *Myodes glareolus*; rodent; speed–accuracy trade-off; temperament.

## Introduction

Cognitive abilities are part of a species’ adaptation to its environment (Dukas, 2004; Shettleworth, 2010). Since cognitive processes are not directly measurable, they are usually inferred by assessing a change in behaviour (e.g. Barron *et al.*, 2015; Bebus, Small, Jones, Elderbrock, and Schoech, 2016; Griffin, Guillette and Healy, 2015). Hence, the individual’s behaviour is used to make inferences about its cognitive abilities (Bebus *et al.*, 2016). Studying individual variation in cognition and individual variation in behaviour, that is, personality, in relation to each other might prove beneficial in multiple contexts. It might help identify responses that underlie specific cognitive abilities (i.e. the mechanistic basis of variation in behaviour), which is the aim of animal cognition researchers, as well as determine the adaptive significance of behavioural and cognitive traits (i.e. the functional basis for variation in behaviour), which is the focus of behavioural ecologists (according to Griffin *et al.*, 2015). However, up to now we have only limited knowledge about patterns of consistent individual differences in various aspects of cognition (e.g. Brust and Guenther, 2017; Chang, Ng, and Li, 2017; Chittka, Dyer, Bock, and Dornhaus, 2003; Wang, Brennan, Lachlan, and Chittka, 2015), even though this field of research is rapidly expanding (e.g. Cussen, 2017; Griffin *et al.*, 2015; Shaw, 2017; Thornton and Lukas, 2012; van Horik, Langley, Whiteside, and Madden, 2017).

Here we investigated whether individual differences in animal personality are related to individual cognitive traits. Personality is defined as the set of individual differences in behaviour that are consistent across time and contexts (Réale, Reader, Sol, McDougall, and Dingemanse, 2007). This variation extends to physiological traits (e.g. Koolhaas *et al.*, 1999), is ecologically relevant (e.g. Wolf & Weissing, 2012) and may affect cognitive performance (e.g. Carere & Locurto, 2011; Locurto, 2007). Specifically, it has been proposed that behavioural types may be markers of different cognitive styles (Carere & Locurto 2011; Sih & Del Giudice 2012), defined as the specific strategies by which different individuals perform cognitive tasks (Bebus *et al.*, 2016). Throughout this article, we use the expression ‘cognitive style’ in this way. It has been suggested that cognitive performance is a combination of cognitive ability and cognitive style (Bebus *et al.* 2016). Cognitive ability is an individual’s capability to acquire, process, store and use information, whereas cognitive style is the specific strategy by which the individual acquires, processes, stores and uses the information (Bebus *et al.*, 2016; Carere & Locurto,

2011; Griffin, Guillette, & Healy, 2015; Sih & Del Giudice, 2012). For example, two test subjects may have similar capability to discriminate between different cues, associate the characteristics of one with the reward, remember this association and recall it when presented again with the same setting. However, the individual cognitive style (e.g. how the individual focuses its attention) may influence the performance (Bebus *et al.*, 2016). One subject may consistently look for the rewarded cue ignoring the, potentially rewarded, other cues, while the second may keep sampling the other cues as well. In an associative task, the first individual will achieve a better performance. In a reversal task, a measure of behavioural flexibility, the second individual will perform better because of the more complete information acquired through extended sampling (Bebus *et al.*, 2016). Sih and Del Giudice (2012) also suggested that these strategies are related to trade-offs between speed and accuracy/flexibility. Their theoretical framework suggests that ‘bolder individuals learn a particular contingency faster (i.e. in fewer trials) than do shyer individuals either because they recognise such contingencies sooner, lay them down in memory more readily, or have lower decision thresholds for association formation’ (Griffin *et al.*, 2015, p. 211). However, because such fast changes in the behavioural response (learning) are bound to the formation of routines (e.g. Benus, Den Daas, Koolhaas & Van Oortmerssen, 1990; Koolhaas *et al.*, 1999), they would also be more challenged in reversal learning tasks that require flexible adjustments in response to altered circumstances. Conversely, shyer individuals might take longer to master a cognitive task (e.g. Sih, Bell, Johnson, & Ziemba, 2004) possibly because they depend more on, and are more sensitive to, environmental stimuli and keep sampling the environment, thus acquiring more complete and accurate information (e.g. Bebus *et al.*, 2016; Benus *et al.*, 1990; Groothuis & Carere, 2005). This strategy would enable them to flexibly adjust to altered circumstances and thus perform better in reversal learning tasks. So far, current empirical evidence for the proposed link between personality and cognition is mixed. Studies reporting connections between personality and cognitive performance have often not included direct reference to a speed–accuracy trade-off (e.g. Guillette *et al.*, 2009, 2011), and some of the studies investigating the presence of speed–accuracy/flexibility trade-offs have not included an assessment of the individuals’ personality (e.g. Raine & Chittka, 2012; Wang *et al.*, 2015). Finally, studies testing the connection between personality and cognition through a speed–accuracy/flexibility trade-off, in both vertebrates and invertebrates, present contradictory findings within and between species (summarized in Table 1).

Therefore, the main aim of this study was to test whether different personality types adopt different strategies to learn a cognitive task, and to test Sih and Del Giudice’s (2012) predictions regarding a speed–accuracy/flexibility trade-off. Our study system was the bank vole, *Myodes glareolus*, a common boreal rodent species that exploits ephemeral food sources (e.g. Imholt, Reil, Plašil, Rödiger, & Jacob, 2016; Reil, Imholt, Eccard, & Jacob, 2015) and is subject to intense predatory pressure (e.g. Jędrzejewski, Rychlik, & Jędrzejewska, 1993). We tested the voles for their olfactory associative learning

speed and flexibility. The reward was the opportunity to return immediately to the vole's own home cage. Believing that associative learning tests should use the predominant sense of a species, we took the set of environmental demands and conditions that shape the species' behaviour and cognition into account when we designed our experiment. We exploited the voles' natural reliance on olfaction to gain information about their environment and the need to find shelter, providing a comparable motivation for all tested individuals. We expected faster learners to be bolder and more active whereas slower learners would show shyer, less active traits. We predicted that bolder, more active faster learners would be less flexible in updating behaviour in response to altered circumstances, and therefore that they would take longer to learn a reversal learning task than shyer, less active slower learners. Since personality might affect learning performance in a sex-dependent way (e.g. Titulaer, van Oers, & Naguib, 2012), we investigated differences between the strategies adopted by males and females to approach the cognitive tasks. Specifically, based on sex differences in space use and territoriality in bank voles (females are territorial and males have large overlapping ranges) and on existing literature on sex differences in cognition, we expected males to be faster learners and females to be more flexible (e.g. Guillamón, Valencia, Calés, & Segovia, 1986; Schuett & Dall, 2009). Lastly, we expected older individuals to be slower learners than younger ones.



	High speed– low accuracy	Low speed– high accuracy	Study	Tested species	Taxon	Supporting
Immediate reward rate	High	Low				
Mortality risk	High	Low				
Exposure to novel environments	Common	Rare	Guillette et al. (2015)	<i>Poecile atricapillus</i>	Bird	Yes
			<b>Present study</b>	<b><i>Myodes glareolus</i></b>	<b>Mammal</b>	<b>Yes</b>
			Brust et al. (2013)	<i>Taeniopygia guttata</i>	Bird	No
	Proactive	Reactive	Ducatez et al. (2014)	<i>Quiscalus lugubris</i>	Bird	Yes
			Guenther et al. (2013)	<i>Cavia aperea</i>	Mammal	Yes
			Griffin et al. (2013)	<i>Sturnus tristis</i>	Bird	Yes
			Guillette et al. (2015)	<i>Poecile atricapillus</i>	Bird	Yes
			<b>Present study</b>	<b><i>Myodes glareolus</i></b>	<b>Mammal</b>	<b>Yes</b>
			Brust et al. (2013)	<i>Taeniopygia guttata</i>	Bird	No
	Fast-exploring	Slow-exploring	Guenther et al. (2013)	<i>Cavia aperea</i>	Mammal	Yes
			Guillette et al. (2015)	<i>Poecile atricapillus</i>	Bird	Partially
			Udino et al. (2016)	<i>Camponotus aethiops</i>	Insect	Yes
			<b>Present study</b>	<b><i>Myodes glareolus</i></b>	<b>Mammal</b>	<b>Yes</b>
			Ducatez et al. (2014)	<i>Quiscalus lugubris</i>	Bird	Yes
	Bold	Cautious	Guenther et al. (2013)	<i>Cavia aperea</i>	Mammal	Yes
			Mamuncas et al. (2015)	<i>Gasterosteus aculeatus</i>	Fish	Partially
			Trompf and Brown (2014)	<i>Poecilia reticulata</i>	Fish	Partially
			Chang et al. (2016)	<i>Portia labiata</i>	Insect	Partially
	Aggressive	Unaggressive	Guenther et al. (2013)	<i>Cavia aperea</i>	Mammal	Yes
	Asocial?	Sociable?	Trompf and Brown (2014)	<i>Poecilia reticulata</i>	Fish	No
	Insensitive	Sensitive	Ducatez et al. (2014)	<i>Quiscalus lugubris</i>	Bird	Yes
	Not choosy	Choosy				
			<b>Present study</b>	<b><i>Myodes glareolus</i></b>	<b>Mammal</b>	<b>Yes</b>
			Burns and Rodd (2008)	<i>Poecilia reticulata</i>	Fish	Yes
	Risk-prone	Risk-averse	Guenther et al. (2013)	<i>Cavia aperea</i>	Mammal	Yes
			<b>Present study</b>	<b><i>Myodes glareolus</i></b>	<b>Mammal</b>	<b>Yes</b>
			Ducatez et al. (2014)	<i>Quiscalus lugubris</i>	Bird	No
			Guenther et al. (2013)	<i>Cavia aperea</i>	Mammal	Yes
			Learning and memory			
			Ducatez et al. (2014)	<i>Quiscalus lugubris</i>	Bird	Yes
			Udino et al. (2016)	<i>Camponotus aethiops</i>	Insect	Yes
			<b>Present study</b>	<b><i>Myodes glareolus</i></b>	<b>Mammal</b>	<b>Yes</b>
			Brust et al. (2013)	<i>Taeniopygia guttata</i>	Bird	Yes
			Griffin et al. (2013)	<i>Sturnus tristis</i>	Bird	Yes
			Guenther et al. (2013)	<i>Cavia aperea</i>	Mammal	Yes
			Mamuncas et al. (2015)	<i>Gasterosteus aculeatus</i>	Fish	No
			Udino et al. (2016)	<i>Camponotus aethiops</i>	Insect	Yes
			<b>Present study</b>	<b><i>Myodes glareolus</i></b>	<b>Mammal</b>	<b>Yes</b>
			Ducatez et al. (2014)	<i>Quiscalus lugubris</i>	Bird	Yes
			Guenther et al. (2013)	<i>Cavia aperea</i>	Mammal	Yes
			Burns and Rodd (2008)	<i>Poecilia reticulata</i>	Fish	Yes
			Burns and Rodd (2008)	<i>Poecilia reticulata</i>	Fish	Yes

**Table 1** – Non exhaustive list of recent empirical studies testing Sih and Del Giudice’s predictions.

The first column reports behavioural and cognitive traits and situations in fast-inaccurate and slow-accurate individuals. The second and third column report Sih and Del Giudice’s predictions regarding such traits. The last column reports whether the study found support for the prediction (modified from Sih and Del Giudice, 2012). The present study is highlighted in bold.

## Methods

### *Animals and housing*

We tested 86 adult bank voles, 45 males and 41 females, born in captivity. Fifty voles originated from laboratory-born mothers; the remaining 36 originated from wild-caught females, trapped in Potsdam (Germany). A maximum of four individuals from the same litter (two males and two females) was included in our sample. At 3–5 weeks of age juveniles were weaned, sexed and assigned a unique identity. From then on, all animals were housed individually in standard polycarbonate cages (Typ III, Ehret GmbH, Mahlberg, Germany; 42 x 27 cm and 16 cm high). Light, temperature and humidity mirrored the natural conditions occurring outside the laboratory. Cages were provided with wood shavings and hay as bedding, and paper rolls for shelter. Water and food pellets (Ssniff V1594 R/M-H Ered II, Soed, Germany) were available *ad libitum*. Bedding was changed every 2 weeks.

### *Personality tests*

We assessed differences between individuals in activity, exploration and boldness using two standardized laboratory tests (Réale *et al.*, 2007), developed for common voles (Herde & Eccard, 2013) and adjusted for bank voles. We conducted the first round of tests 2 days after the cognitive trials; the second round of tests took place 2 weeks later.

### *Open Field Test*

Since bank voles have a polyphasic activity rhythm (e.g. Ylönen, 1988) it is difficult to test all individuals in an active state. However, state differences while testing may account for large variation in behavioural measures in many other studies. We therefore took subjects from their home cage only when they were active, that is, when they were perceived moving in the cage; this allowed us to test all animals during similar activity levels.

A round open field of 100 cm diameter was used as a test arena (Archer, 1973). The concrete floor of the arena was virtually divided into two areas (Herde & Eccard, 2013): a safe peripheral area 10 cm wide and a central unsafe area 80 cm wide. Each animal was placed in the safe area of the arena, and its behaviour was recorded with a video camera (Logitech Quick Cam Pro 9000, PID LZ727BA, Logitech international S.A., Morges, Switzerland) for 10 min. The following parameters were measured: latency to enter the central area, time spent active (that is, moving around the arena) and time spent in the central area. If animals did not enter the central area within 10 min, the latency was set to the maximum of 600 s (24% of all trials). Activity and time in the centre were recorded with instantaneous 1–0 sampling every 10 s (e.g. Martin & Bateson, 1993). Subjects were then transferred into their home cage, and the arena was cleaned with 70% alcohol after each test.

### *Novel Object Test*

Animals were transferred to a new cage (see Animals and Housing) between 1800 and 2000 hours and left to habituate overnight. The new cage was sparsely filled with bedding and contained a plastic roll

for shelter. All other housing conditions were as described above. On each of the 2 test days, a novel object was introduced in the cage, on the side opposite to the shelter. Two different types of novel objects were used for the two test rounds: a plastic toy horse (8 x 4 cm and 6 cm high) and a plastic toy duck (6.5 x 5 cm and 6 cm high). The test started when the novel object was introduced in the cage. If the voles were not in the shelter when the novel object was put in the cage, they were gently guided to it. The subjects' behaviour was then monitored with a video camera (as above) for 30 min. The following parameters were measured: (1) latency to leave the shelter, (2) latency to approach the novel object (defined as coming within 2 cm of it, with the head turned towards it), (3) number of interactions with the novel object (touching, nibbling and sniffing, defined as inspecting the object with the tip of the nose only), and (4) overall duration of interactions. If animals did not approach the novel object at all, the latency was set to 1800 s (13% of all trials). At the end of the test, animals were returned to their home cage.

#### *Associative Learning Test*

We tested the voles for their speed and flexibility in associating a neutral odour cue with a reward. The test consisted of two tasks: an initial learning task and a reversal learning task. The neutral odour cues were fruit juices, orange or pineapple (odours O and P), that are not normally present in the voles' natural environment. The reward was the chance to return to the safety of the home cage, and being left undisturbed for at least 2 h.

The test arena was a plastic Y-maze composed of a path 40 cm long and 5 cm wide, with maze walls 15 cm high (Fig. 1). Animals were placed in a plastic tube (10 cm wide) into a circular start area (10 cm wide) from which a short (10 cm) arm led to an intersection, the 'decision area'. From the decision area, two identical arms 30 cm long each led to an opening to the home cage. The arms were bent, so that the end of the arm was not visible from the shorter arm or from the decision area. One of the openings was closed with wire mesh; the other had a mesh flap of the same material allowing the vole to exit the maze and enter the home cage.

A total of 1 ml of fruit juice was put on a cotton pad (O or P as odour cues). Different odour cues were placed inside each arm of the maze about 5 cm from the intersection. The arena was illuminated with a bright LED lamp, to increase the animals' motivation to find shelter. Preliminary trials following the same protocol described above were run to ensure that voles would be physically able and willing to run the maze, discriminate between the two odours and show preferences for neither. The animals used in the pilot study were not involved in the main experiment.

Voles were always tested between 07.00 and 20.00 h. At the start of each trial, voles were taken from their home cage using a plastic tube 10 cm in diameter and placed in the start area without being directly handled. The home cage was placed at the other end of the maze. The tube was lifted remotely via a string and the voles were free to move through the maze. The trial ended when the voles entered

the home cage with the anterior part of the body (head, front paws and shoulders). The cage was then closed and returned to the housing room. The maze was cleaned with 70% ethanol after each trial. The experimenter (V.M.) was never present in the room while the trials took place. Trials were monitored from the neighbouring room with a video camera. Each animal had a maximum of four trials per day, with a minimum of 2 h between trials. Animals were randomly assigned to one of six successively tested groups, composed of a balanced number of males and females, three of which had odour O as the positive cue, leading to the open door of the maze, in the learning task and odour P as the positive cue in the reversal learning task. The remaining three groups had odour P as the positive cue in the learning task and odour O as the positive cue in the reversal learning task. The side of the open door and associated positive cue were alternated each time a vole entered the maze, to avoid arm bias effects. Before the start of the test procedure voles were allowed a 'trial 0' to explore the maze for 10 min. During trial 0 the setting of the maze was the same as for the other trials, with one door open and one door closed, and the corresponding odour cues in place. Trial 0 ended after 10 min, even if the voles had entered the home cage long before. If after 10 min the voles did not find their way to the home cage (e.g. they froze in the closed arm of the maze), they were gently guided to it. The same time limit would have applied to the rest of the trials; however, during experimental trials, all voles made their way to the home cage by themselves after a maximum of 8 min.

For reversal learning, we switched the positive and the negative cues, so that the previously rewarded odour now led to the blocked door. Both tasks were considered successfully solved when the vole chose (as a first choice) the arm leading to the home cage in seven out of 10 consecutive trials. Voles were considered to have chosen an arm of the maze when they entered it with the entire body (tail excluded), completely leaving the decision area. This definition was used because of the voles' tendency to make numerous 'false starts', moving with only the anterior part of the body and quickly returning to their former position in the decision area. Learning and reversal learning speed were expressed as learning and reversal learning scores, the number of trials necessary to reach the criterion in the two tasks. We used the same criterion in both tasks to have comparable measures of learning and reversal speed (e.g. Guenther *et al.*, 2013). All trials were video-recorded. From these videos the same observer (V.M.) quantified the following variables. (1) Latency to enter the maze: latency to leave the start area with the full body (without tail). We considered this as a measure of the animal's willingness to initiate the test (motivation). (2) Latency to decision: time interval between the vole placing the front paws in the decision area, and the vole leaving this area with the entire body (tail excluded). We considered this a measure of the time required by each individual to choose which route to take. (3) Latency to error correction (persistence): time between the vole arriving at the blocked door and returning to the decision area.

### *Statistical analyses*

We used principal component analyses (PCA) followed by oblimin rotation (Tabachnick & Fidell, 2001) to reduce the number of dependent variables and to summarize the behaviours quantified prior to statistical analyses. We ran PCAs for the open field and the novel object test separately. All trials of both rounds of each test were included in the same PCA.

We performed PCAs with transformed variables to achieve a normal distribution (Table A1 in the Appendix). We retained principal components with eigenvalues greater than 1 (Kaiser–Guttman criterion; Kaiser, 1991). PCA gave a composite score for each round of testing of the open field and for each round of testing of the novel object. We then calculated the individual mean PCA scores for the first factor for the open field and the novel object tests, respectively; these average scores, defined as personality traits ‘activity’ and ‘boldness’ from here on, were used in all further steps of the analysis. They describe the relative position of each individual on the bold–shy and active–inactive axes.

We assessed repeatability of the single recorded behaviours and of the PCA composite scores for each round of testing. We calculated the repeatability of the activity and boldness scores as an intraclass correlation coefficient from a one-way ANOVA with individual as a factor (Lessells & Boag, 1987; Nakagawa & Schielzeth, 2010) using the R package rptR (Stoffel, Nakagawa, Schielzeth, & Goslee, 2017).

We assessed the existence of a behavioural syndrome by Spearman rank correlations between mean composite behavioural variables for each individual. This approach approximates between-individual correlations. However, since the measured behaviours express different, albeit connected, personality traits (activity and boldness), successive analyses were conducted running separate models for either activity or boldness.

We tested relationships between personality scores and learning and reversal learning scores. We initially used restricted maximum-likelihood linear mixed modelling (LMM) to evaluate the relationship between composite behavioural variables from PCA (activity and boldness) and learning and reversal learning scores, including sex and age (in weeks) as fixed effects. We added litter identity and tested group, for example having odour O or P as the positive cue, as random factors in each model, to check for the possible effect of having siblings (maximum of four per litter) in our sample, as well as the possible effect of being tested in successive groups, or a preference for one of the odours. We stepwise compared nested models with both random factors with simpler models without these factors. When a simpler model proved to have a better fit (indicated by  $2 \geq \text{AIC}_{\text{full}} - \text{AIC}_{\text{constrained}}$  where AIC is the Akaike information criterion) the second random factor was dropped (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Since the variance explained by the remaining random factor was relatively low, ranging between 0.009 and 0.136, we ran linear models without random factors and again compared the AICs. In all cases, reduced models, without random effects, were better supported. Therefore, we used linear

models having either learning or reversal learning scores as dependent variables, and personality traits, sex and age as explanatory variables. We included all possible two-way interactions between the explanatory variables and excluded them stepwise if they proved nonsignificant based on log-likelihood ratio tests (Zuur *et al.*, 2009). We used the R package lme4 (Bates, Mächler, Bolker, & Walker, 2015).

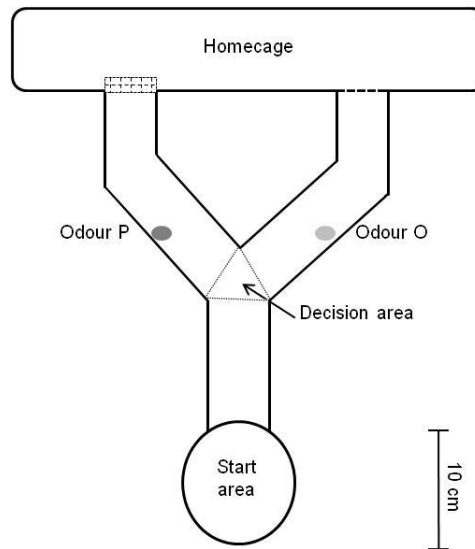
We used LMMs to evaluate the relationship between variables measured during the associative learning test (latency to enter the maze, latency to decision, persistence) and personality scores, sex, age and trial number for each trial. We ran separate models for the learning and reversal learning task, controlling for activity and boldness. In all models, sex, age and trial number, centred to mean trial, were considered as fixed effects. We included all possible two-way interactions between the explanatory variables and excluded them stepwise if they proved nonsignificant based on log-likelihood ratio tests (Zuur *et al.*, 2009). Individual identity was added as a random factor in each model, specified as random intercept. Persistence was log-transformed, and latency to enter the maze was increased by 1 and then log-transformed as well, to meet the normality assumption. We used the R package lme4 (Bates *et al.*, 2015).

Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality, except in the case of latency to enter the maze, although we checked for this being the best suited model to describe the relationship. The accepted significance level was  $\leq 0.05$ . All data analyses were conducted with R version 3.2.3 (R Core Team, 2015).

#### *Ethical note*

All aspects of this study comply with the animal care regulations and applicable national laws of Germany and all research protocols were approved by the ‘Landesamt für Umwelt, Gesundheit und Verbraucherschutz Brandenburg’ (reference number: V3-2347-44-2011, Ä6) and the ethical commissioner for animal experiments of the University of Potsdam.

This study also complies with the ASAB/ABS Guidelines for the Use of Animals in Research. We took great care in ensuring the animals’ welfare throughout the experimental procedure and afterwards. Housing conditions incorporated aspects of the natural living conditions as much as possible, and we provided biologically relevant enrichment features such as natural material and refuges. During testing, we avoided direct handling, preferentially tested subjects during active phases, and chose an alternative reward strategy that allowed us to avoid food deprivation as a motivational procedure.



**Fig. 1** – Schematic representation of the Y-maze used in the associative learning test with olfactory cues. Reaching the home cage served as a reward.

## Results

### *Personality tests*

For each PCA we retained one main component, which explained  $> 65\%$  of the variance, and on which all behaviours loaded significantly (Table A1 in the Appendix). Each test was therefore assumed to have measured one behavioural trait (e.g. Carter *et al.*, 2013), namely activity for the open field test and boldness for the novel object test (e.g. Réale *et al.*, 2007). Both activity in the open field ( $R = 0.74$ , confidence interval, CI = 0.65–0.84) and boldness towards a novel object ( $R = 0.67$ , CI = 0.68–0.89) were highly repeatable over time (Table A1 in the Appendix). Both behavioural traits correlated with each other at the phenotypic level (mean trait value per individual:  $r_s = 0.43$ ,  $P < 0.001$ ; Fig. A1 in the Appendix).

### *Associative Learning Test*

All voles reached the learning criterion in both tasks, after a maximum of 26 trials, but individuals showed much variation in learning speed (see Fig. A2 with learning curves in the Appendix).

The mean ( $\pm$  SD) number of trials required to reach the learning criterion was  $17.1 \pm 3.5$  in the learning task and  $16.2 \pm 3.4$  in the reversal learning task. There was a strong negative correlation between learning and reversal learning scores ( $r_s = -0.77$ ,  $P < 0.001$ ) indicating that animals that learned fast were slow in reversal learning and vice versa. Learning speed increased with both activity and boldness (Fig. 2, Table A2 in the Appendix). Conversely, reversal learning speed increased with decreasing activity and boldness, and shyer, less active individuals were faster to reach the criterion in the reversal learning task than bolder and more active ones (Fig. 2, Table A2 in the Appendix). This pattern was more pronounced for bolder males than for bolder females in the learning task (Fig. 2b). More active males were also slower than active females in the reversal learning task (Fig. 2c). Moreover,

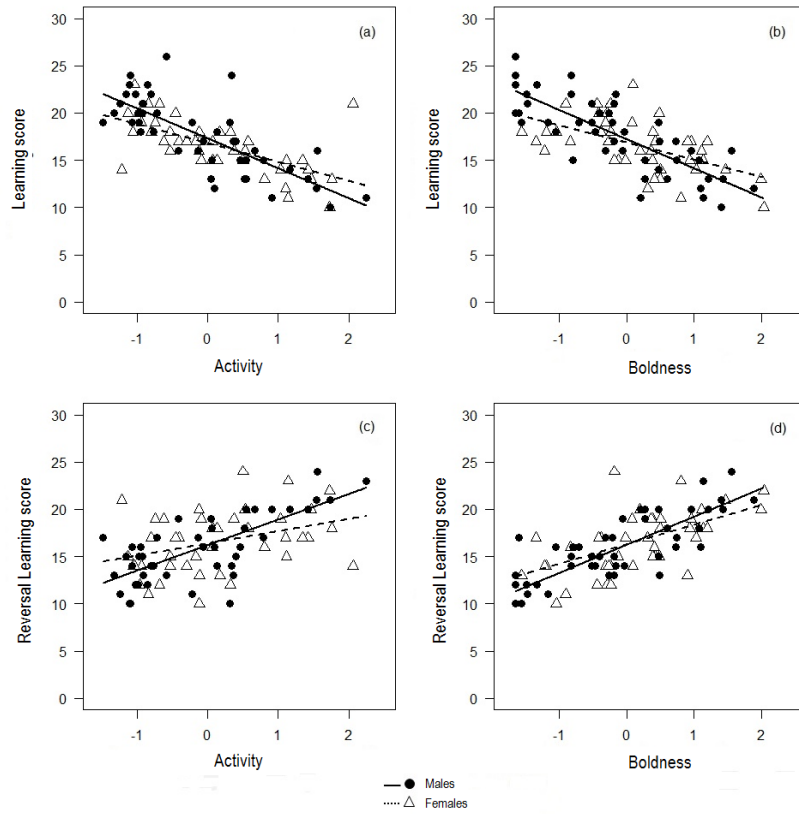
older individuals took more trials to learn the task, but this effect was only present in the model controlling for boldness (Table A2 in the Appendix).

Voles entered the maze after  $7.7 \pm 7.4$  s in the starting area during the learning task, and after  $6.7 \pm 7.0$  s during the reversal learning task. Bolder, more active individuals left the starting area faster than shyer, less active ones in both tasks (Table 2). Older animals took longer to leave the starting area than younger ones in both tasks (Table 2).

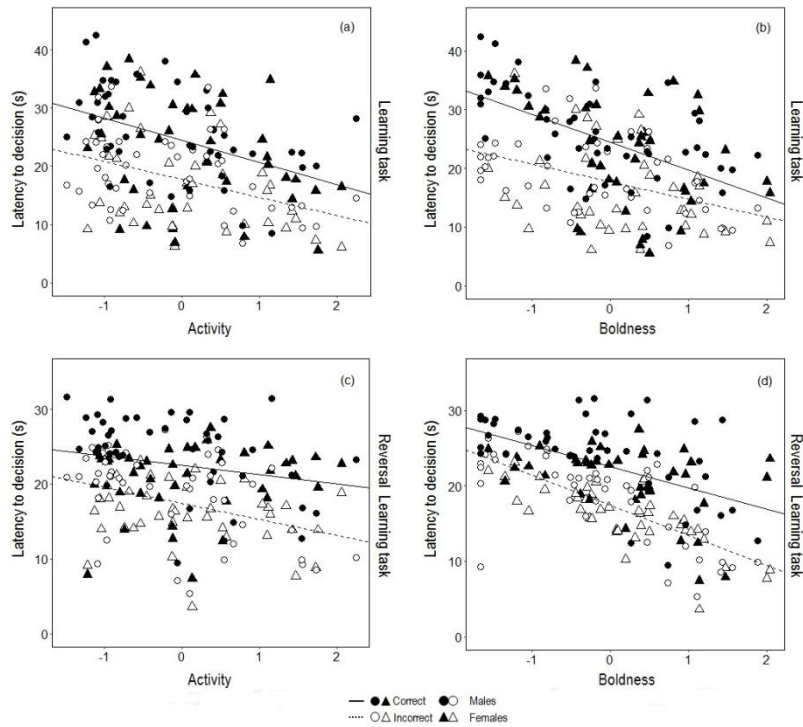
Latency to decision averaged  $22.3 \pm 9.7$  s in the learning task and  $20.1 \pm 6.9$  s in the reversal learning task. Correct choices took longer than incorrect ones for all individuals in both tasks (Fig. 3, Table A3 in the Appendix): on average 6.5 s more in the learning task and 5.6 s more in the reversal learning task. Decisions, correct and incorrect, were faster for bolder and more active individuals than for shyer, less active ones in both tasks (Fig. 3). This pattern remained constant across tasks and did not vary with trial number. For males, correct decisions took significantly longer than for females in the reversal learning task: on average 6.1 s more for males and 5.0 s more for females (Table A3 in the Appendix). The difference between the latencies to a correct and an incorrect decision decreased with increasing boldness in the learning task (Fig. 3a, b), and increased with increasing boldness in the reversal learning task (Fig. 3c, d).

Persistence, expressed here as latency to correct an incorrect decision, averaged  $38.3 \pm 47.0$  s in the learning task and  $46.2 \pm 46.3$  s in the reversal learning task. Persistence increased with boldness in both tasks (Table 3). In both tasks, persistence decreased with increasing trial number (Table 3). Males were more persistent than females in both tasks in the models controlling for boldness (Table 3).





**Fig. 2** – (a, b) Learning and (c, d) reversal learning scores of males and females, represented as number of trials needed to solve the task successfully, in relation to (a, c) activity and (b, d) boldness scores.



**Fig. 3** – Individual mean latency to decision (s) for correct and incorrect choices of males and females, in (a, b) learning and (c, d) reversal learning tasks, in relation to (a, c) activity and (b, d) boldness scores.

	Learning task				Reversal learning task			
	Estimate	SE	<i>t</i>	<i>P</i>	Estimate	SE	<i>t</i>	<i>P</i>
<b>Model controlling for boldness</b>								
Intercept	0.85	0.41	2.07		0.68	0.41	1.68	
Boldness	-1.32	0.47	-2.83	0.005	-0.34	0.08	-4.25	<0.001
Sex (M)	0.14	0.15	0.92	0.36	0.07	0.15	0.45	0.65
No. of trials	-0.003	0.002	-1.64	0.10	-0.002	0.002	-1.66	0.10
Age	0.02	0.01	0.92	0.03	0.03	0.01	2.64	0.01
Boldness*Age	0.03	0.01	2.17	0.03				
<b>Model controlling for activity</b>								
Intercept	0.95	0.43	2.20		0.36	0.18	1.96	
Activity	-0.32	0.09	-3.76	<0.001	-0.14	0.04	-3.77	<0.001
Sex (M)	0.12	0.15	0.78	0.44	0.04	0.07	0.66	0.50
No. of trials	-0.003	0.002	-1.64	0.10	-0.001	0.001	-1.66	0.10
Age	0.02	0.01	1.78	0.07	0.01	0.005	2.12	0.03

**Table 2** – Latency to enter the maze in relation to activity or boldness, age (in weeks), sex and number of test trials for 2866 tests of 86 individual bank voles.

	Learning task				Reversal learning task			
	Estimate	SE	<i>t</i>	<i>P</i>	Estimate	SE	<i>t</i>	<i>P</i>
<b>Model controlling for boldness</b>								
Intercept	3.23	0.44	7.40		2.71	0.45	6.00	
Boldness	0.73	0.08	8.58	<0.001	0.70	0.09	7.94	<0.001
Sex (M)	0.32	0.16	1.98	0.05	0.33	0.17	1.98	0.05
No. of trials	-0.01	0.003	-3.96	<0.001	-0.01	0.004	-4.16	<0.001
Age	-0.003	0.01	-0.23	0.82	0.01	0.01	0.73	0.48
<b>Model controlling for activity</b>								
Intercept	3.15	0.55	5.75		2.66	0.56	4.76	
Activity	0.50	0.11	4.64	<0.001	0.46	0.11	4.13	<0.001
Sex (M)	0.20	0.20	1.04	0.30	0.21	0.20	1.07	0.29
No. of trials	-0.01	0.003	-3.97	<0.001	-0.01	0.004	-4.15	<0.001
Age	0.001	0.01	0.09	0.93	0.01	0.01	0.79	0.44

**Table 3** – Persistence (latency to error correction) in relation to activity or boldness, age (in weeks), sex and number of test trials for 1310 tests of 86 individual bank voles.

## Discussion

Based on olfactory associative learning and reversal learning tests, we showed that learning speed and flexibility are linked to individual differences in boldness and activity in bank voles. Bolder, more active individuals learned the initial association faster but took longer to reverse it, showing less flexibility, whereas shyer, less active individuals were initially slower, but more flexible in acquiring the new association. We also found evidence for a trade-off between decision time and decision outcome, differentially expressed according to personality. Our results support the hypothesis that individual differences in behaviour are reflected in different ‘cognitive styles’, differentially trading off speed for flexibility and accuracy in cognitive tasks. Below we discuss these findings in more detail.

### *Personality differences in associative learning speed and flexibility*

As predicted, bolder and active voles learned faster than shy, less active ones. Bolder, more active individuals might have been faster in forming the association with the reward or they could have established a routine that allowed them to achieve faster responses. Possibly, stop sampling the alternatives leads to better performance in a stable environment, or at least an environment in which the meaning of the cues is unchanged (e.g. Guenther *et al.*, 2014; Griffin, Diquelou, and Perea, 2014; Mamuneas *et al.*, 2014; Chang *et al.*, 2017).

Learning and reversal learning speed, however, were negatively correlated. Bolder, more active individuals that quickly learnt the initial association did not adjust as quickly to the change in meaning of the cues. Shy, less active voles adjusted to the alteration, expressing greater flexibility in their response. Bank voles, thus, showed a trade-off between learning speed and flexibility that aligned with their personality traits, in accordance with previous studies (e.g. Brust *et al.*, 2013; Guillette, Hahn, Hoeschele, Przyslupski, and Sturdy, 2015) and Sih and Del Giudice's (2012) predictions (Table 1).

### *Speed–accuracy trade-off*

Our results clearly indicate the presence of a speed–accuracy trade-off between decision time and choice outcome that applied to all individuals in both tasks. Moreover, this trade-off was linked to personality: different personality types displayed the trade-off between the time required to make a choice and the choice outcome differently and according to the task in which they were more challenged.

Bolder, more active voles made their choices (correct and incorrect) faster than shy, less active ones in both tasks. Individuals may need a variable amount of time to gather information (e.g. Dall, Giraldeau, Olsson, McNamara, and Stephens, 2005; Lotem and Halpern, 2012). Longer latencies to decision might be due to more time spent in assessing the surroundings, examining the cues and making a response by shy, less active individuals (e.g. Burns and Rodd, 2008). Bolder and more active voles, because of routine formation, skip or shorten the process of assessment and decision. Also, bolder and stronger animals might be less affected by a wrong decision (e.g. Luttbegg and Sih, 2010; Sih, 1992; Sih and Del Giudice, 2012), although this may not be true for small mammals with high predation rates (e.g. Norrdahl and Korpimäki, 1995).

We also found that for bolder, more active individuals, the time needed for a correct decision was much longer than the time required for an incorrect one in the reversal task. During initial learning this difference was less pronounced. This was possibly due to the difficulty in updating the response and overcoming the established routine. Shy, less active individuals that do not rely on such routines or need to overcome them when conditions change showed an opposite pattern, that is, their correct decisions took much longer than the incorrect ones in the initial learning, but the difference was less

pronounced in the reversal task. It is also possible that bolder and more active individuals needed more time to retrieve the memory of previous choices' outcomes, given that they are thought to store less information for a shorter period of time if excess information slows decision making (e.g. Kuhl, Dudukovic, Kahn, and Wagner, 2007; Schooler and Hertwig, 2005). Reaume, Sokolowski, and Mery (2011) found that fast-learning explorative 'rover' flies, *Drosophila melanogaster*, are less adept at retrieving previously learned information (retroactive interference) than slow-learning sedentary 'sitter' flies. Rovers experience greater environmental heterogeneity and therefore are less likely to require reference to old information. In vertebrates, however, support for the trade-off between acquisition and retention has been mixed and studies are mostly restricted to humans (e.g. Kyllonen and Tirre, 1988; Slamecka and McElree, 1983; MacDonald, Stigsdotter-Neely, Derwinger, and Bäckman, 2006). In our case, the speed–accuracy trade-off seems linked to the perceived difficulty of the task, which varied between individuals depending on personality and cognitive style.

#### *Personality differences in motivation*

Latency to enter the maze was shorter for more active than less active voles as shown in several studies (e.g. Coleman, Tully, and McMillan, 2005; Griffin *et al.*, 2014; Overington, Cauchard, Côté, and Lefebvre, 2011). This pattern can be explained by a need for less information about the surroundings, higher risk proneness and willingness to explore in bolder, more active individuals (Griffin *et al.*, 2014; Guillette *et al.*, 2011; Lotem and Halpern, 2012), and is in line with Sih and Del Giudice's (2012) hypothesis. We expected that reaching the home cage would particularly motivate shyer animals to engage in the test (e.g. Carrete and Tella, 2009; López, Hawlena, Polo, Amo, and Martín, 2005). This would have balanced out bolder individuals' more pronounced exploratory tendency and activity. The results show that bolder, more active animals were faster to enter the maze than shyer, less active ones, and this pattern did not vary during the experiment. Individuals' motivation to engage in the test would thus appear relatively constant throughout the experiment, minimizing the effect of habituation and different motivational status on our results (e.g. Rowe and Healy, 2014).

#### *Personality differences in persistence*

Persistence decreased with experience in both tasks, indicating a learning process. When faced with the choice to quit an option, for example following a 'win–stay, lose–shift' rule, bolder, more active individuals are expected to persist longer even after some failures (Sih and Del Giudice, 2012). In our study, shyer and less active voles corrected a wrong decision within a few seconds, whereas bolder, more active ones showed greater persistence. Routine formation is well known for bolder, more active individuals (e.g. Koolhaas *et al.*, 1999). More flexible individuals, relying more on environmental information than fixed routines, would be quicker in trying alternatives. Finding alternative solutions seems in fact a recurring feature in shyer, less active individuals. Cole and Quinn (2012) found that it is usually shy low-ranking birds that find innovative solutions to a problem, whereas the so-called 'good

competitors' might not need it, being able to cope with the costs associated with intense competition. Similar findings were also shown in primates (e.g. Kummer and Goodall, 1985; Reader and Laland, 2001), corvids (e.g. Katzir, 1983) and fish (e.g. Laland and Reader, 1999a, 1999b).

Persistence in a wrong choice might also be considered as an example of the Concorde fallacy, the persistence in a non-preferred option owing to prior investment (Dawkins and Carlisle, 1976). In our study, voles that have already put time and effort in running, exposed, the length of the maze might be unwilling to do it again and so would persevere in the choice they have 'invested' in. Sih and Del Giudice (2012) suggested that bolder, more active individuals are more likely to fall victim to this fallacy (but see e.g. Arkes and Ayton, 1999; Magalhães and White, 2014). Several studies have investigated the Concorde fallacy in birds (e.g. Magalhães and White, 2014; Kacelnik and Marsh, 2002; Navarro and Fantino, 2005) and mammals (e.g. Arkes and Blumer, 1985; Cunha and Caldieraro, 2009; Magalhães, White, Stewart, Beeby, and van der Vliet, 2011). However, to our knowledge, the possible connection with personality has not been empirically investigated. Further studies should address this intriguing possibility.

#### *Sex differences in the connection between personality and cognitive style*

Male and female voles did not differ in learning or reversal learning scores per se. However, the relationship between cognitive traits and personality was more pronounced for males than females. In bank voles, males roam through large areas; they are also the dispersing sex (Gipps, 1984, 1985). They would need to acquire and process a constant flow of new information relative to their bearings. Also, frequently moving to a different location might favour shallow sampling and quick, albeit cursory, assessment of new options (Sih and Del Giudice, 2012). Their ever-changing surroundings might promote faster learning compared to females, which occupy and defend small territories (e.g. Guenther *et al.*, 2014; Guillette *et al.*, 2009; Jonasson, 2005; Lucon-Xiccato and Bisazza, 2017).

Females would instead benefit from a more accurate and extensive understanding of the environment they inhabit (Sih and Del Giudice, 2012). Our results seem to indicate that females show more cognitive flexibility than males and are more ready to change their response when a learned rule becomes inappropriate in a new context. This interpretation would be in accordance with previous studies on fish, domestic birds, primates and rodents (e.g. Guillamón *et al.*, 1986; Ha, Mandell, and Gray, 2011; Lucon-Xiccato and Bisazza, 2014; Rogers, 1974).

#### *Slower learning with age*

Older voles were slower to learn than younger ones. Senescence generally brings about a decline in both cognitive and physical functioning (e.g. Barnes, 1979; Languille *et al.*, 2012; Van der Staay, Van Nies, and Raaijmakers, 1990), including the processing of olfactory signals (e.g. Aujard and Némoz-Bertholet, 2004; Nusbaum, 1999; Rosli, Breckenridge, and Smith, 1999), even though both the onset

and which capacities are impaired may vary greatly (e.g. Bachevalier *et al.*, 1991; Languille *et al.*, 2012; Schoenbaum, Nugent, Saddoris, and Gallagher, 2002).

Cognitive flexibility is likewise often affected by age, with older animals expressing difficulty in reversing or shifting previous discriminations to make flexible use of acquired memories (e.g. Barense, Fox and Baxter, 2002; Joly, Deputte, and Verdier, 2006; Moore, Killiany, Herndon, Rosene, and Moss, 2003). This, however, was not the case in the present study. Our voles might not have differed enough in age to show significant patterns and we do not know whether and at what stage in life the effects of senescence on flexibility might appear in captive bank voles (e.g. Bachevalier *et al.*, 1991; Hämäläinen *et al.*, 2014; Lemaître, Gaillard, Lackey, Clauss, and Müller, 2013).

Older voles took longer to enter the maze in all trials. The time required to gather enough information on the surroundings might have increased with age, independent of the amount of information that the individual would deem sufficient (e.g. Deakin, Aitken, Robbins, and Sahakian, 2004). Being older might also entail a decrease in risk taking (e.g. Josef *et al.*, 2016; Lhotellier and Cohen-Salmon, 1989; Wax, 1977).

#### *Possible proximate and ultimate mechanisms*

Taken together, we found that individuals with different personality traits approached cognitive tasks with different strategies. At the proximate level, brain neurochemistry and stress response more typical of a given personality profile could affect cognitive performance (e.g. Coppens, de Boer, and Koolhaas, 2010; Øverli *et al.*, 2007). Some studies have also detected a heritable component in fast and slow learners (e.g. Cape and Vleck, 1981; Tsai, Chen, Ma, Hsu, and Lee, 2002). In our study, we did not detect differences in behaviour or cognition between litters, but since it was not designed to investigate genetic variation, this aspect requires further investigation. The risk–reward trade-off described by Sih and Del Giudice (2012) provides an explanation for the evolutionary maintenance of variation in strategies in populations. Bolder, more active animals would consistently try to maximize reward, at the cost of running higher risks. This would require the animal to quickly process and sort all the relevant information in time to obtain this short-term gain. Conversely, shyer, less active individuals would consistently choose safety, thus needing a slower and thorough processing of information that will ensure accurate decisions and long-term rewards in terms of survival. In addition, while it is true that the most able individuals could be both fast and accurate, the speed–accuracy/flexibility trade-off might eventually promote alternative strategies yielding similar overall fitness (Sih and Del Giudice, 2012). Future empirical studies should consider the fitness consequences of these different strategies. Although studying the effects of cognition on survival and reproduction is challenging, some pioneering studies have started to pave the way (e.g. Boogert, Fawcett, and Lefebvre, 2011; Dukas, 2004; Gaulin and Fitzgerald, 1989; Hollis and Kawecki, 2014; Isden, Panayi, Dingle, and Madden, 2013; Mery and Kawecki, 2002).

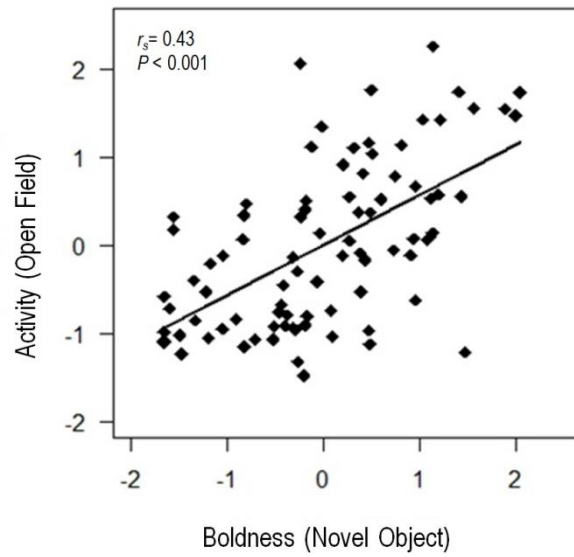
### *Conclusions*

Illuminating the causes and consequences of individual variation in cognition is a current and fascinating area of research (e.g. Griffin *et al.*, 2015). Here, we have provided empirical evidence supporting the hypothesis of personality and cognitive styles being connected through a speed–accuracy/flexibility trade-off (Sih and Del Giudice, 2012). Thus, individual differences in multiple behaviours predicted whether and how individuals differed in trading speed for accuracy and flexibility in a cognitive task. This link between personality and cognition appears to be a valuable tool to interpret otherwise incomprehensible differences in behaviour between conspecifics. Future studies should focus on how personality and cognitive style influence the way individuals behave in their environment, how they approach changes and challenges and how they make decisions regarding resource use, predation, competition, social relationships and reproduction to ultimately illuminate how between-individual differences in cognitive styles are maintained in natural populations.

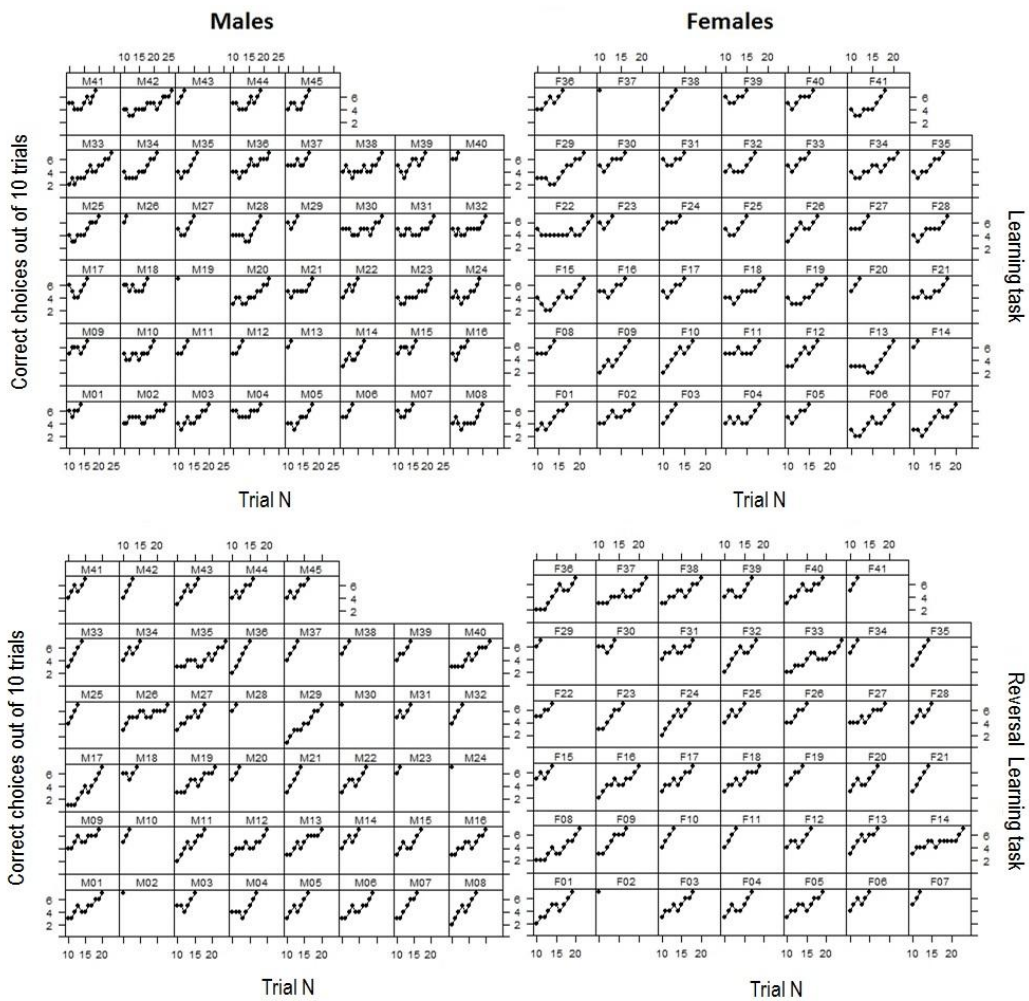
### **Acknowledgments**

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## Appendix



**Fig. A1** – Relationship between activity (open field test) and boldness (novel object test) mean scores per individual for 86 individual bank voles.



**Fig. A2** – Individual learning curves.



Test	Variable	PC 1	PC 2	PC 3	PC 4	Transformation for PCA
Open field	Latency to centre <sup>a</sup>	-0.54	0.82	-0.17		Log
	Time in the centre <sup>b</sup>	0.61	0.24	-0.76		Sqrt, arcsine
	Exploration <sup>c</sup>	0.58	0.52	0.63		Sqrt, arcsine
	Eigenvalue	1.50	0.70	0.51		
	Variance explained	0.75	0.16	0.09		
	Repeatability ( $\pm$ SE)* <i>p</i> *	0.74 $\pm$ 0.05 < 0.001				
Novel object	Latency to exit <sup>d†</sup>	0.48	-0.6	-0.61	-0.19	Log, increased by
	Latency to reach object <sup>e†</sup>	0.50	-0.40	0.71	0.28	/
	Interaction with object <sup>f†</sup>	-0.51	-0.45	-0.17	0.71	Sqrt
	No. of interactions with object <sup>g†</sup>	-0.50	-0.52	0.31	-0.62	Log
	Eigenvalue	1.77	0.73	0.46	0.32	
	Variance explained (%) Repeatability ( $\pm$ SE)* <i>p</i> *	0.78 0.67 $\pm$ 0.05 < 0.001		0.13	0.05	0.02

<sup>a</sup>Latency to enter the central unsafe area.

<sup>b</sup>Proportion of time spent in the central unsafe area.

<sup>c</sup>Proportion of time spent moving in the whole arena.

<sup>d</sup>Latency to leave the nest.

<sup>e</sup>Latency to approach the novel object.

<sup>f</sup>Time spent exploring/interacting with the novel object.

<sup>g</sup>No. of approaches/interactions.

†PCA scores resulting from these components were transformed inverting the signs, so that a higher score expresses higher boldness and a lower score expresses lower boldness.

\*Repeatabilities and their significance were calculated after Lessells and Boag (1987) and Nakagawa and Schielzeth (2010) from a one-way ANOVA with individual as a factor using the R package rptR (Stoffel *et al.*, 2017).

**Table A1** – Loadings, *eigenvalues* and explained variance of PCAs of behaviours in open field test and novel object test as well as repeatability for 86 bank voles.

	Learning task				Reversal learning task			
	Estimate	SE	<i>t</i>	<i>P</i>	Estimate	SE	<i>t</i>	<i>P</i>
<b>Model controlling for boldness</b>								
Intercept	13.17	1.39	9.45		15.77	1.44	10.93	
Boldness	-1.78	0.43	-4.18	<0.001	2.30	0.44	5.21	<0.001
Sex (M)	0.39	0.51	0.76	0.42	0.18	0.53	0.34	0.71
Age	0.10	0.04	2.75	0.007	0.01	0.04	0.28	0.78
Boldness*Sex	-1.15	0.55	-2.09	0.03	0.51	0.57	0.89	0.37
<b>Model controlling for activity</b>								
Intercept	14.53	1.39	9.91		14.92	1.71	8.73	
Activity	-1.91	0.42	-4.54	<0.001	1.34	0.49	2.75	<0.001
Sex (M)	0.55	0.52	1.06	0.35	-0.15	0.61	-0.24	0.70
Age	0.06	0.04	1.60	0.11	0.04	0.04	0.89	0.38
Activity*Sex	-1.11	0.56	-1.96	0.06	1.45	0.66	2.21	0.02

**Table A2** – Learning and reversal learning scores in relation to activity or boldness, age (in weeks), sex and number of test trials for 2866 tests of 86 individual bank voles.

	Learning task				Reversal learning task			
	Estimate	SE	<i>t</i>	<i>P</i>	Estimate	SE	<i>t</i>	<i>P</i>
<b>Model controlling for boldness</b>								
Intercept	13.92	3.70	3.76		17.20	1.97	8.74	
Choice (1)	6.28	0.34	18.73	<0.001	4.08	0.34	12.12	<0.001
No. of trials	0.08	0.03	2.55	0.01	0.04	0.03	1.84	0.07
Boldness	-2.31	0.74	-3.11	0.002	-4.07	0.40	-10.16	<0.001
Age	0.09	0.10	0.92	0.36	-0.01	0.05	-0.15	0.88
Sex (M)	1.66	1.36	1.22	0.22	1.37	0.75	1.82	0.068
Choice*Boldness	-2.24	0.33	-6.72	<0.001	1.55	0.23	6.81	<0.001
Choice*Sex					1.36	0.43	3.19	<0.001
<b>Model controlling for activity</b>								
Intercept	15.23	3.92	3.88		16.51	2.62	6.30	
Choice (1)	6.44	0.34	18.96	<0.001	4.28	0.34	12.71	<0.001
No. of trials	0.08	0.03	2.60	0.01	0.04	0.03	1.93	0.05
Activity	-2.62	0.80	-3.27	0.002	-2.20	0.53	-4.16	<0.001
Age	0.05	0.10	0.44	0.66	-0.002	0.07	-0.03	0.97
Sex (M)	2.01	1.40	1.44	0.15	2.11	0.96	2.21	0.025
Choice*Activity	-1.11	0.35	-3.14	0.002	1.22	0.22	5.44	<0.001
Choice*Sex					1.18	0.43	2.77	0.002

**Table A3** – Latency to decision in relation to activity or boldness, age (in weeks), sex, choice outcome and number of test trials for 2866 tests of 86 individual bank voles.

*“It is our choices that show what we truly are, far more than our abilities.”*

J.K. Rowling, 1998

*“Strategy is a pattern in a stream of decisions.”*

H. Mintzberg, 1978

## Chapter 2

### INDIVIDUAL VARIATION IN COGNITIVE STYLES AFFECTS FORAGING AND ANTI-PREDATORY STRATEGIES IN A SMALL MAMMAL

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#### Abstract

Balancing foraging gain and predation risk is one of the most fundamental trade-offs in the life of animals. Among-individual variation in cognition might affect how individuals balance these conflicting necessities, but the processes underlying individual differences are still unclear. Here we empirically assessed direct consequences of cognitive styles for fitness-determining behaviours, such as foraging and risk-taking behaviour, using a semi-natural setting. We exposed fast/inflexible (N = 21) and slow/flexible (N = 18) learners of bank voles (*Myodes glareolus*) to enclosed landscapes with different risk levels at two food patches. We quantified foraging behaviour, individual giving-up densities for food (a measure for perceived predation risk), and vigilance behaviour, which in a species with high predation pressure directly relate to fitness. Fast learners consumed up to 20% more food than slow learners in the high-risk area, increasingly exploited both food patches, and spent up to 75% of their visit foraging. Slow learners progressively avoided the high-risk area and spent approximately 50% of their visit exercising vigilance even in the low-risk area. Our results indicate that among-individual differences in cognitive styles are indeed reflected in different foraging and anti-predator strategies, providing insights into fitness consequences and differential selection pressures based on individual differences in cognition.

**Keywords:** fitness – giving-up density – animal personality – risk-reward trade-off – rodent.

## Introduction

The ability to gear decisions optimally towards environmental conditions is a fundamental determinant of fitness. Relevant actions include feeding, raising offspring, resting, searching for a suitable habitation, looking for a future mate, guarding a present mate, engaging in social activities, and defending its territory. Engaging in each activity usually prevents the individual from doing any of the others creating lost opportunity cost (e.g. Dunbar *et al.*, 2009). Moreover, each activity potentially exposes the individual to the risk of being attacked by a predator. So the individual's decisions will have to consider not only the behaviour in which to engage, but also the best way to do it safely (e.g. Dall *et al.*, 2005; Lima and Dill, 1990). Successful reproduction and survival thus require an efficient estimate of the value of a resource relative to the risk obtaining it. If these assessments are done correctly, the trade-off between gain and safety will not be too expensive (e.g. Dall *et al.*, 2005; Houston and MacNamara, 1993). The outcome of the animal's assessments will depend on environmental and social context, physical state, life-history and past experiences (e.g. Blumstein and Bouskila 1996; Dubois *et al.*, 2012; Gowaty and Hubbell, 2009; Lima and Dill, 1990; Samia *et al.*, 2013). Also, decisions are often influenced by the individual's bias in favour of either immediate reward over safety or *vice versa* (e.g. Hunt *et al.*, 1989; Martin and Potts, 2009; Zuckerman and Kuhlman, 2000). For example, given the same circumstances, an individual may choose to spend a long time consuming desirable food in an exposed patch, while another may exploit the same patch for a shorter time, or maybe not at all, to avoid exposure to predators.

This bias is part of the individual cognitive style/personality make-up (Sih and Del Giudice, 2012), i.e. the specific strategy by which individuals acquire and process information (Bebus *et al.*, 2016; Griffin *et al.*, 2015; Sih and Del Giudice, 2012). Individual differences in cognitive style may therefore have consequences for the individual's life- and fitness-determining choices and strategies.

In the last decade, there have been appeals for studying cognition at the individual level (e.g. Thornton and Lukas, 2012; Morand-Ferron and Quinn, 2015), for including individual differences and cognition in ecological studies (e.g. Réale *et al.*, 2007; Sih and Del Giudice, 2012), for studying cognition in more natural settings (e.g. Pritchard *et al.*, 2016; Thornton *et al.*, 2014; Morand-Ferron *et al.*, 2016), as well as cautions that none of these tasks is easily accomplished (Rowe and Healy, 2014). Some empirical evidence suggested that cognition might affect reproductive success (reviewed in Boogert *et al.*, 2011; but see Isden *et al.*, 2013) and competitiveness (e.g. Cole and Quinn, 2011). Information about cognitive strategies and risk-reward bias may complement the study of cognitive abilities, and provide a possible explanation for the sustained existence of slow learners in the population. However, there is almost no empirical study addressing the effect of cognitive style on fitness (proxies) in the wild (but see Raine and Chittka, 2008; Cole *et al.*, 2012), and moreover, most studies on cognition are conducted

under laboratory conditions, leaving a gap in our understanding of the ultimate consequences of among-individuals differences in personality and cognition (e.g. Morand-Ferron *et al.*, 2016).

Therefore, the main aim of our study was to test whether individuals with different cognitive styles adopt different foraging and antipredatory strategies in a semi-natural environment. Our study species was the bank vole (*Myodes glareolus*), a rodent common in the Eurasia that subsists on temporally unpredictable food resources such as seed mast (e.g. Abt and Bock, 1998; Hansson 1969-1977; Watts *et al.*, 1968), and is subject to intense predatory pressure by avian and terrestrial predators alike (e.g. Jędrzejewski *et al.*, 1993; Sundell *et al.*, 2003). Bank voles have been shown to be behaviourally and cognitively flexible, adjusting their anti-predatory responses to the perceived predator cues (e.g. Jędrzejewski *et al.*, 1993; Liesenjohann and Eccard, 2008). Bank voles thus make a suitable study species to address how cognition may be involved in the trade-offs caused by the conflicting needs of foraging and avoiding predation.

The giving-up density (GUD) framework provides a powerful experimental approach with a strong theoretical underpinning to quantitatively measure foraging decisions under varying predation risk (Bedoya-Perez *et al.*, 2013; Brown, 1988, Jacob and Brown, 2000). The GUD model predicts that a forager will stop depleting a patch when the benefits of the harvest rate no longer exceed the costs of foraging, expressed as the sum of energetic loss, predation risk and missed opportunity cost (Brown 1988). As the amount of food in a given patch of a food/non-food mixture is progressively depleted, feeding rate decreases and so does the benefit/cost ratio. Therefore, the amount of food that foragers leave in a patch (i.e., the GUD) reflects the harvest rate that is not acceptable to justify associated costs and risks (Brown, 1988). Manipulating cover at the food patch location while keeping all other costs constant allows quantification of perceived predation risk (e.g. Bakker *et al.*, 2005; Jacob, 2008; Pusenius and Schmidt, 2002; Verdolin, 2006).

We hypothesised that individual bank voles with different cognitive style might solve the risk-reward trade-off using different foraging and anti-predatory strategies in a semi-natural setting. Specifically, we predicted that individuals with a fast and inflexible cognitive style would preferentially choose immediate rewards at the cost of higher predation risk. They would exploit more a high-risk food patch and therefore have lower GUDs, and spend comparatively little time exercising vigilance behaviour (Sih and Del Giudice, 2012). Individuals with a slow and flexible cognitive style would instead favour safety and delay rewards. They would exploit the high-risk food patch very little, if at all, thus having higher GUDs, and invest a considerable amount of time in vigilance behaviour (Sih and Del Giudice, 2012) and would be willing to invest more time foraging in the low-risk patch compared to bolder faster, inflexible individuals.

## Methods

### *Animals and housing*

Bank voles (45 males and 41 females) were born in captivity from wild captured mothers. Animals were housed individually in standard laboratory cages (36 x 21 x 15 cm) provided with wood shavings and hay as bedding, and a cardboard shelter. Temperature was set at 21°C and humidity at 50-55%. Commercial food pellets (Altromin 1324; Altromin Spezialfutter GmbH & Co.KG, Lage, Germany) and water *ad libitum* were supplied at all times. Bedding was changed every week.

### *Assessment of cognitive style and personality, and choice of experimental groups*

Individuals were assessed for cognitive style and personality. A detailed description of testing procedures is provided in Mazza *et al.* (in press). Briefly, we tested the voles for their olfactory associative learning speed and flexibility in a reward contingency. We also assessed among-individual differences in activity, exploration and boldness using two standardized laboratory tests (Réale *et al.*, 2007): the open field test and the novel object test. Cognition and personality were closely related (Mazza *et al.*, in press), with faster, inflexible learners being bolder and more active than slower, flexible learners. We selected the 30 males and 30 females that displayed the fastest cognitive style (N = 15 males, N = 15 females, Fig. 1) and the slowest cognitive style (N = 15 males, N = 15 females, Fig. 1). These individuals are termed fast learners and slow learners from here on. The groups differed in activity and boldness, as well as learning and reversal learning speed (Mann-Whitney-U test, all  $p < 0.05$ , Fig. 1). Of the 60 individuals, 9 (4 males and 5 females) were used for preliminary trials, 7 (4 males and 3 females) died before being tested in the enclosures, and 5 (4 males, 1 female) died during the enclosures trials. Age of voles was above average (14 -17 months) and mortality rates were within normal range (e.g. Bujalska, 1975). Therefore, we report results for 39 voles: 21 fast learners (10 males and 11 females) and 18 slow learners (8 males and 10 females).

### *Enclosure trials*

#### *Enclosure setup*

Experiments were conducted in four 3 x 4 m semi-natural enclosures with a concrete base and walls of about 90 cm that were filled with a soil layer of 40 cm. Enclosures were protected against predators and weather conditions by mesh wire and a plastic roof cover 3 m above the enclosures. They were sown with a local grass mix to mimic perennial grassland. Each enclosure was divided into two areas of equal size: a low-risk, high-grass area with ca. 20 cm vegetation height, and a high-risk low-grass area with ca. 2 cm vegetation height. We added camouflage netting (2 x 3 m) above the low-risk area to provide additional cover. The position of low risk and high areas was alternated across enclosures. In each enclosure a plastic nest box (32 x 22 x 16 cm) provided with hay was buried level with the enclosure surface in one corner of the low-risk area to provide a nesting opportunity.

A plastic tray (20 x 15 x 5 cm) was placed level with the enclosure surface in the middle of each low- and high-risk area to create an artificial food patch. Each tray contained 2 g of crushed hazelnuts mixed into 0.75 l of sand (e.g. Jacob and Brown, 2000). Preliminary trials were run to test the appropriateness of food and substrate type and quantity, as well as the overall structure of the feeding station (e.g. Bedoya-Perez *et al.*, 2013). The animals used in the preliminary study were not involved in the main experiment. At the end of each trial, enclosures were watered and mowed to the desired vegetation height, and the hay in the nest-box was replaced.

#### *Experimental procedure*

Experiments were conducted from June to September 2016. At the start of each trial, two fast learners and two slow learners were taken from their home cage and weighed with a spring scale (*PESOLA AG, Schindellegi, Switzerland*) to the nearest gram. They were transferred into a plastic tube of 15 cm diameter and transported to the enclosures where they were placed individually in the low-risk area, between the entrance to the nest-box and the food patch. Voles remained in the enclosures for five days. They were then retrieved using live traps (Ugglan Special Traps n. 2, Grahnb AB, Hillerstorp, Sweden) and weighed.

Food trays were replaced every morning around 08.30 am. The sand was sieved, and recovered food items were dried in a drying cabinet at 60°C for six hours to remove moisture. The dried food was cleaned of remaining sand and debris, and weighed to the nearest centigram to determine GUDs.

Food patches were monitored with motion-sensor, infra-red video-cameras (1/4" CMOS Night Vision Camera, Detec Secure, Detec Handels GmbH, Witzenhausen, Germany). One observer (VM) quantified the following variables from the video footage using the software BORIS (Friard and Gamba, 2016): number of visits to each food patch, visit duration (sec), and proportion of time spent searching for food (e.g. digging, exploring the food patch while looking at the sand), eating (retrieving, handling and consuming hazelnuts) and exercising vigilance (cessation of feeding with head up and inspection of the surroundings – e.g. Lima and Bednekoff, 1999). Behaviours “searching” and “eating” were later pooled and considered as “foraging”.

#### *Statistical analyses*

We used restricted maximum-likelihood linear mixed models (LMMs) to evaluate the relationship between the giving-up densities (GUDs) and cognitive style, risk area (high-risk/low-risk), sex, and mean-centred experimental day, all specified as fixed effects. We also ran separated LMMs to evaluate the relationships between duration of visits to the food patches, proportion of time spent foraging and exercising vigilance, respectively with cognitive style, risk area sex, mean-centred experimental day and time of day (day/night). We used maximum-likelihood generalized linear mixed models (GLMMs) with Poisson-distributed errors to evaluate the relationship between the number of visits to each food patch and cognitive style, risk area sex, mean-centred experimental day and time of day (day/night). In all



models, cognitive style, risk area, sex, experimental day and time of day were considered as fixed effects and individual identity was added as random factor, specified as random intercept. We initially took into account the dependence of the two food trays within each experimental day by adding an additional random factor specifying individual experimental days. Since this factor did not improve the models' AIC, it was removed from the reported models.

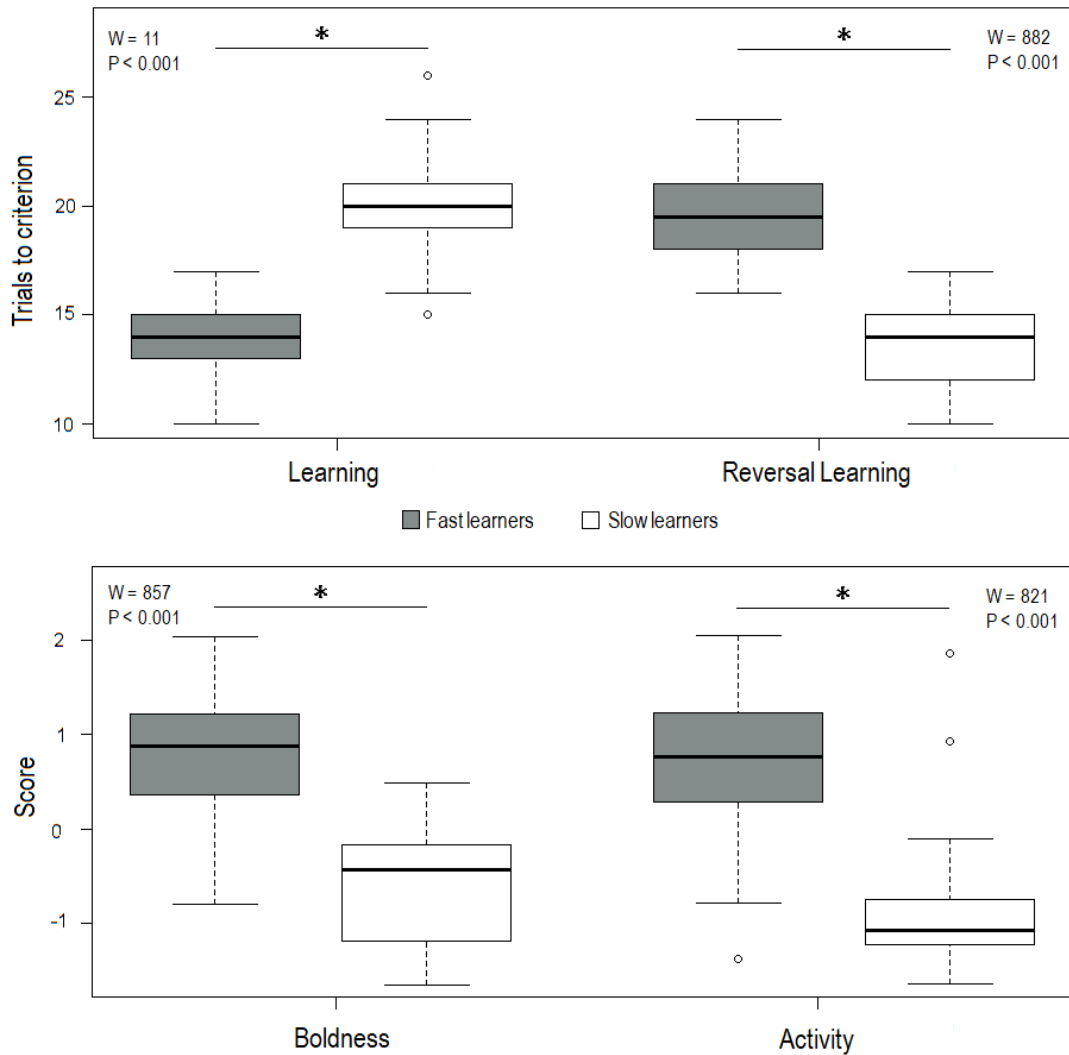
Duration of visits was log-transformed, and GUDs were reversed to food consumption (amount of food provided – amount of food left), increased by 1 and then log-transformed, to meet the normality assumption. The proportions of time spent foraging and in vigilance were square-root transformed to meet the normality assumption. The proportions of time spent foraging and in vigilance were square-root transformed to meet the normality assumption. Based on existing literature (e.g. Jacob and Brown, 2000) and on preliminary data analyses, we included in the initial models 3- and 2-way interactions among all the explanatory variables except sex, that was never found to interact with any other factor. Analyses were first performed on the whole datasets; a 3-way interaction between the explanatory variables cognitive style, risk area and experimental day was found in each case, so we re-ran the analyses on subsets of data including only fast learners or only slow learners, respectively. Subsequently, we ran the analysis on subsets of data including only the high-risk or the low-risk area. In these models, we excluded interactions stepwise if they proved non-significant based on log-likelihood ratio tests (Zuur *et al.*, 2009). All data analyses were conducted with R, version 3.2.3 (R core team, 2015) using the R packages nlme, version 3.1-131, and lme4, version 1.1-12 (Bates *et al.*, 2015; Pinheiro *et al.*, 2017). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality.

We compared the overall food consumption, as well as changes in body weight, expressed as a percentage of the initial body weight, between fast- and slow-learners with Mann-Whitney-U tests.

The accepted significance level was  $\leq 0.05$ .

#### *Ethical note*

All animal experimentation was conducted under the permission of the “Landesamt für Umwelt, Gesundheit und Verbraucherschutz Brandenburg” (reference number: V3-2347-44-2011) and “Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen” (reference number: 84-02.04.2016.A253).



**Fig. A1** – Learning, reversal learning, activity and boldness scores of the 2 groups of bank voles.

Mean ( $\pm$  SD) learning score for fast learners:  $13.6 \pm 1.8$ ; mean learning score for slow learners:  $20.1 \pm 2.3$ . Mean reversal learning score for fast learners:  $19.5 \pm 2.2$ ; mean reversal learning score for slow learners:  $13.9 \pm 2.0$ . Mean boldness score for fast learners:  $0.83 \pm 0.66$ ; mean boldness score for slow learners:  $-0.63 \pm 0.62$ . Mean activity score for fast learners:  $0.85 \pm 0.75$ ; mean activity score for slow learners:  $-0.70 \pm 0.72$ .

## Results

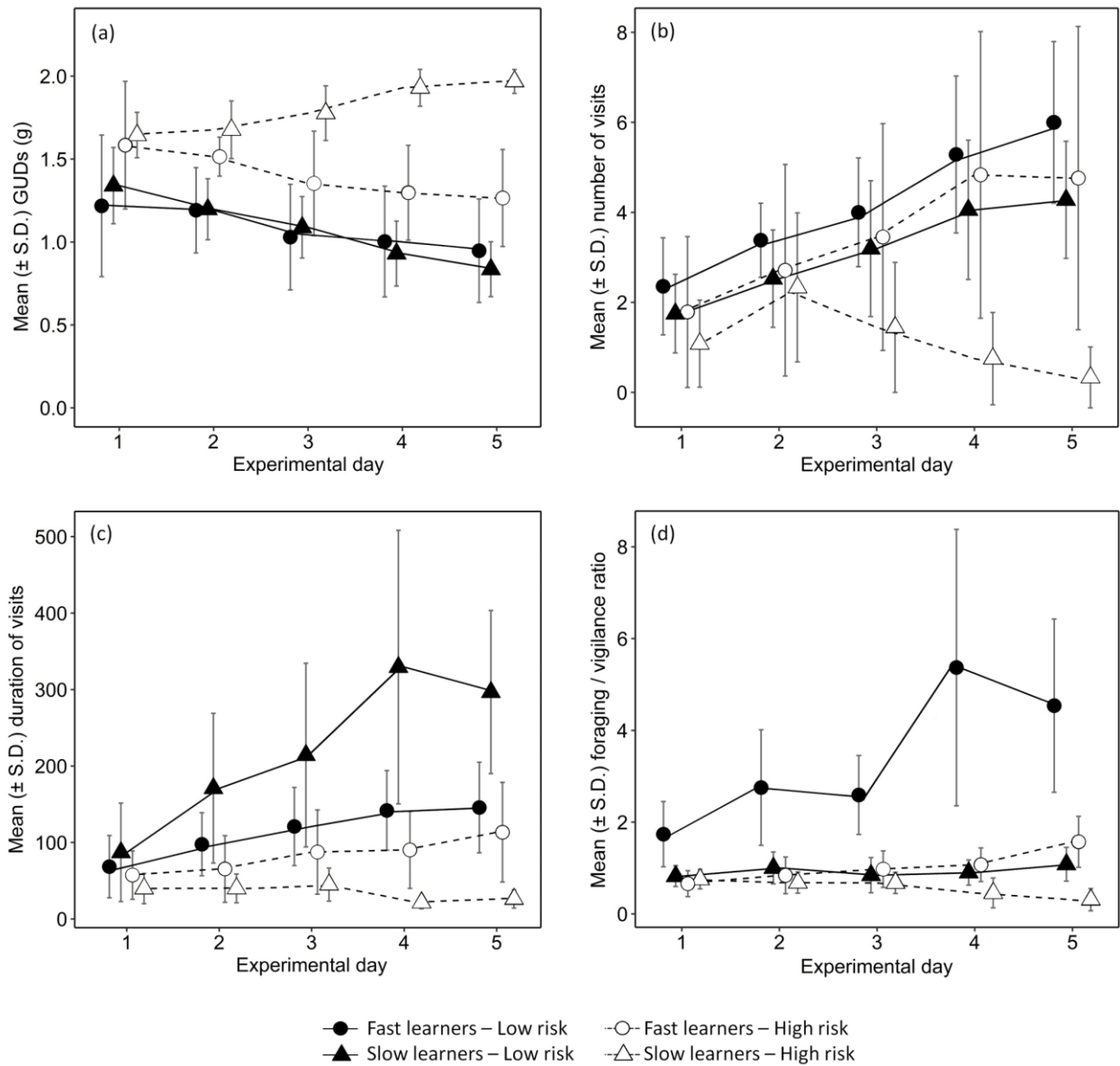
All voles responded to the treatment and exploited the low-risk area more compared to the high-risk area. We found an interaction of risk area and cognitive style (Table 1) for all the variables, and therefore analysed effects of cognitive style within each risk level (Table 2) and effects of risk within each cognitive style (Table 3). Mean GUDs ( $\pm$  S.D.) were  $1.08 \pm 0.35$  g in the low-risk area and  $1.4 \pm 0.31$  g in the high-risk area for fast learners, and  $1.08 \pm 0.26$  g in the low-risk area and  $1.8 \pm 0.19$  g in the high-risk area for slow learners. Voles spent more time in the low-risk area, compared to the high-risk area: fast learners made an average of  $4.2 \pm 1.9$  visits to the low-risk area and  $3.5 \pm 2.9$  visits to the high-risk area, and spent on average 31.4 seconds longer in the low-risk area; slow learners made an

average of  $3.2 \pm 1.6$  visits to the low-risk area and  $1.2 \pm 1.4$  visits to the high-risk area, and spent on average 184.2 seconds longer in the low-risk area.

Fast learners' GUDs progressively decreased in both risk areas over the experimental days (Fig. 1a, Table 2, Table 3). Concurrently, the number and duration of visits progressively increased in both risk areas (Fig. 2b-c, Table 2, Table 3). Fast learners spent on average three times more time exercising foraging than vigilance behaviour in the low risk areas (Fig. 2d, Table 2, Table 3). The proportion of time they spent foraging or in vigilance was approximately the same in the low-risk area (Fig. 2d, Table 2, Table 3). The proportion of time spent in foraging progressively increased in both areas over time, and consequently the proportion of time spent in vigilance decreased (Fig. 2d, Table 2, Table 3).

Slow learners' GUDs progressively decreased in the low-risk area and increased in the high-risk area over experimental days (Fig. 2a, Table 2, Table 3). The number and duration of their visits in the low-risk area increased over time, whereas they became fewer and shorter in the high-risk area (Fig. 2b-c, Table 2, Table 3). Slow learners equally divided the time of their visits to the low-risk area between foraging and exercising vigilance (Fig. 2d, Table 2, Table 3). The proportion of time they spent foraging rather than in vigilance during their visits increased over time in the low-risk area and decreased in the high-risk area (Fig. 2d, Table 2, Table 3).

Food consumption from trays was 30% higher in fast learners ( $7.6 \pm 2.3$  g) than in slow learners ( $5.6 \pm 0.8$  g) (Mann-Whitney-U test:  $W = 305$ ,  $P = 0.001$ ). Slow learners, however, tended to lose slightly less body weight than fast learners during the 5 days in the enclosures (Mann-Whitney-U test:  $W = 3962.5$ ,  $P = 0.051$ ) as weight loss was  $8.7 \pm 6.4$  % of their initial body weight for slow learners and  $9.6 \pm 8.7$  % for fast learners.



**Fig. 2** – Mean ( $\pm$  S.D.) giving-up densities (a), number of visits (b), duration of visits (c) and foraging/vigilance ratio (d) for fast- and slow-learners in high- and low-risk areas for 5 days of observations of 39 individual bank voles (*Myodes glareolus*) in semi-natural enclosures.

	GUDs					Visit N				Visit Duration				
	Estimate	SE	DF	F	P	Estimate	SE	z	P	Estimate	SE	DF	F	P
Intercept	0.64	0.03	1 345	1008.1		1.17	0.05	24.8		4.45	0.09	1 625	7065.9	
Cognitive style (SL)	0.01	0.03	1 36	20.4	<b>&lt;0.001</b>	-0.28	0.06	-5.0	<b>&lt;0.001</b>	0.52	0.11	1 36	1.4	0.25
Area (LR)	-0.19	0.02	1 345	806.1	<b>&lt;0.001</b>	-0.19	0.05	-3.5	<b>&lt;0.001</b>	-0.41	0.05	1 625	580.9	<b>&lt;0.001</b>
Day	0.04	0.01	1 345	39.3	<b>&lt;0.001</b>	0.22	0.02	9.1	<b>&lt;0.001</b>	0.21	0.02	1 625	319.0	<b>&lt;0.001</b>
Sex (M)	-0.01	0.03	1 36	0.1	0.75	-0.10	0.04	-2.4	<b>0.02</b>	-0.06	0.11	1 36	0.2	0.69
Time of day (Night)			/			0.46	0.04	11.1	<b>&lt;0.001</b>	0.36	0.04	1 625	86.6	<b>&lt;0.001</b>
Area:Day	0.02	0.01	1 345	53.4	<b>&lt;0.001</b>	-0.82	0.10	-8.2	<b>&lt;0.001</b>	-0.03	0.03	1 625	47.5	<b>&lt;0.001</b>
Cognitive style:Area	-0.29	0.02	1 345	162.2	<b>&lt;0.001</b>	-0.01	0.04	-0.3	0.78	-1.33	0.08	1 625	247.8	<b>&lt;0.001</b>
Cognitive style:Day	0.03	0.01	1 345	43.0	<b>&lt;0.001</b>	0.01	0.04	0.3	0.74	0.15	0.03	1 625	0.9	0.35
Cognitive style:Area:Day	-0.16	0.02	1 345	99.6	<b>&lt;0.001</b>	-0.49	0.07	-7.1	<b>&lt;0.001</b>	-0.44	0.06	1 625	62.3	<b>&lt;0.001</b>

	Foraging					Vigilance					For / Vig ratio				
	Estimate	SE	DF	F	P	Estimate	SE	DF	F	P	Estimate	SE	DF	F	P
Intercept	73.38	1.48	1 625	4860.1		26.62	1.48	1 625	3249.2		1.16	0.08	1 625	34.74	
Cognitive style (SL)	-26.90	1.76	1 36	138.9	<b>&lt;0.001</b>	26.90	1.76	1 36	138.9	<b>&lt;0.001</b>	-1.31	0.09	1 36	117.67	<b>&lt;0.001</b>
Area (LR)	-25.68	1.19	1 625	433.8	<b>&lt;0.001</b>	25.68	1.19	1 625	433.8	<b>&lt;0.001</b>	-1.26	0.06	1 625	418.10	<b>&lt;0.001</b>
Day	4.79	0.57	1 625	52.7	<b>&lt;0.001</b>	-4.79	0.57	1 625	52.7	<b>&lt;0.001</b>	0.28	0.03	1 625	47.48	<b>&lt;0.001</b>
Sex (M)	0.75	1.58	1 36	0.2	0.67	-0.75	1.58	1 36	0.2	0.67	0.02	0.08	1 36	0.06	0.81
Time of day (Night)	2.61	0.91	1 625	10.1	<b>0.002</b>	-2.61	0.91	1 625	10.1	<b>0.002</b>	0.13	0.05	1 625	9.24	<b>0.003</b>
Area:Day	0.06	0.84	1 625	8.3	<b>0.004</b>	-13.15	1.95	1 625	76.6	<b>&lt;0.001</b>	-0.07	0.04	1 625	22.65	<b>&lt;0.001</b>
Cognitive style:Area	13.15	1.95	1 625	76.6	<b>&lt;0.001</b>	3.72	0.84	1 625	66.0	<b>&lt;0.001</b>	0.60	0.10	1 625	69.98	<b>&lt;0.001</b>
Cognitive style:Day	-3.72	0.84	1 625	66.0	<b>&lt;0.001</b>	-0.06	0.84	1 625	8.3	<b>0.004</b>	-0.24	0.04	1 625	80.50	<b>&lt;0.001</b>
Cognitive style:Area:Day	-5.58	1.41	1 625	15.7	<b>&lt;0.001</b>	5.58	1.41	1 625	15.7	<b>&lt;0.001</b>	-0.26	0.07	1 625	13.05	<b>&lt;0.001</b>

**Table 1** – Results of the full models for giving-up densities (GUDs), number of visits, duration of visits, proportion of time spent foraging and in vigilance in relation to cognitive style, risk area (high-risk/low-risk), experimental day, sex and time of day (day/night) for 5 days of observations of 39 individual bank voles (*Myodes glareolus*) in semi-natural enclosures. Statistically significant effects are highlighted in bold.

	Fast Learners					Slow Learners				
<b>GUDs</b>	Estimate	SE	DF	F	P	Estimate	SE	DF	F	P
Intercept	0,65	0,04	1 187	424,4		0,65	0,02	1 159	1127,1	
Area (LR)	0,19	0,02	1 187	125,4	<b>&lt; 0.001</b>	0,47	0,02	1 159	1017,2	<b>&lt; 0.001</b>
Day	-0,05	0,01	1 187	67,4	<b>&lt; 0.001</b>	-0,07	0,01	1 159	0,4	0,54
Sex (M)	0,02	0,05	1 19	0,1	0,77	0,003	0,02	1 16	0,0	0,89
Area:Day			/			0,14	0,01	1 159	187,2	<b>&lt; 0.001</b>
<b>Visit N</b>	Estimate	SE	z	P		Estimate	SE	z	P	
Intercept	1,39	0,05	25,6			1,13	0,07	16,271		
Area (LR)	-0,90	0,09	-9,9	<b>&lt; 0.001</b>		-1,68	0,15	-11,063	<b>&lt; 0.001</b>	
Day	0,23	0,02	12,6	<b>&lt; 0.001</b>		0,21	0,03	6,958	<b>&lt; 0.001</b>	
Sex (M)	-0,11	0,05	-2,2	<b>0,03</b>		-0,08	0,07	-1,117	0,26	
Time of day (Night)	0,09	0,07	1,4	0,17		0,03	0,08	0,293	0,77	
Area:Day			/			-0,48	0,06	-8,119	<b>&lt; 0.001</b>	
<b>Visit Duration</b>	Estimate	SE	DF	F	P	Estimate	SE	DF	F	P
Intercept	4,62	0,10	1 367	3944,75		5,08	0,12	1 256	3086,78	
Area (LR)	-0,77	0,06	1 367	97,52	<b>&lt; 0.001</b>	-2,14	0,10	1 256	706,90	<b>&lt; 0.001</b>
Day	0,20	0,01	1 367	210,62	<b>&lt; 0.001</b>	0,37	0,03	1 256	106,64	<b>&lt; 0.001</b>
Sex (M)	-0,13	0,14	1 19	0,79	0,38	0,02	0,17	1 16	0,05	0,82
Time of day (Night)	0,09	0,05	1 367	108,87	<b>&lt; 0.001</b>	0,07	0,07	1 256	25,12	<b>&lt; 0.001</b>
Area:Day			/			0,68	0,13	1 256	28,73	<b>&lt; 0.001</b>
<b>Foraging</b>	Estimate	SE	DF	F	P	Estimate	SE	DF	F	P
Intercept	72,96	1,91	1 368	2506,2		46,96	1,44	1 257	3059,7	
Area (LR)	-25,66	1,12	1 368	513,5	<b>&lt; 0.001</b>	-12,35	1,66	1 257	39,3	<b>&lt; 0.001</b>
Day	4,81	0,40	1 368	146,5	<b>&lt; 0.001</b>	1,09	0,67	1 257	1,1	0,30
Sex (M)	1,88	2,53	1 19	0,6	0,47	-0,78	1,63	1 16	0,2	0,67
Time of day (Night)	2,37	1,11	1 368	4,5	<b>0,03</b>	2,97	1,54	1 257	3,8	<b>0,05</b>
Area:Day			/			-5,37	1,21	1 257	19,7	<b>&lt; 0.001</b>
<b>Vigilance</b>	Estimate	SE	DF	F	P	Estimate	SE	DF	F	P
Intercept	27,04	1,91	1 368	838,3		53,04	1,44	1 257	4734,8	
Area (LR)	25,66	1,12	1 368	513,5	<b>&lt; 0.001</b>	12,35	1,66	1 257	39,3	<b>&lt; 0.001</b>
Day	-4,81	0,40	1 368	146,5	<b>&lt; 0.001</b>	-1,09	0,67	1 257	1,1	0,30
Sex (M)	-1,88	2,53	1 19	0,6	0,47	0,78	1,63	1 16	0,2	0,67
Time of day (Night)	-2,37	1,11	1 368	4,5	<b>0,03</b>	-2,97	1,54	1 257	3,8	<b>0,05</b>
Area:Day			/			5,37	1,21	1 257	19,7	<b>&lt; 0.001</b>
<b>For / Vig ratio</b>	Estimate	SE	DF	F	P	Estimate	SE	DF	F	P
Intercept	1,13	0,10	1 368	90,4		-0,13	0,07	1 257	45,0	
Area (LR)	-1,27	0,06	1 368	464,6	<b>&lt; 0.001</b>	-0,65	0,08	1 257	42,0	<b>&lt; 0.001</b>
Day	0,25	0,02	1 368	144,6	<b>&lt; 0.001</b>	0,05	0,03	1 257	3,8	<b>0,05</b>
Sex (M)	0,08	0,14	1 19	0,3	0,59	-0,05	0,08	1 16	0,3	0,58
Time of day (Night)	0,12	0,06	1 368	4,5	<b>0,04</b>	0,13	0,08	1 257	3,1	0,08
Area:Day			/			-0,32	0,06	1 257	29,0	<b>&lt; 0.001</b>

**Table 2** – Giving-up densities (GUDs), number of visits, duration of visits, proportion of time spent foraging and in vigilance in relation risk area (high-risk/low-risk), experimental day, sex and time of day (day/night) for fast learners and slow learners for 5 days of observations of 39 individual bank voles (*Myodes glareolus*) in semi-natural enclosures. Statistically significant effects are highlighted in bold.

GUDs	Low risk					High risk				
	Estimate	SE	DF	F	P	Estimate	SE	DF	F	P
Intercept	0,65	0,03	1 154	1213,87		0,45	0,03	1 154	340,97	
Cognitive style (SL)	0,01	0,04	1 36	0,02	0,88	-0,28	0,04	1 36	64,19	< 0.001
Day	0,04	0,01	1 154	118,88	< 0.001	0,06	0,01	1 154	0,69	0,41
Sex (M)	-0,02	0,04	1 36	0,33	0,57	0,00	0,04	1 36	0,002	0,97
Cognitive style:Day	0,03	0,01	1 154	7,54	<b>0,01</b>	-0,13	0,01	1 154	175,85	< 0.001
<b>Visit N</b>	Estimate	SE		z	P	Estimate	SE		z	P
Intercept	1,40	0,05		27,95		0,50	0,08		6,1	
Cognitive style (SL)	-0,29	0,05		-5,36	< 0.001	-1,10	0,09		-12,0	< 0.001
Day	0,22	0,02		11,44	< 0.001	0,24	0,03		8,7	< 0.001
Sex (M)	-0,10	0,05		-1,81	0,07	-0,11	0,08		-1,5	0,14
Time of day (Night)	0,07	0,05		1,26	0,21	1,17	0,08		15,3	< 0.001
Cognitive style:Day			/			-0,50	0,06		-8,8	< 0.001
<b>Visit Duration</b>	Estimate	SE	DF	F	P	Estimate	SE	DF	F	P
Intercept	4,60	0,13	1 346	4243,18		3,81	0,09	1 241	5255,79	
Cognitive style (SL)	0,52	0,15	1 36	12,44	<b>0,001</b>	-0,89	0,11	1 36	48,18	< 0.001
Day	0,21	0,02	1 346	473,59	< 0.001	0,21	0,02	1 241	43,76	< 0.001
Sex (M)	-0,07	0,15	1 36	0,21	0,65	-0,05	0,11	1 36	0,05	0,83
Time of day (Night)	0,08	0,04	1 346	5,21	<b>0,02</b>	0,77	0,04	1 241	322,73	< 0.001
Cognitive style:Day	0,15	0,03	1 346	34,27	< 0.001	-0,32	0,03	1 241	85,38	< 0.001
<b>Foraging</b>	Estimate	SE	DF	F	P	Estimate	SE	DF	F	P
Intercept	73,96	1,64	1 346	4515,95		46,63	1,83	1 241	2020,57	
Cognitive style (SL)	-26,91	1,87	1 36	206,64	< 0.001	-13,71	2,15	1 36	30,85	< 0.001
Day	4,79	0,51	1 346	68,64	< 0.001	4,92	0,69	1 241	12,89	< 0.001
Sex (M)	0,30	1,87	1 36	0,02	0,88	1,64	2,03	1 36	0,77	0,39
Time of day (Night)	1,87	1,05	1 346	3,16	0,08	3,78	1,59	1 241	4,75	<b>0,03</b>
Cognitive style:Day	-3,73	0,75	1 346	24,76	< 0.001	-9,21	1,26	1 241	53,18	< 0.001
<b>Vigilance</b>	Estimate	SE	DF	F	P	Estimate	SE	DF	F	P
Intercept	26,04	1,64	1 346	1603,96		53,37	1,83	1 241	2939,02	
Cognitive style (SL)	26,91	1,87	1 36	206,63	< 0.001	13,71	2,15	1 36	30,85	< 0.001
Day	-4,79	0,51	1 346	68,65	< 0.001	-4,92	0,69	1 241	12,89	< 0.001
Sex (M)	-0,30	1,87	1 36	0,02	0,88	-1,64	2,03	1 36	0,77	0,39
Time of day (Night)	-1,87	1,05	1 346	3,16	0,08	-3,78	1,59	1 241	4,75	<b>0,03</b>
Cognitive style:Day	3,73	0,75	1 346	24,76	< 0.001	9,21	1,26	1 241	53,18	< 0.001
<b>For / Vig ratio</b>	Estimate	SE	DF	F	P	Estimate	SE	DF	F	P
Intercept	1,18	0,09	1 346	140,82		-0,16	0,09	1 241	22,04	
Cognitive style (SL)	-1,31	0,11	1 36	153,13	< 0.001	-0,71	0,11	1 36	30,17	< 0.001
Day	0,28	0,03	1 346	80,07	< 0.001	0,21	0,03	1 241	5,04	<b>0,03</b>
Sex (M)	0,01	0,11	1 36	0,00	0,95	0,06	0,10	1 36	0,50	0,49
Time of day (Night)	0,09	0,05	1 346	2,90	0,09	0,18	0,08	1 241	4,5	<b>0,04</b>
Cognitive style:Day	-0,24	0,04	1 346	36,98	< 0.001	-0,49	0,06	1 241	63,13	< 0.001

**Table 3** – Giving-up densities (GUDs), number of visits, duration of visits, proportion of time spent foraging and in vigilance in relation cognitive style, experimental day, sex and time of day (day/night) for fast learners and slow learners in the high risk and low risk area for 5 days of observations of 39 individual bank voles (*Myodes glareolus*) in semi-natural enclosures. Statistically significant effects are highlighted in bold.

## Discussion

Based on GUDs and behavioural observations, we showed that individuals with different cognitive styles approach the same challenge (finding food without being food for someone else) in a different way. Individuals with a fast cognitive style appeared biased towards gathering easier to get and greater food rewards at the cost of running higher risks, whereas individuals with a slow cognitive style seemed to favour safety, making a greater foraging effort and avoiding excessive exposure. Despite of these differences, body weight at the end of the enclosure trials was only marginally different between the two groups. To our knowledge, this is the first study to consider individual risk-reward trade-off biases in direct relation to fitness proxies in a small mammal in a semi-natural setting. Our approach combines an individual-level GUD-based perceived risk assessment, direct observation of anti-predator behaviour, with cognitive strategies. Our results provide insights into the mechanisms maintaining individual variation in cognition.

According to our predictions, fast learners increasingly exploited both the high-risk areas and the low-risk areas, made comparatively shorter visits in the low-risk-areas than slow learners, which were mostly devoted to seeking and consuming food. These individuals were characterized by a cognitive style that is fast but superficial, and by a behavioural profile that includes neophilia. They might give up on the protected food patch soon in favour of an unexploited but exposed food patch at the cost of increased perceived predation risk. Fast learners tended to trade the ease of foraging for safety, and accepted predation risk rather than increasing foraging effort. By minimizing the proportion of time spent in vigilance and thus the average visit duration, they had higher food uptake rates and spent overall less time foraging compared to slow learners. This should have minimised missed-opportunity costs. In the wild such activities include looking for mates or defending territories but in the enclosure situation extra time might have simply translated into resting.

According to GUDs slow learners progressively avoided the high-risk area while increasing foraging effort in the low-risk area. They made fewer but comparatively longer visits than fast learners to the food patches, and spent more than half of the time exercising vigilance in both areas. Slow learners have a slow but accurate and flexible cognitive style, and a behavioural type described as shy, neophobic and fearful. They preferred smaller food rewards or increased effort to find them over being at risk. It is likely that the high proportion of time they spent in vigilance in the high-risk area made foraging inefficient and the resulting low feeding rate not worth the risk. They adopted a strategy that favoured safety at the expense of greater food searching effort as well as higher time investment. The time they spent each day foraging was in fact much longer compared to the fast learners. They would therefore be unable to devote much time to other activities, i.e. have larger missed-opportunities cost than fast learners, but this strategy would probably prolong their life-expectancy and thus maximize the survival component of fitness in nature.



While cognitive style refers to the specific strategy by which individuals acquire and process information (Bebus *et al.*, 2016; Griffin *et al.*, 2015; Sih and Del Giudice, 2012), animal personality is defined as the set of among-individual differences in behaviour (or suites of correlated behaviours) that are consistent across time and contexts (Réale *et al.*, 2007; Sih *et al.*, 2004). We showed earlier, that cognitive style and animal personality traits may form a behavioural syndrome, with fast learners being the bolder and more active animals, and slow learners being the shyer and less active animals (Mazza *et al.*, in press). Our results on risk taking indicate that the risk-reward trade-off can provide a first principle link between cognitive decision-making and several personality axes, as suggested by Sih and Del Giudice (2012). Further, the results provide insights into the mechanisms maintaining both individual variation in cognition and individual variation in personality traits.

The results of the present study are in accordance with previous empirical work exploring the connections between foraging, antipredatory behaviour and either personality or cognitive styles. However, none of them considered both personality and cognitive styles, thus providing only a partial reference frame for the present study (but see Zandberg *et al.*, 2017). Griffin *et al.* (2012) found that mud crabs (*Panopeus herbstii*) inhabited reef areas that differ in predation risk depending on their personality. Similarly more active and explorative great tits (*Parus major*) took the risk of moving further and look for new feeding places than less active individuals (e.g. Arvidsson and Matthysen 2016; van Overveld and Matthysen 2010). Šlipogor *et al.* (2016) also found that bolder common marmosets (*Callithrix jacchus*) faced with a desirable food reward “guarded” by a predator-like cue approach the food faster and forage longer compared to shyer conspecifics, who display higher vigilance behaviour and longer latencies to approach the food. Dammhahn and Almeling (2012) found that risk-prone grey mouse lemurs (*Microcebus murinus*) approach a potentially risky foraging platform and start feeding sooner compared to shyer individuals. Lastly, Whiteside and Madden (2014) found shyer pheasants (*Phasianus colchicus*) had longer life-expectancies when released in the wild.

Our results are not consistent with Raine and Chittka’s (2008) seminal work, reporting that fast-learning bumblebees (*Bombus terrestris*) foraged more efficiently than slow-learning ones. However, Burns (2005) suggested that other factors, such as reward availability and distribution as well as predation risk (e.g. Dukas, 2001), might also affect the relationship between cognitive style and fitness-affecting traits such as foraging. Specifically, he found that fast, inaccurate bees forage on “easy” flowers (simple design with short handling times), whereas slow, accurate bees forage on more complex flowers accepting longer handling times. Variation in foraging styles might therefore be maintained if the different styles are equally successful in the long run (Burns, 2005).

Variability between individuals in foraging strategies was also found to improve colony success compared to colonies where all individuals exhibited the same foraging strategy (Burns and Dyer, 2008). Perez *et al.* (2013) also found that individual carpenter ants (*Camponotus aethiops*) differed in their

associative learning abilities and that the best learners would specialise as foragers, thus promoting the whole colony success. Cole *et al.* (2012) demonstrated how problem-solving great tits were more efficient foragers than non-solvers, and that they produced larger clutches. However, the overall reproductive fitness did not differ between solvers and non-solvers because solvers were more likely to desert their nest in response to nest disturbance. Conversely, Cauchard *et al.*, (2013) found that breeding pairs with at least a problem-solver parent had higher clutch sizes and fledgling survival than non-solvers pairs.

Fast learners spent a higher proportion of each visit foraging and exploited both areas increasingly over the experimental days (presumably reducing the searching effort) in our study. In this group it seems plausible to expect a reduction in body weight loss that is common when rodents are introduced to a new environment/diet. However, there was no clear cut difference between the body weight changes of the two groups apart from the tendency of higher body weight in the slow learners at the end of the experiment. This might be due to the fact that explorative and bold individuals were more active and have a faster metabolism than shy, less active individuals (e.g. Careau *et al.*, 2009, 2015; Šíchová *et al.*, 2014; Toscano and Monaco, 2015). The two strategies would thus seem to yield comparable results regarding overall food gain reflected by body weight.

Does this mean that voles simply adjusted their strategy according to their metabolic needs? It is also possible that highly active individuals may require increased foraging activity to sustain the greater energetic demands of their energetically expensive behaviours (Biro and Stamps 2008). As Troxell-Smith and Mella (2017) point out, individual differences “may bias foraging decisions above and beyond a forager’s physiological state”. For instance, Dammhahn and Almeling (2012) found that grey mouse lemurs did not appear to adjust risk taking to their energetic state. Thus, individual differences are likely to encompass physiology, behaviour and cognition, forming an overall trait that will greatly differ among individuals (e.g. Biro and Stamps, 2010; Careau *et al.*, 2008) but might give comparable advantages over a lifetime and hence result in similar fitness. Clarifying this issue requires a combination of measurements to capture individual personality, cognitive style, activity and energy demand/expenditure.

### *Conclusion*

The relationship between cognition and fitness is extremely complex, with many relevant variables that could influence it (e.g. personality, physiology and life-history as well as environmental conditions). More studies conducted in the wild are needed to clarify the relationship between individual cognitive styles and fitness-related success.

We offer the results of the present study as a first step in understanding the mechanisms underlying the maintenance of the variation in decision-making processes and how this variation is connected to

individual differences in cognition and behaviour. These results also highlight how important it is to consider the individual background when testing for effects of cognition in the wild.

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*“Extreme fear can neither fight nor fly.”*

W. Shakespeare, 1594

*“Terror acts in the same manner on them as on us, causing the muscles to tremble, the heart to palpitate, the sphincters to be relaxed, and the hair to stand on end.”*

C. Darwin, 1871

## Chapter 3

### PERSONALITY AND COPING STYLES IN BANK VOLES

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#### **Abstract**

Between-individual differences in coping with stress encompass neurophysiological and behavioural reactions. The coping style model proposes two alternative response patterns to stressors that integrate both types of reactions. Although numerous studies have investigated the possible covariance of behavioural and physiological responses, findings are still mixed. Many of these studies have considered artificially selected lines, and there is reason to believe that in natural populations this relationship may not be as straightforward as predicted. In the present study we tested the predictions of the coping style model in an unselected population of bank voles (*Myodes glareolus*) (N = 70). We measured the voles' faecal corticosterone metabolite levels under different stress conditions (holding in cages/enclosures and during Open Field test) and tested the repeatability of the physiological response and the possible connections with the proactive-reactive behavioural profile.

Individuals were moderately consistent in their physiological state across situations. Proactive voles had significantly lower corticosterone levels than reactive conspecifics under the two less stressful conditions. However, we could not find any co-variation between behaviour and endocrine stress response in the most stressful situation. Our results partially support the coping style model, but suggest a more complicated relationship between behavioural and physiological responses than was initially proposed.

**Keywords:** coping styles; faecal metabolites; flexibility; glucocorticoids; learning; personality; stress.

## Introduction

An individual's response to social and environmental challenges (i.e. stress, Koolhaas *et al.*, 2011; LaDage, 2015) influences its short- and long-term prospects of fitness via rank (e.g. Blanchard *et al.*, 2001; Sapolski, 2004), body condition (e.g. Bartolomucci *et al.*, 2004), reproductive success (e.g. Buchanan *et al.*, 2003; Holberton and Wingfield, 2003), as well as its risk of cardiovascular diseases, depression and immunodeficiency (e.g. Bartolomucci *et al.*, 2005; Henry and Stephens, 1977; Sgoifo *et al.*, 2005). How successfully an individual copes with challenges and changes has therefore relevance for individual fitness (e.g. Bordin *et al.*, 2009). Adaptive responses encompass behavioural, cognitive and neuroendocrine adjustments that will enable the individual to respond while maintaining organismal functioning (e.g. Houslay *et al.*, 2017; McEwen and Wingfield, 2010; Øverli *et al.*, 2007; Romero *et al.*, 2009; Wingfield, 2003). However, there is no single optimal way to respond to challenges. Koolhaas *et al.* (1999) described alternative response patterns in reaction to a stressor, named coping styles, that integrate both neuroendocrine and behavioural traits and place individuals along a proactive-reactive axis. Proactive individuals are characterized by behavioural traits such as aggressiveness, boldness, neophilia and a general fight-flight response (Carere *et al.*, 2010; Koolhaas *et al.*, 1999). They were also described as quickly forming routines and being relatively insensible to environmental change; they would be challenged in reversal learning tasks as well as aversion learning (e.g. Benus *et al.*, 1990; Carere *et al.*, 2010; Koolhaas *et al.*, 1999; Ruiz-Gomez *et al.*, 2011; Sih and Del Giudice, 2012). The reactive strategy instead combines low aggressiveness, risk aversion, neophobia and flexibility, as well as freezing behaviour in response to stress (e.g. Carere *et al.*, 2010; Koolhaas *et al.*, 1999). Reactive individuals are highly sensitive to environmental cues and changes, and quickly learn avoidance and reversal tasks (e.g. Benus *et al.*, 1990; Carere *et al.*, 2010; Koolhaas *et al.*, 1999; Ruiz-Gomez *et al.*, 2011; Sih and Del Giudice, 2012). These suites of traits were shown to correlate with different physiological responses. Compared to reactive individuals, proactive individuals often have lower basal glucocorticoids (e.g. cortisol or corticosterone) levels and lower increases in these hormones under challenging conditions than reactive individuals (e.g. Carere and van Oers 2004; Cockrem, 2007; Koolhaas *et al.* 2010). At the same time, they show a stronger sympathetic activation in terms of plasma noradrenaline and adrenaline (e.g. Koolhaas *et al.*, 1999) and a higher heart and breathing rate (e.g. Koolhaas *et al.*, 1999; but see Ferrari *et al.*, 2013; van Reenen *et al.* 2005). These patterns could be considered basic personality traits (e.g. Carere *et al.*, 2010), defined as among-individuals differences in behaviour consistent across time and contexts (Réale *et al.*, 2007). Recently, however, it was suggested that the terms are not necessarily equivalent and should not be used interchangeably (Zidar *et al.*, 2017). Although the coping style model was supported, completely or partially, by several studies proving consistent individual differences in stress response strategies (reviewed in Carere *et al.*, 2010), the adaptive value and evolutionary maintenance of such different phenotypes are still under debate (Carere

*et al.*, 2010). Furthermore, the relationship between personality traits and the HPA-axis is still not clear. A few recent studies found no evidence of direct co-variation between response to challenge and personality, as initially proposed by the coping style model (e.g. Boulton *et al.*, 2015; Martins *et al.*, 2007; Van Reenen *et al.*, 2005). Besides, only a few studies assessed the repeatability and consistency of the behavioural and physiological responses to stress (but see Boulton *et al.*, 2015; Ellis *et al.* 2004; Ferrari *et al.* 2013; Sebire *et al.* 2007), which are a prerequisite for any kind of among-individual variation assessment (e.g. Dingemanse *et al.* 2010). Lastly, only a few recent studies (e.g. Boulton *et al.*, 2015; Ferrari *et al.*, 2013; Rangassamy *et al.*, 2016) measured differences in stress response considered wild or unselected populations, and their results suggest a more complex relationship between the behavioural and the physiological domains.

Therefore, the aim of this study was to investigate the relationships between behavioural traits consistent with a proactive-reactive axis and HPA-axis reactivity in an unselected population. Our study species was the bank vole (*Myodes glareolus*), a small rodent common in central and northern Europe (e.g. Mazurkiewicz 1983; Sptizenberger, 1999). Bank voles display repeatable personality (e.g. Korpela *et al.*, 2011) and physiological traits (i.e. metabolic rate: Labocha *et al.*, 2014), and some indication of co-variation between the two was recently reported (e.g. Šíchová *et al.*, 2014). Personality in bank voles is related to learning speed and flexibility (Mazza *et al.*, in press). We expanded this previous work to investigate whether behavioural and endocrine profiles were integrated in a manner consistent with the coping style model.

We measured the voles' faecal corticosterone metabolite (FCM) levels after the moderate stress induced by the Open Field test, and undisturbed under two different housing conditions, indoor in cages and outdoor in semi-natural enclosures. The analysis of corticosterone metabolites excreted into faeces and/or urine is a non-invasive and feedback-free technique to assess adrenocortical function (Touma *et al.*, 2003). The measured stress response can thus be disentangled from the stress associated with capturing and handling the animals and collecting the sample. The method is sensitive enough to detect the stress response associated with brief acute stressors as well as prolonged chronic stress, i.e. the exposure to a novel environment (e.g. Harper and Austad, 2000).

We predicted that individuals would show consistent endocrine profiles across different situations. We also predicted that individuals with proactive behavioural traits (i.e. bold, active, fast but unflexible) would show lower HPA-axis activity and reactivity compared to individuals with more reactive-like traits (i.e. shy, less active, slower and more flexible).

## Methods

### *Animals and housing*

We used 86 captive bred voles (45 males and 41 females), removed 1-5 generations from the wild, thus representative of their natural source population. Voles were born between May and October 2015, from unselected lab born and wild-caught parents. A maximum of four individuals from the same litter (two males and two females) was included in our sample. At 3-5 weeks of age juveniles were weaned, sexed and assigned a unique identity.

### *Indoor conditions*

Animals were housed individually in standard polycarbonate cages (Typ III, Ehret GmbH, Germany; dimensions: 42 cm x 27 cm x 16 cm). Light, temperature and humidity mirrored the natural conditions occurring outside the lab. Cages were provided with wood shavings and hay as bedding, and cardboard rolls for shelter. Water and food pellets (Ssniff V1594 R/M-H Ered II, Germany) were available *ad libitum*. Bedding was changed every two weeks.

### *Outdoor conditions*

A subsample of voles was also tested in outdoor conditions. For this part of the experiment we selected/chose the animals which had the highest and lowest boldness and activity scores. We tried to recreate as much as possible the characteristics and challenges of bank voles' natural environment, without actually releasing them in the wild, which would have decreased our chances of retrieving them, due to predation and dispersal. Voles were kept individually in 3 x 4 m semi-natural enclosures, which had a concrete base filled with a 40 cm soil layer; they were protected against predators by mesh wire walls and a plastic roof cover. Enclosures were sown with a local grass mix to mimic perennial grassland. Vegetation height was kept at ca 2 cm in one half of the enclosures and ca 20 cm in the other half, which was additionally covered by camouflage netting, in order to mimic the heterogeneous conditions and exposure voles might experience in their natural habitat. In each enclosure a plastic nest box (32 x 22 x 16 cm) provided with hay was buried level with the enclosure surface in one corner to provide a nesting opportunity. Food was provided in plastic trays (20 x 15 x 5 cm) containing a mixture of crushed hazelnuts (2 g) and sand (0.75 l), so that voles would have to actively search for it. Experiments were conducted between June and September 2016. Voles remained in the enclosures for five days. They were then retrieved using Ugglan multiple capture live traps (Ugglan Special Traps n. 2, Grahnb AB, Hillerstorp, Sweden).

### *Personality assessment*

We assessed among-individual differences in activity, exploration and boldness using two standardized laboratory tests (Réale *et al.*, 2007): the open field test and the novel object test. Each test was repeated twice to calculate repeatabilities.

### *Open Field Test*



The open field test is one of the most widely used tests in personality research to measure activity and exploration (Réale *et al.*, 2007). However, it was originally introduced to measure anxiety-related behaviour, exploiting the natural aversion of rodents to exposed fields (e.g. Carola *et al.*, 2002; Lecorps *et al.*, 2016). Previous studies have used this test as a mild to moderate stressor (e.g. Boulton *et al.*, 2015).

A round open field of 100 cm diameter with a concrete floor and metal walls (Herde and Eccard, 2013) was used as a test arena (Archer, 1973). The floor was virtually divided into two areas: a 10 cm wide safe peripheral area, and a 80 cm wide central unsafe area. At the start of the test, each animal was placed in the peripheral area, and its behaviour was observed via a video camera (Logitech Quick Cam Pro 9000, PID LZ727BA, Logitech international S.A., Morges, Switzerland) for 10 min. We took subjects from their homecage only during their active phase (e.g. Ylönen, 1988), i.e. when they were perceived moving in the cage; this allowed us to test all animals during similar activity levels.

#### *Novel Object Test*

We assessed the animals' approach towards to a novel object that was introduced in the cage, which is usually considered a measure of boldness and neophilia (e.g. Réale *et al.*, 2007; Crane and Ferrari, 2017). We used two different novel objects, one for each round of testing: a plastic toy horse (8 cm x 4 cm x 6 cm) and a plastic toy duck (6.5 cm x 5 cm x 6 cm). The subjects' behaviour was monitored with a video camera (as above) for 30 min. At the end of the test, animals were returned to their homecage.

#### *Association learning and reversal learning*

A detailed description of testing procedures is provided in Mazza *et al.* (in press). Briefly, we tested the voles for their speed and flexibility in associating a neutral odour cue with a reward in a Y-maze. The test consisted of two tasks: an initial learning task and a reversal learning task. The neutral odour cues were fruit juices, orange or pineapple (odours O and P), that are not normally present in the voles' natural environment. The reward was the chance to return to the safety of the homecage, and being left undisturbed for at least 2 hours. Each animal had a maximum of 4 trials per day. We considered the initial learning task solved when the vole made 7 correct choices out of ten consecutive trials. We then reversed the reward contingency and assessed how many trials voles needed to reach again the criterion. This required the animal's attention to external cues and flexible updating of the response to changed conditions; it was therefore considered a measure of cognitive and behavioural flexibility. Learning and reversal learning scores were based on the number of trials necessary to reach the criterion in the two tasks.

#### *Faecal samples collection*

Faecal pellets were collected to determine FCM concentrations that reflect basal values for holding conditions in cages and enclosures and values during Open Field tests. Voles were tested in the Open Filed arena between 08.00 and 10.00 am. They were then transferred from the arena into plastic cages

with mesh floor (20 cm x 39 cm x 15 cm). The cages were provided with the usual food and water, and a cardboard shelter that allowed the faecal pellets from dropping through the bottom of the cage. Faecal pellets dropped through the mesh into a plastic tray lined with paper towels. This allowed us to easily collect them at different times of day without moving, handling and therefore stressing the animals. Paper towels were changed after sampling and whenever they were stained with urine. Voles remained in the cages for ca. 8 hours.

In bank voles, corticosterone metabolites take about 6-8 hours to complete the passage through the intestinal tract and to be excreted with the faeces (Sipari *et al.*, 2017). We collected the faecal pellets excreted within the first 2 h after the Open Field test, and considered them as indicative of the conditions the animals experienced approx. 6-8 h before (Sipari *et al.*, 2017) which we presumed to represent undisturbed basal indoor conditions. We then collected the pellets excreted 6-8 h after the Open Field test and considered them indicative of the stress response to the Open Field test (Sipari *et al.*, 2017). Of the 86 tested animals, 72 produced enough pellets for analyses.

We collected the outdoor samples after retrieving the voles from the enclosures. Traps were equipped with sensors that allowed us to retrieve the voles immediately after capture (Notz *et al.*, 2017). The glucocorticoid metabolites measured in their faeces should therefore reflect the outdoor conditions voles were experiencing in the enclosures. Voles were trapped between 08.30 and 12.00, and moved into standard cages provided with food, water and a cardboard shelter. The cage floor was covered with paper towels. Samples were collected within the first 2.5 hours after capture. As soon as enough faecal pellets were produced, the vole was transferred in a normal cage with hay and bedding (see “Indoor housing conditions” above). Six of 48 voles did not produce the minimum of ca. 20 faecal pellets required for analyses within the first 3 h from capture. All faecal samples were collected from the paper towels into plastic Eppendorf tubes (1.5 ml) using tweezers, and stored in freezer at -20 °C. Pellets clearly contaminated with urine (e.g. lying in urine spots) were not collected. Tweezers were cleaned with 70% alcohol after each sampling.

#### *Faecal sample analysis*

Extraction of steroids was conducted according to the method described by Palme and Möstl (1997), which was adapted for house mice (*Mus musculus domesticus*) by Touma *et al.* (2003, 2004) and recently validated for bank voles (Sipari *et al.*, 2017). Briefly, each faecal sample was homogenized with mortar and pestle and an aliquot of 0.05 g was mixed with 80% methanol (1 ml) and shaken in a multi-vortex. The suspension was then centrifuged for 10 min at 2500G. An aliquot of the supernatant was diluted (1:10) with assay buffer (Tris/HCl 20 mM, pH 7.5) and stored at -20° C until analysis.

To determine the amount of corticosterone metabolites we used a 5a-pregnane-3b,11b,21-triol-20-one enzyme immunoassay (EIA). This EIA utilizes a group-specific antibody measuring steroids with a 5a-3h,11h-diol structure. A detailed description of the procedures is given in Touma *et al.* (2003).

### *Statistical analyses*

Data were normalized through log transformation ( $\log(x+1)$ ) and analysed with R, version 3.2.3 (R Core Team, 2015). We assessed the repeatability (adjusted for treatment) of individual FCM levels using the 'rtpr' package (Nakagawa and Schielzeth, 2010; Nakagawa, Schielzeth, and Stoffel, 2016).

We compared the FCM levels in the three conditions (Cage, Enclosure, Open Field) using Wilcoxon tests. We then used restricted maximum-likelihood linear mixed models to evaluate the relationship between the FCM levels in each treatment and the behavioural/cognitive variables (activity, boldness, learning and reversal learning scores), sex and age, specified as fixed effects. We ran separate models for each variable. In all models sex and age were considered as fixed effects. The EIA plate was added as random factor in each model, specified as random intercept. We used the R packages nlme, version 3.1-131, and lme4, version 1.1-12 (Bates *et al.*, 2015; Pinheiro *et al.*, 2017). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality.

Based on preliminary data exploration, we assessed the relationship between the difference in FCM levels of voles in cages and enclosures and boldness with a Spearman-rank correlation test. We also compared the difference in FCM levels of voles between cages and enclosures between fast/unflexible vs slow/flexible individuals with a Mann-Whitney-U test. The accepted significance level was  $\leq 0.05$ .

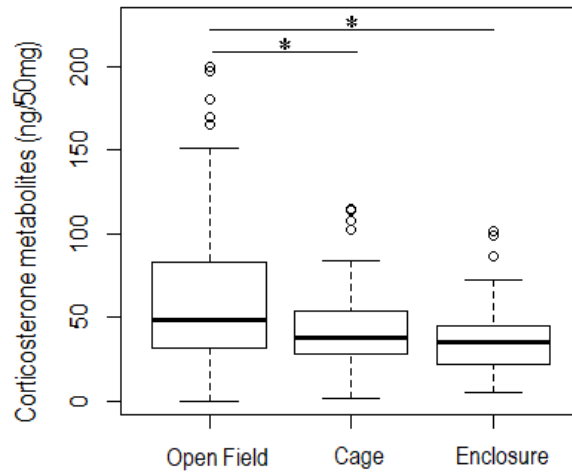
### *Ethical note*

All aspects of this study were in compliance with animal care regulations and applicable national law. The experiments were conducted under the permission of the "Landesamt für Umwelt, Gesundheit und Verbraucherschutz Brandenburg" (reference number: V3-2347-44-2011, Ä6) and "Landesamt für Natur, Umwelt und Verbraucherschutz Nordrhein-Westfalen" (reference number: 84-02.04.2016.A253).

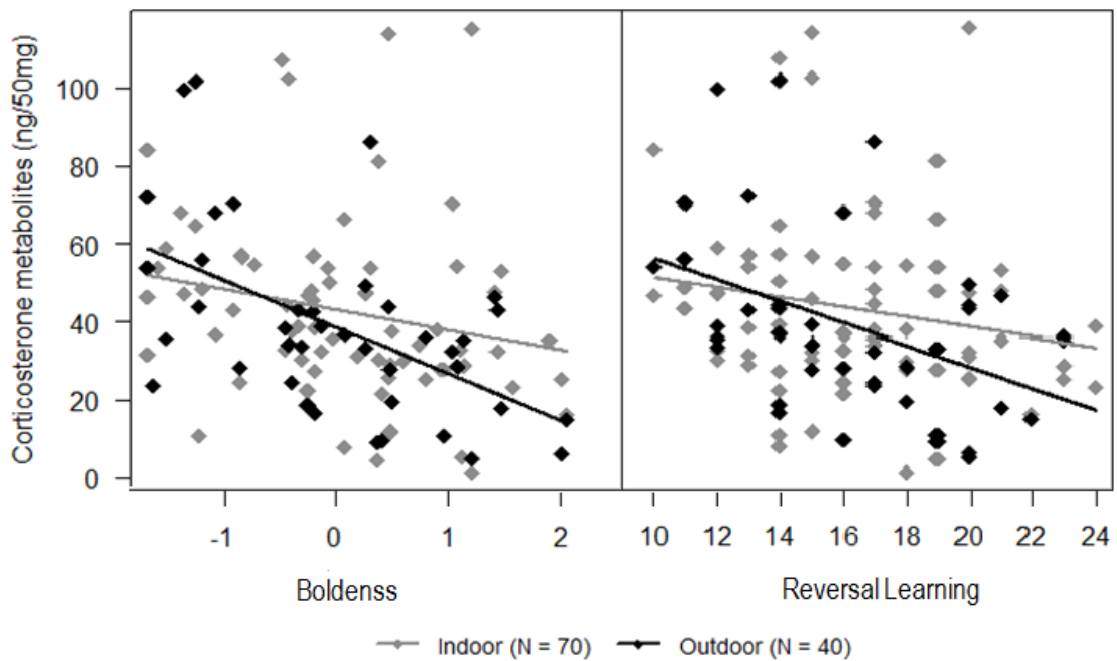
## **Results**

Faecal corticosterone metabolite (FCM) levels were repeatable across contexts ( $R = 0.20 \pm 0.09$ ; C. I. = 0.046 - 0.393;  $P = 0.007$ ). We removed from the dataset two outliers, that had indoor baseline and Open Field values more than 3 standard deviations higher than the means. FCM levels were higher after the Open Field compared to both basal conditions (Fig.1). Overall FCM levels did not differ between basal indoor and outdoor conditions (Fig. 1). The FCM mean ( $\pm$  S.D.) level was  $66.0 \pm 48.6$  ng/50 mg after the open field,  $42.7 \pm 23.9$  ng/50 mg in the cages and  $38.3 \pm 23.5$  ng/50 mg in the enclosures. FCM levels were negatively correlated with boldness in indoor holding conditions (Table 1; Fig.2) and outdoor holding conditions (Table 1; Fig.2). FCM levels were also negatively correlated with reversal learning score both in indoor (Table 1; Fig.2) and outdoor conditions (Table 1; Fig.2). No correlation was observed between FCM levels after the open field and any behavioural/cognitive variable (Table 1). Activity and initial learning score had no significant effect on FCM levels (Table 1). The difference

between FCM levels of voles in cages and enclosures correlated negatively with boldness ( $r_s = -0.42$ ;  $P = 0.009$ ). Fast but rigid learners had lower FCM levels in the enclosures, whereas slow but flexible learners had lower FCM levels in the cages (Mann-Whitney-U test:  $W = 114$ ,  $P = 0.02$ ).



**Fig. 2** – Faecal corticosterone metabolites (ng/50 mg) of bank voles in the three conditions: after the Open Field test, in indoor cages and in outdoor enclosures.



**Fig. 3** – Faecal corticosterone metabolites (ng/50 mg) of bank voles in relation to boldness and reversal learning performance scores in indoor (grey symbols) and outdoor (black symbols) holding conditions.

	Cage					Enclosures					Open Field				
	Estimate	SE	DF	F	P	Estimate	SE	DF	F	P	Estimate	SE	DF	F	P
<b>Boldness</b>															
Intercept	3.48	0.52	1 58	1913.4		3.92	0.63	1 30	509.7		2.95	0.52	1 56	2343.4	
Boldness	-0.18	0.09	1 58	5.6	<b>0.02</b>	-0.37	0.09	1 30	20.6	<b>&lt; 0.001</b>	0.18	0.09	1 56	2.3	0.13
Age	-0.003	0.01	1 58	0.4	0.53	-0.01	0.01	1 30	1.1	0.3	0.02	0.01	1 56	0.8	0.36
Sex (M)	0.48	0.17	1 58	8.4	<b>0.01</b>	0.16	0.25	1 30	0.4	<b>&lt; 0.001</b>	0.61	0.16	1 56	14.0	<b>&lt; 0.001</b>
<b>Activity</b>															
Intercept	3.48	0.54	1 58	1847.7		3.77	0.73	1 30	746.1		2.98	0.54	1 56	2245.4	
Activity	-0.12	0.09	1 58	2.5	0.12	-0.18	0.1	1 30	4.2	<b>0.05</b>	0.1	0.09	1 56	0.27	0.61
Age	-0.003	0.01	1 58	0.4	0.53	-0.01	0.01	1 30	0.6	0.44	0.02	0.01	1 56	0.63	0.43
Sex (M)	0.5	0.17	1 58	8.8	<b>0.004</b>	0.27	0.24	1 30	1.3	0.27	0.6	0.17	1 56	12.8	<b>&lt; 0.001</b>
<b>Learning</b>															
Intercept	3.20	0.59	1 58	1800.1		3.2	0.83	1 30	628.9		3.65	0.57	1 56	2205.6	
Learning	0.005	0.02	1 58	0.4	0.5	0.05	0.03	1 30	4.2	<b>0.05</b>	-0.04	0.02	1 56	1.3	0.27
Age	0.005	0.01	1 58	0.2	0.7	-0.01	0.01	1 30	1.3	0.26	0.02	0.01	1 56	0.9	0.36
Sex (M)	0.52	0.17	1 58	9.1	<b>0.004</b>	0.23	0.26	1 30	0.8	0.37	0.63	0.17	1 56	13.6	<b>&lt; 0.001</b>
<b>Reversal learning</b>															
Intercept	3.9	0.69	1 58	1855.9		5.6	0.77	1 30	616.8		2.4	0.67	1 56	2302.5	
Reversal learning	-0.16	0.02	1 58	4.8	<b>0.04</b>	-0.09	0.03	1 30	10.3	<b>0.003</b>	0.04	0.02	1 56	2.1	0.16
Age	-0.0005	0.01	1 58	0.1	0.75	-0.01	0.01	1 30	0.8	0.37	0.01	0.01	1 56	0.5	0.47
Sex (M)	0.5	0.17	1 58	9.2	<b>0.004</b>	0.32	0.25	1 30	1.6	0.2	0.6	0.17	1 56	13.12	<b>&lt; 0.001</b>

**Table 1** – Faecal corticosterone metabolite levels of bank voles in relation to activity, boldness, learning, reversal learning, age, sex, and treatment (animals exposed to Open Field test, holding conditions in indoor cages or outdoor enclosures).

## Discussion

Overall, our results provide only partial support for among-individual (co)variation in coping styles. Bank voles showed consistent differences among individuals in their physiological response to three different conditions/treatments. We could detect correlations between FCM levels, boldness and flexibility (measured in reversal learning), but only in the two less challenging conditions. Different personality and cognitive profiles were also shown to respond differently to the change from indoor to outdoor conditions. However, contrary to our expectations, we did not detect any effect of any measured trait on the endocrine response to a moderate stressor.

According to our first prediction, individual FCM were moderately repeatable across three conditions that presented low (holding in cages/enclosures) or moderate stress level (Open Field test). These results are in line both with the assumptions of the coping style model and with previous studies conducted on birds, mammals and fish (birds: e.g. Cockrem and Silverin 2002; Kralj-Fiser *et al.* 2007; Martins *et al.* 2007; Stöwe *et al.* 2010; mammals: e.g. Müller and Schrader 2005; van Reenen *et al.* 2005; fish: e.g. Huntingford *et al.*, 2010; Ruiz-Gomez *et al.*, 2011; Schjolden *et al.*, 2005). This is also the case for the study by Ferrari *et al.* (2013), which found repeatable within-individual consistency in physiological profiles in a natural population of marmots (*Marmota marmota*), even after years.

However, our second hypothesis regarding the co-variation of physiological and behavioural/cognitive traits was only partially supported. We found some, but not all, of the correlations we expected between behavioural and endocrine states in different conditions. Proactive individual (bolder, faster to learn but slower to reverse) showed indeed lower FCM levels compared to reactive individuals (shyer, slower to learn but flexible) in conditions of relatively low stress, i.e. undisturbed in their home cages and in outdoor enclosures. This supports the coping style model, showing a direct connection between boldness and flexibility and HPA-axis activity. The coping style model, however, predicts both lower HPA-activity and reactivity to stressful challenges, therefore our results are only partially supporting this model. There was no link between FCM levels and the behavioural/cognitive variables in the moderately stressful conditions of the Open Field test. Furthermore, we found no relation between activity and FCM levels, in any condition. These results are not in line with previous studies who found a correlation between various personality traits and response to an acute stressor (e.g. Carere *et al.*, 2003; Kralj-Fiser *et al.*, 2007; Korte *et al.*, 1992). Other studies demonstrated that individuals with proactive personality traits had the highest HPA response to a stressor (e.g. Boulton *et al.*, 2015; Martins *et al.*, 2007), suggesting a non-linear connection between coping styles and HPA-axis activity and reactivity (Koolhaas *et al.*, 2010). Moreover, Van Reenen *et al.* (2005) found no correlation between Holstein Friesian heifer calves' (*Bos taurus*) glucocorticoid levels and activity, a commonly used measure of personality (e.g. Gosling *et al.*, 2001; Réale *et al.*, 2007). Ferrari *et al.* (2013) showed that cortisol production under restraint was totally independent of other types of reactions to a stressor, both

behavioural and physiological (e.g. locomotion, heart and breathing rate). Based on these and other findings, some authors have suggested that there might be at least two independent components of the stress response: the quantitative component (stress response) that describes the physiological aspects of the glucocorticoid production, whereas the qualitative component (coping style) comprises the behavioural and cognitive strategies employed in coping with the stressor (e.g. Koolhaas *et al.* 2010; van Reenen *et al.* 2005). Thus, individuals showing similar behavioural responses (e.g. activity) may produce very different levels of glucocorticoids (van Reenen *et al.*, 2005). Our results regarding the HPA-axis reactivity to moderate challenges seem more in line with this two-tier model. It is clear that further studies are needed to investigate the relationship between behavioural and endocrine profiles. The updated coping style model requires further attention and formal testing.

An alternative explanation for these mixed findings could be that the predictions made based on results obtained with selected lines might not hold for natural or non selected populations. It is also worth noting that the more robust results in the present study refer to the outdoor condition. The voles assessed for their response to the new environment were chosen among those showing the more extreme proactive and reactive behavioural traits. The responses of the individuals with more moderate behavioural profiles might therefore have clouded the results. If this is the case, future research would have to focus a lot more on natural, unselected populations (see also Holmes *et al.*, 2000).

We assumed that stress levels in undisturbed conditions would be lowest indoors, in the familiar environment in which our voles were born and raised. However, FCM levels were similar in outdoor conditions. Furthermore, the direction of the change in FCM levels differed between proactive and reactive individuals. Proactive individuals had higher FCM in the cages than in the enclosures, whereas for reactive individuals FCM levels were lower in the cages. Previous studies have found that, after a period of adjustment and habituation, individuals show consistent and significant lower stress levels when kept in more natural conditions compared to cages (e.g. Schumann *et al.*, 2014). This is perhaps not surprising, but very rarely tested (but see Bartolomucci *et al.*, 2009) and has important consequences for animal welfare as well as for the reliability of behavioural studies conducted with caged animals. One possible explanation for our results might be that individuals with different coping styles need different amounts of time to adjust to a new environment. Proactive individuals are bolder, more active animals, relatively insensible to change, they explore a new environment faster (albeit superficially), and quickly form routines to cope with/move through it. They might therefore have responded to the change of housing conditions with a lower corticosterone production to begin with, and took less time to adjust to more natural conditions. Reactive individuals, highly sensitive to environmental changes and slower in gathering information/exploring a new territory, might have reacted more strongly to the change, and have been retrieved from the enclosures while they were still in the process of adjusting. This is a rather speculative suggestion, although other observations suggest that reactive individuals

went through a change in their foraging behaviour, concentrating effort in the more protected areas, and showing a significantly higher proportion of vigilance behaviour compared to proactive ones (Mazza *et al.*, submitted). Further studies should investigate whether the change from cages to natural conditions affects proactive and reactive individuals differently, and whether this is only a matter of time.

### *Conclusion*

Endocrine state proved to be a repeatable trait in bank voles and correlated with some personality traits, at least at lower basal levels. Physiological response to induced stress, however, did not correlate with any other trait, and our results might therefore be better explained by the updated coping styles model involving two different and separate axes. Determining whether or not this two-tier model is generally true across species and/or environmental contexts will require further studies, more attention to natural population and wider adoption of repeated measures designs to allow within- and among-individual sources of co-variation to be disentangled.

This study also highlights that experiments conducted in what are supposed to be controlled and protected conditions, might reveal patterns that are not consistent with natural conditions, and that the sole fact of being confined might differentially affect individuals and the responses they display depending on their personality and cognitive types.



## GENERAL DISCUSSION AND CONCLUSIONS

Individuals differ consistently in numerous aspects of their biology including personality, cognition and responsiveness to change and challenges. These domains influence each other, although the mechanisms underlying these links are not entirely understood. The study of individual differences, particularly in behaviour and cognition, is just blooming and as such is still grappling with methodological issues (e.g. Carter *et al.*, 2013; Griffin *et al.*, 2015; Healy and Rowe, 2014). Trying to fathom if and how these domains are inter-related may help shed light on the mechanisms that bring forth among-individual variation and why they are maintained by evolution.

This thesis provides an insight into the links between personality, cognition and responsiveness to challenges, and their potential meaning in terms of fitness in a small mammal. Main results support the hypothesis that individual differences in these domains are related and that they are reflected in ecological and fitness related aspects of their behaviour.

Personality and cognitive style were indeed related in bank voles through a speed-flexibility/accuracy trade-off, in accordance with previous theoretical framework (Carere and Locurto, 2011; Sih and Del Giudice, 2012). Bank voles with proactive personality traits (i.e. activity and boldness) were faster learners, although more rigid and persistent. Voles showing more reactive traits (i.e. shyer and less active) were instead slower but more flexible learners. Proactive individuals took less time than reactive ones to make their choices, both correct and incorrect. Moreover, comparing the latency make a choice and the choice outcome revealed that correct choices required more time. The link between personality and cognition in bank voles thus presented constraints that prevented the same individual from being concurrently fast, accurate and flexible or, in other words, sensitive and insensitive to environmental cues. Differences in performance between the tasks assessing learning speed and flexibility are not likely attributable to difference in motivation, since voles were consistent in their willingness to initiate the test (chapter 1).

Individual differences in personality and cognitive profiles were partially mirrored by the individuals' endocrine profiles, providing some support for the coping style model (chapter 3). As predicted, proactive individuals had lower HPA activity than reactive ones, and this correlation was found in the two less challenging situations. HPA activity affects cognitive functioning (e.g. McEwen and Sapolsky, 1995; but see Medina-García *et al.*, 2017). The effects vary considerably from impairment of the performance (McEwen and Sapolsky, 1995) to its enhancement (e.g. Pravosudov, 2003; Pravosudov and Clayton), depending on different combinations of factors (e.g. Joëls *et al.*, 2005; Kim and Diamond, 2002; Buchanan *et al.*, 2013). Several studies considered whether individual differences might also account for some of the variance in effect of stress and challenges on cognitive performance (e.g. Gouirand and Matuszewich, 2005; Valenchon *et al.*, 2017). In this case, it could be suggested that the higher HPA activity assessed in reactive voles might be a functional cause of their slower learning,

whereas lower levels of corticosterone promoted the fast formation of the association in proactive individuals. However, since there was no clear correlation between personality-cognitive profiles and corticosterone levels under a moderate challenge, this hypothesis remains to be tested. Also, we assessed the response to moderate stress in the Open Field arena, not during the associative learning trials. We therefore have no direct measure of the voles' physiological response the Y-maze. Further work will be necessary to clarify this point.

Although animals were not purposefully subjected to intense challenges, the measured corticosterone levels in holding conditions might not represent real baseline conditions. In fact, housing conditions affected differently proactive and reactive voles. Does this mean that proactive individuals are more suited to thrive outside laboratory conditions? The measured individual variation extends to different ecologically-relevant traits that might differentially influence fitness (chapter 2). However, it does not mean that one behavioural-cognitive-endocrine profile is better than another. From the presented results, it would only appear that they adapt to sudden change more quickly (chapter 3).

As predicted, proactive and reactive individuals had different foraging and antipredatory strategies, reflecting in different approaches to a risk-reward trade-off (chapter 2). Although all animals responded to the differential risk, proactive individuals chose to visit a potentially dangerous exposed area to access the extra food, whereas reactive individuals invested more time and effort in exploiting the safer food patch. Even then, they exercised more vigilance than proactive ones. Although proactive individuals exploited two food patches, they lost as much weight as reactive ones. Taking into account the different metabolic rates that characterize different behavioural types (e.g. Careau *et al.*, 2009, 2015; Šíchová *et al.*, 2014; Toscano and Monaco, 2015), the foraging strategies of proactive and reactive individuals seemed to yield similar overall benefits, at least regarding nutritional gain. Proactive individuals sustained the cost of heightened risk, reactive ones that of time investment which translated into missed opportunity costs. Other studies showed how different anti-predatory strategies of different behavioural types are also linked to corticosterone levels (Rödel *et al.*, 2006). What emerges is again the presence of constraints, likely given by the interaction of personality, cognition and physiology. In the relatively controlled, predator-free and devoid of conspecifics conditions of the experimental enclosures, there is no way of assessing the ultimate fitness consequences of the different strategies. The strategies displayed by individuals with different profiles might have differential adaptive value based on external, environmental circumstances, more than intrinsic features *per se*. Numerous studies have shown how different personalities are differentially favoured according to environmental fluctuating conditions. For example, selection – measured by adult annual survival – acted on great tits' (*Parus major*) exploratory behaviour, but the effects were opposite for males and females, and reversed between years of high and low food availability (Dingemanse *et al.*, 2004). The overall pattern of selection thus turned out to be stabilising (Dingemanse *et al.*, 2004). Similarly, adult survival of bold and

shy bighorn sheep (*Ovis canadensis*) was differentially affected in years of high and low predation pressure (Réale and Festa-Bianchet, 2003). Social environment is another important determinant of the relation between individual profiles and fitness, contributing to the maintenance of high levels of variation (Dingemanse and Réale, 2005). For instance, white-throated sparrows (*Zonotrichia albicollis*) displaying different levels of aggressiveness tended to pair disassortatively (Houtman and Falls, 1994), partly because certain pair combinations achieve better feeding of the nestlings (Knapton and Falls, 1983). On the other hand, Rangassamy *et al.* (2015) found that pairs with assortative personalities with respect to anxiety, starting to reproduce earlier than more dissimilar pairs.

Different sensitivity to external cues and flexibility might prove advantageous depending on the level of unpredictability of the environment itself (Niemelä *et al.*, 2013). Environments with moderate variation allow individuals to gather and use information effectively to their advantage, thus favouring sensitivity to cues and behavioural flexibility. Conversely, in environments that are either invariable or highly variable within an individual's life span, enhanced sensitivity or flexibility would either be unnecessary or not able to keep up with environmental change. This would favour nonflexible, stereotypic profiles (Niemelä *et al.*, 2013).

Although many possible theoretical explanations have been advanced, empirical studies addressing the fitness consequences of individual variation are still scarce, and only a few studies analyse more than one trait or make use of large sample sizes (Dingemanse and Réale, 2005). Further studies, conducted both in laboratory and natural conditions, and comparing populations exhibiting different traits are required to achieve a deeper understanding of the widely-acknowledged but still puzzling phenomenon of consistent among-individual differences.

#### *Concluding remarks and future challenges*

To conclude, this thesis provides an insight into the complex relationship between consistent behavioural, cognitive and endocrine variation, with implications for both animal welfare and behavioural ecology. Next steps in my work that might complement the information presented here include the assessment of exploration patterns of proactive and reactive individuals in a novel natural environment, the evaluation of the effects of old age on the individuals' cognitive abilities, and the investigation of the effects of anthropogenic stress on behavioural and cognitive flexibility in natural populations of voles.

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*“Nothing can be more improving to a young naturalist, than a journey in distant countries.”*

C. Darwin, 1839

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## **Allegato 1 - Relazione sulle attività svolte nel corso del dottorato e pubblicazioni**

Nel corso del primo anno di dottorato ho preso parte al progetto di studio sulla dinamica di popolazione dell'arvicola del Savi (*Microtus savi*) condotta dal gruppo di lavoro del mio tutor, Dr. Zaccaroni. Da novembre 2014 a luglio 2015 ho condotto monitoraggi mensili della durata di 8 giorni sulle popolazioni di arvicole in due aree di studio del centro Italia. Nel corso di questi mesi ho imparato la particolare tecnica di trappolamento necessaria per catturare le arvicole del Savi, e come maneggiare e marcare gli animali con chip sottocutanei. Ho contribuito allo sviluppo e applicazione di metodi volti a diminuire la forte mortalità da trappolamento riscontrata durante i primi mesi dello studio.

Ho inoltre cominciato a elaborare il mio progetto mirato agli aspetti comportamentali e riproduttivi dell'arvicola del Savi, a oggi prevalentemente ignoti. Ho elaborato un disegno sperimentale per lo studio empirico del sistema nuziale della specie e ho condotto alcuni test preliminari sul campo per testare le differenze individuali nel comportamento dei soggetti catturati durante il monitoraggio (febbraio-giugno 2015).

Ho partecipato, insieme al mio tutor, al mio collega Dr Dell'Agnello e a una studentessa magistrale, Matilde Martini, all'incontro di presentazione dei risultati preliminari dello studio tenutosi nella sede della Bayer.

Tra agosto e dicembre 2015, con l'aiuto del mio tutor Dr Zaccaroni e del Prof. Dessì-Fulgheri, il progetto relativo all'analisi comportamentale delle arvicole è stato ampliato e modificato per includere anche aspetti cognitivi. E' stato sviluppato un progetto di collaborazione con il gruppo di Ecologia Animale dell'Università di Potsdam, diretto dalla Prof. Eccard, e con l'Istituto Federale Julius Kühn, condotto dal Dr Jacob, per lo studio delle differenze individuali nei tratti cognitivi delle arvicole rossastre (*Myodes glareolus*). Nell'ambito dell'ecologia comportamentale lo studio delle differenze individuali si è ormai affermato da circa una quindicina di anni. Tuttavia, solo di recente alcune convincenti teorie sono state proposte a riguardo dei collegamenti tra comportamento e cognizione, e in particolare sulla possibilità che questo collegamento sia mediato dai cosiddetti compromessi tra velocità e accuratezza e tra rischio e ricompensa (Carere & Locurto, 2011; Sih & Del Giudice, 2012). Da quando la teoria è stata proposta nel 2012, pochissimi studi l'hanno testata formalmente e con risultati contraddittori.

Da gennaio 2016 mi sono trasferita a Potsdam, dove ho messo a punto il primo esperimento del mio progetto, volto a descrivere una possibile relazione tra le differenze comportamentali e gli stili di apprendimento delle arvicole rossastre. Ho imparato come condurre i test comportamentali classici di questo settore e i relativi metodi di analisi dei dati. Ho iniziato ad apprendere il funzionamento del programma statistico R. Ho disegnato e realizzato un nuovo test per l'apprendimento per le arvicole, utilizzando per la prima volta un sistema di motivazione basato sulla ricerca del riparo invece che sul cibo e una procedura che prevede il coinvolgimento nei test solo di animali già in fase di attività.

Questo ha presumibilmente permesso di ottenere i primi risultati chiari e soddisfacenti sulle capacità di apprendimento delle arvicole rossastre, nonché sul legame tra personalità definite proattive e uno stile cognitivo veloce e rigido e personalità definite reattive e uno stile di apprendimento lento ma flessibile. Da questo studio sono anche emersi elementi a sostegno della teoria di Sih e Del Giudice sulla presenza di un compromesso cognitivo tra velocità e accuratezza, a sua volta collegato ai tratti comportamentali.

A maggio del 2016 ho trasferito 60 degli 86 animali testati nell'Istituto Julius Kühn di Münster, dove ho condotto il secondo esperimento del mio progetto. L'obiettivo di questo esperimento era valutare le possibili conseguenze ecologiche dei diversi stili cognitivi e il legame con il compromesso tra rischio e ricompensa in condizioni semi-naturali. Qui ho imparato ad applicare il metodo delle *giving-up densities* (Brown, 1988) e ad utilizzare il software per analisi comportamentali BORIS. Lo studio ha evidenziato strategie di foraggiamento e antipredatorie diverse tra individui proattivi e reattivi, e una diversa propensione a privilegiare le ricompense a spese della sicurezza o viceversa. A mia conoscenza, questo è il primo studio condotto fuori dal laboratorio volto ad analizzare le relazioni tra cognizione e proxy della fitness in una specie di piccoli mammiferi.

Il terzo esperimento del mio progetto riguarda il legame tra i livelli di stress nei diversi tipi comportamentali e cognitivi e il possibile effetto dello stress sull'apprendimento. Il livello di stress è stato valutato misurando il contenuto di metaboliti di glucocorticoidi nei pellet fecali degli animali a riposo e sottoposti a stress. Questo metodo è non invasivo ed è stato riconosciuto come altrettanto affidabile rispetto al classico prelievo di sangue. In accordo con le aspettative e le letterature, i risultati hanno evidenziato livelli di stress a riposo che correlano con i tratti comportamentali: gli individui reattivi hanno un livello di base di stress più elevato rispetto a individui proattivi. Allo stesso modo, i livelli di stress misurati dopo i 5 giorni passati nelle arene sperimentali sono più alti negli individui reattivi rispetto a quelli proattivi. I risultati evidenziano inoltre come per molti individui (principalmente proattivi) il livello di stress in questa situazione è più basso di quello base misurato in laboratorio.

A ottobre 2016 ho riportato a Potsdam le arvicole e ho condotto un quarto esperimento per valutare come individui con diversi stili cognitivi e comportamentali affrontino esplorazione e colonizzazione di un nuovo ambiente. Ho seguito con la tecnica della radiotelemetria automatizzata e manuale 28 individui che sono stati liberati in grandi arene sperimentali. I dati raccolti serviranno a calcolare home-range, ritmi di attività e latenze di esplorazione degli animali.

Nel corso di questi tre anni ho partecipato ai seguenti convegni nazionali e internazionali:

- I anno:
  - Behavioural Ecology Meeting (Chioggia, VE), 12-13 febbraio 2015;
  - 10<sup>th</sup> European Vertebrate Pest Management Conference (Siviglia, Spagna), 21-25 settembre 2015, presentando i poster “*Savi's pine vole population dynamics in agro-ecosystems*” e “*Spatial behaviour of Microtus savii in Central Italy agro-ecosystems*”.
- II anno:
  - 11<sup>th</sup> Annual Meeting of the Ethological Society “Cognition, Evolution and Behaviour” (Göttingen , Germania), 17-19 febbraio 2016.
- III anno:
  - 12<sup>th</sup> Annual Meeting of the Ethological Society “From Sensory Perception to Behaviour” (Bonn, Germania), 22-24 febbraio 2017, presentando il contributo “*Learning via odour cues and personality in bank voles*”.
  - Behaviour 2017 “joint meeting of the 35th International Ethological Conference (IEC) and the 2017 Summer Meeting of the Association for the Study of Animal Behaviour (ASAB)”, presentando il poster “*Cognitive styles affect foraging and anti-predatory strategies in bank voles*”.

Ho tenuto I seguenti seminari:

- I anno:
  - Seminario “*Ormoni e mating system*”, corso di Etologia (Prof. Dessì-Fulgheri), LM Biologia, Università di Firenze.
- II anno:
  - “*Mating systems*”, corso di Etoecologia (Prof. Dessì-Fulgheri), LM Biologia, Università di Firenze;
  - “*Personality and learning abilities*”, Oberseminar AG Tierökologie, Università di Potsdam.
- III anno:
  - “*Cognition and individual differences*”, corso di Ecologia Animale (Prof. Eccard), LM Biologia, Università di Potsdam;
  - “*Foraging strategies in different bank vole personalities*” , *invited talk* presso lo Julius Kühn Institut;
  - “*Cognitive styles, foraging and anti-predatory strategies in bank voles*”, Oberseminar AG Tierökologie, Università di Potsdam.
  - “*Fitness consequences of variation in cognition: cognitive styles affect foraging and anti-predatory strategies in bank voles*”, workshop “Causes and consequences of individual variation in cognition”(Prof. Madden), Università di Exeter (9-11 ottobre 2017).

I risultati ottenuti hanno permesso di preparare le seguenti pubblicazioni:

- “*From biology to management of Savi's pine vole (Microtus savii)*”. Ranchelli E., Barfknecht R., Capizzi D., Riga F., Mazza V., Dell'Agnello F., & Zaccaroni M. (2016). *Pest Management Science*, 72(5), 857-863, doi: 10.1002/ps.4212.
- “*Trap type and positioning: how to trap Savi's pine voles using the tunnel system*”. Dell'Agnello F., Mazza V., Martini M., Bertolino S., Capizzi D., Riga F., & Zaccaroni M., *Mammalia* (in stampa).
- “*The fast and the flexible: cognitive style drives individual variation in cognition in a small mammal*” Mazza V., Eccard J. A., Zaccaroni M., Jacob J., & Dammhahn M. (2018). *Animal Behaviour* (in revisione).
- “*Consistent demographic trends in Savi's pine vole between two distant areas in central Italy*”. Dell'Agnello F., Barfknecht R., Bertolino S., Capizzi D., Martini M., Mazza V., Riga F., & Zaccaroni M. *Mammalian Biology* (in revisione).
- “*Cognitive styles affect foraging and anti-predatory strategies in bank voles*”, invited contribution to the *Philosophical Transaction of The Royal Society B Special Issue “Causes and consequences of individual differences in cognitive ability”* (in preparazione).
- “*Stress, personality and cognition are linked in bank voles*” (in preparazione).
- “*The mating system in the genus Microtus: a review*” (in preparazione).
- “*Predictions on Microtus savii's mating system*” (in preparazione).

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Firma 