

University of South Bohemia
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CAUSES AND CONSEQUENCES OF PERSONALITIES IN MICROTINE RODENTS

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PhD. thesis

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Annotation:

This thesis focuses on individually specific differences in behavioural strategies, personalities, with two microtine rodents (*Microtus arvalis* and *M. oeconomus*) as study species. The work evaluates methodology necessary to reveal and measure consistent individual differences in behaviour, identifies possible proximate and ultimate mechanisms behind the existence of individual behavioural variability, and describes some ecological, evolutionary and behavioural consequences of personalities.

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List of original papers and author contribution:

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Lantová P., Šíchová K., Sedláček F., Lanta V. Determining behavioural syndromes in voles – the effects of social environment. *Ethology* (2011) 117, 124-132 [IF=2.019]

Paper 2

Lantová P., Šmilauer P., Mappes T. Personalities show contradictory patterns in stability and consistency of behaviour. Manuscript

Paper 3

Lantová P., Šíchová K., Borowski Z., Koskela E., Zub K. Is there a linkage between metabolism and personality in small mammals? The root vole (*Microtus oeconomus*) example. Manuscript submitted to *Physiology & Behavior*, 2nd revision.

Paper 4

Brixová L., Lantová P., Lanta V. Urine marking in male common voles: Does personality matter? Manuscript

The table shows the contributions to the original papers. Smaller contributions are stated as the authorship or in the acknowledgements of the original paper. PL – Petra Lantová, KŠ – Klára Šíchová, VL – Vojtěch Lanta, FS – František Sedláček, PŠ – Petr Šmilauer, TM – Tapio Mappes, ZB – Zbigniew Borowski, EK – Esa Koskela, KZ – Karol Zub, LB – Lenka Brixová, VR – Veronika Roubová

	Paper 1	Paper 2	Paper 3	Paper 4
Original Idea	PL	PL	PL	PL
Data	KŠ, VR, PL, FS	PL, KŠ, VR	PL, KŠ, KZ, ZB	LB, KŠ
Analyses	VL, PL	PŠ, PL	KZ, PL	VL, PL
Writing	PL	PL	PL, EK	LB, PL

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CHAPTER 1

Introduction

General background

Individual phenotypic variability is the keystone for evolution to occur. While the fact that individuals differ systematically in their behaviour is obvious to any observer, it is only recently getting attention in evolutionary ecology. In the past, evolutionary biologists tended to view such variation as stochastic noise, generated by processes as mutation, drift and recombination. This noise was considered important in that it provides the raw material for adaptive evolution, but for the rest the focus was on average or ‘typical’ behaviour. Individual differences in behaviour have thus for long been regarded as the raw material on which selection acts rather than an end product of natural selection (Réale et al. 2007).

According to their behavioural phenotype, animals react differently; some individuals explore the boundaries of their habitat, whereas others stay in well known areas. Some of them take risks (potential predators, novel objects or novel situations) while others avoid them. These individual strategies—**personalities** or temperaments—are defined by two main features. The first characteristic is the **consistency** of an individual’s behavioural responses over time and/or across situations (Budaev 1997, Réale et al. 2007), which means that an individual maintains its rank for a behavioural phenotype relative to the phenotypes of other individuals in the population. The other definition, related to the first one, denotes correlations between behavioural traits and it is referred to as **behavioural syndrome** (i.e. suites of correlated behaviours across contexts and situations, Clark & Ehlinger 1987; Sih et al. 2004).

The personality theory has currently established an accepted position in ecological and behavioural studies and—for its important fitness consequences—represents an important addition to our understanding of the ecology and evolution (e.g. Dingemanse et al. 2004; Wilson et al. 1994; Clarke & Boinski 1995; Carere et al. 2005). During the last decade, personalities have been described in a huge variety of species, ranging from spiders to bumblebees, from octopuses to sticklebacks, and from mice to monkeys (e.g., Clark & Ehlinger 1987, Gosling 2001, Sih et al. 2004). It has been shown that personality traits are associated with survival (Réale & Festa-Bianchet 2003, Dingemanse et al. 2004), reproductive success and strategies (Armitage 1986, Coss & Biardi 1997, Réale et al. 2000, Armitage & van Vuren 2003, Both et al. 2005, Hollander et al. 2008), parental care (Budaev et al. 1999), exploratory behaviour (Verbeek et al. 1994), natal dispersal (Dingemanse et al. 2003), anti-predator behaviour (López et al. 2005, Quinn & Cresswell 2005), and that the expression of these traits is context-dependent (Dingemanse & de Goede 2004, van Oers et al. 2005) and coincides with changes in environmental conditions (Dingemanse et al. 2004).

Personality from evolutionary perspective

The concept of personality has changed substantially the perception of behavioural adaptation, with a shift of interest from a highly plastic conception (i.e. depending mostly on past experience or the immediate environmental conditions) to a conception of behaviour as an intrinsic (i.e. non-flexible) and constrained characteristic of an individual (Réale et al. 2010). The existence of individual differences in wild animal populations raises the questions why different types of individuals often co-exist in a population, whether there is heritable variation in these traits and whether they have fitness consequences. Bergmüller & Taborsky (2010) have recently depicted ‘three evolutionary riddles concerning animal personality’. Firstly, behaviour is generally expected to be flexible rather than consistent over time in order to allow appropriate responses to variation in environmental and social conditions. In contrast to this expectation, many studies have shown that behaviour is often remarkably consistent within individuals over time (Sih et al. 2004; Réale et al. 2007). In other words, the behaviour remains stable over time in the sense that each individual expresses only a part of the behavioural trait values present in a population, even if the absolute level of behaviour of an individual somewhat fluctuates. Secondly, behavioural trait values of individuals in a population should evolve towards a mean optimal phenotype, i.e. evolved traits should show little variance. However, recent research has revealed that individuals in a population frequently differ substantially in their behavioural type (Gosling 2001; Dingemanse & Réale 2005; Réale et al. 2007; Wolf et al. 2007). And thirdly, independent behavioural responses should be favoured over behavioural correlations across functionally unrelated contexts, because uncoupled behaviors might allow for more adequate responses to specific challenges. In contrast to this prediction, a number of studies have shown that seemingly unrelated behaviours are often correlated among each other (e.g. Sih et al. 2004; Dingemanse et al. 2007; Bell & Sih 2007). Looking for explanations of these riddles thus presents principal tasks for personality research.

Causes, mechanisms and theories behind the existence of personality differences

General goals of personality research are to identify causes and consequences of the individual differences in behaviour and correlations among behavioural traits. Various mechanisms have been proposed and described from both proximate (mechanistic) and ultimate (evolutionary) perspective, examples of proximate explanations can be:

- Pleiotropy and linkage disequilibrium. The first one refers to the situation when one gene is involved in the expression of two different traits, the latter one to a state when a gene involved in the expression of one trait is located on the chromosome near a gene involved in the expression of another trait. These are generally the two mechanisms considered to be responsible for the resulting genetic correlation (Lynch & Walsh 1998; Roff 1997).
- Antagonistic pleiotropy. Two traits can be associated at both genetic and phenotypic level in the way that one trait corresponds with fitness costs whereas the second trait corresponds with fitness benefits, which consequently generates evolutionary trade-offs (Roff & Fairbairn 2007; Sih & Bell 2008).
- Heritability. Evolution is manifested only in the traits that are transferable to the next generations and thus the contribution of genetic factors in shaping personality traits (i.e. inheritance) is of fundamental relevance (Dingemanse et al. 2002, Drent et al. 2003). It has been shown that individual differences in behaviour are moderately heritable (heritability estimates of around 20-40%, range 0-66%; Koolhaas et al. 1999; van Oers et al. 2005).
- Neuro-endocrinological pathways. Neuro-endocrinological individual differences influence the differential expression of suites of behavioural traits (Koolhaas et al. 1999; Groothuis & Carere 2005).
- Personality primarily reflects genes, but can be shaped also epigenetically or hormonally during prenatal period, or socially during early postnatal ontogenesis (see indirect genetic effects - Wolf & Brodie 1998, Mousseau & Fox 1998, Wolf 2000). For instance, intrauterine position phenomenon described for rodents (female fetuses are masculinized by testosterone diffusing from adjacent male fetuses; vom Saal 1984) is an example of hormonal impact. Among the epigenetic factors shaping brain and behavior during early postnatal life, social experiences have a major impact. So far most studies have been focused almost exclusively on the mother-offspring interaction (it has been shown that high or low levels of maternal behaviour affects neurobiological and endocrine responses at adulthood and, for instance, stress and anxiety-like behaviour, exploratory behaviour and maze learning; e.g., Liu et al. 1997, 2000; Caldji et al. 1998), but also interaction with peers or other members of the community play important roles (for instance, Dimitantos et al. 2007 showed that litter size can affect emotionality in adult rats independently on maternal care). Additionally, besides social factors, also environmental factors can shape the development of individual personalities (e.g. Carere et al. 2005 showed that food restriction shaped activity, aggressiveness, and begging behaviour of young tits (*Parus major*)).

Further mechanisms described from the ultimate perspective:

- Individual consistency and divergence can be promoted by positive feedback mechanism resulting from getting skilled in a certain task. With the help of specialization, individuals may avoid costs arising from switching between tasks, or they can become better in a task due to learning (Wolf et al. 2008, Bergmüller 2010).
- Specialization may decrease costs involved in interactions among individuals by reducing the level of conflict between conspecifics (see ‘social niche specialization theory’; Bergmüller & Taborsky 2010).
- Consistency in behaviour could be a result of sexual selection, for instance, if females prefer consistent males over inconsistent males or males do better in male-male competition when they are consistent (Schuett et al. 2010).
- Coexistence of different types in a population can be also caused by different forms of balancing selection, such as frequency-dependent selection or spatio-temporal heterogeneity (which may be distinguished also as density-dependent selection). The former one refers to a form of selection in which the relative fitness of a specific phenotype declines if the frequency of that phenotype becomes too high, the latter to a situation when different phenotypes are favoured under different conditions, i.e. when fluctuations in the favoured phenotypes are caused because of environmental heterogeneity in space and time.

Aims and short overview of the dissertation

This work targets some of the above outlined questions and look for possible causes and consequences of personality in small rodents. Two vole species – *Microtus arvalis* and *M. oeconomus* were chose as study species. The structure of the dissertation can be summarized as follows:

First of all it was necessary to validate methodology for measuring personality traits. To be sure that we deal with stable traits, two criteria must be met – (i) experiments should be ‘fine-tuned’ (i.e. neither too strong, nor too weak) to reveal phenotypic variation among individuals, and (ii) the measured traits must be consistent (i.e. repeatable) to assure that we deal with real traits, not with random values. In the first study, we thus target inter-individual variability, and intra-individual consistency in personality traits measured in two traditionally used behavioural experiments, and we also look for correlations among the measured personality traits (so called behavioural syndromes), which result from stable inter-individual differences (if there are any). Moreover, the

work addresses some of the proximate (developmental/social) mechanisms possibly responsible for the existence of identified personalities.

The second study targets a possible consequence of personality differences for behavioural research. Repeated testing and observation of the animals necessary for proving of the consistency of personality traits, may be confounded by individually-specific habituation to experimental procedure, or, to put it more generally, by individually-specific phenotypic plasticity in behaviour. This topic has been recently strongly recommended for study, and to our knowledge, this study is the first one that targets this problem and demonstrates significant results.

The third paper follows another recent calls and hypotheses in personality research and addresses further proximate factors underlying consistent individual differences. By measuring wild living root voles (*Microtus oeconomus*) we tested predicted linkages between behavioural and physiological reactions. Significant correlations between them are generally expected because both energy metabolism and behaviour (specifically reaction to stress) are controlled by the same neurophysiological axis.

The last paper concerns possible consequences of animal personality, specifically, the effect of personality on urine marking behaviour, which is a topic that has not been examined so far. Marking frequency indicates social status or competitive ability of an individual, we, therefore, studied a relationship between male urine-marking in reaction to another male's marks (standard opponent) and individual personality profile, characterized by behavioural activity in open field test (OFT).

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CHAPTER 2

Determining behavioural syndromes in voles – the effects of social environment

Lantová P., Šíchová K., Sedláček F., Lanta V.

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Determining behavioural syndromes in voles – the effects of social environment

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Abstract

Animal personality and behavioural syndromes have experienced rapid increase in interest in the last few years because of their possible role in the evolution of life histories. However, there is still a scarcity of studies concerning the mechanisms maintaining variation in behaviour as well as addressing their relationships to each other. In this paper, we tested the main assumptions of personality, focusing on the individual variability and repeatability of behaviour, and the identification of behavioural syndromes using the common vole (*Microtus arvalis*) as the species being studied. We also studied the effects of family group characters (group size, sex ratio and affinity to family) on the behaviour in this rodent. The animals were repeatedly tested in two behavioural experiments – novel environment (NE) test and radial-arm maze (RAM) test, from which seven personality traits were extracted. The study revealed that inter-individual variance in vole behaviour was consistent and repeatable. Individual-specific responses to NE corresponded with the performance in the maze, which revealed behavioural syndromes and possible trade-offs. Anxiety was determined by the size of the family group, whereas escape-related behaviours and

maze-exploring tactic were more dependent on the affinity to the family. It seems that the development of personality traits we identified here is determined by the effects and structure of the family groups. Further studies are needed to confirm whether the observed variance in vole personalities is maintained by the fitness costs and benefits of the opposite tactics (here fast-random vs. slow-systematic exploration) in more natural circumstances.

CHAPTER 3

Personalities show contradictory patterns in stability and consistency of behaviour

Lantová P., Šmilauer P., Mappes T.

Manuscript

Personalities show contradictory patterns in stability and consistency of behaviour

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Running title: Stability and consistency in behaviour

Key words: activity index, behavioural plasticity, consistency, common vole, habituation, open-field test, personality, stability

Abstract

Consistency of behavioural traits is a crucial requirement for all studies on individual variability in behaviour. The fact that the trait is consistent, however, does not necessarily denote that it is also stable (in absolute values). Here we compare consistency and stability of repeated behavioural performance of common voles (*Microtus arvalis*) in open-field test. We demonstrated that the vole behaviour was consistent, but the consistency (repeatability) was surprisingly higher over the longer compared the shorter interval between observations. Importantly, we showed that the rate and pattern of the change of behaviour (i.e. stability) over the trials was personality- and time-lag specific. Over the short time interval, active individuals decreased their activity, but they increased it again to its original level after the long time interval. On the contrary, less active individuals showed subsequent increase in their activity in the open field. The estimates of behavioural stability and consistency are thus clearly affected by the time span between repeated trials, and show differing patterns for the individuals from the opposite ends of the personality spectra. Both of these

facts can be viewed as differences in phenotypic plasticity in behaviour and should be taken into account in studies where behavioural consistency is a basic requirement. Besides these findings, we also bring a new mathematical approach (activity index) to analyzing animal reaction to a new-environment type of experiments.

CHAPTER 4

Is there a linkage between metabolism and personality in small mammals? The root vole (*Microtus oeconomus*) example

Lantová P., Zub K., Šíchová K., Koskela E., Borowski Z.

Physiology & Behavior, 2nd revision

Is there a linkage between metabolism and personality in small mammals? The root vole (*Microtus oeconomus*) example

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Running title: Linkage between metabolism and personality

Keywords: animal personality, energy metabolism, individual variance, *Microtus oeconomus*, resting metabolic rate, root vole

Abstract

Significant inter-individual variation in the rate of animal metabolism is a widespread phenomenon that has started to accumulate general interest. Here we follow recent calls to focus on linkage between the variation in resting metabolic rate (RMR) and animal personalities. The relationship between these two traits is of central interest not only because of their developing role as important components of individual fitness, but also as behavior and metabolism are both controlled by the

same hormonal and neurological axis. By using wild caught root voles as a study species, we examined the linkage between the behavioral patterns (assessed in open field test) and resting metabolic rate (RMR), both of which are known to show large individual differences and intra-individual consistency in voles. Our results showed weak relationship between variation in personality traits and mass-independent metabolism. Personality trait reflecting proactive behaviors was chosen (according to AICc) together with body mass, sex and season within the best models explaining the level of RMR, but also the model including only body mass and season was within 2 units of the model with the lowest AICc. In all, our study does not provide compelling support for recent ideas of close linkage between behavior and metabolism. Still, our study highlights that even in the case of wild caught individuals when behavior and metabolism often carry effects of both intrinsic and extrinsic conditions, the potential effects of varying behaviors of individuals on their metabolism cannot be neglected.

CHAPTER 5

Urine marking in male common voles: does personality matter?

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Manuscript

Urine marking in male common voles: does personality matter?

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Key words: common vole, *Microtus arvalis*, open field test, personality, urine marking

Abstract

Rodent urine provides animals with a large amount of information, from the identity of the animal through its condition to social status. Many studies therefore focus on rodent urine-marking behaviour and use marking frequency as an indicator of social status or competitive ability. However, marking, like many other aspects of rodent behaviour, may be affected by individual personality, an option that has not been examined so far. We, therefore, studied a relationship between male urine-marking in reaction to another male's marks (standard opponent) and individual personality profile, characterized by behavioural activity in open field test (OFT). The marking appeared to be consistent and specific for the individuals as there was a significant positive relationship between individual markings in two different phases of the experiment. The linkage between behavioural activity in the OFT and urine-marking frequency was non-linear (quadratic), which suggested that males with intermediate activity marked more intensively than males from the extremes of the behavioural spectra. The relationship between the opponent's and the tested males' markings was positive, however, we found no statistically significant evidence that the voles would attempt to overmark the opponent. Marking thus seems to have rather self-advertisement than competitive function in the common vole. Further, as high marking activity is under the strong

intra- or intersexual selection, the result might suggest stabilizing selection on the personality trait described as behavioural activity in our study.

CHAPTER 6

Summary

Acknowledgements

SUMMARY

This dissertation targets the phenomenon of animal personality, which reflects consistent individual differences in animal behaviour and recently experiences rapid increase of interest in evolutionary and behavioural ecology.

In the first paper, the main assumptions of personality (individual variability and repeatability of behaviour), and the existence of behavioural syndromes (correlations among behaviours) were studied. The study revealed that new environment type of experiments (open field test [OFT] and exploration of a maze) are appropriate tools for personality research on study species, voles, as the tests revealed that inter-individual variance in the vole behaviour was consistent and repeatable. Individually-specific responses to the OFT corresponded with the performance in the maze, which revealed behavioural syndromes and possible trade-offs, a mechanism contributing to the maintenance of variable geno-/phenotypes in populations. Some of the identified personality traits were affected by the size, structure or identity of the family group, which implies proximate mechanisms affecting the development of variable personalities.

The second study focuses on consistency and stability of behaviour on individual level. The results showed that the consistency (repeatability) was surprisingly higher over the longer compared the shorter interval between observations and the rate and pattern of the change of behaviour (i.e. stability) over experimental trials was personality- and time-lag specific. The individuals from the opposite ends of the personality spectra showed rather opposite patterns in the stability of their behaviour.

Thirdly, a linkage between energy metabolism (measured as resting metabolic rate) and individual personality was tested. The study showed that metabolism was mostly affected by extrinsic (season) and intrinsic (body mass, sex) conditions, however, weak positive effect of a personality trait reflecting proactive behaviours was identified too.

The last study aims the relationship between vole personality assessed in OFT and marking behaviour, a trait reflecting individual social status or competitive ability. The marking appeared to be consistent and specific for the individuals and can be thus perceived as one of the personality traits. The linkage between behavioural activity in the OFT and urine-marking frequency was non-linear (quadratic), which suggested that males with intermediate activity marked more intensively than males from the extremes of the behavioural spectra. Marking appeared to have rather self-advertisement than competitive function in the common vole.