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Osobnostní rysy chování hraboše polního: Jejich behaviorální plasticita a vliv na rozmnožování

Disertační práce

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Annotation

This thesis is focused on development of individual behavioural tendencies (i.e. animal personality), behavioural plasticity and its influence on reproduction succes in common voles (*Microtus arvalis*). Because common vole is one of our most common rodent species with huge impact in agriculture, we investigated still not studied aspects of common vole's life. The definition of personality traits implies their relative temporal stability as well as, stability under different environmental conditions. In two studies, this personality traits stability/plasticity is approached as phenotypic plasticity using behavioural reaction norm. The first study presents the result of lifelong testing of voles using four open field tests with two-month intervals. The second study, on the other hand, provides insights into the development of personality traits during three days of placing a vole in a new monitoring box environment. The third study analyses one of the possible mechanisms for maintaining personality traits in the vole population. Whether greater similarity in the behavioural personality traits of parental pairs leads to a higher number of offspring.

Prohlášení

Prohlašuji, že jsem autorem této disertační práce a že jsem ji vypracovala pouze s použitím pramenů a literatury uvedených v seznamu použitých zdrojů.

České Budějovice, 20. 7. 2021

Gabriela Urbánková

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Gabriela Urbánková se podílela na návrhu uspořádání laboratorního pokusu, vedla jeho realizaci, sepsala první verzi manuskriptu a následně se podílela na jeho konečné úpravě. (Celkově 50%)

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Gabriela Urbánková navrhla experiment, podílela se na jeho realizaci, sepsala první verzi manuskriptu a také se podílela na konečné úpravě textu. (Celkově 60%)

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Gabriela Urbánková se podílela na návrhu laboratorního pokusu, vedla jeho realizaci a spolupodílela se sepsání manuskriptu. (Celkově 60%)

Prohlášení o autorském podílu

Prof. RNDr. František Sedláček, CSc., který je spoluautorem článků I, II a III, plně souhlasí s uvedenými podíly Gabriely Urbánkové na těchto článcích.

V Českých Budějovicích dne 20. 7. 2021

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prof. RNDr. František Sedláček, CSc.

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Kapitola 1

Úvod do problematiky osobnostních rysů chování u zvířat

Inter-individuální rozdíly v chování (s drobnými rozdíly označované jako personalita zvířat, temperament, copying style, behaviorální syndrom, apod.) jsou v posledních několika desetiletích středem velkého zájmu (Coleman & Wilson, 1998; Dingemanse et al., 2004; Koolhaas et al., 1999; Sih et al., 2004). Bylo zjištěno, že tyto odlišnosti v chování jsou částečně dědičné (Dingemanse, 2002; Drent et al., 2003) a zároveň bylo dokumentováno, že personalita má vliv např. na přežívání (Dingemanse et al., 2004), rodičovské chování (např. Mutzel et al., 2013), zdatnost jedince (např. Jennings et al., 2013) či na učení jedince (např. Carere & Locurto, 2011). Tyto inter-individuální rozdíly byly nalezeny již u širokého spektra živočichů, zahrnujícího jak obratlovce, tak i bezobratlé (přehled v Stamps & Groothuis, 2010b).

U živočichů se brzy ujalo hodnocení osobnostních rysů pomocí polohy na shy-bold, případně slow-fast kontinuu. Tento přístup byl využit u řady živočichů zahrnující primáty (O´Neill et al., 1991), psovité (MacDonald, 1983) a kočkovité šelmy (Feaver, 1986), ptáky (Jones et al., 1991), hlodavce (Blanchard et al., 1986) či ryby (Coleman & Wilson, 1998; Brown et al., 2007). Pozice zvířete (osobnostní typ) v tomto pomyslném gradientu je relativně stabilní v čase (Dzieweczynski & Crovo, 2011) a jeho hraničními body jsou maximální bázlivost (shy) a na opačné straně maximální odvážnost (bold). Rozdíly mezi osobnostními typy lze demonstrovat na příkladu reakce na nový neznámý objekt. Zatímco „bold“ jedinci o něj budou projevovat zájem i za cenu vystavení se nebezpečí (např. predaci), zvířata „shy“ budou reagovat zdrženlivě (Coleman & Wilson, 1998). Tyto vlastnosti mohou např. významně zkreslit výsledky studií mapující početnost zvířat. Pokud jsou k odchytu používány pasti vyžadující aktivní přístup zvířete, budou odchycena převážně zvířata typu „bold“ (Coleman & Wilson, 1998; Biro & Dingemanse, 2008). Zmíněné osobnostní typy se mohou lišit i v jiných rysech, jako je doba vývoje k dosažení pohlavní dospělosti či reprodukční úspěšnost (Réale et al., 2000; Réale & Festa-Bianchet., 2003).

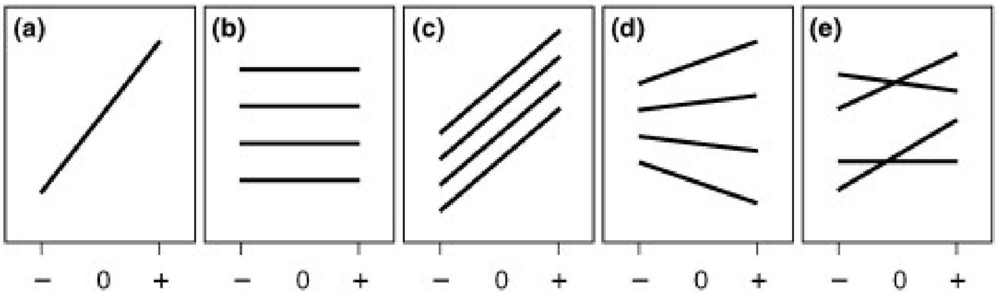
Jak již bylo řečeno výše, obdobou shy-bold kontinua je model fast-slow. Ten je využíván především při studiu vnitrodruhové variability u ptáků a můžeme se s ním setkat především u sýkor (Drent et al., 2003; Marchetti & Drent, 2000). Polohu na gradientu v tomto modelu jedinec může získat na základě reakce opět na nový objekt, tedy jedinec je označen za rychle prozkoumávajícího (fast), nebo pomalu prozkoumávajícího (slow) (Carere et al., 2005; Drent et al., 2003). Dalším podobným modelem je gradient proactive-reactive. Tento model se opírá především o stanovení rysu agresivity a schopností odolávat stresu (Koolhaas et al., 1999; Sih et al., 2004). Využíván je zejména při studiu vnitrodruhové variability u hlodavců – zejména myši domácí (*Mus musculus domesticus*; Benus, 2001; van Oortmerssen & Bakker, 1981). Proaktivní jedinci jsou více agresivní, rychleji útočí, intenzivně kontrolují teritorium. Naopak reaktivní jedinci se projevují spíše imobilitou, náchylností ke stresu a nižší hladinou testosteronu (Benus et al., 1989; Koolhaas et al., 1999). Obecně lze říci, že jedinci na opačném konci osy, ať už v modelu proactive-reactive, slow-fast či shy-bold, se navzájem liší v emocionální stabilitě. Reaktivní, slow nebo shy jedinci jsou v tomto ohledu méně behaviorálně stabilní, ačkoli s věkem se mohou posunout na pomyslné ose blíže k proaktivním, fast či bold jedincům. Jejich skóre však nikdy nedosahují (Carere et al., 2005). Zároveň jsou jedinci reaktivní, slow a shy více obezřetní a nemají sklony k rutinnímu chování.

Z definice zvířecí personality vyplývá, že se jedná o soubor vlastností jedince, které ho odlišují od ostatních jedinců v populaci, a tyto vlastnosti jsou v čase i napříč situacemi konzistentní (Koolhaas et al., 2010). Tato definice v podstatě popírá vývoj osobnosti či osobnostních rysů, ačkoli je jasné, že osobnost představuje dynamickou vlastnost jedince (Stamps & Groothuis, 2010b). Donedávna vycházel výzkum zvířecí personality z dlouho uznávané myšlenky, že osobnost se ustanovuje po dosažení pohlavní dospělosti a že poté jsou její projevy již stabilní či silně konzistentní (Müller & Schrader, 2005). Nicméně zda k ukončení vývoje opravdu dochází, není zatím jasné (Groothuis & Trillmich, 2011). Ukončení vývoje se zdá být poměrně nepravděpodobné vzhledem k faktu, že během života zvíře jednak prochází různými ontogenetickými etapami, které mohou vyžadovat různé behaviorální strategie, ale zvíře se také učí a získává různé zkušenosti, které mohou jeho chování významně měnit (Stamps & Groothuis, 2010b; Groothuis & Trillmich, 2011).

S rostoucím počtem studií zaměřených na osobnostní rysy se tak objevuje také otázka jejich behaviorální fenotypové plasticity podobně jako u jiných fenotypových znaků (Mathot et al., 2012; Kluen & Brommer, 2013; Mackay & Pillay, 2019). Tato plasticita osobnostních rysů je zkoumána např. pomocí tzv. behaviorální reakční normy (BRN) (Griffiths et al., 2000; Fuller et al., 2005), tedy projevených hodnot parametru během postupně se měnících podmínek v čase nebo prostoru (Dingemanse et al., 2010; Dingemanse & Wolf, 2013). Navrženo bylo několik scénářů propojení osobnostních rysů a behaviorální plasticity (Nussey et al., 2007; Dingemanse et al., 2010). Například plasticita může být nízká při malém sklonu proložené přímky a při zachování pořadí jedinců podle skóre na gradientu/osy osobnostního rysu nebo plasticita může být vysoká při velkém sklonu a změně pořadí jedinců podle uvedeného skóre (viz Obr. 1).

Vztahy mezi specifickými osobnostními rysy a jejich plasticitou lze teoreticky vysvětlit jako součást obecného systému vypořádávání se s nejistotou (shrnuto v Mathot et al., 2012). Autoři vysvětlují, že snaha jednotlivců získat dostatek informací o svém okolí (např. o potravě a úkrytech) se pravděpodobně bude měnit v závislosti na individuální aktivitě a chování při průzkumu a současně vytvoří rozdíly mezi populacemi v reakcích na určité změny podmínek prostředí. Byla také pozorována behaviorální plasticita omezená na konkrétní skupinu jedinců v populaci;

například bylo zjištěno, že vysoce agresivní myši neupravují svou agresivitu v různých sociálních kontextech, zatímco opačné typy ano (Koolhass et al., 1999; Natarajan et al., 2009). Mathot et al.



Obrázek 1 Zde jsou zobrazeny modelové situace, které mohou nastat u jedinců s různým osobnostním rysem, který může být spojen s různou behaviorální plasticitou. Vztah mezi uvedenými veličinami je zde podán ve formě tzv. „Behaviorální reakční normy“. Úsekem na ose „Y“ je zobrazena hodnota osobnostního rysu a pozice na ose „X“ obecně představuje časoprostorové podmínky, ve kterých byl osobnostní rys stanoven. Tedy např. měření osobnostního rysu s několikadenním intervalem nebo za různé stoupající či klesající teploty prostředí. Varianta (a) ukazuje, že všichni jedinci v populaci mají teoreticky stejnou hodnotu osobnostního rysu a vykazují stejnou změnu, tedy stejnou behaviorální plasticitu. Varianta (b) ukazuje situaci, kdy rozdílné osobnostní rysy nejsou spojeny s plasticitou (nedochází k žádné změně). Varianta (c) ukazuje rozdílné osobnostní rysy, které jsou spojeny se stejnou hodnotou (sklonem) behaviorální plasticity. Varianta (d) ukazuje spojení vyšších hodnot osobnostního rysu s jejich nárůstem (pozitivním sklonem) a nižších hodnot s jejich poklesem (negativním sklonem). Varianta (e) ukazuje u jedinců v populaci existenci různých osobnostních rysů, které jsou spojeny s různou behaviorální plasticitou, ale chybí zde jakýkoliv vztah mezi těmito veličinami, zde se tedy jedná o absenci kovariance (Dingemanse et al., 2010).

(2012) na základě svého přehledu zjistil, že konkrétních poznatků je velmi málo, a proto doporučil více empirického zkoumání vztahu mezi osobnostním rysem a jeho behaviorální plasticitou. Mezitím se objevila další podnětná idea v problematice plasticity, a to taková, že změny v průběhu života jedince nemusí být pasivní reakcí na aktuální situaci, ale spíše projevem očekávání určitých změn. Tedy že plasticitou by zvířata byla připravena na události nebo podmínky, které mohou nebo nemohou nastat (Stamps & Krishnan, 2014). V návaznosti na tuto studii představili Stamps & Krishnan (2017) svá zjištění, že plasticita (budoucí schopnost) neklesala s věkem, ale byla udržována v podmínkách chovu za absence jakýchkoliv podnětů, čímž se vlastně prodlužovala raná senzitivní perioda. V poslední době se plasticita chování stala součástí širšího paradigmatu fenotypové plasticity (Fox et al., 2019).

Je stále jasnější, že behaviorální plasticita může mít podobu až osobnostních rysů (Dingemanse & Wolf, 2013). Tato plasticita by se mohla chovat podobně jako fyziologické funkce a to např. stresová reakce nebo intenzita metabolismu, které jsou jasně plastické, ale vykazují určitou bazální úroveň regulovanou v relativně úzkém rozmezí (Norin & Metcalfe, 2019). Mitchell & Biro (2017) demonstrovali tento stav u ryby dánio pruhované (*Danio rerio*) jako konzistenci sklonů v reakčních normách. Kromě vztahu mezi osobnostními rysy a behaviorální plasticitou je třeba ještě zmínit také intraindividuální variabilitu, která má také jasné vazby na evoluční ekologii. Ačkoli se tato tři témata překrývají, je třeba zdůraznit, že osobnostní rysy se objevují na úrovni populace jako výsledek intra-populačních procesů, zatímco plasticita chování a intraindividuální variabilita jsou zjevně spojeny s individuální úrovní (Japyassúa & Malangeb, 2014). Ve studii na vlaštovce stromové (*Tachycineta bicolor*) testovaly Betini & Norris (2012) dvě základní hypotézy. První, nazvaná „kvalitní jedinci“, předpokládá, že jedinci s výraznými osobnostními rysy mají také výraznou behaviorální plasticitu. Druhá hypotéza,

„kompenzační“, předpokládá, že jedinci s nízkými hodnotami osobnostních rysů mají zvýšenou plasticitu, tj. mají větší schopnost kompenzovat různé vnější nebo vnitřní vlivy. V uvedené studii bylo zjištěno, že samci se chovali (a byli úspěšní) podle kvalitativní hypotézy, ale stejně úspěšní byli i mírní samci, kteří byli vysoce plastičtí podle druhé hypotézy (Betini & Norris, 2012). Podobně ve studii na koljušce tříostné (*Gasterosteus aculeatus*), Jolles et al. (2019) objevili negativní korelaci mezi behaviorální plasticitou a odvážností a pozitivní korelaci s bázlivostí. Zbytkový rozptyl souvisel s předvídatelností: čím větší byl rozptyl, tím nižší byla předvídatelnost. Rozptyl byl větší u bázlivých jedinců, takže jejich chování bylo méně předvídatelné.

Objevilo se několik teoretických prací, které vyzývají k dlouhodobému studiu vývoje zvířecí osobnosti (např. Stamps & Groothuis, 2010a, b), neboť není dostatek robustních dat v této otázce. Současné studie se zpravidla zaměřují spíše na ekologický a evoluční význam osobnosti či osobnostních rysů a jejich možný postnatální vývoj je zpravidla ignorován, ačkoli je tato informace zcela zásadní (Stamps & Groothuis, 2010b). Skutečnost, že tomuto problému byla zatím věnována jen relativně malá pozornost, částečně pramení i z metodické a časové náročnosti potřebných studií. Při experimentech je nutné se soustředit jak na krátké tak na dlouhé časové intervaly, a to pokud možno po celý život sledovaného jedince (Stamps & Groothuis, 2010b). Dlouhé intervaly mezi testy, které habituaci silně potlačují, mohou přispět k odhalení změn v průběhu života, naopak krátké intervaly mohou sloužit ke zjištění, zda určité chování podléhá habituaci a je tedy plastické. V případě, že je obtížné realizovat eliminaci habituace v konkrétním uspořádání testu, je možné řešit tuto úlohu také použitím hůře zapamatovatelné nebo obměňované baterie testů (viz např. McIlwain et al., 2001).

Že behaviorální plasticita osobnostních rysů nepředstavuje žádnou kontradikci, ukazuje i řada poznatků o behaviorální modulaci z blízkých oblastí biologie. Již v rané ontogenezi působí na jedince vlivy okolního prostředí, které mají zásadní dopad na jeho osobnost, či osobnostní rysy. Mezi těmito vlivy mají zásadní postavení intrauterinní pozice či rané sociální prostředí (Dingemanse et al., 2009; Stamps & Groothuis, 2010a, b). Na fyziologii, morfologii, ale také na chování jedince může mít významný vliv nestejná koncentrace pohlavních hormonů v matčině děloze (Hudson et al., 2011). Tento efekt intrauterinní pozice (Ryan & Vandenbergh, 2002) je důsledkem testosteronu produkovaného samčími zárodky, který proniká do okolních embryí a to buď difúzí přes plodovou vodu nebo prostřednictvím krevního řečiště dělohy (Meisel & Ward, 1981; Ryan & Vandenbergh, 2002).

Vliv na morfologické a behaviorální parametry má nejen prenatální prostředí, ale i postnatální fáze ontogeneze. Ve studii na potkanech (*Rattus norvegicus*) (Gracceva et al., 2011) bylo zjištěno, že samci, kteří vyrůstali mezi sestrami, byli méně agresivní než samci, kteří vyrůstali pouze mezi bratry. Při testování v Open Field testu se samci, kteří vyrůstali mezi bratry, chovali emočně nestabilně, a to zvláště v dospělosti. Byli mnohem bojácnější a trávili více času na periférii arény. Podobný trend byl nalezen i v chování myší domácích (*Mus domesticus*) (Laviola & Alleva, 1995). V mé magisterské práci se vliv pohlaví sourozenců na behaviorální profil hraboše polního sice nepotvrdil, tato skutečnost ale mohla být dána poměrně malými vrhy (průměrně tři mláďata) (Urbánková, 2012).

S behaviorálním profilem jedince může být propojena velikost vrhu, ze kterého konkrétní jedinec pochází (Hudson et al., 2011; Rödel & Meyer, 2011; Stamps & Groothuis, 2010b). Ve více studiích bylo ukázáno, že velikost vrhu ovlivňuje porodní hmotnost a hmotnost při odstavu (Bautista et al., 2005, 2007; Rödel et al., 2008a, b). Mláďata z větších vrhů se rodí až s dvakrát menší porodní hmotností a vzhledem k větší kompetici o mateřské mléko mají i menší hmotnost v době odstavu (Hudson et al., 2011). Z hlediska chování je velikost vrhu spojena s emocionalitou.

Dimitsantos et al. (2007) u dospělých laboratorních potkanů zjistili, že jedinci z menších vrhů vykazovali při testech menší aktivitu a větší sklon k úzkosti. Lze tedy říct, že jedinci z malých vrhů mají větší tendence k emoční nestabilitě. Ze statistických analýz v mé magisterské práci vyplynulo, že právě počet sourozenců má největší vliv na projevy hrabošů v Open field testu (Urbánková, 2012). Dalším důležitým momentem, který vychází z prostředí vrhu je, že relativně větší mláďata (i z různě početných vrhů) jsou více konkurenceschopná, mají rychlejší vývoj motoriky (Muciño et al., 2009), jsou schopna dříve najít bradavku a déle se na ní udržet (Bautista et al., 2005). Větší mláďata mají také lepší sací schopnosti (Nicolás et al., 2011) a častěji zaujímají centrální (a termoregulačně výhodnou) pozici mezi ostatními sourozenci (Bautista et al., 2007; Hudson et al., 2011).

Ve vztahu k osobnostním rysům či obecně vnitrodruhové variabilitě chování zvířat se také často setkáváme s hypotézou tzv. „pace-of-life“ syndromu (POLS). Je založena na tom, že ekologické podmínky formují v živočišných populacích životní strategie („life-history“), kterým by mělo odpovídat také chování jedince (Réale et al., 2010). V této souvislosti se hovoří o tzv. slow-fast life-history kontinuu (Careau & Garland, 2012), čili o rychlém/pomalém způsobu života a rychlosti fyziologických pochodů - např. propojení - intenzivní metabolismus, rychlé dospívání, brzká vlastní reprodukce a naopak (Martin et al., 2006). Prověřovány byly vazby POLS na nejčastěji stanovené osobnostní rysy, jako např. celková aktivita, odvážnost, explorace či agresivita (Le Galliard et al., 2013). Zdá se, že zmíněné rysy by mohly souviset s rychlým způsobem života, jejich protiklady naopak se způsobem pomalým (Careau & Garland, 2012; Réale et al., 2010).

S osobnostními rysy a jejich plasticitou je pochopitelně spojen nedílně mechanismus jejich udržování v populaci. V literatuře je uvedeno několik modelů vysvětlujících, jak se behaviorální osobnostní rysy mohou udržovat. Tyto modely reprezentují řadu mechanismů, například závislost na populační hustotě, specializaci na sociální niku, trade-offs s životními strategiemi či syndrom životního tempa (jak bylo již uvedeno výše) (Tomkins & Brown, 2004; Wolf et al., 2007; Biro & Stamps, 2008; Careau et al., 2008; Bergmüller & Taborsky, 2010; Réale et al., 2010). Dalším často zmiňovaným mechanismem je pohlavní výběr. Význam podobnosti v behaviorálních vlastnostech partnerů pro úspěch reprodukce byl u ptáků a ryb několikrát dokumentován (Schuett et al., 2010; Ihle et al., 2015; Laubu et al., 2016, 2017). Pozornost byla často zaměřena na vliv osobnostního rysu úzce spojeného s průzkumem, který byl zaznamenán např. u sýkory koňadry (*Parus major*) (Dingemanse et al., 2004). Preference podobných fenotypů určitých znaků během reprodukce se označuje jako asortativní párování. Asortativní párování lze rozdělit na pozitivní nebo negativní (disassortativní). Pozitivní párování znamená, že existuje tendence upřednostňovat jedince s podobnými fenotypy, zatímco negativní vede k preferenci spíše odlišných jedinců (Jiang et al., 2013). Thiessen et al. (1997) tvrdili, že asortativní párování může být zásadní strategií, jejíž hlavní výhodou je, že podobné páry ve skutečnosti s větší pravděpodobností předají více než 50% svého genetického materiálu svým potomkům. Inbrední deprese by však mohla ohrozit životaschopnost budoucí reprodukční linie potomků. Je tedy také důležité zmínit, že existuje také opačná tendence udržovat vysokou rozmanitost genů MHC, a proto upřednostňovat co nejvíce odlišného partnera (Leclaire et al., 2017; Santos et al., 2016). Častými morfologickými parametry pro tento výběr jsou velikost těla, tvar nebo barva (Harris & Siefferman, 2014; Hase & Shimada, 2014).

Podobnost rysů chování by měla být častá, zejména u druhů s biparentální péčí o potomky. Existuje několik důvodů pro výběr partnera podle osobnostních rysů, které naznačují individuální kvalitu (Dirienzo & Hedrick, 2014). Některé samice mohou předvídat schopnost samce chránit potomky na základě jeho chování (Teyssier et al., 2014). Důležitou součástí párování je také explorační chování, hledání samic i ve zcela novém neznámém prostředí a s tím spojené schopnosti orientovat se v takovém prostředí (viz např. Spritzer et al., 2005). U křečka Campbellova (*Phodopus campbelli*) byla zaznamenána preference neagresivní péče samce o srst samice během fyzického kontaktu (Rogovin et al., 2017). U monogamního hraboše prérijového (*Microtus ochrogaster*) si solitérní samci upravovali srst častěji než samci spárovaní (Wolff et al., 2002). Tato aktivita mohla být ambivalentním chováním během stresující situace, přičemž ale charakter pohybů mohl naznačovat určité osobnostní rysy hodné výběru. Význam podobnosti v osobnostních rysech, zejména pro reprodukční úspěch u savců, byl poprvé dokumentován u monogamní myši panonské (*Mus spicilegus*). Tento systém párování není u savců běžný, a i zde se rodičovská kompatibilita jeví jako užitečná. Páry s podobným rysem explorace a úzkosti začaly reprodukci dříve než odlišné (Rangassamy et al., 2015). Rodičovská péče je mimochodem u tohoto druhu spojena také s budováním hliněné kupky nad hnízdní dutinou (kurgančik) (Poteaux et al., 2008; Tognetti et al., 2017). Není proto divu, že podobnost v behaviorálních vlastnostech může být pro tuto stavební činnost důležitá. Obecně je tento sociální systém spojen s intenzivní péčí o mláďata, přičemž ale počet mláďat je spíše menší. Za takových podmínek je pozitivní posun v rozmnožování na základě vyššího počtu narozených mláďat pravděpodobně obtížnější a je představován spíše urychlením reprodukce. U tohoto druhu myší zrychlila podobnost párů v úrovni explorace a úzkosti nástup a následně i celkový úspěch reprodukce. Behaviorální kompatibilita v preferenčním testu spojená s reprodukčním úspěchem byla zjištěna také u monogamního křečka kalifornského (*Peromyscus californicus*) (Gleason et al., 2012). Také u pandy velké (*Ailuropoda melanoleuca*) se zdá, že podobnost např. v bázlivosti zasahuje do reprodukce (Martin-Wintle et al., 2017).

Je velmi pravděpodobné, že pozitivní asortativní párování upřednostňuje souhru a spolehlivost rodičů v případě monogamie. Jeho funkce v případě promiskuitního nebo polygynního systému jaký je u hraboše polního, však není tak jasná. Může se jednat o krátkodobé uklidnění nebo vyladění partnera před párováním a kopulací (tj. proximátní příčina, Réale et al., 2009). Podobnost párů fenotyp-genotyp by mohla způsobit také sníženou fluktuující asymetrii ve vývoji potomků (tj. ultimátní příčina). Studie populační genetiky promiskuitních drobných zemních savců (myš, norek) však dosud takové důkazy nepřinesly (Gockel & Ruf, 2001). Je třeba poznamenat, že podobnost v některých parametrech chování nebo osobnostních rysech neznamená automaticky snížení genetické variability, ale jen v některých lokusech. Je zřejmě důležitější, aby volba jedince spojit se s behaviorálně podobným jedincem vedla k uplatnění jeho genů v další generaci, bez ohledu na to, zda pocházejí od sebe nebo od svých partnerů (Thiessen et al., 1997).

Shrnutí výsledků

Předkládaná disertace obsahuje studie, které se zabývaly behaviorálními rozdíly mezi jedinci hraboše polního (*Microtus arvalis*), které jsou označovány jako zvířecí personalita. Pozornost přitom byla zaměřena především na jejich behaviorální plasticitu. V jedné studii byl sledován také vliv podobnosti osobnostních rysů u rodičovských jedinců na produkci mláďat. Úvod seznamuje s problematikou zvířecí osobnosti, seznamuje s termíny a různými mechanismy, jak jsou v populacích udržovány, případně kterými faktory jsou ovlivňovány.

První empirická studie byla věnována téměř celoživotní behaviorální plasticitě. Individuální rozdíly v chování, označované jako zvířecí personalita, jsou v čase a kontextech konzistentní. Osobnostní rysy nicméně vykazují behaviorální plasticitu, podobně jako mnoho jiných fenotypových znaků. V této studii jsme zkoumali vztah mezi osobnostními rysy a behaviorální plasticitou u hraboše polního (*Microtus arvalis*) za dlouhodobě stabilních laboratorních podmínek. V klasickém Open field testu bylo testováno celkem 60 hrabošů, kteří byli během svého života testováni postupně s dvouměsíčním odstupem ve čtyřech termínech. Na základě analýzy hlavních komponent (PCA) byly určeny dvě ordinační osy: „explorace“ a „aktivita“. Pro další analýzy byly vybrány behaviorální parametry, které je sytily: „překonaná vzdálenost“ a „trvání skenování“ z první osy a „trvání lokomoce“ z druhé. Pomocí lineárních modelů se smíšenými efekty (LMM) jsme ve všech třech parametrech chování našli průkazné intercepty (osobnostní rysy). Důkazy o behaviorální plasticitě osobnostního rysu však byly nalezeny pouze u parametru překonaná vzdálenost. Korelace mezi osobnostním znakem a plasticitou nebyla u žádného parametru průkazná. Pozorovaná nízká plasticita chování by mohla odrážet stabilní (laboratorní) podmínky, které by mohly ukazovat původní nastavení osobnostních rysů nebo jejich pozvolnou změnu.

Ve druhé studii jsme zkoumali vztah mezi osobnostními rysy a behaviorální plasticitou u hraboše polního (*Microtus arvalis*) pomocí monitorovacího boxu PhenoTyper (PT, Noldus). Během třídenního testu byly sledovány čtyři parametry lokomotorické aktivity u 47 hrabošů: překonaná vzdálenost, trvání chůze a běhu, frekvence změny pohybu a trvání sprintu. Opakovatelnost (R_C) u všech sledovaných parametrů byla velmi vysoká $\geq 0{,}91$. Pro volbu nejlepších lineárních modelů se smíšenými efekty (LMM) bylo testováno několik prediktorů (den testu, pohlaví, tělesná hmotnost); vybrán byl pouze LMM s testovacím dnem jako prediktorem. Pomocí LMM byly u všech parametrů nalezeny vysoce významné ($p <0{,}001$) náhodné intercepty (osobnostní rysy), sklony (plasticita) a korelace mezi personalitou a plasticitou, což naznačuje orientovanou behaviorální plasticitu osobnostních rysů. Nalezena byla také zajímavá, velmi významná korelace mezi sklony trvání chůze a běhu na jedné straně a frekvence změny pohybu na straně druhé ($r = 0{,}828$, $p <0{,}001$); tento vztah by mohl naznačovat určitou centrální plasticitu. Změny zaznamenané v PT boxu pravděpodobně nastávají vždy, po umístění zvířete do nového chovného boxu a po několik následujících dní.

Ve třetí studii byl analyzován jeden z možných mechanismů udržování osobnostních rysů v populaci u hraboše polního (*Microtus arvalis*). Tato studie se zaměřila na roli asortativního párování na základě podobných osobnostních rysů. U 63 jedinců (34 samců, 29 samic) bylo sledováno 6 behaviorálních parametrů během tří po sobě jdoucích „Open field" testů. Vliv opakování a dalších nezávislých proměnných byl testován pomocí LMM. Ze získaných náhodných efektů pak jako osobnostní rys byl využit opět náhodný intercept jako v předchozích studiích. Rozdíly mezi nimi u jedinců v páru (nezávislá proměnná) pak byly analyzovány pomocí generalizovaného smíšeného modelu (GLMM) ve vztahu k počtu mláďat (závislá proměnná). Významný vliv byl nalezen pouze u podobnosti v délce uběhlé vzdálenost během testu. Výsledky naznačují pozitivní roli podobnosti osobnostních rysů rodičů pro udržení těchto rysů v populaci i možnost účasti indukované ovulace na úspěšném rozmnožování.

Závěry

Disertace přináší poznatky o stabilitě, či z druhé strany o plasticitě, osobnostních rysů u přímo naměřených behaviorálních parametrů a odklání se tak od syntetických parametrů, jakými jsou např. odvážnost a bázlivost, které mohou být v čase skládány proměnlivě. Ze statistického hlediska to byl odklon od analýzy hlavních komponent a místo toho využití lineárních smíšených modelů. Je to cesta, která je bližší genové determinaci a tím také přístupnější fylogenetickému pohledu na různé osobnostní rysy, na jejich homologii či homoplasii. V druhé studii jsme ještě ukázali na přehlížený obecný aspekt behaviorálních testů, kdy např. v „Open field" testu zvíře projevuje své osobnostní rysy za víceméně stresové situace, ale po navyknutí či uklidnění dojde k jejich určitému posunu směrem od výrazných rysů k mírnějším a takto se pak zvíře projevuje např. v domovském chovném boxu. Třetí studie přinesla nové impulzy do studia populačních cyklů hraboše polního, které se zatím plně zaměřují na přesný popis cyklického kolísání početnosti, ale dosti opomíjejí behaviorální mechanismy, které v různých fázích cyklu působí na nárůst početnosti populace, tedy na rozmnožování. Soustředili jsme se na nenáhodné (asortativní) párování podle podobných osobnostních rysů behaviorálních parametrů, které by mohlo probíhat v období gradace uvnitř rozšiřujících se rodinných skupin. Ukázali jsme tak na jeden z možných zdrojů rychlého nárůstu populace.

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Kapitola 2

Lifetime low behavioural plasticity of personality traits in the common vole (*Microtus arvalis*) under laboratory conditions

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Lifetime low behavioural plasticity of personality traits in the common vole (*Microtus arvalis*) under laboratory conditions

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Abstract

Individual differences in behaviour, referred to as animal personality, are consistent across time and contexts. Nevertheless, personality traits show behavioural plasticity, much like many other phenotypic traits. In the present study, we examined the relationship between personality traits and behavioural plasticity in the common vole (*Microtus arvalis*) under stable, long-lasting laboratory conditions. A total of 94 voles were tested in the classic open field test, designed to measure seven behavioural parameters (distance moved, grooming, immobility, rearing, running, scanning, and walking duration) during a three-minute test. A total of 60 voles formed the experimental group and were tested at four different time points over their lifetime (1st, 3rd, 5th, and 7th month); 34 voles formed the control group and were tested only once at the 7th month. All voles were of the same age. Based on principal component analysis (PCA), two ordination axes were determined: “exploration” and “activity”. For further analyses, “distance moved” and “scanning duration” were selected from the first axis and “walking duration” from the second. Using linear mixed-effect models (LMMs), we found highly significant random intercepts (i.e. personality traits) in all three behavioural parameters. However, evidence for behavioural plasticity was only found in the distance moved parameter, as determined from the random slope, and correlations between personality trait (intercept) and plasticity (slope) were not significant for any trait. During the experiment, variances of random effects were high and remained essentially the same, whilst the rank order of many individuals changed. Based on fixed effect slopes and a comparison with the control group, habituation was only significant for “walking duration”. The observed low behavioural plasticity could mirror stable (laboratory) conditions that result in the manifestation of original trait settings (genetic, early postnatal) or their gradual overcoming. These findings provide a starting point for further tests on free-living voles.

Keywords: Open field test, animal personality trait, repeated testing, behavioural plasticity, common vole

Introduction

Over the past few decades, the study of animal personality has brought a great deal of knowledge and new ideas to behavioural ecology (Wilson et al., 1994; Koolhass et al., 1999; Dingemanse et al., 2003; Sih et al., 2004; Carere et al., 2005). Personality traits are understood as individual differences in behaviour that are consistent across time and ecological contexts (Réale et al., 2007, 2010). These traits have been well-documented in a wide array of species, including both vertebrates (Gosling, 2001) and invertebrates (Mather & Logue, 2013), and several models explaining how they are maintained have been suggested. These models emphasise a variety of mechanisms; for example, density dependence, life-history trade-offs, sexual selection, and social niche specialisation (Tomkins & Brown, 2004; Wolf et al., 2007; Biro & Stamps, 2008; Schuett et al., 2010; Bergmüller & Taborsky, 2010). The study of personality traits is still revealing new links between behaviour and population ecology, evolutionary and developmental biology (Nussey et al., 2007; Carere et al., 2015; Dingemanse, 2017; Stamps & Krishan, 2014, 2017). The fact that they are maintained as traits in populations does not mean that there are no changes in how these personality traits manifest.

With an increasing number of studies on personality traits, a close link with behavioural plasticity has been recognized (Mathot et al. 2012, Kluen & Brommer, 2013; Mackay & Pillay 2019). The behavioural plasticity of personality traits has generally been investigated using the approach of behavioural reaction norms (BRN) (Griffiths et al., 2000; Fuller et al., 2005) during gradually changing conditions (Dingemanse et al., 2010; Dingemanse & Wolf, 2013), and several different scenarios of animal personality and behavioural plasticity linkage have been suggested (Nussey et al., 2007; Dingemanse et al., 2010). For example, the plasticity could be low with the rank order of individuals on the personality gradient being maintained or the plasticity could be high with a change in rank order. However, it is important to stress that personality traits can be also successful in intra-population competition without behavioural plasticity, when animals choose the habitat and/or microhabitat that best fits their personality (Holtmann et al. 2017).

Relationships between specific personality traits and their plasticity can be explained as part of a general management system of uncertainty (reviewed in Mathot et al., 2012). The authors explain that the effort exhibited by an individual to acquire enough information on its surroundings (e.g. food, shelters) is likely to co-vary with individual activity and exploration behaviours, while simultaneously creating population variation in reactions to certain changes in environmental conditions. Behavioural plasticity limited to a specific group of individuals in the population has also been observed; for example, highly aggressive mice were found not to adjust their aggressiveness across different social contexts, while the opposite types did (Koolhass et al., 1999; Natarajan et al., 2009). Therefore, Mathot et al. (2012) recommended that more empirical investigation is needed on the link between consistency and plasticity. Meanwhile, a new perspective in plasticity topics has appeared, namely that changes during the life of an individual may not be a passive reaction to an actual situation, but rather adjusted to their expectations, i.e. they are prepared for events or conditions that may or may not occur (Stamps & Krishnan, 2014). Subsequent to this study, Stamps & Krishnan (2017) presented their findings that the plasticity of belief was maintained with age when individuals were reared in the absence of cues. More recently, behavioural plasticity has become a part of a broader phenotypic plasticity paradigm (Fox et al., 2019).

It is becoming increasingly clear that behavioral plasticity can take the form of personality traits (Dingemanse & Wolf 2017). This plasticity could behave in a similar manner to physiological functions (e.g. stress reactions or metabolic rate, which are clearly plastic), albeit over a more limited range (Norin & Metcalfe, 2019). Mitchell & Biro (2017) demonstrated this mechanism in zebrafish as consistency of slopes in reaction norms. In addition to the relationship between personality traits and behavioural plasticity, attention must also be paid to intra-individual variability, which has clear links to evolutionary ecology. Although these three topics overlap, it should be emphasized that personality traits appear at the population level as result of intra-population processes, while behavioural plasticity and intra-individual variability are apparently linked to the individual level (Japyassúa & Malangeb 2014). In a study of tree swallows, Betini & Norris (2012) tested two fundamental hypotheses. The first, called "quality individuals", predicts that individuals with strong personalities also have a pronounced plasticity. The second, called "compensatory", predicts that individuals with low personality trait values have an increased plasticity, i.e. have a greater ability to compensate for various external or internal factors. It was found that males behaved (and were successful) according to the qualitative hypothesis, but equally successful were mild males who were highly plastic (Betini & Norris 2012). Similarly, in a study of fish (three-spined sticklebacks), Jolles et al. (2019) discovered a negative correlation between plasticity and bold personality and a positive correlation with shy personality. Residual variance was related to predictability: the greater the variance, the lower the predictability. Variance was greater in shy individuals, making their behaviour less predictable.

In studies of personality traits and behavioural plasticity, the repetition of tests is essential and therefore it is always necessary to deal with its consequences, i.e. habituation. In fact, some studies have repeated tests so often that the traits no longer change, considering this point the basal level (Žampachová et al., 2017). Of course, even in a familiar environment, some information is required to acknowledge that the surroundings are familiar. However, this can no longer be described as an exploration of an unknown environment. In many studies, the number of repetitions was not high and inseparable habituation was accepted. Under these conditions, determined behaviour repeatability reaches an average value of around 0.37 (Bell et al., 2009). Another approach is to undertake the tests in the field and to use the "capture-mark-recapture" (CMR) method for tested animals. After the test, animals are released again into their habitats, and then caught for another test. This arrangement decreases the habituation process markedly (Martin et al., 2008). Whilst the effects of habituation or other forms of learning in long-term studies can be mitigated, they cannot be avoided completely (Bolivar et al., 2000). Activity levels may be affected by the length of the inter-session interval (e.g. in mice; Paylor et al., 2006). When sessions are separated by a short gap (e.g. 24 h), test-retest activity values may reflect strong habituation or sensitisation that could overlay spontaneous behaviour (Whimbey & Denenberg, 1967). On the other hand, activity displayed under a long-term arrangement may be also affected by memory capacity (Clemens et al., 2009) and, moreover, by shifted internal states of individuals (e.g. age, hierarchical position, body size; Bell et al., 2009). Therefore, in order to minimise the effect of test repetition, an optimal test structure should be prepared. The measurement interval and number of repetitions should be sufficiently large, but measurement duration should be sufficiently short in order to limit its memory footprint.

Since we have previously determined personality traits in the common vole (*Microtus arvalis*) (Lantová et al., 2011) and have extensive (more than ten years) experience with their breeding (Řičánková et al., 2007), we further aimed to determine the extent of behavioural plasticity of the personality traits. This species is a suitable animal for such studies due to its overall biological and ecological plasticity. Across its distribution range within the Palaearctic region, voles are exposed to a great variety of climatic and biotic conditions. This can involve extensive seasonal changes, with temperatures in their steppe/meadow habitats reaching over 35 °C in the summer to below 0 °C in the winter under snow. Furthermore, populations undergo three- to five-year cycles of population density variation, during which vole numbers range from thousands to only a few individuals per hectare (Lambin et al., 2006; Andreassen et al., 2013). This is connected with changes of food and shelter availability as well as health conditions, i.e. parasitic, bacterial, and viral load (Niethammer & Krapp, 1982). Under these changes, it could be expected that each individual would adjust its behaviour. For example, Gracceva et al. (2014) found that laboratory voles became less active and more cautious as the light regime was changed from summer to winter. This behavioural plasticity could also be a potential cause of the typical rapid increase in vole populations under gradation conditions (Niethammer & Krapp, 1982). According to Wolf et al. (2008), this picture can be explained through a rather different mechanism, namely responsiveness. Under low density (before gradation) conditions, responsive (i.e. highly plastic) voles could be more successful, whereas unresponsive voles could be more successful under high-density conditions. The positive feedback mechanism in responsiveness stabilises the coexistence of traits in a population.

We developed our study to answer one main question: What is the behavioural plasticity of personality traits in the common vole under constant laboratory conditions and minimized habituation during the tests? We consider this the first step in understanding the behavioural plasticity of personality traits in free-living voles. Under stable laboratory conditions and maybe also under “conservative“ expectation in animals (sensu Stamps & Krishnan, 2014, 2017), we hypothesised three different scenarios. (i) Due to the stable conditions, no behavioural plasticity could be expected in voles. However, variance would be high because of the different values of personality traits; during the experiment, the rank order of individuals would be maintained. This scenario was considered the null hypothesis. (ii) Individual animal housing could cause behavioural plasticity because of habituation and/or aging. The trait values would convergence to the mean population values, i.e. an increase in low starting values and a decrease of high starting values (negative correlation) would be observed. During the experiment, the variance will decrease; the rank order would change. (iii) Individual animal housing could cause spontaneous (not affected) development of innate behavioural plasticity independent on personality traits. Changes of their trait values would not show any prevailing direction and the variance would be high and stable; the rank order would change.

Material and Methods

Animals

For the present study, we selected the common vole (*Microtus arvalis*) as a model species. A sample size of 94 spring-born voles (male, n = 33; female, n = 61) was used, originating from 34 families established from voles caught during the summer and autumn. They were reared under standard laboratory conditions, at room temperature (18–22 °C) and with a 12:12 photoperiod (lights on at 06.00 h). After weaning at 21 days, voles were marked and kept individually in standard polycarbonate cages (31 × 21 × 15 cm) containing wood shavings, hay, and plastic tubes as shelters. Water and food were available ad libitum, with the commercial food pellet diet (MOK and ST-1; VELAZ Prague) enriched with fresh grass and vegetables three times per week. The voles were weighed weekly, starting at two days after birth, and also the day following each open field test (OFT). Other human disturbances were limited to feeding and new bedding replacement, which were performed randomly according to a time schedule prepared in advance.

Open field test (OFT)

The open field test is a commonly used method to study personality traits in voles (see e.g. Eilam, 2010; Osako et al., 2018). In this test, the animal is confronted with an open illuminated area that is an appropriate stressful stimulus (Walsh & Cummins, 1976). Since voles are fossorial rodents, the light intensity was maintained at about 100 lx to ensure equal illumination and rather low stress conditions. Voles are animals with polyphasic circadian activity (Niethammer & Krapp, 1982; Gerkema et al., 1993) and, in our laboratory, often showed spontaneous locomotor activity during daylight. Based on this experience, we performed all behavioural personality tests between 9 am and 4 pm under laboratory conditions (as already described). During individual test days, the testing order of the voles was completely random according to a time schedule prepared in advance. Each OFT trial was initiated by placing a vole in the peripheral zone (approximately 5 cm from the arena wall) of a square, non-transparent plastic arena (75 × 75 × 50 cm). In each case, the start location was identical. The animal was allowed to explore the arena freely for 3 min. The relatively short duration of the test was chosen to provide a valid measure of exploratory activity during the OFT (Montiglio et al., 2010), whilst limiting memory-related effects/habituation. Behaviour was video-recorded from overhead by a digital camera (BASLER acA1300) connected with camera software (NUUO Surveillance System, v.3.3.12). The distance moved (m) during the complete test was determined using a custom-designed modular tracking system (MTS v.1.07, Inst. of Physiology CAS, Prague, Czech Republic). Observer XT 8.0 coding software (Noldus) was used to evaluate six behavioural parameters [measured as total duration (s) during the 3 min OFT]. All studied parameters are presented below:

1) Distance moved – during the complete test
2) Grooming duration – behaviour focused on own body surface/fur
3) Immobility duration – state without any movement
4) Rearing duration – standing on hind legs, occurs often during locomotion
5) Running duration – high rate of locomotion in a straight line, often along arena walls
6) Scanning duration – stationary, but turning head

7) Walking duration – forward locomotion, often interrupted by other behaviour

The arena was cleaned between animals with a solution of 30 % ethanol.

Experimental design

Two groups of voles were tested: a repeatedly exposed (RE) experimental group (n = 60) and a singly exposed (SE) control group (n = 34). The proportion of males to females was consistent with that of the breeding colony, i.e. 20 males to 40 females in the RE group and 13 males to 21 females in the SE group. In the RE group, weaning voles (aged 21 days at the first test) were subjected to a 3-min OFT, and subsequently tested every two-months until senescence (seven months; total of four OFTs). Because we planned to study life-long changes in behavioural traits, it was necessary to differentiate between the effects of habituation and those of aging: this was the purpose of the SE control group, which was tested only on month seven. It is important to stress that SE animals were reared in the same breeding room: food, water, and bedding were changed together with other RE animals. They were also weighed at the same intervals, so they differed only in the number of experienced OFTs.

Ethical note

All procedures were conducted in accordance with the principles and guidelines of ethical standards implemented in the basic national law of the Czech Republic related to animal protection, Act no. 246/1992 Coll., on the protection of animals against cruelty and Regulation no. 419/2012 Coll. on the protection of experimental animals. The project was approved by the Departmental Commission for Animal Protection and the Ministry of Education, Youth and Sports under reference 7945/2010-30. Laboratory breeding conditions, as well as all the behavioural tests, also complied with the ASAB/ABS Guidelines for the Use of Animals in Research.

Statistical analyses

The distribution of our data was tested for normality using a Kolmogorov-Smirnov test; data used for final calculations were found not to differ significantly from a Gaussian distribution. As an initial evaluation, a principal component analysis (PCA) was performed to obtain an overview of the relationships among behavioural traits (Budaev, 2010). Behavioural traits in the RE group were analysed using Canoco v.5.0 software for the multivariate analysis (ter Braak & Šmilauer, 2012). Based on this analysis, we chose three behavioural parameters (distance moved, scanning duration, and walking duration) with the highest positive/negative correlation coefficients with the first and second ordination axes. These traits significantly contributed to two non-correlated gradients of vole behaviour (Tab. 1). Consistency repeatability R_C was calculated according to Biro and Stamps (2015) based on variance component estimates produced by the linear mixed models LMMs (Tab. 2). Conditional repeatability was calculated because it takes into account changes between individuals at different times and with different directions (see Figs. 1–3).

Behavioural plasticity of personality traits was evaluated using the reaction norm approach. This approach allows variations in individual reactions to the environment to be tested, using two parameters of a linear model: intercept (~ expected trait value in the average environment) and slope (~ value by which the trait changes per unit change in the environment) (Nicolaus et al., 2013). Mixed-effect models were used to estimate the variation in the random intercepts and slopes, and the correlations between them for the three behavioural parameters using the four measurements (i.e. the four different time points) on each individual. We used the statistical software R v.3.5.2 (R Core Team, 2018) and the software package lme4 (Bates et al., 2015) to build mixed effect models for each dependent variable (e.g. Schaeffer, 2004; Nussey et al., 2007; Brommer et al., 2012; Dingemanse & Dochtermann, 2013; Bates et al., 2015). We applied only the first polynomial order to fit the values among the four measurements (time). Statistical significances for fixed (time, sex, weight), as well as, random (individual - id) effects were obtained using a likelihood-ratio test, which compared a particular model with the null model. The factor "age" was not used because all tested individuals were born within several days.

For all tests, we considered the cutoff for statistical significance as $p < 0.05$. To indicate the amount of uncertainty in the estimates, bootstrap confidence intervals (CI) were also calculated. We also checked for homogeneity in residuals using Q-Q plots of the models to avoid biases caused by heterogenous residuals (e.g. Nicolaus et al., 2013; Araya-Ajoy & Dingenmanse, 2017). To visualise behavioural plasticity in personality traits, the random intercepts and slopes were used to calculate a behavioural reaction norm for each trait and individual. Calculation of the y value point was as follows: $y = slope * x + intercept$, where x is test order (time). On the y-axis, the zero point corresponded to the mean population level. In order to compare the RE group with the SE control group, a Mann-Whitney test was used, *implemented* within *STATISTICA v.*13.2 (Dell Inc., 2016).

3. Results

Selection of behavioural parameters

PCA was used to obtain an overview of the relationships among the observed behavioural parameters and canonical axes (Tab. 1). The two ordination axes explained 33.3 % and 22.0 % of variability, respectively. These axes could be considered as exploration and activity gradients according to the highest correlation coefficient values (> 0.7). Distance moved was negatively correlated with the first ordination axis ($r = -0.75$) and a positive correlation was found for scanning duration ($r = 0.73$). Walking duration was negatively correlated with the second ordination axis ($r = -0.92$, Tab. 1). These behavioural parameters fitted the LMM criteria in R software for convergence, after correction for so-called "tolerances and stopping criteria".

Repeatability of behavioural traits

Distance moved and walking duration were both found to be highly repeatable (0.51 and 0.39, respectively; $p < 0.001$; for H_o: $R_c = 0$). Scanning duration showed rather low repeatability (0.20); nevertheless, it was still statistically significant ($p = 0.031$, Tab. 2).

Table 1 Correlation coefficients of behavioural parameters with the first and second PCA ordination axis. Explained variation according to the axes was 33.3 % and 22.0 %, respectively. Axis 1: from negative to positive values = increase in scanning duration and decrease in distance moved ("exploration"). Axis 2: from negative to positive values = decrease in walking duration ("activity")

Variable	PCA axis 1, "Exploration"	PCA axis 2, "Activity"
Distance moved	-0.7527	-0.0170
Scanning duration	0.7290	0.1344
Walking duration	0.2203	-0.9170
Grooming duration	0.5719	0.0875
Immobility duration	0.1204	0.6684
Rearing duration	-0.5907	-0.4040
Running duration	-0.7102	0.4695

Table 2 Repeatability of selected behavioural parameters

Parameters	Consistency repeatability $R_C \pm SE$	Confidence interval CI 95 %	p
Distance moved	0.51 ± 0.07	0.37 – 0.65	**< 0.001**
Scanning duration	0.20 ± 0.07	0.08 – 0.37	**0.031**
Walking duration	0.39 ± 0.08	0.24 – 0.53	**< 0.001**

Fixed and random effects and individual profiles

The best LMM was selected for three response variables (distance moved, scanning duration and walking duration) considering following fixed predictors: time, sex, and weight. The best LMMs were with the fixed effect time only, other predictors (sex, weight) did not improve the models (Tab. 3).

Table 3 Selection of the best LMM for three response variables with different fixed factors (time, sex, weight). All models used (1+time|id) specification as their random effects, therefore estimating the random effect of intercept, the random effect of the slope of the time effect, and their mutual correlation. Presented likelihood-ratio tests compare the particular model with a reduced model of the preceding row. Effect of time is not tested here, as its use in the model is implied by the model design

Response variable	Model	AIC	BIC	logLik	df	p
Distance	time	1658.0	1678.8	-823.0		
	time+sex	1659.8	1684.2	-822.9	1	0.667
	time+sex+weight	1661.5	1689.4	-822.8	1	0.608
Scanning	time	1857.9	1878.8	-923.0		
	time+sex	1859.7	1884.1	-922.9	1	0.670
	time+sex+weight	1860.3	1888.2	-922.2	1	0.242
Walking	time	2374.8	2395.7	-1181.4		
	time+sex	2375.5	2399.9	-1180.8	1	0.262
	time+sex+weight	2375.4	2403.3	-1179.7	1	0.148

AIC - Akaike information criterion; BIC - Bayesian information criterion; logLik - log-likelihood estimates; df – degrees of freedom; p – significance level

Based on the LMM with the fixed predictor of time only, we interpreted the fixed effects and the random effects of the models for the three mentioned behavioural parameters. Tab. 4 shows the significance levels of individual random factors based on likelihood-ratio tests. Tab. 5 shows variances and bootstrap confidence intervals in random effects (Tab. 5A) and mean values in fixed effects (Tab. 5B).

Table 4 Tests of individual random effects of individual-specific intercept, of individual-specific dependency of the response variable on time, and of the correlation between these two random effects

Response variable	Random factors	AIC	BIC	logLik	df	p
Distance	without	1701.1	1711.6	-847.6		
	id	1661.4	1675.3	-826.7	1	**<0.001**
	id+time	1659.0	1676.5	-824.5	1	**0.037**
	id*time	1658.0	1678.8	-823.0	1	0.079
Scanning	without	1860.8	1871.2	-927.4		
	id	1854.2	1868.1	-923.1	1	**0.003**
	id+time	1855.9	1873.3	-923.0	1	0.634
	id*time	1857.9	1878.8	-923.0	1	0.846
Walking	without	2397.4	2407.9	-1195.7		
	id	2372.6	2386.5	-1182.3	1	**<0.001**
	id+time	2374.2	2391.6	-1182.1	1	0.526
	id*time	2374.8	2395.7	-1181.4	1	0.236

Note: Differences between models, based on likelihood-ratio tests. Abbreviations (Tab. 4): AIC, Akaike information criterion; BIC, Bayesian information criterion; logLik, log-likelihood *estimates*; df, degrees of freedom; p, significance level; id – identity; time, trial order; id*time, correlation id-time; bold p level indicates a statistically significant random effect.

Table 5 Estimated parameters of the LMM for three behavioural variables with time as an explanatory variable with fixed effect. A) Estimates of random effects: variances in intercepts, slopes (time), residuals (within-individual), and the correlation between random intercepts and slopes. B) Fixed effect estimates

A	Response variables		
Random effects	Distance moved	Scanning duration	Walking duration
Intercept σ^2 and CI	45.1 (11.6, 84.6)	28.4 (0.38, 123)	736 (102, 1490)
Slope (time) σ^2 and CI	5.05 (1.08, 10.4)	2.09 (0.02, 13.6)	56.5 (0.74, 154)
Intercept–slope correlations and CI	-0.63 (-0.84, 0.16)	-0.46 (-1, 1)	-0.66 (-1, 1)
Residual σ^2 and CI	33.9 (25.9, 41.7)	108 (81.0, 128)	774 (576, 973)

B	Response variables		
Fixed effects	Distance moved	Scanning duration	Walking duration
Intercept estimate ± SE	17.3 ± 1.26	14.3 ± 1.78	108.5 ± 5.62
Slope (time) estimate ± SE	-0.25 ± 0.44	0.14 ± 0.63	-20.9 ± 1.88
df	59	59	59
t-values	-0.572	0.224	-11.2
p	0.570	0.823	**< 0.001**

Abbreviations: CI, bootstrap confidence interval; df, degrees of freedom; p, significance level; SE, standard error; t-values, t-test statistics; σ^2, variance; bold p level indicates a statistically significant slope fixed effect

For distance moved, the random effects were significant for the intercept as well as for the slope (Tab. 4). The intercept-slope correlation was not significant (r = -0.63, p = 0.079), and the bootstraps confidence interval calculation did not show a significant negative correlation (CI = -0.84, 0.16), see Tab. 4 and 5. For both scanning duration and walking duration, only the random intercepts were significant; the slopes (Tab.4) and intercept-slope correlations were not significant (Tab. 4 and 5). In all response variables, the distance moved, scanning and walking durations, we found relatively high residual variances $\sigma^2 = 33.9$, 108, and 774, respectively, see Tab. 5A.

The reaction norms showed changes in the personality ranking order of the voles during the experiment. The most noticeable were in the distance moved trait; the least noticeable changes were in scanning duration (Figs. 1 – 3).

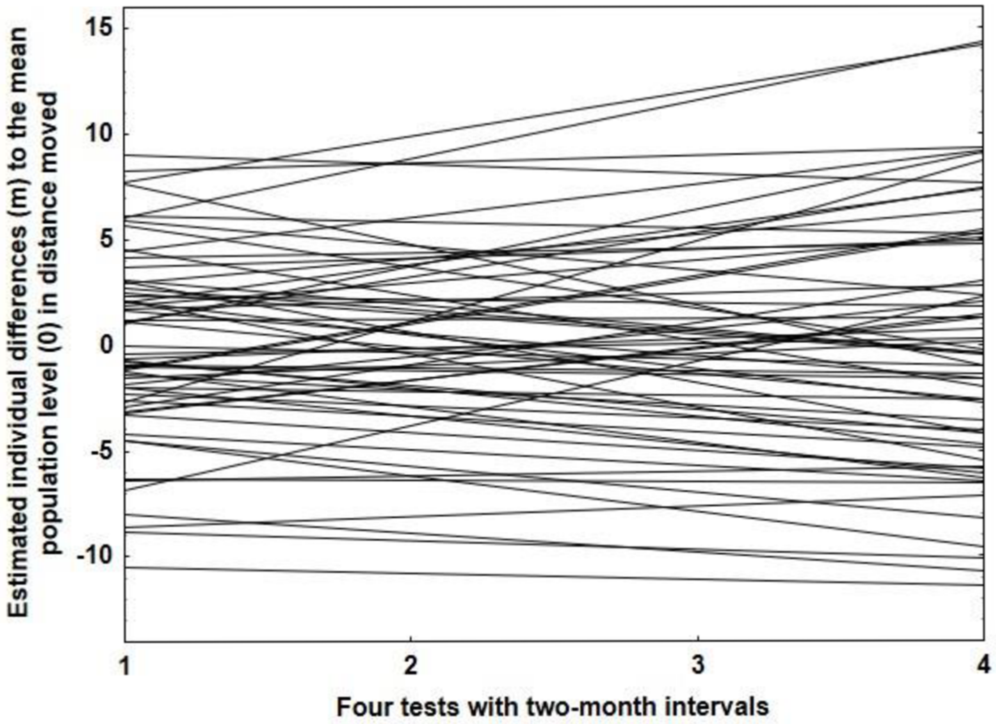

Figure 1 Behavioural plasticity of the distance moved personality trait in 60 voles. The behavioural reaction norms (black lines) were calculated using the random effects values (intercepts and slopes) from the LMM. Separate intercepts ($p < 0.001$) and slopes ($p = 0.037$) are significant; the corresponding variances are $\sigma^2 = 45.1$ and $\sigma^2 = 5.05$, respectively. The intercept-slope correlation was not significant ($r = -0.63$, $p = 0.079$), highlighted by the bootstrap confidence interval (CI = -0.84, 0.16)

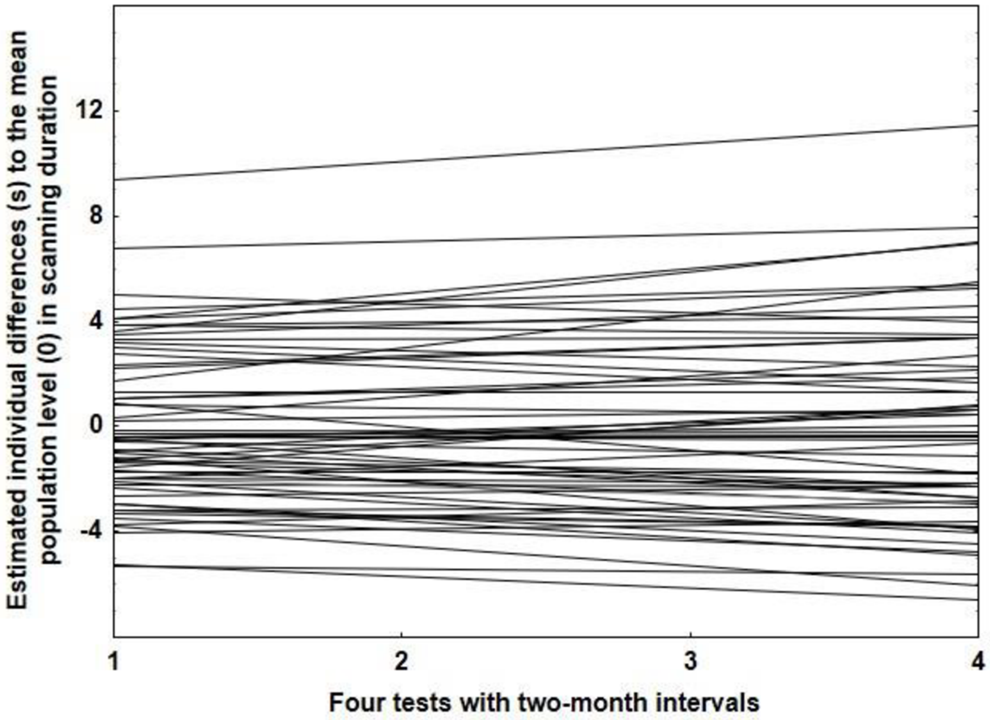

Figure 2 Behavioural plasticity of the scanning duration personality trait in 60 voles. The behavioural reaction norms (black lines) were calculated using the random effects values (intercepts and slopes) from the LMM. Separate intercepts are significant ($p < 0.003$), separate slopes are not significant ($p = 0.634$); the corresponding variances are $\sigma^2 = 28.4$, $\sigma^2 = 2.09$, respectively. The intercept-slope correlation was not significant ($r = -0.46$, $p = 0.846$), bootstrap confidence interval (CI = -1, 1)

Concerning the fixed effects in the distance moved, scanning duration, and walking duration, the intercept mean values were 17.3 m, 14.3 s, and 108.5 s, respectively. In the distance moved and scanning duration, the mean slopes were very low and insignificant (-0.25 m, 0.14 s, respectively). However, the situation for walking duration was quite different, where the values decreased highly significantly (-20.9 ± 1.88 s, $p < 0.001$), see Tab. 5 B.

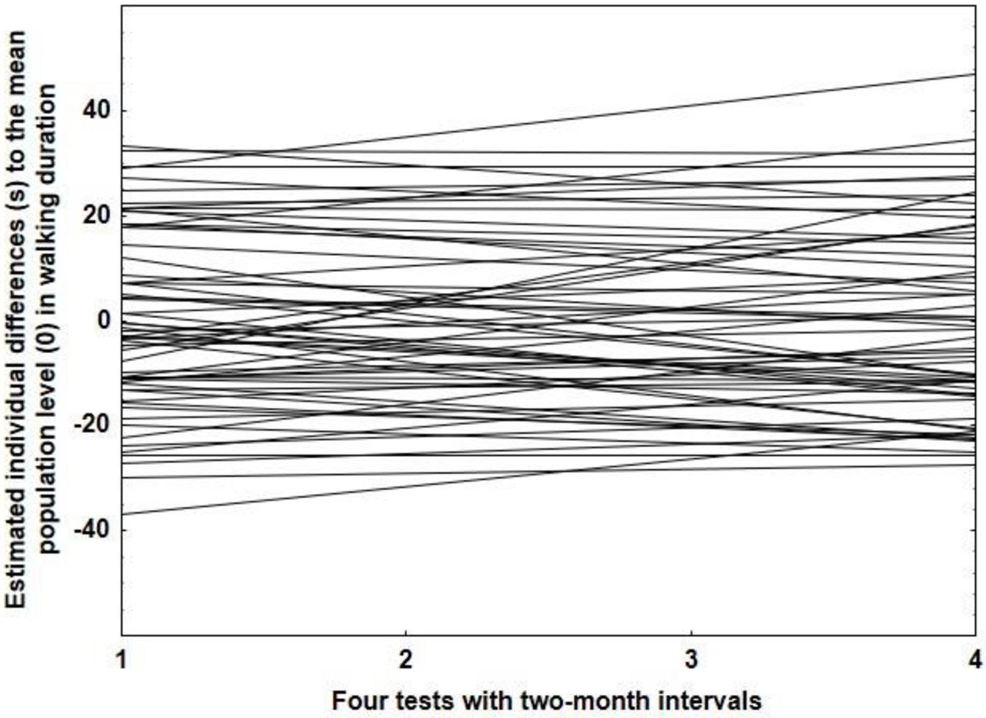

Figure 3 Behavioural plasticity of the walking duration personality trait in 60 voles. The behavioural reaction norms (black lines) were calculated using the random effects values (intercepts and slopes) from the LMM. Separate intercepts are significant ($p < 0.001$), separate slopes are not significant ($p = 0.526$); the corresponding variances are $\sigma^2 = 736$ and $\sigma^2 = 56.5$, respectively. The intercept-slope correlation was not significant ($r = -0.66$, $p = 0.236$), bootstrap confidence interval (CI = -1, 1)

Concerning the fixed effects in the distance moved, scanning duration, and walking duration, the intercept mean values were 17.3 m, 14.3 s, and 108.5 s, respectively. In the distance moved and scanning duration, the mean slopes were very low and insignificant (-0.25 m, 0.14 s, respectively). However, the situation for walking duration was quite different, where the values decreased highly significantly (-20.9 ± 1.88 s, $p < 0.001$), see Tab. 5 B.

Comparison of the RE group with the SE group

To assess the influence of habituation, a comparison was performed between the fourth test of the RE group and the SE control group. For walking duration, the value for the RE group was half that of the SE control group (Mann-Whitney U-test, $Z = -4.702$, $p < 0.001$); in both of the other parameters, the differences were not statistically significant (distance moved: -1.727, $p = 0.084$; scanning duration: $Z = 1.704$, $p = 0.088$) (Fig. 4). To assess the influence of age, a comparison was also performed between the first test of the RE group (1 month old) and the SE control group (7 months old, control with the last RE group). In the selected behavioural parameters, the differences were not significant: distance moved: $Z = 1.161$, $p = 0.246$; scanning duration: $Z = -1.822$, $p = 0.069$; walking duration: $Z = -1.857$, $p = 0.063$.

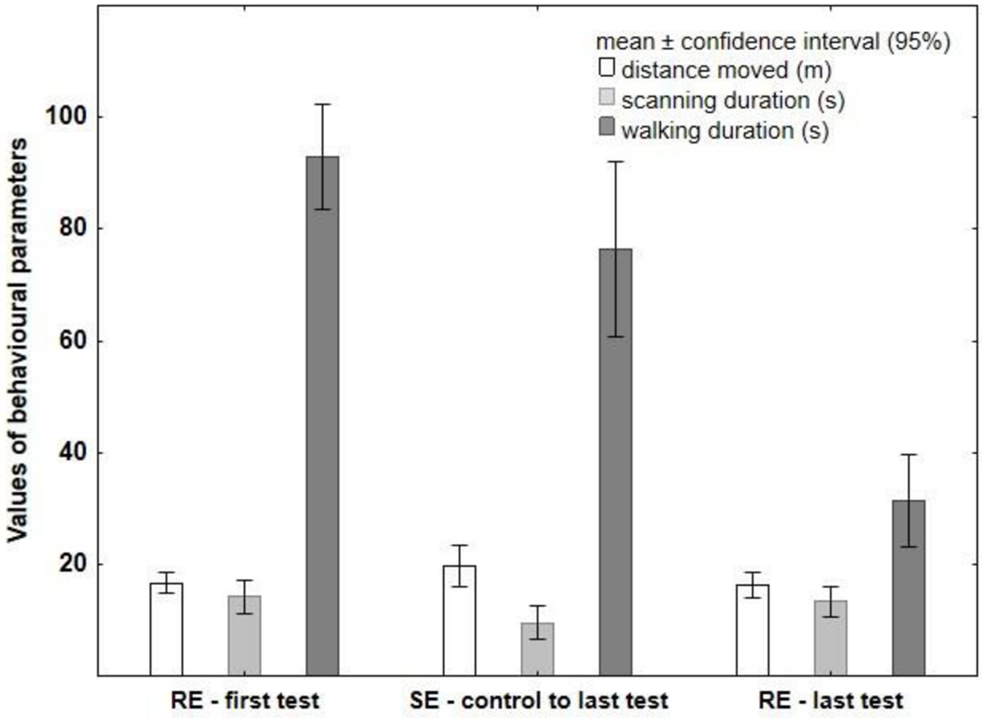

Figure 4 A) Comparison of the studied behavioural parameters between the last test of the RE group and the SE control group (to assess habituation). Mann-Whitney U-test – distance moved: $Z = -1.727$, $p = 0.084$; scanning duration: $Z = 1.704$, $p = 0.088$; walking duration: $Z = -4.702$, $p < 0.001$. B) Comparison between the first test of RE group and the SE control group (to assess aging): distance moved: $Z = 1.161$, $p = 0.246$; scanning duration: $Z = -1.822$, $p = 0.069$; walking duration: $Z = -1.857$, $p = 0.063$

Discussion

Our multivariate analysis of behavioural traits showed the same or very similar results to that reported in previous studies ("activity" or "exploration", see Lantová et al., 2011; Herde & Eccard, 2013; Gracceva et al., 2014). Similar results have also been described in other rodents (Eilam et al., 2003; Martin & Réale, 2008; Vošlajerová et al., 2016; Žampachová et al., 2017). In our case, the most important trend was represented by the "exploration" axis, explaining most of the variability (33 %). This axis represented a gradient between distance moved and scanning duration. The second axis, "activity", accounted for less of the explained variation (22 %), with walking duration being the most substantial contributor.

Personality trait involved in a behavioural parameter could be revealed by a repeatability (R) evaluation. Wilson (2018) emphasizes that the repeatability index R should be used in a defined context and with clear intention. In our study, the repeatability was calculated according to Biro and Stamps (2015) as a consistency repeatability (R_C). The determined values (distance moved $R_C = 0.51$; walking duration 0.39; scanning duration 0.20; Tab. 2) correspond to the significances of the random factors (Tab. 4). Based on a literature review, Bell et al. (2009) calculated that the mean repeatability of behavioural parameters is around 0.37. Comparable values were found also in agreement repeatability (R_A) in voles (0.25–0.63, Lantová et al., 2011; Herde & Eccard, 2013) or for R_C in the black rat (0.22–0.81, Žampachová et al., 2017). Nevertheless, these comparisons between species must be treated cautiously, because the same repeatability can be achieved in samples with completely different population structures (Dochtermann & Royauté 2019).

In the present study, we controlled as many influencing factors as possible. This involved using animals of an almost identical age, breeding care, and a randomised test order. However, some factors could not be eliminated. To select the best LMM, several predictors [test order (time), sex, and body weight] were tested; only the LMM with the predictor "time" was selected, since other predictors did not improve the models (Tab. 3). This was unsurprising, since the animals had no experience of the opposite sex since weaning and had not been exposed to stress situations such as lack of food or temperature fluctuations. Body weight or sex were also not significant fixed effects in linear models in similar studies of voles (e.g. Lantová et al., 2011, Herde & Eccard, 2013) or e.g. in chipmunks (Martin & Réale, 2008).

In all three examined behavioural parameters (distance moved, scanning duration, walking duration) we found significant random intercepts and, for distance moved, we also found a significant random slope (plasticity itself). However, the personality-plasticity correlation was not significant. This means that whilst the behavioural plasticity in “distance moved” was high, it was not bound to the personality trait. If we supposed that the distance moved random effects had a slightly greater correlation, we could consider that also an oriented plasticity appeared. A negative correlation could mean that the higher the intercept, the more negative the slope and *vice versa*, i.e. voles with the most-expressed personality traits could possess the highest plasticity. From another perspective, it could be also considered that a certain tendency towards the average population value is indicated. This would be an interesting result in voles kept under long-lasting stable laboratory conditions. Unfortunately, these conclusions are not supported by a significant correlation. Such a correlation has, however, been observed in other studies; for example, boldness and temporal plasticity were negatively correlated in three-spined sticklebacks (Jolles et al., 2019).

Based on a study of tree swallows, Betini & Norris (2012) formulated two hypotheses concerning the personality-plasticity correlation. Whilst they cannot be reliably assigned to our results in the common vole, due to the lack of significant correlation, their hypothesis on “quality individuals” (individuals with strong personality have also a pronounced plasticity) does show some relevance to our study (see Fig. 1).

Attention should be also paid to residual variances which were high in all three evaluated parameters. This is not simply unexplained unassigned variability, but suggests that there may be other factors which could not be recognized. The term intra-individual variability is used in this context (Japyassúa &

Malangeb, 2014) and could mean that the open-field behaviour was affected by something other than personality, i.e. an emotional component such as the feeling of safety. Since this is a subjective emotional state dictated by various inputs, control of this parameter is not practically possible (Eilam, 2010). Accordingly, high variance can also be interpreted as low behavioural predictability (Jolles et al., 2019).

To highlight behavioural plasticity in the personality traits, the random effects (intercepts and slopes) were used to calculate a behavioural reaction norm for each trait and individual (Figs. 1 – 3). The results showed that, especially in distance moved, the ranking among individuals noticeably changed. This overall picture of state (a number of crossing individual reaction norms) has also been observed in other species (Carter et al. 2012, Kluen & Brommer 2013, Jolles et al., 2019). On the other hand, the overall lower plasticity and lowest change in the ranking order for scanning duration showed that high behavioural plasticity in this personality trait is not useful. Even after many repeated exposures to the test space, the animal must still scan to know that it is a familiar surrounding (see Žampachová et al. 2017).

It is important to add that our study is based on an overall large number of measurements; however, the ratio between the number of observations through time and the number of observed individuals does not match the recommended value of 0.5 and might therefore limit the power of our tests (see Martin et al., 2011).

Concerning fixed effects, the intercept estimate of distance moved shows that during the first test the animals moved approximately 17 m, and spent about 14 s by scanning, and 88 s by walking. These “mean” values correspond completely with other open field tests on voles (Eilam, 2010; Lantová et al., 2011; Maiti et al., 2019). The significant negative value of slope in walking duration (-20.9) signals potential habituation. Even though we tried to mitigate habituation, some occurred. This corresponds to an extensive study in black rats, which showed that after several repetitions, habituation was clearly expressed by a decrease in distance moved (Žampachová et al., 2017). Other similar results have also been frequently found (Drent et al., 2003; Sih et al., 2004; Carere et al., 2005**;** Leussis & Bolivar, 2006; Finger et al., 2016 etc.). Habituation speed is negatively related to the length of the inter-session (retention) interval (Bolivar et al., 2000; *Bouton, 2007*). It has been observed that in the case of OFTs, spatial information can be retained for relatively long periods (e.g. laboratory rats: two months, Broadbent et al., 2004; marmots: six months, Clemens et al., 2009). A comparison of the last test of the RE group with that of the SE control group showed that walking duration was reduced to half in the RE group, that corresponds with the, above mentioned, clear negative slope of the fixed effect estimates. As mentioned above, such a decrease in a behavioural parameter is commonly observed in repeated behavioural tests. Regarding personality traits, the situation could be slightly different. It is not possible to exclude the fact that the repetition may also have some influence on random effects, i.e. overstressed shy individuals move greater distances in a gradually more familiar environment whereas for bold individuals the effect is reversed (Thiel et al., 1999). However, no such significant changes (habituation) were observed in walking duration random effects.

The second comparison between the first test of the RE group with that of the SE control group to check aging effect was not significant, but in scanning and walking durations a trend toward significance was found. This indicate the age should be also taken into considerations. Stamps and Krishnan (2014) described the issue of predictability and appropriate personality trait strategy based on past genetic “experiences” and actual state. The authors modelled these processes and, for example, correlated a stable environment with an increasing stability of personality traits, but also with a negative correlation between intercept and slope in boldness. We observed similar trends in behavioural plasticity but unfortunately, due to the absence of a statistically significant correlation in our study, comparisons can only be speculative. The authors also linked this issue to the gradual loss of behavioural plasticity during aging (Stamps & Krishnan, 2017). For example, in rats, enrichment in the breeding boxes and two age categories showed different effects on plasticity in a cognitive test (Mora-Gallegos et al., 2015). From this point of view, our laboratory experiments can be considered as tests in a stable environment whereby a slightly indicated convergence in plasticity to a mean population value can have two explanations: (i) it confers a greater selective advantage in predictable conditions, or (ii) it is the result of lower behavioural plasticity due to aging (Roberts & DelVecchio, 2000; Stamps & Krishnan, 2017).

In less predictable conditions, Eccard and Herde (2013) found certain shifts in voles' behaviour according to postnatal periods and seasonal environmental conditions. This could be a consequence of programmed responses to the distinct conditions in the summer and winter. Similarly, in another study by the same research group, Gracceva et al. (2014) found that if voles experiencing summer light conditions were then exposed to winter conditions, their personality traits changed to more cautious (less explorative) and less active overall. This is quite understandable for winter conditions, especially under snow cover. However, the results were reported as a shift of the whole dataset, without detailed evaluation at the individual level. The question is whether the observed shifts in personality traits are due to a direct impact of an external climatic factor, or if the common vole anticipates the next season. In our laboratory study, the voles were kept in a stable environment and responded in a very specific way. During our experiment, some animals from extreme trait positions (random intercepts) shifted towards the mean population value and often behind this value (see above all Fig. 1). Such a pattern led to variance maintenance or a slight increase whereas the personality rank order was completely changed. We think that this could result from the undeveloped potential of behavioural plasticity that is expressed under stable conditions corresponding to ideas of Stamps and Krishnan (2014, 2017), rather than simply a consequence of habituation or aging. These results would be thus closer to the third hypothesis. During population density cycles, it is easy to imagine that individuals with different fully developed levels of personality traits and their different behavioural plasticity could have competitive advantage in different microhabitats (Holtmann et al., 2017) or in different phases of the population cycle (Lambin et al., 2006; Andreassen et al., 2013).

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Kapitola 3

Behavioural plasticity of motor personality traits in the common vole under three-day continual observation in a test box

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Behavioural plasticity of motor personality traits in the common vole under three-day continual observation in a test box

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Abstract

In animals, behavioural personality traits have been well-documented in a wide array of species. However, these traits, different between individuals, are not completely stable in individuals. They show behavioural plasticity like many other phenotypic traits. This plasticity is able to overcome some weak aspects of personality trait behavioural strategy. In the present study, we examined the relationship between motor personality traits and behavioural plasticity in the common vole (*Microtus arvalis*) using a PhenoTyper (PT) box (Noldus). During a three-day test, four behavioural motor activity parameters were monitored in 47 voles: distance moved, (loco)motion duration, motion change frequency, sprint duration. Consistency repeatability (R_C) of the parameters from the PT test was very high, with all values ≥ 0.91. To select the best linear mixed-effect models (LMMs), several predictors (test day, sex, body weight) were tested. Only test day had a significant effect on the dependent variables and other predictors did not improve the LMMs. Further, we found significant effects of random intercepts (motor personality traits) and slopes (behavioural plasticity), as well as significant negative correlations between them for all behavioural parameters. Our results indicate that motor personality traits were connected with behavioural plasticity. Moreover, we revealed a significant positive correlation between the random slopes of (loco)motion duration and motion change frequency. This relationship could indicate some central plasticity of motor personality traits. In conclusion, negative correlations between the motor personality traits and the behavioural plasticity demonstrate expression of convergent tendency from both opposite trait values. This corresponds with different ideas on ability to compensate personality effects or to prepare for potential future conditions. In the laboratory, plasticity of personality traits take place whenever an animal is placed e. g. in a breeding box for the first time or is left for a long time in an experimental apparatus.

Keywords: common vole, PhenoTyper box, behavioural plasticity, motor personality traits

Introduction

Personality traits have been well-documented in a wide array of species (Gosling, 2001; Mathot et al., 2012; Mather & Logue, 2013), and several models have been suggested to explain how they are maintained in populations. These models emphasise a variety of mechanisms, including density dependence, life-history trade-offs, sexual selection, and social niche specialisation (Tomkins & Brown, 2004; Wolf et al., 2007; Biro & Stamps, 2008; Schuett et al., 2010; Bergmüller & Taborsky, 2010). The fact that personality traits are maintained in populations does not mean that there are no changes in how these traits manifest. With an increasing number of studies on personality traits, a close link with behavioural plasticity has been recognized (Mathot et al., 2012; Kluen & Brommer, 2013; Mackay & Pillay, 2019). Relationships between specific personality traits and their plasticity can be explained as part of a general management system of uncertainty (reviewed in Mathot et al., 2012) or of a system that is able to adjust to expectations (Stamps & Krishnan, 2014). Behavioural plasticity can act as a personality trait, i.e., it can be consistent over time and / or context (Dingemanse & Wolf, 2013). This plasticity could behave in a similar manner to physiological functions (e.g. stress reactions or metabolic rate, which are clearly plastic), albeit over a more limited range (Norin & Metcalfe, 2019). It is important to emphasize that personality traits appear primarily (but not only) at the population level because of the processes within the population, while plasticity of behaviour is primarily associated with the individual level (Japyassúa & Malangeb, 2014).

In a study on tree swallows, Betini & Norris (2012) tested two fundamental hypotheses. The first, called “quality individuals”, predicts that individuals with extreme personality traits (both bold and shy) also have significant plasticity. The second, called "compensatory", predicts that individuals with indistinct personality traits have increased plasticity, i.e., they have an increased ability to compensate for various external or internal factors. The authors found that males could be successful according to either of hypotheses. Similarly, in a study of three-spined stickleback (*Gasterosteus aculeatus*), Jolles et al. (2019) discovered a negative correlation between plasticity and bold personality, and a positive correlation with shy personality. Residual variance was related to predictability: the greater the variance was, the lower was the predictability. Simultaneously, variance was greater in shy individuals, making their behaviour less predictable.

In studies of personality traits and behavioural plasticity, the repetition of tests is essential and therefore it is necessary to control the habituation process. Some studies have repeated tests until changes of the traits no longer occurred, considering this point as the basal level (Žampachová et al., 2017). Another approach to address this is to continuously monitor animals placed in a new box (similar to the Open field test, OFT), which gradually becomes their home environment. This is for example possible using the PhenoTyper (PT; Noldus) box, in which the movement activity of laboratory rodents can be monitored. PhenoTyper in connection with automated tracking software provides a useful alternative system for the reliable and accurate measurement of movement activity and fear-related behaviour in a high-throughput manner (Pham et al., 2009; van Dam et al., 2013). Tang et al. (2002) emphasised the relevance of studying baseline activity in the home cage to interpret behaviour within novel environment using such devices. Robinson et al. (2013) used a PT box to monitor activity in mice documenting a prominent reduction in overall locomotor activity, while circadian rhythms were maintained. The PT box has also been used to determine similar drug and strain effects on behaviour to those observed using traditional methods (Robinson & Riedel, 2014), as well as for assessing behavioural parameters in different strains of mice (de Visser et al., 2006). The authors of the latter study observed mice in the PT box over several days to determine baseline motor activity levels and compared them with those established in OFTs and elevated plus-maze tests. (Loco)motion activity is of considerable interest when phenotyping rodents. This is reflected by the numerous studies on locomotor activity as a proxy of overall behavioural activity and emotional states (Tang et al., 2002; Uchiumi et al., 2008; Kostrzewa & Kas, 2014). For example, Wistar-Kyoto rats showed, in addition to an attenuated locomotor activity, fewer entries into the central area of the open field and fewer visits to the open arms of the elevated plus-maze (Gentsch et al., 1987). In a study on mice (Careau et al., 2012), a positive correlation between the distance run in wheels and the distance moved in the OFT was observed.

In the common vole, a number of studies have identified the main personality traits as boldness, exploration, anxiety, and behavioural activity (Lantová et al., 2011; Eccard & Herde, 2013; Herde & Eccard, 2013; Gracceva et al., 2014; Urbánková et al., 2020). This species is a suitable animal for such studies due to its overall biological and ecological plasticity. Across its distribution range within the Palaearctic region, voles are exposed to a great variety of climatic and biotic conditions. This can involve extensive seasonal changes, with temperatures in their steppe/meadow habitats reaching over 35 °C in summer to below 0 °C under the snow cover during the winter. Furthermore, populations undergo three- to five-year cycles of population density variation, during which vole numbers range from thousands to only a few individuals per hectare (Lambin et al., 2006; Andreassen et al., 2013). This is connected with changes in food and shelter availability as well as health conditions, i.e. parasitic, bacterial, and viral load (Niethammer & Krapp, 1982).

In our previous study (Urbánková et al., 2020), we found that personality traits in voles determined in four OF tests within two-month intervals showed little plasticity. In the present study, we tested whether the motor personality traits would be more plastic under different experimental conditions. Our main question was what will be the several-day development of motor personality traits after exposure to a new, moderate stressful, test-box environment? Temporal plasticity, a special case of phenotypic plasticity, occurs when individuals habituate to a stressful stimulus. It is represented by a change in the behavioural response to repeated exposure to a stimulus that does not involve action inhibition of the organs (sensory, muscles) on the periphery of the neural system (Rankin et al., 2009).

The following hypotheses with predictions of the results were formulated as follows:

H_0: Motor personality traits are not affected by habituation. They are not plastic and they are stable. Prediction: Random slopes are not significant, as well as correlations between the intercepts and slopes.

H_A: Motor personality traits are affected by habituation and they are plastic. Prediction: Random slopes are significant, as well as correlations between the intercepts and slopes.

Materials and methods

Vole individuals

We tested 47 adult individuals of the common vole (*Microtus arvalis*) (18 males and 29 females) at the age of 3 months. All tested vole individuals belonged to the first offspring generation of wild-caught animals. The parental pairs came from two distant localities to preclude inbreeding (locality 1: České Budějovice, 48.977821°N, 14.441390°E; locality 2: Lužnice, 49.080373°N, 14.755786°E). Voles were kept individually in polycarbonate breeding cages 58 × 36 × 20 cm (VELAZ Prague) with wood shavings, hay, and plastic tubes as shelter. Food and water, including fresh carrots and commercial pellets (for mice, guinea pigs and rabbits; VELAZ Prague), was available *ad libitum*. All individuals were identified by labels on the breeding boxes. The laboratory conditions were stable, with the room at a temperature of 22 ± 1°C and a L:D 12:12 photoperiod. Initial body weights showed low variation in both sexes (males 25 ± 3 g, females 20 ± 2 g).

Voles were bred and tested in accordance with the principles of animal welfare and guidelines of the Departmental Commission for Animal Protection of the Ministry of Education, Youth and Sports, permit number 7945/2010-30 according to the law 246/1992 on the protection of animals against cruelty. After the experiments, the voles stayed in the laboratory and were used for further research.

PhenoTyper (PT) test

PhenoTyper is a box that, in conjunction with EthoVision software, enables a continual measurement and differentiation between novelty-induced and baseline behaviours (de Visser et al., 2006). This activity was measured in three PT Perspex test boxes (45 × 45 × 45 cm, Noldus) in parallel. Each vole was placed separately into the PT box from its home box, in a plastic tube shelter. In each PT box the bottom was covered with wood shavings, food and water were available *ad libitum*, and light and temperature conditions were consistent with the breeding room. Measurements lasted for 72 h (3 successive days) since our pilot test established that the data did not change significantly during the third day. All animals were weighed pre- and post-testing to check they had retained their body weight and mastered the test well (Riedel et al., 2009).

Behavioural activity was recorded with digital cameras placed in the heads of the PT boxes. The cameras in the three box heads were connected via Videoswitcher Viq601a to a computer. In this relatively long-lasting test, data were collected and evaluated by EthoVision software. Similarly, to de Visser et al. (2006), four behavioural motor parameters were scored. The common vole has a polyphasic activity in which two to three-hour intervals of activity and rest alternate. Their sums, however, vary between days minimally (Gerkema et al., 1993; Niethammer & Krapp, 1982). Therefore, we assessed the following measured variables within a time period of 24 h within a 3-day observations:

1) Distance moved – total distance covered (m).
2) (Loco)motion duration – percentage of time spent moving activity. The parenthesis is used because the automatically recorded motion may have been also without clear locomotion.

3) Motion change frequency – each motion change (number/h).

4) Sprint duration – percentage of stereotyped straightforward high-rate locomotion (> 0.6 m/s), often along walls.

Statistical analyses

The distributions of our dependent variables (distance moved, [loco]motion duration, motion change frequency and sprint duration) were tested for normality using a Kolmogorov-Smirnov test. Some of dependent variables did not display a Gaussian distribution and we used arcsin*√p transformation for them. Consistency repeatability R_C was calculated according to Biro and Stamps (2015) based on variance component estimates produced by the linear mixed models (LMMs). Mixed-effect models were used to estimate variation in the random intercepts and slopes of our four independent variables, and the correlations between them. The statistical software R v.3.5.2 (R Core Team, 2018) and the software package lme4 (Bates et al., 2015) were used to build mixed effect models for each dependent variable (e.g. Schaeffer, 2004; Nussey et al., 2007; Brommer et al., 2012; Dingemanse & Dochtermann, 2013; Bates et al., 2015). Only the first polynomial order was used to fit the values among the three individual day values (time). Statistical significances for both fixed (time, sex, weight) and random (individual - id) effects were obtained using a likelihood-ratio test, which compared a particular model with the null model. The age of tested individuals was not used since all of them were born within several days.

For all statistical tests, we considered the cut-off for statistical significance as $p < 0.05$. To indicate the amount of uncertainty in the estimates, bootstrap confidence intervals (CI) were also calculated. We also checked for homogeneity of residual variance using Q-Q plots of the models to avoid bias (e.g. Nicolaus et al., 2013; Araya-Ajoy & Dingenmanse, 2017). The relationship between intercept and slope (based on random effect of time) for each dependent variable was visualised by a linear regression, for correlations of slopes the Spearman coefficient was used in Statistica 13 (TIBCO Software Inc., 2017).

Results

The highest repeatability was found in the (loco)motion duration ($R_C = 0.98$), the lowest value (although still quite high) was found in the motion change frequency ($R_C = 0.91$). All confidence intervals (CI) closely corresponded to the mean values. In all behavioural motor variables, the significance level was very high ($p < 0.001$; for H_o: $R_c = 0$; Table 1).

Table 1 Repeatability of PT behavioural motor parameters

Variable	Consistency repeatability R_C ± SE	Confidence interval 95 %
Distance moved	0.96 ± 0.01	0.93 – 0.98
(Loco)motion duration	0.98 ± 0.01	0.97 – 0.99
Motion change frequency	0.91 ± 0.02	0.86 – 0.95
Sprint duration	0.93 ± 0.02	0.88 – 0.96

In all variables $p < 0.001$

The best LMM was selected for each of four PT dependent variables (distance moved, (loco)motion duration, motion change frequency, sprint duration) against time, sex, and weight. The best LMMs included only time when considering fixed effects (Table 2). Based on the best LMMs, we also calculated the random effects for the models for four PT dependent variables (Table 3). In all cases, inclusion of individual random factors significantly improved the basic model. This means that the behavioural plasticity, as well as the correlation between intercepts and slopes, was found in all observed dependent variables. For all dependent variables, we found a negative relationship between intercept and slope for random effects (Figure 1). The strongest intercept-slope correlation was found in motion change frequency ($r = -0.74$, $p < 0.001$), with the confidence interval ranging from -0.856 to -0.563 (Table 4). Despite the generally high significance of results for random effects, relatively high residual variances (σ_r^2) were found in the original data (e.g. motion frequency, $\sigma_s^2/\sigma_r^2 = 20483/5645$), as well as in the transformed data (e.g. sprint duration, $\sigma_s^2/\sigma_r^2 = 0.005/0.002$, Table 4). Considering the fixed effects on the behavioural motor variables, the highest changes during the three days were observed in distance moved (intercept = 713 ± 67 m, slope = -83 m, $t_{test} = -3.706$, $p < 0.001$). However, no significant changes during days (slopes) were observed in the motion change frequency (Table 4).

Table 2 Comparison of fixed effects of independent variables (time, sex and weight) and their combinations on four PT dependent variables. Presented likelihood-ratio tests compare each model with the reduced model on the preceding row

Response variable	Independent variables	logLik	df	p
Distance moved	Time	-953.3	3	**<0.001**
	Time+sex	-953.2	2	0.696
	Time+sex+weight	-952.7	1	0.324
(Loco)motion duration	Time	94.53	3	**<0.001**
	Time+sex	95.23	2	0.496
	Time+sex+weight	95.58	1	0.402
Motion change frequency	Time	-988.9	3	**<0.001**
	Time+sex	-988.3	2	0.561
	Time+sex+weight	-988.0	1	0.484
Sprint duration	Time	122.5	3	**<0.001**
	Time+sex	122.7	2	0.754
	Time+sex+weight	123.3	1	0.303

logLik, log-likelihood estimates

Table 3 Comparison of random effects of independent variables (time and individual id) and their combinations on four PT dependent variables. Presented likelihood-ratio tests compare each model with the reduced model on the preceding row. Differences between models were calculated using likelihood-ratio tests

Response variable	Random factors	logLik	df	p
Distance moved	Null model	-1027		
	Id	-975.3	1	**<0.001**
	Id+time	-965.6	1	**<0.001**
	Id*time	-953.3	1	**<0.001**
(Loco)motion duration	Null model	-16.32		
	Id	67.58	1	**<0.001**
	Id+time	86.00	1	**<0.001**
	Id*time	94.53	1	**<0.001**
Motion change frequency	Null model	-1040		
	Id	-1004	1	**<0.001**
	Id+time	-1002	1	**0.037**
	Id*time	-988.9	1	**<0.001**
Sprint duration	Null model	65.18		
	Id	100.5	1	**<0.001**
	Id+time	113.1	1	**<0.001**
	Id*time	122.5	1	**<0.001**

Id, individual identity; time, day 1–3; id*time interaction between id and time; logLik, log-likelihood estimates

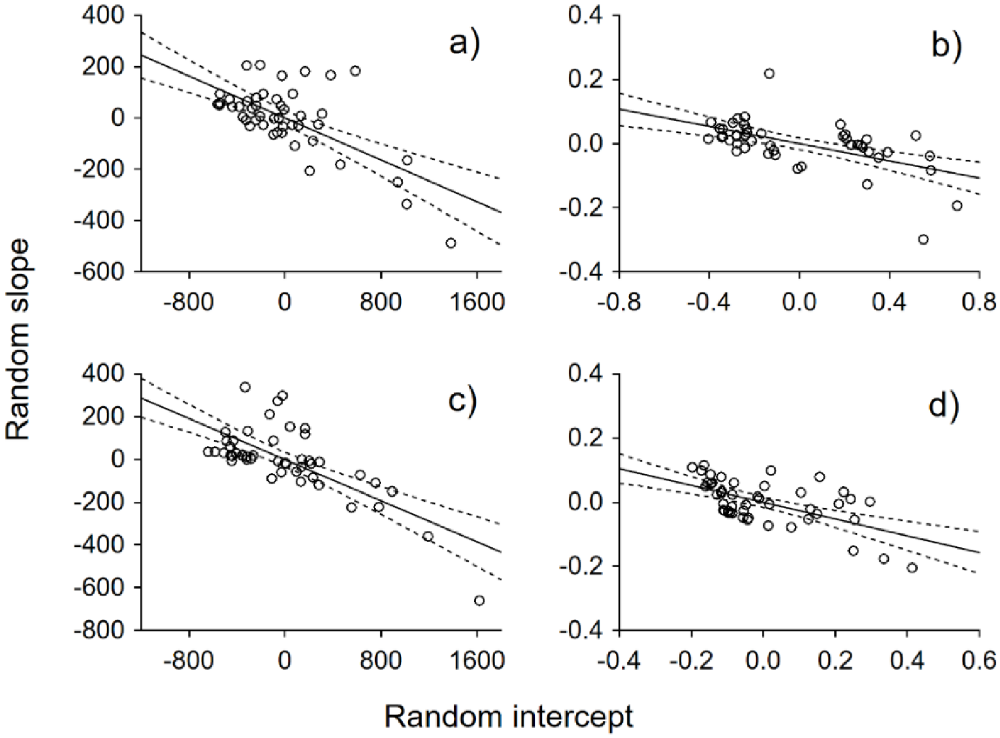

Figure 1 Correlation between random intercepts (motor personality traits) and random slopes (behavioural plasticity) in 47 voles (Tab. 3 and 4). Zero on the axis is the LMM mean of the vole file. The relationships show the opposite motor personality traits (positive and negative values) are connected with decreasing or increasing behavioural plasticity, respectively, causing convergent trend of personality trait expression. a) “distance moved” (m) (r = -0.68); b) “(loco)motion duration” after *arcsin*√*p* transformation (r = -0.58); c) “motion change frequency” (number/hour) (r = -0.74); d) “sprint duration” after *arcsin*√*p* transformation (r = -0.64).

Table 4 Estimated parameters of the LMMs for four behavioural dependent variables with time as an independent variable with fixed effect. Estimates of fixed effect include intercepts with SE, slopes (time) with SE. Slope significances are expressed as t-statistic (**A**). Estimates of random effects include variances in intercepts, slopes (time), residuals (within-individual), and the correlation between random intercepts and slopes (**B**)

Tab. **A** Fixed effects

Response variables	Intercept ± SE	Slope ± SE (time)	t-statistics	p
Distance moved (m)	713.4 ± 67.14	-82.53 ± 22.27	**-3.706**	**<0.001**
(Loco)motion duration *arcsin*$\sqrt{p}$	0.667 ± 0.048	-0.032 ± 0.012	**-2.648**	**< 0.02**
Motion change frequency (h^{-1})	741.8 ± 78.84	-54.43 ± 28.74	-1.894	> 0.05
Sprint duration *arcsin*$\sqrt{p}$	0.121 ± 0.026	0.031 ± 0.012	**2.662**	**< 0.02**

Tab. **B** Random effects

Response Variables	Intercept variance σ_i^2	Slope variance σ_s^2	Residual variance σ_r^2	IS corr.	CI
Distance moved (m)	198682	20483	5645	**-0.68**	-0.81, -0.48
(Loco)motion duration *arcsin*$\sqrt{p}$	0.104	0.006	0.001	**-0.58**	-0.75, -0.31
Motion change frequency (h^{-1})	259808	31894	13861	**-0.74**	-0.86, -0.56
Sprint duration *arcsin*$\sqrt{p}$	0.028	0.005	0.002	**-0.64**	-0.79, -0.38

Abbreviations (Tab. 4): IS corr., Intercept-Slope correlation; CI, Bootstrap Confidence Interval; significant values bold

To evaluate behavioural plasticity, correlations between random slopes were also determined. A positive correlation was found between (loco)motion duration and motion change frequency ($r = 0.828$, $p < 0.001$), while other correlations were non-significant (Table 5).

Table 5 Correlations between random slopes of PT behavioural dependent variables

Variable	(Loco)-motion duration	Motion change frequency	Sprint duration
Distance moved	0.043	0.066	-0.105
(Loco)motion duration		0.828*	-0.147
Motion change frequency			-0.044

* $p < 0.001$, $n = 47$

Discussion

The PhenoTyper test

Similar to OF tests, putting voles in the PT boxes meant that the voles were introduced into a new environment. However, the presence of a shelter profoundly influenced their activity from the beginning. This is not surprising, because we tested animals born in a laboratory environment, however, unlike to laboratory animals these individuals exhibited an instinctive clear search for a safe place. Voles were able to move approximately 35 m during the first hour. These results agree with a similar study using laboratory mice in a PT, where the mean values ranged between approximately 6 and 60 m (Robinson et al., 2013; Robinson & Riedel, 2014).

In our study, repeatability was calculated according to Biro and Stamps (2015) as a consistency repeatability (R_C). Based on mean values for individual days (1–3) we reached surprisingly high R_C values that ranged from 0.91 to 0.98. This probably corresponds to experimental settings since each animal is still in the same closed test box and gradually adapts to its new conditions. Under quite different conditions (four 3 min OFTs with a two-month interval) the voles showed $R_C = 0.51$ in distance moved, $R_C = 0.39$ in walking duration, and $R_C = 0.20$ in scanning duration (Urbánková et al., 2020). Based on a literature review, Bell et al. (2009) calculated that the mean repeatability of behavioural parameters is around 0.37. Somewhat lower values were found in agreement repeatability (R_A) in voles (0.25–0.63, Lantová et al., 2011; Herde & Eccard, 2013). However, in the black rat, many repetitions over a short time were able to produce very high values (R_C = 0.22–0.81; Žampachová et al., 2017). Nevertheless, these comparisons between species must be treated cautiously because the same repeatability can be achieved in samples with completely different population structures (Dochtermann & Royauté, 2019).

Fixed effects

To select the best LMM, several predictors were tested: test day (time), sex, and body weight. However, only the LMM with the predictor “time” was selected, as other predictors did not improve the models. This result was an expected scenario since the animals had no experience of the opposite sex since weaning and had not been exposed to stress situations such as lack of food or temperature fluctuations. Furthermore, previous similar studies also showed that body weight and sex were not significant fixed effects in linear models for voles (e.g. Lantová et al., 2011; Herde & Eccard, 2013; Urbánková et al., 2020) or chipmunks (Martin & Réale, 2008).

In distance moved the intercept was 713 m and slope -83 m and animals moved 630, 547, and 464 m in each of three days, respectively. Similar decreases in distance moved (i.e. habituation) occurred in mice during 3–4 day trials (de Visser et al., 2006; Riedel et al., 2009). Using the PT box, Robinson et al. (2013) also documented a certain reduction of overall locomotor activity in mice, while another motion parameter, the circadian rhythm, was maintained. This also corresponds to an extensive study in black rats, which showed that after several repetitions, habituation was clearly expressed by a decrease in distance moved (Žampachová et al., 2017). In our study, the significant negative value of the slope for (loco)motion duration parameter may also signal such habituation. Similar results have been frequently reported by other studies (Drent et al., 2003; Sih et al., 2004; Carere et al., 2005; Leussis & Bolivar, 2006; Finger et al., 2016). On the other hand, an increase in sprint duration could mirror a certain need for higher locomotor activity (compensation) that may correspond to the reinforcing properties of the running wheel of experiments for locomotor activity determination (Sherwin, 1998; de Visser et al., 2005).

Random effects

In all examined behavioural motor parameters, we found significant random intercepts, random slopes (plasticity itself), and negative intercept-slope (personality-plasticity) correlations. This means that the behavioural plasticity was high and bound to the personality traits, i. e. the behavioural plasticity was oriented. A negative correlation also means that the higher the intercept is, the more negative is the slope and *vice versa*, i. e. voles with the most-expressed personality traits could possess the highest plasticity (Figure 1). From another perspective, it could also be considered that a certain tendency towards the average population value is indicated. This would be an interesting result in voles kept under short but intensive exposition to specific conditions. Similar correlation has been observed between boldness and temporal plasticity in three-spined sticklebacks (Jolles et al., 2019). Our results also correspond to the first hypothesis of Betini & Norris (2012) called "quality individuals". It states that individuals with extreme personality traits also have pronounced plasticity.

Attention should also be paid to residual variances, which were relatively high in all parameters. Unassigned variability suggests that there may be other factors, which were not recognised. The term intra-individual variability is used in this context (Japyassúa & Malangeb, 2014) and could mean that behaviour inside the PT box was affected by something other than motor personality, i. e. an emotional component, such as the feeling of safety and/or anxiety. Since this is a subjective emotional state dictated by various inputs, control of this parameter is not practically possible (Eilam, 2010).

Behavioural plasticity

We found that in all parameters, slopes and correlations between random intercepts and slopes were negative and statistically significant. To test the idea that behavioural plasticity represents a personality trait (Dingemanse & Wolf, 2013), we correlated random effects (slopes) in individual parameters to reveal the internal interconnection (common plasticity). Among all positive correlations, we found a strong relationship ($r = 0.828$, $p < 0.001$) between (loco)motion duration and frequency of motion changes. The results suggest that as the duration of the (loco)motion increases, the frequency of motion changes also increases. This relationship is not easily explainable and could indicate some central behavioural plasticity. However, more general plasticity has been found in somewhat more distant physiological-behavioural parameters than we have achieved using relatively close motor activity parameters. For example, zebrafishes that were thermally responsive were not more responsive to food deprivation, but they exhibited greater unexplained variation (Mitchell & Biro, 2017). Finally, it should be emphasized that the motor personality trait changes that we have recorded in the PT box most likely take place each time an animal is first placed in a breeding box.

Ecological consequences

In terms of the ultimate goal of explaining the relationships between specific personality traits and their plasticity, it should be considered part of a general management system of uncertainty (reviewed in Mathot et al., 2012) or a part of a system that is able to adjust to expectations (Stamps & Krishnan, 2014). Accordingly, high variance can also be interpreted as low behavioural predictability (Jolles et al., 2019).

Stamps and Krishnan (2014) described the issue of predictability and appropriate personality trait strategy based on past genetic "experiences" and actual state. The authors modelled these processes and correlated a stable environment with an increasing stability of personality traits, but a negative correlation between intercept and slope in boldness. We observed similar trends in all evaluated parameters. Therefore, our laboratory experiments could be considered as tests in a new stable environment with low population density, whereby plasticity leads up, more or less, to the mean motor personality trait values across the population. This phenomenon could be explained by an increased selective advantage in predictable conditions.

In less predictable conditions, Eccard and Herde (2013) found certain shifts in vole behaviour according to postnatal periods and seasonal environmental conditions. This could be a consequence of programmed responses to the distinct conditions in the summer and winter. Similarly, in another study by the same research group, Gracceva et al. (2014) found that if voles experiencing summer light conditions were then exposed to winter conditions, their personality traits changed to being more cautious (less explorative) and less active overall.

In the case of the voles, behavioural plasticity allows to better cope with large fluctuations in the population density (Korpela et al., 2011; Schirmer et al., 2019; Morris et al., 2016; Wright et al., 2019), as well as, with fluctuations in predation pressure and climate changes during the winter and summer period. It should be emphasized that the plastic motor personality traits may change behaviour effectively. In the familiar home range, these motor personality traits may not be manifested fully and only with the presence of an intruder they can be shown on the appropriate level. On the other hand, increased phenotypic plasticity buffers strong directional selection and evolutionary shifts. However, such situations also often support new selective pressures (Losos et al., 2006; Price, 2006). Given that vole populations are subjects of pronounced cyclical changes (Lambin et al., 2006; Andreassen et al., 2013), disruptive or stabilising selection of motor personality traits could be still expected accordingly. It is also easy to imagine that individuals with different levels of personality traits and behavioural plasticity could have a competitive advantage in different microhabitats (Holtmann et al., 2017).

Since population density has been recently recognized as an important factor affecting behavioural plasticity (Wright et al., 2019), we suggest to repeat our experiment with implementing a social context. Particularly, we plan to observe behavioural parameters of small groups (2-4 individuals), which would simulate a higher population density.

CRediT authorship contribution statement

Gabriela Urbánková: Conceptualization, Methodology, Investigation, Writing - original draft. **Jan Riegert:** Methodology, Formal analysis. **Nella Mladěnková:** Methodology, Investigation. **Petra Kolářová:** Investigation, Resources. **Zdeněk Eliáš:** Investigation, Resources. **František Sedláček:** Supervision, Conceptualization, Validation, Writing - review & editing.

Declaration of Competing Interest

We declare that we have no conflicts of interest.

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Kapitola 4

Similarity of behavioural traits within parents improves their reproduction: The case study on the common vole (*Microtus arvalis*)

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Similarity of behavioural personality traits within parents improves their reproduction: The case study on the common vole (*Microtus arvalis*)

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Abstract

Individual differences in behaviour, referred to as animal personality were described in a broad spectrum of animal taxa. Several models explaining how they are maintained have been suggested; for example, density dependence, life-history trade-offs, sexual selection, and social niche specialisation. In the last decade the personality traits were described also in the common vole (*Microtus arvalis*). However, the mechanisms by which they are maintained in the vole populations has not yet been studied. Inspired by a study on mound-building mouse, the present study focused on the possible role of assortative mating based on similar personality traits within the parental pairs. Six behavioral parameters were evaluated in 63 individuals (34 males, 29 females) during three successive Open field (OF) tests. Using linear mixed models (LMMs), personality traits were considered intercepts of random effects. Then, male-female intercept difference were related to presence (0/1) and number (1-5) of offspring using generalized linear mixed models (GLMMs). Significant results were obtained in the male-female difference of intercepts of the total distance covered during the test. Presence of offspring was connected with low intercept difference (i.e. increased similarity) in the total distance covered ($p < 0.022$); number of offspring was negatively related to this difference ($p < 0.010$). The results indicate a possible mechanism of assortative mating and personality trait maintenance in the vole population.

Keywords: Common vole, behavioural personality trait,
assortative mating, offspring production

Introduction

Personality traits are understood as individual differences in behaviour that are consistent across time and ecological contexts (Réale et al. 2009, 2010). These traits have been well-documented in a wide array of species, including both vertebrates (Gosling 2001) and invertebrates (Mather and Logue 2013). Several models explaining how personality traits are maintained have been suggested. These models emphasise a variety of mechanisms, for example, density dependence, social niche specialisation, life-history trade-offs or pace-of-life syndrome (Tomkins and Brown 2004; Wolf et al. 2007; Biro and Stamps 2008; Careau et al. 2008; Bergmüller and Taborsky 2010; Réale et al. 2010; Schuett et al. 2010). The next mechanism recently often mentioned is sexual selection. The importance of similarity in behavioural traits of partners for the success of reproduction has been documented several times in bird and fish species (e.g. Ihle et al. 2015; Laubu et al. 2016, 2017). Attention has been often focused on the influence of a personality trait closely associated with exploration that was reported for example in the great tit (*Parus major*) (Dingemanse et al. 2004).

The preference for similar trait phenotypes during the reproduction is referred to as assortative mating. Assortative pairing can be divided into positive or negative (disassortative). Positive pairing means that there is a tendency to prefer individuals with similar phenotypes, while negative one lead to preference of rather different individuals (Jiang et al. 2013). Thiessen et al. (1997) argued that assortative mating may be a strategy since the main advantage is that similar couples are actually more likely to pass on more than 50% of their genetic material into their offspring. However inbreeding depression could endanger the viability of the future offspring reproductive line. So, it is also important to mention that there is also an opposite tendency to maintain high diversity of the MHC genes and therefore to prefer a partner different as much as possible (Leclaire et al. 2017; Santos et al. 2016). The frequent morphological parameters for this selection are body size, shape, or colour (Harris and Siefferman 2014; Hase and Shimada 2014). Similar behavioural traits should be probably common, especially in species with biparental care for offspring, and should be an essential part of the ethogram at least during the breeding season. There are several reasons for choosing a partner according to personality traits that indicate individual quality (Dirienzo and Hedrick 2014). Some females can predict the male's ability to protect offspring based on its behaviour (Teyssier et al. 2014).

Exploratory behaviour, searching for females even in a completely new environment and orientation in such an environment is also an important part of mating (see e.g. Spritzer et al. 2005). In the Campbell's hamster (*Phodopus campbelli*), a preference for the male's non-aggressive care of the female's hair during physical contact was recorded (Rogovin et al. 2017). In the monogamous prairie vole (*Microtus ochrogaster*), males combed their hair more often without pairing than already mated individuals (Wolff et al. 2002). These activities could be an ambivalent behaviour during a stressful situation, however, the movements could demonstrate also certain personality traits.

The importance of similarity in personality traits especially for reproductive success in mammals was documented for the first time in the monogamous mound-building mouse. This mating system is not common in mammals, but even there, parental compatibility appears to be useful. Couples with similar levels of anxiety started reproduction earlier than dissimilar ones (Rangassamy et al. 2015). In a very rare species, the giant panda (*Ailuropoda melanoleuca*), it is quite understandable that the all potential factors affecting the reproduction success were analysed, including the personality traits. It seems, mutual fear is not beneficial in reproduction, both in males and females (Martin-Wintle et al. 2017).

Based on the above-mentioned data, the aim of this study was to determine whether the similarity in partner behaviour will affect reproduction in a solitary-living rodent, the common vole. Therefore the main hypothesis of our study was that pair similarity of behavioural traits enhances 1) the number of vole pairs that produce at least one young and 2) the total offspring number in vole pairs.

Material and Methods

Animals

Wild common voles were caught using Sherman live traps for small mammals. In our breeding colony, we tested 63 adult individuals (34 males and 29 females) at the age of 3 months, which were the first offspring generation of wild-caught animals. Thanks to the possibility of preparing experimental animals from captured parents, we used animals of an almost identical age/weight. The parental pairs came from two distant localities to prevent inbreeding (locality 1: České Budějovice, 48.977821 N, 14.441390 E, locality 2: Lužnice, 49.080373 N, 14.755786 E).

Voles were kept individually in polycarbonate breeding cages 58 x 36 x 20 cm (VELAZ Prague) with wood shavings, hay, and plastic tubes as shelters. Commercial pellets for rats and mice as well as pellets for guinea pigs and rabbits (VELAZ Prague), fresh carrots, and water were available *ad libitum*. All individuals were individually marked on the breeding boxes. The laboratory conditions were stable, with the room temperature of 22 ± 1°C and under a L:D 12:12 photoperiod. Body weights in both sexes showed low variability (males 25 ± 3g, females 20 ± 2g). The voles were tested between 9 a.m. and 4 p.m. in a random order, because vole are animals with polyphasic circadian activity in which alternate 2-3 hours of moving and rest (Gerkema et al. 1993).

The voles were bred and tested in accordance with the principles of animal welfare and guidelines of the Departmental Commission for Animal Protection of the Ministry of Education, Youth and Sports, permit number 7945/2010-30 and the animal treatment conforming also the journal ethics guidelines. After the experiments, the voles stayed in the laboratory and were used for further breeding and behavioural tests.

Experimental design

The behavioural personality trait was determined during three Open field (OF) tests with two-week intervals. Each test session was recorded on a digital camera (Panasonic Color CCTV Camera WV-CP500/G) placed 150 cm above the test arena. The video sequence was analysed using the EthoVision 8.0 TX (Noldus) software. In the tests, we focused on the usually observed behavioural parameters (Lantová et al., 2011) as described below. Individuals were tested in the OF test in a random order to avoid biases of results. After the third test, vaginal smears were evaluated and the voles were paired (Cora et al. 2015; Nubbemeyer 1999). In total, proestrus-like stage was observed in 40 females (70.2 %), estrus in 15 (26.3 %) and diestrus in two females (3.5 %). The males were placed into the female home boxes. If the males still tried to escape from the female home box, they were removed after 15 minutes. If the males did not try to escape, they were left in the female home box maximally for four days. The relationships between the number of offspring and the behavioural personality trait differences of parents were calculated based on male - female absolute differences (|m - f| after Rangassamy et al. 2015).

Open field (OF) test

Our OF test was carried out in a square Perspex arena (75 L x 75 W x 50 H cm) with non-transparent walls. In the test room, the light intensity was maintained at about 100 lx to ensure equal illumination and a stress level slightly increased only for the tested voles. All experimental animals were carried from their home boxes to the experimental arena in their plastic home tubes, and were subsequently gently placed in the peripheral zone on the same place and direction (i.e. forced OF test). Each session lasted 5 min since prolonged tests cause habituation in voles, i.e. less frequent and less pronounced exploration as observed in previous studies (Lantová et al. 2011, Urbánková et al. 2020). The arena was cleaned with watered-down ethanol after each experiment. The behavioural parameters were scored as follows: 1) “Central distance” – distance covered inside the central area (m), 2) “Total distance” – total distance covered during the test (m), 3) “Grooming” – behaviour focused on own body surface/fur (s), 4) “Jumping” – jumping up the walls often quickly repeated (s), 5) “Locomotion” – forward movement often interrupted by other behaviours (s), 6) “Scanning” - staying on place and turning head (s).

Statistical analyses

In the beginning of the evaluation, the behavioural personality traits (intercepts of random effects for each individual for each behavioural trait) were obtained using linear mixed models (LMMs). First, selection of the best LMM for six response variables (observed behavioural parameters) with different fixed factors (time, sex, weight) was carried out. All models used (1+time|id) specification of random effects, for estimating the random effect of intercept as personality trait. Consistency repeatability R_C was calculated according to Biro and Stamps (2015). For both calculations, the package lme4 using lmer function and the package rptR was used in R 4.0.2 software (R Core Team 2020).

Next, the effect of independent variables (intercepts of random effects for each individual for each behavioural trait) on presence of young (0/1) and number of young (1-5) produced by the vole breeding pairs was determined. Firstly, we built null model without factors. Then, we built two groups of original models (for 0/1 and for 1-5 offspring) that differed in combination of factors. The relationship between the number of young (dependent variable) and the similarity in personality traits (male - female trait difference), pairing round (first and second), male and female body weight and their difference within a breeding pair, occurrence of female proestrus and estrus (independent variables) was determined using generalized linear models (GLMMs) and LMMs.

Multi model inference (Anderson and Burnham 2002; Burnham et al. 2011; Whittingham et al. 2006) was calculated using package MuMIn in R 4.0.2 software (R Core Team 2020). We used localities where the individuals were captured in the field for male and female within the pair as random factors. We show results for full average procedure (i.e. the results from comparison of all models). For visualization of the results (occurrence 0/1 and the number of offspring) we used Statistica 13 software (TIBCO Software Inc. 2017). For all tests, we considered the cut-off for statistical significance as $p < 0.050$.

Results

The OF test

Consistency repeatability was in all behavioural parameters very high and highly significant (Table 1). The highest value showed the distance covered during the all test ($R_C = 0.93$). On the other hand, the lowest value was determined also in distance, however, in this case it was the distance covered in the central area ($R_C = 0.55$).

Table 1 Repeatability of behavioural parameters. In all parameters $p < 0.001$

Parameters	Consistency repeatability $R_C \pm SE$	Confidence interval CI 95 %
Distance total	0.93±0.02	0.89, 0.96
Distance central	0.55±0.07	0.41, 0.70
Locomotion	0.72±0.06	0.59, 0.83
Scanning	0.81±0.04	0.74, 0.88
Jumping	0.87±0.03	0.80, 0.91
Grooming	0.87±0.03	0.79, 0.92

Reproduction

A total of 57 pairs of voles were involved into the experiment, 33 pairs were created during the first round and 24 new ones during the second round. In both rounds of mating, 72 pups were obtained, with 33 offspring produced in the first round and 39 in the second one. The number of pups among pairs was strongly unbalanced (Fig. 1). More than half of the pairs (32 i.e. 56 %) produced no offspring. The final production was 1.3 ± 1.6 (SD) offspring per all pairs, or 2.9 ± 1.0 (SD) offspring per fertile pair.

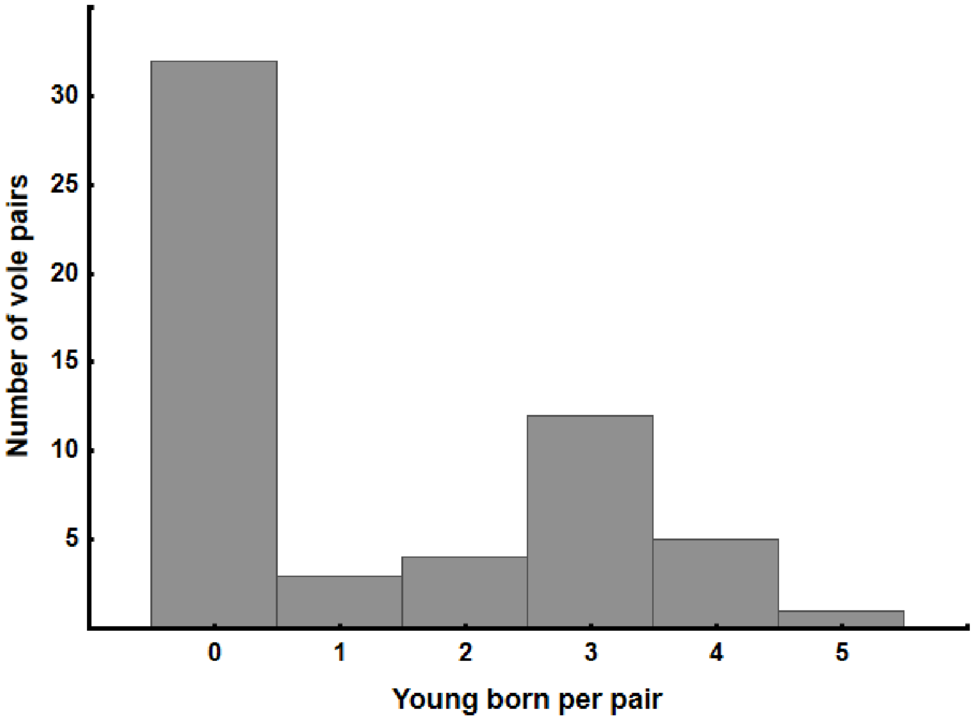

Figure 1 Histogram of the number of young born in the setup pairs

Behavioural parameters and personality trait differences versus reproduction

In all behavioural parameters, the best LMM was for the fixed factor time (repetition of tests) only (Table 2). Therefore, the intercepts of random effects calculated in the LMMs with factor time were used only. Differences of these intercept values (behavioural personality traits) between male and female in the vole pairs were then tested for the relation to the number of offspring (Table3). The difference between males and females in the total distance intercept was significantly different only. Higher difference was determined in pairs without offspring (Table 3, upper part, p = 0.022, Fig. 2). Similarly, significant negative correlation was found between the number of offspring and males – females total distance intercept difference (Table 3, lower part, p = 0.010, Fig. 3). Concerning this behavioural personality trait, the more the pairs were similar, the more offspring they produced.

Table 2 Selection of the best LMM for six response variables with different fixed factors (time, sex, weight). All models used (1+time|id) random effects, for estimating the random effect of intercept as a personality trait. Likelihood-ratio tests compare the particular model with the reduced model of the preceding row, the first one with the null model: response variable ~ +1 + (1 + 1 | id)

Response variable	Model	logLik	df	p
Distance total	~time	-611.7	3	**<0.001**
	~time+sex	-610.6	1	0.138
	~time+sex+weight	-609.0	1	0.079
Distance central	~time	-309.6	3	**<0.001**
	~time+sex	-309.6	1	0.914
	~time+sex+weight	-309.3	1	0.425
Locomotion duration	~time	-897.5	3	**0.015**
	~time+sex	-895.9	1	0.069
	~time+sex+weight	-894.8	1	0.145
Scanning duration	~time	-643.2	3	**0.016**
	~time+sex	-642.7	1	0.292
	~time+sex+weight	-640.9	1	0.063
Jumping duration	~time	-658.9	3	**<0.001**
	~time+sex	-657.9	1	0.162
	~time+sex+weight	-657.9	1	0.869
Grooming duration	~time	-752.7	3	**<0.001**
	~time+sex	-751.0	1	0.068
	~time+sex+weight	-751.0	1	0.945

logLik, log-likelihood estimates

Table 3 The effect of independent variables on production of young (0/1) and number of young (1-5) produced by the vole breeding pairs. GLMM analyses with different independent variables were compared using model averaging (Appendix 1). Statistically significant p (< 0.05) or marginally significant values (< 0.10) are bold. M-F – difference between male and female intercepts based on previous LMM analyses (Tab. 2)

Variable	**Estimate**	**SE**	**z**	**p**
Dependent young presence (0/1)				
Independent (Intercept)	-0.74	2.81	0.26	0.794
M-F distance total (m)	-0.15	0.06	2.30	**0.022**
M-F distance central (m)	0.98	1.14	0.84	0.401
M-F locomotion (s)	0.02	0.02	0.81	0.416
M-F scanning (s)	-0.03	0.04	0.59	0.558
M-F jumping (s)	0.02	0.03	0.63	0.526
M-F grooming (s)	0.00	0.01	0.19	0.846
Male body weight (g)	0.04	0.11	0.33	0.740
Female body weight (g)	-0.01	0.07	0.13	0.897
Body weight diff. m–f (g)	0.00	0.04	0.00	0.997
Female proestrus (0/1)	0.00	0.06	0.01	0.995
Female estrus (0/1)	0.00	0.05	0.01	0.995
Pairing round (1 and 2)	0.30	0.67	0.45	0.653
Dependent young number (1-5)				
Independent (Intercept)	2.92	0.67	4.23	0.000
M-F distance total (m)	-0.08	0.03	2.58	**0.010**
M-F distance central (m)	-0.08	0.54	0.14	0.892
M-F locomotion (s)	-0.02	0.01	1.86	0.062
M-F scanning (s)	0.00	0.02	0.06	0.953
M-F jumping (s)	-0.01	0.01	0.89	0.371
M-F grooming (s)	0.00	0.01	0.36	0.720
Male body weight (g)	0.05	0.07	0.73	0.465
Female body weight (g)	0.10	0.08	1.24	0.214
Body weight diff. m–f (g)	-0.08	0.09	0.82	0.410
Female estrus (0/1)	0.28	0.76	0.35	0.727
Female proestrus (0/1)	-0.33	0.73	0.42	0.672
Pairing round (1 and 2)	-0.21	0.41	0.49	0.627

Figure 2 Fertile vole pairs showed much lower difference between male and female LMM random intercepts, considered personality traits, than the pairs without offspring (Table 3, p = 0.022)

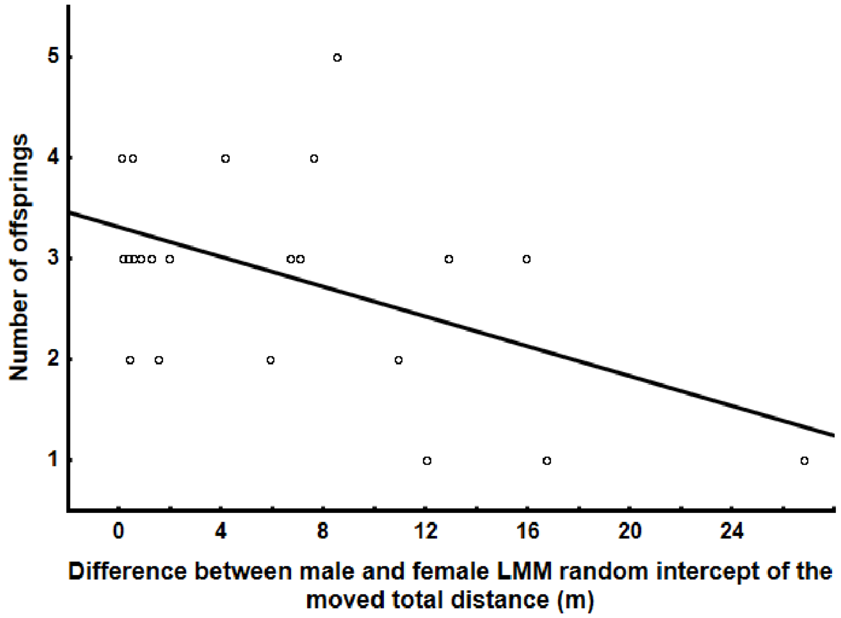

Figure 3 In vole pairs, the higher is the difference between male and female LMM random intercepts (considered personality trait) the lower number of offspring is produced (Table 3, p = 0.010)

Discussion

The study was inspired by the finding of the effect of behavioural similarity on the reproduction success of the mound-building mouse (Rangassamy et al. 2015). We found that in a solitary rodent, the common vole, the similarity of personality trait in parents has a positive effect on reproduction, i.e. the number of offspring.

The OF test

Our set of three OF tests showed that the behaviour of animals and test conditions correspond with previous results gathered by our laboratory (Lantová et al. 2011; Urbánková et al. 2020) as well as by other common vole study groups elsewhere (Eccard and Herde 2013; Gracceva et al. 2014; Herde and Eccard 2013). Similar results have also been described in other rodents (Eilam et al. 2003; Martin and Réale 2008; Vošlajerová et al. 2016; Žampachová et al. 2017). Voles were able to cover, more or less the similar distance (2-8 m/min), and the explorative behaviour dominated (locomotion, scanning, jumping). Low number of individuals manifested grooming behaviour considered rather anxiety indication of the need to care for fur. Similar results were also obtained by the seminal study of mound-building mouse (Rangassamy et al. 2015).

Presence of personality traits should be always considered when high repeatability is recorded. The values determined in our study were generally high, they ranged between $R_C = 0.55$ and 0.93. Therefore, it is possible to state, at least for total distance covered, the presence of a personality trait associated with this behaviour. On the contrary, the lowest repeatability was found for the covered distance in the central area. This parameter is always largely linked to the emotional state of the animal, which can vary from test to test (Eilam 2010). Wilson (2018) emphasized that the repeatability index R should be used in a defined context and with clear intention. In our study, repeatability was calculated according to Biro and Stamps (2015) as a consistency repeatability (R_C) for three tests. This type of repeatability respects individual trajectory, which is especially useful in the case of behavioural plasticity of personality traits. Among other factors, repeatability depends mainly on the intervals between tests (Bolivar et al. 2000; Bouton 2007) and those were relatively short (two weeks). Based on extensive literature review, Bell et al. (2009) calculated, according to Lessells and Boag (1987), the mean agreement repeatability of behavioural parameters (R_A= 0.37). However, it is a slightly different index, more sensitive to systematic shifts. Comparably higher values were found at the upper value ranges for agreement repeatability (R_A) in voles (0.25–0.63, Herde and Eccard 2013; Lantová et al. 2011) and for consistency repeatability (R_C) in the black rat (0.22–0.81, Žampachová et al. 2017). It should be emphasized that these comparisons between species must be treated cautiously, because the same repeatability can be achieved in samples with completely different population structures (Dochtermann and Royauté 2019).

Reproduction

Females in central Europe produce about four litters with 1 – 13 young during the year, with an average of 5.5 young (Reichstein 1957, 1960 ex Niethammer and Krapp 1982). Under laboratory conditions, the average value of the litter is 4.2 young. The decrease in value is explained by less suitable breeding conditions and embryonic mortality (Reichstein 1964 ex Niethammer and Krapp 1982). These authors calculated the mean value based on the number of young in litters of fertile females only. In our case, the mean value shifted to 1.3 offspring in all pairs, or 2.9 offspring in all fertile females. This shift could be caused just by our random pairing creating pairs with unsuitable differences in behavioural traits, rather than the effect of natural preference.

Similarity of behavioural traits supported reproduction also in the mound-building mouse (Rangassamy et al. 2015), a species living in monogamous couples, where the father helps in the upbringing of the offspring. In such a social system, it is quite understandable that similarity in behavioural manifestations is useful. In the common vole, males and females live in completely different social conditions. However, at the moment of a total population collapse (see e.g. Lambin et al. 2006), when several individuals remain per ha, induced ovulation would be very useful in a random contact of partners (Katandukila and Bennett 2016). Such a contact could be supported by a same character of (loco)motor activity of pairs driven by female preference (Larivière and Ferguson 2003; Jiang et al. 2013). Clulow and Mallory (1970) suggest that induced ovulation may be a general feature of the genus *Microtus*. Induced ovulation is probably quite widespread in mammals, for example in carnivores (Larivière and Ferguson 2003), but also in other mammals such as rabbits (Dutch-belted) (Staples 1967), alpacas (Fernandez-Baca et al. 1970) or sheeps (Perkins and Fitzgerald 1994). The direct mechanism can be different, but reproductive success often depends on behavioural motor activity.

Behavioural trait differences versus reproduction

In the above-mentioned monogamous mouse species (Rangassamy et al. 2015), the parental care is also connected with huge mound building (Poteaux et al. 2008; Tognetti et al. 2017). Therefore, no wonder that similarity in behavioural traits could be important for this building activity. In general, this social system is connected with an intensive care for the young. On the other hand, the number of young is rather smaller. Under such conditions, positive shift in reproduction is probably more difficult and is represented by the timing of reproduction. In this mouse species, pair similarity in the exploration / anxiety traits accelerated the onset and consequently also the total success of reproduction. Similar behavioural compatibility and reproductive success have been apparently found previously in the monogamous California hamster (*Peromyscus californicus*) (Gleason et al. 2012).

The importance of similarity in (loco)motor activity traits of partners for the success of reproduction has been documented also several times in some fish and bird species (see e.g. Ihle et al. 2015; Laubu et al. 2016, 2017). Attention has been often focused on the influence of a personality trait closely associated with exploration, as was found in the great tit (Dingemanse et al. 2004). Great tits were more successful in reproduction (their offspring were in better condition) if both individuals in the parent pairs were marked as "slow". If both individuals were considered "fast", they were more successful in defending their territory and thus actually food sources (Both et al. 2005). Chira (2014) does not deny the influence of personality traits, but noted that it is not clear how or why personality traits affect individual fitness.

Assortative mating seems to favour interplay and parental reliability in the case of monogamy. However, its function in the case of a promiscuous or polygynous system is not so clear. It may be a short-term calming or tuning of the partner before mating and copulation (i.e. proximate causation, Réale et al. 2009). Phenotype-genotype pair similarity could cause also reduced fluctuating asymmetry in developing offspring (i.e. ultimate causation). However, studies on the population genetics of promiscuous small terrestrial mammals (mice, minks) has not yet yielded such evidence (Gockel and Ruf 2001). It should be noted that similarity in some behavioural parameters or personality traits does not automatically mean reduction of genetic variability, but in some traits only. It is more important that an individual's decision to mate with a behaviourally similar individual leads to exercising of his or her genes to the next generation, regardless of whether they came from themselves or their partners (Thiessen et al. 1997). A convergent approximation of the personality traits of one parent to another was also noted. This means that the manifestations of personality traits become more similar only after individuals come together (Laubu et al. 2016, 2017). This plasticity shows how important is the behavioural compatibility of the parental pairs as confirmed by our results.

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Appendix 1 The results of averaging models for presence of young (no/yes, 0/1) and number of young (1-5) with different combinations of independent variables based on AIC values. Legend to numbering of independent variables: 1 – Difference between male and female LMM random intercept of distance moved on the central area (m); 2 – Difference of male and female body weight (g); 3 – Difference between male and female LMM random intercept of the moved total distance (m); 4 – Female estrus (0/1); 5 – Female body weight (g); 6 – Difference between male and female LMM random intercept of the grooming duration (s); 7 – Difference between male and female LMM random intercept of the jumping duration (s); 8 – Difference between male and female LMM random intercept of locomotion duration (s); 9 – Male body weight (g); 10 – Female proestrus (0/1); 11 - Pairing round (1-2); 12 – Difference between male and female LMM random intercept of scanning (s)

Dependent variable young presence (0/1)	**df**	**logLik**	**AICc**	**Delta**	**Weight**
Model					
3	4	-32.63	74.03	0.00	0.23
1/3	5	-31.76	74.70	0.67	0.16
1/3/6/7/8/12	9	-26.74	75.31	1.28	0.12
1/3/6/7/8	8	-28.30	75.59	1.56	0.10
1/3/6/7/8/9/11/12	11	-23.88	75.63	1.59	0.10
1/3/6/7/8/11/12	10	-25.45	75.69	1.65	0.10
1/3/6/8	7	-29.96	76.20	2.17	0.08
1/3/6	6	-31.50	76.67	2.64	0.06
1/3/5/6/7/8/9/11/12	12	-23.39	77.86	3.83	0.03
1/2/3/5/6/7/8/9/11/12	13	-23.39	81.24	7.20	0.01
8	4	-37.72	84.21	10.18	0.00
7	4	-37.87	84.51	10.48	0.00
1/2/3/5/6/7/8/9/10/11/12	14	-23.27	84.54	10.50	0.00
Null	3	-39.08	84.61	10.57	0.00
9	4	-38.07	84.90	10.86	0.00
11	4	-38.41	85.59	11.56	0.00
12	4	-38.42	85.61	11.57	0.00

6	4	-38.82	86.42	12.38	0.00
2	4	-38.83	86.42	12.39	0.00
5	4	-38.96	86.70	12.66	0.00
10	4	-39.03	86.83	12.79	0.00
4	4	-39.05	86.86	12.83	0.00
1	4	-39.07	86.91	12.88	0.00
1/2/3/4/5/6/7/8/9/10/11/12	15	-23.12	87.95	13.91	0.00
4/10	5	-39.02	89.23	15.19	0.00
2/4/10	6	-38.81	91.30	17.27	0.00
2/4/5/9/10	8	-37.27	93.54	19.51	0.00
2/4/5/10	7	-38.80	93.89	19.85	0.00
2/4/5/9/10/11	9	-36.22	94.27	20.24	0.00
2/4/5/9/10/11/12	10	-35.44	95.66	21.63	0.00
2/4/5/7/8/9/10/11/12	12	-32.32	95.73	21.69	0.00
2/4/5/7/9/10/11/12	11	-34.89	97.65	23.61	0.00
2/4/5/6/7/8/9/10/11/12	13	-32.30	99.06	25.02	0.00
1/2/4/5/6/7/8/9/10/11/12	14	-32.13	102.25	28.22	0.00

Dependent variable Number of young (1-5)	**df**	**logLik**	**AICc**	**Delta**	**Weight**
Model					
3	4	-35.98	81.96	0.00	0.32
Null	5	-35.27	83.71	1.75	0.13
4	5	-35.53	84.21	2.25	0.10
10	5	-35.55	84.26	2.30	0.10
1	5	-35.69	84.54	2.58	0.09
11	5	-35.81	84.78	2.83	0.08
4/10	6	-34.52	85.72	3.76	0.05
1/3	6	-34.94	86.56	4.60	0.03
5	5	-36.73	86.62	4.66	0.03
2	5	-37.18	87.52	5.56	0.02
9	5	-37.45	88.07	6.11	0.02
8	5	-37.99	89.13	7.17	0.01
12	5	-38.94	91.04	9.08	0.00
2/4/10	7	-35.37	91.33	9.37	0.00
7	5	-39.27	91.69	9.73	0.00
6	5	-39.94	93.04	11.08	0.00
2/4/5/10	8	-36.29	97.59	15.63	0.00

1/3/6	7	-38.99	98.58	16.62	0.00
2/4/5/9/10	9	-36.13	102.25	20.29	0.00
1/3/6/8	8	-39.99	104.99	23.03	0.00
2/4/5/9/10/11	10	-35.89	107.49	25.53	0.00
1/3/6/7/8	9	-43.07	116.15	34.19	0.00
2/4/5/9/10/11/12	11	-38.67	119.65	37.69	0.00
1/3/6/7/8/12	10	-46.14	127.99	46.03	0.00
1/3/6/7/8/11/12	11	-45.83	133.97	52.01	0.00
2/4/5/7/8/9/10/11/12	13	-42.39	143.87	61.91	0.00
1/3/6/7/8/9/11/12	12	-47.34	144.68	62.72	0.00
1/3/5/6/7/8/9/11/12	13	-48.15	155.39	73.43	0.00
2/4/5/6/7/8/9/10/11/12	14	-45.69	161.38	79.42	0.00
1/2/3/5/6/7/8/9/11/12	14	-47.83	165.65	83.69	0.00
1/2/4/5/6/7/8/9/10/11/12	15	-45.23	173.78	91.82	0.00
1/2/3/5/6/7/8/9/10/11/12	15	-46.87	177.08	95.12	0.00
1/2/3/4/5/6/7/8/9/10/11/12	16	-45.52	191.05	109.09	0.00

Curriculum vitae

Curriculum vitae k 20. 7. 2021

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2007-2011: Bc. studium na Přírodovědecké fakultě Jihočeské univerzity, obor Biologie (Téma: Jsou živochytné pasti selektivní pro norníky rudé (*Myodes glareolus*) lišící se v reakcích na signály ohrožení?)

2003-2007: Gymnázium Třeboň

Publikace:

Urbánková G, Riegert J, Mladěnková N, Dikošová T, Janochová L, Sedláček F (submitted) Similar behavioural traits in the common vole pairs enhance offspring production.

Urbánková G, Riegert J, Mladěnková N, Kolářová P, Eliáš Z, Sedláček F (2021) Behavioural plasticity of personality traits of the common vole under three-day continual observation in a test box. Behavioural Processes, 188, 104418. https://doi.org/10.1016/j.beproc.2021.104418; *IF2020: 1,777; Q2.*

Urbánková G, Šíchová K, Riegert J, Horsley R, Mladěnková N, Starck-Lantová P, Sedláček F (2020) Lifetime plasticity of personality traits in the common vole (*Microtus arvalis*) under laboratory conditions. Ethology, 126, 812-823. https://doi.org/10.1111/eth.13039; *IF2020: 1,897; Q2.*

Vybrané mezinárodní konference (postery; *prezentující):

Sedláček F*, Eliáš Z, Kolářová P, Mladěnková N, **Urbánková G** (2018) Low correlation between parameters from different behavioral tests in the common vole. 6th International Conference of Rodent Biology and Management & 16th Rodens et Spatium, Sep 3-7, 2018 Potsdam, Germany, p. 197; poster.

Sedláček F*, Janochová L, Mladěnková N, Šíchová K, **Urbánková G** (2018) Relationship of breathing frequency to the personality trait in the common vole (*Microtus arvalis*). 6th International Conference of Rodent Biology and Management & 16th Rodens et Spatium, Sep 3-7, 2018 Potsdam, Germany, p. 198; poster.

Sedláček F*, Mladěnková N, Šíchová K, **Urbánková G** (2016) On the determination of personality traits in the common vole. In: Abstracts of 15th Int. Conf. Rodens et Spatium, Jul 25–29, 2016, Olomouc, Czech Republic, p. 93; oral presentation.

Urbánková G*, Mladěnková N, Sedláček F (2014): The relationship between daily activity and behavioural display in open field test and elevated plus maze in common voles (*Microtus arvalis*). In:

Abstracts of 14th Int. Conf. Rodens et Spatium, Jul 28–Aug 2, 2014, Lisbon, Portugal, p. 7; poster.

Urbánková G*, Šíchová K, Mladěnková N, Sedláček F (2013): Does the travelled distance in Open field test provide reliable information about personality traits in common vole? In: Abstracts of 33rd International Ethological Conference, Behaviour 2013, Aug 4–8, 2013, Newcastle, Gateshead, UK, p. 215; poster.

Vybrané tuzemské konference (přednášky a postery; *prezentující):

Janochová L, Dikošová T, Mladěnková N, **Urbánková G***, Sedláček F (2019) U hraboše polního s jeho chováním korelovaly změny stresových parametrů a nikoliv jejich absolutní hodnoty. In: Sborník abstraktů z konference Zoologické dny, 7.-8. února 2019, Brno, str. 86; poster.

Urbánková G*, Eliáš Z, Kolářová P, Mladěnková N, Sedláček F (2018) Na hraboše polního působí behaviorální testy komplexně, aneb není běh jako běh a skok jako skok. In: Sborník abstraktů z konference Zoologické dny, 8.-9. února 2018, Praha, str. 224-225; poster.

Dikošová T, **Urbánková G***, Janochová L, Mladěnková N, Sedláček F (2017) Handling u dospělých hrabošů nezměnil výsledky behaviorálních testů. In: Sborník abstraktů z konference Zoologické dny, 9.-10. února 2017, Brno, str. 42-43; poster.

Janochová L*, Šíchová K, **Urbánková G**, Mladěnková N, Sedláček F (2015) Vztah dechové frekvence k osobnostním rysům u hraboše polního (*Microtus arvalis*). In: Sborník abstraktů z 42. etologické konference, 4.-7. listopadu 2015, České Budějovice, str. 70; poster.

Janochová L, Šíchová K, **Urbánková G***, Mladěnková N, Sedláček F (2015) Vztah dechové frekvence k osobnostním rysům chování u hraboše polního (*Microtus arvalis*). In: Sborník abstraktů z konference Zoologické dny, 12.-13. února 2015, Brno, str. 101; poster.

Schmidtmajerová E, Šíchová K, **Urbánková G***, Mladěnková N, Sedláček F (2015) Rychlost postnatálního růstu u hraboše polního neovlivňuje osobnostní rysy chování. In: Sborník abstraktů z konference Zoologické dny, 12.-13. února 2015, Brno, str. 221-222; poster.

Sedláček F*, Elexhauserová A, Mladěnková N, Šíchová K, **Urbánková G** (2014) Opakovatelnost chování u hrabošů. In: Sborník abstraktů z konference Zoologické dny, 6.-7. února 2014, Brno, str. 175-176; přednáška.

Urbánková G*, Mladěnková N, Šíchová K, Sedláček F (2014) Informace o chování zvířete v OFT – stačí pouze měření ušlé vzdálenosti? In: Sborník abstraktů z konference Zoologické dny, 6.-7. února 2014, Ostrava, str. 212; poster.

Školitelství:

Boříková A, Vývoj motorických schopností hraboše polního, Bc. práce, zadáno 2015 – školitel specialista

Dikošová T, Vliv handlingu na osobnostní rysy hraboše polního (*Microtus arvalis*), Mgr. práce, zadáno 2013, obhájeno 2017 – školitel specialista

Eliáš Z., Osobnostní rysy hraboše polního (*Microtus arvalis*): Chování ve vyvýšeném labyrintu. Bc. práce, zadáno 2014, obhájeno 2015 – školitel specialista

Kolářová P, Koreluje denní aktivita ve známém prostředí s aktivitou v experimentálních aparaturách? Bc. práce, zadáno 2013, obhájeno 2015 – školitel specialista

Martínková M, Vliv postnatálního prostředí na motorické schopnosti hraboše polního (*Microtus arvalis*), Bc. práce, zadáno 2015 – školitel specialista

Pracovní zkušenosti:

Vědecko-pedagogický asistent na PřF JU od 2016 do 2019

Veterinární asistent a practice manager, BUDvet s.r.o, 2019- dosud

Účast na organizaci tuzemských konferencí: konference České a Slovenské etologické společnosti 2015, Zoologické dny 2016

Pedagogické zkušenosti:

FBI 002 Terénní praktická cvičení - zimní semestr 2013/2014, 2014/2015, 2015/2016

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