Behavioural Processes 157 (2018) 133–141

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Behavioural strategies of three wild-derived populations of the house mouse (*Mus m. musculus* and *M. m. domesticus*) in five standard tests of exploration and boldness: Searching for differences attributable to subspecies and commensalism

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ARTICLE INFO

Keywords:
Boldness
Exploration
House mouse
Synanthropic

ABSTRACT

Animal populations adopting a commensal way of life, e. g. house mice in buildings and stores, are subject to different selection pressures than those living in a non-commensal environment. This may radically influence their behaviour. This study investigated the effects of a commensal way of life on exploratory behaviour in mice. The focal population was non-commensal *Mus musculus musculus* from Northern Iran. To assess the effect of commensal way of life on exploratory behaviour, it was compared with commensal *M. m. musculus* from the Czech Republic and to assess the effect of subspecies, it was compared to non-commensal *M. m. domesticus* from Eastern Syria.

We compared their behaviour in five tests of exploratory behaviour and boldness: an open field test with 1) free exploration and 2) forced exploration, 3) hole-board test, 4) test of vertical activity and 5) elevated plus maze. We detected a significant effect of population on behaviour in all five tests. *M. m. domesticus* was generally bolder and more active than *M. m. musculus*. Commensal mice were characterized by a higher level of vertical activity (climbing, rearing, jumping). These results suggest that the specific selection pressures of the commensal lifestyle select mice for higher affinity towards elevated places.

1. Introduction

The house mouse is currently a cosmopolitan rodent inhabiting various habitats and represents the third most important vertebrate pest (Capizzi et al., 2014). Moreover, a laboratory mouse is a prominent model species in experimental research. Despite general importance of the house mouse species for humans, only limited attention has been devoted to its wild populations so far (but see e.g. Macholán et al., 2012a,b). Such disproportion especially concerns mice populations adopting a non-commensal way of life, i.e. those inhabiting steppes and fields outside buildings and stores. Comparative studies are more focused on comparing subspecies and seldom consider the effect of commensal (or synanthropic) lifestyle (Frynta et al., 2005; Ganem, 1991). In this study, we aim to compare behaviour in tests of exploratory behaviour and boldness in three populations of *Mus musculus*. Our focal population is non-commensal *Mus musculus musculus* from Northern Iran and we compare it to *M. m. domesticus* from Eastern Syria and to commensal *M. m. musculus* from the Czech Republic.

The genus *Mus* originating in Asia started its radiation approximately 7.8 Mya (Chevret et al., 2005). Recent species *Mus musculus* sensu lato probably emerged from the north of the Indian subcontinent, where it appeared about 0.5 Mya (Boursot et al., 1993; Geraldes et al., 2008; Karn et al., 2002). It has been hypothesized that mice colonized Europe through at least two different routes: *M. m. musculus* followed the route leading north of the Black Sea, while *M. m. domesticus* came into the Mediterranean basin across Asia Minor (Boursot et al., 1993; Macholán et al., 2012a,b; Rajabi-Maham et al., 2008; Sage et al., 1993). During secondary contact in the Holocene (Macholán et al., 2007) these

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https://doi.org/10.1016/j.beproc.2018.09.008
Received 23 July 2018; Received in revised form 18 September 2018; Accepted 21 September 2018
Available online 26 September 2018
0376-6357/

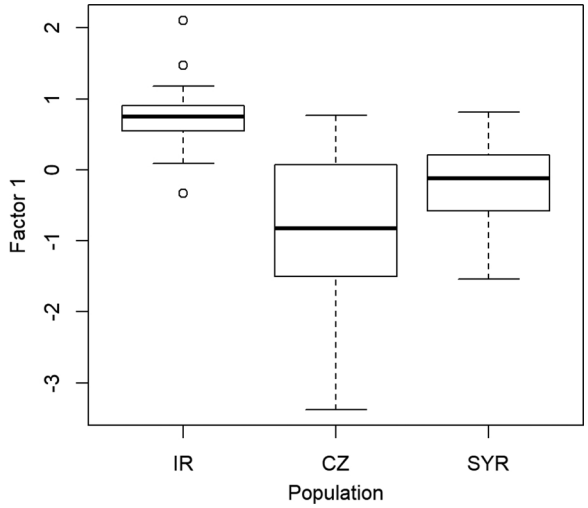

Fig. 1. Factor scores of Factor 1, interpreted as exploratory behaviour, derived from the overall factor analysis – comparison of three different populations. **IR** = non-commensal *M. m. musculus* (Now Kandeh population), **CZ** = commensal *M. m. musculus* (Prague population), **SYR** = non-commensal *M. m. domesticus* (Halabiyah population). For the p-values of the post-hoc comparison see Table 2.

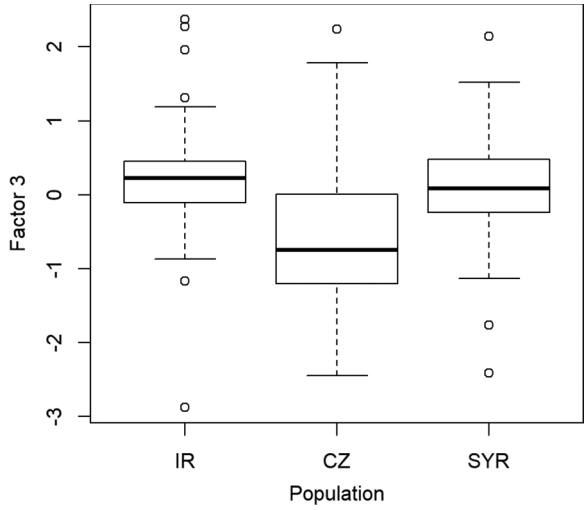

Fig. 2. Factor scores of Factor 3, interpreted as vertical activity, derived from the overall factor analysis – comparison of three different populations. **IR** = non-commensal *M. m. musculus* (Now Kandeh population), **CZ** = commensal *M. m. musculus* (Prague population), **SYR** = non-commensal *M. m. domesticus* (Halabiyah population). For the p-values of the post-hoc comparison see Table 2. Note that the willingnes to climb is correlated negatively with this factor, therefore the population with the lowest factor scores is in fact climbing the most.

two subspecies formed a narrow hybrid zone through the central Europe (Boursot et al., 1993; Duvaux et al., 2011; Macholán et al., 2012a,b). In the house mouse (*Mus musculus* sensu lato), one of the important differences between populations is whether they live in a commensal environment. The commensal house mouse has probably originated in West-central Asia (Iran, Iraq, Pakistan) (Prager et al., 1998) or in North India (Berry and Scriven, 2005). Around 10,000 BC (Cucchi and Vigne, 2006) the house mouse in the Near East (the Fertile Crescent region) lived as a cohabitant in human dwellings (Auffray et al., 1990; Cucchi et al., 2005; Prager et al., 1998; Rajabi-Maham et al., 2008). Although diffusion of mice inside this region was fast, the colonization of the rest of the Mediterranean area occurred later: the Eastern Mediterranean was not colonised before first millennium BC (Cucchi and Vigne, 2006), when the mice most likely came with Neolithic people (Cucchi et al., 2005). After reaching this eastern part, the mice invaded the Western Mediterranean rapidly, within next few centuries (Cucchi and Vigne, 2006) (Figs. 1 and 2).

The commensal environment presents different challenges for rodents. It offers more food, is more complex, but also poses different dangers, such as traps, poisoned baits or different predators (Pocock et al., 2005, 2004; Redhead, 1982; Singleton and Redhead, 1990). These conditions provide selective pressures different from non-commensal habitats (Pocock et al., 2004; Žampachová et al., 2017). Conditions in commensal habitats favour a high rate of reproduction, a high population turnover and lower rates of dispersal in comparison with non-commensal environment (Pocock et al., 2004). Previous research showed that commensal mice (living in relatively stable habitats) have very small home ranges with abundant food (Bronson, 1979; Brown, 1953; Hurst, 1987; Pocock et al., 2004). Commensal house mice are usually less aggressive than their non-commensal conspecifics as well as related non-commensal mice species (Frynta et al., 2005; Simeonovska, 1994; Suchomelová et al., 1998). The pattern of their exploratory behaviour is also different (Frynta, 1994; Kotenkova et al., 1994; Meshkova et al., 1999): under experimental conditions, the commensal mice leave their shelter quickly and explore both the horizontal and vertical plane of an unfamiliar territory. The non-commensal mice leave the shelter less willingly, often return inside and investigate only the horizontal level of the experimental area (Kotenkova et al., 1994, 2003).

Exploratory behaviour is one of the most studied aspects of animal behaviour (Fonio et al., 2009; Renner, 1990), especially in relation to animal personality (Careau and Garland, 2012; Lantová et al., 2011; Réale et al., 2010, 2007; Šíchová et al., 2014). The most common method of testing exploratory behaviour is a novel environment test, such as the open field test (Hall, 1934) or hole-board test (Boissier and Simon, 1962), others include tests of neophobia, for example the novel object test (Cowan, 1976; Ennaceur and Delacour, 1988; Hughes, 2007; Powell et al., 2004).

In the classic open field test, originally designed for rats, the animal is put in an unknown environment without any additional stimuli and the variables measured usually include the distance covered by the animal, the number of rears, and the number of fecal boli produced during the test (Hall, 1934). The basic paradigm is sometimes referred to as 'forced exploration', because the animal is not provided with any shelter or place to hide. Therefore, it is difficult to distinguish between true (intrinsic) exploration, which is motivated purely by the animal's curiosity (Berlyne, 1966; Hughes, 1997), and stress reactions, e.g. attempts to escape the arena (Renner, 1990). One solution to this problem is the so-called 'free exploration' (Fonio et al., 2009; Griebel et al., 1993; Hughes, 1997), when the animal is placed in an open field in some sort of a shelter and can choose whether at all and when it will emerge from this shelter and start exploring. Another variation of the open field test is the hole-board test (Boissier and Simon, 1962), which is forced exploration in an arena with holes in the floor that provides additional opportunities for exploratory behaviour. However, all these tests measure only exploration of the horizontal surface and do not consider the willingness to explore vertical surfaces as well, even though the ability to climb and utilize vertical spaces can be a key factor for mamals when avoiding competition (Buesching et al., 2008; Jones and Barmuta, 2000; King et al., 2011). Alternatively, absent fear of heights can serve as a measure of boldness, which can interfere with the measures of exploration (Réale et al., 2007; Rodgers and Dalvi, 1997; Žampachová et al., 2017). A traditional test for measuring boldness is the elevated plus maze or EPM (Carobrez and Bertoglio, 2005; Lister, 1987; Pellow et al., 1985). In this test, the animal is placed on an elevated platform in the shape of a plus, where two of the arms are 'closed' (they have walls providing shelter) and two are 'open' (they consist solely of a rather narrow walkway without any walls). The animal is considered bold when it spends a relatively long amount of time