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Is water really a barrier for the house mouse? A comparative study of two mouse subspecies

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Abstract. House mice are believed to be, unlike rats, only reluctant swimmers. If water is a barrier to mouse dispersal water bodies and streams can have a substantial impact on the genetic structure of populations. Previous studies revealed influence of rivers on the position and structure of the European hybrid zone between two house mouse subspecies, *Mus musculus musculus* and *M. m. domesticus*. In this study, we used a simple motivation experiment to test the disposition of both wild and inbred mice representing the subspecies to overcome a water barrier. As the more dispersing sex, males were chosen for the experiment. Mice were tested under two air/water temperature regimes, 20 °C and 10 °C. Contrary to a common belief tested animals entered water rather easily, often even engaging in repeated swimming. We found significant differences in scored behavioural parameters between the subspecies. Under the 20 °C regime, both wild and inbred *domesticus* males entered and crossed the water earlier and more often swam even when satiated. Strikingly, under the 10 °C regime, the results were rather equivocal but with the opposite tendencies, with *musculus* males being more willing to swim. We discuss implications of these findings for the hybrid zone dynamics.

Key words: dispersal, *Mus musculus domesticus*, *M. m. musculus*, swimming, water barrier

Introduction

Hybrid zones are often viewed as natural laboratories where various questions of speciation can be studied. However, natural experiments in these "labs" are not carried out in a controlled uniform environment. This holds especially for commensal species such as the house mouse (*Mus musculus*) which is, at least in central Europe, confined to buildings during winter, making its distribution rather patchy on a local scale. Moreover, mouse populations are usually structured into small and relatively closed demes with a single dominant male siring most of its offspring (Crowcroft 1955, Reimer & Petras 1967, Bronson 1979, Drickamer et al. 2000, Dean et al. 2006). The demes are strongly defended, which further reduces gene flow between them, though a deme's lifespan is rather short (Hauffe et al. 2000, Pocock et al. 2005).

It has been shown (Barton & Hewitt 1985, Raufaste et al. 2005, Macholán et al. 2007, Baird & Macholán 2012) that the zone of secondary contact between two house mouse subspecies, *M. m. musculus* Linnaeus, 1758, and *M. m. domesticus* Schwarz & Schwarz, 1943, is a tension zone (Key 1968). This type of hybrid zone is maintained by a balance between dispersal of genetically pure individuals into the centre and endogenous selection against admixture. Due to differential migration a tension zone will move so that to minimize its length. For the same reason, it will tend to move across landscape till it stops at a population density trough or a geographic barrier (Barton 1979, Barton & Gale 1993). The same effect will push clines for individual traits towards each other (Barton

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& Bengtsson 1986) – the greater the selection against hybrids, the larger this tendency. Hence the position of clines maintained even by entirely endogenous selection will tend to correlate with environmental features reducing density or dispersal.

In temperate areas, house mice can move between adjacent farms during spring and summer. This movement is likely to be more intense through suitable corridors while being strongly hampered by unsuitable habitats, e.g. large forests (Zejda 1975). In addition, house mice as small and warm-blooded animals may avoid crossing water, a good conductor of heat. It has been suggested that contrary to rats, known to be strong swimmers, mice enter water only reluctantly or not at all. Several types of behavioural experiments such as Morris water maze test (Morris 1981, 1984) or the forced swimming test, using mostly laboratory mice, have worked on this assumption, to test diverse hypotheses concerning stress, learning, memory, orientation and other parameters (Francis et al. 1995, Wolfer et al. 1998, D'Hooge & De Deyn 2001, Petit-Demouliere et al. 2005). Similar results have been revealed in wild mice living in semi-natural enclosures (Gerlach 1990, 1996, 1998, Nelson 2002). Moreover, some studies reported changes in levels of blood hormones and neurotransmitters indicating extreme stress (Francis et al. 1995).

If water is a barrier to mouse dispersal then rivers will not only affect the centre of the hybrid zone. For example, presence of rivers and a water reservoir (along with forests and steep slopes) was shown to narrow the zone in comparison with areas without these geographic barriers in the Czech Republic (Baird & Macholán 2012). Moreover, studies of mouse genetic variation across the central European and Danish portions of the zone revealed a rather complex structure on a fine scale caused by even small water courses (Baird & Macholán, unpublished results). Rivers can thus have important effects on both the position and the internal structure of the house mouse hybrid zone (the same holding also for areas well outside the zone). However, besides environmental factors the zone can be affected by differences in biology between the subspecies. For example, both males and females of *M. m. domesticus* are more aggressive than males and females of *M. m. musculus* (Thuesen 1977, van Zegeren & van Oortmerssen 1981, Munclinger & Frynta 2000, Frynta et al. 2005). The two subspecies were also shown to differ in their exploration strategies (Hiadlovská et al. 2012). Obviously, if water barriers impact on the structure of mouse populations within the zone its dynamics can be influenced by potential differences in the ability to overcome these barriers. Indeed, using a modified water-escape test (Essman & Jarvik 1961), Brubaker (1970) suggested that *M. m. domesticus* is a better swimmer than *M. m. musculus*.

In this study, we used a simple experimental setup to test the disposition of both wild and inbred house mice representing the two subspecies to overcome a small water barrier. We found that contrary to a common belief house mice enter water easily, often even engaging in repeated and voluntary swimming. In addition, we show differences in scored behavioural parameters between the subspecies and discuss their implications for the hybrid zone dynamics.



Fig. 1. *The course of the* M. m. musculus – M. m. domesticus *hybrid zone in central Europe. Localities at which founding pairs of inbred strains used in this study have been trapped are indicated. Below are sampling sites of wild* M. m. domesticus and M. m. musculus *(see Table 1 and text for more details). The dashed line in the bottom panel indicates the approximate course of the zone defined in Macholán et al. (2007).*

Material and Methods

Tested animals

For the experiments described below both inbred and wild house mice representing the two subspecies were used. The group of inbred mice comprised three

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Table 1. *The origin of wild mice founder pairs with geographic coordinates of the localities sampled and the number of captive-born individuals – G1 males used in this study.*

	M. m. domesticus			*M. m. musculus*	
Locality	Coordinates	***N***	Locality	Coordinates	***N***
Ottmannsreuth	49° 53′ N, 11° 37′ E	2	Krasíkov	49° 53′ N, 12° 56′ E	3
Röthelbach	49° 59′ N, 11° 35′ E	4	Přílezy	50° 06′ N, 12° 57′ E	1
Unterweissenbach	50° 09′ N, 12° 06′ E	4	Vrbička	50° 11′ N, 13° 18′ E	4
Weickenreuth E	50° 10′ N, 11° 40′	1	Žihle	50° 03′ N, 13° 22′ E	3

strains derived from *M. m. musculus* (BUSNA, STUF, PWD) and two of the *M. m. domesticus* origin (STRA, Schweben). Details on the strains STRA, BUSNA, and STUF are given in Piálek et al. (2008), whereas the PWD strain is described in Gregorová & Forejt (2000). The "Schweben" group is a lineage established with a pair captured in Schweben, western Germany, and kept in the Institute of Vertebrate Biology in Studenec. The tested individuals represented the 8th and 9th generation of brother-sister mating (thus, strictly speaking, these mice were not fully inbred even though this lineage is denoted as "inbred" for simplicity in this study). Most of these strains have been proven as suitable surrogates of the two subspecies in various behavioural studies (Piálek et al. 2008, Bímová et al. 2009, Ďureje et al. 2010, Vošlajerová Bímová et al. 2011, Hiadlovská et al. 2012). Obviously, inbred lineages cannot encompass the whole genetic variation present in natural populations. Therefore, we carried out the same experiments also with wild mice. To avoid undesirable effects of different age, diet, health condition, and previous experiences of wild-captured animals, we used mice of the first generation born in captivity (see below).

Wild mice were live-trapped using wooden traps at localities outside the central European portion of the hybrid zone, four sites on the *M. m. musculus* side and four on the *M. m. domesticus* side (Fig. 1), during September and October 2010. Details on the sampling sites and numbers of tested individuals are given in Table 1. After transport to a breeding facility of the Institute of Vertebrate Biology, male-female pairs of individuals trapped at the same sites were put together. The first-generation mice resulting from their mating were used for experiments. These mice, here designated G1 *musculus* and G1 *domesticus*, keep the same variability as wild-caught individuals but can be standardized with regard to age, living conditions or life experience (Garland & Stephen 1991, Clément et al. 2002, Bímová et al. 2005). Only males were tested as they are predominant among dispersing animals (van Zegeren 1980).

All mice were kept in polycarbonate (PC) cages (16 × 28 × 15 cm) under the light: dark regime 14:10 (light starting at 06:00 a. m.) and temperature 20 °C. Pelleted food (ST1, VELAZ, Prague, Czech Republic) and water were provided *ad libitum*. Sawdust bedding and nesting material (shredded papers) were changed every fifth day. Males were weaned at the age of 20 days and isolated at 55 days. Each male was tested under two different temperature regimes (i.e. same individuals have been tested two times – see below). The first experimental trial was carried out at the age of 90-139 days in G1 males and 90-117 days in inbreds, the second between 133 and 161 days in G1's and between 104 and 154 days in inbreds, respectively.

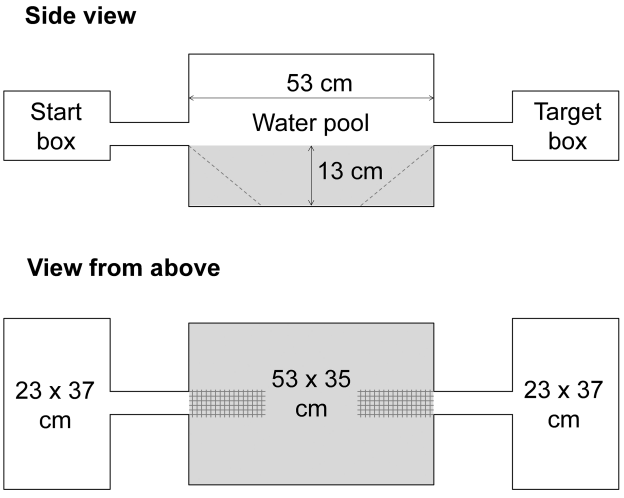


Fig. 2. *The experimental setup, consisting of a start and target boxes connected with a water pool. Food and water is available in the target box but not in the start box during experiments while bedding material is provided in both cages.*

Experimental design

To test the motivation and swimming ability we used food deprivation of tested mice. The experimental setup (Fig. 2) comprised the starting and target boxes (PC cages covered with a glass pane, 23 × 28 × 15 cm) with a swimming pool in between. The pool (transparent plastic box covered with a glass pane, 53 × 35 × 33 cm) was filled with water (13 cm deep). The cages were connected to the pool with Perspex

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tubes (17 cm long, 5 cm in diameter) with a sliding door on the starting box side. The tubes opened into the pool at the water level. Strips of wire mesh were placed in the swimming pool from the openings to the bottom to facilitate animals entering/getting out from the water. Both starting and target box were provided with bedding and nesting material.

At 18:00, a tested mouse was put to the starting box with the sliding door closed. Nesting material was transported to the box with the animal to reduce stress. During a habituation period, food and water were available *ad libitum*. After 26 h food and water were removed and the box was connected to the swimming pool. A 12 h trial period started with opening the sliding door at 20:00 and finished at 08:00 next morning. By removing food mice were moderately motivated to cross the water barrier. After the experiment, mice were put back to their home cages.

Trials were video recorded with infra-red camera and swimming episodes were then digitized and processed using the MTS program (Modular Tracking Software; custom designed and provided by M. Kučera). The following parameters were measured:

Latency to swim – time from the beginning of the trial to the first swimming episode; if there was no swimming, animal was scored with 12 h penalty;

Latency to cross – time from the beginning of the trial to the first successful crossing of the pool; if there was no cross, animal was scored with 12 h penalty;

Voluntary swim – presence/absence of swimming episodes occurring after the first successful crossing the pool (note: as we do not know what actually motivates a mouse to enter the water pool we cannot rule out a possibility that also the first overcoming the barrier was voluntary or that also repeated entering the water is motivated by hunger; "voluntary swim" is thus just a technical term describing the given type of behaviour);

Path – total length of swimming path a mouse covered during a single trial.

Mouse movements increase during summer when the first generation born in the respective year is weaned and especially in the beginning of autumn (Walkowa et al. 1989) when the population peaks (Brown 1953). The mouse, as a small mammal with a relatively large body surface, loses heat rapidly (Feldhamer et al. 2007) and this loss is especially grave in cold water. However, negative effects of loss of insulation and resulting increased physiological demands continue even after the mouse gets out from the water, when it needs to dry itself quickly. Hence water is likely to be a stronger barrier during autumn when ambient temperature drops. Therefore, we used two water/air temperature regimes in the present study, 20 °C (common laboratory temperature, approximating summer conditions), and 10 °C, the average October temperature of rivers in the area under study (data Czech Hydrometeorological Institute). The latter experimental design was used to simulate more natural conditions occurring in the area where the parents of the G1 mice were trapped. At least two weeks were left between subsequent tests. A potential effect of the order of temperature regimes was tested so that for each inbred strain five randomly chosen individuals started in 10 °C and another five randomly chosen mice started in 20 °C. Since repeated measures ANOVA revealed no significant effect of the order of trials on the scored behavioural parameters all other

Table 2. *Results of statistical tests for inbred mice under the 20 °C regime.* Z *and* H *are the Mann-Whitney* U *test and Kruskal-Wallis ANOVA statistics, respectively;* χ^2*: Pearson's chi-squared test. Fisher's exact test was used for voluntary swim in comparisons between two* domesticus *strains and between pooled* musculus *and* domesticus *groups.*

Variable	*domesticus*-derived strains	*musculus*-derived strains	pooled *domesticus* vs. *musculus* groups
Latency to swim	$Z = -0.076$	$H_{(2, n=30)} = 4.286$	$Z = 3.664$
	$P > 0.05$	$P > 0.05$	$P = 0.000$
	$N_{STRA} = 10$, $N_{Schweben} = 10$	$N_{STUF} = 10$, $N_{PWD} = 10$, $N_{BUSNA} = 10$	$N_D = 20$, $N_M = 30$
Latency to cross	$Z = 0.567$	$H_{(2, n=30)} = 1.962$	$Z = 2.990$
	$P > 0.05$	$P > 0.05$	$P = 0.003$
	$N_{STRA} = 10$, $N_{Schweben} = 10$	$N_{STUF} = 10$, $N_{PWD} = 10$, $N_{BUSNA} = 10$	$N_D = 20$, $N_M = 30$
Voluntary swim		$\chi^2 = 3.536$	-
	$P = 0.029$	$P > 0.05$	-
	$N_{STRA} = 9$, $N_{Schweben} = 9$	$N_{STUF} = 10$, $N_{PWD} = 8$, $N_{BUSNA} = 7$	-
Path	$Z = 1.715$	$H_{(2, n=24)} = 4.628$	$Z = 0.980$
	$P > 0.05$	$P > 0.05$	$P > 0.05$
	$N_{STRA} = 9$, $N_{Schweben} = 10$	$N_{STUF} = 9$, $N_{PWD} = 8$, $N_{BUSNA} = 7$	$N_D = 19$, $N_M = 24$

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Table 3. *Results of statistical tests for inbred mice under the 10 °C regime.* Z *and* H *are the Mann-Whitney* U *test and Kruskal-Wallis ANOVA statistics, respectively;* χ^2*: Pearson's chi-squared test. Fisher's exact test was used for voluntary swim in comparisons between two* domesticus *strains and between pooled* musculus *and* domesticus *groups.*

Variable	*domesticus*-derived strains	*musculus*-derived strains	pooled *domesticus* vs. *musculus* groups
Latency to swim	$Z = -1.134$	$H_{(2, n=30)} = 12.916$	-
	$P > 0.05$	$P = 0.002$	-
	$N_{STRA} = 10$, $N_{Schweben} = 10$	$N_{STUF} = 10$, $N_{PWD} = 10$, $N_{BUSNA} = 10$	-
Latency to cross	$Z = 2.003$	$H_{(2, n=30)} = 11.511$	-
	$P = 0.045$	$P = 0.003$	-
	$N_{STRA} = 10$, $N_{Schweben} = 10$	$N_{STUF} = 10$, $N_{PWD} = 10$, $N_{BUSNA} = 10$	-
Voluntary swim		$\chi^2 = 8.306$	-
	$P > 0.05$	$P = 0.016$	-
	$N_{STRA} = 2$, $N_{Schweben} = 7$	$N_{STUF} = 8$, $N_{PWD} = 10$, $N_{BUSNA} = 5$	-
Path	$Z = 1.171$	$H_{(2, n=28)} = 1.487$	$Z = 1.493$
	$P > 0.05$	$P > 0.05$	$P > 0.05$
	$N_{STRA} = 7$, $N_{Schweben} = 10$	$N_{STUF} = 10$, $N_{PWD} = 10$, $N_{BUSNA} = 8$	$N_D = 17$, $N_M = 28$

Table 4. *Results of statistical tests* for differences between *G1 musculus and G1 domesticus* mice*.* Z *is the Mann-Whitney* U *test statistic; voluntary swim was tested with Fisher's exact test.*

Variable	Regime	
	10 °C	20 °C
Latency to swim	$Z = 1.609$	$Z = -2.003$
	$P > 0.05$	$P = 0.045$
	$N_D = 11$, $N_M = 11$	$N_D = 11$, $N_M = 11$
Latency to cross	$Z = 1.215$	$Z = -2.068$
	$P > 0.05$	$P = 0.039$
	$N_D = 11$, $N_M = 11$	$N_D = 11$, $N_M = 11$
Voluntary swim	$P > 0.05$	$P = 0.007$
	$N_D = 5$, $N_M = 8$	$N_D = 8$, $N_M = 7$
Path	$Z = -1.735$	$Z = 2.083$
	$P > 0.05$	$P = 0.037$
	$N_D = 6$, $N_M = 10$	$N_D = 8$, $N_M = 7$

experiments started in 10 °C and then continued under the 20 °C regime.

Statistical analyses

Since Shapiro-Wilk's test showed most data to have non-normal distribution non-parametric tests were used. In two-group comparisons (STRA vs. Schweben, G1 *musculus* vs. G1 *domesticus*), Mann-Whitney *U* test was applied whereas three *musculus*-derived strains were compared with Kruskal-Wallis ANOVA. Where there was no significant difference between consubspecific inbred strains, the strains were pooled as the *domesticus*-inbred and *musculus*-inbred group, respectively, for a corresponding trait. The two groups were then compared using Mann-Whitney *U* test. Since for *voluntary swim* there were no entries in some groups (i.e., no voluntary swimming was recorded), either Fisher's exact test (G1 *domesticus* vs. G1 *musculus*, STRA vs. Schweben) or Pearson's

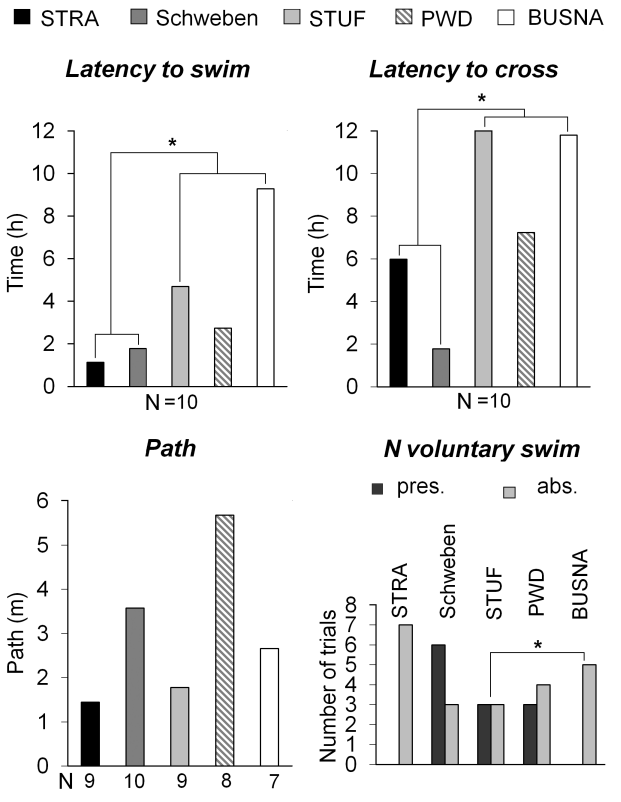


Fig. 3. *Medians of the four measured parameters for inbred mice tested under the 20 °C regime. Significant differences (P < 0.05) are indicated with asterisks; N – number of individuals; pres./abs. – presence or absence of the corresponding behaviour.*

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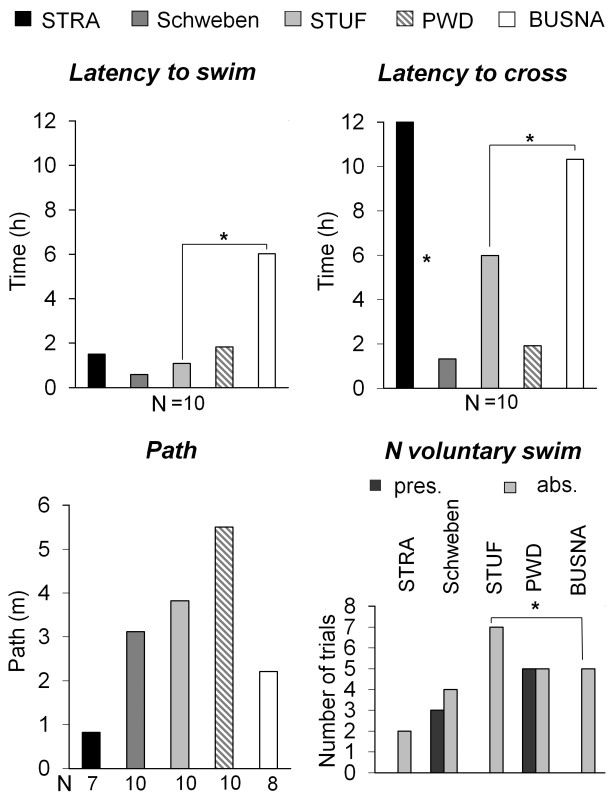


Fig. 4. *Medians of the four measured parameters for inbred mice tested under the 10 °C regime. Significant differences (P < 0.05) are indicated with asterisks; N – number of individuals; pres./abs. – presence or absence of the corresponding behaviour.*

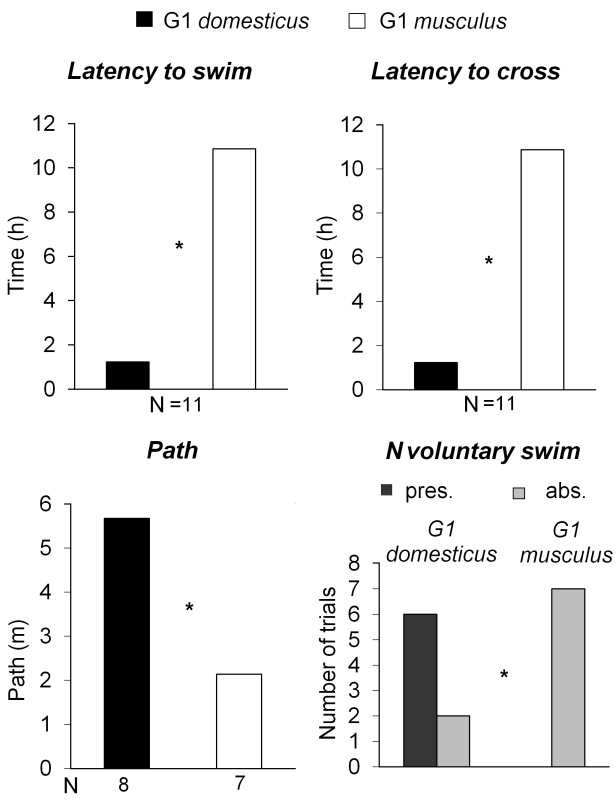


Fig. 5. *Medians of the four measured parameters for G1 mice tested under the 20 °C regime. Significant differences (P < 0.05) are indicated with asterisks; N – number of individuals; pres./abs. – presence or absence of the corresponding behaviour.*

chi-squared test (STUF, PWD, BUSNA) was used in these cases. Pooled *musculus*-inbred and *domesticus*-inbred groups were compared with Fisher's exact test. All these analyses were done in Statistica 6.0 (StatSoft, Inc. 2006).

Results

Inbred mice

Under the 20 °C regime, variation among *musculus*-derived and *domesticus*-derived strains, respectively, was not significant in three variables (*Latency to swim*, *Latency to cross*, *Path*; Table 2) and so these parameters could be compared between the two groups. Of these, only the two latency parameters were significantly different (Table 2, right column). As shown in Fig. 3, both latencies are higher in the pooled group of the *musculus*-derived strains, i.e., males of these strains were more reluctant to enter the water pool and took them more time to get over it. In other parameters, there were neither significant differences between the groups nor any consistent tendency. Males of the Schweben strain appeared to be the most ardent swimmers that entered and crossed the pool most frequently (data not shown; see also *N* for *Path* in Table 2 and Fig. 3) and also more often engaged in voluntary swimming.

Contrary to the previous experiment, only *Path* appeared homogenous within the two groups of inbred strains under the 10 °C regime. The difference between *musculus*-derived and *domesticus*-derived groups was not significant (Table 3). Again, the Schweben males seem to be more zealous swimmers compared to the STRA males as indicated by shorter latency times before entering and overcoming the pool (Fig. 4).

G1 mice

Under the 20 °C regime, the G1 groups significantly differed in four parameters: *domesticus* males revealed a shorter latency before entering the water and reaching the opposite side of the pool. More *domesticus* individuals also engaged in voluntary swimming and followed a shorter path (Table 4, Fig. 5).

Strikingly, when the mice were tested under the 10 °C regime, they showed opposite tendencies. Although

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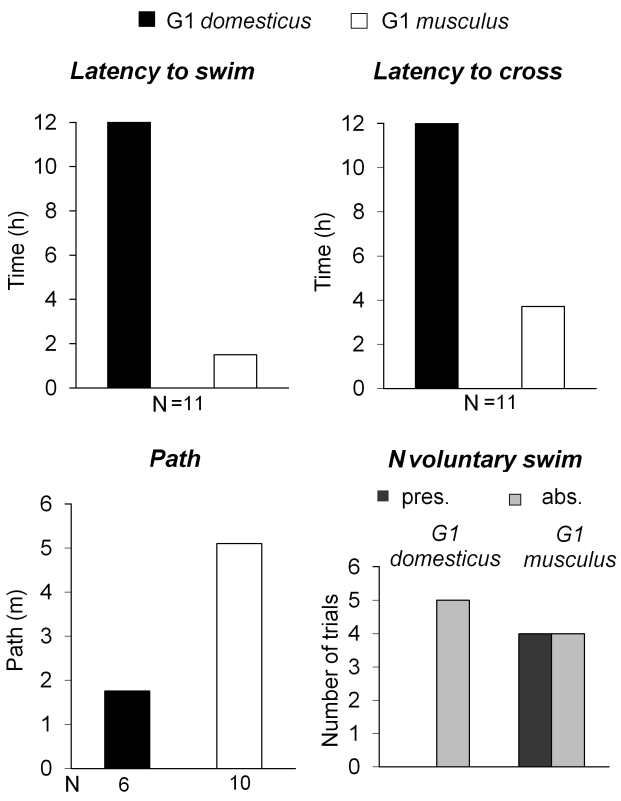


Fig. 6. *Medians of the four measured parameters for G1mice tested under the 10 °C regime. N – number of individuals; pres./abs. – presence or absence of the corresponding behaviour.*

the differences were not significant for all parameters, it took *longer* before *domesticus* males entered the pool and got over it. Moreover, no *domesticus* individual entered the water more than once (Table 4, Fig. 6).

Discussion

In this study we tested whether and to what extent water can act as a barrier to mouse dispersal and thus to affect the genetic structure of mouse populations. More specifically, since the zone of secondary contact between the two house mouse subspecies has been shown to be a tension zone (Barton & Hewitt 1985, Raufaste et al. 2005, Macholán et al. 2007, Baird & Macholán 2012) such barriers can have a potentially strong influence on its position and structure on a local scale.

Contrary to the common notion of house mice as reluctant swimmers (Gerlach 1990, 1996, 1998, Wolfer et al. 1998, D'Hooge & De Deyn 2001, Nelson 2002, Petit-Demouliere et al. 2005) we found that tested males of all experimental groups entered the water (6-10 individuals per group; see *N* for *Path* in Figs. 3-5). It should be noted that all the mice were left unmolested for 26 hours so that the observed behaviour do not represent any panic or extreme reactions to disturbance. Since physiological effects of starving is detected after 24-60 h after removing food (Leone et al. 1999, Raffaghello et al. 2008) mice tested in this study were not probably strongly coerced to swim across the pool for food. Moreover, many males swam repeatedly, even after they reached the target box and fed themselves. These results are consistent with pilot experiments in which some individuals swam even when food was provided *ad libitum* (Hiadlovská, unpublished results). Therefore, the inbred and G1 individuals were likely to be motivated by other factors than food deprivation. In conclusion, a water pool such as that used in our experiments does not appear a strong barrier for house mice under both experimental conditions (i.e., 10 °C and 20 °C regime). Though sporadic reports on swimming abilities of wild mice describe them as good swimmers (Randall 1999, Singleton & Krebs 2007) especially in habitats where water dominates (such as rice fields), our results appear to contradict the majority of published data (Francis et al. 1995, Wolfer et al. 1998, Gerlach 1990, 1996, 1998, D'Hooge & De Deyn 2001, Nelson 2002, Petit-Demouliere et al. 2005).

Under the 20 °C regime, both *domesticus*-derived inbred strains and the G1 *domesticus* group revealed a higher propensity for swimming. These mice entered the water pool and crossed it mostly within the first two hours of the experiment whereas *M. m. musculus* displayed longer latencies. In addition, more G1 *domesticus* mice engaged in repeated swimming after previous reaching the target box (six times on average, data not shown). Why should the mice enter the water when they have already come by food in a dry box similar to their home cage? A possible explanation can be differences in exploratory strategies between the two subspecies. Open field experiments showed that *M. m. domesticus* males are less thigmotactic, i.e., less fearful of open areas than *M. m. musculus* males (Hiadlovská et al. 2012). These results correspond with a higher movement activity, including swimming (Brubaker 1970), escape activity (Hunt & Selander 1973), and aggression (Thuesen 1977, van Zegeren & van Oortmerssen 1981, Munclinger & Frynta 2000, Frynta et al. 2005) evidenced in *M. m. domesticus*. However, open field tests carried out by Hiadlovská et al. (2012) also showed a longer latency before entering the arena in this subspecies, suggesting a stronger risk assessment prior to stepping into an unfamiliar area.

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This behaviour is probably an adaptation to higher danger of encountering an aggressive dominant male. Why did not *domesticus* males wait longer also before entering the water pool? We may hypothesize that the reason lies in different designs of the open field experiment (Hiadlovská et al. 2012) and the present study. Specifically, the present experiment lasted much longer compared to the open field test. Hence the tested male had sufficient time to get olfactory information about potential threat from behind the pool.

Interestingly, when the air and water temperature was decreased to 10 °C, the results were reversed: G1 *domesticus* males displayed longer latency phases before entering and crossing the pool, and engaged less in voluntary swimming than G1 *musculus* males. As indicated by *N* for *Path* in Table 4 (see also Figs. 5 and 6), the number of males entering the water decreased by 14.3 % compared to the 20 °C in *M. m. domesticus* while in *M. m. musculus* this value increased by 25.0 %. The results for inbred strains are less clear than for G1 males. It seems that reactions of individual strains to cold conditions were rather random. However, the number of males entering the water consistently increased in all *musculus*-derived strains and decreased in one of the *domesticus* strains (STRA). The only exception was the Schweben group in which the value remained unchanged (Figs. 3, 4). In total, the number of recorded swimming individuals decreased by 10.5 % in the *domesticus* group and increased by 16.7 % in the *musculus* group of inbred strains.

Decreasing swimming activity under cold conditions is not surprising. For example, Mount & Willmott (1967) reported reduction of activity in a strain of albino mice. Though the authors did not specify the strain, it is known that albino mice (both inbred and outbred) are predominantly of the *M. m. domesticus* origin (Berry 1981, Yang et al. 2011). What is less clear, however, is why the *M. m. musculus* males tested in this study increased their swimming activity under the 10 °C regime. This is especially puzzling in repeated, "voluntary", swimming (Figs. 3, 4). In central Europe, *M. m. musculus* males are in general smaller than *M. m. domesticus* (Macholán 1996) and thus may react more strongly to food deprivation. For example, Lynch & Sulzbach (1984) and Lynch et al. (1988) found increased food consumption in mice kept in 4 °C, however, this increase was stronger in females than in males who also displayed lower heritability of this trait (0.32 compared to 0.39 in females). Therefore, it is not clear if the size difference between the subspecies is sufficiently large to explain the different reaction to decreased temperature (10 °C/38 h compared to 4 °C/4 days in the studies of Lynch & Sulzbach 1984 and Lynch et al. 1988). All the more so that the *musculus* males swam repeatedly, even after reaching food in the target box.

In summary, we found that house mice are capable of entering and overcoming at least small and still bodies of water and that they often engage in voluntary and repeated swimming events. This does not mean, however, that larger water bodies and/or fast-running streams are not strong barriers to mouse natural dispersion. Moreover, if a male mouse is given a possibility to choose between two sources of food or a potential sexual partner, one easy to achieve and the other separated by a small and surmountable barrier, he is likely to choose the former, easier, alternative. Thus even tiny water barriers can, in principle, affect genetic structure of mouse populations. To what extent small watercourses really do act as barriers to mouse dispersal is not clear for now. However, this study at any rate showed that house mice are not as fearful of water as suggested in literature.

The differences in the disposition to enter water as well as in swimming abilities are not easy to interpret. As discussed above, *M. m. domesticus* is more aggressive and active with respect to exploratory behaviour than *M. m. musculus*. Having higher potential for overcoming barriers, *M. m. domesticus* might be less limited by presence of water bodies during dispersion. Moreover, studies focused on mate choice discrimination and subspecies specific assortative mating have reported lower assortative preference in *M. m. domesticus* (Smadja & Ganem 2002, Bímová et al. 2005, 2009, Vošlajerová Bímová et al. 2011; see also Ganem 2012 for a recent review). This subspecies thus can be expected to invade the territory of *M. m. musculus*. However, there are no indications of this process along the whole stretch of the European hybrid zone. Conversely, Macholán et al. (2011) found genetic evidences of a past westward movement of the zone, i.e. the movement from *M. m. musculus* territory to *M. m. domesticus* range. Anyway, although at present we can only speculate about actual effects of different behavioural/ecological strategies on the structure and dynamics of the European hybrid zone, both published data (see Ganem 2012 for review; see also Vošlajerová Bímová et al. 2011, Hiadlovská et al. 2012) and the present study suggest that behaviour has played an important role in house mouse evolution.

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Literature

Baird S.J.E. & Macholán M. 2012: What can the *musculus/domesticus* hybrid zone tell us about speciation? In: Macholán M., Baird S.J.E., Munclinger P. & Piálek J. (eds.), Evolution of the house mouse. *Cambridge studies in morphology and molecules: new paradigms in evolutionary biology. Cambridge University Press, Cambridge: 334–372.*

Barton N.H. 1979: The dynamics of hybrid zones. *Heredity 43: 341–359.*

Barton N.H. & Bengtsson B.O. 1986: The barrier to genetic exchange between hybridising populations. *Heredity 57: 357–376.*

Barton N.H. & Gale K.S. 1993: Genetic analysis of hybrid zones. In: Harisson R.G. (ed.), Hybrid zones and evolutionary process. *Oxford University Press, Oxford: 13–45.*

Barton N.H. & Hewitt G.M. 1985: Analysis of hybrid zones. *Annu. Rev. Ecol. Syst. 16: 113–148.*

Berry R.J. 1981: Town mouse, country mouse: adaptation and adaptability in *Mus domesticus* (*M. musculus domesticus*). *Mamm. Rev. 11: 91–136.*

Bímová B., Albrecht T., Macholán M. & Piálek J. 2009: Signalling components of the house mouse mate recognition system. *Behav. Process. 80: 20–27.*

Bímová B., Karn R.C. & Piálek J. 2005: The role of salivary androgen-binding protein in reproductive isolation between two subspecies of house mouse: *Mus musculus musculus* and *Mus musculus domesticus*. *Biol. J. Linn. Soc. 84: 349–361.*

Bronson F.H. 1979: The reproductive ecology of the house mouse. *Q. Rev. Biol. 54: 265–299.*

Brown R.Z. 1953: Social behavior, reproduction, and population changes in the house mouse (*Mus musculus* L.). *Ecol. Monogr. 23: 218–240.*

Brubaker L.L. 1970: A behavior-genetic study of race and deme differences in *Mus musculus*. *Doctoral dissertation, University of Texas at Austin.*

Clément Y., Calatayud F. & Belzung C. 2002: Genetic basis of anxiety-like behaviour: a critical review. *Brain Res. Bull. 57: 57–71.*

Crowcroft P. 1955: Territoriality in wild house mice, *Mus musculus* L. *J. Mammal. 36: 299–301.*

D'Hooge R. & De Deyn P.P. 2001: Applications of the Morris water-maze in the study of learning and memory. *Brain Res. Rev. 36: 60–90.*

Dean M.D., Ardlie K.G. & Nachman M.W 2006: The frequency of multiple paternity suggests that sperm competition is common in house mice (*Mus domesticus*). *Mol. Ecol. 15: 4141–4151.*

Drickamer L.C., Gowaty P.A. & Holmes C.M. 2000: Free female mate choice in house mice affects reproductive success and offspring viability and performance. *Anim. Behav. 59: 371–378.*

Ďureje Ľ., Vošlajerová Bímová B. & Piálek J. 2010: No postnatal maternal effect on male aggressiveness in wild-derived strains of house mice. *Aggressive Behav. 35: 1–8.*

Essman W.B. & Jarvik M.E. 1961: A water-escape test for mice. *Psychol. Rep. 8: 58.*

Feldhamer G.A., Drickamer L.C., Vessey S.H., Merritt J.F. & Krajewski C. 2007: Mammalogy: adaptation, diversity, ecology. 3rd edn. *John Hopkins University Press, Baltimore, MD.*

Francis D.D., Zaharia M.D., Shanks N. & Anisman H. 1995: Stress-induced disturbances in Morris water-maze performance: interstrain variability. *Physiol. Behav. 58: 57–65.*

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Frynta D., Slábová M., Váchová H., Volfová R. & Munclinger P. 2005: Aggression and commensalism in house mouse: a comparative study across Europe and Near East. *Aggressive Behav. 31: 283–293.*
Ganem G. 2012: Behaviour, ecology and speciation in the house mouse. In: Macholán M., Baird S.J.E., Munclinger P. & Piálek J. (eds.), Evolution of the house mouse. *Cambridge studies in morphology and molecules: new paradigms in evolutionary biology. Cambridge University Press, Cambridge: 373–406.*
Garland T., Jr. & Stephen C.A. 1991: Physiological differentiation of vertebrate populations. *Annu. Rev. Ecol. Syst. 22: 193–228.*
Gerlach G. 1990: Dispersal mechanism in a captive wild house mouse population (*Mus domesticus* Rutty). *Biol. J. Linn. Soc. 41: 271–277.*
Gerlach G. 1996: Emigration mechanisms in feral mice – a laboratory investigation of the influence of social structure, population density, and aggression. *Behav. Ecol. Sociobiol. 39: 159–170.*
Gerlach G. 1998: Impact of social ties on dispersal, reproduction and dominance in feral house mice (*Mus musculus domesticus*). *Ethology 104: 487–499.*
Gregorová S. & Forejt J. 2000: PWD/Ph and PWK/Ph inbred mouse strains of *Mus m. musculus* subspecies – a valuable resource of phenotypic variations and genomic polymorphisms. *Folia Biol. (Praha) 46: 31–42.*
Hauffe H.C., Piálek J. & Searle J.B. 2000: The house mouse chromosomal hybrid zone in Valtellina (SO): a summary of past and present research. *Hystrix 11: 17–25.*
Hiadlovská Z., Vošlajerová Bímová B., Mikula O., Piálek J. & Macholán M. 2012: Explorative behaviour in two house mouse subspecies and their hybrids. *Biol. J. Linn. Soc., in press.*
Hunt W.G. & Selander R.K. 1973: Biochemical genetics of hybridisation in European house mice. *Heredity 31: 11–33.*
Key K.H. 1968: The concept of stasipatric speciation. *Syst. Zool. 17: 14–22.*
Leone T.C., Weinheimer C.J. & Kelly D. 1999: A critical role for the peroxisome proliferator-activated receptor (PPARα) in the cellular fasting response: the PPARα-null mouse as a model of fatty acid oxidation disorders. *Proc. Natl. Acad. Sci. USA 96: 7473–7478.*
Lynch C.B. & Sulzbach D.S. 1984: Quantitative genetic analysis of temperature regulation in *Mus musculus*. II. Diallel analysis of individual traits. *Evolution 38: 527–540.*
Lynch C.B., Sulzbach D.S. & Connolly M.S. 1988: Quantitative-genetic analysis of temperature regulation in *Mus domesticus*. IV. Pleiotropy and genotype-by-environment interactions. *Am. Nat. 132: 521–537.*
Macholán M. 1996: Morphometric analysis of European house mice. *Acta Theriol. 46: 255–275.*
Macholán M., Baird S.J.E., Dufková P., Munclinger P., Vošlajerová Bímová B. & Piálek J. 2011: Assessing multilocus introgression patterns: a case study on the mouse X chromosome in central Europe. *Evolution 65: 1428–1446.*
Macholán M., Munclinger P., Šugerková M., Dufková P., Bímová B., Božíková E., Zima J. & Piálek J. 2007: Genetic analysis of autosomal and X-linked markers across a mouse hybrid zone. *Evolution 61: 746–771.*
Morris R. 1981: Spatial localization does not require the presence of local cues. *Learn. Motiv. 12: 239–260.*
Morris R. 1984: Developments of a water-maze procedure for studying spatial learning in the rat. *J. Neurosci. 11: 47–60.*
Mount L.E. & Willmott J.V. 1967: The relation between spontaneous activity, metabolic rate and the 24 hour cycle in mice at different environmental temperatures. *J. Physiol. 190: 317–380.*
Munclinger P. & Frynta D. 2000: Social interactions within and between two distant populations of house mouse. *Folia Zool. 49: 1–6.*
Nelson A.R., Johnson C.L., Matter W.J. & Mannan R.W. 2002: Test of emigration in small mammals under experimental conditions. *Can. J. Zool. 80: 2056–2060.*
Petit-Demouliere B., Chenu F. & Bourin M. 2005: Forced swimming test in mice: a review of antidepressant. *Psychopharmacology 177: 245–255.*
Piálek J., Vyskočilová M., Bímová B., Havelková D., Piálková J., Dufková P., Bencová V., Ďureje Ľ., Albrecht T., Hauffe H.C., Macholán M., Munclinger P., Strochová R., Zajícová A., Holáň V., Gregorová S. & Forejt J. 2008: Development of unique house mouse resources suitable for evolutionary studies of speciation. *J. Hered. 99: 34–44.*
Pocock M.J.O., Hauffe H.C. & Searle J.B. 2005: Dispersal in house mice. *Biol. J. Linn. Soc. 84: 565–583.*
Raffaghello L., Lee C., Safdie F.M., Wei M., Madia F., Bianchi G. & Longo V.D. 2008: Starvation-dependent

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differential stress resistance protects normal but not cancer cells against high-dose chemotherapy. *Proc. Natl. Acad. Sci. USA 105: 8215–8220.*

Randall C. 1999: Vertebrate pest management – a guide for commercial applications (Extension bulletin E-2050). *Michigan State University, East Lansing, MI.*

Raufaste N., Orth A., Belkhir K., Senet D., Smadja C., Baird S.J.E., Bonhomme F., Dod B. & Boursot P. 2005: Inferences of selection and migration in the Danish house mouse hybrid zone. *Biol. J. Linn. Soc. 84: 593–616.*

Reimer J.D. & Petras M.L. 1967: Breeding structure of the house mouse, *Mus musculus* in a population cage. *J. Mammal. 48: 88–99.*

Singleton G.R. & Krebs C.J. 2007: The secret world of wild mice. In: Fox J.G., Davisson M.T., Quimby F.W., Barthold S.W., Newcomer C.E. & Smith A.L. (eds.), The mouse in biomedical research. Vol. 1. History, wild mice and genetics. *Academic Press/Elsevier, San Diego: 25–51.*

Smadja C. & Ganem G. 2002: Subspecies recognition in the house mouse: a study of two populations from the border of a hybrid zone. *Behav. Ecol. 13: 312–320.*

StatSoft, Inc. 2006: Statistica Cz (Software system for data analysis), version 7.1. *www.statsoft.com*

Thuesen P. 1977: A comparison of the agonistic behaviour of *Mus musculus musculus* L. and *Mus musculus domesticus* Rutty (Mammalia, Rodentia). *Vidensk. Medd. Dan. naturhist. Foren. 140: 117–128.*

van Zegeren K. 1980: Variation in aggressiveness and the regulation of numbers in house mouse population. *Neth. J. Zool. 30: 635–770.*

van Zegeren K. & van Oortmerssen G.A. 1981: Frontier disputes between the West- and East-European house mouse in Schleswig-Holstein, West Germany. *Z. Säugetierkd. 46: 363–369.*

Vošlajerová Bímová B., Macholán M., Baird S.J.E., Munclinger P., Dufková P., Laukaitis C.M., Karn R.C., Luzynski K., Tucker P. & Piálek J. 2011: Reinforcement selection acting on the European house mouse hybrid zone. *Mol. Ecol. 20: 2403–2424.*

Walkowa W., Adamczyk K. & Chełkowska H. 1989: Characteristics of migrants in a free-living population of the house mouse. *Acta Theriol. 34: 305–313.*

Wolfer D.P., Stagljar-Bozicevic M., Errington M.L. & Lipp H.-P. 1998: Spatial memory and learning in transgenic mice: fact or artifact? *News Physiol. Sci. 13: 118–123.*

Yang H., Wang J.R., Didion J.P., Buus R.J., Bell T.A., Welsh C.E., Bonhomme F., Yu A.H.-T., Nachman M.W., Piálek J., Tucker P., Boursot P., McMillan L., Churchill G.A. & de Villena F.P.-M. 2011: Subspecific origin and haplotype diversity in the laboratory mouse. *Nat. Genet. 45: 648–655.*

Zejda J. 1975: Habitat selection in two feral house mouse (*Mus musculus*) lowland populations. *Zool. listy 24: 99–111.*

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