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The influence of familiarity and temperature on the huddling behavior of two mouse species with contrasting social systems

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A B S T R A C T

Huddling with other individuals is an effective way to reduce heat loss. This cooperative behavior requires that the individuals tolerate each other's presence at least for a certain time or under certain circumstances. In our study, we investigated the effects of ambient temperature and familiarity on the huddling behavior of two closely related mouse species, the mound-building mouse (*Mus spicilegus*) and the house mouse (*Mus musculus musculus*). While their geographic distribution overlaps, their social systems differ in many aspects. Whereas house mice are territorial, mound-building mice tolerate each other and live in groups during winter. In laboratory experiments we found that familiarity and ambient temperature influenced the huddling behavior of both species. Familiar individuals were more likely to huddle, but while mound-building mice did so at all temperatures, huddling in house mice increased with lower temperatures. Our results are consistent with the previous knowledge about these species' social systems and might provide us with more details about their sociality. Investigating huddling behavior might be a good way to measure social tolerance between individuals within a species and compare social systems of different species.

1. Introduction

In colder climates, physiological and behavioral strategies to survive the winter are of crucial importance. Especially in small mammals where the body surface area-to-volume ratio is higher (McNab 2008) maintaining constant body temperature is more demanding. One option to lower these costs is to engage in social thermoregulatory behavior with other individuals like huddling (Gilbert et al. 2010). To form and maintain such social aggregations it is essential that individuals tolerate each other's presence at a certain level. The extent individuals tolerate or behave aggressively towards others depends on a complex set of traits including their age, sex, the social and mating system of the population and in many cases the environmental conditions they live under (Armitage 1981; Crowcroft and Rowe 1963; Livoreil et al., 1993; Pulliam and Caraco 1984). Overwintering in groups can increase survival, and even individuals of otherwise solitary species may gather and tolerate each other under harsh environmental conditions (e.g. wood mice (*Apodemus sylvaticus*), Wolton (1985); golden mice (*Ochrotomys nuttalli*), Springer et al. (1981); red squirrels (*Tamiasciurus hudsonicus*), Williams et al. (2013); Siberian flying squirrels (*Pteromys volans*), Selonen et al. (2014) ; brush-tailed phascogales (*Phascogale tapoatafa*), Rhind (2003).

Huddling, which is defined as an active and close aggregation of animals (Gilbert et al., 2010), helps them overcome not only cold, but other harsh conditions such as food or water scarcity due to reduced energy expenditure. This allows more energy to be allocated to other important processes like growth or reproduction (Bautista et al., 2017; Madison et al., 1984; Rödel et al., 2008; Scantlebury et al., 2006; Schradin et al., 2006; Sealander, 1952; Wolff and Lidicker, 1981). It is often observed in the field and the laboratory in many small mammals (Alberts, 1978; Batchelder et al., 1983; Gilbert et al., 2010; Sánchez et al., 2015; Sokoloff and Blumberg, 2002; Terrien et al., 2011). Huddling – despite the obvious benefits for each individual– can be in conflict with other traits, such as territoriality and dominance, therefore it is more frequent among kin than non-related individuals (Gilbert et al., 2010). However, even unrelated individuals can form huddling groups (Schradin et al., 2006; Selonen et al., 2014; Wolff and Lidicker, 1981).

The house mouse (*Mus musculus musculus* Linnaeus 1758) and the mound-building mouse (*Mus spicilegus* Petényi 1882) are

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morphologically similar, closely related rodent species with overlapping distribution, but living under different ecological and social conditions (Dobson and Baudoin, 2002; Mitsainas et al., 2009; Orsini et al., 1983; Sokolov et al., 1998). One of the main differences between the social systems of the two species is that the house mouse has a polygynous mating system with social group territoriality where males develop dominance–submission relationships within the social group (Bronson, 1979; Brown, 1953; Crowcroft and Rowe, 1963; Latham and Mason, 2004; Lidicker, 1976; Reimer and Petras, 1967), while the mound-building mouse exhibits a mating system of social monogamy (Baudoin et al., 2005; Gouat and Féron, 2005; Patris and Baudoin, 1998; Patris and Baudoin, 2000). They establish a strong social bond between partners (Patris and Baudoin, 1998). Both female and male adult mice are highly aggressive toward unfamiliar, but not toward familiar individuals (Patris et al., 2002; Simeonovska-Nikolova, 2003; Suchomelova et al., 1998; Szenczi et al., 2012). In contrast to the house mouse, the mound-building mouse shows a unique communal overwintering behavior. They construct large mounds in autumn and they overwinter together under these structures (Murariu, 1981; Naumov, 1940; Sokolov et al., 1998). During autumn/winter the young delay their sexual maturation, as a consequence of staying in groups for overwintering (Gouat et al., 2003), although they start to show more agonistic behaviors toward strangers than familiar individuals as early as 21 days of age (Szenczi et al., 2012). Individuals inhabiting a mound might derive from related female parents and their unrelated mates (Garza et al., 1997), or just from one litter (c.f. Szenczi et al., 2011, own observation). This kind of cooperative overwintering behavior requires that juveniles must recognize and be tolerant toward each other, but possibly defend their mound and protect it from intruders. However, this kind of behavior has not yet been observed in the wild. House mice show different behavior toward familiar and unfamiliar individuals. Young adults of both sexes remain social with their siblings they were raised with, but start to show agonistic behavior toward strangers and at adulthood males become highly aggressive towards same-sex individuals, while females remain social with familiars (Szenczi et al., 2012).

It is well-known that mice like to huddle, although information is scanty on how the thermoregulatory requirements of mice influence their social behavior and willingness to huddle. Batchelder et al. (1983) found that house mice huddled more at 5 °C than 26 °C. They also noted comparing single and mixed sex groups that huddling behavior was more consistent in female groups, and changed less in response to variations in temperature, while males were more likely to huddle at low temperatures. According to the authors, the difference is due to males establishing dominance hierarchies. However, the animals in the Batchelder et al. experiment were not siblings or cage-mates, although this can be a strong influential factor, especially in adult animals.

Therefore, the aims of the present study are to examine if ambient temperature and familiarity of individuals affect huddling behavior in two mouse species with contrasting social systems, the mound-building mouse and the house mouse. We expected to find differences dependent on the ambient temperature and familiarity of the animals in the group. We predicted that huddling will occur between familiar individuals, especially in the case of mound-building mice, and lowering the ambient temperature may facilitate huddling among non-familiar individuals in both species.

2. Material and methods

2.1. Ethics statement

Throughout the study, animals were kept and treated according to the ASAB/ABS (2016) Guidelines for the treatment of animals in behavioral research and testing. The experimental protocol was approved by the Governmental Office of Pest County, Directorate for Food Chain Safety and Animal Health, File Nr: XIV-001/525-4/2012

2.2. Housing conditions

The experiments were carried out at the Biological Research Station of the Eötvös Loránd University in Göd on fifth and sixth generation randomly bred descendants of wild caught mound-building mice and house mice originating from three different regions of Hungary. Mice were maintained in the breeding facilities under reversed day-night 12:12 light conditions. Temperature in the rooms was kept constant at $20-22$ °C. Mice were housed in standard polycarbonate T4 cages (35 × 20 × 15 cm). Sawdust (Lignocell from J. Rettenmaier und Söhne GmbH, Rosenberg, Germany) was used as bedding material and hay was provided as nest material. The animals were provided with food pellets (S8106-S011, Ssniff Spezialdiäten GmbH, Soest, Germany) and water ad libitum.

2.3. Test design

In two experiments we arranged four treatment groups, each consisting of four animals in a fixed sex ratio of 1:1; familiar mound-building mice, non-familiar mound-building mice, familiar house mice and non-familiar house mice. Familiar individuals were always siblings from the same litter and were kept together until the experiments. Non-familiar animals were same age conspecifics from 4 different litters. Four mice of the same treatment group were considered as an experimental unit. The animals were 60 ± 5 days old at the time of the testing, considered to be young adults in these species.

Animals were separated in individual cages one day before the tests. After the separation, the groups were formed and the mice were placed into the experimental boxes (35 × 20 × 15 cm) – same size as used for housing – which contained only fresh wood shavings as bedding material. The animals were allowed 15 min of habituation to the new box in the pre-set temperature room, but under continuous observation before the test started (see below). One set of the four treatment groups was tested simultaneously at a time (see below for the number of replicates in each experiment). The four boxes were placed next to each other in random order between sets while separated visually with non-transparent plastic panels. The duration of the test was 60 min. In every 15 min for 15 s we scan-sampled the whole group and recorded the number of huddling individuals; huddling was considered when at least two individuals maintained body contact for more than 10 s with body parts other than head and extremities. Additionally, we recorded the number of mice climbing on the wire mesh top of the box, since we assumed this behavior can reflect social intolerance between the individuals (c.f. Batchelder et al., 1983). When all individuals in the cage were separate from the others we scored the number of huddling individuals as 1, when two individuals were in a huddle we scored it as 2, and so on. We also observed if severe aggression occurred. In the case of one group of non-familiar house mice and one group of non-familiar mound building mice we did not begin the test because the animals showed aggressive behavior during the habituation period and they were excluded from the analysis. In the rest of the animals actually tested, no injuries were observed during the experiments.

2.4. First experiment

We aimed to test whether the huddling behavior of the two mouse species is different and if it changes with the familiarity of group members. We expected that familiar individuals would engage in more huddling than non-familiar individuals, especially in the case of the mound-building mice. The four treatment groups were tested at 19 °C. Twelve replicates were conducted, totaling 192 animals.

2.5. Second experiment

We investigated the effect of temperature on huddling in a similar set of groups of animals, but used different individuals than in the first