

# House mouse subspecies do differ in their social structure

Ondřej Mikula<sup>1,2</sup>, Miloš Macholán<sup>1,3</sup>, Ľudovít Ďureje<sup>2</sup>, Zuzana Hiadlovská<sup>1</sup>, Kristina Daniszová<sup>1</sup>, Kateřina Janotová<sup>2</sup>, Barbora Vošlajerová Bímová<sup>1</sup>

<sup>1</sup>Laboratory of Mammalian Evolutionary Genetics, Institute of Animal Physiology and Genetics, Czech Academy of Sciences, 602 00 Brno, Czech Republic

<sup>2</sup>Institute of Vertebrate Biology, Czech Academy of Sciences, Brno; Research Facility Studenec, 675 02 Koněšín, Czech Republic

<sup>3</sup>Department of Botany and Zoology, Faculty of Science, Masaryk University, 625 00 Brno

**Author for correspondence:** Miloš Macholán, macholan@iach.cz

## Keywords:

*Mus musculus musculus*, *M. m. domesticus*, radio-frequency identification, social networks, modularity, demes

## Abstract

It is widely acknowledged that population structure can have a substantial impact on evolutionary trajectories. In social animals, this structure is strongly influenced by relationships among the population members, so studies of differences in social structure between diverging populations or nascent species are of prime interest. Ideal models for such a study are two house mouse subspecies, *Mus musculus musculus* and *M. m. domesticus*, meeting in Europe along a secondary contact zone. Though the latter subspecies has usually been supposed to form tighter and more isolated social units than the former, the evidence is still inconclusive. Here, we carried out a series of radio-frequency identification experiments in semi-natural enclosures to gather large longitudinal datasets on individual mouse movements. The data were summarised in the form of uni- and multi-layer social networks. Within them, we could delimit and describe the social units ('modules'). While the number of estimated units was similar in both subspecies, *domesticus* revealed a more 'modular' structure. This subspecies also showed more intramodular social interactions, higher spatial module separation, higher intramodular persistence of parent-offspring contacts, and lower multiple paternity, suggesting more effective control of dominant males over reproduction. We also demonstrate that long-lasting modules can be identified with basic reproductive units or demes. We thus provide the first robust evidence that the two subspecies differ in their social structure and dynamics of the structure formation.

## 1. Introduction

Knowledge of population structure is crucial for understanding many evolutionary phenomena, including the relative importance of genetic drift and selection (Wright, 1931), adaptation (Kemppainen et al., 2021; Kryvokhyzha et al., 2016; Vahdati & Wagner, 2018), dispersal (Clutton-Brock & Lukas, 2012; Slatkin, 1987; Stenseth & Lidicker, 1992), the spread of pathogens (Sattenspiel, 1987; Thrall & Burdon, 1997; Lopes et al. 2016), mating patterns (Jarne & Städler, 1995; Odden et al., 2014; Ferrari et al., 2019; Evans et al., 2021b,c), or speciation (Coyne & Orr, 2004). In social animals, populations are strongly affected by social interactions and resulting relationships among their members, i.e., their social structure (Kappeler & de Schaik, 2002). In some groups, especially mammals, these interactions are further intensified by physical and alimentary bonds between mothers and their offspring. Trade-offs between competition and cooperation may interplay in various ways with environmental conditions, resulting in different levels of group cohesion across taxa (Drobniak et al., 2015; Kramer & Meunier, 2019). If parental or communal care increases fitness (König, 1994; Rymer & Pillay, 2018), an evolutionary pathway for more complex sociality may be opened. Moreover, populations can be influenced by a particular mating system. Social and mating systems are thus coupled (Dewsbury, 1990; Kappeler, 2019). For example, small groups usually comprise a single breeding male monopolising copulations with several adult females. Such units tend to be, to a large extent, isolated from other subpopulations. This isolation may be further strengthened if several group members participate in the defence of its territory. By contrast, insufficient control over reproduction by dominant males can result in less close groupings, with extended male-male contests, potentially leading to changes in female mating strategies (Clutton-Brock, 2017).

Differences in social structure can exist even between closely related species (e.g., Stone et al., 2010). However, whether these differences drive the formation of reproductive barriers between nascent species or are a consequence of the isolation is unclear. It is, therefore, necessary to study diverging populations within a single species, just displaying some degree of differentiation in their social structure.

An excellent model for such a study seems to be two house mouse subspecies, *Mus musculus musculus* and *M. m. domesticus*, which diverged ~500.000 years ago (Geraldes et al., 2008; Macholán et al., 2012). These are known to differ in several behavioural traits that can potentially affect population structure, such as higher aggressiveness of *M. m. domesticus* (Đureje et al., 2011; Piálek et al., 2008; Thuesen, 1977; van Zegeren & van Oortmerssen, 1981) and higher choosiness of *M. m. musculus*, preferring consubspecific mates Bímová et al., 2005; Smadja et al., 2004; Vošlajerová Bímová et al., 2011). *Mus m. domesticus* males showed longer primary risk assessment but a more active exploration of an unfamiliar space (Hiadlovská et al., 2013; Vošlajerová Bímová et al., 2016) than *musculus* males. By contrast, *musculus* males performed better in challenging situations (Hiadlovská et al., 2014) and were less stressed by handling (Daniszová et al., 2017). More importantly, *domesticus* males appear to establish a social hierarchy faster, leading to reduced stress, while the social tension tends to persist much longer in *musculus* males (Hiadlovská et al., 2015). Higher social stress can be the reason why subordinate *musculus* males leave their homes more often than dominant males, whereas the opposite holds for *M. m. domesticus* (Hiadlovská et al., 2021).

On the other hand, despite dozens of studies over eight decades of research (see Berry, 1981; Sage, 1981; Boursot et al., 1993; Krasnov & Khokhlova, 1994), our knowledge of ecology and population structure in each mouse subspecies is still equivocal (Ganem, 2012). Mouse populations are generally considered to be subdivided into small, more or less isolated units, usually called demes. Typically, these demes consist of one dominant male monopolising reproduction, several subordinate males and females with their juvenile offspring. Females can move freely within the deme's territory, whereas subordinate males are usually forced to stay on its periphery. Upon reaching maturity, young males are often coerced into leaving the group, whereas females usually stay and reproduce within the natal deme (see, e.g., Vošlajerová Bímová et al., 2016 and references therein). However, the mouse population structure may vary depending on ecological, climatic, or density situations (Butler, 1980; Noyes et al., 1982; Pocock et al., 2004; Singleton & Krebs, 2007). For example, feral male mice on islands and elsewhere are known to defend individual, exclusive territories that usually overlap with those of several females (Berry, 1970; Krasnov & Khokhlova, 1994; Sage, 1981). Moreover, mice can switch from strong territoriality to a gregarious life during population outbreaks (Singleton & Krebs, 2007). Similar flexibility conditional on or triggered by external conditions has also been described in other species such as dunnocks (Davies, 1992), African striped mice (Schradin et al., 2012), and primates (Kappeler & van Schaik, 2002). In the house mouse, the ecological and social plasticity is largely associated with the level of its commensal bond with humans. In any case, there is a widespread notion that *M. m. domesticus* is more strictly commensal and hence more 'demic' than *M. m. musculus*. However, as Ganem (2012) pointed out, this has not ever been appropriately documented.

This study tested whether the subspecies differ in their social structure using a combination of radio-frequency identification (RFID) and parentage analysis in a series of longitudinal semi-natural breeding experiments. To control for the possible influence of different external conditions, we ran the *musculus* and *domesticus* experiments simultaneously, and these parallel runs were repeated for two consecutive years to increase the robustness of the results. The movement data from each experimental run were summarised in the form of social networks.

The structure of time-extended social networks can be analysed in various ways (Holme, 2015; Finn et al., 2019). We used a recently published multi-layer adaptation of map equation module detection (Aslak et al., 2018), which has several advantages over other approaches since it explicitly estimates the modules as multi-layer ones. The identity of modules in different time layers need not be assessed *post hoc*, which is necessary when analysing such data separately, layer by layer (Liechti & Bonhoeffer, 2019; Evans et al., 2021c). In this way, we could, for the first time, quantitatively demonstrate differences between the subspecies in the social structure of their commensal populations and the dynamics of its formation under semi-natural conditions.

## 2. Methods

### 2.1. Source data

The source data come from semi-natural enclosures inspired by Perony et al. (2012) and König et al. (2015), furnished with nest boxes, each monitored by two RFID readers recording all in/out moves of mice provided with RFID transponders (see (Supplementary Material; Fig. S1. The two collateral

experiments ran for two consecutive years (2013 and 2014), each with *M. m. musculus* and *M. m. domesticus* individuals populating separate enclosures. We thus worked with four data sets: 'musculus 2013', 'domesticus 2013', 'musculus 2014', and 'domesticus 2014'. To simulate the subspecies' secondary contact, we interconnected the enclosures with a tube containing two transponder readers at the end of the 2014 experiment (see Supplementary Material for details about animals and enclosures design).

## 2.2. Statistical processing of data

### 2.2.1. Pre-processing of the movement data

We defined a visit to a nest box as the time between entering it (recorded as a twofold signal: the first from the outer reader followed by that from the inner reader) and leaving it (recorded in the reverse order, i.e., the inner→outer reader). We cleared the record from equivocal signals, retaining only the credible visits. The record was then divided into discrete time layers. Ideally, these should be of equal length, but enclosure checks made the record semi-continuous with gaps that were just approximately equally spaced and long. Therefore, we set criteria ensuring the record is not biased by the checks but keeps as much information as possible, and the time layers are long enough to allow a description of the social structure but short enough not to encompass major changes in the structure. First, we ignored the records made during and after enclosure checks (till midnight of the concerned day). Then, we defined the layers as the record fragments no longer than 48 hours and involving no gap exceeding one hour. Finally, we merged the layers shorter than 24 hours with their nearest layers. The resulting time layers varied in length (24 to 107, although usually < 72 hours between the first and the last entry), but each of them could provide a snapshot of social structure. The position of the layers along the time axis corresponds to their mid-times (in units of days since the start of the experiment). For assessment of movement between the subspecies/enclosures (2014 runs, see above), we considered as proven all those movements, which were recorded by a reader from one enclosure followed by a record from the other enclosure. Note that a record from a reader does not imply box entrance but still proves presence in the enclosure.

### 2.2.2. The social network in a single time layer and its structure

We expressed a social contact between two individuals within a single time layer as the total time they spent together in any of the nest boxes, irrespective of other individuals potentially present therein. If  $N_m$  is the total number of individuals present in the enclosure during day  $m$ , the overall daily summary of pairwise social contacts is represented by the  $N_m \times N_m$  matrix with the zero diagonal. This can be interpreted as an adjacency matrix (**A**) of a weighted graph, whose vertices are individuals and undirected edges are interactions between them. The presence of an edge between vertices  $i$  and  $j$  is indicated in the matrix by a positive value of the element  $A_{ij}$  (or, equivalently,  $A_{ji}$ ). This value itself represents the weight of the edge, expressing the strength of the interaction. In biological terms, we may interpret this graph as a social network.

As noted above, an observed social network may show some degree of regularity in the arrangement of its edges, which enables describing its structure more concisely. If vertices form clusters whose members are connected more often to each other than to other vertices, we can simplify the network's description by partitioning the vertices into a comprehensive set of non-overlapping clusters. The map equation introduced by Rosvall and Bergstrom (2008) calculates the

description length of a given network. The network structure represents a random variable, which can be thought of as a sequence of vertices visited in a stochastic walk along the edges. Then we can describe the sequence by binary numbers playing the role of codewords denoting vertices visited during the walk. The codewords are chosen in a parsimonious way so that shorter ones are reserved for more frequently visited vertices. The less regular the structure, the more specific and hence longer codewords are required for its description. The average codeword length ( $L$ ), in the bit units, is thus a suitable measure of the description length. The map equation provides a basis for optimal network partitioning, which is carried out through the minimisation of  $L$  as described in detail in Rosvall and Bergstrom (2008) and Rosvall et al. (2009).

The clusters of vertices corresponding to the optimal partitioning are called ‘communities’ or ‘modules’ in the social network literature. Modularity  $M$  is then a quantity expressing the tightness and exclusiveness of the estimated modules. A new module is created in the map equation framework only if it helps to describe the network structure more concisely. Hence, modularity can be quantified using the average codeword length  $L$ , but this value is dependent on the network size. Therefore, we define  $M$  as a compression rate of  $L$ , i.e., the ratio of its value before and after partitioning into the modules:

$$M = \frac{L_{before}}{L_{after}}.$$

In practice, optimal partitioning is found using the Louvain algorithm (Blondel et al. 2008) with  $L$  as the objective function. The search is not constrained in any specific way, and the modules can thus be of any size and composition; it only matters if their delimitation reduces  $L$ . Note that our definition of modularity is different from the most common use of the term (Newman & Girvan, 2004). We use the word as a general term expressing the degree of partitioning into modules.

### 2.2.3. Time dimension

Social relations may change during time, for example, due to birth, death, and migration that change population size and composition. We created a time-ordered collection of layer-specific social networks for each of the four experimental runs. Then we estimated time-extended modules under the extension of map equation formalism described by Aslak et al. (2018) and implemented in the program Infomap (Rosvall & Bergstrom, 2008). In this algorithm, vertices are linked to their neighbours within the same layer as well as with the same set of neighbours in all other layers. The weights of these cross-layer links depend on the similarity of neighbourhood patterns in two particular layers. If a vertex has the same neighbours and similar edge weights in both layers, the cross-layer links are strong. The algorithm then clusters vertices across the layers with the probability dependent on the weight of cross-layer links and a tuneable relaxing rate parameter  $r \in (0,1)$  which balances the importance of within-layer and cross-layer links. The clustering criterion is still the same,  $L$ , and so is the definition of modularity  $M$ . Every individual is assigned to a single module in any particular time layer, but the assignment may change between time layers. Choosing the relaxing rate and the randomisation procedure used for assessing the robustness of the differences in modularity are described in more detail in Supplementary Material. Finally, we examined the sex-specific roles in the social structure dynamics. We re-calculated  $M$  in each experiment from only female-female, male-male, or female-male interactions while keeping the clustering of individuals fixed to the estimated solution. In these calculations, we included only adults ( $\geq 50$  days old individuals).

For illustrative purposes, we depicted three selected social networks from each experiment. The selection was motivated by the observed results (see below). Specifically, we used the networks from (i) the initial period when most of the founders were still present (the first 10 time layers); (ii) 10 time layers covering the period after the establishment of new major modules (starting thirty days after their appearance); and (iii) the last 10 time layers of the experiment when the population structure can be considered ‘mature’. For this display, we calculated the mean interaction strength in the time layers involved. Only the founder and/or already reproducing individuals were included in the calculation (reproduction being proven by parentage analysis, see below).

#### 2.2.4. Spatial dimension

In time layer summaries and all other analyses described above, the location of encounters was ignored. Nevertheless, once the network is partitioned, we can work backwards and detect where the identified modules were settled. Separately for each layer, we calculated the total amounts of time spent by members of particular modules in each of the six boxes. These times were divided by the total usage of the box, which is the sum of times spent by all individuals in the box. The resulting proportions can be understood as box possession values, and their maximum was taken as a measure of the box usage exclusivity. Then, for a given time layer, we calculated an index of spatial separation as a weighted mean of box usage exclusivities, weights being proportional to the total usage of the boxes.

The connection of enclosures brought an extra spatial dimension to the two 2014 parallel runs. Therefore, we examined how often mice moved between the enclosures (evidenced by any signal from the opposite side) and whether they participated in the other subspecies’ social network (evidenced by box entrances).

#### 2.2.5. Software

Apart from Infomap (Rosvall & Bergstrom, 2008), all the statistical analyses described above were implemented in the computing language and environment R (RCore Team, 2019). A collection of functions performing the core of our analyses and drawing the main figures is available at the publicly available repository ([https://github.com/onmikula/movement\\_networks](https://github.com/onmikula/movement_networks)). Included is also a worked-out example based on *domesticus* 2013 experiment. The scripts relied on the functionality of the packages igraph (Csardi & Nepusz, 2006), Matrix (Bates & Maechler, 2019), abind (Plate & Heiberger, 2016), and stringr (Wickham, 2019). For plotting, we used package vioplot (Adler & Kelly, 2018), TeachingDemos (Snow, 2020). The colour palette used for the module display was designed by A. Trubetskoy (<https://sashamaps.net/docs/resources/20-colours>).

### 2.3. Parentage assignment and inference of demes

From founder mice and all their descendants, we collected samples of tissues for subsequent parentage analysis. DNA was then extracted from these ethanol-preserved tissues using DNeasy 96 Blood & Tissue Kit (Qiagen, Düsseldorf, Germany). Panels of 25 and 26 microsatellites were used for parentage assignment (see (Supplementary Material, Table S1). Parentage analysis was performed using CERVUS v. 3.0.3 (Kalinowski et al., 2007) at the 95% confidence level. Individuals meeting defined requirements (e.g., reaching sexual maturity at the estimated time of conception) were



included in the analysis as candidate parents. Based on these data, we assessed the reproductive success of all males and females during the whole experiment.

We quantified multiple paternity for each experimental run as the mean probability that two offspring from the same litter have different fathers. We also examined the association between the modular structure and reproductive behaviour. Specifically, we assessed whether the offspring remain in the same module as their parents or whether they emigrate. It was accomplished by constructing parentage networks with arrows leading from parents to their offspring. We calculated the persistence of family bonds as the proportion of the parentage arrows found within modules for each time layer and each experimental run. These statistics were also evaluated specifically for mother-daughter and father-son interactions.

Parentage data also allow us to address one of the paramount issues of this study, i.e., whether and how the inferred social network modules can be related to basic reproductive units or demes. A module was considered a deme if the coincidence of social and reproductive relations could be proved. A parental pair was assigned to a module in accord with the assignment of the mother at the estimated time of conception. Then, we considered whether both parents interacted preferentially with members of this module. More precisely, we calculated a proportion of time layers from conception to delivery where it holds true and this proportion served as a measure of support for the demic nature of the module. When summed over all parental pairs, the sum can be thought of as an effective number of parental pairs whose reproduction took place in a particular social environment (see also Supplementary Material).

## 3. Results

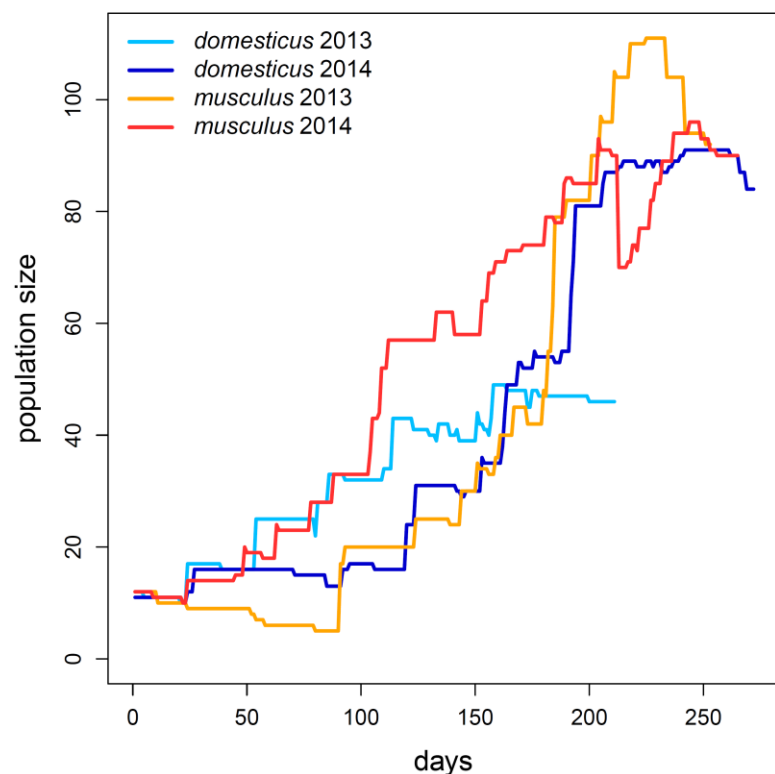
### 3.1. Populations

All but one of the experimental runs revealed a similar trend in population growth. The only exception was the ‘*musculus* 2013’ population in which the growth period was preceded by a severe decline (Fig. 1; see also Fig. S2). Maximum population sizes were 49 in *domesticus* 2013, 91 in *domesticus* 2014, 111 in *musculus* 2013, and 96 in *musculus* 2014. There were usually only 1–2 (occasionally up to five) pregnant or nursing females at the same time until the 150<sup>th</sup> day. After that, there were large fluctuations in all runs (Fig. S2c, d). Table S2 shows details on the total numbers of individuals, numbers of those that reached adulthood and sexual maturity, as well as those participating in reproduction. Reported is also the number of delivered offspring and the number of litters. (Note that while the numbers shown in the figures refer to individuals involved in RFID-tracked interactions, those in the tables refer to all registered individuals.)

### 3.2. Modules

The analysis integrating multiple time layers revealed 4–11 modules in each experiment. The modules varied greatly in their size and lifespan, some comprising a few isolated individuals and lasting no longer than one or a couple of days. The number of long-lasting modules (> 50 days) was just 3–5 (see Table S3 for an overview). The number of modules was not dependent on the population size in any obvious way, but new modules sometimes arose with the introduction of new

offspring, i.e., with the appearance of new vertices. This is because the algorithm does not explicitly consider the appearance of new vertices or the disappearance of old ones, and hence a sudden significant change in population composition results in introducing new modules to minimise the description length.

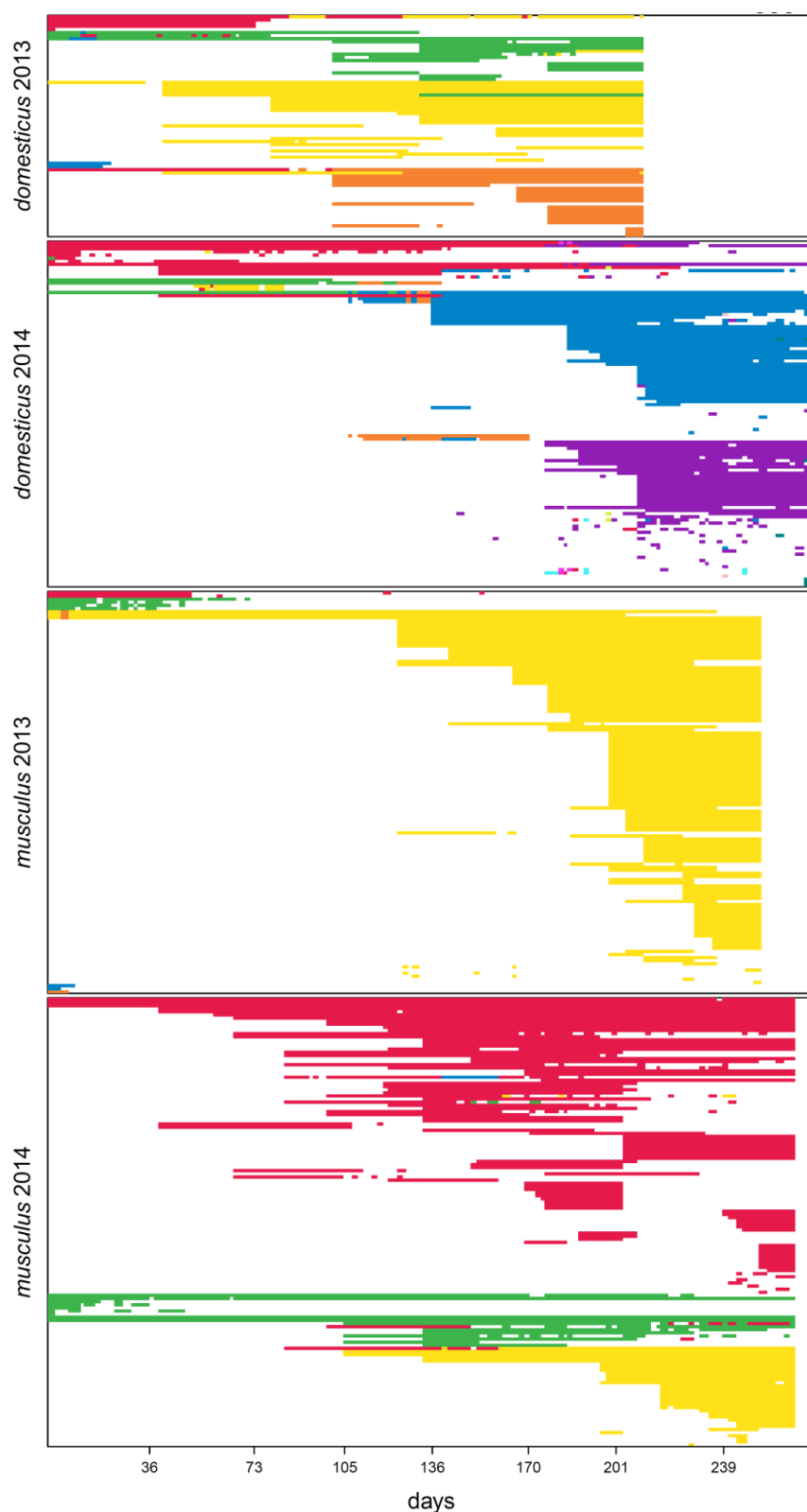


**Figure 1.** Population changes during four experiments. On the abscissa are days since the beginning of each run. On the ordinate are the total numbers of individuals present in the enclosure.

The multi-layer modular structure is graphically depicted in Fig. 2. Each row corresponds to a single individual in this figure, while each column represents one time layer; assignments of individuals to modules are shown in different colours. Immediately after launching the *domesticus* 2013 experiment, four modules were formed, but one of them ('blue') survived only until the 21<sup>st</sup> day, and another ('red') dissolved into 'yellow' and 'orange' modules, respectively. The latter was estimated to form at about the 104<sup>th</sup> day when the offspring of the 'red' module's founding female were weaned, received transmitters, and thus entered the record. In the *domesticus* 2014 run, two modules that arose initially ('red' and 'green') were gradually transformed into two modules dominating the social structure at the end of the experiment ('blue' and 'purple'). The transformation reflected a gradual extinction of founding individuals and their replacement by newly born offspring. In addition, there were seven modules, often representing a temporary association of siblings with some of their parents or an episodic interaction of immigrants with local inhabitants. The *musculus* 2014 run started with two modules ('red' and 'green', both persisting until the end), from the 106<sup>th</sup> day on, accompanied by the third module ('yellow'). In both persisting initial modules, three of their founders also survived until the end, whereas the later-appearing one was established by the first-generation offspring born in the enclosure. The fourth module, which also appeared in this experiment, was marginal. Finally, as noted above, the *musculus* 2013 run was very different from the remaining experiments. While five modules occurred initially, two of them were



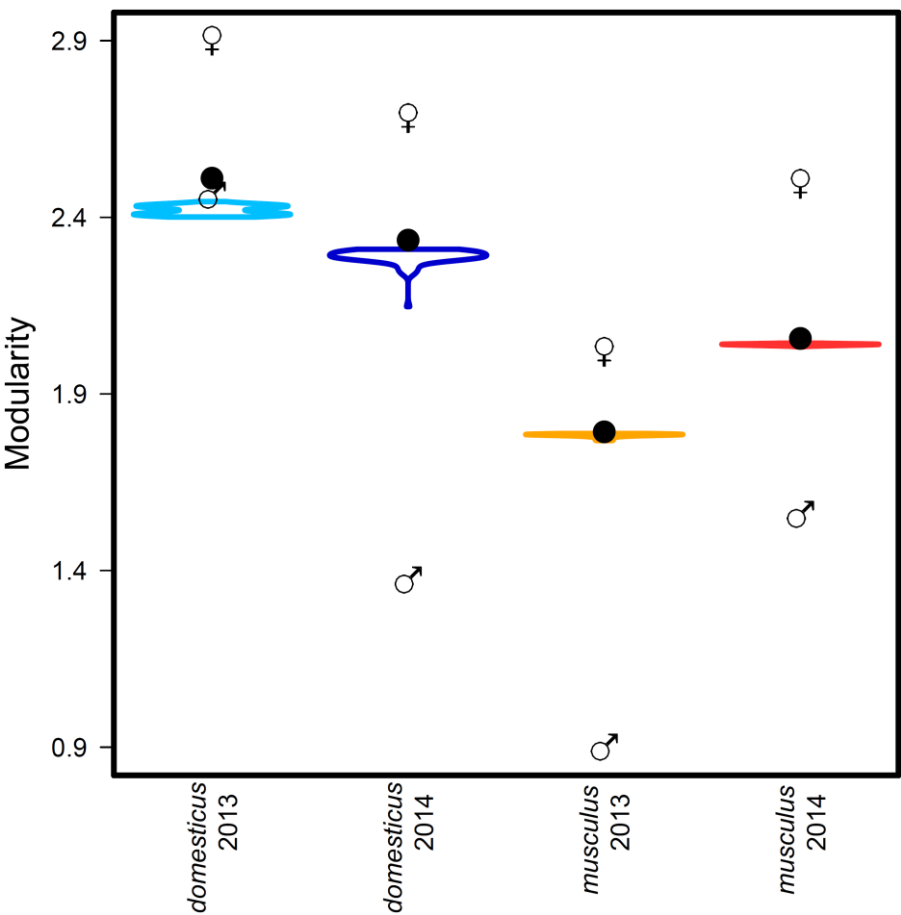
318 substantially short-lived, and only one module ('yellow') survived, dominating the rest of the  
 319 experiment.



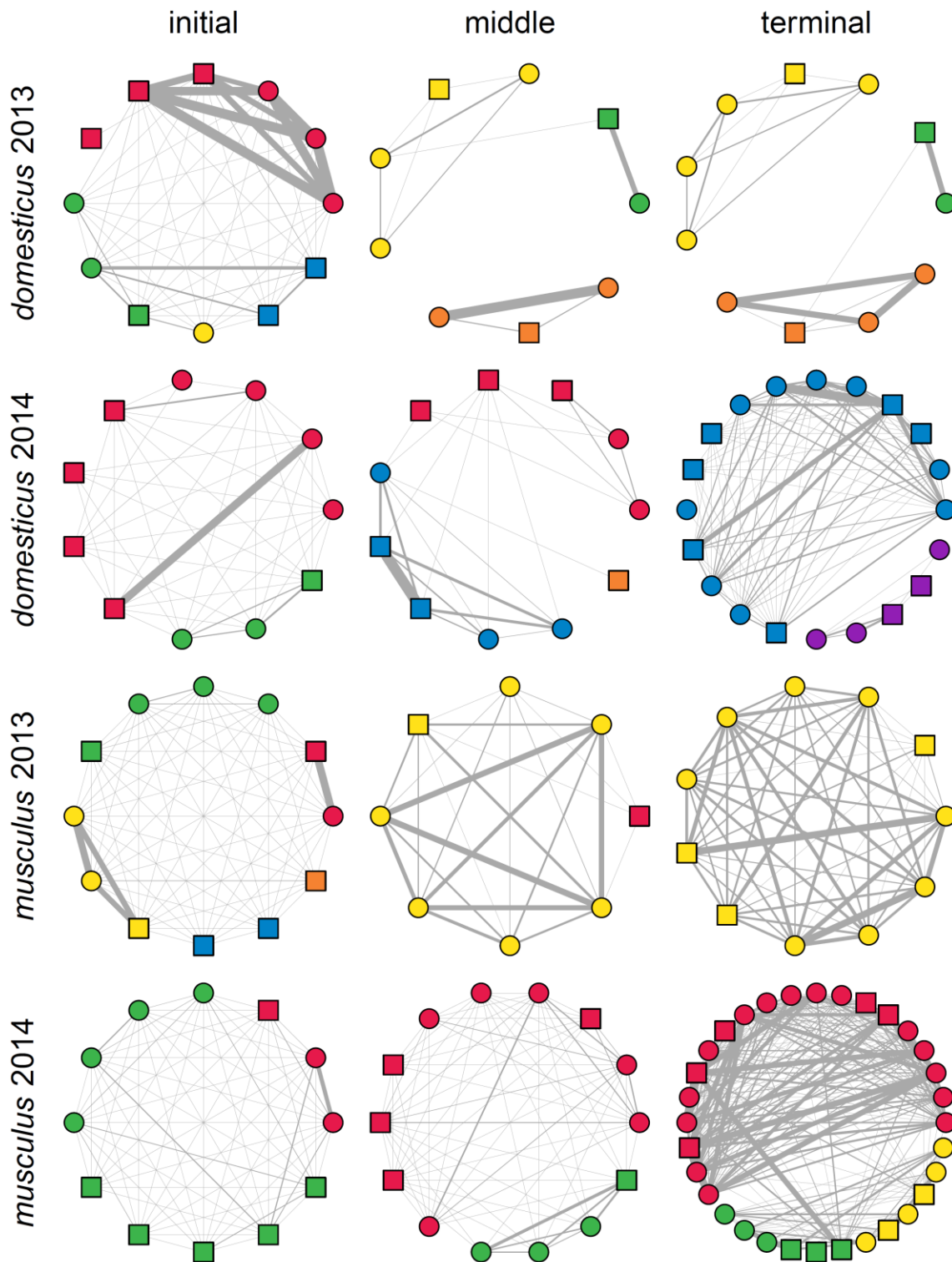
**Figure 2.** The modular structure of the experimental populations. Rows of the bar plots correspond to individuals and columns to time layers. On the abscissa is time in days. Colours indicate module membership, while blank spaces indicate time layers in which the individuals did not enter any box. Note that in the 'musculus 2013' experiment, the red module persists considerably long via the episodic occurrence of a single 'red' individual. This is the trace of a subpopulation allowed to survive in the exit box (see Supplementary Material).

### 3.3. Modularity

To quantify the degree of tightness and exclusiveness of the estimated modules, we introduced a new index of modularity,  $M$  (see Methods for details). The most fundamental result of our study is the difference in this index between the subspecies. While in *M. m. musculus*,  $M$  was 1.78 (2013) and 2.05 (2014), respectively, in *M. m. domesticus*, it was as high as 2.51 (2013) and 2.33 (2014), respectively (Table 1). Fig. 3 shows these estimates together with the randomisation support (represented by violin plots). The difference between subspecies is apparent even in the ordination of randomised distributions. The modularity of *M. m. domesticus* populations seems to be slightly more dependent on individual movement details, but it still holds their minimum randomised  $M$  was higher than that observed in *M. m. musculus* populations (Table S2). In all cases,  $M$  values calculated from female-female interactions were considerably higher than those based solely on male-male interactions within individual runs (see gender symbols in Fig. 3). By contrast,  $M$ s calculated from male-female interactions (Table S2) were all close to the overall values. The presented solution was obtained with the relaxing rate parameter  $r = 0.60$ . However, the full sequence of  $M$  values obtained under different relaxing rates also supports the conclusion that *M. m. domesticus* is more ‘demic’ than *M. m. musculus* (Fig. S3) and confirms, via randomisation, that differences in  $M$  are reasonably robust to accidental details of movement records.



**Figure 3.** Modularity quantified for each experimental run as the compression rate of the description length (see Methods for details) compared between original data (black dots) and randomised replicates (violin plots). Venus and Mars’s symbols show values based on female-female and male-male interactions, respectively.



**Figure 4.** Summary of social networks calculated for three periods, each consisting of ten time layers. Line widths reflect the strength of social interaction; vertex colours indicate prevailing module membership, and their shapes correspond to sex (squares are for males, circles for females). The networks cover the following time spans (in days since the start of the experiment): 1–25, 136–155, 195–211 (*domesticus* 2013); 1–21, 134–156, 250–272 (*domesticus* 2014); 1–25, 136–155, 233–253 (*musculus* 2013) and 1–21, 134–156, 245–265 (*musculus* 2014). The displayed networks contain only individuals involved in reproduction.

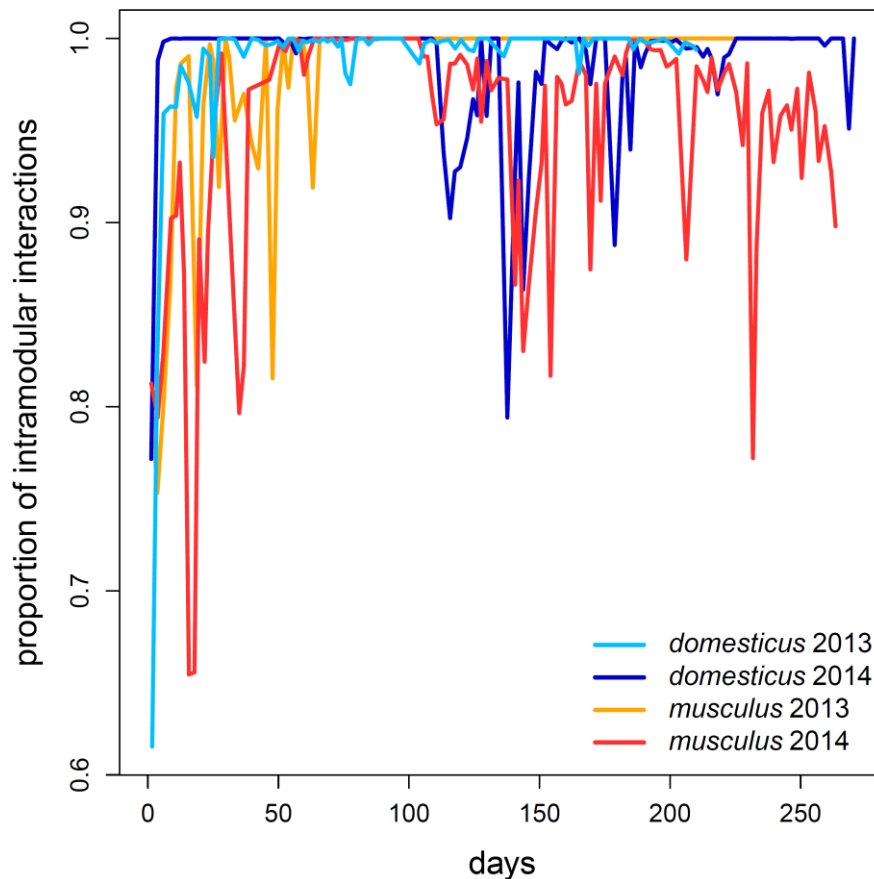
**Table 2.** Modularity in the four experimental populations, calculated with  $r = 0.60$ .

	Full data	Female-female	Male-male	Male-female	Minimum randomised value	Maximum randomised value
<i>domesticus</i> 2013	2.51	2.91	2.46	2.44	2.40	2.44
<i>domesticus</i> 2014	2.33	2.68	1.36	2.38	2.14	2.31
<i>musculus</i> 2013	1.78	2.01	0.88	1.88	1.76	1.78
<i>musculus</i> 2014	2.05	2.50	1.54	2.13	2.03	2.04

Summary networks are depicted for the three selected periods: the first ten layers of each experiment (initial), ten layers covering an advanced phase of the demic dynamics (middle), and the last ten layers (terminal). These graphs render an illustrative picture of the social structure difference between the two subspecies: while *M. m. musculus* displays multiple and recurrent intermodular interactions, these vanish with time in *M. m. domesticus* (Fig. 4).

The between-subspecies difference in the level of modularity is corroborated by module distinctiveness expressed as the proportion of intramodular interactions (Fig. 5). The maximum value of 1.00 means all individuals met in the boxes only with members of their modules). In both *M. m. domesticus* populations, this proportion approached 1.00 in 5–30 days after launching the experiments and tended to remain close to the maximum value until the end. Even in *domesticus* 2014, occasional deep drops were followed by a fast recovery of high distinctiveness. A more detailed examination revealed these drops could be explained by the temporary relaxation of father-son bonds (Fig. S6). In *musculus* 2014, module distinctiveness reached its maximum later (after ~50 days), and it remained high only until the rise of the third module ('yellow' in Fig. 2) on the 106<sup>th</sup> day. Since then, it fluctuated between 0.77 and 1.00. Again, loose father-son bonds can be largely responsible for the lower distinctiveness of the modules (Fig. S6). From around the 50<sup>th</sup> day onwards, only a single module existed in the *musculus* 2013 population. The mice could only interact within their group, and distinctiveness was 1.00, thus resembling *M. m. domesticus*.

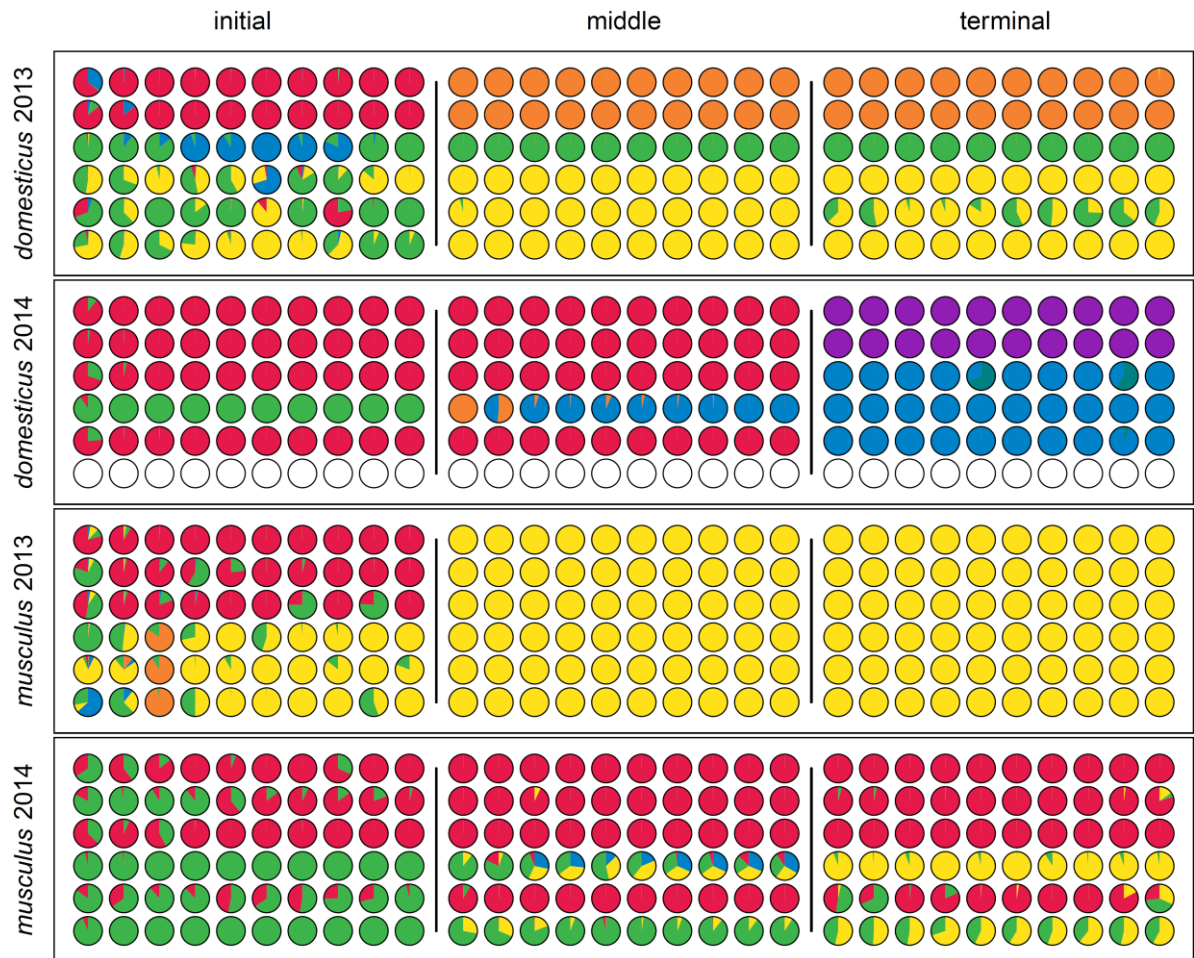
The spatial separation of modules (Fig. S4, Supplementary Material) closely parallels the picture revealed by module distinctiveness. These differences are further corroborated if we look at each of the six nest boxes' occupancies by members of individual modules (Fig. 6) in the same periods as covered by the summary networks shown in Fig. 4. In both subspecies, a substantial spatial admixture can be seen in the initial period. Later on, a visible difference arises. In *M. m. domesticus* runs, the admixture is very limited, confined to a single nest box, a few time layers, and in *domesticus* 2014, also to marginally significant modules. On the contrary, in *M. m. musculus* the admixture persisted in four nest boxes and was quite extensive, especially between the green module and the rest (in *musculus* 2014 run, which was the only informative in this respect, containing more than one module).



**Figure 5.** Module distinctiveness quantified as a mean proportion of time spent by individuals in interactions with their module members.

### 3.4. Connecting enclosures

During the last part of the 2014 experiment, connecting the arenas resulted in the migration of some individuals to the opposite enclosure. We recorded 266 such events, but 154 of them (58%) were due to just five males: four *domesticus* and one *musculus* male. The remaining 112 migrations were due to 49 individuals (9 females/19 males in *domesticus* and 11 females/10 males in *musculus*) distributed in time are shown in Fig. S5 (Supplementary Material). The migration rate was highest shortly after interconnecting the enclosures in both subspecies, yet this remained high much longer in *M. m. domesticus*, with another peak ~50 days after the interconnection, short before the end of the experiment. These remaining migrations were distributed between the subspecies and sexes as follows: 20 in *domesticus* females, 54 in *domesticus* males, 14 in *musculus* females, and 24 in *musculus* males. These numbers are negligible compared to thousands of movements recorded within every time layer in both enclosures, but on the other hand, they indeed underestimate real figures. Due to design limitations (just one reader on each side of the connecting tube), it was hard to distinguish real migration from the background of unrealised migration attempts. In total, we detected as many as 3813 attempts, but we do not know for sure how many of them were successful. Interactions of the migrants with residents were scarce. First, we did not find their co-occurrence within a single nest box. And second, although five *musculus* individuals were occasionally involved in *domesticus* networks and one *domesticus* individual entered *musculus* boxes, all these cases were detected within just a single time layer shortly after interconnecting the arenas. In no case the intruders stayed and reproduced in the opposite enclosure.



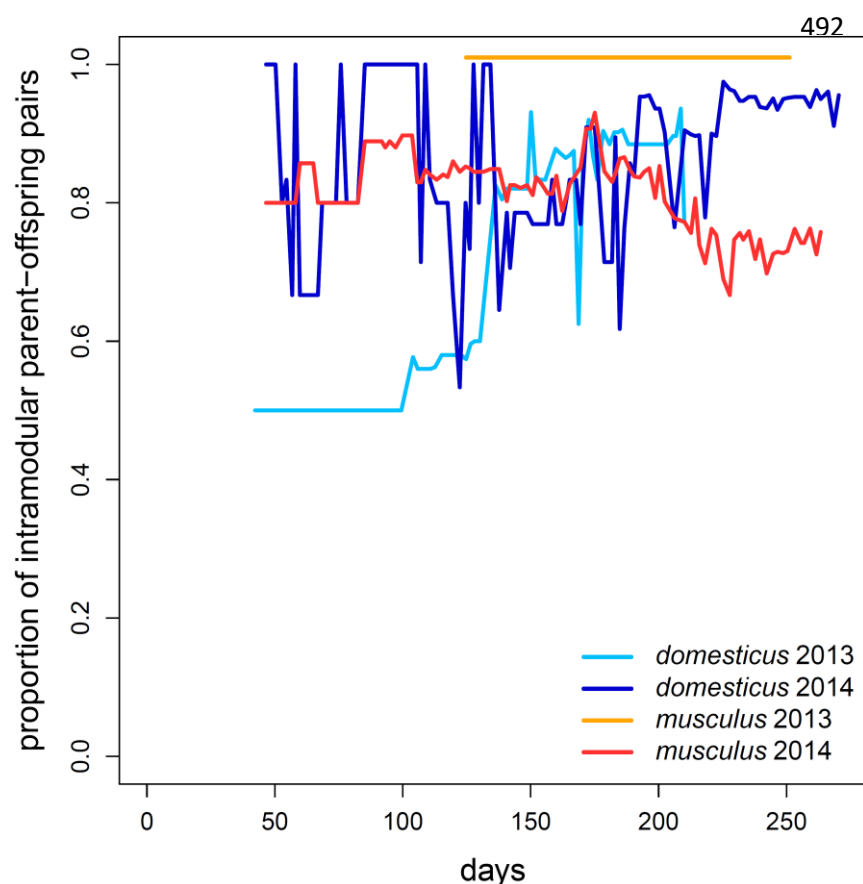
**Figure 6.** The spatial separation of modules in three selected periods of the four experimental runs. Rows correspond to nest boxes, columns to time layers, and pies show the proportions of box occupancy by members of different modules (with colour code as in Fig. 2; empty circles depict unoccupied boxes). Every period consists of 10 time layers, the same as in summary networks.

### 3.5. Parentage and demic structure

In *M. m. domesticus*, the offspring appears more likely to remain with their parents in the same module (Fig. 7). Sex-focused analyses reveal that this is mainly due to mother-daughter interactions (Fig. S6). Multiple paternity (i.e., probability that two siblings have different fathers) was equal to 0.04 in *domesticus* 2013, 0.15 in *domesticus* 2014, 0.11 in *musculus* 2013, and 0.42 in *musculus* 2014. Note that the value in *musculus* 2013, where a single module was present for most of the trial duration, is almost as high as in *domesticus* 2014. It is also striking because the time window when this multiple fathering came about was relatively narrow – reproduction started with just one male surviving in the enclosure, and the first offspring sired by someone else appeared as late as 94 days after the first offspring male was born. These results suggest looser intramodular bonds and/or lower control of a dominant male over reproduction in *M. m. musculus* relative to *M. m. domesticus*.



Knowledge of associations between parents, their offspring, and modules they are mostly associated with allows us to relate individual modules to reproductive units (demes), i.e., inferring the number of presumed demes in each experiment. Overall, inferred demes perfectly matched the long-lasting modules persisting for more than 50 days. Support for individual demes ranged from 0.92 ('red' module in '*domesticus* 2013') to 33.04 ('red' module in '*musculus* 2014'; cf. Fig. 2 and Table S3). All other modules could not be considered true demes.



**Figure 7.** The persistence of family bonds within modules shown as changes in the proportion of parent-offspring pairs found within modules through time.

## 4. Discussion

In all experimental runs, *M. m. domesticus* displayed higher modularity than *M. m. musculus* (with the difference ranging from 0.28 between the '*domesticus* 2014' and '*musculus* 2014' population to 0.73 between the '*domesticus* 2013' and '*musculus* 2013' population). It means that the former subspecies has a closer population structure, which can involve either subdivision into modules or a higher degree of regularity in intramodular interactions (recall that module tightness is defined in terms of compressibility in the map equation framework, which is unrelated to internal link density).

Since we could run only two replicates of RFID experiments per subspecies, we could not test whether the contrast in modularity between them was significant. However, there are reasons to believe the difference is real. First, there is a clear difference in the distinctiveness of the estimated modules (Fig. 4). In *M. m. domesticus*, their boundaries were very sharp, with little or no contact between members of different modules. In contrast, contacts between different modules' members were commonplace in *M. m. musculus* (cf. Figs. 4 and 5). Second, within *M. m. domesticus* modules, nest boxes were shared much less often than in *M. m. musculus*. Although sharing a nest box does

not always mean a direct encounter, higher vs. lower spatial separation indicates a real behavioural/ecological difference (Evans et al. 2021a). Third, more intramodular parent-offspring pairs in *M. m. domesticus* than in *M. m. musculus* (Figs. 7 and S6) are consistent with the higher modularity of the former subspecies. Finally, multiple paternity was considerably lower in *M. m. domesticus*, suggesting higher dominance and control over reproduction in this subspecies. This contrasts with previous studies reporting comparable or only slightly lower multiple paternities in *M. m. domesticus* (Dean et al., 2006; Firman & Simmons, 2008; Thornhauser et al., 2014; our unpublished data).

Although this study focuses on contrasting *musculus* and *domesticus* in the first place, we should also note higher modularity in females than males within each subspecies (Fig. 3). This is consistent with the higher persistence of mothers-daughters bonds than fathers-sons interactions (Fig. S6), possibly suggesting higher philopatry of females. Our study thus corroborates the results of Evans et al. (2021b) and Königin et al. (2021), who found that females of *M. m. domesticus* preferentially breed within their maternal community.

Since the 1950s, lots of ecological and genetic studies have suggested that *M. m. domesticus* populations are structured into small and relatively rigid and closed units (Anderson, 1964; Crowcroft, 1955; Crowcroft & Rowe, 1963; Lewontin & Dunn, 1960; Lidicker, 1976; Reimer & Petras, 1967; Selander, 1970) and that these units or demes do not survive longer than a few months (Singleton, 1983; Pocock et al., 2005; König et al., 2015; Evans et al., 2021c). However, considerable evidence has also been gathered that many *domesticus* populations are not so tightly organised (Berry, 1981; Sage, 1981). Nevertheless, this subspecies has generally been considered more ‘demic’ than *M. m. musculus*. Such the opinion is based on two tenets: first, the demic structure is characteristic of commensal populations, and second, *domesticus* is often believed to be more commensal than *musculus*. However, as Ganem (2012) pointed out, the latter assumption has never been reliably documented.

Moreover, it should be mentioned that *M. m. musculus* is also ecologically highly flexible, as shown by many studies (Krasnov, 1988; Krasnov & Khokhlova, 1994; Pelikán, 1981; Petrusiewicz & Andrzejewski, 1962; Walkova, 1981). On the other hand, permanent non-commensal *M. m. domesticus* populations are relatively common (e.g., Cassaing & Croset, 1985; Hardouin et al., 2010; Navarro et al., 1989; Sage, 1981; Triggs, 1991; Webb et al., 1997). In this context, it is important that we seeded all the experimental populations with individuals collected from the same central European area (two within the *M. m. domesticus* distribution area and the other two within the *M. m. musculus* range). The sampling sites are located at similar latitudes and altitudes and represent the same indoor, commensal habitat. This way, we avoided potential confounding effects of different environmental conditions known to affect house mouse ecological strategies (Butler, 1980; Noyes et al., 1982; Pocock et al., 2004; Singleton & Krebs, 2007) and hence demonstrated a significant distinction in the social structure between the two subspecies without any reference to (either real or suspected) differences in the level of commensalism. Likewise, owing to identical conditions in the enclosures, we assume the differences revealed in this study are not simply a manifestation of the social flexibility reported in several bird and mammal species (Davies, 1992; Kappeler & van Schaik, 2002; Schradin et al., 2012).

Given our method of detecting social network modules, one key question arises: How can the identified modules be related to basic reproductive units or demes? We believe this issue can be addressed by combining paternity data with information on associations with individual modules across time layers. Our results show a close relation between demes and stable modules persisting for more than seven weeks (Table S3; Supplementary Material).

The higher modularity of *M. m. domesticus* appears consistent with about twice as high global effective population size ( $N_e$ ) as that of *M. m. musculus* (Gerlandes et al., 2008; Phifer-Rixey et al., 2012; Salcedo et al., 2007). (Interestingly, the Asian subspecies *M. m. castaneus*, considered the most strictly commensal of the three main house mouse subspecies (Sage, 1981), also has the highest  $N_e$  (Gerald et al., 2008; Phifer-Rixey et al., 2012). Therefore, it would be useful to extend the experiment reported here also to *castaneus*.) In contrast, socially mediated reduction of gene flow, in combination with polygynous mating, should decrease  $N_e$  of *local* demes more in *M. m. domesticus* than in *M. m. musculus*. Joint effects of genetic drift and inbreeding in small, socially structured subpopulations can facilitate the fixation of underdominant chromosomal rearrangements such as Robertsonian fusions (Britton-Davidian et al., 2007; Dallas et al., 1998; Nachman & Searle, 1995). According to Bush (1975) and Wilson et al. (1975), this process can result in establishing postzygotic reproductive isolation promoting stasipatric speciation (White, 1978; Sites & Moritz, 1987). However, given the great ecological plasticity of house mice, it is unclear how the differences in social structure between the two taxa evidenced in this study relate to the dynamics of secondary contact between them.

By connecting the enclosures around the last quarter of the 2014 experiments, we wanted to simulate an initial contact between the subspecies and appraise potential differences in their dispersal and exploration strategies. Surprisingly, migrations between the arenas were infrequent, and their frequency was even decreasing with time (Fig. S5). This finding may correspond with the poor ability of mice to re-invade sub-Antarctic Kerguelen islands already populated by residents (Hardouin et al., 2010). We further corroborated the higher dispersion rate of males in both taxa as well as a more active exploration of an unfamiliar space by *M. m. domesticus* of both sexes (Hiadlovská et al., 2013; Vošlajerová Bímová et al., 2016). However, all the migration events were ephemeral, reflecting the inherent neophilia of house mice (Barnett, 1988; Chitty, 1954), although this may apply more to lab mice than wild mice, as shown by Kronenberg & Medioni (1985) rather than actual dispersal.

To conclude, we showed that describing network structures through binary codeword lengths estimated by the map equation (Rosvall & Bergstrom, 2008) and the vertex-level coupling method (Aslak et al., 2018) is very useful for treating large RFID-based longitudinal data sets. This method not only avoids the need for analysing successive time layers one by one but also separates two conceptually different issues: the quantification of cross-layer coupling and its weighting relative to intra-layer connectivity. While the cross-layer coupling reflects the similarity of intra-layer connectivity patterns, the relative weights are given by choice of some relaxing rate. In contrast, the multi-layer generalisation of Newman and Girvan's modularity (Mucha et al., 2010) conflates these issues by relying on tunable weights of links connecting identical vertices in different layers. As a result, the persistence of modules through multiple layers is less likely due to the particular choice of the tuning parameter. It is also worth stressing that although modularity defined by the compression rate of the average code length is unbounded at its upper end, it is independent of network size, a

favourable property it shares with Newman and Girvan's modularity. Finally, it is expected to suffer less from the resolution limit problem (Kawamoto & Rosvall, 2015), i.e., the impossibility of detecting modules that are too small relative to the overall size of the network (Fortunato & Barthelemy, 2007). In this way, we could render, for the first time, robust quantitative evidence that commensal populations of the two European house mouse subspecies subjected to identical environmental conditions develop diverse social networks and hence differ in their social structure.

## Ethics

The experiments were performed in the Institute of Vertebrate Biology breeding facility, Czech Academy of Sciences (License No. 227203/2011-MZE-17214 2011-2016). Animals were handled by authorised persons only (Licenses No. CZ 01267 (LĎ), CZ 01293 (BVB), and CZ 01271 (ZH). The experimental protocols (145/2010) were approved by the Ethical Commission of the IVB and followed the EU Directive 2010/63/EU.

## Acknowledgements

We are grateful to U. Aslak and M. Rosvall for their advice on the application of Infomap algorithm to this specific research task. I. Pospíšilová, J. Růžičková, and L. Rousková is acknowledged for help in the enclosures. We thank B. König for offering a member of our team (ZH) a short stint in her lab to gain skills in performing experiments with mice in semi-natural enclosures and for useful comments on an earlier version of the manuscript.

## Funding

The study was funded with the Czech Science Foundation grants Nos. P506-11-1792, 19-19056S (to MM), and 17-25320S (to BVB). Computational resources were supplied by the project 'e-Infrastruktura CZ' (e-INFRA LM2018140) provided within the program Projects of Large Research, Development and Innovations Infrastructures.

## Competing interests

The authors declare no competing interests.

## 636 **Authors' contributions**

637 B.V.B. and M.M. designed the study, Ľ.Ď., Z.H., K.D., and K.J. collected the data, K.D. carried out the  
638 analysis of parentage, O.M. statistically processed the data, O.M. and M.M. drafted the manuscript,  
639 and O.M., M.M., Z.H., K.D., and B.V.B. contributed to the final version of the manuscript.

## References

- Adler D, Kelly ST. 2018 vioplot: violin plot. R package version 0.3.2.  
(<https://github.com/TomKellyGenetics/vioplot>)
- Anderson PK. 1964 Lethal alleles in *Mus musculus*: local distribution and evidence for isolation of demes. *Science* **145**, 177–178.
- Aslak U, Rosvall M, Lehmann S. 2018 Constrained information flows in temporal networks reveal intermittent communities. *Phys. Rev. E* **97**, 062312.  
(<https://doi.org/10.1103/PhysRevE.97.062312>)
- Barnett SA. 1988 Exploring, sampling, neophobia, and feeding. In *Rodent pest management* (ed I Prakash), pp. 295–320. Boca Raton, FL: CRC Press.
- Bates D, Maechler M. 2019. Matrix: Sparse and Dense Matrix Classes and Methods. R package version 1.2-18. (<https://CRAN.R-project.org/package=Matrix>)
- Berry RJ. 1970 The natural history of the house mouse. *Fld. Stud.* **3**, 219–262.
- Berry RJ. 1981 Population dynamics of the house mouse. In *Biology of the house mouse* (ed RJ Berry), pp. 395–425. Symposia of the Zoological Society of London, vol. 47. London: Academic Press, Ltd.
- Bímová B, Karn RC, 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. (doi: 10.1111/j.1095-8312.2005.00439.x)
- Blondel VD, Guillaume J-L, Lambiotte R, Lefebvre E. 2008. Fast unfolding of communities in large networks. *Journal of Statistical Mechanics: Theory and Experiment* **2008**, P10008.  
(doi:10.1088/1742-5468/2008/10/P10008)
- Boursot P, Auffray J-C, Britton-Davidian J, Bonhomme F. 1993 The evolution of house mice. *Ann. Rev. Ecol. Syst.* **24**, 119–152. (doi: <https://doi.org/10.1146/annurev.es.24.110193.001003>)
- Britton-Davidian J, Catalan J, Lopez J, Ganem G, Nunes AC, Ramalhinho MG, Auffray J-C, Searle JB, Mathias ML. 2007 Patterns of genic diversity and structure in a species undergoing rapid chromosomal radiation: an allozyme analysis of house mice from the Madeira archipelago. *Heredity* **99**, 432–442. (doi: 10.1038/sj.hdy.6801021)
- Bush GL. 1975 Modes of animal speciation. *Annu. Rev. Ecol. Syst.* **6**, 339–364.
- Butler RG. 1980 Population size, social behaviour, and dispersal in house mice: a quantitative investigation. *Anim. Behav.* **28**, 78–85.
- Cassaing J, Croset H. 1985 Spatial organisation, competition and dynamics of wild mice populations (*Mus spretus* Lataste and *Mus domesticus* Ratty) in Southern France. *Z. Säugetierk.* **50**, 271–284.
- Chitty D. 1954 *Control of rats and mice*. Oxford: Clarendon Press.



673 Clutton-Brock T. 2017 Reproductive competition and sexual selection. *Phil. Trans. R. Soc. B* **372**,  
674 20160310. <http://dx.doi.org/10.1098/rstb.2016.0310>

675 Clutton-Brock TH, Lukas D. 2012 The evolution of social philopatry and dispersal in female mammals.  
676 *Mol Ecol.* **21**, 472–492. (doi: 10.1111/j.1365-294X.2011.05232.x)

677 Coyne JA, Orr HA. 2004 *Speciation*. Sunderland, MA: Sinauer Associates.

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

679 Crowcroft P, Rowe FP. 1963 Social organisation and territorial behaviour in the wild house mouse  
680 (*Mus musculus* L.). *Proc. Zool. Soc. Lond.* **140**, 517–531.

681 Csardi G, Nepusz T. 2006 The igraph software package for complex network research. *InterJournal*,  
682 *Complex Systems* 1695, 1–9. (doi: <http://igraph.org>)

683 Dallas JF, Bonhomme F, Boursot P, Britton-Davidian J, Bauchau V. 1998 Population genetic structure  
684 in a Robertsonian race of house mice: evidence from microsatellite polymorphism. *Heredity* **80**,  
685 70–77. (doi: 10.1046/j.1365-2540.1998.00258.x)

686 Daniszová K, Mikula O, Macholán M, Pospíšilová I, Vošlajerová Bímová B, Hiadlovská Z. 2017  
687 Subspecies-specific response to ACTH challenge test in the house mouse (*Mus musculus*). *Gen.*  
688 *Comp. Endocrinol.* **252**, 186–192. (doi: 10.1016/j.ygcen.2017.06.023)

689 Dean M, Ardlie G, Nachman M. 2006 The frequency of multiple paternity suggests that sperm  
690 competition is common in house mice (*Mus domesticus*). *Mol. Ecol.* **15**, 4141–4151. (doi:  
691 10.1111/j.1365-294X.2006.03068.x)

692 Dewsbury DA. 1990 Individual attributes generate contrasting degrees of sociality in voles. In *Social*  
693 *systems and population cycles in voles*. Advances in life sciences (eds RH Tamarin, RS Ostfeld, SR  
694 Pugh, G Bujalska), pp. 1–9. Basel: Birkhäuser.

695 Drobnia SM, Wagner G, Mouroucq E, Griesser M. 2015 Family living: an overlooked but pivotal social  
696 system to understand the evolution of cooperative breeding *Behav. Ecol.* **26**, 805–811. (doi:  
697 10.1093/beheco/arv015)

698 Ďureje L, Vošlajerová Bímová B, Piálek J. 2011 No postnatal maternal effect on male aggressiveness  
699 in wild-derived strains of house mice. *Aggress. Behav.* **35**, 48–55. (doi: 10.1002/ab.20371)

700 Evans J, Liechti JL, Silk MJ, Bonhoffer S., König B. 2021a Quantifying the influence of space on social  
701 group structure. *bioRxiv* doi: <https://doi.org/10.1101/2020.12.10.419317>

702 Evans J, Lindholm A, König B. 2021b Family dynamics reveal that female house mice preferentially  
703 breed in their maternal community. *Behav. Ecol. Arab* **128**.  
704 (<https://doi.org/10.1093/beheco/arab128>)

705 Evans JC, Lindholm AK, König B. 2021c Long-term overlap of social and genetic structure in free-  
706 ranging house mice reveals dynamic seasonal and group size effects. *Curr. Zool.* **67**, 59–69.  
707 (<https://doi.org/10.1093/cz/zoaa030>)

708 Ferrari M, Lindholm AK, König B. 2019 Fitness consequences of female alternative reproductive  
709 tactics in house mice (*Mus musculus domesticus*). *Am. Nat.* **193**, 106–124.

710 Finn KR, Silk MJ, Porter MA, Pinter-Wollman N. 2019 The use of multi-layer network analysis in  
711 animal behaviour. *Anim. Behav.* **149**, 7–22. (doi: 10.1016/j.anbehav.2018.12.016)

712 Fortunato S, Barthelemy M. 2007 Resolution limit in community detection. *Proc. Natl. Acad. Sci. USA*  
713 **104**, 36–41. (doi: 10.1073/pnas.0605965104)

714 Firman RC, Simmons LW. 2008 The frequency of multiple paternity predicts variation in testes size  
715 among island populations of house mice. *J. Evol. Biol.* **21**, 1524–1533. (doi:  
716 <https://doi.org/10.1111/j.1420-9101.2008.01612.x>)

717 Ganem G. 2012 Behaviour, ecology and speciation in the house mouse. In *Evolution of the house*  
718 *mouse* (eds M. Macholán, SJE Baird, P Munclinger, J Piálek), pp. 373–406. Cambridge, UK:  
719 Cambridge University Press.

720 Geraldès A, Basset P, Gibson B, Smith KL, Harr B, Yu HT, Bulatova N, Ziv Y, Nachman MW. 2008  
721 Inferring the history of speciation in house mice from autosomal, X-linked, Y-linked and  
722 mitochondrial genes. *Mol Ecol.* **17**, 5349–5363. (doi: 10.1111/j.1365-294X.2008.04005.x)

723 Hardouin EA, Chapuis J-L, Stevens MI, van Vuuren JB, Quillfeldt P, Scavetta RJ, Teschke M, Tautz D.  
724 2010 House mouse colonisation patterns on the sub-Antarctic Kerguelen Archipelago suggest  
725 singular primary invasions and resilience against re-invasion. *BMC Evol. Biol.* **10**, 325.  
726 (<http://www.biomedcentral.com/1471-2148/10/325>)

727 Hiadlovská Z, Hamplová P, Berchová Bímová K, Macholán M, Vošlajerová Bímová B. 2021 Ontogeny  
728 of social hierarchy in two European house mouse subspecies and difference in the social rank of  
729 dispersing males. *Behav. Proc.* **183**, 104316. (doi: <https://doi.org/10.1016/j.beproc.2021.104316>)

730 Hiadlovská Z, Macholán M, Mikula O, Vošlajerová Bímová B. 2014 The meek inherit the earth: less  
731 aggressive wild mice are more successful in challenging situations. *Biol. J. Linn. Soc.* **113**, 310–319.  
732 (<https://doi.org/10.1111/bij.12307>)

733 Hiadlovská Z, Mikula O, Macholán M, Hamplová P, Vošlajerová Bímová B, Daniszová K. 2015 Shaking  
734 the myth: body mass, aggression, steroid hormones, and social dominance in wild house mouse.  
735 *Gen. Comp. Endocrinol.* **223**, 16–26. (doi: 10.1016/j.ygcen.2015.09.033)

736 Hiadlovská Z, Vošlajerová Bímová B, Mikula O, Piálek J, Macholán M. 2013 Transgressive segregation  
737 in a behavioural trait? Explorative strategies in two house mouse subspecies and their hybrids.  
738 *Biol. J. Linn. Soc.* **108**, 225–235. (<https://doi.org/10.1111/j.1095-8312.2012.01997.x>)

739 Holme P. 2015 Modern temporal network theory: a colloquium. *Eur. Phys. J. B* **88**, 234. (doi:  
740 10.1140/epjb/e2015-60657-4)

741 Jarne P, Städler T. 1995 Population genetic structure and mating system evolution in freshwater  
742 pulmonates. *Experientia* **51**, 482–497. (<https://doi.org/10.1007/BF02143200>)

743 Kalinowski ST, Taper ML, Marshall TC. 2007 Revising how the computer program CERVUS  
 744 accommodates genotyping error increases success in paternity assignment. *Mol. Ecol.* **16**, 1099–  
 745 1106. (doi:10.1111/j.1365-294X.2007.03089.x)

746 Kappeler PM. 2019 A framework for studying social complexity. *Behav. Ecol. Sociobiol.* **73**, 13.  
 747 (<https://doi.org/10.1007/s00265-018-2601-8>)

748 Kappeler PM, van Schaik CP. Evolution of Primate social systems. *Int. J. Primatol.* **23**, 707–740.  
 749 (<https://doi.org/10.1023/A:1015520830318>)

750 Kawamoto T, Rosvall M. 2015 Estimating the resolution limit of the map equation in community  
 751 detection. *Phys. Rev. E*. **91**, 012809. (doi: 10.1103/PhysRevE.91.012809)

752 Kemppainen P, Li Z, Rastas P, Löytynoja A, Fang B, Yang J, Guo B, Shikano T, Merilä J. 2021 Genetic  
 753 population structure constrains local adaptation in sticklebacks. *Mol. Ecol.* **30**, 1946–1961. (doi:  
 754 10.1111/mec.15808)

755 König, B. 1994 Fitness effects of communal rearing in house mice: The role of relatedness versus  
 756 familiarity. *Anim. Behav.* **6**, 1449–1457 (<https://doi.org/10.1006/anbe.1994.1381>)

757 König B, Lindholm AK, Lopes PC, Dobay A, Steinert S, Buschmann FJU. 2015 A system for automatic  
 758 recording of social behavior in a free-living wild house mouse population. *Anim. Biotelemetry*. **3**,  
 759 39. (doi: 10.1186/s40317-015-0069-0)

760 Kramer J, Meunier J. 2019 The other facets of family life and their role in the evolution of animal  
 761 sociality. *Biol. Rev.* **94**, 199–215. (<https://doi.org/10.1111/brev.12443>)

762 Krasnov BR. 1988 Ecology of *Mus musculus* (Rodentia, Muridae) in the north-east of the USSR. *Zool.*  
 763 *Zh.* **67**, 102–110. [In Russian with English summary]

764 Krasnov BK, Khokhlova IS. 1994 Spatial-behavioural structure of subpopulations. In *The house mouse.*  
 765 *Origin, distribution, systematics, behaviour* (eds EV Kotenkova, NS Bulatova), pp 188–214.  
 766 Moscow: Nauka.

767 Kronenberger J-P, Medioni J. 1985 Food neophobia in wild and laboratory mice *Mus musculus*  
 768 *domesticus*. *Behav. Proc.* **11**, 53–60.

769 Kryvokhyzha D, Holm K, Chen J, Cornille A, Glémin S, Wright SI, Lagercrantz U, Lascoux M. 2016 The  
 770 influence of population structure on gene expression and flowering time variation in the  
 771 ubiquitous weed *Capsella bursa-pastoris* (Brassicaceae). *Mol. Ecol.* **25**, 1106–1121. (doi:  
 772 10.1111/mec.13537)

773 Lewontin RC, Dunn LC. 1960 The evolutionary dynamics of a polymorphism in the house mouse.  
 774 *Genetics* **45**, 705–722.

775 Lidicker WZ, Jr. 1976 Social behaviour and density regulation in house mice living in large enclosures.  
 776 *J. Anim. Ecol.* **45**, 677–697.

777 Liechti JI, Bonhoeffer S. 2019 A time resolved clustering method revealing longterm structures and  
 778 their short-term internal dynamics. *arXiv pre-print arXiv:191204261*.

779 Lopes C, Block P, König B. 2016 Infection-induced behavioural changes reduce connectivity and the  
780 potential for disease spread in wild mice contact networks. *Sci. Rep.* **6**, 31790. doi:  
781 10.1038/srep31790

782 Macholán M, Mrkvicová Vyskočilová M, Bejček V, Šťastný K. 2012 Mitochondrial DNA sequence  
783 variation and evolution of Old World house mice (*Mus musculus*). *Folia Zool.* **61**, 284–307.  
784 (<https://doi.org/10.25225/fozo.v61.i3.a12.2012>)

785 Mucha PJ, Richardson T, Macon K, Porter, MA, Onnela, J-P. 2010 Community structure in time-  
786 dependent, multiscale, and multiplex networks. *Science* **328**, 876-878. (doi:  
787 10.1126/science.1184819)

788 Nachman MW, Searle JB. 1995 Why is the house mouse karyotype so variable? *Trends Ecol. Evol.* **10**,  
789 397–402. (doi: 10.1016/s0169-5347(00)89155-7)

790 Navarro MN, Cassaing J, Croset H 1989 Demography and dispersal of one feral insular population of  
791 *Mus domesticus*: comparison with one mainland population. *Z. Säugetierk.* **54**, 286–295.

792 Newman MEJ, Girvan M. 2004 Finding and evaluating community structure in networks. *Phys. Rev. E*  
793 **69**, 026113. (doi: 10.1103/PhysRevE.69.026113)

794 Noyes RF, Barrett GW, Taylor DH. 1982 Social structure of feral house mouse (*Mus musculus* L.)  
795 populations: effects of resource partitioning. *Behav. Ecol. Sociobiol.* **10**, 157–163.

796 Odden M, Ims R, Støen OG, Swenson JE, Andreassen HP. 2014 Bears are simply voles writ large: social  
797 structure determines the mechanisms of intrinsic population regulation in mammals. *Oecologia*  
798 **175**, 1–10. (<https://doi.org/10.1007/s00442-014-2892-z>)

799 Pelikán J. 1981 Patterns of reproduction in the house mouse. In *Biology of the house mouse* (ed RJ  
800 Berry), pp. 205–224. Symposia of the Zoological Society of London, vol. 47. London: Academic  
801 Press, Ltd.

802 Perony N, Tessone CJ, König B, Schweitzer F. 2012 How random is social behaviour? Disentangling  
803 social complexity through the study of a wild house mouse population. *PLoS Comput. Biol.* **8**,  
804 e1002786. (<https://doi.org/10.1371/journal.pcbi.1002786>)

805 Petruszewicz K, Andrzejewski R. 1962 Natural history of a free-living population of house mice (*Mus*  
806 *musculus* Linnaeus), with particular reference to groupings within the population. *Ekol. Polska A*  
807 **10**, 85–122.

808 Phifer-Rixey M, Bonhomme F, Boursot P, Churchill GA, Piálek J, Tucker PK, Nachman MW. 2012  
809 Adaptive evolution and effective population size in wild house mice. *Mol. Biol. Evol.* **29**, 2949–  
810 2955. (doi:10.1093/molbev/mss105)

811 Piálek J, Vyskočilová M, Bímová B, Havelková D, Piálková J, Dufková P, Bencová V, Ďureje L, Albrecht  
812 T, Hauffe HC, Macholán M, Munclinger P, Strochová R, Zajícová A, Holáň V, Gregorová S, Forejt J.  
813 2008 Development of unique house mouse resources suitable for evolutionary studies of  
814 speciation. *J. Hered.* **99**, 34–44. (doi: 10.1093/jhered/esm083)

815 Plate T, Heiberger R. 2016. abind: Combine Multidimensional Arrays. R package version 1.4-5.

- 816 Pocock MJO, Hauffe HC, Searle JB. 2005 Dispersal in house mice. *Biol. J. Linn. Soc.* **84**, 565–583.  
817 (<https://doi.org/10.1111/j.1095-8312.2005.00455.x>)
- 818 Pocock MJO, Searle JB, White PCL. 2004 Adaptations of animals to commensal habitats: population  
819 dynamics of house mice *Mus musculus domesticus* on farms. *J. Anim. Ecol.* **73**, 878–888.
- 820 RCore Team 2019 R: A language and environment for statistical computing. *Vienna, Austria:*  
821 *Computing R Foundation for Statistical Computing.*
- 822 Reimer JD, Petras ML. 1967 Breeding structure of the house mouse, *Mus musculus* in a population  
823 cage. *J. Mammal.* **48**, 88–99.
- 824 Rosvall M, Axelsson D, Bergstrom CT. 2009 The map equation. *Eur. Phys. J. Special Topics* **178**, 13–23.  
825 (doi: : 10.1140/epjst/e2010-01179-1)
- 826 Rosvall M, Bergstrom CT. 2008 Maps of random walks on complex networks reveal community  
827 structure. *Proc. Natl. Acad. Sci. USA* **105**, 1118–1123. (doi:  
828 <https://doi.org/10.1073/pnas.0706851105>)
- 829 Rymer TL, Pillay N. 2018 An integrated understanding of paternal care in mammals: lessons from the  
830 rodents. *J. Zool.* **306**, 69–76. (doi: 10.1111/jzo.12575)
- 831 Sage RD. 1981 Wild mice. In *The mouse in biomedical research* (eds HL Foster, JD Small, JG Fox), pp.  
832 39–90, vol. 1. New York: Academic Press.
- 833 Salcedo T, Geraldles A, Nachman MW. 2007 Nucleotide variation in wild and inbred mice. *Genetics*  
834 **177**, 2277–2291. (doi: 10.1534/genetics.107.079988)
- 835 Sattenspiel L. 1987 Population structure and the spread of disease. *Hum. Biol.* **59**, 11–438.
- 836 Selander RK. 1970. Behavior and genetic variation in natural populations. *Am. Zool.* **10**, 53–66.
- 837 Schradin C, Lindholm AK, Johannesen J, Schoepf I, Yuen C-H, König B, Pillay N. 2012 Social flexibility  
838 and social evolution in mammals: a case study of the African striped mouse (*Rhabdomys pumilio*).  
839 *Mol. Ecol.* **21**, 541–553. (doi: 10.1111/j.1365-294X.2011.05256.x)
- 840 Singleton GR. 1983 The social and genetic structure of a natural colony of house mice, *Mus musculus*,  
841 at Healesville Wildlife Sanctuary. *Austr. J. Zool.* **31**, 155–166.
- 842 Singleton GR, Krebs CJ. 2007 The secret world of wild mice. In *The mouse in biomedical research* (eds.  
843 JG Fox, MT Davisson, FW Quinby, SW Barthold, CE Newcomer, AL Smith), pp. 25–52, vol. 1, 2<sup>nd</sup> ed.  
844 Amsterdam: Elsevier. (doi: 10.1016/B978-012369454-6/50015-7)
- 845 Sites JW Jr, Moritz C. 1987 Chromosomal evolution and speciation revisited. *Syst. Zool.* **36**, 153–174.
- 846 Slatkin M. 1987 Gene flow and the geographic structure of natural populations. *Science* **15**, 787–792.  
847 (doi: 10.1126/science.3576198)
- 848 Smadja C, Catalan J, Ganem G. 2004 Strong premating divergence in a unimodal hybrid zone between  
849 two subspecies of the house mouse. *J. Evol. Biol.* **17**, 165–176. (doi: 10.1046/j.1420-  
850 9101.2003.00647.x)

851 Snow G. 2020. TeachingDemos: Demonstrations for Teaching and Learning. R package version 2.12.  
852 (<https://CRAN.R-project.org/package=TeachingDemos>)

853 Stenseth NC, Lidicker Jr WZ (eds). 1992 *Animal dispersal*. London, UK: Chapman and Hall.

854 Stone AC, Battistuzzi FU, Kubatko LS, Perry GH Jr, Trudeau E, Lin H, Kumar S. 2010 More reliable  
855 estimates of divergence times in *Pan* using complete mtDNA sequences and accounting for  
856 population structure. *Phil. Trans. R. Soc. Lond. B Biol. Sci.* **365**, 3277–3288.  
857 (doi: 10.1098/rstb.2010.0096)

858 Thornhauser KE, Thoß M, Musolf K, Klaus T, Penn DJ. 2014 Multiple paternity in wild house mice  
859 (*Mus musculus musculus*): effects on offspring genetic diversity and body mass. *Ecol. Evol.* **4**, 200–  
860 209. (doi: 10.1002/ece3.920)

861 Thrall PH, Burdon JJ. 1997 Host-pathogen dynamics in a metapopulation context: the ecological and  
862 evolutionary consequences of being spatial. *J. Ecol.* **85**, 743–753. (doi: 10.2307/2960598)

863 Thuesen P. 1977 A comparison of the agonistic behaviour of *Mus musculus musculus* L. and *Mus*  
864 *musculus domesticus* Ratty (Mammalia, Rodentia). *Vidensk. Medd. Fra. Dansk. Naturh. Foren.* **140**,  
865 117–128.

866 Triggs GS. 1991 The population ecology of house mice (*Mus domesticus*) on the Isle of May, Scotland.  
867 *J. Zool.* **225**, 449–448.

868 Vahdati AR, Wagner A. 2018 Population size affects adaptation in complex ways: simulations  
869 on empirical adaptive landscapes. *Evol. Biol.* **45**, 156–169 ([https://doi.org/10.1007/s11692-017-](https://doi.org/10.1007/s11692-017-9440-9)  
870 [9440-9](https://doi.org/10.1007/s11692-017-9440-9))

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

873 Vošlajerová Bímová B, Macholán M, Baird SJE, Munclinger P, Dufková P, Laukaitis CM, Karn RC,  
874 Luzynski K, Tucker PK, Piálek J. 2011 Reinforcement selection acting on the European house mouse  
875 hybrid zone. *Mol Ecol.* **20**, 2403–2424. (doi: 10.1111/j.1365-294X.2011.05106.x)

876 Vošlajerová Bímová B, Mikula O, Macholán M, Janotová K, Hiadlovská Z. 2016 Female house mice do  
877 not differ in their exploratory behaviour from males. *Ethology* **122**, 298–307.  
878 (<https://doi.org/10.1111/eth.12462>)

879 Walkowa W. 1981 Structure, dynamics and productivity of mouse populations: A review of studies  
880 conducted at the Institute of Ecology, Polish Academy of Sciences. In *Biology of the house mouse*  
881 (ed RJ Berry), pp 427–437. Symposia of the Zoological Society of London, vol. 47. London:  
882 Academic Press, Ltd.

883 Webb PI, Ellison GTH, Skinner JD, van Aarde RJ. 1997 Are feral house mice from the sub-Antarctic  
884 adapted to cold? *Z. Säugetierk.* **62**, 58–62.

885 White MJD. 1978 *Modes of speciation*. San Francisco, CA: W. H. Freeman and Co.



886 Wickham H. 2019 stringr: Simple, Consistent Wrappers for Common String Operations. R package  
887 version 1.4.0. <https://CRAN.R-project.org/package=stringr>

888 Wilson, AC, Bush GL, Case SM, King MC. 1975 Social structuring of mammalian populations and the  
889 rate of chromosomal evolution. *Proc. Natl. Acad. Sci. USA* **72**, 5061-5065.

890 Wright S. 1931 Evolution in Mendelian populations. *Genetics* **16**, 97–159.

891

## Figure legends

**Figure 1.** Population changes during four experiments. On the abscissa are days since the beginning of each run. On the ordinate are the total numbers of individuals present in the enclosure.

**Figure 2.** The modular structure of the experimental populations. Rows of the bar plots correspond to individuals and columns to time layers. On the abscissa is time in days. Colours indicate module membership, while blank spaces indicate time layers in which the individuals did not enter any box. Note that in the ‘*musculus* 2013’ experiment, the red module persists considerably long via the episodic occurrence of a single ‘red’ individual. This is the trace of a subpopulation allowed to survive in the exit box (see Supplementary Material).

**Figure 3.** Modularity quantified for each experimental run as the compression rate of the description length (see Methods for details) compared between original data (black dots) and randomised replicates (violin plots). Venus and Mars’s symbols show values based on female-female and male-male interactions, respectively.

**Figure 4.** Summary of social networks calculated for three periods, each consisting of ten time layers. Line widths reflect the strength of social interaction; vertex colours indicate prevailing module membership, and their shapes correspond to sex (squares are for males, circles for females). The networks cover the following time spans (in days since the start of the experiment): 1–25, 136–155, 195–211 (*domesticus* 2013); 1–21, 134–156, 250–272 (*domesticus* 2014); 1–25, 136–155, 233–253 (*musculus* 2013) and 1–21, 134–156, 245–265 (*musculus* 2014). The displayed networks contain only individuals involved in reproduction.

**Figure 5.** Module distinctiveness quantified as a mean proportion of time spent by individuals in interactions with their module members.

**Figure 6.** The spatial separation of modules in three selected periods of the four experimental runs. Rows correspond to nest boxes, columns to time layers, and pies show the proportions of box occupancy by members of different modules (with colour code as in Fig. 2; empty circles depict unoccupied boxes). Every period consists of 10 time layers, the same as in summary networks.

**Figure 7.** The persistence of family bonds within modules shown as changes in the proportion of parent-offspring pairs found within modules through time.