

1 House mouse subspecies do differ in their social structure

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17

18 **Abstract**

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

36 1. Introduction

37 Knowledge of population structure is crucial for understanding many evolutionary phenomena,
38 including the relative importance of genetic drift and selection (Wright, 1931), adaptation
39 (Kemppainen et al., 2021; Kryvokhyzha et al., 2016; Vahdati & Wagner, 2018), dispersal (Clutton-
40 Brock & Lukas, 2012; Slatkin, 1987; Stenseth & Lidicker, 1992), the spread of pathogens (Sattenspiel,
41 1987; Thrall & Burdon, 1997; Lopes et al. 2016), mating patterns (Jarne & Stadler, 1995; Odden et
42 al., 2014; Ferrari et al., 2019; Evans et al., 2021b,c), or speciation (Coyne & Orr, 2004). In social
43 animals, populations are strongly affected by social interactions and resulting relationships among
44 their members, i.e., their social structure (Kappeler & de Schaik, 2002). In some groups, especially
45 mammals, these interactions are further intensified by physical and alimentary bonds between
46 mothers and their offspring. Trade-offs between competition and cooperation may interplay in
47 various ways with environmental conditions, resulting in different levels of group cohesion across
48 taxa (Drobniak et al., 2015; Kramer & Meunier, 2019). If parental or communal care increases fitness
49 (Konig, 1994; Rymer & Pillay, 2018), an evolutionary pathway for more complex sociality may be
50 opened. Moreover, populations can be influenced by a particular mating system. Social and mating
51 systems are thus coupled (Dewsbury, 1990; Kappeler, 2019). For example, small groups usually
52 comprise a single breeding male monopolising copulations with several adult females. Such units
53 tend to be, to a large extent, isolated from other subpopulations. This isolation may be further
54 strengthened if several group members participate in the defence of its territory. By contrast,
55 insufficient control over reproduction by dominant males can result in less close groupings, with
56 extended male-male contests, potentially leading to changes in female mating strategies (Clutton-
57 Brock, 2017).

58 Differences in social structure can exist even between closely related species (e.g., Stone et al.,
59 2010). However, whether these differences drive the formation of reproductive barriers between
60 nascent species or are a consequence of the isolation is unclear. It is, therefore, necessary to study
61 diverging populations within a single species, just displaying some degree of differentiation in their
62 social structure.

63 An excellent model for such a study seems to be two house mouse subspecies, *Mus musculus*
64 *musculus* and *M. m. domesticus*, which diverged ~500.000 years ago (Geraldes et al., 2008; Macholan
65 et al., 2012). These are known to differ in several behavioural traits that can potentially affect
66 population structure, such as higher aggressiveness of *M. m. domesticus* (Đureje et al., 2011; Pialek
67 et al., 2008; Thuesen, 1977; van Zegeren & van Oortmerssen, 1981) and higher choosiness of *M. m.*
68 *musculus*, preferring consubspecific mates Bimova et al., 2005; Smadja et al., 2004; Vořlajerova
69 Bimova et al., 2011). *Mus m. domesticus* males showed longer primary risk assessment but a more
70 active exploration of an unfamiliar space (Hiadlovska et al., 2013; Vořlajerova Bimova et al., 2016)
71 than *musculus* males. By contrast, *musculus* males performed better in challenging situations
72 (Hiadlovska et al., 2014) and were less stressed by handling (Daniszova et al., 2017). More
73 importantly, *domesticus* males appear to establish a social hierarchy faster, leading to reduced stress,
74 while the social tension tends to persist much longer in *musculus* males (Hiadlovska et al., 2015).
75 Higher social stress can be the reason why subordinate *musculus* males leave their homes more
76 often than dominant males, whereas the opposite holds for *M. m. domesticus* (Hiadlovska et al.,
77 2021).

78 On the other hand, despite dozens of studies over eight decades of research (see Berry, 1981;
79 Sage, 1981; Boursot et al., 1993; Krasnov & Khokhlova, 1994), our knowledge of ecology and
80 population structure in each mouse subspecies is still equivocal (Ganem, 2012). Mouse populations
81 are generally considered to be subdivided into small, more or less isolated units, usually called
82 demes. Typically, these demes consist of one dominant male monopolising reproduction, several
83 subordinate males and females with their juvenile offspring. Females can move freely within the
84 deme's territory, whereas subordinate males are usually forced to stay on its periphery. Upon
85 reaching maturity, young males are often coerced into leaving the group, whereas females usually
86 stay and reproduce within the natal deme (see, e.g., Vošlajerová Bímová et al., 2016 and references
87 therein). However, the mouse population structure may vary depending on ecological, climatic, or
88 density situations (Butler, 1980; Noyes et al., 1982; Pocock et al., 2004; Singleton & Krebs, 2007). For
89 example, feral male mice on islands and elsewhere are known to defend individual, exclusive
90 territories that usually overlap with those of several females (Berry, 1970; Krasnov & Khokhlova,
91 1994; Sage, 1981). Moreover, mice can switch from strong territoriality to a gregarious life during
92 population outbreaks (Singleton & Krebs, 2007). Similar flexibility conditional on or triggered by
93 external conditions has also been described in other species such as dunnocks (Davies, 1992), African
94 striped mice (Schradin et al., 2012), and primates (Kappeler & van Schaik, 2002). In the house mouse,
95 the ecological and social plasticity is largely associated with the level of its commensal bond with
96 humans. In any case, there is a widespread notion that *M. m. domesticus* is more strictly commensal
97 and hence more 'demic' than *M. m. musculus*. However, as Ganem (2012) pointed out, this has not
98 ever been appropriately documented.

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

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

113

114 2. Methods

115 2.1. Source data

116 The source data come from semi-natural enclosures inspired by Perony et al. (2012) and König et al.
117 (2015), furnished with nest boxes, each monitored by two RFID readers recording all in/out moves of
118 mice provided with RFID transponders (see (Supplementary Material; Fig. S1. The two collateral

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

125 2.2. Statistical processing of data

126 2.2.1. Pre-processing of the movement data

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

145 2.2.2. The social network in a single time layer and its structure

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

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

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

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

$$176 \quad M = \frac{L_{before}}{L_{after}}.$$

177 In practice, optimal partitioning is found using the Louvain algorithm (Blondel et al. 2008) with L as
178 the objective function. The search is not constrained in any specific way, and the modules can thus
179 be of any size and composition; it only matters if their delimitation reduces L . Note that our
180 definition of modularity is different from the most common use of the term (Newman & Girvan,
181 2004). We use the word as a general term expressing the degree of partitioning into modules.

182 2.2.3. Time dimension

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

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

210 2.2.4. Spatial dimension

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

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

224 2.2.5. Software

225 Apart from Infomap (Rosvall & Bergstrom, 2008), all the statistical analyses described above were
226 implemented in the computing language and environment R (RCore Team, 2019). A collection of
227 functions performing the core of our analyses and drawing the main figures is available at the
228 publicly available repository (https://github.com/onmikula/movement_networks). Included is also a
229 worked-out example based on *domesticus* 2013 experiment. The scripts relied on the functionality of
230 the packages igraph (Csardi & Nepusz, 2006), Matrix (Bates & Maechler, 2019), abind (Plate &
231 Heiberger, 2016), and stringr (Wickham, 2019). For plotting, we used package vioplot (Adler & Kelly,
232 2018), TeachingDemos (Snow, 2020). The colour palette used for the module display was designed by
233 A. Trubetskoy (<https://sashamaps.net/docs/resources/20-colours>).

234 2.3. Parentage assignment and inference of demes

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

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

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

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

261

262 **3. Results**

263 **3.1. Populations**

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

274 **3.2. Modules**

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

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

284

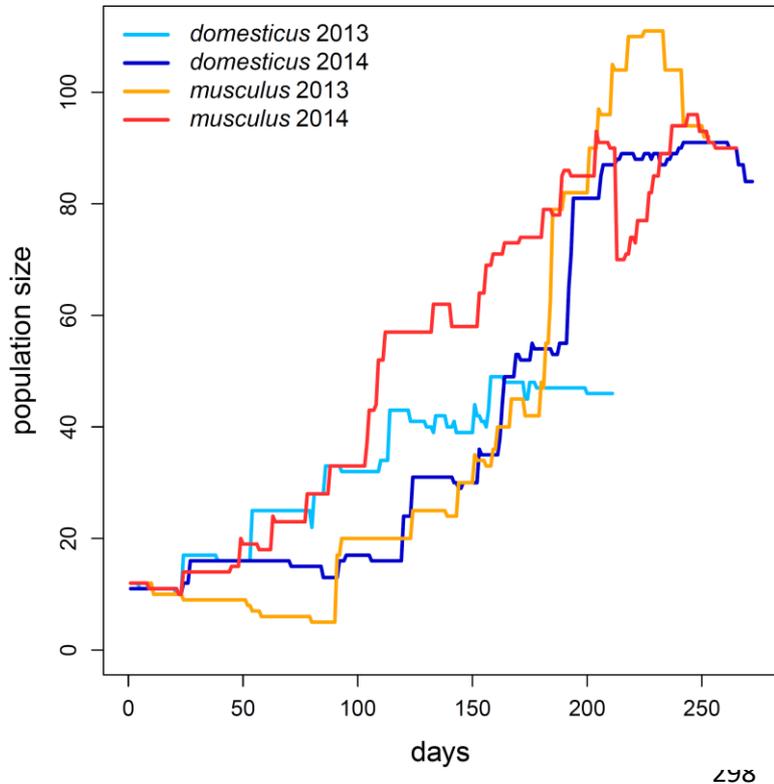


Figure 1. Population changes during four experiments. On the abscissa are days since the beginning of each run. On the ordinate are the total numbers of individuals present in the enclosure.

299

300 The multi-layer modular structure is graphically depicted in Fig. 2. Each row corresponds to a
 301 single individual in this figure, while each column represents one time layer; assignments of
 302 individuals to modules are shown in different colours. Immediately after launching the *domesticus*
 303 2013 experiment, four modules were formed, but one of them ('blue') survived only until the 21st
 304 day, and another ('red') dissolved into 'yellow' and 'orange' modules, respectively. The latter was
 305 estimated to form at about the 104th day when the offspring of the 'red' module's founding female
 306 were weaned, received transmitters, and thus entered the record. In the *domesticus* 2014 run, two
 307 modules that arose initially ('red' and 'green') were gradually transformed into two modules
 308 dominating the social structure at the end of the experiment ('blue' and 'purple'). The
 309 transformation reflected a gradual extinction of founding individuals and their replacement by newly
 310 born offspring. In addition, there were seven modules, often representing a temporary association of
 311 siblings with some of their parents or an episodic interaction of immigrants with local inhabitants.
 312 The *musculus* 2014 run started with two modules ('red' and 'green', both persisting until the end),
 313 from the 106th day on, accompanied by the third module ('yellow'). In both persisting initial modules,
 314 three of their founders also survived until the end, whereas the later-appearing one was established
 315 by the first-generation offspring born in the enclosure. The fourth module, which also appeared in
 316 this experiment, was marginal. Finally, as noted above, the *musculus* 2013 run was very different
 317 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.

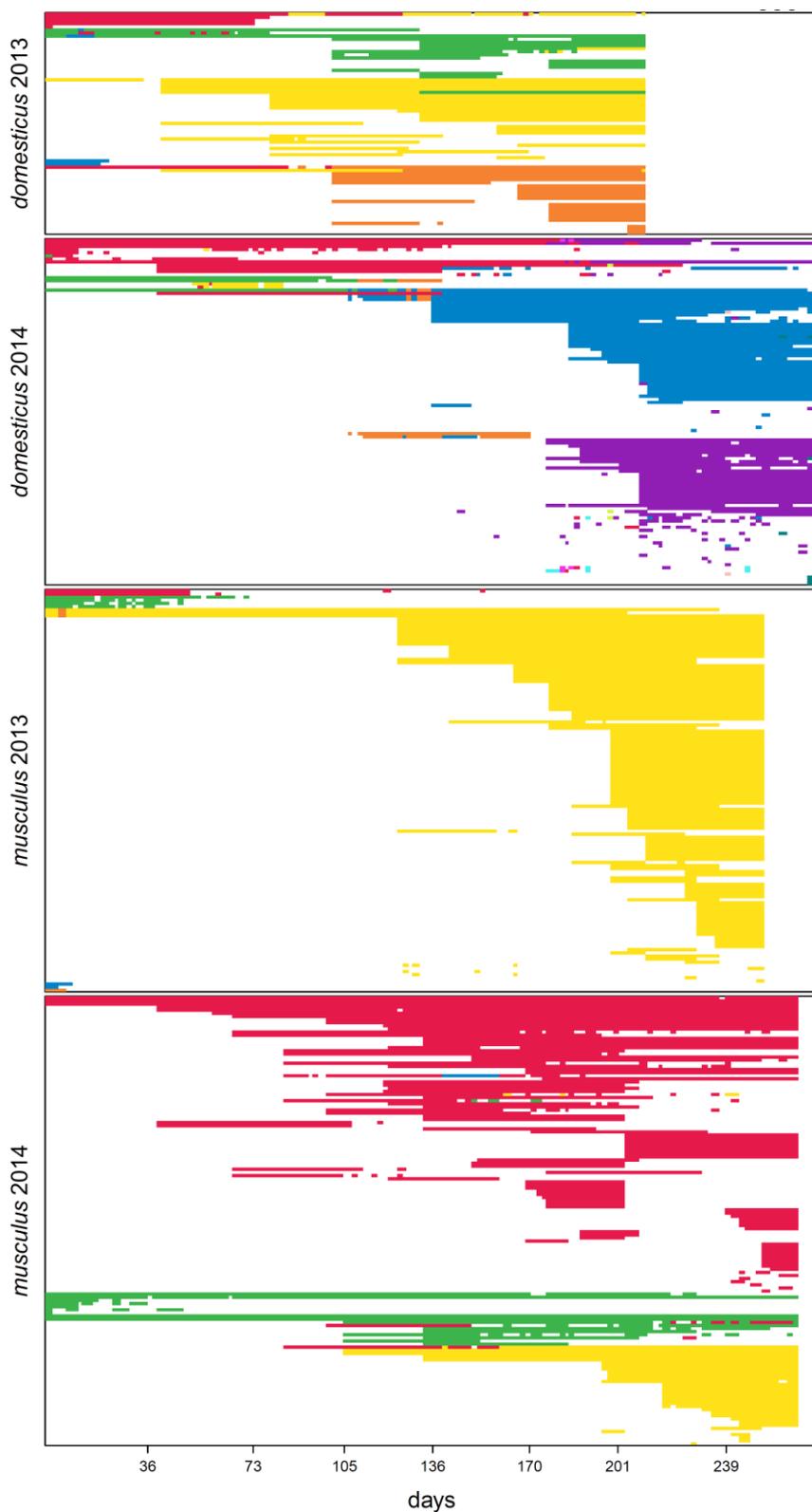


Figure 2. The modular structure of the experimental populations. Rows of the bar plots correspond to individuals and columns to time layers. On the abscissa is time in days. Colours indicate module membership, while blank spaces indicate time layers in which the individuals did not enter any box. Note 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).

352

353 **3.3. Modularity**

354 To quantify the degree of tightness and exclusiveness of the estimated modules, we introduced a
 355 new index of modularity, M (see Methods for details). The most fundamental result of our study is
 356 the difference in this index between the subspecies. While in *M. m. musculus*, M was 1.78 (2013) and
 357 2.05 (2014), respectively, in *M. m. domesticus*, it was as high as 2.51 (2013) and 2.33 (2014),
 358 respectively (Table 1). Fig. 3 shows these estimates together with the randomisation support
 359 (represented by violin plots). The difference between subspecies is apparent even in the ordination
 360 of randomised distributions. The modularity of *M. m. domesticus* populations seems to be slightly
 361 more dependent on individual movement details, but it still holds their minimum randomised M was
 362 higher than that observed in *M. m. musculus* populations (Table S2). In all cases, M values calculated
 363 from female-female interactions were considerably higher than those based solely on male-male
 364 interactions within individual runs (see gender symbols in Fig. 3). By contrast, M s calculated from
 365 male-female interactions (Table S2) were all close to the overall values. The presented solution was
 366 obtained with the relaxing rate parameter $r = 0.60$. However, the full sequence of M values obtained
 367 under different relaxing rates also supports the conclusion that *M. m. domesticus* is more ‘demic’
 368 than *M. m. musculus* (Fig. S3) and confirms, via randomisation, that differences in M are reasonably
 369 robust to accidental details of movement records.

370

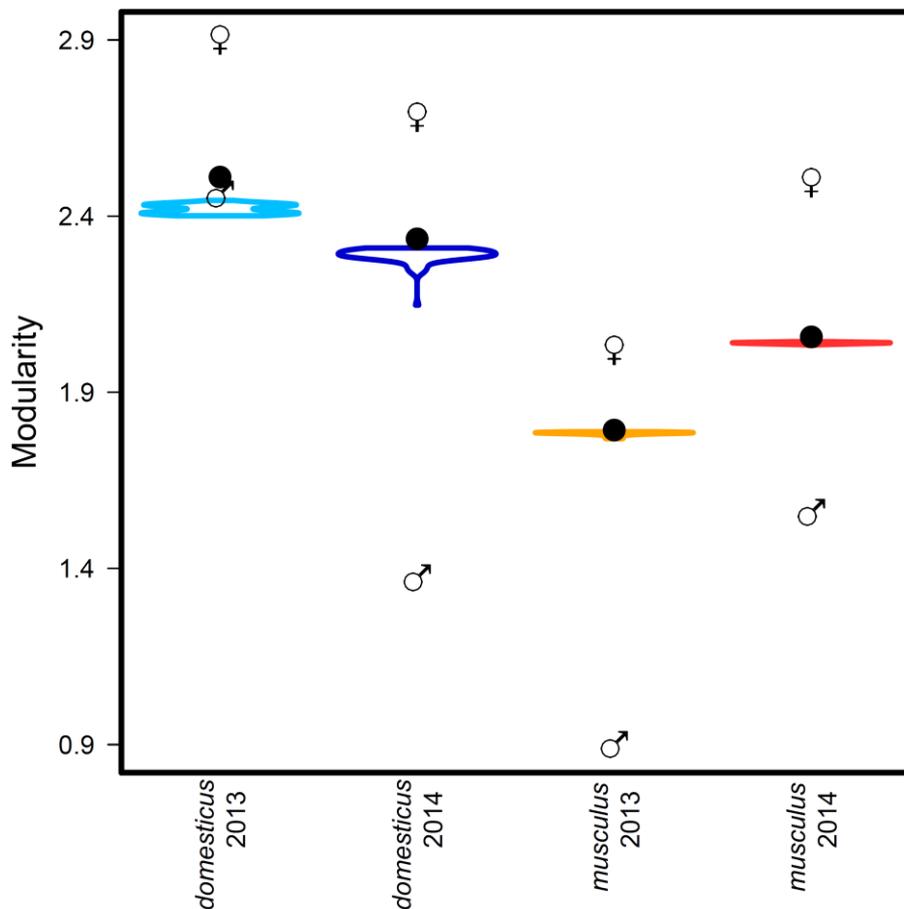
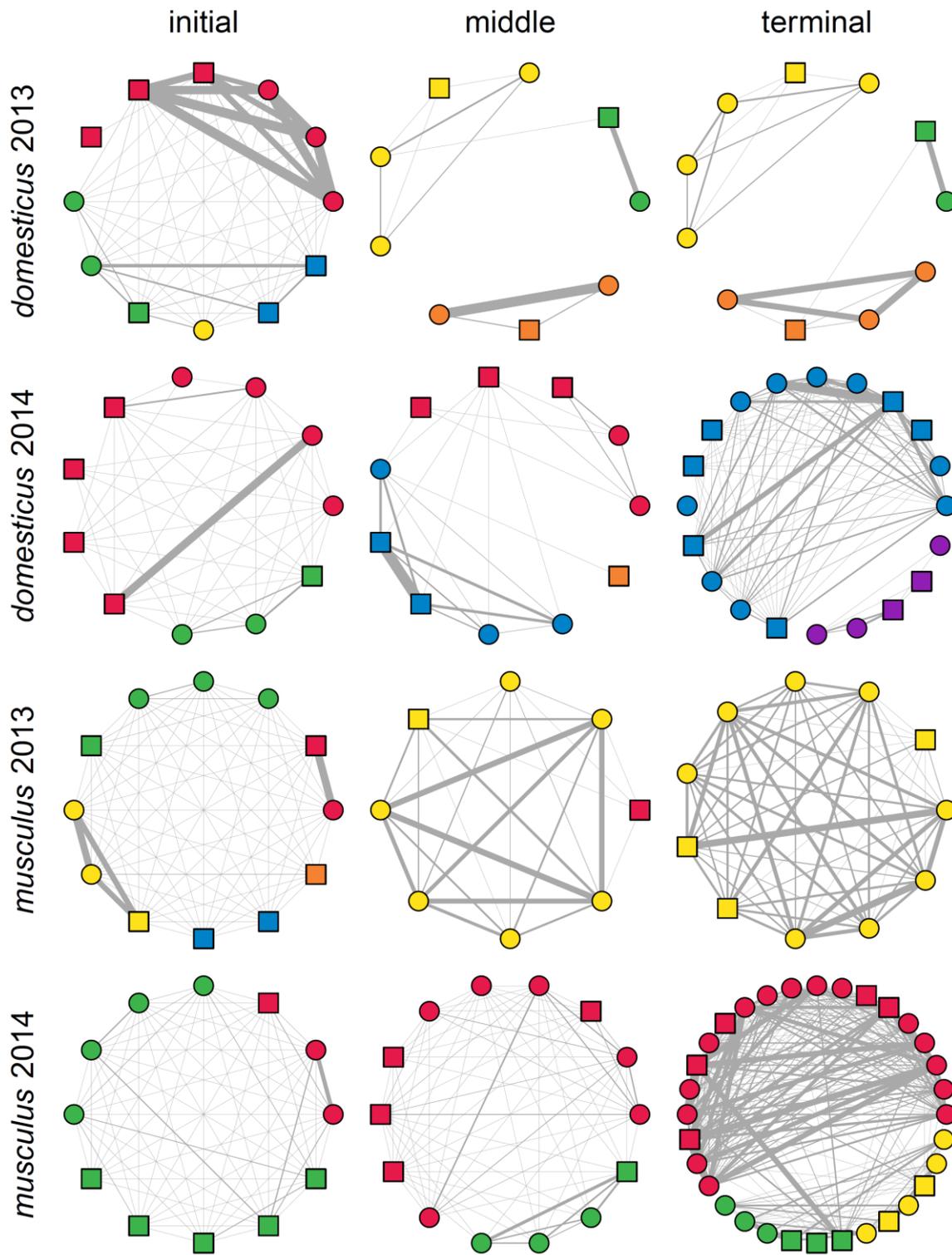


Figure 3. Modularity quantified for each experimental run as the compression rate of the description length (see Methods for details) compared between original data (black dots) and randomised replicates (violin plots). Venus and Mars’s symbols show values based on female-female and male-male interactions,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

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394 **Figure 4.** Summary of social networks calculated for three periods, each consisting of ten time layers.
 395 Line widths reflect the strength of social interaction; vertex colours indicate prevailing module
 396 membership, and their shapes correspond to sex (squares are for males, circles for females). The
 397 networks cover the following time spans (in days since the start of the experiment): 1–25, 136–155,
 398 195–211 (*domesticus* 2013); 1–21, 134–156, 250–272 (*domesticus* 2014); 1–25, 136–155, 233–253
 399 (*musculus* 2013) and 1–21, 134–156, 245–265 (*musculus* 2014). The displayed networks contain only
 400 individuals involved in reproduction.

401 **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

402

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

408 The between-subspecies difference in the level of modularity is corroborated by module
 409 distinctiveness expressed as the proportion of intramodular interactions (Fig. 5). The maximum value
 410 of 1.00 means all individuals met in the boxes only with members of their modules). In both *M. m.*
 411 *domesticus* populations, this proportion approached 1.00 in 5–30 days after launching the
 412 experiments and tended to remain close to the maximum value until the end. Even in *domesticus*
 413 2014, occasional deep drops were followed by a fast recovery of high distinctiveness. A more
 414 detailed examination revealed these drops could be explained by the temporary relaxation of father-
 415 son bonds (Fig. S6). In *musculus* 2014, module distinctiveness reached its maximum later (after ~50
 416 days), and it remained high only until the rise of the third module ('yellow' in Fig. 2) on the 106th day.
 417 Since then, it fluctuated between 0.77 and 1.00. Again, loose father-son bonds can be largely
 418 responsible for the lower distinctiveness of the modules (Fig. S6). From around the 50th day onwards,
 419 only a single module existed in the *musculus* 2013 population. The mice could only interact within
 420 their group, and distinctiveness was 1.00, thus resembling *M. m. domesticus*.

421 The spatial separation of modules (Fig. S4, Supplementary Material) closely parallels the picture
 422 revealed by module distinctiveness. These differences are further corroborated if we look at each of
 423 the six nest boxes' occupancies by members of individual modules (Fig. 6) in the same periods as
 424 covered by the summary networks shown in Fig. 4. In both subspecies, a substantial spatial
 425 admixture can be seen in the initial period. Later on, a visible difference arises. In *M. m. domesticus*
 426 runs, the admixture is very limited, confined to a single nest box, a few time layers, and in *domesticus*
 427 2014, also to marginally significant modules. On the contrary, in *M. m. musculus* the admixture
 428 persisted in four nest boxes and was quite extensive, especially between the green module and the
 429 rest (in *musculus* 2014 run, which was the only informative in this respect, containing more than one
 430 module).

431

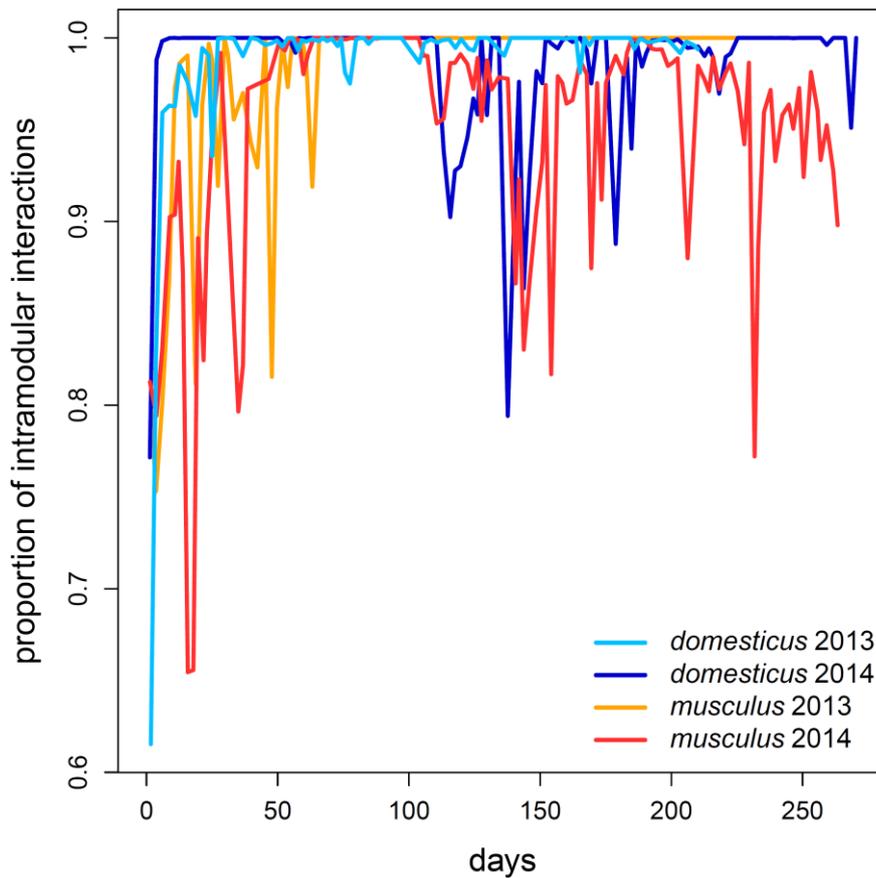
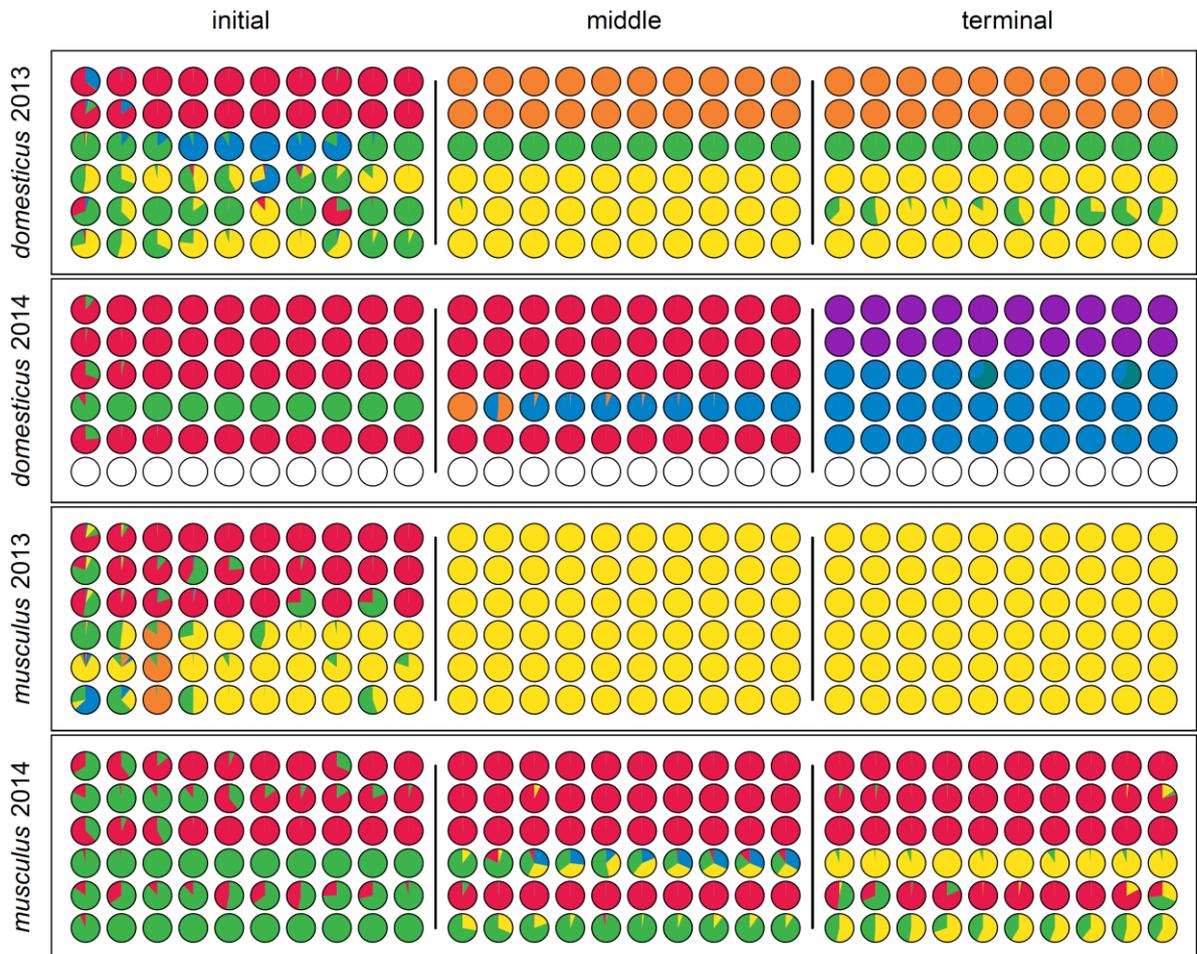


Figure 5. Module distinctiveness quantified as a mean proportion of time spent by individuals in interactions with their module members.

447

448 3.4. Connecting enclosures

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



468

469

470 **Figure 6.** The spatial separation of modules in three selected periods of the four experimental runs.

471 Rows correspond to nest boxes, columns to time layers, and pies show the proportions of box

472 occupancy by members of different modules (with colour code as in Fig. 2; empty circles depict

473 unoccupied boxes). Every period consists of 10 time layers, the same as in summary networks.

474

475 3.5. Parentage and demic structure

476 In *M. m. domesticus*, the offspring appears more likely to remain with their parents in the same

477 module (Fig. 7). Sex-focused analyses reveal that this is mainly due to mother-daughter interactions

478 (Fig. S6). Multiple paternity (i.e., probability that two siblings have different fathers) was equal to

479 0.04 in *domesticus* 2013, 0.15 in *domesticus* 2014, 0.11 in *musculus* 2013, and 0.42 in *musculus* 2014.

480 Note that the value in *musculus* 2013, where a single module was present for most of the trial

481 duration, is almost as high as in *domesticus* 2014. It is also striking because the time window when

482 this multiple fathering came about was relatively narrow – reproduction started with just one male

483 surviving in the enclosure, and the first offspring sired by someone else appeared as late as 94 days

484 after the first offspring male was born. These results suggest looser intramodular bonds and/or lower

485 control of a dominant male over reproduction in *M. m. musculus* relative to *M. m. domesticus*.

486 Knowledge of associations between parents, their offspring, and modules they are mostly
 487 associated with allows us to relate individual modules to reproductive units (demes), i.e., inferring
 488 the number of presumed demes in each experiment. Overall, inferred demes perfectly matched the
 489 long-lasting modules persisting for more than 50 days. Support for individual demes ranged from
 490 0.92 ('red' module in '*domesticus* 2013') to 33.04 ('red' module in '*musculus* 2014'; cf. Fig. 2 and
 491 Table S3). All other modules could not be considered true demes.

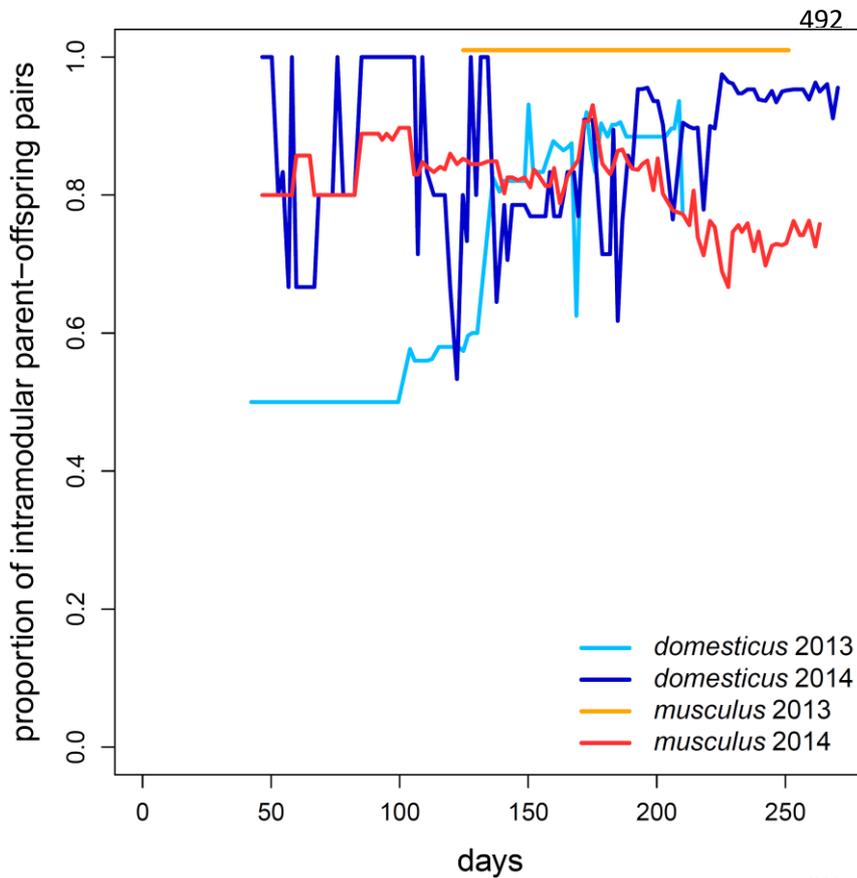


Figure 7. The persistence of family bonds within modules shown as changes in the proportion of parent-offspring pairs found within modules through time.

508 4. Discussion

509 In all experimental runs, *M. m. domesticus* displayed higher modularity than *M. m. musculus* (with
 510 the difference ranging from 0.28 between the '*domesticus* 2014' and '*musculus* 2014' population to
 511 0.73 between the '*domesticus* 2013' and '*musculus* 2013' population). It means that the former
 512 subspecies has a closer population structure, which can involve either subdivision into modules or a
 513 higher degree of regularity in intramodular interactions (recall that module tightness is defined in
 514 terms of compressibility in the map equation framework, which is unrelated to internal link density).

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

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

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

536 Since the 1950s, lots of ecological and genetic studies have suggested that *M. m. domesticus*
537 populations are structured into small and relatively rigid and closed units (Anderson, 1964;
538 Crowcroft, 1955; Crowcroft & Rowe, 1963; Lewontin & Dunn, 1960; Lidicker, 1976; Reimer & Petras,
539 1967; Selander, 1970) and that these units or demes do not survive longer than a few months
540 (Singleton, 1983; Pocock et al., 2005; König et al., 2015; Evans et al., 2021c). However, considerable
541 evidence has also been gathered that many *domesticus* populations are not so tightly organised
542 (Berry, 1981, Sage, 1981). Nevertheless, this subspecies has generally been considered more 'demic'
543 than *M. m. musculus*. Such the opinion is based on two tenets: first, the demic structure is
544 characteristic of commensal populations, and second, *domesticus* is often believed to be more
545 commensal than *musculus*. However, as Ganem (2012) pointed out, the latter assumption has never
546 been reliably documented.

547 Moreover, it should be mentioned that *M. m. musculus* is also ecologically highly flexible, as
548 shown by many studies (Krasnov, 1988; Krasnov & Khokhlova, 1994; Pelikán, 1981; Petruszewicz &
549 Andrzejewski, 1962; Walkova, 1981). On the other hand, permanent non-commensal *M. m.*
550 *domesticus* populations are relatively common (e.g., Cassaing & Croset, 1985; Hardouin et al., 2010;
551 Navarro et al., 1989; Sage, 1981; Triggs, 1991; Webb et al., 1997). In this context, it is important that
552 we seeded all the experimental populations with individuals collected from the same central
553 European area (two within the *M. m. domesticus* distribution area and the other two within the *M.*
554 *m. musculus* range). The sampling sites are located at similar latitudes and altitudes and represent
555 the same indoor, commensal habitat. This way, we avoided potential confounding effects of different
556 environmental conditions known to affect house mouse ecological strategies (Butler, 1980; Noyes et
557 al., 1982; Pocock et al., 2004; Singleton & Krebs, 2007) and hence demonstrated a significant
558 distinction in the social structure between the two subspecies without any reference to (either real
559 or suspected) differences in the level of commensalism. Likewise, owing to identical conditions in the
560 enclosures, we assume the differences revealed in this study are not simply a manifestation of the
561 social flexibility reported in several bird and mammal species (Davies, 1992; Kappeler & van Schaik,
562 2002; Schradin et al., 2012).

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

568 The higher modularity of *M. m. domesticus* appears consistent with about twice as high global
569 effective population size (N_e) as that of *M. m. musculus* (Gerlandes et al., 2008; Phifer-Rixey et al.,
570 2012; Salcedo et al., 2007). (Interestingly, the Asian subspecies *M. m. castaneus*, considered the most
571 strictly commensal of the three main house mouse subspecies (Sage, 1981), also has the highest N_e
572 (Geraldes et al., 2008; Phifer-Rixey et al., 2012). Therefore, it would be useful to extend the
573 experiment reported here also to *castaneus*.) In contrast, socially mediated reduction of gene flow, in
574 combination with polygynous mating, should decrease N_e of *local* demes more in *M. m. domesticus*
575 than in *M. m. musculus*. Joint effects of genetic drift and inbreeding in small, socially structured
576 subpopulations can facilitate the fixation of underdominant chromosomal rearrangements such as
577 Robertsonian fusions (Britton-Davidian et al., 2007; Dallas et al., 1998; Nachman & Searle, 1995).
578 According to Bush (1975) and Wilson et al. (1975), this process can result in establishing postzygotic
579 reproductive isolation promoting stasipatric speciation (White, 1978; Sites & Moritz, 1987). However,
580 given the great ecological plasticity of house mice, it is unclear how the differences in social structure
581 between the two taxa evidenced in this study relate to the dynamics of secondary contact between
582 them.

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

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

606 favourable property it shares with Newman and Girvan's modularity. Finally, it is expected to suffer
607 less from the resolution limit problem (Kawamoto & Rosvall, 2015), i.e., the impossibility of detecting
608 modules that are too small relative to the overall size of the network (Fortunato & Barthelemy,
609 2007). In this way, we could render, for the first time, robust quantitative evidence that commensal
610 populations of the two European house mouse subspecies subjected to identical environmental
611 conditions develop diverse social networks and hence differ in their social structure.

612

613 **Ethics**

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

619

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626

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632

633 **Competing interests**

634 The authors declare no competing interests.

635

636 **Authors' contributions**

637 B.V.B. and M.M. designed the study, L.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.

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892 Figure legends

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

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

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

905 **Figure 4.** Summary of social networks calculated for three periods, each consisting of ten time layers.
906 Line widths reflect the strength of social interaction; vertex colours indicate prevailing module
907 membership, and their shapes correspond to sex (squares are for males, circles for females). The
908 networks cover the following time spans (in days since the start of the experiment): 1–25, 136–155,
909 195–211 (*domesticus* 2013); 1–21, 134–156, 250–272 (*domesticus* 2014); 1–25, 136–155, 233–253
910 (*musculus* 2013) and 1–21, 134–156, 245–265 (*musculus* 2014). The displayed networks contain only
911 individuals involved in reproduction.

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

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

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