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Long-term overlap of social and genetic structure in free-ranging house mice reveals dynamic seasonal and group size effects

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Abstract

Associating with relatives in social groups can bring benefits such as reduced risk of aggression and increased likelihood of cooperation. Competition among relatives over limited resources, on the other hand, can induce individuals to alter their patterns of association. Population density might further affect the costs and benefits of associating with relatives by altering resource competition or by changing the structure of social groups; preventing easy association with relatives. Consequently, the overlap between genetic and social structure is expected to decrease with increasing population size, as well as during times of increased breeding activity. Here, we use multi-layer network techniques to quantify the similarity between long-term, high resolution genetic, and behavioral data from a large population of free-ranging house mice (*Mus musculus domesticus*), studied over 10 years. We infer how the benefit of associating with genetically similar individuals might fluctuate in relation to breeding behavior and environmental conditions. We found a clear seasonal effect, with decreased overlap between social and genetic structure during summer months, characterized by high temperatures and high breeding activity. Though the effect of overall population size was relatively weak, we found a clear decrease in the overlap between genetic similarity and social associations within larger groups. As well as longer-term within-group changes, these results reveal population-wide short-term shifts in how individuals associate with relatives. Our study suggests that resource competition modifies the trade-off between the costs and benefits of interacting with relatives.

Key words: genetic relatedness, long-term data, multilayer networks, seasonal, social behavior

Many animals live in groups based on extended families, leading to aggregations of individuals with varying levels of genetic similarity (Emlen 1997). As a result, we might expect a high level of overlap between the genetic structure and social associations of a population, with individuals frequently interacting with genetically similar individuals within social groups. As well as the commonly assumed benefits of group living (Krause and Ruxton 2002), a high level of relatedness within a group is thought to promote the evolution of cooperative behaviors (Hamilton 1964; Sherman 1981; Baglione et al.

2003; Ruch et al. 2009). Other advantages of associating with relatives include a reduced chance of aggression (König 1994a; McComb et al. 2001; Pravosudova et al. 2001; Carazo et al. 2014), support during agonistic interactions (Smith et al. 2010), or increased likelihood of engaging in affiliative interactions such as grooming (Silk 2007; Ren et al. 2017). In several cases, individuals living in closely related groups have shown an increase in traits such as growth speed and reproductive success, indicating that associating with relatives has direct fitness benefits (Mappes et al. 1995; Gerlach et al. 2007;

Silk 2007; Carazo et al. 2014), in addition to potential indirect fitness benefits (Hamilton 1964; Lehmann and Rousset 2019).

Despite the potential benefits of associating with related individuals, not all animals show a clear relationship between social and genetic structure (Liker et al. 2009; King et al. 2011; Croft et al. 2012; Hirsch et al. 2013). This suggests that associating with relatives might not always be advantageous. If average relatedness is high, breeding within a social group can carry a high risk of inbreeding (Keller and Waller 2002; Annavi et al. 2014). Individuals may, therefore, seek out extra group matings, leading to an increased frequency of associations with unrelated individuals (Emlen 1997; Kurvers et al. 2013). It might also be undesirable to compete with relatives over limited resources such as shelter, food, or suitable mating partners, due to indirect fitness costs (Hamilton and May 1977; Perrin and Mazalov 2000). The overlap between genetic and social structure within a population is therefore expected to change depending on the level of resource competition. Increased population density and reduced resource availability could lead to the fission of larger groups or increased movement between groups. These changes have the potential to reduce the overlap between genetic and social structure (Bowler and Benton 2005; Matthysen 2005; Sutherland et al. 2005) or enhance it if a group splits based on relatedness (Archie et al. 2006). On the other hand, increased density as well as lack of resources might also reduce opportunities to disperse or move to other groups, leading to "social crowding" effects (Matthysen 2005). This could cause an increase in the genetic similarity within groups as individuals are unable to disperse. Species that suffer from social crowding will generally show greater amounts of dispersion when populations drop to lower densities (Richardson et al. 2002; Frantz et al. 2010).

Given that the benefits and costs of interacting with relatives might vary with season, resource availability, population density, or group size, detailed long-term data on the genetic and social structure of a population are required to provide insights into the factors shaping its dynamics. While there are many studies examining individual aspects that may drive changes in the relationship between genetic similarity and sociality, being able to quantify long-term changes from a population perspective is rare. In this article, we use multilayer network analysis (Silk et al. 2018; Finn et al. 2019) to investigate the extent to which social structure coincides with genetic structure in a large population of free-ranging house mice (*Mus musculus domesticus*), analyzed over 10 years. The relationship between social and genetic structure is important in house mice, with populations divided into distinct social groups. Within these groups, individuals with higher relatedness and familiarity appear to be less likely to engage in aggressive interactions and, at least among females, are more likely to engage in cooperation (Parmigiani 1989; König 1994b; Hurst and Barnard 1995; Rusu and Krackow 2004; Ensminger and Meikle 2005; Harrison et al. 2018). Our study population has increased substantially in size since its founding in 2002, leading us to expect an increase in local resource competition among both male (over access to females in oestrus and areas or nest-boxes containing multiple females) and female mice (over access to safe nesting sites to rear a litter). Competition among males can be extremely fierce, resulting in mortalities and severe wounds (König and Lindholm 2012). Similarly, females unable to successfully gain access to a nest-box are unlikely to breed successfully as they cannot effectively defend litters from infanticidal conspecifics (Harrison et al. 2018).

By taking a multilayer network approach, we were able to analyze high-resolution genetic and social association data and examine how their structures relate to each other over time. This allowed us to quantify both long-term trends and seasonal patterns in the whole population and within social groups. From this, we inferred how the benefit of associating with genetically similar individuals fluctuates in response to population density, or breeding season, in parallel to environmental effects such as ambient temperature. We predicted that increasing population size would result in a decrease in overlap between genetic similarity and social associations because of increasing local resource competition. Similarly, we expected lower overlap between social and genetic structures during times of high breeding activity, due to individuals attempting to reduce competition and inbreeding with relatives.

Materials and Methods

Study population

Our study population is located in a $72\,m^2$ barn near Zurich, Switzerland. Within the barn, mice have access to 40 artificial nest boxes divided between 4 sections (Figure 1). As well as spending a large period of time resting in nest boxes while inactive during the day, mice also spend 3–4 h in nest boxes in their periods of activity during the night (Lopes et al. 2016). Litters are also born and raised in nest boxes. Within a nest box, individuals regularly meet with conspecifics, meeting an average of 7 partners over 24 h (Perony et al. 2012), though 30 individuals (adults and sub-adults) can fit in a nest box. Meetings can last for up to several hours, with high variability (Perony et al. 2012). The number of individuals in a box can also vary depending on the level of breeding activity, with a single or small group of males more likely to monopolize a nest box during periods of high breeding activity (Liechti et al. 2020). In each section, there are also 5–7 additional shelters (wood or brick), providing further places to rest or sleep, and allowing juveniles or subordinates to hide from older or dominant individuals. Food, water, and nesting material are freely available. Individuals are able to move freely about the barn and utilize any nest boxes, or leave entirely, with both sexes dispersing (Runge and Lindholm 2018). The population is regularly monitored, with attempts made to capture the entire population every 6–8 weeks. During these population checks, mice weighing $\geq 18\,g$ (i.e., young adults) are equipped with passive integrated transponder (PIT) tags which are read by radio frequency identification (RFID) antennae attached to the entrance tubes through which the mice enter and leave a nest box (2 antennae per entrance tube). Additionally, a tissue sample is taken via ear punch for genetic analysis. Nest boxes are also regularly checked for litters, with a full nest box check carried out every 8–12 days (for further details on the methods used to monitor the population see König et al. 2015).

For this study, we used data collected from 2008, which was the first full year in which the RFID antennae were operational, to 2017. The total number of pups found per year increased over the 10 years from 783 pups found in 2008 to 1,553 pups found in 2017. Temperature data are recorded hourly by a HOBO U12-013 Data Logger (Onset Computer Corporation, USA). The lowest average monthly temperature was -2.6 ± 3 SD (standard deviation) °C in January 2010 and the highest was 21.6 ± 3.1 SD °C in July 2017.

Network construction

As mice fitted with PIT tags pass through the entrance tubes to nest boxes, the antennae system recorded whether they were first passing the outermost or innermost antenna, from which entrances or exits
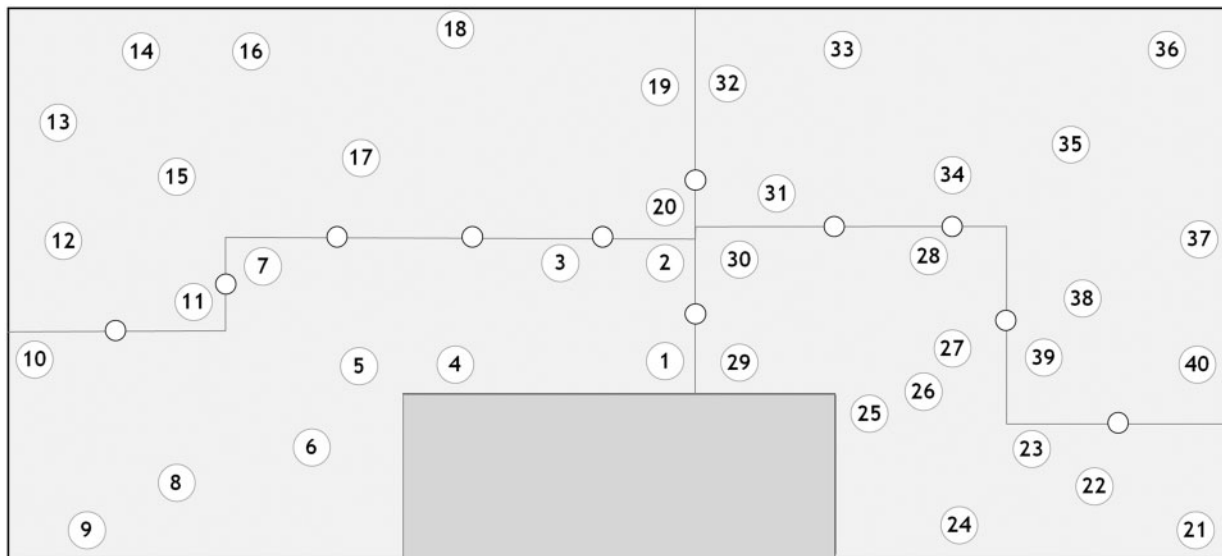
Figure 1. Schematic map of the barn showing locations of nest boxes equipped with RFID antennae (numbered 1–40, 10/section). Open circles indicate holes in the plastic walls that structure the building. Mice can access the entire area and also leave the building through holes or under the roof. Food and water are freely available (3 feeding stations and 5 water bottles) in each section (see König et al. 2015).

from the nest box could be deduced. From this, we could ascertain which individuals were present in a nest box and when. Networks of social associations were therefore constructed based on the proportion of time 2 individuals spent in nest boxes together out of the entire time they spent in nest boxes (simple ratio index, where 0 indicates that individuals spent no time together and 1 indicates that individuals spent all their time in nest boxes together). We calculated monthly networks for the entire 10 years of data. In order for an individual to be included in a social network, it had to be present in the antennae data on at least 75% of the days of the month. This provided a balance between supplying a sufficient amount of data per individual to avoid biases when constructing social networks and including as many individuals as possible in the network to avoid biases when considering whole network metrics. For each of these networks, we also assigned individuals to social groups using the clustering algorithm developed by Blondel et al. (2008). This starts by assigning each individual their own group, and then sequentially moves allocated individuals between groups so as to achieve maximum modularity (proportion of connections within groups compared to proportion of connections between groups).

Genetic similarity was calculated based on markers at 25 polymorphic microsatellite loci (Bult et al. 2008; Teschke et al. 2008; Ferrari et al. 2019, see Supplementary Table S1 for summary). These markers were used to calculate the Wang coefficient (Wang 2002) of pairwise relatedness among mice. Wang relatedness is an estimator of coefficient of relatedness between pairs of individuals, generally considered to be robust to uncertainties about allele frequency and useful for populations with complex pedigrees. In our study population, this measure has previously been found to highly correlate with Hamilton's degree of relatedness *r*, making it an appropriate metric to determine pairwise relatedness (Harrison et al. 2018). Wang relatedness was calculated using the R package relatedness (Pew et al. 2018), an R implementation of the software COANCESTRY (Wang 2011). Networks of genetic similarity were constructed by taking the Wang relatedness coefficient between each dyad and scaling it between 0.0001 and 1. The lowest value of dyadic relatedness ever recorded in the barn was set to 0.0001, and the

dyad of highest relatedness set to 1. This value of rescaled genetic similarity was used as the edge weights in genetic networks. The value of 0.0001 was used because an edge with a weight of 0 would not technically exist in a network. As with the social data, we calculated monthly genetic networks for the entire study period. Individuals that were not present in the social network for a month were removed from the corresponding genetic network. Similarly, individuals for whom we could not calculate genetic relatedness were removed from the social network. This ensured that exactly the same individuals were present in each monthly social and genetic network. All networks were constructed in R (R Development Core Team 2019) using the igraph package (Csardi and Nepusz 2006).

Multilayer networks and edge overlap

To assess the correlation between the networks of genetic similarity and social association we employed multilayer network methods (Finn et al. 2019). Given our long-term dataset and our hypotheses regarding population size and environmental conditions, a multilayer approach allowed us to efficiently quantify and compare changes in social and genetic network structure over time. We chose to treat each network type as a layer in a 2-layer multilayer network and calculated the global edge overlap between them, for each of the 120 pairs of genetic and social networks. This whole-network multilayer metric quantifies the overlap in edges between 2 networks (Bianconi 2013; De Domenico et al. 2015a). Thus, 2 networks with identical edges would have a global edge overlap of 1. In our case, the edge weights of the social layer were always lower than the edge weights in the genetic layer. In addition, the edge weights between a dyad in the genetic layer were always the same between months, meaning that any changes in edge overlap represent sociality being more or less similar to relatedness. Multilayer networks were constructed using the R package MuxViz (De Domenico et al. 2015b), which was also used to calculate global edge overlap. Two types of edge overlap were calculated. The first used all edges in the genetic layer, which were between every dyad included in the network (rescaled Wang relatedness calculated between all individuals present in the network, represented by edge color in Figure 2). As the
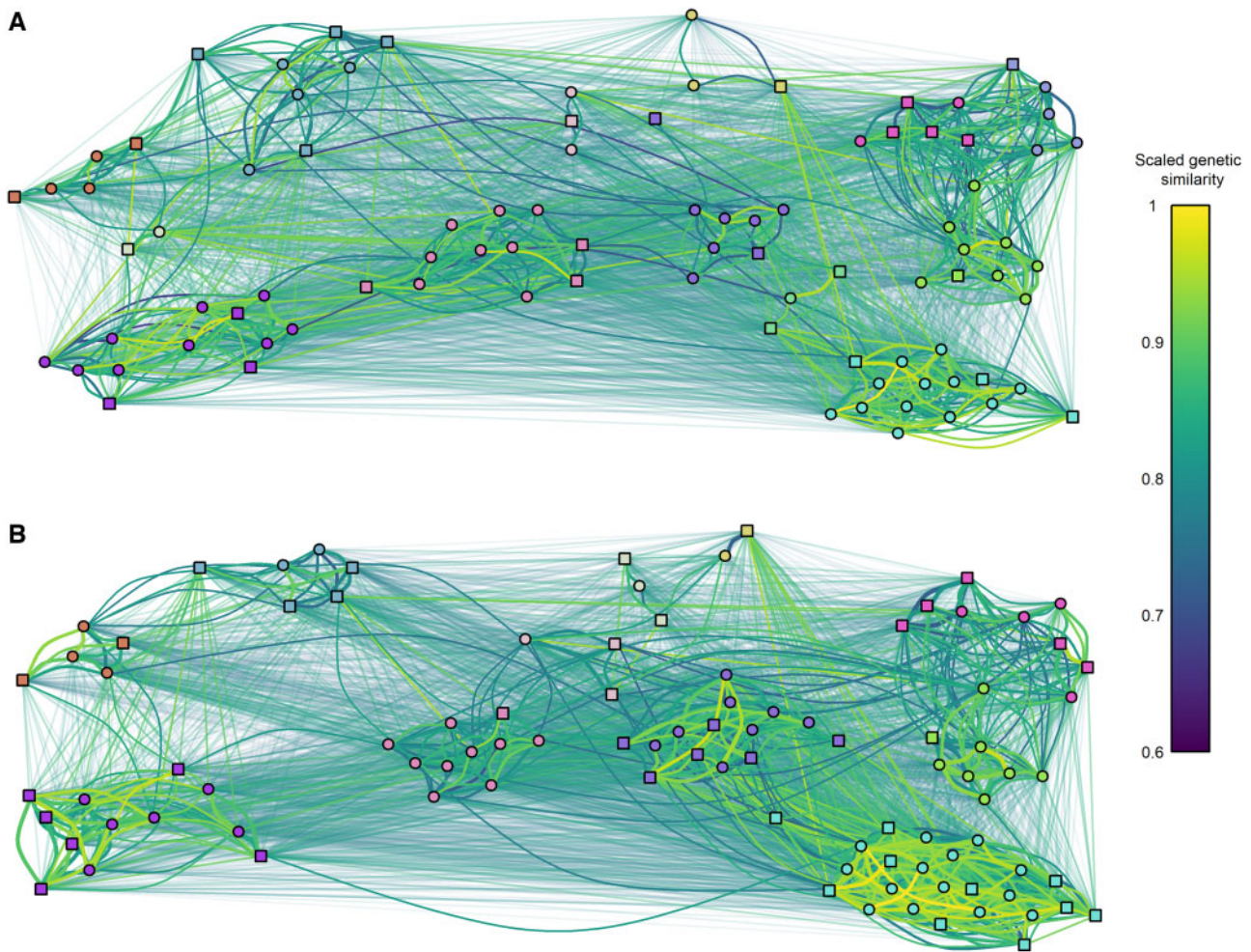
Figure 2. Illustration of the networks used to calculate full global edge overlap between social associations and genetic similarity in the entire population. The color of edges represents rescaled genetic similarity between a pair of individuals, with brighter colors indicating higher genetic similarity. Curved edges represent social associations, with the thickness of edges indicating the strength of association (the proportion of time a dyad spent together). Straight edges indicate a social association of strength 0, illustrating the genetic similarity of individuals who did not interact. These edges were removed from the restricted versions of these networks in order to calculate restricted global edge overlap, see Supplementary Figure S1. Square nodes are males although round nodes are females. Node color indicates social group (as detected from the social associations). Node layout is based approximately on the spatial location of individuals, when using nest boxes within the barn. (**A**) A network from September 2009, with a full global edge overlap of 0.018. (**B**) A network from November 2009, with a full global edge overlap of 0.042. These networks were chosen due to their relative similarity in size and proximity in time, although nevertheless showing a difference in edge overlap.

genetic layer contained a large number of edges that effectively did not exist in the social layer due to certain individuals never interacting with each other (leading to an edge strength of 0 in the social layer, indicated by straight edges in Figure 2), this measure of edge overlap (henceforth: full edge overlap) was expected to be very low. The second used a restricted genetic layer, which consisted only of edges that existed in the social layer (edge strength of >0 in the social layer, see Supplementary Figure S1). This measure (henceforth: restricted edge overlap) focused only on how much overlap social associations had with the genetic relatedness between 2 individuals. Full edge overlap provided a more conservative estimate, accounting for individuals who had high relatedness but never interacted with each other (a high edge weight in the genetic layer but an edge weight of 0 in the social layer, as represented by bright, straight edges in Figure 2), which would lead to decreased overlap. As well as calculating these values for the monthly whole-barn networks, we also calculated them for networks restricted to individual groups (as detected from the social layer for that month) consisting of >3

individuals. Detected groups consisting of single individuals or dyads were not considered as we did not believe these to represent biologically meaningful social groups. The edges considered in these networks were restricted to those between members of the same social group, ignoring connections with other groups. These networks allowed us to compare the effect of overall barn population size to local group size, as the density of an individual's immediate social group might be argued to have more of an effect on that individual. This comparison also helped determine if any effects found in the full-barn networks might be driven by, for example, a small number of large groups. For both whole-barn and within-social group networks, we also calculated edge overlap in networks consisting only of male–male and female–female interactions.

Analyses

Monthly global edge overlap values were fitted as response variables in Bayesian regression models using the R package BRMS (Bayesian Regression Models using 'Stan', Bürkner 2017). In all whole-barn

models, adult population size was fitted as an explanatory variable. Adult population size was estimated based on the total number of individuals recorded by any antenna for that month. While this gives an estimate of the number of adults present which may have an effect on individual behavior, not all of these individuals were always included in the networks for that month due to not meeting the necessary criteria. We therefore also fitted the interaction between the estimated population size with the proportion of these individuals who were actually included in the multilayer network. This controlled for potential overestimation of global edge overlap when a smaller proportion of individuals were included in the analyzed network, and vice versa. The year was fitted as a random effect to control for other aspects that might differ between years (e.g., a disease outbreak in 2012, Dobay et al. 2015).

For both measures of edge overlap, we fitted 3 models. The first model included month of the year fitted as a smoothing factor, thus modeling a nonlinear change in season. The other 2 models substituted month for variables that might be correlated with season, in order to investigate what relevant biological effects might drive any changes in overlap found with season. These models fitted average monthly temperature and level of breeding activity (as represented by total number of pups sampled per month), in place of month, respectively. All these models included the effect of number of tagged adults, proportion of these included in the network and the interaction between them. As population size was one of the effects we were interested in, caution was taken to consider all models while interpreting this effect.

In order to gain better understanding of the influence of overall barn population size compared to the size of social groups, the same models were then also fitted using the within-group networks. Finally, as we were interested in whether the patterns found in the overall network might be driven by or restricted to a particular sex, we repeated all analyses on sex-restricted networks. All numeric explanatory variables were mean-centered and rescaled so that 1 was equal to 1 SD of the original variable. When examining results, we primarily focused on variables where confidence intervals (CIs) did not cross 0.

Results

Over the 10-year study period, population size increased from a yearly average of 97.5 ± 11.3 SD tagged individuals in 2008, with 4.8 ± 0.9 SD detected groups (>3 individuals), to an average of 357.9 ± 70.5 SD tagged individuals with 14.8 ± 1.5 SD detected groups in 2017. This corresponds to a density of 1.3 tagged adults/m^2 in 2008, to 5 tagged adults/m^2 in 2017. Though there was a general trend of growth, there was some pronounced variation between seasons and years (Dobay et al. 2015). The greatest recorded number of tagged adults was 540, in October 2016. Over the entire study period, 3,459 individuals were included in our networks. As expected, in whole-barn networks the full overlap measure was generally quite low (mean 0.04 ± 0.04), whereas restricted overlap tended to be somewhat higher (mean 0.23 ± 0.05). In the within-group networks, these 2 measures were more similar with a mean of 0.29 ± 0.12 for full edge overlap and 0.30 ± 0.11 for restricted edge overlap. This is likely due to the lower number of individuals and higher level of connectivity within a group compared to the whole-barn networks.

In the whole-barn networks, a strong seasonal effect was immediately apparent in both measures of edge overlap. This was confirmed by the strength of the smoothing term (Tables 1A and 2A,

Figures 3A and 4A). Both overlap measures dipped from April to September, returning to higher values in the winter (October to December). The models fitting variables that might explain the observed seasonal variation found that both temperature and the number of pups were strong predictors of the 2 edge overlap measures (as might be expected due to the high correlation between these variables), with both leading to reduced edge overlap in their respective models (Tables 1B, C and 2B, C, Figures 3C, D and 4C, D). Of these models, those with temperature as an explanatory variable appeared to be better fitting than those with the number of pups as an explanatory variable, based on their R^2 values (Tables 1B, C and 2B, C). The interaction between monthly adult population size and the proportion of individuals in a network was more important in the model of restricted edge overlap in the whole-barn network (Table 2A, CIs did not cross 0) than in the model of full edge overlap (Table 1A). This is to be expected as the number of edges (representing actual social connections) in restricted networks will be more directly influenced by the number of individuals present in that network. When controlling for the proportion of individuals included in networks and seasonal variation, both types of overlap appeared to decrease slightly as number of adults increased (Figures 3B and 4B, Tables 1A and 2A). This effect was generally rather weak in all models however, appearing strongest in the model fitting restricted edge overlap against month as a smoothing factor (Table 2A).

Although the effect of overall population size seemed relatively weak, the models of within-group networks indicated that group size had a strong influence on the overlap between genetic and social networks, with larger groups having lower overlaps (Figures 3F and 4F, Tables 1D and 2D). Other than this, the within-group results followed qualitatively similar seasonal patterns and effects of temperature and number of pups to the whole-barn network (Figures 3C–H and 4C–H, Tables 1D–F and 2D–F). Similarly, within the sex-restricted networks, the female only whole-barn and per group models followed qualitatively similar trends to the networks including both sexes (Supplementary Figure S2, Supplementary Tables S2 and S3). In models of male only networks, the number of males in the overall population and the number of males in a group appeared to have no effect on edge overlap (Supplementary Tables S4a, d and S5a, d, Supplementary Figures S4b, f and S5b, f).

Discussion

We used multilayer techniques to quantify long- and short-term changes in the relationship between social associations and genetic similarity, both at a population level and within groups. Our findings reveal a distinct change in the level to which social structure coincided with genetic structure from winter to summer months, both in the population as a whole and within groups. This change correlated with temperature and breeding activity (as indicated by the number of pups sampled per month). While the steady increase in population size over the years appeared to cause a slight reduction in the overlap between genetic and social networks, this effect was far weaker than expected. This was despite a clear trend for social structure to diverge from genetic structure within larger groups. Taken together, these results indicate that the overlap in social structure and genetic structure in our population underwent seasonal changes, but that no strong long-term increase or decrease was observed. We therefore conclude that the observed changes were caused by dynamic changes in the benefits of associating with

Table 1. Model summary tables for full average global edge overlap in whole-barn networks

(A–C) and within-group (D–F) networks. This table shows the effect of month fitted as a smoothing effect (A and D), temperature (B and E) and number of pups (C and F) as well as the effect of number of tagged individuals and proportion of tagged individuals in network. Effects, where CIs do not cross 0 are highlighted in bold. Each model's R^2 value and SD of the random intercept, year, are also provided. All continuous variables were mean-centered and rescaled so that 1 was equivalent to 1 SD.

Whole-barn edge overlap (full):

A)

	Estimate (2.5–97.5% C)
R^2	0.360 (0.200 to 0.487)
Year (random intercept SD)	0.016 (0.003 to 0.032)
Intercept	0.040 (0.027 to 0.052)
No. of tagged adults	−0.008 (−0.017 to 0.002)
Prop. adults in network	**−0.019 (−0.028 to −0.010)**
No of adults: prop. in network	0.001 (−0.007 to 0.008)
Month	−0.004 (−0.304 to 0.198)
Month (smoothing term)	**0.084 (0.020 to 0.261)**

B)

	Estimate (2.5–97.5% CI)
R^2	0.330 (0.183 to 0.449)
Year (random intercept SD)	0.017 (0.004 to 0.035)
Intercept	0.039 (0.026 to 0.052)
No. of tagged adults	−0.005 (−0.015 to 0.005)
Prop. adults in network	**−0.021 (−0.029 to −0.012)**
No. of adults: prop. in network	0.001 (−0.007 to 0.008)
Temperature	**−0.014 (−0.021 to −0.007)**

C)

	Estimate (2.5–97.5% CI)
R^2	0.259 (0.116 to −0.389)
Year (random intercept SD)	0.013 (0.001 to 0.030)
Intercept	0.040 (0.028 to 0.052)
No. of tagged adults	−0.007 (−0.016 to 0.003)
Prop. adults in network	**−0.017 (−0.026 to −0.009)**
No. of adults: prop. in network	0.002 (−0.006 to 0.010)
No. of pups	**−0.010 (−0.018 to −0.003)**

Within-group edge overlap (full):

D)

	Estimate (2.5–97.5% CI)
R^2	0.350 (0.308 to 0.388)
Year (random intercept SD)	0.071 (0.044 to 0.116)
Intercept	0.274 (0.227 to 0.319)
Group size	**−0.055 (−0.063 to −0.048)**
Prop. adults in network	−0.003 (−0.014 to 0.008)
Group size: prop. in network	0.001 (−0.005 to 0.006)
Month	0.315 (−0.005 to 0.674)
Month (smoothing term)	**0.213 (0.093 to 0.447)**

E)

	Estimate (2.5–97.5% CI)
R^2	0.313 (0.272 to 0.351)
Year (random intercept SD)	0.074 (0.045 to 0.126)
Intercept	0.275 (0.229 to 0.319)
Group size	**−0.051 (−0.059 to −0.044)**
Prop. adults in network	−0.007 (−0.018 to 0.005)
Group size: prop. in network	0.001 (−0.004 to 0.007)
Temperature	**−0.051 (−0.058 to −0.044)**

F)

	Estimate (2.5–97.5% CI)
R^2	0.259 (0.219 to 0.298)
Year (random intercept SD)	0.077 (0.047 to 0.133)
Intercept	0.274 (0.224 to 0.324)
Group size	**−0.043 (−0.051 to −0.036)**
Prop. adults in network	−0.003 (−0.014 to 0.009)
Group size: prop. in network	0.003 (−0.003 to 0.009)
No. of pups	**−0.039 (−0.046 to −0.032)**

Table 2. Model summary tables for restricted average global edge overlap in whole-barn networks

(A–C) and within-group (D–F) networks. This table shows the effect of month fitted as a smoothing effect (A and D), temperature (B and E), and number of pups (C and F) as well as the effect of number of tagged adults and proportion of tagged adults in network. Effects, where CIs do not cross 0 are highlighted in bold. Each model's R^2 value and SD of the random intercept, year, are also provided. All continuous variables were mean centered and rescaled so that 1 was equivalent to 1 SD.

Whole-barn edge overlap (restricted)

A)

	Estimate (2.5–97.5% CI)
R^2	0.663 (0.563 to 0.725)
Year (random intercept SD)	0.045 (0.024 to 0.081)
Intercept	0.222 (0.192 to 0.251)
No. of tagged adults	−0.014 (−0.030 to 0.002)
Prop. adults in network	0.002 (−0.008 to 0.011)
No. of adults: prop. in network	**−0.014 (−0.022 to −0.006)**
Month	0.068 (−0.241 to 0.369)
Month (smoothing term)	**0.171 (0.067 to 0.381)**

B)

	Estimate (2.5–97.5% CI)
R^2	0.542 (0.415 to 0.625)
Year (random intercept SD)	0.038 (0.018 to 0.071)
Intercept	0.223 (0.196 to 0.249)
No. of tagged adults	−0.003 (−0.019 to 0.014)
Prop. adults in network	−0.002 (−0.013 to 0.009)
No. of adults: prop. in network	**−0.013 (−0.022 to −0.004)**
Temperature	**−0.031 (−0.040 to −0.021)**

C)

	Estimate (2.5–97.5% CI)
R^2	0.412 (0.256 to 0.522)
Year (random intercept SD)	0.042 (0.017 to 0.083)
Intercept	0.224 (0.193 to 0.252)
No. of tagged adults	−0.005 (−0.028 to 0.016)
Prop. adults in network	0.005 (−0.007 to 0.017)
No. of adults: prop. in network	−0.011 (−0.022 to 0.000)
No. of pups	**−0.020 (−0.031 to −0.009)**

Within-group edge overlap (restricted):

D)

	Estimate (2.5–97.5% CI)
R^2	0.352 (0.309 to 0.390)
Year (random intercept SD)	0.068 (0.041 to 0.114)
Intercept	0.282 (0.239 to 0.325)
Group size	**−0.053 (−0.060 to −0.046)**
Prop. adults in network	−0.002 (−0.012 to 0.009)
Group size: prop. in network	0.001 (−0.004 to 0.007)
Month	**0.329 (0.015 to 0.671)**
Month (smoothing term)	**0.209 (0.092 to 0.442)**

E)

	Estimate (2.5–97.5% CI)
R^2	0.315 (0.274 to 0.354)
Year (random intercept SD)	0.070 (0.043 to 0.115)
Intercept	0.281 (0.239 to 0.324)
Group size	**−0.049 (−0.057 to −0.042)**
Prop. adults in network	−0.006 (−0.016 to 0.005)
Group size: prop. in network	0.002 (−0.004 to 0.007)
Temperature	**−0.051 (−0.059 to −0.045)**

F)

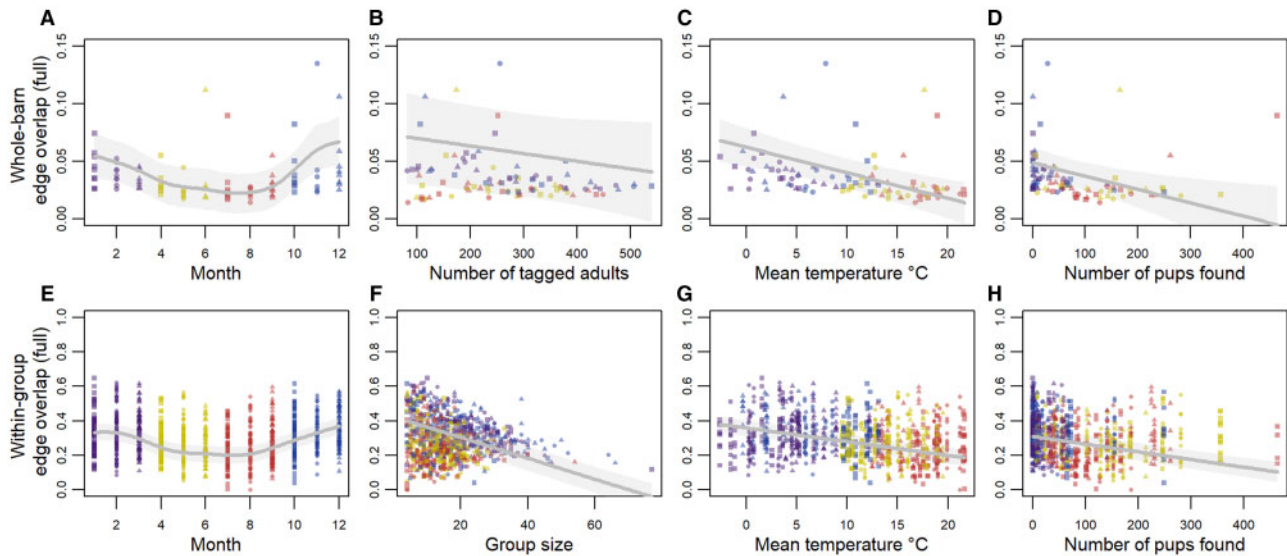|	Estimate 2.5% CI 97.5% CI
R^2	0.253 (0.212 to 0.293)
Year (random intercept SD)	0.074 (0.046 to 0.125)
Intercept	0.281 (0.238 to 0.333)
Group size	**−0.041 (−0.048 to −0.034)**
Prop. adults in network	−0.001 (−0.012 to 0.009)
Group size: prop. in network	0.003 (−0.003 to 0.009)
No. of pups	**−0.038 (−0.045 to −0.031)**

Figure 3. Predicted effects of explanatory variables on full global edge overlap in the whole-barn (**A–D**; Table 1A–C) and within-group (**E–H**, Table 1D–F) networks, plotted against raw data. Variables not on the *x*-axis are held at 0 (mean) when plotting estimates. Raw data have different shape and color depending which month they represent, as seen in **A** and **E**. **B** draws estimates for the effect of number of tagged mice from the model of full global edge overlap in the whole-barn network with the month as a smoothing factor (Table 1A) and *F* does the same for within-group networks (Table 1D).
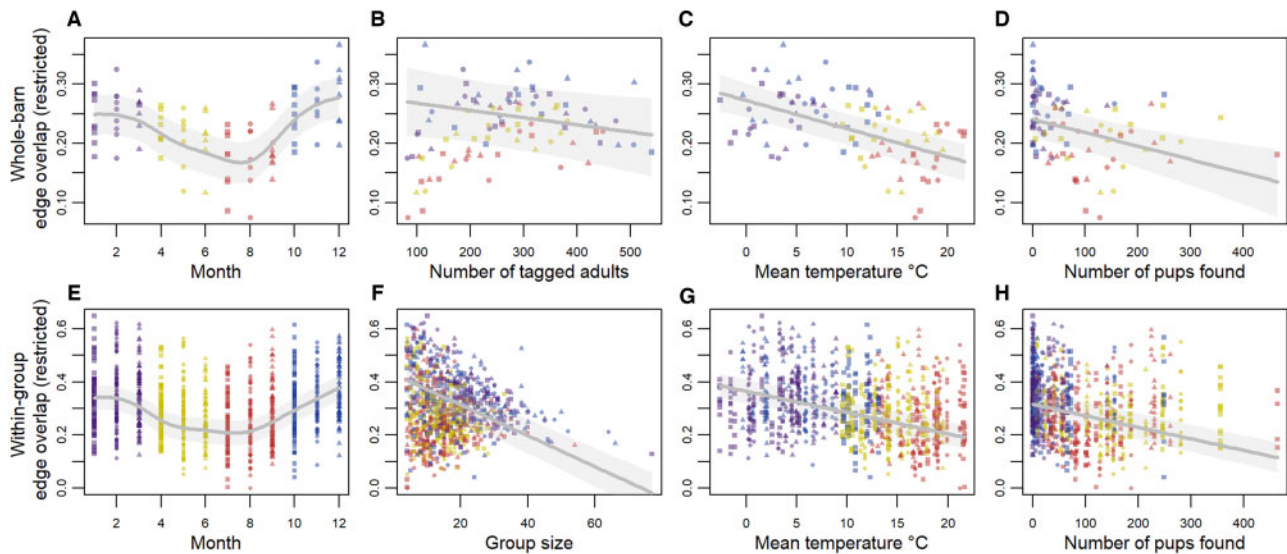
Figure 4. Predicted effects of explanatory variables on restricted global edge overlap in whole-barn (**A–D**, Table 2A–C) and within-group (**E–H**, Table 2D–F) networks, plotted against raw data. Variables not on the *x*-axis are held at 0 (mean) when plotting estimates. Raw data have different shape and color depending which month they represent, as seen in A and E. B draws estimates for the effect of number of tagged mice from the model of full edge overlap in the whole-barn network with month as a smoothing factor (Table 2A) and F does the same for within-group networks (Table 2D).

relatives, rather than population pressure forcing changes in group structure.

Although some models suggested a slight negative effect of population density on the overlap between genetic and social groups, this was generally not a strong effect. Despite the dramatic increase in population density (by almost 4-fold) over the years, which we assumed would result in increased competition for resources (access to females for males and nest boxes for females), the level to which social structure relates to genetic structure appears unchanged at the population level. Similarly, we expected the level of inbreeding within the barn to increase (given the apparent lack of immigration, see Runge and Lindholm 2018, Supplementary material). We predicted

that this would result in a decrease in full edge overlap, due to individuals being unable to associate with all genetically similar individuals in an increasingly genetically homogeneous population. However, while full edge overlap was generally always low, we found no evidence of this change, suggesting that increased inbreeding, if present, was insufficient to stop social groups differing genetically. Though the increase in population size had less effect than predicted, in the within-group networks a larger group size clearly resulted in a lower overlap between social and genetic networks. As there were more social groups present in the barn toward the end of the study period than at the beginning, some groups clearly underwent fission as the population grew (see also Liechti et al. 2020 for

detailed quantification of changes in group structure during some of the years analyzed here). Given our within-group and population-level results, this increase in number of groups could suggest that fission occurred along genetic lines when groups exceeded a certain size (Chepko-Sade and Sade 1979; Whitlock 1994; Archie et al. 2006; Patriquin et al. 2013). Fission occurring along genetic lines could explain why group size has a clear effect on edge overlap, while the effect of population size is negligible. There was also no sign of social crowding leading to an increase in relatedness within groups (which would lead to an increase in overlap between sociality and genetic similarity with increasing population size) as has been described for other species (Matthysen 2005; Frantz et al. 2010). This might anyway not be expected to happen in our population, as even if there were no available social groups to join (potentially due to lack of resources in a group's home range or aggression from existing group members), mice were always free to leave the barn entirely.

Our results demonstrated a strong seasonal trend, with the overlap between social and genetic layers decreasing during spring and summer. This may be due to mice changing association patterns as reproductive competition increases during times of high breeding activity. The number of pups found in a month was a strong predictor of edge overlap in both full and restricted edge overlap and both network types, suggesting that the benefit of associating with genetically similar individuals decreases during these times. Such a change in behavior could be to avoid competition with relatives (Hamilton and May 1977; Clutton-Brock et al. 1982; Perrin and Mazalov 2000; West et al. 2002) and/or reduce risk of inbreeding (Keller and Waller 2002; Annavi et al. 2014). Individuals might visit other social groups to seek extra-group matings, allowing them access to preferred mates and avoiding competition with relatives, as observed in species where reproduction is more tightly controlled (Clutton-Brock et al. 1982). It should be noted that the similarity in patterns observed in sex-restricted and both-sex networks make it less likely that the patterns we observed are purely due to inbreeding avoidance. How much inbreeding/competition avoidance might cause changes in social behavior in a species will be dependent on both the cost of inbreeding and the ability to recognize relatives (König 1994b; Hurst and Barnard 1995). In house mice, lab studies have found that females prefer genetically dissimilar males (Roberts and Gosling 2003; Green et al. 2015). Females of other social mammal and bird species that mostly associate with related individuals have also been found to mate with unrelated individuals where possible (Double et al. 2005; Kerth and van Schaik 2012; Kurvers et al. 2013). Nevertheless, in our population females continue to interact with relatives in social groups during the breeding season, and will also regularly communally nest with related females (Green et al. 2015; Harrison et al. 2018). It could be suggested that it might be desirable to actually avoid aggregating with relatives so as to avoid inflicting any potential costs of such aggregations on relatives, such as attracting predators (Griffiths et al. 2003). Predation pressure, however, is unlikely in our system as predators which might be attracted by an aggregation can rarely access the barn (though see: Evans et al. 2020).

An alternative explanation is that the seasonal patterns are caused by a change in behavior during the winter. We found that temperature had a strong effect on both full and restricted edge overlap. Many species engage in some form of social thermoregulation, particularly mammals (Terrien et al. 2011). Thermoregulation via huddling behavior is well-documented in house mice (Batchelder et al. 1983; König and Lindholm 2012). We might predict a decrease in overlap between social and genetic structure as individuals become less choosy with whom they share a nest, as found in other mammals (Morton 1978; Rhind 2003; Elmhagen et al. 2014). However, in our data, the opposite trend was observed, with models suggesting that social structure follows genetic structure more during colder months. This could indicate that it is beneficial to engage in social thermoregulation with relatives, potentially due to the reduced likelihood of aggression (König 1994b; Thorington et al. 2010; Robert et al. 2013; Williams et al. 2013). Additionally, when engaging in thermoregulatory behavior, individuals on the outer edge of a group will receive less benefit than those closer to the center (Alberts 1978). There may therefore also be indirect selection benefits to engaging in social thermoregulation with relatives, which mitigates the potential costs of being on the periphery of a group (Hamilton 1964; Arnold 1988). Lab studies of house mice have shown that mice will prefer to huddle with familiar/related individuals, but the relative importance of social association and relatedness when engaging in this behavior was uncertain (Groó et al. 2018). Relatedness is likely to be important, as nonbreeding female house mice prefer to nest with related over unrelated individuals, when familiarity is controlled for (Green et al. 2015). Similar preferences have also been found in other mammals (Mateo 2003; Patriquin et al. 2013; Flores et al. 2020).

Due to the strong correlation between number of pups and temperature, we are unable to rule out either one of these hypotheses. A first step might be to establish the extent to which increases in breeding behavior alters sociality in a controlled environment. This would help disentangle the relative influence of temperature and breeding behavior on changes in patterns of association. Similarly, experiments attempting to discern the relative importance of familiarity compared with relatedness in huddling behavior would be useful in testing the social thermoregulation hypothesis. This might be challenging as familiarity and kin-recognition appear to be linked in house mice, as familiar mice are usually kin (König 1994b; Hurst and Barnard 1995). Our study population is spatially and genetically structured (König et al. 2015), and within groups females prefer familiar partners for communal nesting (Harrison et al. 2018). In terms of examining whether the decrease in overlap between social behavior and genetic structure is linked to avoiding competition or inbreeding with relatives, detailed examination of how the decisions of females of different breeding status relate to social network structure and relatedness is necessary. This will require construction of a detailed pedigree, and will need to account for female multiple mating, which is common in our study population (Auclair et al. 2014).

In conclusion, we used multilayer network techniques to reveal changes in how house mice associate with relatives at different scales. We found only weak evidence of the relationship between population social and genetic structure being altered by population pressure, but changes were observed in larger groups. Our results did show a distinct seasonal change in how social structure relates to genetic structure. These results could be due to changes in behavior related to breeding activity or in response to environmental effects. Further study will be required to link how such changes in individual behavior combine to lead to these population-level effects. Our study emphasizes the importance of analyzing the mechanisms trading-off the costs and benefits of interacting with relatives dependent on resource competition.

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Author Contributions

J.C.E. devised the study, processed, and analyzed the data and wrote the manuscript. B.K. initiated and maintains the long-term study, A.K.L. is involved in long-term data collection, and maintains the genetic data. All authors discussed the results and contributed to the final manuscript.

Ethics Statement

Data were collected under the permits ZH 210/2003, ZH 215/2006, ZH 51/2010, ZH 56/2013, and ZH 91/2016 from the Cantonal Veterinary Office Zürich, Switzerland.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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