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Split between two worlds: automated sensing reveals links between above- and belowground social networks in a free-living mammal

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Many animals socialize in two or more major ecological contexts. In nature, these contexts often involve one situation in which space is more constrained (e.g. shared refuges, sleeping cliffs, nests, dens or burrows) and another situation in which animal movements are relatively free (e.g. in open spaces lacking architectural constraints). Although it is widely recognized that an individual's characteristics may shape its social life, the extent to which architecture constrains social decisions within and between habitats remains poorly understood. Here we developed a novel, automated-monitoring system to study the effects of personality, life-history stage and sex on the social network structure of a facultatively social mammal, the California ground squirrel (*Otospermophilus beecheyi*) in two distinct contexts: aboveground where space is relatively open and belowground where it is relatively constrained by burrow architecture. Aboveground networks reflected affiliative social interactions whereas belowground networks reflected burrow associations. Network structure in one context (belowground), along with preferential juvenile–adult associations, predicted structure in a second context (aboveground). Network positions of individuals were generally consistent across years (within contexts) and between ecological contexts (within years), suggesting that individual personalities and behavioural syndromes, respectively, contribute to the social network structure of these free-living mammals. Direct ties (strength) tended to be stronger in belowground networks whereas more indirect paths (betweenness centrality) flowed through individuals in aboveground networks. Belowground, females fostered significantly more indirect paths than did males. Our findings have important potential implications for disease and information transmission, offering new insights into the multiple factors contributing to social structures across ecological contexts.

This article is part of the theme issue 'Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour'.

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1. Introduction

Behavioural ecologists have long understood that social decisions have important fitness consequences for individuals, shaping key processes including foraging decisions, information flow, disease transmission and reproduction [1]. It has become increasingly clear that who-meets-whom within animal societies is rarely random [2] and that social structure is often produced by individual variation in social preferences within groups [3,4]. Social network theory offers useful tools for quantifying and understanding how this variation contributes to social structure [5–7]. This framework formalizes the classical

view that repeated pairwise interactions give rise to social relationships that in turn contribute to emergent social structures [8]. Importantly, network analysis extends traditional approaches by offering well-defined, standardized metrics for characterizing the effect of an individual's characteristics on *direct* and *indirect* social connections [9–11]. Network metrics are, therefore, offering new insights into the ways that individual characteristics (e.g. life-history stage, sex), preferential relationships (e.g. coalition partners) and the presence of key individuals shape group stability and structure [3,12–18].

A parallel, but largely distinct, literature has emerged showing that many animals exhibit 'personalities' [19], defined as consistent individual differences in behaviour; e.g. in aggressiveness, boldness or sociability. Only a handful of studies have explicitly linked personality traits to animal social networks [20–24]. A closely related literature examines behavioural syndromes, defined as consistent and/or correlated behaviour across two or more situations [19,25,26]. In nature, the two situations for animals often involve one situation where space is more constrained (e.g. shared use of refuges, sleeping cliffs, nests, or burrows) and another situation in which movements are relatively free (e.g. in open spaces lacking architectural constraints). The latter may, therefore, permit a richer range of social behaviours and interactions.

Interestingly, although most animals live in two or more distinct habitats or major situations, most social network studies are limited to a single context or rely upon combined data without explicit considerations of ecological context [27]. Thus, despite definitive evidence that individuals in different situations often differ in their patterns of space use [28,29] and sociality [30], and this notion being discussed extensively in review articles [7,10,31], very few empirical studies explicitly examine links between social networks derived from different situations [27]. This is unfortunate because connectivity may contribute to important processes such as disease and information transfer [32–34]. For example, understanding whether networks are more connected in one habitat than the other may offer insights into contexts as a 'hot spot' of transmission [35–37]. Moreover, partitioning the differences in social network metrics between contexts for individuals of different life-history stages and sexes will likely provide insights into how social roles (e.g. for juveniles versus adults [3,38]) vary or remain consistent across situations. Thus, although data collected using different sampling methods are inherently challenging to compare [39], efforts to assess the effects of life-history stage and sex on *context-specific* social metrics for individuals should provide an enhanced understanding of mechanisms contributing to social structure [2].

Within a social network framework, three major, non-mutually-exclusive mechanisms may generate social structure: 'movement rules', 'social interaction rules' and 'individual characteristics' [3,6,40]. First, movement rules refer to the ways that daily patterns of travel to and from limited resources, such as a shared refuge or a clumped food source, can produce repeated spatial associations even in the absence of social preference [41]. For individuals that travel away from refuges each day to search for food, movement rules predict that animals sharing similar refuges will be most likely to socialize due to increased encounter rates. Second, social interaction rules describe the extent to which social partner choice drives social structure [6].

These rules emphasize factors such as homophily [42], the tendency for similar individuals (e.g. same life-history stage, same sex) to preferentially interact. For example, homophily occurs among juveniles during play [43,44] or among adult females with enduring social bonds [45]. Finally, individual characteristics, such as personality, life-history stage or sex of an individual may predict social network metrics within a context [3,31,38]. An individual's network position may also remain consistent across contexts, indicating a behavioural syndrome, or vary between contexts if individuals engage in context-specific social roles.

Here we studied a semi-fossorial mammal, the California ground squirrel, *Otospermophilus beecheyi*, to gain insights into the factors contributing to social network structures of free-living mammals who split their lives between two major contexts: above- and belowground. This is important because very few studies simultaneously seek to explain the ecological aspects of above- and belowground behaviours in semi-fossorial mammals; for notable exceptions, see [46,47]. California ground squirrels are facultatively social rodents that offer an interesting mammalian system for elucidating the extent to which movement rules, social interaction rules, and/or individual characteristics (e.g. personality, behavioural syndromes, life stage, sex) predict social structure. Individuals reside at distinct geographical sites, called colonies, at which group members regularly socialize, forage and collectively mob predators aboveground, but also seek refuge belowground in communal burrow systems for protection from predation and harsh weather [48–50].

Our current study capitalized upon the natural history of these animals to examine the mechanisms promoting social structure in two distinct contexts: above- and belowground. First, movement rules predict that because burrows are refuges limited in their size capacity as well as in their spatial distribution and abundance across the landscape, individuals that share burrows may also socialize to the greatest extent aboveground due to their increased tendency to interact as they travel to and from the same location (burrow) each day to forage aboveground. Specifically, if movements away from refuges spatially constrain opportunities for aboveground social exchanges, then social network structure in one context (belowground) should predict that in a second context (aboveground). Second, social interaction rules predict that if individuals exhibit social preferences based on homophily, then they should associate most often with others of the same stage and sex. Finally, we investigated how individual characteristics shape *direct* and *indirect* social connectivity within above- and belowground social networks. If networks reflect animal personalities and/or behavioural syndromes, then the relative network positions of individuals should be consistent over time (between years) and between contexts (aboveground versus belowground), respectively [31,51]. Beyond the effects of individual identity, we also predicted that juveniles of both sexes and adult females should be the most connected within their social networks. Although surprisingly little is known about kinship and dispersal patterns for the California ground squirrel [50], groups are likely matrilineal (female-based kin structure) with male-biased dispersal, as seen across the ground squirrel lineage [52]. If this is the case, then adult females and their immature offspring should promote connectivity, as seen in other matrilineal mammals [3,53,54].

Figure 1. Novel automated-tracking system. (*a*) Live trapping and release of free-living California ground squirrels allow researchers to provide each individual with a unique fur mark for visual identification during social observations, ear tag for identification during trapping and passive integrated transponder (PIT) tag beneath the skin for detection by the monitoring system. (*b*) Movements are detected by scanning an individual's PIT tag every time it passed through a secure antenna loop inside of a burrow opening. (*c*) Data logger (Biomark, Inc., Boise Idaho) records information about the time of day, squirrels' PIT tag ID and burrow location for each movement event. (Online version in colour.)

2. Material and methods

(a) Field site and study subjects

We studied free-living California ground squirrels at Briones Regional Park in Contra Costa County, California (37.9377014 N, 122.1388542 W). At this field site, at least some members of the population remain active aboveground all year [55]. Breeding largely occurs from mid-February to April, with females typically only producing a single litter per year [55]. Adult females rear young in burrows until offspring emerge as fully weaned young (age: 45–60 days), after which young of the year spend the remainder of their first year as juveniles (61–364 days) before maturing into reproductive adults (older than 364 days) [55,56]. We focused on juveniles and adults in the current study because these individuals are regularly observed socializing aboveground and, thus, have ample opportunities to visit burrows belowground and to affiliate with colony members aboveground.

The precise connectivity of California ground squirrel burrow complexes is largely unknown [50]. Although most burrows are presumed of to lack connections, excavations show that some are comprised of interconnected tunnels with multiple openings (e.g. 6–20 openings) at the surface [55]. Most tunnels are 4.6 m long, but extreme cases report tunnels of up to 70 m [55,57]. Regardless of the precise interconnectivity or length of burrow systems, individuals that share any burrow opening on a given day have opportunities to socialize, share space and exchange parasites [58].

(b) Live trapping of free-living individuals

The current study was part of a long-term study at our main colony site (Crow). Since 2013, we have live-trapped, marked and released California ground squirrels using squirrel traps (Tomahawk Live-Trap Company, Hazelhurst, Wisconsin, USA) baited with black oil sunflower seeds and peanut butter at and around burrow entrances. This is primarily done during the summer months, from late May to early August (figure 1*a*). Traps were covered with pieces of cardboard for shade and checked at intervals of ≤30 min. While safely contained in a cone-shaped, cloth handling bag [59], we noted the individual's weight, sex, anogenital distance and reproductive status and then released each individual at its site of capture. We used this information to assign the life-history stage and sex to each individual for each year of the study.

Upon first capture, individuals were given three types of identification (figure 1). First, a Monel metal ear tag (National Band and Tag Co., Newport, Kentucky, USA) was attached to one pinna for permanent identification. Second, a unique Nyanzol cattle dye mark (Greenville colorants: New Jersey) was applied to the back for visual identification during social observations. Third, we inserted a unique passive integrated transponder (PIT) tag (Biomark, Inc., Boise Idaho) beneath the skin as a reliable 'lifetime' barcode [60]. In 2016 and 2017, respectively, we live-trapped and monitored a total of 131 and 158 marked individuals across the entire colony site.

(c) Automated sensing of belowground activity

Automated tracking offers exciting opportunities for the study of animal social networks [61]. Because the social lives of subterranean animals are largely hidden from researchers due to the small size of the openings to belowground refuges [62,63], we developed a new method for monitoring belowground activity of burrowing animals reliant upon radio-frequency identification to detect small (less than 1 g) and inexpensive PIT tags. We stored information from each burrow complex on an external data logger powered by a single 6 V rechargeable battery (Model DC224-6 AGM, Full River Battery, USA). A single battery powered each system for two weeks. This approach offers advantages over other reality-mining approaches because of its low cost, extended battery life and low disturbance to subjects [61].

Starting April 2016, we deployed data loggers (Biomark, Inc., Boise Idaho, figure 1a–c) at two distinct data monitoring stations within the colony site. The first station covered activity over an area of $15.0. \times 14.8$ m^2 ('Logs' area), whereas the second station covered an area of 17.8×7.7 m^2 ('580' area). The two areas were separated by 86 m and squirrels were regularly observed travelling aboveground between them. A total of 12 antennae loops were attached to each data logger at each station. Each loop was placed at an active burrow entrance and detected movements by scanning the unique PIT tags of visitors (figure 1b). We validated that each loop accurately detected PIT tags by scanning tags in and out of loops and confirming that their time–date stamps were accurately stored on the SD card at each station. These 12 loops provided substantial coverage of active openings, covering roughly 90% of active burrow entrances at each burrow complex. We secured each antennae loop at a single burrow entrance with 10 cm $\times$ 2.5 cm Fabric & Garden Staples (Easy Gardener Products, Inc., Waco, TX). Staples were placed into the dirt using a mallet without damaging the burrow architecture, obstructing the ability for the antenna to effectively read the PIT tag, or jeopardizing animal safety as squirrels passed through the antenna (figure 1b).

The data logger recorded the specific time, date and unique PIT tag number each time a tagged individual passed in or out of an antenna's loop (figure 1c). Each data logger and battery were hidden under their own $24'' \times 12'' \times 13''$ artificial rocks (Orbit granite valve box cover, Model # 53016) to protect equipment from weather and other disturbances. Squirrels adjusted quickly to the equipment; we detected the first squirrel entering a loop within 20 min. of deploying it. The automated-sensing system remains on-site and currently records data year-round. Loops are monitored weekly and reinforced with additional staples or repaired with electrical tape as needed. On rare occasions, we moved antennae from previously active burrows to newly active ones to ensure continuous coverage of most burrows; most changes occurred outside of our summer sampling periods, such as after a winter rainstorm or juveniles emerged at the start of the summer.

(d) Behavioural observations at field site

Social observations were conducted from 27 May to 27 July in two separate years: 2016 and 2017. Whereas the field site experienced a severe drought in 2016, rainfall returned to typical regional levels in 2017 (http://cdec.water.ca.gov/index.html). Most juveniles and adults of the year were marked during these entire periods and, thus, were easily observed during social observations and detected by the data loggers. We recognized animals aboveground in daylight within open grasslands by the unique fur marks we gave them. Animals were also detected belowground by their unique PIT tags at the two focal burrow complexes with consistently high antennae coverage.

The diurnal lifestyles of these animals make them particularly straightforward to observe aboveground [48,50]. Trained observers monitored the study colony primarily in the mornings (0800 to 1200 h) and some afternoons (1200 to 1400 h); most affiliative exchanges occurred between 0900 and 1100 h. Observers sat at a distance (≥ 20 m) to avoid influencing behaviour. Observers monitored multiple areas within the study colony each observation day of this study; at least two groups of observers simultaneously collected social data from each of the two areas being monitored belowground. Thus, these data provided excellent knowledge of affiliative interactions for animals observed at, between- or surrounding the two belowground monitoring stations.

We recorded all occurrences [64] of affiliative behaviours (socio-positive interactions) including greetings, proximity maintenance, social foraging and playing (for details, see ethogram

[48,50]) using 10×14 binoculars (Eagle Optics Ranger Extra-Low Dispersion Middleton, WI). Briefly, greetings involved two individuals meeting head-on and touching noses, one individual rubbing its cheek on that of another squirrel, or one individual approaching a second head-on and rubbing its nose near the corner of the receiver's mouth [48,50]. Proximity maintenance occurred when one individual approached a second and sat in direct body contact or within less than 1 m of the second individual [50]. Individuals foraged socially when they consumed seeds, grass or other forage within less than 1 m [50]. Each unique play bout started with one individual initiating play slapping, boxing, chasing, mounting, pouncing or wrestling with a second individual and ended when one of the two individuals moved apart from the other [50].

(e) Above- and belowground social network parameters

Networks are comprised of individuals (nodes) connected to each other (by 'ties' or 'edges'). In this study, nodes represented individual squirrels and ties represented weighted, symmetric connections between them. We selected colony-year as the unit of analysis to account for annual changes in colony composition attributed to births, deaths and dispersal [65]. We therefore constructed a total of four separate networks—one belowground network and one aboveground network for each year.

Ties within a network reflected the proportion of days each pair, A and B, were detected at the same burrow reader (belowground) or exchanged affiliative behaviours (aboveground). We elected to use the same sampling period (day) for both contexts to minimize differences in network construction. Day was used as the sampling period for two reasons. First, although recording the precise amount of time pairs of semi-fossorial rodents are simultaneously aboveground is challenging, measures of daily rates of behaviour offer robust measures of affiliation [65]. Second, because the precise connectivity of burrow entrances and exits is unknown, this measure captures daily overlap within a burrow opening regardless of whether pairs shared the burrow at the same time for a given day. We calculated simple association indices to measure the daily rates of pairwise associations in each context [2,66]. This index was appropriate for our study because all subjects in the current study were equally likely to be detected in both contexts [2,66].

Belowground associations were calculated as: (the number of days A and B were detected using the same burrow)/ (the number of days A and/or B were detected at one or more burrows). Aboveground associations were also calculated as: (the number of days A and B exchanged affiliative interactions)/(the number of days A and/or B were observed engaging in at least one affiliative interaction). Because even weak associations are potentially important for the maintenance of social structure, we analysed weighted, unfiltered networks based on all associations [67]. However, an individual had to be logged (via its PIT tag) at least once and observed engaging in at least one affiliative interaction aboveground to be included in the final aboveground and belowground networks for a given year. This was done to avoid spurious correlations between empty cells and to ensure that each pair had the opportunity to associate in both contexts [68].

We constructed each of the four networks using the package 'igraph' [69]. For each network, we calculated two different node-based metrics. First, we calculated the 'strength', the weighted equivalent to degree in binary networks, as the sum of its association indices with all colony-mates divided by the number of other potential actors (minus the focal individual) [70]. This standardized metric corrects for the number of nodes in the network to measure the extent to which each individual node *directly* associates with all potential actors in the network. Second, we calculated 'betweenness centrality', defined as a count of the

number of shortest paths through a node. This *indirect* metric reflects how important a node is for connecting disparate parts of the network, offering insights into the roles that key individuals may play in the spread of disease or information transmission across networks [6,31,32]. Because investigating the distributions of metrics (e.g. degree distribution for binary networks) is the preferred method for comparing node-based metrics between networks [2], we plotted cumulative distributions for metrics derived from above- and belowground networks to describe their relative properties.

(f) Statistical analyses

All statistical tests were conducted in R v. 3.4.1 [71]. To account for the non-independence in our data, we implemented permutation tests when using relational data (dyads within social networks) to test hypotheses [67,72] and included random effects in generalized linear mixed effects models (GLMMs) to account for repeated measures [3].

First, to test the predictions of movement and social interaction rules, we implemented multiple regression quadradic assignment procedures (MRQAPs) to assess the extent to which belowground network structure (predicted by movement constraints) and/or trait similarity (predicted by the social interaction rule of homophily) predicted aboveground network structure. This regression framework was superior to the univariate quadratic assignment procedure (QAP) because it allowed us to simultaneously test for the effects of multiple predictor matrices on the aboveground affiliative association matrix. For each year, we constructed a model in which we regressed three predictor matrices: (i) belowground association matrix, (ii) stage similarity (juvenile−juvenile = 1, juvenile−adult = 0, adult−adult = 1), (iii) sex similarity (male−male = 1, female−male = 0, female−female = 1) on the response matrix: aboveground affiliative associations. Permutation tests used the 'double-semi-partialing' method [73] developed in the mrqap.dsp function from the R package 'asnipe', each with 10 000 permutations [74]. We deemed P-values of less than 0.05 to be statistically significant.

Second, we tested for the effects of individual characteristics. To examine the potential for individual consistency in network position across contexts and years, we implemented consistency tests designed to compare the ranks of node-based metrics derived from different networks [51]. We therefore compared ranked values for a single metric (e.g. strength, betweenness) for each test [51]. First, to examine the effects of individual identity across contexts, we conducted a single test for individual consistency of each node-based metric (strength or betweenness) between ecological contexts (above- or belowground network) within a year. Second, we evaluated individual consistency across time by comparing each node-based metric (strength or betweenness) within an ecological context (above- or belowground network) between the two years of study.

We also tested whether the fixed effects of an individual's life-history stage and sex were significantly associated with the node-based metrics (strength or betweenness) within each ecological context using randomized network permutations. To account for the non-independence of relational data, we permuted the nodes (individuals) of networks (while holding the edges constant) to create a set of 10 000 randomized networks for each year within each ecological context [72,75]. We then calculated the node-based metrics based on each of the four sets of permuted data. From the observed data, we constructed separate models to explain the following predictor variables: (i) strength belowground, (ii) strength aboveground, (iii) betweenness belowground and (iv) betweenness aboveground. That is, we calculated the estimates (slopes) for the fixed effects of stage and sex on each context-specific node-based metric using GLMMs in lme4 [76] with a restricted maximum likelihood method, Gaussian

Table 1. All occurrences of pair-wise affiliative behaviours aboveground.*

proximity maintenance ($N = 5555$ events)
  a) sitting <1 m ($N = 3373$)
  b) collective foraging ($N = 1727$)
  c) sitting in body contact ($N = 326$)
  d) following ($N = 129$)
greetings ($N = 1228$ events)
  a) nose to nose ($N = 720$)
  b) nose to cheek ($N = 508$)
play ($N = 1967$ events)
  a) play wrestle ($N = 952$)
  b) play pounce ($N = 384$)
  c) play chase ($N = 234$)
  d) play slap ($N = 227$)
  e) play mount ($N = 85$)
  f) play grab ($N = 45$)
  g) play push ($N = 28$)
  h) play bite ($N = 12$)
allogrooming ($N = 4$ events)

*Exchanges involved juveniles (2016: $N_F = 36$, $N_M = 26$; 2017: $N_F = 36$, $N_M = 27$) and/or adults (2016: $N_F = 28$, $N_M = 11$; 2017: $N_F = 35$, $N_M = 21$).

distributions and the random effects of identity and year for the observed data. We also extracted 10 000 model estimates from GLMMs run on the 10 000 permuted values of the fixed effects of stage or sex on each metric within an ecological context. We tested the statistical significance of the effects of stage and sex for each model by comparing the parameter estimates from the observed data to randomizations of each dependent variable. In electronic supplementary material, S1, we compared the estimates from our observed dataset (blue lines) to the distribution of randomly generated estimates and considered those effects falling outside of the 95% confidence interval (within the areas with red bars at the tails of each distribution) to be statistically significant.

3. Results

From 27 May to 27 July, we monitored a total of 101 (2016) and 119 (2017) individuals aboveground during social observations and 98 (2016) and 89 (2017) individuals belowground. Aboveground, we recorded a total of 10 975 affiliative social interactions over 297 observation hours (2016: $N = 5662$; 2017: $N = 5313$ affiliative interactions). Of these, both identities were known for 8754 affiliative interactions (table 1). We also collected 17 726 recordings of individuals moving in or out of burrows. On average, each loop detected 2.0 ± 0.3 (2016) and 2.3 ± 0.1 (2017) unique squirrel visitors per day (range: 0 to 16 squirrels per loop per day). We detected belowground movements for juveniles (2016: $N_F = 28$, $N_M = 28$; 2017: $N_F = 22$, $N_M = 15$) and adults (2016: $N_F = 29$, $N_M = 13$; 2017: $N_F = 35$, $N_M = 17$). In 2016 and 2017, only 16% ($N = 16$) and 18% ($N = 16$) of these individuals, respectively, were detected at both monitoring stations within the same summer; this suggests that a small proportion of individuals bridged connections in belowground networks.
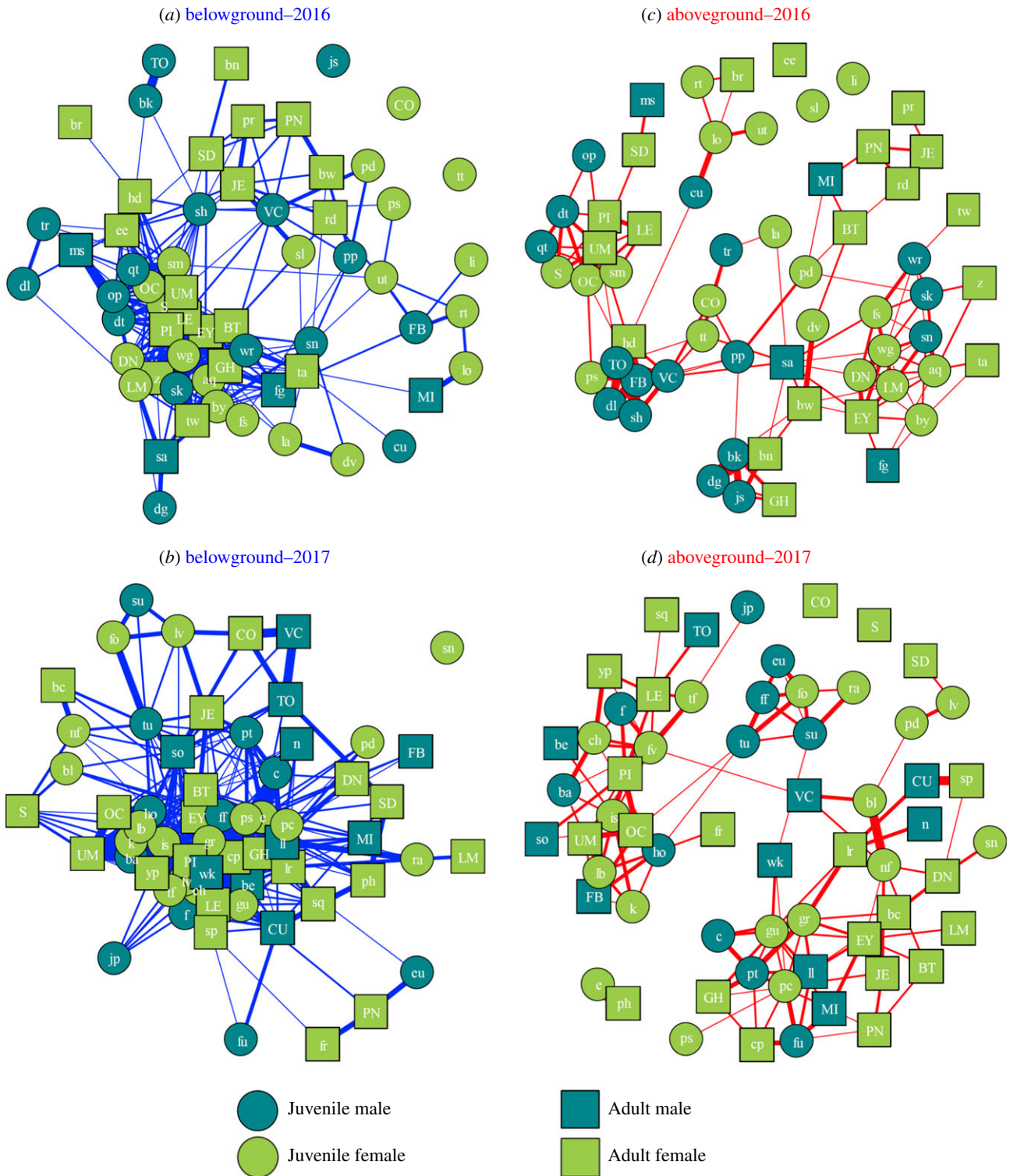
Figure 2. Below- and aboveground social networks. (a,b) Belowground networks: blue ties reflect shared daily burrow associations. (c,d) Aboveground networks: red ties reflect daily exchanges of affiliative behaviours. To enhance the visibility of network features, node positions within networks were placed using the Fruchterman–Reingold algorithm (igraph R package [69]). For all networks, tie thickness is proportional to the simple association index (AI). For visualization purposes only, networks are shown as filtered networks (AIs > 0.08). Individual attributes are reflected by node shape (circle: juveniles; square: adult) and colour (turquoise: male; green: female). The 2016 network contained 37 juveniles (number of females (N_F) = 20, number of males (N_M) = 17) and 23 adults (N_F = 19, N_M = 4) and the 2017 network contained 29 juveniles (N_F = 18, N_M = 11) and 32 adults: N_F = 22, N_M = 10). Letters represent abbreviations that correspond to fur marks for each individual squirrel (capital letters: in networks for both years; lower-case letters: in networks for a single year). (Online version in colour.)

(a) Distributions of node-based metrics in two ecological contexts

Overall, the *direct* metric of network connections (strength) was generally higher for nodes within below- (figure 2a,b) than aboveground networks (figure 2c,d), a pattern reflected by comparing the cumulative distributions of strength for each network (figure 3a). In 2016, strength belowground was roughly twice as high (mean ± s.e.: 0.039 ± 0.004, range: 0.00 to 0.137) as aboveground (0.020 ± 0.002, range: 0.00 to 0.060, $N = 60$ individuals). In 2017, strength was roughly four times higher below- (0.063 ± 0.006, range:
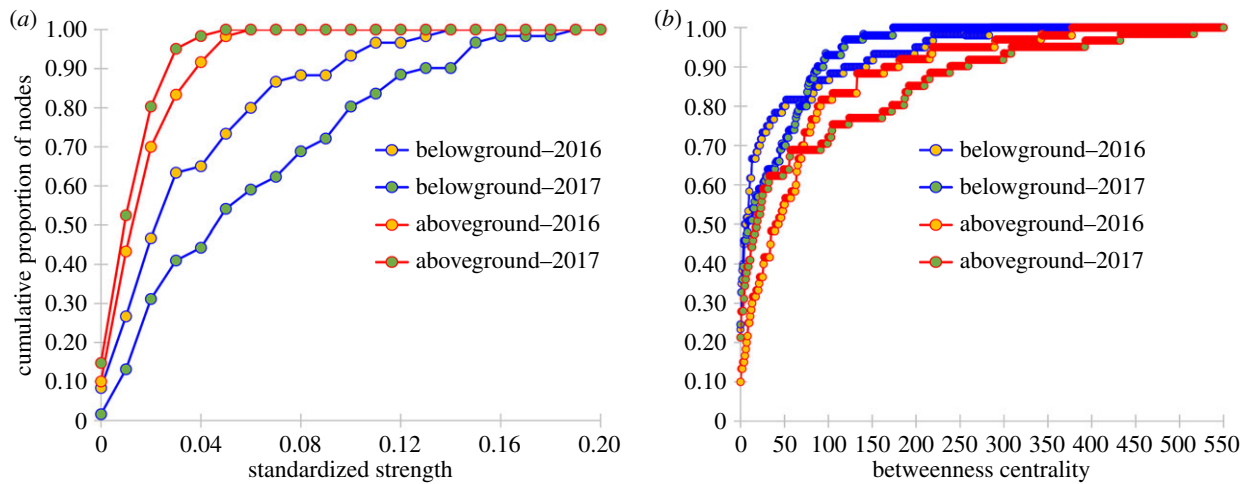
Figure 3. Cumulative distribution of node-level network measures. (*a*) Standardized strength: average level of association for each node, a weighted measure equivalent to node degree in binary networks. (*b*) Betweenness centrality: number of unique path lengths that flow through each individual node. Measurements are plotted for spatial and social networks in 2016 and 2017. (Online version in colour.)

0.000 to 0.187) than aboveground (0.016 ± 0.001, range: 0.000 to 0.047, $N = 61$ individuals). By contrast, the *indirect* metric (betweenness), defined as the number of shortest paths that pass through an individual, was consistently higher for aboveground networks (2016: 67 ± 11 paths, range: 0 to 378 paths; 2017: 79 ± 15 paths, range: 0 to 517 paths, figure 2*c,d*) than for belowground networks (2016: 35 ± 8 paths, range: 0 to 284; 2017: 33 ± 5 paths, range: 0–174 paths, figure 2*a,b*). The cumulative distributions reflect these patterns (figure 3*b*).

(b) Belowground networks, but not homophily, predict aboveground social networks

For both years, the full models including all three predictor matrices (belowground associations, stage similarity and sex similarity) captured a statistically significant amount of variation contributing to aboveground affiliative networks (MRQAP: 2016: $F_{3,1766} = 58.37$, $p < 0.0001$; 2017: $F_{3,1825} = 55.78$, $p < 0.0001$). Despite their statistical significance and, thus, statistical support of our predictions, these models only captured a small portion of the variability of the aboveground networks (adjusted $R^2 = 0.089$ in 2016 and 0.082 in 2017).

As predicted by movement rules, the structure of belowground networks (figure 2*a,b*) was positively correlated with that of aboveground affiliative networks (MRQAP: $R = 0.228$ in 2016; $R = 0.130$ in 2017; $p < 0.0001$ for both years, figure 2*c,d*). That is, pairs that occupied burrows at the same location on the same days were significantly more likely to exchange affiliative behaviours aboveground than were pairs that rarely visited similar burrows. This finding is consistent with the notion of movement rules because individuals seeking safety at similar burrow complexes (home bases) were presumably also most likely to encounter each other aboveground as they moved towards or away from these refuges. Beyond these effects, stage similarity negatively predicted aboveground networks such that juvenile–adult dyads tended to socialize most often aboveground (figure 2). These effects were statistically significant in 2016 ($R = -0.008$, $p = 0.001$) but not in 2017 ($R = -0.003$, $p = 0.184$). Although consistent with the notion that social interaction rules matter, our finding that individuals tended to

associate most often with individuals belonging to a life-history stage different from their own is in direct contrast to the prediction of homophily. Sex similarity, however, failed to predict aboveground networks (2016: $R = -0.001$, $p = 0.807$; 2017: $R = -0.001$, $p = 0.836$).

(c) Node-based metrics consistent for individuals between contexts

Within a year, an individual's strength in its social network was consistent between above- and belowground ecological contexts (consistency permutation tests: 2016: $N = 60$, $p = 0.001$; 2017: $N = 61$, $p < 0.0001$). This confirms that individuals highly connected belowground are also the most socially connected aboveground. Moreover, an individual's metric of betweenness within a year was generally consistent between above- and belowground contexts; betweenness was significantly consistent for individuals between contexts during the summer with typical rainfall (2017: $N = 61$, $p = 0.031$) but not in the summer during a drought year (2016: $N = 60$, $p = 0.311$).

(d) Node-based metrics only consistent between years belowground

To test for consistency between years, we applied consistency tests to data for the subset of individuals ($N = 19$) monitored in both years. Belowground, an individual's strength ($p = 0.033$) and betweenness ($p = 0.033$) were consistent between years. However, individuals were not statistically consistent across years in their aboveground strength ($p = 0.073$) or betweenness ($p = 0.098$).

(e) Females important in fostering indirect connectivity belowground

After accounting for variation attributed to the random effects of individual identity and year, life-history stage and sex had limited effects on node-based metrics (see electronic supplementary material, S1). Life-history stage failed to significantly predict either the *direct* metric of strength or *indirect* metric of betweenness above- or belowground ($p > 0.05$ for all comparisons with null models; for details, see

electronic supplementary material, S1). We also did not detect an effect of sex on strength in either context or on betweenness aboveground ($p > 0.05$, S1). However, sex had a statistically significant effect on betweenness belowground ($p < 0.01$, S1). That is, on average, roughly five times as many of the shortest paths between nodes passed through females (betweenness: 44+7 paths) as through males (9+4 paths; figure 2).

4. Discussion

(a) Social selectivity in networks across ecological contexts

Our study uncovers new linkages between belowground architecture and the patterns of aboveground sociality for subterranean mammals, suggesting that social interactions belowground indeed are correlated with (and likely constrain) those occurring aboveground. Consistent with movement constraints, belowground associations predicted aboveground affiliative networks, but social interaction rules were also important because we found preferential juvenile–adult associations (regardless of the sexes involved). These relationships persist despite the inherent challenges of comparing data collected using different methods. The unexplained variation between our networks might be attributed to methodological and/or ecological differences. Individual characteristics also contributed to social structure. Although the explanatory value of life-history stage and sex on social structure was generally low, females had the highest betweenness belowground, fostering more indirect connections than males. Beyond this, social metrics were generally consistent for individuals over time (suggesting personalities) and between two major ecological contexts (suggesting behavioural syndromes) [51,77]. Both of these final findings contradict the common simplifying assumption of random mixing within populations made by traditional game theoretical models [31].

(b) Movement rules and social partner choice influence network structure

Although aboveground networks are relatively open and free compared to those occurring inside the confines of belowground tunnels, our finding of correlated network structures is consistent with the notion that movements away from burrows influence aboveground behaviours. Access to limited refuges is likely a major factor shaping movements, and thus, patterns of social behaviour, as occurs in other species of mammals [14,78,79] as well as in birds [17,80], reptiles [40] and insects [81,82]. Ground squirrel burrows are limited refuges that offer protection from weather, safety from predators, and a place for hoarding food or rearing offspring [50,57,83]. Whereas social partners may simply interact most often with those they encounter near shared burrows, individuals may alternatively actively seek associations with the same partners aboveground independent of burrow preferences [84,85]. Distinguishing between these factors is important because models of social evolution, regardless of whether behaviours are favoured by direct or indirect fitness benefits, often require viscosity, defined as environmental restrictions on movements [4,86,87]. Empirical data such as ours are important because

game-theoretic models often make opposing predictions, predicting that spatial constraints may either promote [88,89] or inhibit [90] the emergence of socio-positive behaviours, both of which may be shaped by the animal's built environment [62,91].

Social interaction rules explained network structure. We documented preferential *direct* associations between juveniles and adults as well as the importance of *indirect* connectivity by females in belowground networks. These findings are consistent with the presumed matrilineal structure for this species [50] and what is known about other mammalian species living in matrilineal societies [18,92,93]. First, preferential aboveground connections between juveniles and adults suggest that parent–offspring bonds likely persist after weaning; pedigree information is required to confirm this and is not yet established for our subjects. Second, juvenile–adult preferential connections are also largely expected; juveniles often associate with adults to reduce predation risk [65] and sometimes initiate play with adults [43,44]. Finally, females likely reside at their natal burrows, fostering indirect links with other members of the social group. Kinship explains social network structures in many mammalian societies (e.g. [3,14,94–96]). Studying its effects on California ground squirrel networks should prove fruitful after a pedigree is established.

(c) Individual consistency in network position

Our finding that some individuals consistently occupied key positions in social networks across time (personalities) and major ecological contexts (behavioural syndromes) extends previous studies documenting consistent personality traits across time, seasons and/or behavioural categories [22,97]. These traits likely have fitness consequences for individuals [51] and may predict patterns of group-level behaviour [31], such as mobbing of predators [98] or policing of social conflicts [12]. Our results should inform our understanding of how connectivity by key individuals shapes the transmission of disease, information and genetic material within animal populations [51].

Despite our general finding of individual consistency in network metrics, betweenness was consistent between contexts in the summer with typical rainfall (2017), but not in the summer during a drought year (2016). Several other mammalian species [54,99,100] vary the strength of their direct associations in response to rainfall. Future studies spanning additional years should, therefore, conclusively elucidate whether ecological perturbations associated with drought disrupted otherwise consistent network positions in the California ground squirrel.

(d) Implications for understanding flow across dynamic networks

Our finding that individuals tend to occupy consistent network positions from one ecological context to another has important implications for understanding transmission networks. Within the context of disease, heterogeneity in contact rates may determine whether a disease dies out or becomes epidemic [36,101,102]. Parasites may be directly transmitted from one individual to the next (e.g. via direct social interactions) or transferred indirectly when potential hosts visit locations used earlier by infected hosts (e.g. via

space-use overlap [103]). This may produce time-lagged interactions [104]. Modelling pathways for parasite (disease) transmission in the ground squirrel system should prove particularly useful; these hosts may carry fleas and ticks that transmit zoonotic diseases (e.g. plague, Lyme disease, tularaemia and relapsing fever [50,105]). Flea density varies among burrows [58] and flea abundance on hosts varies with microhabitat use by hosts [106]. Study of individual differences in social personalities should thus offer additional insights into parasite transmission.

Applications of automated technologies are also revealing how social information spreads across animal groups [107]. For example, these technologies offer a rare glimpse into how social innovations spread across foragers [108]. Network structure also has implications for prey species, fostering the detection of and cooperative protection against predators [109]. Because California ground squirrels rely upon multiple modes of communication to locate food and cope with intense predation via the production of alarm calls [50], studies of communication networks may similarly explain the extent to which acoustic and/or olfactory information about food sources and predation risk flows across the social networks of ground squirrels.

(e) Conceptual framework for uncovering animal social networks

Our research establishes a novel approach for future studies aiming to understand how interactions in constrained spaces (that may or may not involve direct contact) and those occurring in relatively unconstrained spaces (e.g. aboveground, in the air, or in open aquatic environments) contribute to social structure. First, we offer a dependable, inexpensive alternative to heavier and more expensive proximity collars [47,110,111] and extend previous network studies that capture activity in other closed spaces, such as at nests and roosts [85,108,112], by capturing belowground activity. Second, we establish a conceptual framework for combining the use of two straightforward methods—direct social observations and passive data logging—to study networks in multiple contexts and across time. Automated measures should, therefore, complement insights gained from direct observations. Going forward, integration of both approaches should offer new insights into social structures for animals that socialize in easily observable, open spaces but that also visit relatively hidden architectural structures at fixed spatial locations for which direct observation is

prohibitive, such as occurs in fishes [113], birds [108,114], bats [85,95] and other semi-fossorial mammals [63,110]. Comparing networks should prove particularly useful for understanding how heterogeneities in node connectivity may affect disease [36,37,115] and information [116,117] transmission (flow) dynamics across contexts. Further investigations into the processes producing social structures and the role of key individuals across multiple habitats or major situations should, therefore, elucidate the ecological rules that generate and maintain social structures across animal societies more broadly.

References

1. Alexander Richard D. 1974 The evolution of social behavior. *Annu. Rev. Ecol. Syst.* **5**, 325–383. (doi:10.1146/annurev.es.05.110174.001545)

2. Whitehead H. 2008 *Analyzing animal societies: quantitative methods for vertebrate social analysis*. Chicago, IL: University of Chicago Press.

3. Wey T, Blumstein DT. 2010 Social cohesion in yellow-bellied marmots is established through age and kin structuring. *Anim. Behav.* **79**, 1343–1352. (doi:10.1016/j.anbehav.2010.03.008)

4. Lion S, van Baalen M. 2008 Self-structuring in spatial evolutionary ecology. *Ecol. Lett.* **11**, 277–295. (doi:10.1111/j.1461-0248.2007.01132.x)

5. Wey T, Blumstein DT, Shen W, Jordán F. 2008 Social network analysis of animal behaviour: a promising tool for the study of sociality. *Anim. Behav.* **75**, 333–344. (doi:10.1016/j.anbehav.2007.06.020)

6. Sih A, Hanser SF, McHugh KA. 2009 Social network theory: new insights and issues for behavioral ecologists. *Behav. Ecol. Sociobiol.* **63**, 975–988. (doi:10.1007/s00265-009-0725-6)

7. Kurvers RHJM, Krause J, Croft DP, Wilson ADM, Wolf M. 2014 The evolutionary and ecological consequences of animal social networks: emerging issues. *Trends Ecol. Evol.* **29**, 326–335. (doi:10.1016/j.tree.2014.04.002)

8. Hinde RA. 1976 Interactions, relationships and social structure. *Man* **11**, 1–17. (doi:10.2307/2800384)

9. Farine DR, Whitehead H. 2015 Constructing, conducting and interpreting animal social network analysis. *J. Anim. Ecol.* **84**, 1144–1163. (doi:10.1111/1365-2656.12418)

10. Pinter-Wollman N *et al.* 2014 The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behav. Ecol.* **25**, 242–255. (doi:10.1093/beheco/art047)

11. Brent LJN. 2015 Friends of friends: are indirect connections in social networks important to animal behaviour? *Anim. Behav.* **103**, 211–222. (doi:10.1016/j.anbehav.2015.01.020)

12. Flack JC, Girvan M, De Waal FBM, Krakauer DC. 2006 Policing stabilizes construction of social niches in primates. *Nature* **439**, 426–429. (doi:10.1038/nature04326)

13. Pinter-Wollman N, Wollman R, Guetz A, Holmes S, Gordon DM. 2011 The effect of individual variation on the structure and function of interaction networks in harvester ants. *J. R. Soc. Interface* **8**, 1562–1573. (doi:10.1098/rsif.2011.0059)

14. Viblanc VA, Pasquaretta C, Sueur C, Boonstra R, Dobson FS. 2016 Aggression in Columbian ground squirrels: relationships with age, kinship, energy allocation, and fitness. *Behav. Ecol.* **27**, arw098. (doi:10.1093/beheco/arw098)

15. Rimbach R, Bisanzio D, Galvis N, Link A, Di Fiore A, Gillespie TR. 2015 Brown spider monkeys (*Ateles hybridus*): a model for differentiating the role of social networks and physical contact on parasite transmission dynamics. *Phil. Trans. R. Soc. B* **370**, 20140110. (doi:10.1098/rstb.2014.0110)

16. Smith JE, Van Horn RC, Powning KS, Cole AR, Graham KE, Memenis SK, Holekamp KE. 2010 Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behav. Ecol.* **21**, 284–303. (doi:10.1093/beheco/arp181)

17. Podgórski T, Lusseau D, Scandura M, Sönnichsen L, Jędrzejewska B. 2014 Long-lasting, kin-directed female interactions in a spatially structured wild boar social network. *PLoS ONE* **9**, e99875. (doi:10.1371/journal.pone.0099875)

18. Wolf JBW, Trillmich F. 2008 Kin in space: social viscosity in a spatially and genetically substructured network. *Proc. R. Soc. B* **275**, 2063–2069. (doi:10.1098/rspb.2008.0356)

19. Sih A, Bell AM, Johnson JC, Ziemba RE. 2004 Behavioral syndromes: an integrative overview. *Q. Rev. Biol.* **79**, 241–247. (doi:10.1086/422893)

20. Aplin LM, Farine DR, Morand-Ferron J, Cole EF, Cockburn A, Sheldon BC. 2013 Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). *Ecol. Lett.* **16**, 1365–1372. (doi:10.1111/ele.12181)

21. Pike TW, Samanta M, Lindström J, Royle NJ. 2008 Behavioural phenotype affects social interactions in an animal network. *Proc. R. Soc. B* **275**, 2515–2520. (doi:10.1098/rspb.2008.0744)

22. Kulahci IG, Ghazanfar AA, Rubenstein DI. 2017 Consistent individual variation across interaction networks indicates social personalities in lemurs. *Anim. Behav.* **136**, 217–226. (doi:10.1016/j.anbehav.2017.11.012)

23. Spiegel O, Leu ST, Bull CM, Sih A. 2017 What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecol. Lett.* **20**, 3–18. (doi:10.1111/ele.12708)

24. Croft DP, Krause J, Darden SK, Ramnarine IW, Faria JJ, James R. 2009 Behavioural trait assortment in a social network: patterns and implications. *Behav. Ecol. Sociobiol.* **63**, 1495–1503. (doi:10.1007/s00265-009-0802-x)

25. Sih A, Bell A, Johnson JC. 2004 Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol. Evol.* **19**, 372–378. (doi:10.1016/j.tree.2004.04.009)

26. Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ. 2007 Integrating animal temperament within ecology and evolution. *Biol. Rev.* **82**, 291–318. (doi:10.1111/j.1469-185X.2007.00010.x)

27. Jandt JM, Bengston S, Pinter-Wollman N, Pruitt JN, Raine NE, Dornhaus A, Sih A. 2014 Behavioural syndromes and social insects: personality at multiple levels. *Biol. Rev.* **89**, 48–67. (doi:10.1111/brv.12042)

28. Pearish S, Hostert L, Bell AM. 2013 Behavioral type–environment correlations in the field: a study of three-spined stickleback. *Behav. Ecol. Sociobiol.* **67**, 765–774. (doi:10.1007/s00265-013-1500-2)

29. Wilson ADM, McLaughlin RL. 2007 Behavioural syndromes in brook charr, *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel laboratory situations. *Anim. Behav.* **74**, 689–698. (doi:10.1016/j.anbehav.2007.01.009)

30. Wright CM, Holbrook CT, Pruitt JN. 2014 Animal personality aligns task specialization and task proficiency in a spider society. *Proc. Natl Acad. Sci. USA* **111**, 9533–9537. (doi:10.1073/pnas.1400850111)

31. Krause J, James R, Croft DP. 2010 Personality in the context of social networks. *Phil. Trans. R. Soc. B* **365**, 4099–4106. (doi:10.1098/rstb.2010.0216)

32. Silk MJ, Croft DP, Delahay RJ, Hodgson DJ, Weber N, Boots M, McDonald RA. 2017 The application of statistical network models in disease research. *Methods Ecol. Evol.* **8**, 1026–1041. (doi:10.1111/2041-210X.12770)

33. Craft ME. 2015 Infectious disease transmission and contact networks in wildlife and livestock. *Phil. Trans. R. Soc. B* **370**, 20140107. (doi:10.1098/rstb.2014.0107)

34. White LA, Forester JD, Craft ME. 2017 Using contact networks to explore mechanisms of parasite transmission in wildlife. *Biol. Rev.* **92**, 389–409. (doi:10.1111/brv.12236)

35. Chen S, White BJ, Sanderson MW, Amrine DE, Ilany A, Lanzas C. 2014 Highly dynamic animal contact network and implications on disease transmission. *Sci. Rep.* **4**, 4472. (doi:10.1038/srep04472)

36. Danon L, House TA, Read JM, Keeling MJ. 2012 Social encounter networks: collective properties and disease transmission. *J. R. Soc. Interface* **9**, 2826–2833. (doi:10.1098/rsif.2012.0357)

37. Paull SH, Song S, McClure KM, Sackett LC, Kilpatrick AM, Johnson PT. 2012 From superspreaders to disease hotspots: linking transmission across hosts and space. *Front. Ecol. Environ.* **10**, 75–82. (doi:10.1890/110111)

38. Turner JW, Bills PS, Holekamp KE. 2018 Ontogenetic change in determinants of social network position in the spotted hyena. *Behav. Ecol. Sociobiol.* **72**, 10. (doi:10.1007/s00265-017-2426-x)

39. Castles M, Heinsohn R, Marshall HH, Lee AEG, Cowlishaw G, Carter AJ. 2014 Social networks created with different techniques are not comparable. *Anim. Behav.* **96**, 59–67. (doi:10.1016/j.anbehav.2014.07.023)

40. Spiegel O, Leu ST, Sih A, Bull CM. 2016 Socially interacting or indifferent neighbours? Randomization of movement paths to tease apart social preference and spatial constraints. *Methods Ecol. Evol.* **7**, 971–979. (doi:10.1111/2041-210X.12553)

41. Ramos-Fernández G, Boyer D, Gómez VP. 2006 A complex social structure with fission–fusion properties can emerge from a simple foraging model. *Behav. Ecol. Sociobiol.* **60**, 536–549. (doi:10.1007/s00265-006-0197-x)

42. McPherson M, Smith-Lovin L, Cook JM. 2001 Birds of a feather: homophily in social networks. *Annu. Rev. Sociol.* **27**, 415–444. (doi:10.1146/annurev.soc.27.1.415)

43. Nunes S, Muecke E-M, Lancaster LT, Miller NA, Mueller MA, Muelhaus J, Castro L. 2004 Functions and consequences of play behaviour in juvenile Belding's ground squirrels. *Anim. Behav.* **68**, 27–37. (doi:10.1016/j.anbehav.2003.06.024)

44. Blumstein DT, Chung LK, Smith JE. 2013 Early play may predict later dominance relationships in yellow-bellied marmots (*Marmota flaviventris*). *Proc. R. Soc. B* **280**, 20130485. (doi:10.1098/rspb.2013.0485)

45. Sterck EHM, Watts DP, van Schaik CP. 1997 The evolution of female social relationships in nonhuman primates. *Behav. Ecol. Sociobiol.* **41**, 291–309. (doi:10.1007/s002650050390)

46. Hayes LD, Chesh AS, Ebensperger LA. 2007 Ecological predictors of range areas and use of burrow systems in the diurnal rodent, *Octodon degus*. *Ethology* **113**, 155–165. (doi:10.1111/j.1439-0310.2006.01305.x)

47. Blyton MDJ, Banks SC, Peakall R, Lindenmayer DB, Gordon DM. 2014 Not all types of host contacts are equal when it comes to *E. coli* transmission. *Ecol. Lett.* **17**, 970–978. (doi:10.1111/ele.12300)

48. Owings DH, Borchert M, Virginia R. 1977 The behaviour of California ground squirrels. *Anim. Behav.* **25**, 221–230. (doi:10.1016/0003-3472(77)90085-9)

49. Owings DH, Virginia RA. 1978 Alarm calls of California ground squirrels (*Spermophilus beecheyi*). *Z. Tierpsychol.* **46**, 58–70. (doi:10.1111/j.1439-0310.1978.tb01438.x)

50. Smith JE, Long DJ, Russell ID, Newcomb KL, Muñoz VD. 2016 *Otospermophilus beecheyi* (Rodentia: Sciuridae). *Mamm. Species* **48**, 91–108. (doi:10.1093/mspecies/sew010)

51. Wilson ADM, Krause S, Dingemanse NJ, Krause J. 2013 Network position: a key component in the characterization of social personality types. *Behav. Ecol. Sociobiol.* **67**, 163–173. (doi:10.1007/s00265-012-1428-y)

52. Hare JF, Murie JO. 2007 ecology, kinship, and ground squirrel sociality: insights from comparative analyses. In *Rodent societies: an ecological and evolutionary perspective* (eds J Wolff, P Sherman), pp. 345–355. Chicago, IL: University of Chicago Press.

53. Silk JB, Alberts SC, Altmann J. 2003 Social bonds of female baboons enhance infant survival. *Science* **302**, 1231–1234. (doi:10.1126/science.1088580)

54. Holekamp KE, Smith JE, Strelioff CC, Van Horn RC, Watts HE. 2012 Society, demography and genetic structure in the spotted hyena. *Mol. Ecol.* **21**, 613–632. (doi:10.1111/j.1365-294X.2011.05240.x)

55. Grinnell J, Dixon JS. 1918 *Natural history of the ground squirrels of California*. Sacramento, CA: California State Printing Office.

56. Hanson MT, Coss RG. 2001 Age differences in the response of California ground squirrels (*Spermophilus beecheyi*) to conspecific alarm calls. *Ethology* **107**, 259–275. (doi:10.1046/j.1439-0310.2001.00659.x)

57. Van Vuren DH, Ordeñana MA. 2011 California levee vegetation research program habitat associations of burrowing mammals along levees in the Sacramento Valley, California. In *Proceedings of the 2012 California Levee Vegetation Research Program Symposium*, Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA, 22 September 2011, pp. 1–32. Davis, CA: University of California.

58. Stewart MA, Evans FC. 1941 A comparative study of rodent and burrow flea populations. *Exp. Biol. Med.* **47**, 140–142. (doi:10.3181/00379727-47-13066P)

59. Koprowski JL. 2002 Handling tree squirrels with a safe and efficient restraint. *Wildl. Soc. Bull.* **30**, 101–103. (doi:10.2307/3784642)

60. Gibbons JW, Andrews KM. 2004 PIT tagging: simple technology at its best. *Bioscience* **54**, 447–454. (doi:10.1641/0006-3568(2004)054[0447:PTSTAI]2.0.CO;2)

61. Krause J, Krause S, Arlinghaus R, Psorakis I, Roberts S, Rutz C. 2013 Reality mining of animal social systems. *Trends Ecol. Evol.* **28**, 541–551. (doi:10.1016/j.tree.2013.06.002)

62. Hansell MH, Michael H. 2005 *Animal architecture*. Oxford, UK: Oxford University Press.

63. Ellwood SA *et al.* 2017 An active-radio-frequency-identification system capable of identifying co-locations and social-structure: validation with a wild free-ranging animal. *Methods Ecol. Evol.* **8**, 1822–1831. (doi:10.1111/2041-210X.12839)

64. Altmann J. 1974 Observational study of behavior: sampling methods. *Behaviour* **49**, 227–266. (doi:10.1163/156853974X00534)

65. Smith JE, Chung LK, Blumstein DT. 2013 Ontogeny and symmetry of social partner choice among free-living yellow-bellied marmots. *Anim. Behav.* **85**, 715–725. (doi:10.1016/j.anbehav.2013.01.008)

66. Ginsberg JR, Young TP. 1992 Measuring association between individuals or groups in behavioural studies. *Anim. Behav.* **44**, 377–379. (doi:10.1016/0003-3472(92)90042-8)

67. James R, Croft DP, Krause J. 2009 Potential banana skins in animal social network analysis. *Behav. Ecol. Sociobiol.* **63**, 989–997. (doi:10.1007/s00265-009-0742-5)

68. Hemelrijk CK. 1990 Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. *Anim. Behav.* **39**, 1013–1029. (doi:10.1016/S0003-3472(05)80775-4)

69. Csardi GN, Nepusz TT. 2006 The igraph software package for complex network research. *InterJournal* **1695**, 1–9.

70. Barthélemy M, Barrat A, Pastor-Satorras R, Vespignani A. 2005 Characterization and modeling of weighted networks. *Phys. A Stat. Mech. Appl.* **346**, 34–43. (doi:10.1016/j.physa.2004.08.047)

71. R Development Core Team. 2017 R: A language and environment for statistical computing. Vienna, Austria: The R Foundation for Statistical Computing.

72. Croft DP, Madden JR, Franks DW, James R. 2011 Hypothesis testing in animal social networks. *Trends Ecol. Evol.* **26**, 502–507. (doi:10.1016/j.tree.2011.05.012)

73. Dekker D, Krackhardt D, Snijders TAB. 2007 Sensitivity of MRQAP tests to collinearity and autocorrelation conditions. *Psychometrika* **72**, 563–581. (doi:10.1007/s11336-007-9016-1)

74. Farine DR. 2013 Animal social network inference and permutations for ecologists in R using *asnipe*. *Methods Ecol. Evol.* **4**, 1187–1194. (doi:10.1111/2041-210X.12121)

75. Farine DR. 2017 A guide to null models for animal social network analysis. *Methods Ecol. Evol.* **8**, 1309–1320. (doi:10.1111/2041-210X.12772)

76. Bates D, Mächler M, Bolker B, Walker S. 2014 Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:1406.5823. (doi:10.18637/jss.v067.i01)

77. Croft DP, Darden SK, Wey TW. 2016 Current directions in animal social networks. *Curr. Opin. Behav. Sci.* **12**, 52–58. (doi:10.1016/j.cobeha.2016.09.001)

78. Wolf JBW, Mawdsley D, Trillmich F, James R. 2007 Social structure in a colonial mammal: unravelling hidden structural layers and their foundations by network analysis. *Anim. Behav.* **74**, 1293–1302. (doi:10.1016/j.anbehav.2007.02.024)

79. Grabowska-Zhang AM, Hinde CA, Garroway CJ, Sheldon BC. 2016 Wherever I may roam: social viscosity and kin affiliation in a wild population despite natal dispersal. *Behav. Ecol.* **27**, 1263–1268. (doi:10.1093/beheco/arw042)

80. Shizuka D, Chaine AS, Anderson J, Johnson O, Laursen IM, Lyon BE. 2014 Across-year social stability shapes network structure in wintering migrant sparrows. *Ecol. Lett.* **17**, 998–1007. (doi:10.1111/ele.12304)

81. Pie MR, Rosengaus RB, Traniello JFA. 2004 Nest architecture, activity pattern, worker density and the dynamics of disease transmission in social insects. *J. Theor. Biol.* **226**, 45–51. (doi:10.1016/j.jtbi.2003.08.002)

82. Pinter-Wollman N. 2015 Nest architecture shapes the collective behaviour of harvester ants. *Biol. Lett.* **11**, 20150695. (doi:10.1098/rsbl.2015.0695)

83. Kinlaw A. 1999 A review of burrowing by semi-fossorial vertebrates in arid environments. *J. Arid Environ.* **41**, 127–145. (doi:10.1006/jare.1998.0476)

84. Smith JE, Memenis SK, Holekamp KE. 2007 Rank-related partner choice in the fission–fusion society of the spotted hyena (*Crocuta crocuta*). *Behav. Ecol. Sociobiol.* **61**, 753–765. (doi:10.1007/s00265-006-0305-y)

85. Kerth G, Perony N, Schweitzer F. 2011 Bats are able to maintain long-term social relationships despite the high fission–fusion dynamics of their groups. *Proc. R. Soc. B* **278**, 2761–2767. (doi:10.1098/rspb.2010.2718)

86. Hamilton WD. 1964 The genetical evolution of social behaviour. II. *J. Theor. Biol.* **7**, 17–52. (doi:10.1016/0022-5193(64)90039-6)

87. Taylor PD, Day T, Wild G. 2007 Evolution of cooperation in a finite homogeneous graph. *Nature* **447**, 469–472. (doi:10.1038/nature05784)

88. Nowak MA, May RM. 1992 Evolutionary games and spatial chaos. *Nature* **359**, 826–829. (doi:10.1038/359826a0)

89. Ohtsuki H, Hauert C, Lieberman E, Nowak MA. 2006 A simple rule for the evolution of cooperation on graphs and social networks. *Nature* **441**, 502–505. (doi:10.1038/nature04605)

90. Hauert C, Doebeli M. 2004 Spatial structure often inhibits the evolution of cooperation in the snowdrift game. *Nature* **428**, 643–646. (doi:10.1038/nature02360)

91. Pinter-Wollman N, Fiore SM, Theraulaz G. 2017 The impact of architecture on collective behaviour. *Nat. Ecol. Evol.* **1**, 1–2. (doi:10.1038/s41559-017-0111)

92. Smith JE. 2014 Hamilton's legacy: kinship, cooperation and social tolerance in mammalian groups. *Anim. Behav.* **92**, 291–304. (doi:10.1016/j.anbehav.2014.02.029)

93. Silk JB. 2007 The adaptive value of sociality in mammalian groups. *Phil. Trans. R. Soc. B* **362**, 539–559. (doi:10.1098/rstb.2006.1994)

94. Wittemyer G, Douglas-Hamilton I, Getz WM. 2005 The socioecology of elephants: analysis of the processes creating multitiered social structures. *Anim. Behav.* **69**, 1357–1371. (doi:10.1016/j.anbehav.2004.08.018)

95. Patriquin KJ, Leonard ML, Broders HG, Garroway CJ. 2010 Do social networks of female northern long-eared bats vary with reproductive period and age? *Behav. Ecol. Sociobiol.* **64**, 899–913. (doi:10.1007/s00265-010-0905-4)

96. Wey TW, Burger JR, Ebensperger LA, Hayes LD. 2013 Reproductive correlates of social network variation in plurally breeding degus (*Octodon degus*). *Anim. Behav.* **85**, 1407–1414. (doi:10.1016/j.anbehav.2013.03.035)

97. Blaszczyk MB. 2018 Consistency in social network position over changing environments in a seasonally breeding primate. *Behav. Ecol. Sociobiol.* **72**, 11. (doi:10.1007/s00265-017-2425-y)

98. Croft DP, Krause J, James R. 2004 Social networks in the guppy (*Poecilia reticulata*). *Proc. R. Soc. Lond. B* **271**, S516–S519. (doi:10.1098/rsbl.2004.0206)

99. Henzi SP, Lusseau D, Weingrill T, Van Schaik CP, Barrett L. 2009 Cyclicity in the structure of female baboon social networks. *Behav. Ecol. Sociobiol.* **63**, 1015–1021. (doi:10.1007/s00265-009-0720-y)

12

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100. de Silva S, Ranjeewa ADG, Kryazhimskiy S. 2011 The dynamics of social networks among female Asian elephants. *BMC Ecol.* **11**, 17. (doi:10.1186/1472-6785-11-17)

101. Pastor-Satorras R, Castellano C, Van Mieghem P, Vespignani A. 2015 Epidemic processes in complex networks. *Rev. Mod. Phys.* **87**, 925–979. (doi:10.1103/RevModPhys.87.925)

102. Read JM, Eames KTD, Edmunds WJ. 2005 Dynamic social networks and the implications for the spread of infectious disease. *J. R. Soc. Interface* **5**, 1001–1007. (doi:10.1098/rsif.2008.0013)

103. Riley S. 2007 Large-scale spatial-transmission models of infectious disease. *Science* **316**, 1298–1301. (doi:10.1126/science.1134695)

104. Anderson RM, May RM. 1992 *Infectious diseases of humans: dynamics and control.* Oxford, UK: Oxford University Press.

105. Holdenried R, Evans FC, Longanecker DS. 1951 Host–parasite–disease relationships in a mammalian community in the central coast range of California. *Ecol. Monogr.* **21**, 1–18. (doi:10.2307/1948643)

106. Hubbart JA, Jachowski DS, Eads DA. 2011 Seasonal and among-site variation in the occurrence and abundance of fleas on California ground squirrels (*Otospermophilus beecheyi*). *J. Vector Ecol.* **36**, 117–123. (doi:10.1111/j.1948-7134.2011.00148.x)

107. Aplin LM, Farine DR, Morand-Ferron J, Cockburn A, Thornton A, Sheldon BC. 2014 Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* **518**, 538–541. (doi:10.1038/nature13998)

108. Aplin LM, Farine DR, Morand-Ferron J, Sheldon BC. 2012 Social networks predict patch discovery in a wild population of songbirds. *Proc. R. Soc. B* **279**, 4199–4205. (doi:10.1098/rspb.2012.1591)

109. Kelley JL, Morrell LJ, Inskip C, Krause J, Croft DP. 2011 Predation risk shapes social networks in fission–fusion populations. *PLoS ONE* **6**, e24280. (doi:10.1371/journal.pone.0024280)

110. Silk MJ, Weber N, Steward LC, Delahay RJ, Croft DP, Hodgson DJ, Boots M, McDonald RA. 2017 Seasonal variation in daily patterns of social contacts in the European badger *Meles meles*. *Ecol. Evol.* **7**, 9006–9015. (doi:10.1002/ece3.3402)

111. Sih A, Spiegel O, Godfrey S, Leu S, Bull CM. 2018 Integrating social networks, animal personalities, movement ecology and parasites: a framework with examples from a lizard. *Anim. Behav.* **136**, 195–205. (doi:10.1016/J.ANBEHAV.2017.09.008)

112. Alanärä A, Burns MD, Metcalfe NB. 2001 Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. *J. Anim. Ecol.* **70**, 980–986 (doi:10.1046/j.0021-8790.2001.00550.x)

113. Klefoth T, Skov C, Krause J, Arlinghaus R. 2012 The role of ecological context and predation risk-stimuli in revealing the true picture about the genetic basis of boldness evolution in fish. *Behav. Ecol. Sociobiol.* **66**, 547–559. (doi:10.1007/s00265-011-1303-2)

114. Galbraith JA, Jones DN, Beggs JR, Parry K, Stanley MC. 2017 Urban bird feeders dominated by a few species and individuals. *Front. Ecol. Evol.* **5**, 81. (doi:10.3389/fevo.2017.00081)

115. Bull CM, Godfrey SS, Gordon DM. 2012 Social networks and the spread of *Salmonella* in a sleepy lizard population. *Mol. Ecol.* **21**, 4386–4392. (doi:10.1111/j.1365-294X.2012.05653.x)

116. Lusseau D. 2003 The emergent properties of a dolphin social network. *Proc. R. Soc. Lond. B* **270**, S186–S188. (doi:10.1098/rsbl.2003.0057)

117. Fewell JH. 2003 Social insect networks. *Science* **301**, 1867–1870. (doi:10.1126/science.1088945)

118. Sikes RS and Animal Care and Use Committee of the American Society of Mammalogists, 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *J. Mamm.* **97**, 663–688.

119. Smith JE, Gamboa DA, Spencer JM, Travenick SJ, Ortiz CA, Hunter RD, Sih A. 2018 Data from: Split between two worlds: automated sensing reveals links between above- and belowground social networks in a free-living mammal. Dryad Digital Repository. (doi:10.5061/dryad.8nq547q)