# Cockroach social network position does not influence dispersal tendency

**Authors**

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## Abstract

In group-living organisms, we might expect relationships between social position and dispersal, such as if certain patterns of social associations lead to dispersal or if certain personality types both link different groups and are more likely to disperse. However, directly testing these ideas is challenging as dispersal is hard to track in the field and is a difficult trait to measure in the laboratory. Furthermore, invertebrate dispersal is less commonly quantified as their small size makes them hard to track. Here we quantified social networks in multiple groups of the gregarious cockroach *Blaptica dubia* in the laboratory and related three measures of social network position (representing overall sociability, connectedness in local cliques, and connectedness to the wider network) to two different measures of dispersal. We found none of the social network measures related to either of the measures of dispersal, which were themselves not correlated. We also found that sociability and connectedness to the wider network were negatively correlated, with males falling towards the low-sociability/high global connectedness part of the continuum compared to females. We found no effects of mass, but there were differences between the two blocks our experiments were performed in, suggesting some effect of observer variability. Overall, our results suggest assays of dispersal may not effectively capture the underlying trait we hope to quantify, that cockroaches differ in the social behaviour along a syndrome integrating sociability and the tendency to move between groups, and that study replication should be encouraged so we can be confident identified trends are robust.

**Key words**: Blaptica, cockroach, dispersal, exploration, invertebrate, social network analysis

## Introduction

Organisms often disperse from their natal or breeding habitat to find resources elsewhere and avoid competition in their local environment (Matthysen, 2012). By facilitating the movement of individuals, their genetic material, and any parasites they bear (among other

things) to new locations, dispersal plays a vital role in various ecology and evolutionary processes such as the spread of disease, population demographics, and the rate of adaptive change (Clobert, 2012). Identifying drivers of dispersal and associations with other traits is therefore key for understanding and predicting dispersal's importance and influence in the natural world.

As organisms disperse to both avoid others due to competition and find others to mate with, social interactions are likely to be key for predicting dispersal tendencies (Kurvers et al., 2014; Louca et al., 2009; Wey et al., 2015). Animals engage in social interactions when they mate and cooperate, but also when they fight or compete, and so essentially all animals engage in social interactions of some sort (Székely et al., 2010). The great diversity of social interactions in the natural world, both within and across species, makes it difficult to relate individual social behaviour to other traits such as dispersal in a manner that facilitates the synthesis of findings across taxa. A potential solution is to use a common quantitative framework to analyse social interactions and then relate to traits such as dispersal. An example of such a framework is social network analysis (SNA; Krause et al., 2007; Wey et al., 2008). In SNA individuals are represented as "nodes" or "vertices" and are connected with other individuals with "ties", "edges", or "links" (see: Croft et al., 2008; and: Krause et al., 2014 for introductions). This approach is represented mathematically as a matrix, where positive valued cells are present between individuals when they interact and 0 values are used when they do not. We can then use the extensive suite of measures in SNA (Sosa et al., 2021) to quantify different aspects of social behaviour, including those depending on both direct and indirect interactions (Brent, 2015), and relate to other traits and compare across species (Farine & Whitehead, 2015; e.g.: Sueur et al., 2011).

Although substantial information is available on how individuals dispersing into and out of groups affects the group's social network structure (Borgeaud et al., 2017; Shizuka & Johnson, 2020), it is less clear how the social position of individuals within the group influences the tendency to disperse. It is conceivable that, social interactions are expected to be related to dispersal in various ways. Negative interactions may stimulate an individual to leave their current group or area (e.g. in the western bluebird Sialia mexicana; Aguillon & Duckworth, 2015; Christian, 1970). In contrast, positive associations may encourage an individual to stay (the "social cohesion hypothesis"; Bekoff, 1977; e.g. in yellow-bellied marmots Marmota flaviventris; Blumstein et al., 2009). Meanwhile, an organism's own social tendencies might be related to its dispersal tendency, for instance unsociable individuals might be more willing to disperse from groups of high densities, while sociable individuals might be more willing to disperse when at low densities (as seen in the common lizard Lacerta vivipara; Cote & Clobert, 2007). In the males of the spotted hyena (*Crocuta crocuta*),

there is evidence that during ontogeny, network connections tend to weaken, which eventually leads to individuals dispersing from their natal groups (Turner et al., 2018). These relationships may differ between the sexes, for example if females compete for resources they may disperse more at high density, while if males compete for access to females they may disperse more at low densities (as seen in feral horses *Equus ferus caballus*; Marjamäki et al., 2013). There may also be confounding factors for these relationships, for instance higher body condition may effect position in a social group (for example in female reindeer *Rangifer tarandus*; Holand et al., 2004) but also the probability of dispersal (such as in greater flamingos *Phoenicopterus ruber*; Barbraud et al., 2003), creating the illusion of a positive relationship between social phenotype and dispersal when in fact none exists. Explicitly testing the relationship between dispersal and social behaviour, and how it depends on context, is therefore essential. This is especially true in invertebrates, as their dispersal is relatively understudied (Wey et al., 2015).

While using SNA allows us to quantitatively study social behaviour, relating social behaviours to dispersal can be difficult as dispersal is often rare, hard to observe in the wild, and difficult to re-create in the laboratory. Here we develop methods to quantify dispersal tendency using two different approaches. We relate each measure of dispersal to three measures of social behaviour based on social networks in a laboratory population of the cockroach *Blaptica dubia*. We also compare the sexes and control for body mass. This allows us to measure how different aspects of social behaviour relate to dispersal and how these traits are affected by sex while controlling for key confounding variables.

We predict that individuals with a higher dispersal tendency will have a higher strength (a measure of gregariousness), lower clustering coefficient (a measure of the density of only local interactions), and higher closeness (a measure of connectedness across the entire network). We also predict that males, which unlike females in this species have fully developed wings (but with limited ability to fly; Kesel et al., 2009) and are likely the dispersing sex, will show higher dispersal tendencies. Body condition could affect dispersal in either direction; better condition individuals may have the stored resources to take on the risk of dispersing (Barbraud et al., 2003), but alternatively poor condition individuals may disperse to find more resources (Lowe, 2009). As such, we do not make a directional prediction (see also the model of Bonte & De La Peña, 2009 which demonstrates how both positive- and negative-condition dependent dispersal can evolve).

## Methods

### Study population

A population of *B. dubia* was founded in the lab in Aberdeen in March 2021 by purchasing a mixed colony online. They were then maintained at 28°C, 50% humidity, and a 12:12 light:dark cycle. Stock was maintained in 48L plastic boxes (610 × 402 × 315 mm), with cardboard egg tray as shelter, carrot for hydration and Sainsbury's dog food for nutrition (approx. nutritional composition = 1527 kJ energy, 24 g protein, 12 g fat per 100 g). Boxes of immature nymphs were of mixed ages and sexes, with individuals that eclosed into adults moved to adult-only boxes within three-four days of eclosion. Some adult boxes were used for breeding and so contained both sexes, while others were for experimental animals and were single-sex. The colony showed no infection in this time and low mortality in all life stages, and so presumed to be healthy (for further details on the stock population see: Fisher, 2023). Data collection took place in two blocks with one researcher conducting the majority of the work in each, the first from 26/5/22 to 14/7/22 (led by SS), the second from 7/10/22 to 14/11/22 (led by NV). The methods were the same in each block unless we note otherwise.

## Data collection

We collected data in each block in three stages, first measuring social associations to construct social networks, then assaying the cockroaches' dispersal in a group setting, before measuring dispersal tendency alone. To create groups to quantify social networks, we selected unmated adult males and females from single-sex stock boxes and placed them into single-sex groups of ten (selection of individuals was not random, as that would have required labelling each individual in the stock population, but we removed shelters from boxes before selecting individuals to avoid only selecting "bolder" individuals). We created 12 groups in the first block (six of each sex) and ten in the second block (five of each sex). The high level of replication of networks (22 in total) in a particular strength of our study; while most studies on social networks in animals only have a single or few networks, we have multiple independent networks. This replication prevents the behaviour of a few individuals influencing the social phenotypes of every individual in the study (as social network measures often depend on connections in across the whole network). We weighed each individual and, so that we could recognise individuals, for the first block marked each with a unique combination of two colours (red, green, blue, white and gold) on their wing cases using paint pens (Edding 780 Extra-fine paint markers). As we filmed the second block in darkness, here we instead marked individuals with a unique combination of dot locations (dots present/absent on head, left wing case and right wing case, with the head occasionally having 2 dots to reach a unique code for all 10 individuals) using only white paint pens. We

placed each group of ten into a plastic box (340 × 200 × 125 mm) with four cardboard egg-tray shelters (approx. 100 x 120 mm), one in each corner taped along the long wall (see: Fisher, 2023). We placed dog food (enough to ensure cockroaches have excess food, around 3-5g) and carrot (for hydration, around 10g) in each box between the shelters and replaced it each time we recorded associations. To record associations, we observed which individuals were using the same shelter on six dates between two to four days apart (from 26/5/22 to 13/6/22 in the first block and from 7/10/22 to 19/10/22 in the second). Observations were only roughly evenly spaced due to avoiding data collection at weekends and other occasional scheduling constraints, but observations never took place on consecutive days. After recording the associations of all individuals in a box they were removed from the shelters and placed in the centre of the box, so any associations would be re-formed each observation. In this manner we gain six snapshots of the social associations in each group of cockroaches, much like observations of flocks of birds or herds of ungulates. We then aggregated these data to build a single social network for each group by assuming those in the same shelter are associated in some way (the “gambit of the group”; Whitehead & Dufault, 1999). While a single observation of two individuals sharing a shelter does not imply they are close social associates, consistently observing them together would allow us to infer some degree of social preference. Using the R package *asnipe* (Farine, 2013), we converted the data on co-occurrence in groups into an undirected weighted social network, where edge weights equalled the “simple ratio index”; the number of times the two individuals were using the same shelter divided by the total number of times they were seen (Cairns & Schwager, 1987). This value is 1 if two individuals are always seen together and near zero if they are very rarely seen together (it is exactly zero if they are never seen together). We did this separately for each group, giving 22 independent social networks, 11 of each sex.

For each individual we calculated three social network measures, each representing a different aspect of social behaviour. These measures all are weighted, and hence account for the frequency of the associations. First was “strength”, the sum of all an individual’s weighted interactions, representing overall gregariousness (function **rowSums** in the package *Matrix*). Second was “clustering coefficient”, the sum of the weighted edges involved in *closed* triads centred on the focal node divided by the sum of all weighted edges in triads centred on the focal node (Barrat et al., 2004; Opsahl & Panzarasa, 2009), which represents whether individuals invest in a closed circle of associates by regularly interacting with others who they share a mutual association with or not (function **clustering_local_w** in *tnet*; Opsahl, 2009). Finally, there was “closeness”, which is the inverse of the mean of the weighted pathlengths between an individual and all others in the network (Freeman, 1978),

representing how well connected to all parts of the group the individual is (function **closeness** in *sna*; Butts, 2008).

After the sixth observation of associations, individuals in block 1 were immediately moved to the next stage of data collection. However, individuals in block 2 were observed a further four times (giving 10 in total). To better compare the blocks, we do not use the extra four observations in block 2 here (social network measures from networks based on six observations are either strongly or moderately positively correlated with measures from networks based on ten observations; Supplementary Materials Fig. S1). In the next stage we tested the individuals for dispersal tendency in group setting (hereafter “dispersal-group”). We removed the carrot from the groups for 24 hours in block 1 and 48 hours in block 2 to increase their need for hydration and so willingness to disperse; the change between groups was made to encourage more individuals to disperse (although this was unsuccessful as there was no difference in mean dispersal group time between the blocks, see Results). We then transferred all group members into a single large plastic box (610 × 402 × 315 mm) with the four shelters used in the social association stage placed at one end of the box, evenly spaced. At the other end of the box we placed 10g of carrot and three pellets of dry dog food (Sainsbury’s Complete Nutrition Adult Small Dog Dry Dog Food, approx. nutritional composition = 1527 kJ energy, 24g protein, 12g fat per 100g) to act as a goal. We placed each box in a room maintained at 22-26°C (although with no humidity control), with a pet heating pad placed beneath each box to raise the temperature closer to that of the stock room to encourage movement (22-24$^{0}$ C). Above each box, at approximately 50cm, we placed an IP camera (ABUS IP video surveillance 8MPx mini tube camera) pointing directly downwards to record the box from above. We then left the room for 24 hours, with the camera recording continuously. For block 1, the lights were left on, while for block 2 the lights were turned off as, similarly to the above-mentioned difference in carrot deprivation between groups, this was to encourage more individuals to disperse, although as noted above this was unsuccessful.

We were able to record up to four groups simultaneously, and so we filmed them in batches of two to four (which means groups had different periods between the end of the recording of the social associations and the start of the dispersal-group trial). In block 1 we initially made recordings on 14-23/6/22, but due to computer error these were not useable, and so we repeated the trials on 1-6/7/22 (therefore starting at least 22 days after the final observation of social associations) and only used the data from the second run. In block 2 the recordings were made from 7-9/11/22 (therefore starting at least 18 days after the final observation of social associations). From the video recordings we extracted the number of minutes between the start of the trial and when each individual first crossed the half-way point of the

box (i.e., it left the shelter and travelled a distance of approx. 200 mm). This measure of dispersal is therefore low when individuals are quick to disperse, and high when they are slow/unwilling to disperse (with a theoretical maximum of 1440). We gave individuals who never dispersed values of NA to avoid a data distribution with a spike at high values (n = 11). We also repeated the analysis with those that did not disperse given a score of 1440; the clear results in the original analysis are maintained in the second analysis with the additional presence of a mass-dispersal relationship in males (see Supplementary Materials). After 24 hours we returned each group to the box it had recorded associations in with fresh carrot and cardboard shelters and returned them to the stock room.

For the third stage we measured a proxy for dispersal tendency while alone (hereafter "dispersal-alone") by placing each individual in a small plastic box (200 × 100 × 70 mm) with a grid of 18 rectangles (each 32 by 27 mm) drawn onto paper underneath the box's (clear) floor. In the same room as we recorded dispersal-group, again using pet heating pads to raise the temperature, we placed boxes with cockroaches in sets of four beneath the same IP cameras, switched off the lights (as *B. dubia* is more active in the dark; Bouchebti et al., 2022), and filmed continuously for 30 minutes. These cameras automatically use infrared LEDs to film in the dark, which we presume the cockroaches cannot see. We ignored the first 10 minutes of the recording as we did not want to record the individual's immediate response to being placed in a box, and instead counted the number of unique squares each individual visited in 20 minutes as a measure of dispersal tendency (counting unique areas visited as opposed to total amount of movement separates this from a measure of general activity and instead comes closer to "exploration"; Réale et al., 2007). In block 1 we made recordings on 12-14/7/22 (therefore starting at least 7 days after assaying dispersal-group), while in block 2 we made recordings on 10-14/11/22 (with trials staggered so that individuals were tested 3 or 4 days after being assayed for dispersal-group). After the dispersal-alone trials we returned individuals to the stock population. Individuals that died part way through the experiment had the values for the behavioural trials they completed retained in the dataset and NA values entered for any missing (n = 7).

## Data analysis

Our final dataset comprised of 215 individuals measured for each of the three social network traits, 199 of which recorded a non-NA value for dispersal-group, and 208 which recorded a measure of dispersal-alone. To determine how the different behaviours were associated, and if any were influenced by mass or sex, we entered the five behaviours into a multivariate mixed-effects model using function **MCMCglmm** in the R package *MCMCglmm* (Hadfield,

2010). We used each social network trait, dispersal-alone, and the log of dispersal-group as response variables and estimated the covariances among each of them simultaneously (10 covariances in total). We included block number and sex as two-level categorical variables, and cockroach mass as a continuous predictor, mean centred and scaled to a variance of 1 (Schielzeth, 2010). We also included the interaction between (scaled) mass and sex to test whether the effect of mass differed between the sexes. We estimated an intercept and the relationship with each fixed effect for each response variable, giving 25 coefficients in total. We included the random effect of group identity, to estimate any among-group variation that may have arisen due to emergent group dynamics and to account for differences in what the groups experiences e.g., the slightly different periods of time between behavioural tests. We did not estimate the among-group covariance in behavioural traits, leaving the covariance as the phenotypic covariance, once the effect of the fixed effects and the variation in means among groups was accounted for.

We ran the model for 550,000 iterations, discarding the first 50,000 (as parameter estimates change most at the start of the chain), and using 1 in each 100 iterations to generate the posterior distributions. We used a very weakly informative prior with a variance of 1 and a degree of belief of 0.002 for the random effect and residual variance. For dispersal-alone we used a Poison error distribution, while for the other four traits we used a Gaussian error distribution as the raw data distributions were not too far from normality and we achieved satisfactory convergence with these error distributions. We calculated the among-trait correlations as the covariance divided by the square root of the product of the variances of the two traits. We did this for each draw in our posterior distribution, allowing us to estimate the mode and 95% credible intervals for each correlation; those with credible intervals that do not overlap zero are considered clearly different from zero. For the fixed effects we used the posterior distributions; those with 95% credible intervals that did not overlap zero have a relationship with the trait in question. The author that ran the analysis (DNF) did not conduct the behavioural trials or extract data from the video, and so was blind to any impressions developed during those stages.

## Results

Closeness was negatively associated with strength (R = -0.643, CrIs = -0.715 to -0.540; we show the raw correlations in Fig. 1 and the correlation posterior distribution modes and the 95% credible intervals estimated from the model in Fig. 2), and with clustering coefficient (R = -0.270, CrIs = -0.388 to -0.117). Clustering coefficient and strength were not associated (R = 0.010, CrIs = -0.130 to 0.150). Neither dispersal-group nor dispersal-alone were

associated with any of the social network traits (dispersal-alone – strength R = 0.046, CrIs = -0.120 to 0.046; dispersal-alone – clustering coefficient R = -0.017, CrIs = -0.182 to 0.154; dispersal-alone – closeness R = -0.043, CrIs = -0.227 to 0.092; dispersal-group – strength R = -0.058, CrIs = -0.219 to 0.079; dispersal-group – clustering coefficient R = -0.067, CrIs = -0.245 to 0.053; dispersal-group – closeness R = 0.032, CrIs = -0.137 to 0.160). The two measures of dispersal were not associated with each other (R = -0.104, CrIs = -0.242 to 0.089). The residual variances and covariances are given in Table S1.

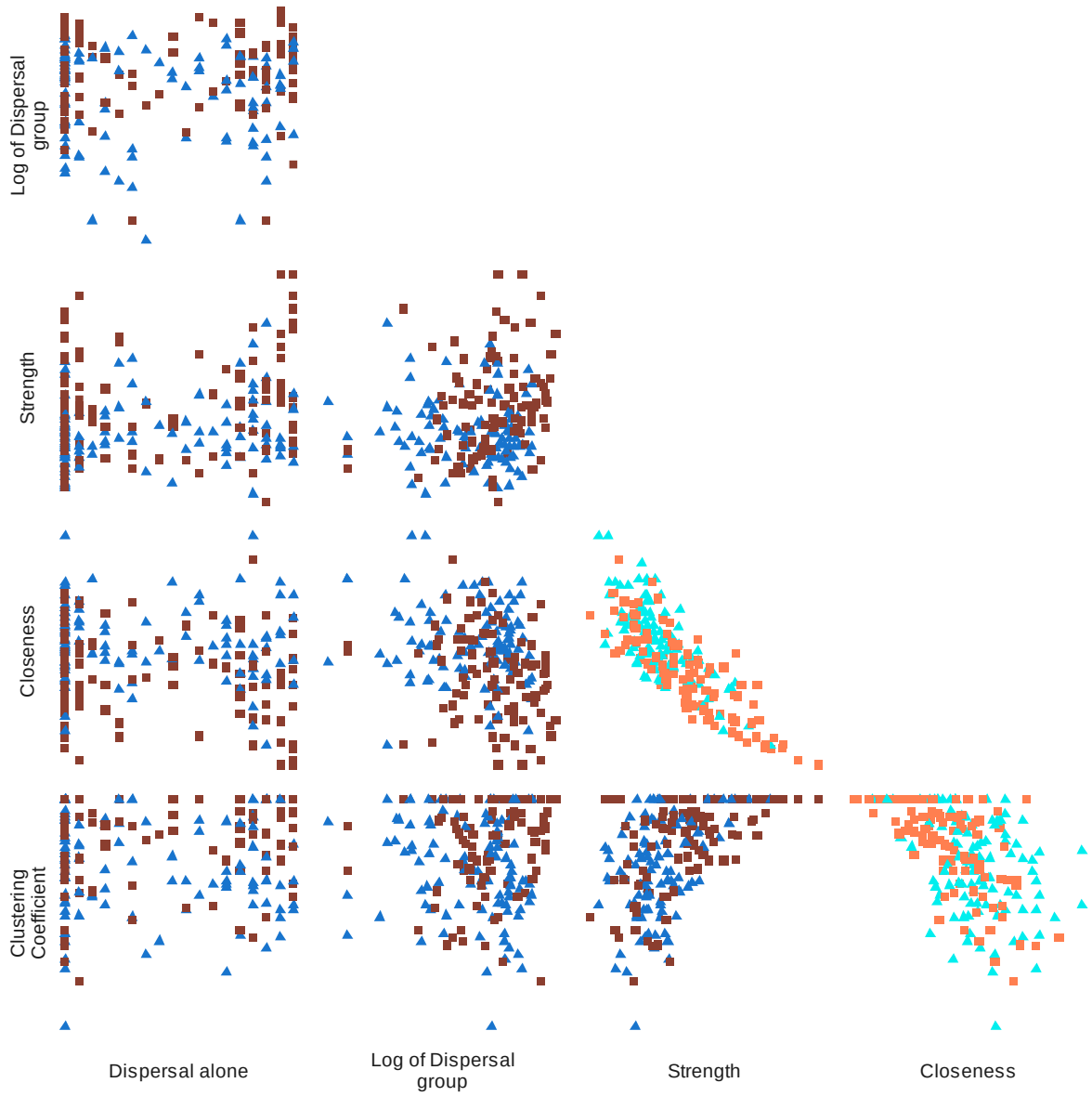
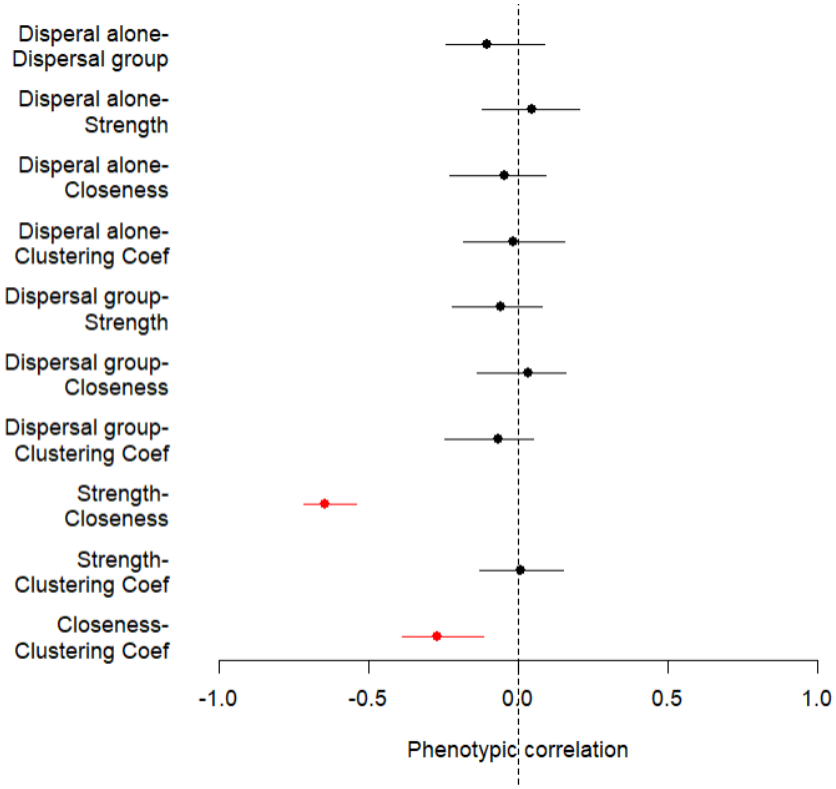



Figure 1. A pairs plot showing the relationship between each pair of traits. Females are orange squares, males are blue triangles, with the statistically significant correlations (closeness – strength and closeness – clustering coefficient) highlighted in lighter colours.

295 Cockroach mass was not associated with any behavioural trait in either sex. Males had
296 higher closeness scores than females, and marginally lower strength scores, although this
297 latter effect overlapped with zero (Fig. 1). The sexes did not differ in any other trait.
298 Individuals in block 1 had lower strengths, higher closeness scores, and lower dispersal-
299 alone scores than individuals in block 2 (model results in Table 1).

300




301

302 Figure 2. Correlations between traits as estimated from the model., Points show the
303 posterior distribution mode, the horizontal lines show the 95% credible intervals. The
304 correlations that do not overlap with zero have been highlighted in red.

305

## 306 Discussion

307 Our study investigated aspects of individual social network position within groups of *Blaptica*
308 *dubia* cockroaches and demonstrated that different measures of dispersal are not linked to
309 these positions. Two of the social network measures, strength and clustering coefficient,
310 were negatively correlated with a third, closeness, but not with each other. Meanwhile, our
311 two measures of dispersal were not correlated. Therefore, while we had predicted social
312 interactions may be associated with dispersal (with the direction of causality plausibly in
313 either direction, or both being affected by a third variable) we found no evidence for this
314 prediction. Instead, dispersal in *B. dubia* might depend strongly on other aspects of

behaviour, such as the motivation to mate and reproduce (which since all our individuals were unmated did not vary in this study), such that the variables we did measure were unimportant.

**Table 1**. Additional effect estimates from our statistical model. For each of the five traits (dispersal alone, dispersal group, strength, closeness, and clustering coefficient) we give the intercept, the effect of mass, the effect of sex (females are the default, so this effect represents how males deviate from females), the mass:sex interaction (again, as females are the default this effect indicates how the effect of mass on male traits differs from that for females, which is indicated by the main effect of mass), the effect of block (block 1 is the default, and so this effect indicates how block 2 differs), and the random effect of group. As group is a random effect, we only report the posterior mode, mean, and lower and upper 95% credible intervals (CrI), while as the remaining terms are fixed effects we also report the pMCMC value, which represents two times the probability the effect is either greater or smaller than zero (whichever is smaller), and can be interpreted in a similar way to traditional (frequentist) p-values. Terms where the 95% CrIs do not overlap with zero are highlighted in bold.

| Variable | Posterior mode | Posterior mean | Lower 95% CrI | Upper 95% CrI | pMCMC | Effect |
|---|---|---|---|---|---|---|
| Intercept - Dispersal alone | 1.1293 | 1.0876 | 0.6622 | 1.5590 | 0.0002 | fixed |
| Intercept - Dispersal group | 4.9290 | 4.8186 | 4.0583 | 5.6829 | 0.0002 | fixed |
| Intercept - Strength | 2.3732 | 2.3380 | 1.8801 | 2.8451 | 0.0002 | fixed |
| Intercept - Closeness | 0.5342 | 0.5383 | 0.4646 | 0.6062 | 0.0002 | fixed |
| Intercept - Clustering Coefficient | 0.9498 | 0.9327 | 0.8895 | 0.9792 | 0.0002 | fixed |
| Mass – Dispersal alone | 0.0336 | 0.0876 | -0.2877 | 0.5124 | 0.6620 | fixed |
| Mass – Dispersal group | 0.0957 | 0.0411 | -0.4941 | 0.5529 | 0.8724 | fixed |
| Mass - Strength | 0.0754 | 0.0758 | -0.1602 | 0.3006 | 0.5204 | fixed |

| | | | | | | |
|---|---|---|---|---|---|---|
| Mass - Closeness | -0.0131 | -0.0142 | -0.0456 | 0.0179 | 0.3720 | fixed |
| Mass - Clustering Coefficient | -0.0010 | -0.0006 | -0.0121 | 0.0117 | 0.9256 | fixed |
| Sex – Dispersal alone | -0.0325 | -0.1244 | -1.0238 | 0.7681 | 0.7880 | fixed |
| Sex – Dispersal group | 0.2122 | 0.2178 | -1.2025 | 1.6551 | 0.7712 | fixed |
| Sex - Strength | -0.5928 | -0.6517 | -1.3758 | 0.0986 | 0.0876 | fixed |
| **Sex - Closeness** | **0.1430** | **0.1355** | **0.0324** | **0.2438** | **0.0148** | fixed |
| Sex - Clustering Coefficient | -0.0455 | -0.0450 | -0.1031 | 0.0117 | 0.1264 | fixed |
| Mass:Sex – Dispersal alone | -0.3949 | -0.1935 | -1.1410 | 0.7480 | 0.6692 | fixed |
| Mass:Sex – Dispersal group | 0.9968 | 1.0352 | -0.2887 | 2.2945 | 0.1184 | fixed |
| Mass:Sex - Strength | -0.1389 | -0.1580 | -0.7448 | 0.4142 | 0.5928 | fixed |
| Mass:Sex - Closeness | 0.0734 | 0.0586 | -0.0196 | 0.1377 | 0.1464 | fixed |
| Mass:Sex - Clustering Coefficient | -0.0157 | -0.0100 | -0.0403 | 0.0191 | 0.5028 | fixed |
| **Block – Dispersal alone** | **1.0619** | **1.0059** | **0.6806** | **1.3197** | **0.0002** | fixed |
| Block – Dispersal group | 0.4524 | 0.5098 | -0.2867 | 1.2855 | 0.2000 | fixed |
| **Block - Strength** | **0.6462** | **0.6529** | **0.1286** | **1.1858** | **0.0212** | fixed |
| **Block - Closeness** | **-0.1079** | **-0.0961** | **-0.1729** | **-0.0193** | **0.0208** | fixed |
| Block - Clustering Coefficient | 0.0217 | 0.0224 | -0.0253 | 0.0777 | 0.3840 | fixed |
| Group – Dispersal alone | 0.0013 | 0.0128 | 0.0002 | 0.0477 | N/A | random |
| Group – Dispersal group | 0.4688 | 0.6758 | 0.1722 | 1.3146 | N/A | random |

| | | | | | | |
|---|---|---|---|---|---|---|
| Group - Strength | 0.2555 | 0.3477 | 0.1277 | 0.6247 | N/A | random |
| Group - Closeness | 0.0069 | 0.0078 | 0.0032 | 0.0143 | N/A | random |
| Group - Clustering Coefficient | 0.0029 | 0.0038 | 0.0016 | 0.0066 | N/A | random |

Cockroach mass was not found to influence dispersal (or social network position) in either sex, demonstrating either that animal condition is not a driver for dispersal or that mass is not a good proxy for body condition in our system. There is evidence that in German cockroaches (*Blattella germanica*) dispersal is linked to food availability and starvation (Ross & Tignor, 1985; Tignor & Ross, 1987), which might indicate that in some cockroach populations lack of food and hunger might initially be a driver for dispersal, but in a stable laboratory population with ample access to resources such as ours, there is not sufficient pressure on the lighter/poorer condition individuals to disperse. We could test this by experimentally limiting food availability, beyond the 48 hours we used in block 2 of this study. This manipulation would also be instructive for understanding the relationship between mass/condition and social behaviour, as we found no relationship here. Studies on some species, such as sleepy lizards (*Tiliqua rugosa*) and great tits (*Parus major*), have also suggested limited relationship between body condition and social network structure (Godfrey et al., 2013; Snijders et al., 2014), but other studies have suggested relationships between connectedness and body mass (e.g., in prairie voles *Microtus ochrogaster*; Sabol et al., 2020). As the number of studies using social network analysis grows, we may be able to integrate across studies (either informally or formally as a meta-analysis) to determine the typical relationship between mass/condition and centrality measures, and if this relationship varies systematically across certain categories (such as females) or groups (such as mammals) of animals.

Perhaps the most surprising result of our study is the lack of a clear relationship between our two measures of dispersal. We had designed our assays to capture dispersal tendency in two different contexts, but it is possible that instead we measured two different traits. One possibility is that dispersal alone, which was quantified as searching a small arena, functions to locate food or water, while dispersal in a group, which was assayed in a larger arena, functions to location mating patterns. Along these lines, dispersal over longer distances in the German cockroach (*Bl. germanica*) is often linked to searching for mates for breeding (Ross & Tignor, 1985), which may assist with avoiding inbreeding (Lihoreau & Rivault, 2010). In contrast, exploring the more immediate area (which is similar to our dispersal alone

assay) may serve to search for food, rather than dispersal (Durier & Rivault, 2001). Despite the different functions, we might still have expected such similar behaviours to be positively correlated, such as if individuals with a higher metabolic rate both moved around their immediate environment more and travelled long distances more (Biro & Stamps, 2010). In other species positive correlations are seen, such as in roe deer (*Capreolus capreolus*) and a colonial spider (*Cyrtophora citricola*), where different measures of dispersal (exploration beyond the home range and natal dispersal, and exploration of a new environment and "tiptoeing" to release silk into air, respectively) are positively correlated (Debeffe et al., 2013; Yip et al., 2021, p. 202). As Dochtermann (2023) highlights, we still have a limited understanding of when and how different behavioural traits covary. Therefore, until we generate better theoretical predictions, we will have to sift through published examples and try to detect broader patterns.

A not-mutually-exclusive alternative to these measures of dispersal being different behaviours is that dispersal shows such high within-individual variability that a correlation across the two contexts (as well as across the time between the assays) was too weak to be detected. Some personality traits in cockroaches are consistent (Arican et al., 2020; Planas-Sitja & Deneubourg, 2018; Stanley et al., 2017), suggesting we might expect dispersal behaviours to be consistent too. However, further data on cockroach dispersal in controlled conditions (as opposed to in uncontrolled settings such as through apartment buildings; Barcay et al., 1990; Crissman et al., 2010) is lacking for us to suggest why in our study we might not have found this. In great tits (*P. major*) exploration of a novel environment is repeatable and heritable (Dingemanse et al., 2002), and genetically correlated with dispersal distance, yet the phenotypic correlation between exploration and dispersal is not different from zero (Korsten et al., 2013), or is only positive for females in some seasons, and never in males (van Overveld et al., 2014). In the case of the great tits, a negative environmental covariance counters the positive genetic one to give the phenotypic null covariance (Korsten et al., 2013); the same might be true in our system, but we would need further work on the genetics underpinning cockroach behaviour to find out.

We found that males had higher closeness scores (and nearly lower strength scores) than females. Work in another Blaberid, *Diploptera punctata*, found that females were more gregarious and formed the core of a proximity network (Stanley et al., 2018). This result is similar to ours, as in our study males were marginally less gregarious (lower strength) and instead formed links with different parts of the network (higher closeness), implying they were at the periphery of the network core (although note we did not assay male and females together in a social network, whereas Stanley et al. did). These results suggest that males and females may generally have different positions within cockroach aggregations, with

398 females possibly being more central as they are larger, and so more able to displace others
399 from preferred spots in an aggregation, or as they are preferred associates of both males
400 and other females, causing them to end up in the centre of an aggregation (Stanley et al.,
401 2018).

402 In a related result, we also found strength was strongly negatively correlated with closeness.
403 Therefore, within our study population there appears to be an axis of variation from high-
404 strength/low-closeness to low-strength/high-closeness, and females fall more towards the
405 first of these, and males the latter. However, the relationship is not entirely defined by sex, as
406 this covariance was present in our results despite modelling the effect of sex simultaneously.
407 We also found a negative relationship between clustering coefficient and closeness, which
408 likely represents a trade-off between making strong local connections with a few individuals
409 (giving a higher clustering coefficient) *or* making connections with a wide range of individuals
410 (giving a high closeness). The strong negative correlation between strength and closeness
411 suggests variation in social behaviour in *B. dubia*, with some individuals being less
412 gregarious and moving between groups, while others remaining in larger groups. Planas-
413 Sitja and Deneubourg (2018) found that collective aggregation formation in the American
414 cockroach (*Periplaneta americana*) is influenced by the social behaviour of individuals in the
415 aggregations, suggesting substantial differences among-individuals. Such differences in
416 social behaviour will likely expose an individual to a range of different selection pressures,
417 such as differential exposure to directly transmitted infections, variation in competition for
418 resources and mates, and different risk of desiccation. Understanding what drives this
419 variation in social behaviour and what consequences it has for the ecology and evolution of
420 cockroach groups are important next steps.

421 Our study has also demonstrated that three traits (dispersal alone, strength, and closeness)
422 differed between blocks, which indicates the presence of observer induced variation.
423 Observer-induced variation seems more plausible than an environmental change between
424 the boxes, as we used standardised environmental conditions. That the mean level of a
425 behaviour that is observed differs between blocks within a single study should be considered
426 in other studies and when making conclusions from single studies at single point in time by a
427 single laboratory, reinforcing the need for more extensive replication in such experiments
428 (Brecht et al., 2021; Farrar et al., 2021; Gaona-Gordillo et al., 2023).

429 In conclusion, our results suggest care should be taken when measuring dispersal in the
430 laboratory, as assays designed to capture dispersal may actually measure different traits or
431 not capture the consistent component of dispersal. We also found no support for the
432 suggestion that social behaviour and dispersal are associated. We found limited importance

of mass in our system, while there were some differences between males and females that reflected broader trade-offs in social behaviour. Finally, our results indicate that repeating experiments, even in the same lab, can give different results, and so add strength to the call that study replication should be an important component of animal behaviour research if we are to detect general pattens.

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No specific funding was received for this project.

## Conflict of interest

We have no conflicts of interest.

## Ethical approval

No specific approval was required for this work. We did follow the Association for the Study of Animal Behaviour's "Guidelines for the ethical treatment of nonhuman animals in behavioural research and teaching", notably using a non-invasive marking system (using non-toxic paint on the outer carapace) and performing no other procedures. Our level of replication, both number of groups and individuals per group, was high enough to detect clear trends but not unnecessarily large. Our study species is naturally aggregative and so is not stressed by being kept in groups, and periods kept alone were short (30 minutes). We used short periods (24 or 48 hours) without access to food to increase motivation to disperse, but all animals were given access to food in the subsequent behavioural trial and when returned to housing afterwards. At the end of the experiments individuals were returned to the stock population.

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## References

Aguillon, S. M., & Duckworth, R. A. (2015). Kin aggression and resource availability influence phenotype-dependent dispersal in a passerine bird. *Behavioral Ecology and Sociobiology*, *69*(4), 625–633. https://doi.org/10.1007/s00265-015-1873-5

Arican, C., Bulk, J., Deisig, N., & Nawrot, M. P. (2020). Cockroaches Show Individuality in Learning and Memory During Classical and Operant Conditioning. *Frontiers in Physiology*, *10*, 1539. https://doi.org/10.3389/FPHYS.2019.01539/BIBTEX

Barbraud, C., Johnson, A. R., & Bertault, G. (2003). Phenotypic correlates of post-fledging dispersal in a population of greater flamingos: The importance of body condition. *Journal of Animal Ecology*, *72*(2), 246–257. https://doi.org/10.1046/j.1365-2656.2003.00695.x

Barcay, S. J., Schneider, B. M., & Bennett, G. W. (1990). Influence of Insecticide Treatment on German Cockroach (Dictyoptera: Blattellidae) Movement and Dispersal within Apartments. *Journal of Economic Entomology*, *83*(1), 142–147. https://doi.org/10.1093/jee/83.1.142

Barrat, A., Barthélemy, M., Pastor-Satorras, R., & Vespignani, A. (2004). The architecture of complex weighted networks. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(11), 3747–3752. https://doi.org/10.1073/pnas.0400087101

Bekoff, M. (1977). Mammalian Dispersal and the Ontogeny of Individual Behavioral Phenotypes. *The American Naturalist*, *111*(980), 715–732. https://doi.org/10.1086/283201

Biro, P. A., & Stamps, J. A. (2010). Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends in Ecology & Evolution*, *25*(11), 653–659. https://doi.org/10.1016/j.tree.2010.08.003

Blumstein, D. T., Wey, T. W., & Tang, K. (2009). A test of the social cohesion hypothesis: Interactive female marmots remain at home. *Proceedings of the Royal Society of London B: Biological Sciences*, *276*(1669), 3007–3012.

Bonte, D., & De La Peña, E. (2009). Evolution of body condition-dependent dispersal in metapopulations. *Journal of Evolutionary Biology*, *22*(6), 1242–1251. https://doi.org/10.1111/j.1420-9101.2009.01737.x

Borgeaud, C., Sosa, S., Sueur, C., & Bshary, R. (2017). The influence of demographic variation on social network stability in wild vervet monkeys. *Animal Behaviour*, *134*, 155–165. https://doi.org/10.1016/J.ANBEHAV.2017.09.028

Bouchebti, S., Cortés-Fossati, F., Estepa, Á. V., Lozano, M. P., Calovi, D. S., & Arganda, S. (2022). Sex-Specific Effect of the Dietary Protein to Carbohydrate Ratio on Personality in the Dubia Cockroach. *Insects 2022, Vol. 13, Page 133*, *13*(2), 133. https://doi.org/10.3390/INSECTS13020133

Brecht, K. F., Legg, E. W., Nawroth, C., Fraser, H., & Ostojic, L. (2021). The Status and Value of Replications in Animal Behavior Science. *Animal Behavior and Cognition*, *8*(2), 97–106. https://doi.org/10.26451/abc.08.02.01.2021

Brent, L. J. N. (2015). Friends of friends: Are indirect connections in social networks important to animal behaviour? *Animal Behaviour*. https://doi.org/10.1016/j.anbehav.2015.01.020

Butts, C. C. T. (2008). Social network analysis with sna. *Journal of Statistical Software*, *24*(6), 13–41. https://doi.org/10.1111/j.1467-839X.2007.00241.x

Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indices. *Animal Behaviour*, *35*(5), 1454–1469. https://doi.org/10.1016/S0003-3472(87)80018-0

Christian, J. J. (1970). Social Subordination, Population Density, and Mammalian Evolution. *Science*, *168*(3927), 84–90. https://doi.org/10.1126/science.168.3927.84

Clobert, J. (2012). *Dispersal Ecology and Evolution*. Oxford University Press.

Cote, J., & Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1608), 383–390. https://doi.org/10.1098/rspb.2006.3734

Crissman, J. R., Booth, W., Santangelo, R. G., Mukha, D. V., Vargo, E. L., & Schal, C. (2010). Population Genetic Structure of the German Cockroach (Blattodea: Blattellidae) in Apartment Buildings. *Journal of Medical Entomology*, *47*(4), 553–564. https://doi.org/10.1603/me09036

Croft, D. P., James, R., & Krause, J. (2008). *Exploring Animal Social Networks*. Princeton University Press. http://opus.bath.ac.uk/25878/

Debeffe, L., Morellet, N., Cargnelutti, B., Lourtet, B., Coulon, A., Gaillard, J. M., Bon, R., & Hewison, A. J. M. (2013). Exploration as a key component of natal dispersal: Dispersers explore more than philopatric individuals in roe deer. *Animal Behaviour*, *86*(1), 143–151. https://doi.org/10.1016/j.anbehav.2013.05.005

Dingemanse, N., Both, C., Drent, P., Van Oers, K., & Van Noordwijk, A. J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, *64*(6), 929–938. https://doi.org/10.1006/anbe.2002.2006

Dochtermann, N. A. (2023). The role of plasticity, trade-offs, and feedbacks in shaping behavioral correlations. *Behavioral Ecology*, *34*(6), 913–918. https://doi.org/10.1093/beheco/arad056

Durier, V., & Rivault, C. (2001). Effects of spatial knowledge and feeding experience on foraging choices in German cockroaches. *Animal Behaviour*, *62*(4), 681–688. https://doi.org/10.1006/anbe.2001.1807

Farine, D. R. (2013). Animal social network inference and permutations for ecologists in R using asnipe. *Methods in Ecology and Evolution*, *4*(12), 1187–1194. https://doi.org/10.1111/2041-210X.12121

Farine, D. R., & Whitehead, H. (2015). Constructing, conducting, and interpreting animal social network analysis. *The Journal of Animal Ecology*, *84*(5), 1144–1163. https://doi.org/10.1111/1365-2656.12418

Farrar, B. G., Voudouris, K., & Clayton, N. S. (2021). Replications, Comparisons, Sampling and the Problem of Representativeness in Animal Cognition Research. *Animal Behavior and Cognition*, *8*(2), 273–295. https://doi.org/10.26451/abc.08.02.14.2021

Fisher, D. N. (2023). Direct and indirect phenotypic effects on sociability indicate potential to evolve. *Journal of Evolutionary Biology*, *36*(1), 209–220. https://doi.org/10.1111/jeb.14110

Freeman, L. C. (1978). Centrality in social networks conceptual clarification. *Social Networks*, *1*(3), 215–239. https://doi.org/10.1016/0378-8733(78)90021-7

Gaona-Gordillo, I., Holtmann, B., Mouchet, A., Hutfluss, A., Sánchez-Tójar, A., & Dingemanse, N. J. (2023). Are animal personality, body condition, physiology and structural size integrated? A comparison of species, populations and sexes, and the value of study replication. *Journal of Animal Ecology*, *92*(9), 1707–1718. https://doi.org/10.1111/1365-2656.13966

Godfrey, S. S., Sih, A., & Bull, C. M. (2013). The response of a sleepy lizard social network to altered ecological conditions. *Animal Behaviour*, *86*(4), 763–772. https://doi.org/10.1016/j.anbehav.2013.07.016

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, *33*(2), 1–22.

Holand, Ø., Gjøstein, H., Losvar, A., Kumpula, J., Smith, M. E., Røed, K. H., Nieminen, M., & Weladji, R. B. (2004). Social rank in female reindeer (Rangifer tarandus): Effects of body mass, antler size and age. *Journal of Zoology*, *263*(4), 365–372. https://doi.org/10.1017/S0952836904005382

Kesel, A. B., Martin, A., & Hoffmann, F. (2009). *Quantifying the Landing Reaction of Cockroaches* (Final Report 08/6302; 21958/08/NL/CBI, p. 56). European Space Agency.

Korsten, P., van Overveld, T., Adriaensen, F., & Matthysen, E. (2013). Genetic integration of local dispersal and exploratory behaviour in a wild bird. *Nature Communications*, *4*(1), 2362. https://doi.org/10.1038/ncomms3362

Krause, J., Croft, D. P., & James, R. (2007). Social network theory in the behavioural sciences: Potential applications. *Behavioral Ecology and Sociobiology*, *62*(1), 15–27. https://doi.org/10.1007/s00265-007-0445-8

Krause, J., James, R., Franks, D. W., & Croft, D. P. (2014). *Animal Social Networks*. Oxford University Press. http://ukcatalogue.oup.com/product/9780199679058.do

Kurvers, R. H. J. M., Krause, J., Croft, D. P., Wilson, A. D. M., & Wolf, M. (2014). The evolutionary and ecological consequences of animal social networks: Emerging issues. *Trends in Ecology & Evolution*, *29*(6), 326–335. https://doi.org/10.1016/j.tree.2014.04.002

Lihoreau, M., & Rivault, C. (2010). German cockroach males maximize their inclusive fitness by avoiding mating with kin. *Animal Behaviour*, *80*(2), 303–309. https://doi.org/10.1016/j.anbehav.2010.05.011

Louca, V., Lindsay, S. W., & Lucas, M. C. (2009). Factors triggering floodplain fish emigration: Importance of fish density and food availability. *Ecology of Freshwater Fish*, *18*(1), 60–64. https://doi.org/10.1111/j.1600-0633.2008.00323.x

Lowe, W. H. (2009). What drives long-distance dispersal? A test of theoretical predictions. *Ecology*, *90*(6), 1456–1462. https://doi.org/10.1890/08-1903.1

Marjamäki, P. H., Contasti, A. L., Coulson, T. N., & McLoughlin, P. D. (2013). Local density and group size interacts with age and sex to determine direction and rate of social dispersal in a polygynous mammal. *Ecology and Evolution*, *3*(9), 3073–3082. https://doi.org/10.1002/ece3.694

Matthysen, E. (2012). Multicausality of dispersal: A review. In *Dispersal ecology and evolution* (Vol. 27, pp. 3–18). Oxford University Press.

Opsahl, T. (2009). *Structure and Evolution of Weighted Networks*. University of London (Queen Mary College).

Opsahl, T., & Panzarasa, P. (2009). Clustering in weighted networks. *Social Networks*, *31*(2), 155–163. https://doi.org/10.1016/j.socnet.2009.02.002

Planas-Sitja, I., & Deneubourg, J. L. (2018). The role of personality variation, plasticity and social facilitation in cockroach aggregation. *Biology Open*, *7*(12). https://doi.org/10.1242/BIO.036582/2072

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, *82*(2), 291–318. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Ross, M. H., & Tignor, K. R. (1985). Response of german cockroaches to a dispersant emitted by adult females. *Entomologia Experimentalis et Applicata*, *39*(1), 15–20. https://doi.org/10.1111/j.1570-7458.1985.tb03537.x

Sabol, A. C., Lambert, C. T., Keane, B., Solomon, N. G., & Dantzer, B. (2020). How does individual variation in sociality influence fitness in prairie voles? *Animal Behaviour*, *163*, 39–49. https://doi.org/10.1016/j.anbehav.2020.02.009

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, *1*(2), 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x

Shizuka, D., & Johnson, A. E. (2020). How demographic processes shape animal social networks. *Behavioral Ecology*, *31*(1), 1–11. https://doi.org/10.1093/beheco/arz083

Snijders, L., van Rooij, E. P., Burt, J. M., Hinde, C. A., van Oers, K., & Naguib, M. (2014). Social networking in territorial great tits: Slow explorers have the least central social network positions. *Animal Behaviour*, *98*, 95–102. https://doi.org/10.1016/j.anbehav.2014.09.029

Sosa, S., Sueur, C., & Puga-Gonzalez, I. (2021). Network measures in animal social network analysis: Their strengths, limits, interpretations and uses. *Methods in Ecology and Evolution*, *12*(1), 10–21. https://doi.org/10.1111/2041-210X.13366

Stanley, C. R., Liddiard Williams, H., & Preziosi, R. F. (2018). Female clustering in cockroach aggregations-A case of social niche construction? *Ethology*, *124*(10), 706–718. https://doi.org/10.1111/eth.12799

Stanley, C. R., Mettke-Hofmann, C., & Preziosi, R. F. (2017). Personality in the cockroach Diploptera punctata: Evidence for stability across developmental stages despite age effects on boldness. *PLoS ONE*, *12*(5). https://doi.org/10.1371/journal.pone.0176564

Sueur, C., Petit, O., De Marco, A., Jacobs, A. T., Watanabe, K., & Thierry, B. (2011). A comparative network analysis of social style in macaques. *Animal Behaviour*, *82*(4), 845–852. https://doi.org/10.1016/j.anbehav.2011.07.020

Székely, T. (Tamás), Moore, A. J. (Allen J., & Komdeur, J. (2010). *Social behaviour: Genes, ecology and evolution*. Cambridge University Press. https://www.cambridge.org/gb/academic/subjects/life-sciences/animal-behaviour/social-behaviour-genes-ecology-and-evolution?format=PB&isbn=9780521709620

Tignor, K. R., & Ross, M. H. (1987). Effect of starvation on secretion of a dispersal pheromone by female german cockroaches. *Entomologia Experimentalis et Applicata*, *45*(3), 245–249. https://doi.org/10.1111/j.1570-7458.1987.tb01090.x

Turner, J. W., Bills, P. S., & Holekamp, K. E. (2018). Ontogenetic change in determinants of social network position in the spotted hyena. *Behavioral Ecology and Sociobiology*, *72*(1). https://doi.org/10.1007/s00265-017-2426-x

van Overveld, T., Careau, V., Adriaensen, F., & Matthysen, E. (2014). Seasonal- and sex-specific correlations between dispersal and exploratory behaviour in the great tit. *Oecologia*, *174*(1), 109–120. https://doi.org/10.1007/s00442-013-2762-0

Wey, T. W., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal behaviour: A promising tool for the study of sociality. *Animal Behaviour*, *75*(2), 333–344. https://doi.org/10.1016/j.anbehav.2007.06.020

Wey, T. W., Spiegel, O., Montiglio, P.-O., & Mabry, K. E. (2015). Natal dispersal in a social landscape: Considering individual behavioral phenotypes and social environment in dispersal ecology. *Current Zoology*, *61*(3), 543–556. https://doi.org/10.1093/czoolo/61.3.543

Whitehead, H., & Dufault, S. (1999). Techniques for Analyzing Vertebrate Social Structure Using Identified Individuals: Review and Recommendations. *Advances in the Study of Behavior*, *28*. http://www.sciencedirect.com/science/article/pii/S0065345408602156

Yip, E. C., Smith, D. R., & Lubin, Y. (2021). Causes of plasticity and consistency of dispersal behaviour in a group-living spider. *Animal Behaviour*, *175*, 99–109. https://doi.org/10.1016/j.anbehav.2021.02.019

656