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Social interactions shape individual and collective personality in social spiders

Edmund R. Hunt[1*], Brian Mi[2], Camila Fernandez[2], Brandyn M. Wong[2], Jonathan N. Pruitt[3], and Noa Pinter-Wollman[1]

[1] Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095
[2] BioCircuits Institute, University of California, San Diego, La Jolla CA 92093
[3] Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106
*Corresponding author / Lead contact

Abstract

The behavioural composition of a group and the dynamics of social interactions can both influence how social animals work collectively. For example, individuals exhibiting certain behavioural tendencies may have a disproportionately large impact on the group, and so are referred to as keystone individuals, while interactions between individuals can facilitate information transmission about resources. Despite the potential impact of both behavioural composition and interactions on collective behaviour, the relationship between consistent behaviours, also known as personalities, and social interactions remains poorly understood. Here, we use stochastic actor oriented models to uncover the interdependencies between boldness and social interactions in the social spider *Stegodyphus dumicola*. We find that boldness has no effect on the likelihood of forming social interactions, but interactions do affect boldness, and lead to an increase in the boldness of the shyer individual. Furthermore, spiders tend to interact with the same individuals as their neighbours. In general, boldness decreases over time but once an individual's boldness begins to increase, this increase accelerates, suggesting a positive feedback mechanism. These dynamics of interactions and boldness result in skewed boldness distributions of a few bold individuals and many shy individuals, as observed in nature. This group behavioural composition facilitates efficient collective behaviours, such as rapid collective prey attack. Thus, by

examining the relationship between behaviour and interactions, we reveal the mechanisms that underlie the emergence of adaptive group composition and collective behaviour.

Keywords: Collective behaviour, Stochastic Actor Oriented Models, Personality, Keystone individual, Social network analysis, *Stegodyphus dumicola*

Introduction

Collective phenomena, where interactions among individuals produce emergent behaviours, are ubiquitous in biology. Previous work on collective behaviour [1] typically assumes homogeneity of agents' intrinsic characteristics and interaction rules. However, heterogeneous interaction and consistent individual variation in behaviour over time, often described as 'personality', are both increasingly recognized as pervasive and important for emergent group function within animal societies [2-6]. Even limited behavioural heterogeneity can be highly impactful. For example, just one 'keystone' individual, such as a leader or a tutor, can affect the whole group [7, 8]. As such, the behavioural composition of a group can be crucial to its success [9], and thus it is a key research challenge to explain how such behavioural heterogeneity emerges.

The particular mechanism(s) by which keystone individuals' influence on other group members is imparted can be direct, e.g., by leading a collective behaviour, or indirect, e.g., by catalysing particular behaviours of others in the group [10]. Keystone individuals can induce long-term changes in others' behaviour [11], however, it is not known how these behavioural changes occur. The impact on the behaviour of group members may be mediated via social interactions, which can be studied using social networks [5, 12-14]. Such network representations of social interactions often reveal highly heterogeneous interaction patterns that can influence collective outcomes [6, 15].

Behavioural plasticity is often overlooked in consideration of animal personality [16], perhaps because of the seeming tension between behavioural consistency (the definition of personality) and development [17]. Nevertheless, social interactions likely have a strong influence on both short-term individual behaviour [18], and the development of group members' behavioural traits [19]. This influence can be manifest over an individual's lifetime: for example, in the long-tailed manakin, network position of juveniles predicts later social status [20]. Generally however, the effect of social interactions on behavioural plasticity has been comparatively understudied, probably in part because it is methodologically challenging to estimate the relative influence of individual behavioural traits on dynamic social interactions, and vice versa. Perhaps as a result, personality has typically been assessed by observations across a short time period, often just a few days, because it may not be stable in the longer-term [21, 22].

Explicit empirical work to identify joint changes in both interaction networks and behaviour is therefore necessary to make further progress in attributing causal priority to either internal processes that affect personality, or external forces such as social interactions, in determining group behavioural compositions. Fortunately, a recently developed simulation-based method of statistical inference, known as stochastic actor oriented models (SAOMs) [23], now enables such studies of dynamic animal social networks [24].

Stochastic actor oriented models (SAOMs) represent network dynamics of longitudinal data, and can estimate the mutual effects of multiple micro-mechanisms that may be operating simultaneously, such as personality and social influence. Importantly, the

SAOM framework allows one to study changing nodal variables alongside the network dynamics: behavioural characteristics can be dependent variables, whereby the social network influences the dynamics of behaviour, and the behaviour influences the dynamics of the network. Thus, one can establish the relative influence of networks and behaviour as they change over time (Figure 1). The actor-oriented aspect of SAOM refers to the changes in network structure being modelled as stepwise choices by individuals, represented as nodes in a network. The framework describes the agency of individuals deciding with whom to form, maintain and dissolve social ties, as a function of their local social structure and neighbours' behavioural traits [23, 25]. So far, there has been fairly limited use of SAOMs to study animal systems (but see examples in: hyenas [26], vervet monkeys [27], rooks [28], and *Drosophila* flies [29]).

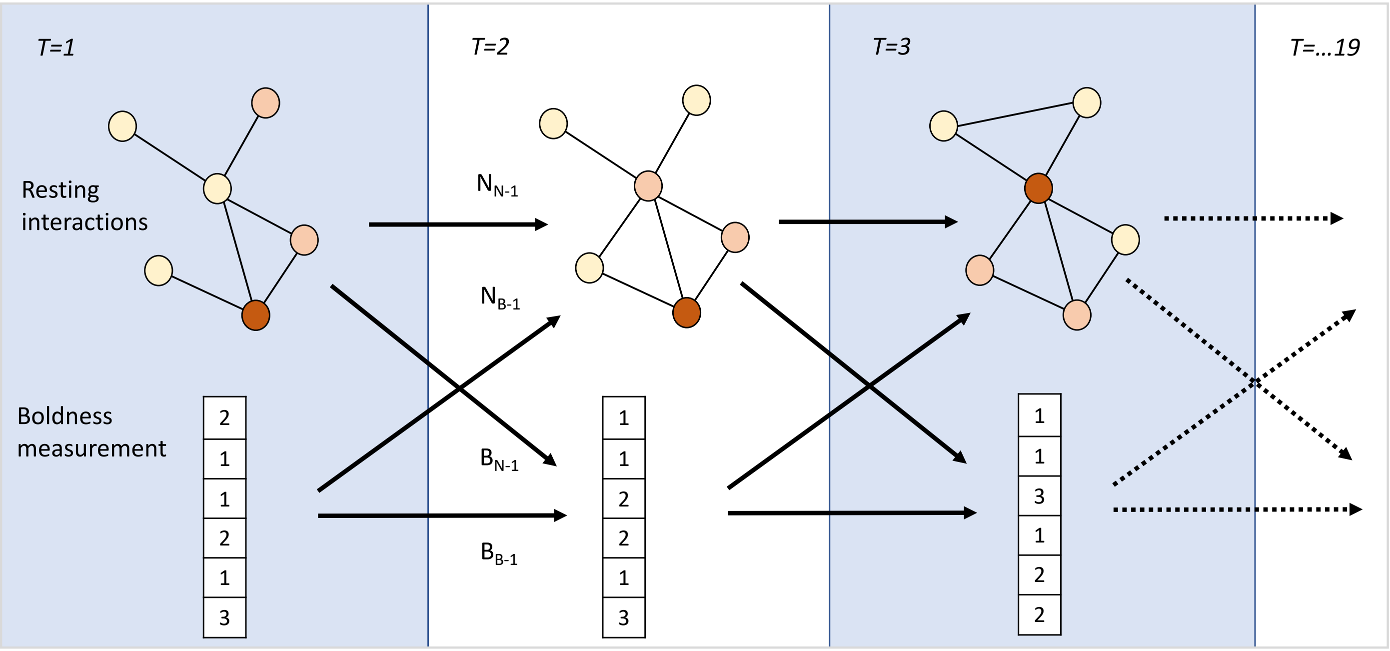

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Figure 1: Network-boldness co-dynamics in the SAOM framework. Each panel is one time point (observation), denoted as T=1-19. Node (spider) colors indicate boldness which is also listed for each individual in the table below each network. Spider social interactions, which are physical contacts between resting spiders, are represented, for each observation, by undirected, unweighted edges. Arrows between observations indicate possible mechanisms of causal influence: current boldness measurement may depend on the social position of individuals in the previous observation (B_{N-1}); network interactions may be shaped by the individuals' boldness in the previous observation (N_{B-1}); network structure in one observation may result from the social interactions in the previous observation (N_{N-1}), and boldness in one observation may result from the boldness in the previous observation (B_{B-1}). SAOM allows us to estimate all 4 effects. Figure adapted from [24].

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Stegodyphus dumicola are social spiders that live in colonies of up to several hundred individuals and exhibit cooperative behaviours such as prey capture and allo-maternal care [30, 31]. The presence of just one very bold individual (keystone) in a group of *S. dumicola* can substantially boost the prey capture success and mass gain of the whole colony [32], with that individual's presence having long-term effects on other spiders' boldness [11]. Boldness in this system is measured as the latency to resume movement after experiencing an aversive stimulus [33, 34] and it is a repeatable behaviour, with a repeatability of 0.63 measured when spiders are kept in isolation [35]. Boldness has been shown to correlate with aggression [35], and thus provides insight into more general behavioural tendencies. However, behavioural consistency seems to be contingent on a stable social environment: boldness repeatability is much-reduced following social disturbance [36] and such a disturbance reduces group performance [37]. This makes it challenging to assess the mechanism of influence and longer-term identity of keystone individuals. Furthermore, the identity of the boldest individual in the group does not influence its impact on prey capture dynamics [38] – in this system, keystone refers to a behavioural role rather than a specific individual [7].

Investigation into potential mechanisms of keystone influence on the group has been conducted using computer simulations [39]. A priori, one can expect behavioural variation among individuals in the same group to arise from either internal differences (genetics and development) or external conditions (social context and ecological conditions) [40]. Simulation investigation indicates that the effect of keystone individuals on social organization could be mediated through either internal (behavioural persistence) or external (social interaction) forces, as these models generate boldness distributions that match the empirical distribution of *Stegodyphus* colonies found in the field [39]. Here, we apply the SAOM framework to uncover the temporal dynamics of physical interaction patterns and boldness in the social spider S. *dumicola*, and to determine if social interactions affect boldness, and/or whether boldness affects who interacts with whom (Figure 1).

Methods

Animal collection and maintenance

Colonies of adult *S. dumicola* were collected from roadside *Acacia* trees in the Northern Cape of South Africa in March 2016. After transportation to the laboratory, they were fed crickets weekly. Lab colonies contained only females – males are short-lived and rare (12%) in natural colonies [41]. We created 24 groups of 10 adult female spiders each, from 3 source colonies. Groups were housed in large round containers (11cm diameter, 10cm depth) with a vertical wire mesh (a 5x5cm sheet) to allow the spiders to build both a retreat and a capture web. Experimental observations were made during June-August, 2016.

Boldness

Each spider’s boldness was measured once a week using an established assay that recorded the recovery of a spider from exposure to air puffs, which mimic the approach of an avian predator [33]. After placing spiders individually in a plastic container (15x15cm) we waited for 30sec until the spiders were acclimated and stopped moving around the arena, as in recent studies [42-45]. We then administered two puffs of air to the anterior prosoma using an infant nose-cleaning bulb. Spiders react to the air puffs by huddling, i.e. pulling their legs under their body, and remaining motionless. Boldness was measured as the latency to resume movement and move one body length. Because bolder individuals resume movement faster, the latency to resume movement was subtracted from the maximum duration of the procedure (600s) to create a metric that increases with boldness. We designated as 'shy' those individuals with a latency to resume movement of 400-600s (boldness of 0-200), while 'bold' individuals were those with a latency to resume movement of 0-200s (boldness of 400-600). The abdomen of each spider was given a unique marking with acrylic paint to track their behaviour over time.

Group boldness composition

We artificially created groups of 10 spiders with one of three boldness compositions: all bold spiders, all shy spiders, and 9 shy individuals with one bold individual. Overall, these groups contained more initially shy individuals than bold individuals because this represents the spiders' natural boldness distribution (see figure 4 in Pinter-Wollman et al 2016 [39]). Group composition converged after the first week (supplementary information and Figure S1). To examine changes in groups' boldness compositions, we compared the boldness distributions in week 1 to week 7.

Social interactions

We manually recorded the physical contacts among spiders three times a week (see below), during the day, while spiders are inactive for long periods of time. Therefore, we refer to these interactions as 'resting interactions' and define an interaction as a physical contact between any body parts of two spiders, when the colony is not active. Colony activity is minimal in the lab (initial web construction and collective predation when fed) and most of the time spiders are resting. Therefore, observing their interactions every 2-3 days samples most social interactions. We used the interactions to construct unweighted (binary), undirected (symmetrical), networks for each spider group during each observation.

We calculated the skewness of each resting network's degree distribution (N=456), to assess whether the spiders in each observed network tended to have a similar number of interactions (skewness close to 0) or if degree was heterogeneous (skewness different from 0).

Experimental procedure

Each group was observed for 6.5 weeks. Boldness was measured once a week and resting interactions, later translated into social networks, were observed three times a week with 2-3 days separating each observation. We recorded the first set of resting interactions each week immediately before measurement of boldness ('Day 1'). We recorded the second resting network on Day 3, and the third resting network was recorded on Day 5. After interactions were observed on Day 5, we fed each colony a single 4-week-old cricket, hence all colonies had an equal opportunity to consume prey. This spacing of measures of interactions allowed time for the spiders to recover from the disturbance caused by measuring boldness on Day 1 (after observing the resting interaction). In week 7 we made a final observation of boldness and the resting network. In total, there were 7 boldness measures for each individual spider and 19 resting networks for each group.

Stochastic actor oriented models

To determine the relationship between boldness and social interactions using the SAOM method, we first ensured that our data met the model assumptions. The SAOM method requires an appropriate level of tie turnover between successive network observations (i.e., edges being created, maintained, or removed) measured using the Jaccard index of similarity between successive observation waves [46]. Because several spider groups did not have a Jaccard index greater than 0.2 when modelled individually, we aggregated groups by source colony and group composition treatment, such that 24 groups became 8 (Table S1). This aggregation allowed us to compare the different group composition treatments as detailed in the supplementary material. We aggregated groups using structural zeros, whereby two or more networks are included in one adjacency matrix, but the two sets of nodes are not allowed to form edges between groups, only within them. This aggregation achieved the appropriate level of tie turnover and allowed us to proceed with the SAOM analysis. When nodes were removed because of spider death we specified structural zeros for the relevant node in the time periods after its death, such that it can no longer participate in network dynamics, and is not included in statistical estimation from that time point.

Boldness was measured once per week, to minimize disruption to the spiders, and so we interpolated the boldness measure to obtain boldness measures for all 3 sets of network observations made each week. To calculate boldness at intermediate days (3 and 5), we used a linear interpolation between the two known points on day 1 of that week and the next week. The SAOM framework simulates network and behaviour changes through a series of microsteps, i.e. the addition, maintenance or dissolution of a single network tie, or a -1, 0, or +1 change in a spider's boldness covariate. The boldness range of 0-600 is too wide for such microsteps, and therefore we translated it to a 1-3 scale, from 0-200, 200-400, and 400-600. These groupings match the criteria we used for creating group compositions of all shy and all-bold groups.

Although we created three group composition treatments, the behavioural composition of the groups converged after the first week, and thus after the first week all treatments had similar boldness compositions.

We used the SIENA framework (*Simulation Investigation for Empirical Network Analysis*), to implement the SAOM analysis in the R package RSiena version 1.2.3 [46, 47], with R version 3.3.3 [48]. To construct models we followed an iterative approach guided by existing scientific insight and the hypotheses tested, as detailed in Fisher et al [24]. We started with a simple set of core effects and then introduced further complexity to the model. We were primarily interested in the effect of boldness on tie formation, and the effect of social ties on boldness, and used effects that are specific to undirected (symmetrical) ties.

SAOM effects

We included the following structural and behavioural effects in our SAOMs:

(1) **Network on boldness** – to measure the influence of network ties on boldness we included the *average alter* effect (*avAlt*). This is the influence of the (averaged) behaviour of alters (i.e. neighbouring spiders) upon interaction with a focal individual (i.e. the 'actor' in SAOM). Here, a positive effect indicates that the formation of a social interaction tends to increase boldness of the individual with lower boldness, while a negative effect indicates that interactions tend to reduce boldness.

(2) **Boldness temporal dynamics** – to examine general tendencies in boldness over time across all the spiders we included both a *linear shape* effect and a *quadratic shape* effect. A zero value for the linear shape effect indicates drift toward the midpoint of the range of the behavioural variable. A positive value indicates an increase, and a negative

value a decrease, in boldness over time. The quadratic shape effect indicates the presence of feedback: positive values imply that an increase in boldness tends to be followed by another boldness increase, as a self-reinforcing, ‘addictive’ behaviour [47]. A negative value indicates a self-correcting negative feedback: boldness increases tend to be followed by reductions in boldness and when boldness decreases, the push toward further decreases is curtailed.

(3) **Boldness on interactions** – to measure the effect of boldness on the tendency to form ties we included the *covariate effect*, *egoPlusAltX* (the covariate being boldness, in this case). A positive covariate effect would indicate that bolder spiders are more likely to form ties in general, while a negative effect would indicate that bolder spiders tend to be more isolated.

The following effects depend on the network itself, separately from individual behavioural co-variates.

(4) **Structural equivalence** – We examined two measures of structural equivalence: (i) *Jaccard similarity effect* (*Jout*) – the extent to which two actors (connected or not) are connected with the same third parties [49]. Thus, a positive Jout effect indicates that individuals share a similar social environment. (ii) *Weighted structural equivalence effect* (*from.w.ind*) – measures a preference to interact with individuals who have similar ties to other individuals, weighted by the degrees (number of neighbours) of those others. A positive *from.w.ind* suggests that structural equivalence is achieved by ties to third parties with high degree.

(5) **Degree plus popularity** (d*egPlus*) – a feedback effect for undirected networks, representing (if positive) a tendency for nodes with high-degree (many neighbours) to

create and maintain relatively more ties than low-degree nodes. If negative, this indicates a constraint on node degrees becoming too dispersed.

Network density and period-specific network and boldness effects were also included. Network density (*density*), which is the ratio of observed ties to all possible ties, takes the role of an intercept in a regression model, by controlling for the overall density given all the other effects included in the models. Thus, while it is a necessary effect it is not biologically informative. Finally, because we model the change in network tie formation and boldness change over 19 observations, there are 18 period-specific rate constants for each of these (inter-)dependent variables. Similar to network density, these constants are not of focal interest [46].

To ensure that our data fit the SAOM we ran post-hoc statistical goodness-of-fit (GOF) tests. We ensured that the simulated networks and behaviour variables in the SAOM are sufficiently similar to empirical observations, across various relevant characteristics, and that model convergence has been obtained (maximum convergence ratio < 0.25, [46]). We run 4 such GOF tests, on the Degree distribution, Geodesic distribution (the number of nodes connected at a certain network distance), Triad census (the number of node triplets with 1, 2, or 3 edges), and Behavior Distribution (the discrete behaviour dependent variable ranged 1-3) (Table S2).

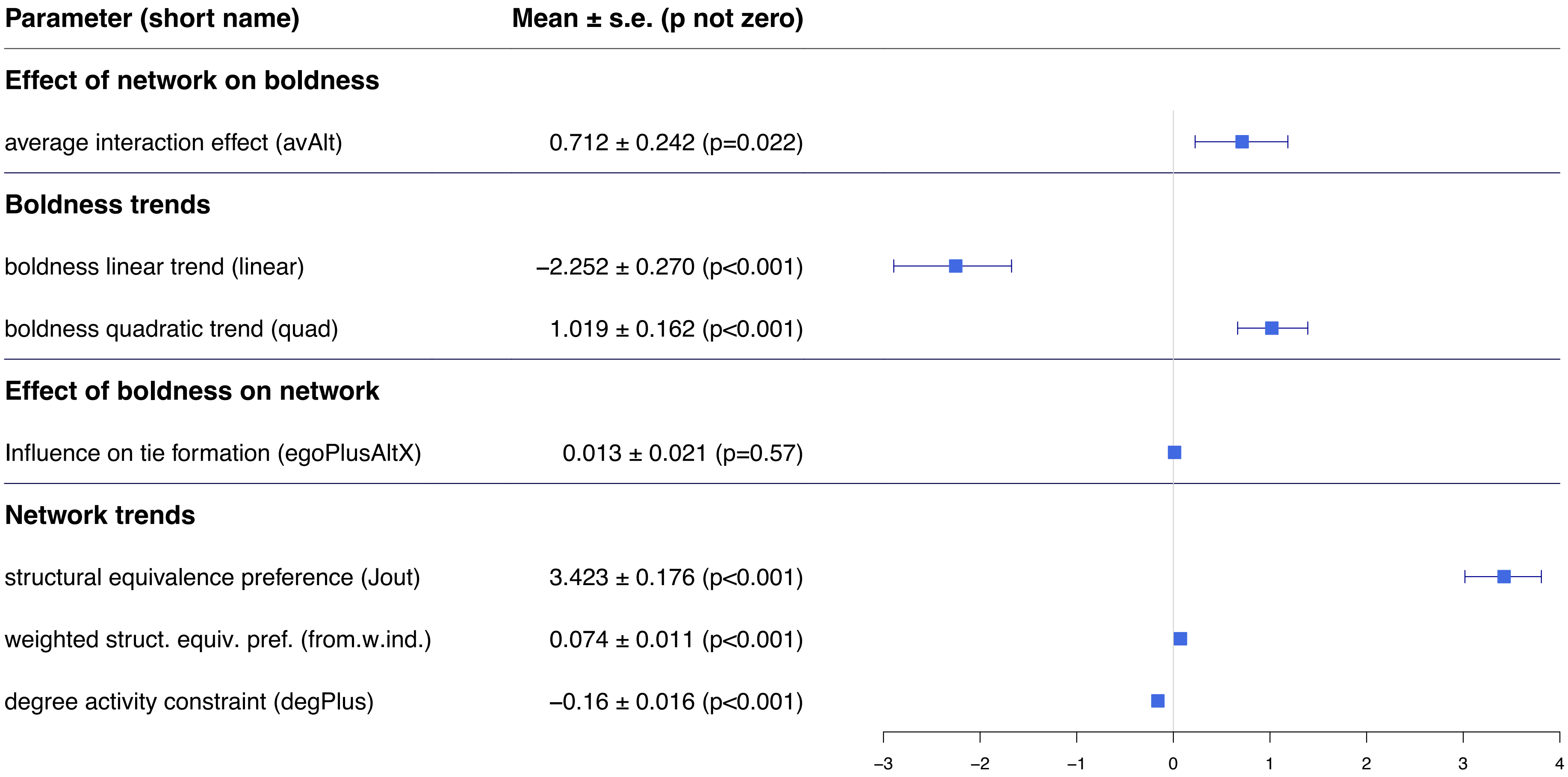
To assess the overall results of the SAOM analysis we conducted meta-analysis of the 8 SAOMs. When a common set of effects was identified that led to good model convergence and adequate post-hoc goodness-of-fit tests across all 8 models, we performed a meta-analysis of the model effects, to see if they are significantly different from zero. We did this using the RSiena function *siena08*, which weights model effects according to their standard error, into a final mean effect value with associated estimated 95% confidence interval. The *siena08* function provides means, standard errors, and p values under a normality assumption, and also under an alternative approach of modified iterated re-weighted least squares (IWLS) developed by Snijders & Baerveldt for meta-analysis [50]. We present the normality assumption results in the main text but both sets of results are presented in Table S2, with the same overall results.

Results

Interactions and time affected boldness, but boldness did not affect interactions. We found several significant effects in our meta-analysis of the 8 SAOM models. When spiders interacted with others that had a different boldness than themselves, the spider with the lower boldness tended to increase its boldness in the next time step (significantly positive *average alter* effect (p=0.024, Figure 2)). Boldness tended to decrease over time (significantly negative *bold linear* effect (p<0.001, Figure 2)). However, once an individual's boldness increased, there was a positive feedback pushing toward higher boldness (positive *bold quadratic* effect (p<0.001, Figure 2)). Boldness distributions changed over the course of 7 weeks (Figure 3) such that by the end of the 7 weeks, boldness distributions resembled those observed in the field and generated by models in which boldness tends to decrease over time and increase when spiders interact [39].

Individuals' social interactions were not impacted by boldness but they were influenced by the surrounding social environment. We did not detect a significant effect of boldness on the tendency to form (or avoid) ties (p=0.445, Figure 2). At the same time, spiders tended to interact with similar individuals as their nestmates: both *Jout* and *from.w.ind* were positive effects (p<0.001 in both cases, Figure 2). Positive *from.w.ind* further indicates that individuals with high-degree make a larger contribution to achieving structural equivalence. Finally, we found a restriction on the dispersion of spider degrees (negative *degPlus*, $p<0.001$, Figure 2), likely because of physical limits on how many individuals a spider can touch at once (i.e., a cap on higher degrees).

These observed trends were seen in all three behavioural composition treatments (Figure 2, Table S2). For example, all the SAOMs, including the all-shy and all-bold treatments, had a negative linear boldness trend. Furthermore, boldness compositions of the three treatments converged within the first week (Figure S1). Thus, our findings reveal that in a social context, boldness is more plastic than in isolation, and artificially manipulating group boldness compositions is quickly rectified by endogenous group processes.



Parameter (short name)	Mean ± s.e. (p not zero)
Effect of network on boldness	
average interaction effect (avAlt)	0.712 ± 0.242 (p=0.022)
Boldness trends	
boldness linear trend (linear)	–2.252 ± 0.270 (p<0.001)
boldness quadratic trend (quad)	1.019 ± 0.162 (p<0.001)
Effect of boldness on network	
Influence on tie formation (egoPlusAltX)	0.013 ± 0.021 (p=0.57)
Network trends	
structural equivalence preference (Jout)	3.423 ± 0.176 (p<0.001)
weighted struct. equiv. pref. (from.w.ind.)	0.074 ± 0.011 (p<0.001)
degree activity constraint (degPlus)	–0.16 ± 0.016 (p<0.001)

Figure 2: A forest plot showing meta-analysis results of the SAOMs' parameters. Social interactions between spiders exhibiting different boldness tend to increase the boldness of the shyer spider (*avAlt* effect). There is a general decrease in boldness over time (*linear)* but boldness increases are self-reinforcing (*quad*). There is no effect of boldness on the likelihood of forming (or avoiding) social ties (*egoPlusAltX*). Positive *Jout* and *from.w.ind* indicate a tendency for spiders to form ties with nestmates that interact with their neighbours: the positive *from.w.ind* effect suggests that individuals with high-degree centrality drive this trend. Negative *degPlus* implies a cap on the dispersion of spider degrees, likely because of physical restrictions on the maximum number of individuals a spider can touch.

The average degree distribution across all networks was unimodal (Figure S2), and the skewness of the degree distributions of all networks was centred around zero (Figure S3). This indicates that all spiders in a network tend to physically interact with a similar number of nestmates when resting.

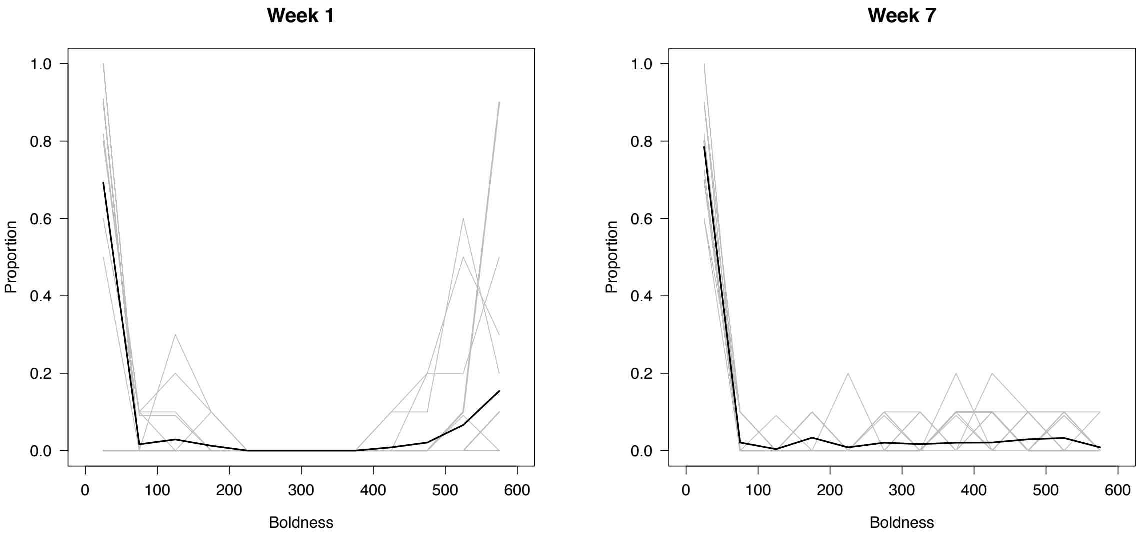


Figure 3: The empirical boldness distribution for each of the 24 groups (grey lines) and the average boldness distribution for all groups (black line), at (left) week 1 and (right) week 7.

Discussion

We found that social interactions promote changes in individual boldness in social spider groups. While boldness is a highly repeatable trait for spiders kept in isolation [35], in a social context we find that individuals' boldness is plastic. Specifically, social interactions tend to increase boldness, such that a spider whose physical neighbours have overall higher average boldness at one point in time, tends toward higher boldness values itself. Here, where boldness has been analysed on a 1-3 scale, this finding is an aggregate trend that encompasses any interactions in which one individual is bolder and the other shyer (i.e., 3-1, 3-2, and 2-1). The boldness-promoting effect of social interactions is balanced against an overall decrease in boldness over time. Furthermore, spiders tend to interact with the same individuals as their neighbours, especially those that are well connected. This finding likely results from the spiders' preference to huddle together in the nest retreat. This finding also suggests that an individual with high boldness (or even the highest boldness, i.e., the keystone individual) could promote increases in boldness across several individuals simultaneously, if more than one shyer individual is socially connected to that bold individual. Different spiders tend to interact with the same individuals, thus boldness increases to a few central spiders may have widespread effects. We did not find evidence that boldness influences the likelihood of forming social interactions. A question for future research is how social interactions influence boldness. Perhaps spiders cue on chemicals present on the body surface, like ants [51], or influence each other through small movements. For example, if bold individuals are more agitated than others, their proximity could affect their neighbours, directly or through web vibrations.

Our finding that bold spiders are no more or less likely to interact with other individuals than their shyer nestmates could be seen as contrary to expectations. For example, social assortment according to behavioural type has been recognised in fish shoals [52]. On the other hand, bolder spiders might be thought to prefer social isolation: bolder three-spined stickleback fish have been observed to keep a greater distance from a partner, while showing more leadership behaviour [53]. However, it is possible that boldness does not correlate with sociability. Indeed, in a review of behavioural syndromes by Réale et al [54] the shyness–boldness axis is distinguished from sociability. The natural distribution of boldness in *Stegodyphus* groups is a few bolder individuals among a majority of shyer individuals [39], and hence with no behavioural assortment bold individuals are more likely to interact with shy individuals by simple probability. Bolder individuals are more likely to interact with the environment outside the nest during foraging, given increased participation in prey capture in both the laboratory [32] and the field [55, 56], and thus may be a source of disease vulnerability for other group members. Yet our findings here point toward bold-shy interactions being an indispensable element in determining the behavioural composition of the group, whereby boldness is ‘passed on’ by an as-yet unidentified mechanism from bolder to shyer individuals. Bold-shy interactions thus maintain a suitable group-level boldness distribution that promotes effective prey capture [32, 57].

A general trend toward decreases in boldness over time, occurring separately from the influence of the spiders’ interaction network, is consistent with past findings. Recently disturbed colonies of *S. dumicola* become shyer over time before recovering in boldness [58]. However, the significantly positive quadratic shape effect on boldness that we identified indicates that an increase in spider boldness generally tends to be self-reinforcing, or ‘addictive’. In this way, a spider with a low boldness rating, that transitions to a medium rating, will be more likely to increase its boldness still further rather than reduce its boldness. Thus, individuals with small initial increases in their boldness are more likely to become a group’s boldest group member in subsequent weeks. These boldest individuals are known to be major determinants of the behaviour and success of the colony as a whole [59]. Interestingly, despite different initial boldness compositions, by week 2 of the experiment the average boldness of all groups was not different (see supplementary material and Figure S1). This change, and the SAOM findings, indicate that social interactions are apparently instrumental in changing artificially manipulated *S. dumicola* boldness distributions to resemble those found in nature [39], which facilitate rapid prey attack [32].

The results we present here corroborate the assumptions made in simulation work on how the dynamics of boldness and social interactions result in skewed behavioural distributions and can point to the model parameters that best fit the biological system [39]. The observed resting networks' degree distribution was unimodal (Figure S2), and the skewness of the degree distributions of all networks was centred around zero (Figure S3), similar to the uniform interaction rule in previous simulation work. These characteristics indicate that all individuals are equally likely to interact with one another, regardless of their boldness. Furthermore, our finding that boldness tends to decrease over time and that boldness is acquired from bolder neighbours, points toward a scenario in the theoretical model in which there is low persistence of boldness and high acquisition of boldness from others. Indeed, the simulated boldness distributions for this parameter setting (low persistence, high acquisition – LPHA) and a uniform interaction rule [39] qualitatively match well with the empirical observations presented here (Figure 3).

One remaining open question, regarding influential keystone individuals in animal collectives, is their replaceability: whether the specific individual or the role performed by that individual is the most important [16]. Our results, indicating social plasticity of boldness in accordance with [38], point to the existence of a keystone role rather than a keystone individual [7]. With relatively low behavioural persistence, and high acquisition of behaviour from others via social interactions, the boldest spiders in the group – the keystone(s) – are highly influential but likely to change in identity over time. Indeed, in the case of *S. dumicola*, while keystone individuals are important, they do not seem to be irreplaceable. For example, iteratively removing and replacing shy individuals has a greater impact on the colony's behaviour than replacing bold individuals [38].

One question arising from the boldness dynamics that we observed is what occurs when there are no bolder individuals to impart their positive catalytic influence on the boldness of other shyer individuals. In this case, one can see the importance of the significant quadratic shape effect (the ‘addictive’ boldness increase effect), to magnify even small boldness increases over time such that they become self-sustaining and do not require constant social contact to support them. In a real-world system, small boldness differences will always exist for such dynamics to work upon [39]. Such an inherent robustness of the group-level skewed boldness phenotype, dependent on social dynamics alone, seems to downplay the importance of internal, genetic or developmental differences for the ontogenesis of keystones. Instead, it indicates that external factors, such as social and ecological conditions, may be sufficient. In practice, boldness may be contingent on physiological factors such as satiation, i.e. the time since last feeding, though evidence for this idea are mixed [35, 60]. For periods longer than a few weeks, i.e. beyond the observation range of the data examined here, life history stages relating to reproduction are also likely to be important given the relatively short lives of female *Stegodyphus* of 1-2 years [41].

Conclusions

Many animal groups are increasingly recognised to rely on heterogeneity in the behaviour and social interactions of the group members for effective group function. However, the relative importance of behaviour for shaping interactions, and interactions for shaping behaviour, is poorly understood. We show that social interactions promote the increase of boldness in social spiders, such that an optimal collective distribution in boldness is attained. Boldness, however, does not make individuals more or less likely to physically interact with others. Our findings are consistent with the uniform interactions, high acquisition, low persistence model of keystone influence on groups of Pinter-Wollman et al [39], and thus suggest that it is the keystone role, rather than the identity of the individual acting it, that is important to such social groups [38]. Our findings have implications for the understanding of personality in social groups, indicating a priority of an animal's social environment for the development of personality. Future research should address in more detail the specific mechanisms of how social interactions promote boldness, and the dynamics of social networks and boldness in different ecological conditions in the field. This should further elucidate the relative importance of internal vs. external factors for the emergence of adaptive collective phenotypes.

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Author contributions

NPW and JNP designed the study, ERH analysed the data and wrote the first draft of the manuscript, and BM, CF, BW, and NPW collected the data. All co-authors gave approval to the final version of the paper.

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Data accessibility

The network and boldness data analysed in this paper is available on Dryad at…

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