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https://doi.org/10.1038/s41559-019-0852-z
nature ecology & evolution

Experimental evidence of frequency-dependent selection on group behaviour

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Evolutionary ecologists often seek to identify the mechanisms maintaining intraspecific variation. In social animals, whole groups can exhibit between-group differences in their collective traits. We examined whether negative frequency-dependent selection (that is, a rare-type advantage) could help to maintain between-group variation. We engineered neighbourhoods of social spider colonies bearing bold or shy foraging phenotypes and monitored their fecundity in situ. We found that bold colonies enjoyed a rare-type advantage that is lost as the frequency of bold colonies in a neighbourhood increases. The success of shy colonies was not frequency dependent. These dynamics seem to be driven by a foraging advantage of bold colonies that is lost in bold neighbourhoods because prey become scarce, and shy colonies perform better than bold colonies under low-resource conditions. Thus, to understand selection on collective traits, it is insufficient to examine groups in isolation. The phenotypic environment in which groups reside and compete must also be considered.

Identifying the forces maintaining intraspecific variation has been a perennial goal in evolutionary biology because selection is predicted to cull low-performing phenotypes and reduce trait diversity. Yet, intraspecific variation varies across taxa[1–3]. In social animals, intraspecific trait variation occurs at two levels: individual animals may differ from each other in their individual traits, and whole groups can differ from each other in terms of their collective traits[4,5]. Recent studies have demonstrated considerable intraspecific variation in collective traits in natural populations[4], and a handful of studies have documented selection acting on collective traits[6–8]. For instance, colonies of harvester ants that exhibit greater restraint during foraging produce more offspring colonies in arid climates[8], selection on group size in cliff swallows alternates across wet/cold and hot/dry years[6], and more aggressive honeybee colonies are better able to survive harsh winters[9]. Unlike individual-level traits, however, there has been little exploration of how between-group variation in collective traits is maintained in spite of selection[6].

We propose that negative frequency-dependent selection could help maintain intraspecific variation in collective traits. Negative frequency-dependent selection ensures that rare phenotypes experience an advantage that prevents elimination of that phenotype from a population[10,11]. For instance, under some pay-off conditions of the hawk–dove game, aggressive hawks outperform doves when hawks are rare in a population, because hawks consistently secure contested resources when interacting with non-combative doves. However, hawks are outperformed by deferential doves in hawk-rich populations, because the costs incurred by hawk–hawk interactions (for example, injury) outweigh the rare benefits secured when interacting with an uncommon dove phenotype[12]. Individual-level traits are often subject to negative frequency-dependent selection[11,13,14]. We therefore examined whether similar mechanisms could act at the level of collective traits.

We tested for frequency-dependent selection acting on colony foraging behaviour using the African social spider *Stegodyphus dumicola* (Araneae, Eresidae). Colonies of *S. dumicola* vary in their boldness during foraging[15]. Bold colonies of *S. dumicola* exhibit greater prey capture efficiency and more pronounced collective defence against threats than shy colonies[15,16]. In *S. dumicola*, colony phenotypes are influenced by the relative frequency of bold and shy individual spiders in the group[15,16]. Previous studies have detected positive selection acting on colony foraging behaviour at dry sites, but not wet sites[17]. However, all sites contain colonies with varying ratios of bold/shy individuals and contrasting foraging strategies[15]. Thus, how such variation in collective traits is maintained despite ongoing selection is of interest.

Selection on colony-level traits is likely to be especially effective in *S. dumicola* because, as in other social spiders, there is little and often no detectable genetic variation present within colonies[18]. The individual bold/shy phenotypes used to engineer colony phenotypes here are exceedingly plastic within individuals[19,20] and are not, by our present understanding, heritable (heritability (H^2) < 0.16, $N_{broods} = 14$; see Supplementary Fig. 1). Yet, the collective phenotypes that they create at the colony level are temporally consistent for extended periods, even when some bold/shy group members are subsequently removed[21]. Importantly, colony behavioural differences are transmitted from parental to daughter colonies in *S. dumicola* during fission (that is, budding) events and are maintained across generations within colonies (Supplementary Figs. 2 and 3). This is consistent with the finding that there is limited gene flow in the population, which leads to large genetic differences between colonies of *S. dumicola*[18], indicating that genetic differences between colonies could underlie differences in their foraging behaviour. Thus, colony behaviour has the potential to respond to between-group selection in this system. Finally, there is greater diversity in the foraging phenotypes of naturally occurring colonies within clustered neighbourhoods versus those in isolation (Levene test: $F_{1,115} = 22.49$, $P < 0.0001$; see Supplementary Fig. 4). This suggests that a special diversity maintenance mechanism might be acting under clustered conditions.

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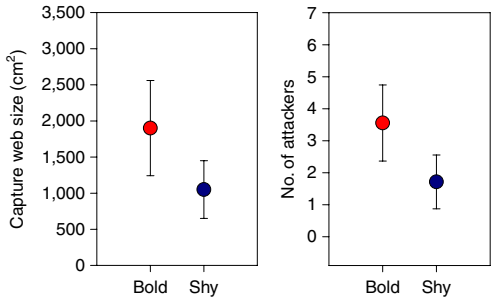

Fig. 1 | Capture web size and attacker deployment across colonies. The capture web area (left) and number of attackers deployed during an attack on prey (right) are shown for colonies comprising all bold versus all shy individuals. Data represent mean ± s.d.; $P < 0.0001$ (LMM).

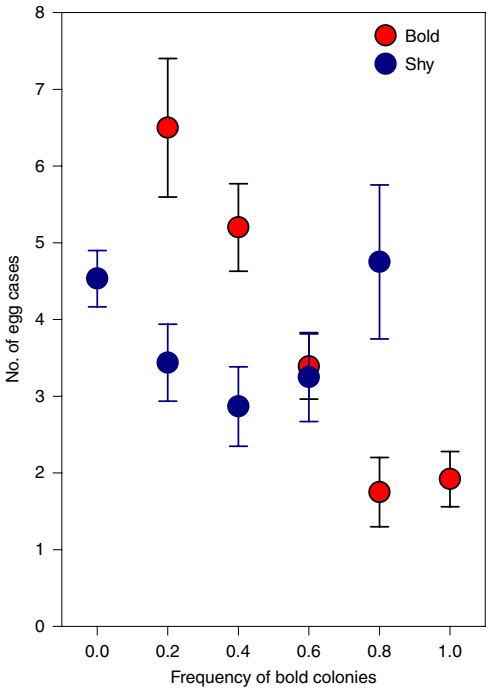

Fig. 2 | Egg case production and the frequency of bold colonies. The number of egg cases (mean ± s.e.m.) produced by bold and shy colonies are shown as a function of the frequency of nearby bold colonies. Bold colonies outperform shy colonies when they are rare, but are outperformed by shy colonies when bold colonies are abundant (LMM: $F_{1,23.24} = 42.05$, $R^2 = 0.47$, $\beta = -5.89 \pm 0.91$, $P < 0.0001$). Shy colony performance is not frequency dependent (LMM: $F_{1,20.54} = 2.60$, $R^2 = 0.05$, $\beta = -1.57 \pm 0.97$, $P = 0.12$) ($N_{\text{neighbourhoods}} = 17$ at Drakensberg; 13 at Avis Dam). s.e.m. values are computed directly from the observed phenotypes without adjusting for other explanatory variables, such as colony size and site. Sample sizes: 100% bold ($N_{\text{neighbourhoods}} = 5$), 80% bold ($N_{\text{neighbourhoods}} = 4$), 60% bold ($N_{\text{neighbourhoods}} = 6$), 40% bold ($N_{\text{neighbourhoods}} = 5$), 20% bold ($N_{\text{neighbourhoods}} = 4$), 0% bold ($N_{\text{neighbourhoods}} = 6$).

Although colonies of *S. dumicola* do not compete with one another directly (as territorial societies do), *S. dumicola* individuals frequently reside in clusters of colonies on the same host plant[22], possibly resulting in resource competition. *S. dumicola* colonies use two-dimensional traps (capture webs) to ensnare prey. Thus, like other trap-building predators, clustered *S. dumicola* colonies can eclipse each other's capture web surfaces and potentially interfere with prey interception. We therefore predicted that colonies that are able to capture more prey or that can persist with fewer resources will have a selective advantage over rival colonies—these predictions are termed the optimal foraging hypothesis and Tilman's R* rule, respectively[23,24]. Both types of strategy are important for determining competition at the individual level.

Results and discussion

We created phenotypic neighbourhoods (clusters) of *S. dumicola* colonies on *Senegalia mellifera* trees at two sites in southern Africa (Avis Dam, Namibia, 22° 33' 27.78" S, 17° 8' 0.52" E (arid climate); Drakensberg, South Africa, 29° 0' 20.11" S, 29° 32' 28.13" E (wet climate)) in February–March 2018. Spiders were collected from the site where they were subsequently deployed. Field-collected colonies were subsetted to produce experimental colonies of two collective phenotypes: bold colonies were made up of 100% bold individuals, and shy colonies were composed of 100% shy individuals (10 spiders per colony). Although these ratios are more polarized than those observed in natural colonies of *S. dumicola*[15], the compositions engineered sound differences in colony traits to test for frequency-dependent selection (Supplementary Figs. 4 and 5). Individual boldness was determined by puffing spiders with two rapid jets of air and measuring the latency for individuals resuming activity following the stimulus[15]. Individual differences in boldness are repeatable in *S. dumicola* and associated with responsiveness towards predators, web repair and prey[15,16], but not with individual differences in body condition[17]. Our experimental design notably involves the binning of individuals and colonies into discrete types (bold versus shy). This practice was adopted for experimental convenience. However, it is important to note that negative frequency-dependent selection, and fluctuating selection in general, has the potential to maintain variation in continuous traits too[3,25].

Each colony neighbourhood contained five experimental colonies (total $N_{\text{neighbourhoods}} = 30$), and each five-colony neighbourhood was deployed on a single host tree (*S. mellifera*). Colonies were separated by 1–2 m on each tree, and trees of different neighbourhoods were selected to be at least 20 m apart ($N_{\text{neighbourhoods}} = 17$ at Drakensberg; 13 at Avis Dam). The five colonies in each neighbourhood were all-bold colonies or all-shy colonies, or a ratio of these two types of colony (100% bold ($N_{\text{neighbourhoods}} = 5$), 80% bold ($N_{\text{neighbourhoods}} = 4$), 60% bold ($N_{\text{neighbourhoods}} = 6$), 40% bold ($N_{\text{neighbourhoods}} = 5$), 20% bold ($N_{\text{neighbourhoods}} = 4$), 0% bold ($N_{\text{neighbourhoods}} = 6$)). A neighbourhood size of five colonies bears close resemblance to the average colony neighbourhood size observed in natural populations of this species (mean = 3.63 colonies, s.d. = 2.49; see Supplementary Fig. 6). We tested the collective foraging behaviour of colonies three times following deployment using a simulated prey capture assay, and measured their total capture web area (cm²). We returned to both sites four months later (June–July 2018), after *S. dumicola* individuals produced egg cases, and counted the number of egg cases produced by each colony and the number of prey carcasses incorporated into the nests. These metrics provided us with an estimate of the total fecundity of each colony, as well as its foraging success (see Methods).

Bold and shy colonies differed in their collective foraging behaviour. Bold colonies attacked more prey with ~200% more individuals (linear mixed model (LMM): variance ratio (F)$_{1,143.7} = 63.55$, the proportion of variation explained by the model (R^2) = 0.65, regression coefficient of the population (β) = 0.87 ± 0.11 (mean ± s.e.m.), $P < 0.0001$) and produced ~180% larger capture webs than shy colonies (LMM: $F_{1,144.9} = 55.57$, $R^2 = 0.28$, $\beta = 0.87 \pm 0.11$, $P < 0.0001$) (Fig. 1). The web sizes and foraging behaviour of our bold and shy colonies closely resemble those of natural colonies (Supplementary Fig. 5).

To test whether the effect of neighbourhood composition differed according to colony behavioural phenotype (colony phenotype × frequency of bold neighbours), the 100% bold and 100% shy colony treatments were trimmed from the analysis. Even within this

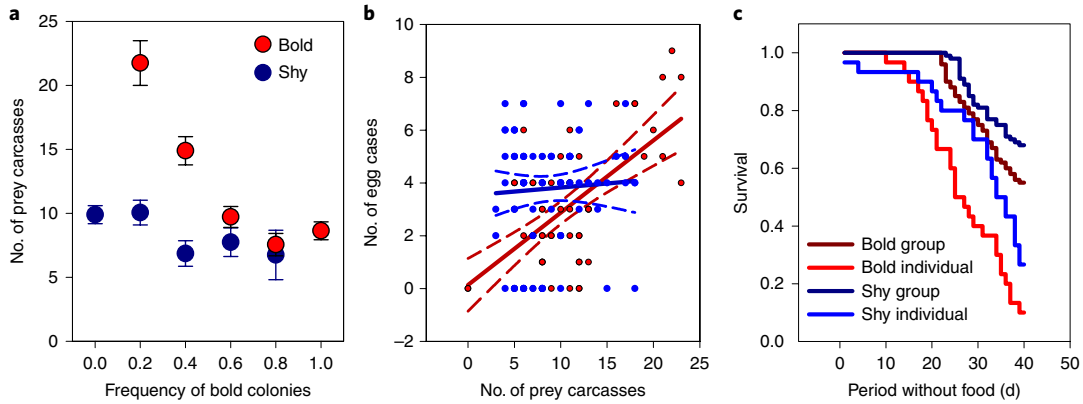

Fig. 3 | The relationship between the number of prey carcasses and egg cases produced by colonies, and survival curves. **a**, The number of prey carcasses recovered (mean ± s.e.m.) in the retreat web of bold and shy *S. dumicola* colonies as a function of the proportion of neighbouring bold colonies. Bold colonies capture more prey when rare in the phenotypic neighbourhood (LMM: $F_{1,23.17}=32.94$, $R^2=0.57$, $\beta=-13.75\pm2.39$, $P<0.0001$) ($N_{neighbourhoods}=17$ at Drakensberg; 13 at Avis Dam). Sample sizes: 100% bold ($N_{neighbourhoods}=5$), 80% bold ($N_{neighbourhoods}=4$), 60% bold ($N_{neighbourhoods}=6$), 40% bold ($N_{neighbourhoods}=5$), 20% bold ($N_{neighbourhoods}=4$), 0% bold ($N_{neighbourhoods}=6$). **b**, The relationship between the number of prey carcasses present in retreat webs and fecundity for bold and shy colonies (colours as in **a**), measured as the number of egg cases. Bold colonies produce more egg cases than shy colonies when they capture a large number of prey, but fewer egg cases when they capture few prey. Shy colonies produce a similar number of egg cases regardless of the number of prey captured ($N_{neighbourhoods}=17$ at Drakensberg; 13 at Avis Dam). The solid lines are the best-fit linear regressions, and dashed lines demarcate the 95% CI surrounding that estimate. **c**, Survival curves depicting the number of days that individuals survived without food as a function of individuals' behavioural phenotype (bold/shy) and whether they were isolated or in a group setting. Bold individuals (Wilcoxon: $\lambda^2=7.99$, d.f. = 1, $P=0.005$) and colonies (Wilcoxon: $\lambda^2=4.54$, d.f. = 1, $P=0.033$) die sooner when deprived of food as compared to shy individuals or colonies ($N_{individuals}=10$ per phenotype, $N_{groups}=10$ per phenotypic composition). s.e.m. values are computed directly from the observed phenotypes without adjusting for other explanatory variables, such as colony size and site.

restricted composition space, however, we found that the effects of neighbourhood composition differed strongly on the basis of the focal colony's foraging phenotype (colony phenotype × frequency of bold neighbours; LMM: $F_{1,89.07}=19.33$, $R^2=0.33$, $\beta=-4.74\pm1.08$, $P<0.0001$; see Fig. 2). Bold colonies performed best in neighbourhoods composed of predominantly shy colonies (frequency of bold neighbours; LMM: $F_{1,23.24}=42.05$, $R^2=0.47$, $\beta=-5.89\pm0.91$, $P<0.0001$; see Fig. 2). By contrast, shy colonies produced a similar number of egg cases regardless of the neighbourhoods in which they resided (frequency of bold neighbours; LMM: $F_{1,20.54}=2.60$, $R^2=0.05$, $\beta=-1.57\pm0.97$, $P=0.12$; see Fig. 2). When rare, bold colonies produced 1.5–2 times more egg cases than shy colonies in the same neighbourhood (Fig. 2). We predict that this occurs because bold colonies produce larger capture webs and deploy a more pronounced foraging response, thus allowing them to capture more prey than their shy counterparts. However, in neighbourhoods dominated by bold colonies, shy colonies outperformed their bold rivals, producing twice as many egg cases (Fig. 2). Thus, at either extreme, colonies possessing the rarer collective phenotype outperformed the dominant strategy, which should help maintain the diversity of collective phenotypes in the population.

Shy colonies seem to benefit from an advantage under low-resource conditions, such as those created by bold neighbourhoods. The number of prey captured per bold colony decreased sharply as bold colonies became common in a neighbourhood (frequency of bold neighbours; LMM: $F_{1,23.17}=32.94$, $R^2=0.57$, $\beta=-13.75\pm2.39$, $P<0.0001$; see Fig. 3a). Shy colonies also captured fewer prey in bolder neighbourhoods, although the slope of this relationship was less pronounced (frequency of bold neighbours; LMM: $F_{1,29.11}=7.10$, $R^2=0.17$, $\beta=-4.56\pm1.17$, $P=0.012$; see Fig. 3a). The reproductive output of bold colonies was positively correlated with prey capture success, but no such relationship was recovered for shy colonies (number of prey carcasses × colony behavioural phenotype; LMM: $F_{1,137.5}=9.35$, $R^2=0.28$, $\beta=0.12\pm0.04$, $P=0.003$; see Fig. 3b). This could be because shy colonies produce smaller capture webs (Fig. 1) and therefore have reduced energetic demands in the form of web investment. Indeed, shy individuals and shy colonies are able to withstand starvation conditions better than their bold counterparts (Fig. 3c). When bold and shy colonies (Wilcoxon test: $\lambda^2=4.54$, degrees of freedom (d.f.) = 1, $P=0.033$) and bold and shy individuals (Wilcoxon: $\lambda^2=7.99$, d.f. = 1, $P=0.005$)[26] were experimentally subjected to prolonged starvation in a follow-up lab experiment, colonies composed of shy spiders and shy singleton individuals both survived at higher rates than their bold counterparts (Fig. 3c). The reason(s) why neighbourhoods that are dominated by the bold phenotype capture fewer prey overall remains unclear. Many large webs, such as those produced by bold colonies (Fig. 1), may be more easily detected and avoided by prey, or it may be that large capture webs risk shadowing each other's capture surface areas, thereby reducing per capita prey acquisition rates (similar to that in ref. [27]).

It is curious that the reproductive output of shy colonies was not linked with their prey capture success (Fig. 3b). The finding that shy colonies are better able to endure low-resource conditions than their bold counterparts (Fig. 3c) suggests that the success of shy colonies should indeed be less dependent on prey availability, but not independent of it. One plausible explanation is that we observed too little variability in prey capture success to detect its effects on colony performance for shy colonies. Shy colonies could also be less efficient at prey extraction or metabolization than bold colonies. Alternatively, shy colonies may feed less on the prey that they do capture, which is common in spiders[28–30]. Notably, we do observe some variation in reproductive output in shy colonies (Fig. 3b). This variation hints that other environmental factors might limit the success of shy colonies, and the environmental factors that are important for colony success may therefore differ depending on colony phenotype. Prey capture success is an important factor driving colony success in bold colonies of *S. dumicola*, whereas the factors driving the differential success of shy colonies remain unknown.

Our findings demonstrate that shy colonies deploy a low-requirement strategy (that is, a Tilman's R* rule strategy) that may never achieve a reproductive rate as high as the most successful bold colonies (Fig. 2), but will never suffer very low success. In contrast,

bold colonies represent a high-variance strategy with higher reproductive potential when conditions are right, but one that is sensitive to resources in the environment (that is, an optimal foraging strategy) (Fig. 2). Thus, the relative performance of these two strategies is predicted to vary depending on both prey availability and the competitive environment in which the colonies reside.

Negative frequency-dependent selection is one of the most commonly proposed mechanisms for maintaining intraspecific variation in individual-level traits[11,13,14]. While additional work is necessary to confirm that negative frequency-dependent selection is the causal agent maintaining between-group behavioural differences in *S. dumicola*, our results provide robust evidence to support this prediction. Such frequency-dependent effects could in turn help to maintain intraspecific diversity in individual-level traits by ensuring that no single combination of individual traits, which underlie collective phenotypes[31–33], outperforms rival trait combinations in other colonies. Thus, at least in principle, frequency-dependent selection on collective behaviour could help maintain diversity in individual-level traits and in how those traits are organized spatially and socially into groups, thereby maintaining diversity across multiple tiers of biological organization in social systems. Data from mixed-composition colonies of *S. dumicola* are still needed to fully evaluate whether this is the case in this system.

Several recent studies have detected ongoing selection acting on collective behaviour in situ[6,8,34,35]. A smaller number of studies have further shown that, like individual-level phenotypes, the optimal collective strategy depends on the environment in which a colony resides (for example, desert versus savannah habitats)[17,36]. The data herein add another layer of complexity by revealing that the optimal strategy for a group could be further dependent on the strategies deployed by nearby groups—that is, the competitive and social environment of a group. We detected these effects in experimental settings using a sedentary species in which groups do not interact physically. We therefore reason that frequency-dependent selection could be even more powerful in systems where interactions between groups are direct and intense. Thus, our understanding of how collective behaviour evolves seems more nuanced now than ever, and there is great potential for further collaborative work.

Methods

Source colony collection. Source colonies of *S. dumicola* containing 158–823 female spiders were collected in February and March 2018 (Namibia $N_{colonies} = 13$, 22° 33' 27.78" S, 17° 8' 0.52" E; South Africa $N_{colonies} = 17$, 29° 0' 20.11" S, 29° 32' 28.13" E). We collected colonies by placing the nest of the colony within a cloth pillowcase and trimming the supporting branching using pruning snips. Colonies were transported back to hotels adjacent to each site for dissection.

Colonies were dissected by hand and all resident females were counted and isolated in 59 ml plastic deli cups. All spiders were run through a boldness assay three times over the next three days to determine their individual phenotypes. After their boldness was assessed, we haphazardly subsetted individuals of the desired behavioural phenotypes into experimental colonies of ten individuals. Experimental colonies contained either all bold individuals or all shy individuals. We refer to these as bold and shy colonies. Before admitting individuals into an experimental colony, individuals were assigned a colour ID to identify them as belonging to that experimental colony. This enabled us to track movement between experimental colonies over the duration of the study.

This work was conducted under research and export permit numbers ODB3130 FAUNA1691 and ODB3129 FAUNA1692.

Boldness assay. The boldness of individual *S. dumicola* was estimated using each individual's latency to resuming movement following an aversive stimulus. Trials were initiated by removing an individual from its container and placing it in an open field (diameter = 16 cm). After 30 s of acclimation, 2 rapid puffs of air were administered using an infant nose-cleaning bulb positioned approximately 5 cm away from the spider's anterior prosoma. This procedure resulted in the spider pulling its legs tight against its body in a huddled death feign. We then recorded the latency of each individual to resuming movement and moving one body length following the puff stimulus. Spiders that resumed movement quickly (<200 s) were deemed bold, and spiders that resumed movement slowly (>400 s) were deemed shy. Individual differences in boldness are repeatable across days to months in *S. dumicola*[37–39], and are associated with the role that individuals play in society[16,38,40]. Bold individuals are more likely to participate in prey capture events[40], assist in web repair[41] and transmit cuticular microbes than their shy counterparts[42,43].

Experimental colony establishment. Two experimental colony compositions were created: shy and bold. Shy colonies were composed entirely of individuals that averaged a shy score across their three consecutive boldness assays. Bold colonies were composed entirely of individuals that averaged a bold score across their three consecutive boldness assays. All experimental colonies were composed of individuals from the same source colony to preserve natural levels of relatedness and familiarity. Both of these factors are known to influence collective behaviour and colony success in *S. dumicola*[22,38,39,44,45]. Colonies were permitted three days to construct their nest (that is, a silken retreat) before deployment. Assignment of individuals to experimental colonies was performed randomly by drawing individuals from cloth pillow cases containing spiders of the desired behavioural phenotype (bold versus shy individuals). The average boldness of group constituents varied by colony phenotype (colony bold/shy phenotype; LMM: $F_{1,147.2} = 89{,}596.16$, $R^2 = 0.99$, $P < 0.0001$), but did not vary across sites (Kalkrand versus Drakensburg; LMM: $F_{1,28} = 0.01$, $R^2 = 0.99$, $P = 0.93$), and there were no detectable differences in the average of boldness of bold or shy colonies assigned to particular neighbourhood compositions (frequency of bold phenotype × colony phenotype, Kalkrand versus Drakensburg; LMM: $F_{1,145.1} = 1.44$, $P = 0.23$). Thus, variation among colonies in the average boldness of their group constituents is unlikely to be a confounding factor in our results.

Experimental colonies were arranged into phenotypic neighbourhoods in the field. Neighbourhoods of colonies always contained five experimental colonies deployed on the same host tree. Neighbourhoods were composed of six contrasting ratios of bold versus shy colony phenotypes: 100% bold colonies, 80% bold colonies and 20% shy colonies, 60% bold colonies and 40% shy colonies, 40% bold colonies and 60% shy colonies, 20% bold colonies and 80% shy colonies, and 100% shy colonies. Experimental colonies were deployed 1–2 m apart, each on a different branch of the host tree. The arrangement of the colonies on the host tree was determined haphazardly by pulling colonies blindly from a white pillowcase. Before deployment, spiders were provided a series of twigs to facilitate web construction. Each nest was then adhered to a host tree using zip ties and wooden clothespins. The following day, we returned to each colony to ensure that it had successfully established and constructed a two-dimensional capture web. We then counted the number of spiders present within each nest and assayed the foraging behaviour of each colony.

Colony foraging behaviour was evaluated by placing a 1.5 cm × 1.5 cm piece of computer paper into the capture web and vibrating it using a vibrator. A thin metal wire extending from the head of the vibrator was placed in contact with the computer paper, causing it to flutter back and forth to mimic the behaviour of a struggling insect ensnared in the web[46,47]. We assayed each colony's behaviour three times over the next 48 h: twice within the first 24 h, and a third time in the second 24 h period. We recorded the number of colony members that emerged in response to the prey item until the first spider seized the paper with its chelicerae.

Colony performance metrics. We returned to monitor the success of the colonies four months later. We counted the number of egg cases produced by each colony and noted whether or not the colony had collapsed. Colonies were deemed to have collapsed if they contained no living members of the society and no egg cases. *S. dumicola* naturally produce egg cases by this time of year and living nests should contain early instar juveniles. Nearly all of the colonies containing egg cases contained juveniles at a normal developmental stage. For our analyses, we focused on the number of egg cases produced by a colony as our composite metric of colony performance because it summarizes both colony fecundity and survival.

We also measured the diameter of two egg cases from within each colony that contained them. This was to evaluate whether egg size varied as a consequence of colony behaviour (bold/shy) and the phenotypic neighbourhood in which colonies resided. In 2013, we measured the diameter of 29 egg cases collected from 29 different *S. dumicola* source colonies from Namibia (Avis Dam). Egg case diameter (mm) was positively correlated with the number of eggs therein (LMM: $F_{1,27} = 50.04$, $R^2 = 0.65$, $\beta = 3.63 \pm 0.51$, $P < 0.0001$) and, to a lesser degree, the size of individual eggs (LMM: $F_{1,27} = 4.45$, $R^2 = 0.14$, $\beta = 3.96 \times 10^{-6} \pm 1.87 \times 10^{-6}$, $P = 0.044$). No differences in egg case diameter were noted between shy and bold colonies in our study (colony behavioural type; LMM: $F_{1,96.29} = 0.012$, $P = 0.91$), or in colonies of contrasting phenotypic neighbourhoods (all $P > 0.31$). Although egg case cannibalism is common in other social spiders (for example, in *Anelosimus studiosus*[36] and *Anelosimus eximius*[48]), we failed to observe any evidence of egg case cannibalism or egg predation by heterospecifics. This may be the case because, in *S. dumicola*, egg cases are collectively deposited in a centralized interior chamber[48–50].

We further collected each colony's web (nest and capture web) and counted the number of prey carcasses that had been ensnared. *S. dumicola* ensnare flying prey on their two-dimensional capture web surfaces but then transport the prey back to a three-dimensional nest for consumption. Carcasses are incorporated into the nest and webbed over in time. This behaviour allows us to excavate nests of colonies to unearth their prey capture history over the duration of their time in the field. Unlike Keiser and Pruitt[15], where spiders were permitted ~12 h to produce capture webs, the colonies used in the present study had several months to construct their webs.

Starvation resistance. We deployed a starvation study to evaluate how bold/shy individuals and colonies perform under low-resource conditions. We examined the starvation performance of 60 isolated individuals: 30 of each bold versus shy phenotype. Phenotypes were determined by an individual's average boldness score across three consecutive daily assays. We further evaluated the starvation resistance of entire colonies composed of shy or bold individuals. Groups were composed of ten individuals of similar phenotype. Experimental groups (10 shy, 10 bold) were composed of spiders subsetted from the same source colony to ensure natural levels of relatedness and familiarity. Before the starvation experiment, all spiders were fed an ad libitum meal of domestic crickets. Single spiders and groups were held in 590 ml containers with a network of *S. mellifera* twigs to facilitate web construction. Each container had a screen top to permit air to flow freely in and out of the container. Spiders were subsequently held under ambient conditions in a laboratory for 40 days. We monitored the survival of spiders in both social settings three times daily by gently blowing on the spiders and documenting the number of unresponsive, dead individuals. Blowing on living *S. dumicola* causes spiders to adjust their positions in the web. To prevent spiders from gaining foraging opportunities through cannibalism, spider carcasses were removed from groups when they were discovered. No evidence of postmortem cannibalism was observed during the study.

Statistical methods. We deployed a series of LMMs to evaluate the impacts of variation in colony behavioural phenotype (bold/shy) and phenotypic neighbourhood (proportion of neighbours with the bold phenotype) on colony performance.

To determine how colony phenotype influences collective foraging behaviour, we constructed two models: one with the average number of attackers deployed in response to a vibratory stimulus across three trials as the response variable, and a second model with the estimated capture web area as the response variable. Colony phenotype, colony size (number of females remaining after 48 h) and the proportion of neighbours exhibiting the bold phenotype were included as fixed effects, and neighbourhood ID was included as a random effect.

To determine whether the performance of colonies was frequency dependent, we constructed an LMM with the number of egg cases produced as the response variable, and colony size and the proportion of neighbours bearing the bold collective phenotype as predictor variables. An independent analysis was run for shy versus bold colonies because each phenotype experienced a different range of neighbourhood compositions. Thus, there were no shy colonies in neighbourhoods of 100% bold colonies and vice versa. Neighbourhood ID was included as a random effect.

To evaluate the degree to which colony success (number of egg cases produced) depended on colony foraging history, we constructed an LMM with the number of egg cases produced as a response variable and colony phenotype (bold/shy), number of prey carcasses recovered in the web, and the interaction term between colony phenotype and number of of prey carcasses recovered as predictor variables. Neighbourhood ID was included as a random effect.

To determine how the phenotypic composition of colony neighbourhoods influences prey intake, we constructed an LMM with the number of prey carcasses recovered as our response variable and the frequency of neighbours bearing the bold phenotype as a fixed predictor variable. An independent analysis was run for shy versus bold colonies because each phenotype experienced a different range of compositions: there were no shy colonies in neighbourhoods of 100% bold colonies and vice versa. Neighbourhood ID was included as a random effect.

To determine the effect of individual phenotype (bold/shy) and colony-level phenotype (bold/shy) on survival rates under prey-restricted conditions, we performed a Kaplan–Meier survival analysis. We compared the proportion of spiders alive after 40 days without food. We compared group verus singleton individual and shy versus bold phenotypes at both the individual and colony level using paired Wilcoxon and log-rank tests. These statistical tests always produced the same results and all possible pairwise contrasts were highly significant.

All statistical tests were two-sided.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data used in this study are available from Dryad (https://doi.org/10.5061/dryad.m592p4g). Raw data are depicted in Fig. 3b,c and Supplementary Figs. 1–6.

Received: 22 November 2018; Accepted: 25 February 2019;
Published online: 25 March 2019

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Acknowledgements

We thank A. Santoro, E. Eliason, H. Moeller, D. Fisher, A. Little and A. Radford for their help in improving previous versions of this manuscript. Funding was provided by NSF IOS grant numbers 1455895 to J.N.P., 1456010 to N.P.W., NIH GM115509 to N.P.W. and J.N.P., and the Tricounsel Agencies of Canada in association with a Canada 150 Research Chair Professorship to J.N.P.

Author contributions

All authors contributed to study design, data collection, statistical analysis, and composing of the manuscript. All authors were included in all aspects of the pipeline.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41559-019-0852-z.

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Last updated by author(s): Feb 22, 2019

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Software and code

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Data collection	NA
Data analysis	All of these analyses were run in JMP Pro 13.0

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Study description

wo experimental colony compositions were created: shy and bold. Shy colonies were composed entirely of individuals averaging a shy score across their three consecutive boldness assays. Bold colonies were composed entirely of individuals average a bold score across their three consecutive boldness assays. All experimental colonies were composed of individuals from the same source colony to preserve natural levels of relatedness and familiarity. Colonies were provided three days to construct their nest (i.e., a silken retreat) prior to deployment.
Experimental colonies were arranged into phenotypic neighborhoods in the field. Neighborhoods of colonies always contained five experimental colonies deployed on the same host tree. Neighborhoods were composed of six contrasting ratios of bold vs. shy colony phenotypes: 100% bold colonies, 80% bold colonies and 20% shy colonies, 60% bold colonies and 40% shy colonies, 40% bold colonies and 60% shy colonies, 20% bold colonies and 80% shy colonies, and 100% shy colonies. Experimental colonies were deployed 1-2m apart, each on a different branch of the host tree. The arrangement of these colonies on the host tree was determined haphazard by pulling colonies blindly from a white pillowcase. Prior to deployment, spiders were provided a series of twigs to facilitate web construction. Each nest was then adhered to a host tree using zip ties and wooden clothespins. The following day we returned to each colony to ensure that it had established successful and had constructed a two-dimensional capture web. We then counted the number of spiders present within each nest and assayed the foraging behavior of each colony.

Research sample

Wild captured social spiders, Stegodyphus dumicola from Namibia and South Africa

Sampling strategy

Source colonies were collected opportunistically based on their sizes. We needed very large colonies in order to ensure that we could subset experimental groups of the desired phenotypic compositions.

Data collection

Boldness Assay

The boldness of individual S. dumicola was estimated using individual's latency to resume movement following an aversive stimulus. Trials were initiated by removing individuals from their containers and placing them in an open field (diameter = 16cm). After 30 seconds of acclimation two rapid puffs of air were administered using an infant nose-cleaning bulb from approximately 5cm away from the spider's anterior prosoma. This procedure results in the spider pulling its legs tight against its body in a huddled death feign. We then recorded the latency of each individual to resume movement and move one body length following the puff stimulus. Spiders that resumed movement quickly (<200 seconds) were deemed "bold" and spiders the resumed movement slowly (>400 seconds) were deemed "shy". Individuals differences in boldness are repeatable across days to months in S. dumicola 1-3, and are associated with the role individuals play in societies. Bold individuals are more likely to participate in prey capture events 5, assist in web repair 6, and transmit cuticular microbes than their shy counterparts.

Colony Performance Metrics

We returned to colonies four months later to monitor their success. We counted the number of egg cases produced by each colony and whether or not the colony collapsed. Colonies were deemed to have collapsed if they contained no living members of the society and no egg cases. S. dumicola naturally produce egg cases by this time of year and living nests should contain early instar juveniles. Nearly all of the colonies containing egg cases contained juveniles at a normal developmental stage. For our analyses we focus on the number of egg cases produced by a colony as our composite metric of colony performance because it summarizes both colony fecundity and survival.

We also measured the diameter of two egg cases from within each colony that contained them. We did this to evaluate whether egg size might have varied as a consequence of colony behavior (shy/bold) and the phenotypic neighborhood in which colonies resided. In 2013, we measured the diameter of 29 egg cases collected from 29 different S. dumicola source colonies from Namibia (Avis Dam). Egg case diameter (mm) was positively correlated with the number of eggs therein ($F_{1,27}=50.04$, $R^2 = 0.65$, $\beta = 3.63 \pm 0.51$, $p < 0.0001$) and to a lesser degree the size of individual eggs ($F_{1,27}= 4.45$, $R^2 = 0.14$, $\beta = 3.96 \times 10\text{-}6 \pm 1.87 \times 10\text{-}6$, $p = 0.044$). No differences in egg case diameter were noted between shy and bold colonies in our study (Colony BT: $F_{1,96.29} = 0.012$, $p = 0.91$) nor in colonies of contrasting phenotypic neighborhoods (all $p > 0.31$).

We further collected each colony's web (nest and capture web) and counted the number of prey carcasses that had been ensnared. S. dumicola ensnare flying prey on their two-dimensional capture web surfaces but then transport prey back to a three-dimensional nest for consumption. Carcasses are then incorporated into the nest and are webbed over in time. This behavior allows us to excavate nests of colonies to unearth their prey capture history over the duration of their time in the field.

Blind: Data were collected by all listed observers blind with regard to the focal colony's behavioral composition and phenotypic neighborhood treatment.

Timing and spatial scale

Source Colony Collection

Source colonies of S. dumicola containing 158-823 female spiders were collected in February and March 2018 (Avis Dam Namibia Ncolonies=13, 22°33'27.78"S, 17° 8'0.52"E; Drakensberg South Africa Ncolonies = 17, 29° 0'20.11"S, 29°32'28.13"E). Colony performance metrics were evaluated June 2018.

Data exclusions

In order to test whether the effect of neighborhood composition differed by colony behavioural phenotype (Colony Phenotype x

Data exclusions	Frequency of Bold Neighbors), we needed to trim the 100% bold and 100% shy colony treatments from the analysis. Even within this restricted composition space, however, we found that the effects of neighborhood composition differed strongly based on the focal colony's foraging phenotype (Colony Phenotype x Frequency of Bold Neighbors [LMM]: F1,89.07 = 19.33, R2 = 0.33, β = -4.74± 1.08, p < 0.0001, Fig 2).
Reproducibility	We conducted parallel studies at two sites, and Site ID never proved to be an important predictor of any response variable considered. Thus, the results appear robust for at least these two sites.
Randomization	Individuals of the desired phenotypes were haphazardly assigned to focal colonies by drawing them from cloth pillow cases containing spiders of the desired phenotype. The same procedure was deployed when selecting specific colony phenotypes for creating contrasting phenotypic neighborhoods. While this is not a truly random procedure, individuals and colonies were well mixed within pillow cases before selecting them.
Blinding	Observers were blind to the focal colony's phenotype and its neighborhood composition at the time of sampling.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Austral Summer and Fall 2018
Location	Avis Dam Namibia N colonies=13, 22°33'27.78"S, 17° 8'0.52"E; Drakensberg South Africa N colonies = 17, 29° 0'20.11"S, 29° 32'28.13"E
Access and import/export	No living samples were transported from the field for these studies.
Disturbance	Care was taken not to collect more than 30% of the road side S. dumicola colonies at a specific collection locality.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

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☒	☐ ChIP-seq
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Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	NA
Wild animals	Mature female S. dumicola colonies collected from the field and deployed to their collection site in experimental compositions and contrasting competitive conditions.
Field-collected samples	Source colonies of S. dumicola containing 158-823 female spiders were collected in February and March 2018 (Namibia Ncolonies=13, 22°33'27.78"S, 17° 8'0.52"E; South Africa Ncolonies = 17, 29° 0'20.11"S, 29°32'28.13"E). We collected colonies by placing the nest of the colony within a cloth pillowcase and then tripping the supporting branching using pruning snips. Colonies were then transported back to hotels adjacent to each site for dissection. Colonies were dissected by hand and all of the resident females were counted and isolated in 59ml plastic deli cups. All spiders were run through a boldness assay three times over the next three days in order to determine their individual phenotypes. After their boldness was assessed, we haphazardly subsetted individuals of the desired behavioral phenotypes into experimental colonies of ten individuals. Experimental colonies contained either all bold individuals or all shy individuals. Hereafter we will refer to these as "bold" and "shy" colonies. Prior to admitting individuals into an experimental colony, they were assigned a color ID to identify them as belonging to that experimental colony. This enabled us to track movement between experimental colonies over the duration of our study.
Ethics oversight	No ethics oversight are needed for invertebrates in the United States, Canada, South Africa, or Namibia.

Note that full information on the approval of the study protocol must also be provided in the manuscript.