Report

Current Biology

Selection for Collective Aggressiveness Favors Social Susceptibility in Social Spiders

Highlights

- Bold individuals emerge as influential leaders in arid, but not wet, habitats
- Geographic variation in leadership is caused by changes in following behavior
- Shy followers from arid sites will follow bold conspecifics and even heterospecifics
- Followership is under positive colony-level selection at sites where it occurs

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In Brief

Pruitt et al. show that arid environments favor more aggressive societies and that site-specific variation in followership enables groups to achieve these collective phenotypes. The followers that emerge will naively follow any bold conspecific and even bold heterospecifics.

Pruitt et al., 2018, Current Biology *28*, 100–105
January 8, 2018
https://doi.org/10.1016/j.cub.2017.11.038

CellPress

Current Biology
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Selection for Collective Aggressiveness Favors Social Susceptibility in Social Spiders

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https://doi.org/10.1016/j.cub.2017.11.038

SUMMARY

Particularly socially influential individuals are present in many groups [1–8], but it is unclear whether their emergence is determined by their social influence versus the social susceptibility of others [9]. The social spider *Stegodyphus dumicola* shows regional variation in apparent leader-follower dynamics. We use this variation to evaluate the relative contributions of leader social influence versus follower social susceptibility in driving this social order. Using chimeric colonies that combine potential leaders and followers, we discover that leader-follower dynamics emerge from the site-specific social susceptibility of followers. We further show that the presence of leaders increases colony survival in environments where leader-follower dynamics occur. Thus, leadership is driven by the "social susceptibility" of the population majority, rather than the social influence of key group members.

RESULTS AND DISCUSSION

In virtually any social group, some individuals are more influential than others [10–14]. Knowledgeable matriarchs in elephant [15] or orca [16] societies, ringleaders in chimpanzees hunting groups [17], and movement initiators in schooling fish [18] are all examples in which one or a few individuals strongly influence the behavior and success of their group. Such phenomena have inspired many scientists to ask what causes individuals to become so influential [1–5, 18–21]. Yet an equally important, but potentially inconspicuous and overlooked, contributor to these dynamics is the social susceptibility of other group members [18–20, 22–24]. We define "social susceptibility" as an individual's tendency to alter its behavior in response to influential social partners (see glossary in Table 1). Previous studies have demonstrated links between individuals' tendency to assume leader versus follower roles during movement decisions and individual temperament [21, 25] and that the strength of these roles can differ as a consequence of individuals' previous social experience [5]. Here we experimentally determine the relative contributions of "social influence" versus "social susceptibility" in generating habitat-specific variation in apparent leader-follower dynamics and collective behavior. "Leader" is broadly defined here as an individual that influences, leads, or commands a group.

The spider *Stegodyphus dumicola* lives in colonies of up to a few thousand individuals [26]. Social spiders exhibit a highly female-biased primary sex ratio [27], and females perform the vast majority of colony maintenance tasks in these systems. Female social spiders cooperate in collective prey capture and food sharing, web maintenance, and alloparental care [27]. *S. dumicola* also exhibits temporally consistent individual differences in behavior that are associated with the roles that individuals play in groups [28, 29]. Prior lab studies on *S. dumicola* have shown that a colony's boldest group member wields a large influence over the behavior and success of its colony. Boldness is defined as an individual's willingness to place itself at risk, and bold individuals constitute 3%–10% of a mature *S. dumicola* colony. Bold *Stegodyphus* are more likely to be initiators and participators in prey capture events, in both *S. dumicola* [28, 30] and other social congeners [31]. In *S. dumicola* from arid sites in the Kalahari desert, previous research has shown that boldness is not associated with individual body condition in these spiders, although bold individuals do tend to be slightly smaller than their shy counterparts (r^2 only 0.03) [32].

Importantly, adding just one bold individual to a laboratory colony of all shy individuals increases the number of colony members that respond to prey by >400% and increases the mass gained by other colony members by 200% [30, 33]. Such effects on colony behavior and performance persist even weeks after bold individuals are removed from groups, thus conveying that their "social influence" over groups is enduring [34]. Yet, other studies have also shown that, in lab environments with enemies, a bold individual can spread misinformation about predator identity and decrease colony mass gain and survival [35]. Given that the same kind of key individual can enhance colony success under some situations but diminish it in others, it is likely that such social dynamics will not be universal across environments. We therefore predict variation among populations in this unique social relationship.

Here we focus on differences between arid and wet environments because prior work has shown local behavioral adaptation in spiders associated with aridity [36, 37]. Specifically, arid

Table 1. Glossary Describing the Terminology Used Here to Describe Individual Behavioral Tendencies, the Collective Behavioral Tendencies of Groups, and Social Roles

Definition	Metric and Interpretation
Boldness: an individual's willingness to place itself at risk. Individuals that tolerate risk are termed "bold," whereas more cautious individuals are termed "shy."	Boldness is measured in *Stegodyphus* by administering an aversive stimulus to spiders that causes a death feigning response. Boldness is then measured as the latency for individuals to leave their death feigning posture and resume normal activity. The majority of *S. dumicola* are shy, and only a small number exhibit a bolder phenotype (3%–6% of the mature spiders assayed here). This metric is continuously distributed.
Aggressiveness: hostile or forceful behavior, here measured in the context of foraging responsiveness.	Aggressiveness is measured in *Stegodyphus* using spiders' responsiveness toward prey. Greater responsiveness is interpreted as more aggressive foraging behavior. For individuals, this is measured as an individual's tendency to join hunting groups. Colony-level aggressiveness is measured as the number of colony members that participate in a hunting group.
Leader: an individual that influences, leads, or commands a group.	Leadership in *S. dumicola* is measured as an individual's ability to alter the collective behavior of their group. In arid regions, bold individuals are able to dramatically enhance the foraging aggressiveness of their colony. Bold individuals from wet sites have no such effect. Although initiators of group movement, typically located at the front of the group, are often hypothesized to be group leaders, leaders need not always reside at the front of groups to exact their social power.
Social susceptibility: an individual's tendency to alter its behavior in response to influential social partners.	Social susceptibility is measured in *S. dumicola* as an individual's tendency to respond to the movement or excitatory actions of other individuals. Shy individuals from arid sites are socially susceptible, as evidenced by their willingness to follow the vibratory cues of foraging conspecifics and by their tendency to model the foraging behavior of bold group members, even long after bold group members have been removed from the colony.

habitats are generally prey limited and thus favor more aggressive behavior, whereas wetter habitats have more prey but more enemies too [36, 37]. Thus, we predicted that bold individuals would have a positive effect on colony aggressiveness, and therefore on colony performance, in harsher desert sites where aggressive hunting may be essential.

We established 242 experimental colonies of 19 shy spiders and one bold spider of varying degrees of boldness in the field (see STAR Methods for details). For some colonies, the single bold spider was only slightly bolder than the shy spiders, but in other colonies the bold individual was far bolder than other group members. We first determined whether the boldness of the single boldest group member predicts colonies' foraging aggressiveness. We measured the foraging aggressiveness of each colony three times by recording the number of spiders that responded to simulated prey. We then deployed 28–32 colonies at each of eight sites along two orthogonal precipitation gradients: one extending from the Namib Desert north (810 km) and one extending from the Kalahari Desert east (981 km) (Figure S2). All of the spiders used to create experimental colonies were mature females, and only native spiders were used to construct colonies at each site. Colonies were established in the field in November–December 2016, and their status was checked in February of the following year. In particular, we noted whether each colony survived this time period and whether produced offspring. We used these data to determine (1) whether the boldness of the single boldest group member predicts colonies' foraging aggressiveness and (2) whether colony foraging aggressiveness is linked with colony survival and reproductive success.

At the four arid sites, we found that colony aggressiveness toward prey increased up to 300% in groups containing just one very bold spider, as compared to colonies in which a less bold spider was added ($F_{1,\ 111.4} = 50.17$, $\beta = 0.008 \pm 0.001$, $p < 0.0001$; Figure 1A). At the four wet sites, we did not find an effect of the boldness of colonies' boldest spiders on colony aggression ($F_{1,\ 120.5} = 0.01$, $\beta = -3.539e{-6} \pm 5.95e{-5}$, $p = 0.98$; Figure 1B). Thus, an apparent leader-follower relationship, in which group members alter their foraging behavior in the presence of a bold individual, exists only in arid sites and not in wet ones. To further test whether the establishment of this social order is beneficial, we examined the colonies' survival and reproduction in the field. We detected positive selection on colony aggressiveness at all arid sites: aggressive colonies were more likely to survive (likelihood ratio [L-R] $\chi^2_1 = 75.44$, $p < 0.0001$; Figure 1A) and produce offspring (L-R $\chi^2_1 = 21.13$, $p < 0.0001$), whereas no selection was detected at the wet sites (colony survival: L-R $\chi^2_1 = 0.03$, $p = 0.85$; Figure 1B; offspring production: L-R $\chi^2_1 = 0.002$, $p = 0.95$) (Data S1). Thus, bold individuals have a pronounced positive effect on colony aggressiveness, and this collective aggressiveness has a positive effect on colony survival and reproductive success only in arid sites, as predicted. Perhaps in response to this selection, colonies at arid sites are, on average, more aggressive than colonies at wet sites ($F_{1,\ 10.23} = 7.22$, $\beta = 0.83 \pm 0.31$, $p = 0.02$).

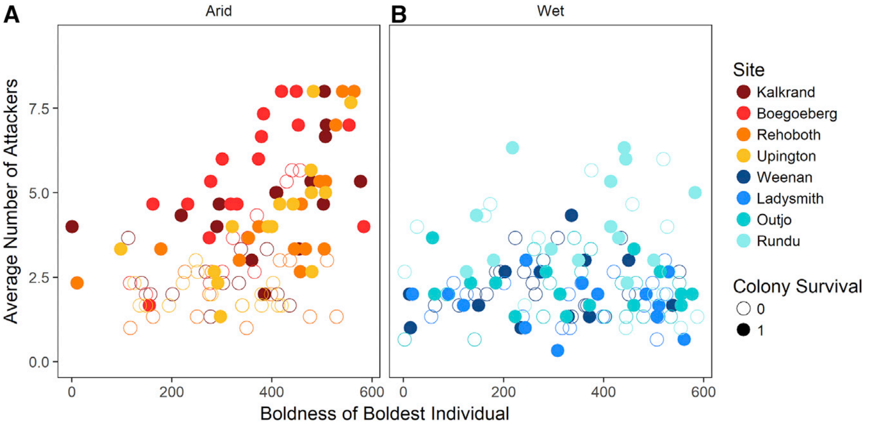

Figure 1. Regional Variation in Colony Performance and Survival

Relationship between the number of spiders that attacked a simulated prey and the boldness of the boldest individual in the group (i.e., the leader) in arid (A) and wet (B) sites. Each site is depicted in a different color. Open circles indicate colonies that did not survive after 2 months in the field, and closed circles indicate colonies that persisted. See Figure S2 for site locations.

Colonies of *S. dumicola* from arid and wet sites also differ in a number of other respects. For instance, naturally occurring arid-dwelling colonies contain 40% more individuals than their wet-site counterparts ($F_{1,\ 51} = 12.34$, $p = 0.0009$). However, the more plentiful colony constituents in arid-site colonies are also smaller in size (prosoma width: $F = 8.52$, $\beta = -0.45 \pm 0.15$, $p = 0.03$). Bold individuals are also slightly rarer at arid sites than at wet sites. Bold individuals constitute 5.4% of mature individuals in wet sites but only 3.6% of individuals at dry sites ($F_{1,\ 51} = 6.13$, $p = 0.02$). Together, the ecology and functioning of natural *S. dumicola* colonies in arid versus wet sites appear to differ in a number of respects.

The effect of bold *S. dumicola* on colony behavior and success in arid sites could be due to the "social influence" of bold individuals or the "social susceptibility" of shy individuals, or both. To disentangle these effects, we created 96 chimeric colonies in the laboratory with different compositions of individuals from arid and wet sites. The arid-wet chimeric colonies included two treatments in which the followers (shy) were from either an arid or a wet site and the leader (bold) was from the opposing habitat type. We found that bold individuals from arid sites are not uniquely influential (Figure 2B). When bold individuals from arid sites were mixed with shy individuals from wet sites, we did not recover a positive association between the boldness of the group's boldest member and colony aggressiveness ($F_{1,\ 44.24} = 1.07$, $\beta = -0.0007 \pm 0.0007$, $p = 0.31$; Figure 2B). In contrast, when we mixed shy individuals from arid sites with bold individuals from wet sites, we recovered a positive association between the boldness of singularly bold individuals and group foraging aggressiveness ($F_{1,\ 44} = 1.07$, $\beta = 0.006 \pm 0.0008$, $p < 0.0001$; Figure 2C). Thus, habitat-specific differences in leader-follower dynamics appear to be generated by site-specific variability in the "social susceptibility" of shy individuals and not the "social influence" of bold individuals.

To determine whether mixing individuals across populations that share a similar climate affects colony foraging behavior, we generated two control treatments in which the leader and followers were from two different sites that were both either arid ($n_{\text{colonies}} = 24$) or wet ($n_{\text{colonies}} = 15$) (see STAR Methods). These control chimeric colonies revealed that mixing individuals from populations that share the same climate had no effect on colony foraging behavior (Figures 2A and 2D). The leader-follower dynamics observed at arid sites do not break down in response to mixing, despite reduced familiarity or relatedness ($F_{1,\ 20} = 26.74$, $\beta = 0.006 \pm 0.001$, $p < 0.0001$; Figure 2A), and the wet-wet chimeras never produced the behavioral patterns observed in arid populations ($F_{1,\ 11} = 2.96$, $\beta = -0.0062 \pm 0.0016$, $p = 0.11$; Figure 2D).

To determine whether the shy spiders from arid sites are susceptible to any indication of boldness in their group, we produced interspecific-chimeric colonies. Here we constructed colonies of 19 shy *S. dumicola* from two arid sites (Kalkrand, Namibia and Upington South Africa; total n = 48) and two wet sites (Rundu, Namibia and Ladysmith, South Africa; total n = 37) with a single heterospecific congener *Stegodyphus mimosarum*. Like *S. dumicola*, *S. mimosarum* exhibits temporally stable individual differences in boldness that are linked with individual social roles [38]. This species has independently evolved sociality, and it last shared a common ancestor with *S. dumicola* several million years ago [39]. Despite these differences, adding a bold *S. mimosarum* to a colony of shy *S. dumicola* from arid sites enhanced the collective foraging aggressiveness of chimeric colonies to the same degree as adding a bold conspecific ($F_{1,\ 44} = 35.78$, $\beta = 0.006 \pm 0.001$, $p < 0.0001$; Figure 2E). In contrast, adding a bold *S. mimosarum* to a colony of shy *S. dumicola* from wet sites did not enhance colony aggressiveness ($F_{1,\ 44} = 2.07$, $\beta = 0.002 \pm 0.0013$, $p = 0.16$; Figure 2F). Thus, shy individuals from arid sites are obligatorily socially susceptible, as evidenced by their willingness to respond to bold conspecifics from any source, as well as heterospecifics, to the same degree that they respond to native bold individuals.

One possible mechanism behind the leader-follower dynamics observed at arid sites is within-colony competition for resources. If colonies at arid sites are more food starved, it may benefit shy colony members to quickly join bold individuals during prey attack sequences, as to secure limited resources, particularly if bold individuals are disproportionately able to monopolize resources for themselves. One might also expect within-colony competition over resources to be less pronounced at high resource sites. However, the majority of the available data are mixed or at odds with this hypothesis. Colonies at arid sites were of no lower body condition than their counterparts at wet sites ($F_{1,\ 5.89} = 3.21$, $\beta = -0.002 \pm 0.001$, $p = 0.12$). Furthermore, body condition is unrelated to boldness at both wet and dry sites (boldness: $F_{1,\ 236.8} = 0.28$, $\beta = -3.772\text{e}{-6} \pm 7.172\text{e}{-6}$, $p = 0.60$, boldness × site type: $F_{1,\ 236.8} = 0.28$, $\beta = -2.237\text{e}{-6} \pm 7.172\text{e}{-6}$, $p = 0.76$) (Data S1). Thus, bold individuals are not consistently able to secure more resources than their shy

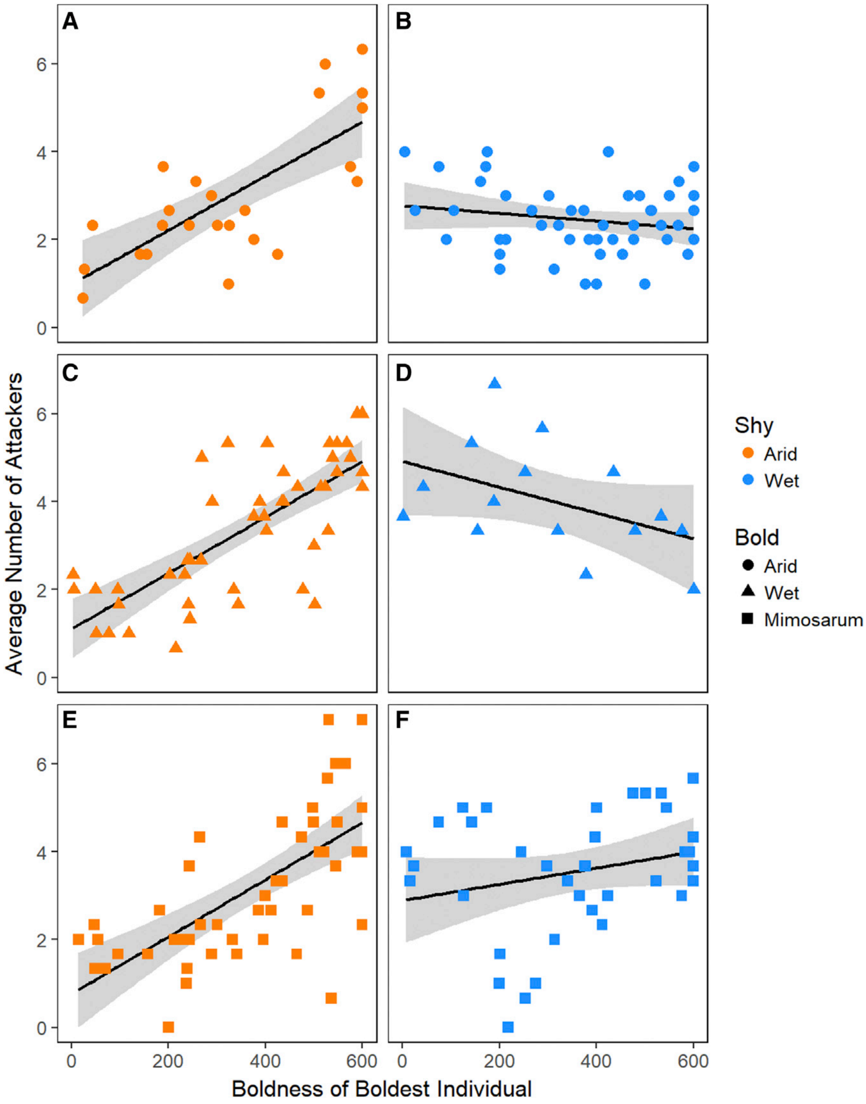

Figure 2. Chimeric Colonies Reveal "Social Susceptibility" of Shy Individuals from Arid Sites

Relationship between the number of spiders that attacked a simulated prey and the boldness of the boldest individual in the group (i.e., the leader) in chimeric colonies. Color denotes the origin of the shy individuals (followers) in the chimeric colonies: orange, arid; blue, wet. Shapes denote the origin of the bold individuals (leaders): circles, arid; triangles, wet; squares, heterospecifics (*S. mimosarum*). (A) and (D) are controls in which both the leaders and followers come from arid (A) or wet (D) sites. Shy followers from wet sites are not susceptible to bold leaders from arid sites (B) or from another species (F). However, shy followers from arid sites are susceptible to the influence of bold leaders from wet sites (C) and to bold leaders from a different species (E). See Figure S1 for more information on following behavior.

counterparts, nor are they more food deprived, and colonies at arid sites are not in poorer body condition. Instead, shy colony members at arid sites actually benefit by the presence of bold individuals because they enhance colony survival (Figure 1), reproductive output (Data S1), and the collective mass gain of shy colony members [30, 33]. Finally, the social dynamics observed at arid sites are seemingly unresponsive to manipulations to resource availability (see additional results in Figure S1) [30]. In sum, this suggests that ongoing differences in hunger among individuals within colonies or across sites are not sufficient to explain our results. Instead, we propose that an early developmental or evolutionary history of food limitation may be key.

Socially influential individuals can provide their groups with benefits [15, 30] but also situationally associated costs [35, 40]. In the social spider *S. dumicola*, a leader-follower dynamic is established in a habitat-specific manner and is restricted to arid environments. This social order also enhances colony survival and reproduction at arid sites and is therefore subject to ongoing site-specific selection. Most interestingly, we discover that this leader-follower relationship depends on habitat-specific "social susceptibility" of shy spiders from arid sites, because these shy individuals are uniquely influenced by the social cues of conspecifics (Figure S1). Notably, *post hoc* behavioral analyses showed that even bold individuals from arid sites exhibit some degree of heightened social responsiveness, at least as compared to their counterparts from wet sites (Figure S1), though not nearly so much as shy individuals. Therefore, the emergence of leadership is not driven by the unique traits of leaders, but by the population majority's willingness to follow. In the hands of the socially susceptible, anything approximating the phenotype of a leader, even a heterospecific sham, is sufficient to elicit a response. Though naive followership appears to be advantageous in particular settings (e.g., in arid habitats for *S. dumicola*), such susceptibility may one day provide an easy point of manipulation whereby enemies or selfish phenotypes could evolve to exploit entire societies.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information includes two figures and one data file and can be found with this article online at https://doi.org/10.1016/j.cub.2017.11.038.

ACKNOWLEDGMENTS

We are indebted to J.W. Jolles, S.E. Bengston, R. Wollman, C.N. Keiser, J.E. Smith, D.R. Farine, A. Gardner, and two anonymous reviewers for comments on prior versions of this manuscript. Funding was provided by NSF IOS grants 1352705 and 1455895 to JNP, 1456010 to N.P.-W. and NIH grant GM115509 to N.P.-W. and J.N.P.

AUTHOR CONTRIBUTIONS

J.N.P., C.M.W., J.L.L.L., G.T.C., and B.L.M. all contributed to study design, data collection, writing, and analyses. A.K. contributed to writing, data analyses, and figure production. N.P.-W. contributed to study design, writing, and data analyses.

Received: August 19, 2017
Revised: September 29, 2017
Accepted: November 16, 2017
Published: December 21, 2017

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological Samples		
Healthy mature *Stegodyphus dumicola* & *Stegodyphus mimosarum*	Southern Africa	N/A
Deposited Data		
Raw & Analyzed Behavioral & Colony Survival Data	Dryad	https://doi.org/10.5061/dryad.7p090

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Jonathan N. Pruitt (pruitt@ucsb.edu).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Colony Selection Study

Study Sites and Collection

Whole *S. dumicola* colonies (n = 212) were collected along roadside *Acacia mellifera* and barbwire fencing at eight study sites. These sites were arranged along two orthogonal precipitation gradients: one extending from the Namib Desert north toward Angola (810km) and a second extending from the Kalahari Desert east toward Lesotho (981km). Along each gradient, care was taken to select two arid desert sites (*Namib Gradient*: Kalkrand [-24.065027, 17.580452] and Rehoboth [-23.209881, 17.092]; *Kalahari Gradient*: Upington [-28.403361, 21.071249] and Boegoeberg [-29.037819, 22.027999]) and two wetter savannah sites (*Namib Gradient*: Outjo [-20.233099, 16.354468] and Rundu [-18.299209, 19.407636]; *Kalahari Gradient*: Ladysmith [-38.65655, 29.625249] and Weenen [-28.856239, 30.142306]) per gradient (Figure S2). A total of 211 source colonies were collected ranging in size from 75-512 mature female *S. dumicola*. The sequence of colony creation and deployment was arranged to prevent linearly conflating aridity with time of deployment (Nov 1- Dec 15, 2016): Wet (Rundu) → Wet (Outjo) → Arid (Rehoboth) → Arid (Kalkrand) → Arid (Upington) → Arid (Boegoeberg) → Wet (Ladysmith) → Wet (Weenen)

Colonies were collected by covering the nest containing all the spiders in a cloth pillowcase and snipping off the supporting branches using pruning snips. Whole colonies were then transported to nearby hotels and lodges. Each source colony was then dissected by hand by gently pulling open the nest and counting all of the spiders therein. Spiders were isolated in 59 mL deli containers and their prosoma widths, masses, and individual boldness scores were obtained before assigning them to an experimental colony. When assigning spiders to an experimental colony, care was taken never to mix spiders from multiple source colonies in order to preserve natural levels of within-colony relatedness and familiarity, both of which can impact collective behavior and foraging performance in this or other species of *Stegodyphus* [41–44].

Experimental colonies used in our selection studies were subsequently deployed at the same source site where the original colonies were collected, i.e., experimental colonies were never moved across sites. We avoided moving spiders across sites to preserve natural population genetic structure, which is the subject of ongoing genomic investigations by other investigators.

METHOD DETAILS

Boldness Assay

Boldness is defined as an individual's willingness to place itself at risk [45]. In *S. dumicola*, boldness is assessed by measuring the duration of an individual's antipredator response following an aversive stimulus [31, 46]. Boldness trials are initiated by placing each individual spider in the center of a clean open field container (radius = 12cm) and giving the spider 30 s to acclimate. Two puffs of air are then administered toward the dorsal anterior end of the spider using an infant nose-cleaning bulb. These puffs universally result in *S. dumicola* pulling in its legs in a death feign, which varies in duration. Spiders that remain in the death feign for longer are deemed shyer than spiders that emerge from a death feign sooner. We recorded individuals' latency to emerge from a death feign and move one full body length in the open field. Individuals are given a maximum duration of 10 min to emerge and move one body length. Individuals that fail to move a body length in this time receive a maximum score of 600 s. We then take individuals' latency to resume movement and subtract it from the maximum time provided in the trial (600 s) to obtain a boldness index that scales positively with boldness. All behavioral assays were conducted during daylight hours under artificial lighting in the absence of air drafts.

Individual differences in this test are repeatable over the duration of several months [47, 48]. Moreover, individual differences in boldness are tightly linked with these spiders' tendency to participate in a variety of cooperative tasks, including colony defense [29], prey capture [28], and web construction and maintenance [49]. The majority (90%–95%) of adult *S. dumicola* exhibit a shy behavioral type (latency to emerge and resume movement > 600 s) [47]. Bold individuals, while rare, are known to have a large impact on colony behavior and performance in the laboratory [30, 35].

The truncated dataset associated with a 10-min termination to our trials raises the concern that shy individuals from arid sites might be shyer than their counterparts from wet sites (or vice versa), and that this variation could be concealed by the design of our assay. However, a more open-ended 3 hr trial where we tracked the emergence time of shy individuals from wet (Ladysmith, Weenan) versus arid (Upington, Groblershoop [near Boegoeberg]) sites reveals (1) that there are no concealed differences in the shyness of individuals that receive as boldness score of 0 (latency to emerge > 600 s) in our truncated trials, and that many of these individuals would take hours to emerge from their huddles (see supplementary statistics). Thus, conducting these trials over a duration which would not truncate the dataset for the ~10,000 spiders assayed here was not feasible.

Experimental Colony Construction

We created experimental colonies of 20 adult female spiders. 19 of these females exhibited a latency to resume movement of 600 s or greater (boldness index = 0), and the 20th spider was randomly pulled from a pool of spiders that varied in their boldness scores from 1-600. This created a set of experimental colonies of identical size and developmental stage, but which varied in the boldness score of the single boldest member of the group. Prior studies have referred to these individuals as 'keystone individuals' because they exhibit a disproportionately large influence over the collective behavior and success of their colony.

Experimental colonies were housed in 390 mL plastic cups containing three *Acacia mellifera* twigs to facilitate web construction. Colonies were provided two days to construct a rudimentary nest and capture web. Colonies were then run through three collective foraging aggressiveness assays (1/day for 3 days) before being deployed into the field. The temperature in the lodge/hotel rooms where individual boldness assays, colony assembly, and colony foraging aggressiveness assays occurred varied from 22.2-25.5C. All behavioral assays were conducted during daylight hours under artificial lighting in the absence of air drafts.

Colony Foraging Aggressiveness Assay

Colony foraging aggressiveness is quantified as the number of colony members that leave the nest during a staged prey capture event, where more aggressive colonies deploy more attackers [30]. Foraging aggressiveness assays are initiated by placing a 1 × 1cm piece of paper in the colony capture web ~5cm away from the nest entrance, and then vibrating the piece of paper using a 1.5mm diameter wire attached to the end of a handheld vibratory device (Magic Purple Bullet). The device was set on a pulse setting, as to mimic the irregular thrashing movements of insect prey captured in the web. We then recorded the number of spiders that left the nest to capture the simulated prey item, until the first individual contacted the piece of paper. Colony prey capture behavior was assessed once per day for three consecutive days. At the end of the third day, colonies were deployed at one of our eight field sites during the evening hours. Nearly all individuals that emerge in response to stimulated prey eventually attempted to attack and subdue the stimulus, which conveys that emergence is an indication of individuals' desire to attack prey, and not merely to acquire information about it.

This assessment of colony aggressiveness does raise the potential concern that if one individual is very fast and contacts the paper rapidly, then its fellow colony members may not have time to emerge. However, at odds with this inference we actually find that fast-responding *Stegodyphus* colonies also attack prey with larger numbers of individuals in a smaller amount of time [30, 46, 50]. Additionally, the number of attackers that emerge in response to prey until contact is ecologically realistic because, once the first few individuals contact and subdue the prey, the attack ceases and the prey is dragged back to the next entrance where it is shared. Thus, in nature, the time for the attack sequence to occur is actually smaller for aggressiveness colonies. All colony aggressiveness assays were conducted during daylight hours under artificial lighting in the absence of air drafts in lodges and hotels.

Colony Deployment and Monitoring

Experimental colonies (28-33 colonies per sites) were deployed at our eight sites by using clothespins to attach the colony in its container to resident *Acacia* trees. We used the preexisting presence of *S. dumicola* colonies on nearby trees as an indicator of habitat quality and substrate suitability. Care was taken not to place colonies on *Acacia* trees actively being guarded or patrolled by ants (genus *Anoplolepis* and *Crematogaster*), which can destroy *S. dumicola* colonies before they establish [51, 52]. Prior studies have shown that setting colonies out in the evening hours provides them with an opportunity to produce a functional nest and a sizable capture web before the following sunrise [46].

We then left these experimental colonies in the field for the next several months and checked their performance in February 2017. During these checks, we determined if there were any spiders living within the colonies, noted the presence and number of egg cases, noted the presence of spiderlings, and, in cases where the colony had perished, we noted situational factors that provide clues as to why the colony may have perished. For instance, a large number of predatory ant carcasses remaining in the colony retreat and in the plastic deli cup was taken as evidence of a raid by predatory ants, which kill a large number of natural colonies each year. The presence of sporulated fungus emerging from the carcasses of colony members was interpreted as evidence that fouling by fungus had contributed to colony demise. Entomopathogenic fungus is a common driver of colony demise in this system [52]. In this study we focus on whether or not colonies survived the duration of study, meaning that at least one colony member was left alive, and whether or not colonies successfully reproduced, i.e., produced viable egg cases or spiderlings during this time period.

The phenology of our experimental colonies (e.g., timing of egg case production, presence of spiderlings, age of spiderlings) closely matched those of native naturally-occurring colonies. Experimental colonies were composed of mature females only that came from colonies containing mature males, and thus, were likely mated prior to colony establishment. Although, immigration of some foreign males to the colonies was evident during our February check.

Chimeric Colony Study

Because the influence of bold spiders on colony foraging behavior was only detected at arid sites, we used chimeric colonies (n = 96) to determine whether this dynamic was driven by the "social influence" of bold individuals from arid sites or the "social susceptibility" of shy individuals from arid sites. We created colonies of bold individuals from arid sites with shy individuals from wet sites (N = 48), and vice versa (N = 48). We also executed a set of control chimeras (n = 39) where we mixed individuals from different sites with similar climatic conditions (arid with arid [n = 24], wet with wet [n = 15]). This allowed us to determine if merely mixing colonies alters associations between group composition and group behavior, and whether the mechanisms governing the influence of bold individuals at arid sites are mutually cross-compatible. Mixtures involve 19 shy individuals from one population with 1 bold individual from another, and vice versa (Wet: Ladysmith → Rundu, Rundu → Ladysmith, Arid: Kalkrand → Upington, Upington → Kalkrand).

Chimeric colony studies were carried out under standardized laboratory conditions at the University of California Santa Barbara. Twenty intact *S. dumicola* colonies were collected form each site and transported to laboratory in January 2017. Colonies were dissected out and the prosoma width, mass, and boldness of each colony constituent were determined over a 72 hr period. We then constructed chimeric colonies (n = 96) of the same behavioral composition (19 spiders with a boldness index of 0, and 1 spider with a boldness index between 1 and 600). Colonies were then subjected to foraging aggressiveness assays identical to those detailed above.

To determine if the shy spiders from arid sites are socially susceptible to any indication of boldness in their group, we produced a third set of interspecific-chimeric colonies. Here we constructed colonies of 19 shy *S. dumicola* from two arid sites (Kalkrand, Namibia and Upington South Africa, total n = 48) and two wet sites (Rundu, Namibia and Ladysmith, South Africa, total n = 37) with a single heterospecific congener *Stegodyphus mimosarum*. Like *S. dumicola*, *S. mimosarum* exhibits temporally stable individual differences in boldness that are linked with individual social roles [38]. This species has independently evolved sociality and shared a common ancestor with *S. dumicola* several million years ago [39].

Web Recruitment Study

We designed a final study to determine 1) whether shy individuals from arid sites are uniquely drawn to the cues of conspecific on the capture web, and 2) whether food restriction could cause shy individuals from wet sites to become more socially susceptible (see Figure S1). To do this, we created colonies of 19 shy spiders or 19 bold spiders from two arid (Kalkrand, Namibia and Upington South Africa) and two wet (Rundu, Namibia and Ladysmith, South Africa) sites (total N = 33). We then subjected these colonies to two different sensory stimuli at three time points (in a fully factorial design), where each colony was tested in each of the six different treatment combinations. To test responsiveness to conspecifics we introduced a bold conspecific taken from the same source colony to the experimental colony's capture web. To test change over time in responsiveness to prey, we introduced a domestic cricket on the capture web. Colonies were presented with each of these stimuli in a randomized order one, two, and five days after an *ad libitum* feeding event and we recorded the number of spiders that responded to each of these stimuli. The ordering of prey-response treatments (1, 2 or 5 days post-feeding) was likewise alternated among focal colonies.

Timeline

Colony Establishment in the Field: November-December 2016
Colony Performance Assessment: February 2017, July 2017
Chimeric Colony Experiment (Lab): February-April 2017
Web Recruitment Studies: April-May 2017

QUANTIFICATION AND STATISTICAL ANALYSIS

Our statistical analyses were performed in JMP 12.0. In brief, we constructed a variety of GLMs and LMMs to evaluate associations between group composition and various behavioral and colony performance response variables (see Data S1 for full model descriptions). Statistical significance was evaluated using an $\alpha = 0.05$. Sample sizes were determined by the availability of spiders of specific behavioral tendencies and general feasibility based on personnel limitations. No replicates were excluded from our statistical analyses. The distribution of residuals and the nature of our response variables (e.g., binary versus continuous) were used to determine our model structures.

DATA AND SOFTWARE AVAILABILITY

Behavioral and colony performance data summarized in this paper are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.7p090.