Behavioral
Ecology

The official journal of the
ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2018), XX(XX), 1–8. doi:10.1093/beheco/ary158

Original Article

Collective behavior and colony persistence of social spiders depends on their physical environment

Ambika Kamath,[a,b] Skylar D. Primavera,[a] Colin M. Wright,[a,c] Grant N. Doering,[a]
Kirsten A. Sheehy,[a] Noa Pinter-Wollman,[d] and Jonathan N. Pruitt[a,e]
[a]Department of Ecology, Evolution, and Marine Biology, 2124 Noble Hall, University of California Santa Barbara, Santa Barbara, CA 93106, USA, [b]Department of Environmental Science, Policy, and Management & Miller Institute for Basic Research in Science, 137 Mulford Hall, University of California Berkeley, Berkeley, CA 94720, USA, [c]Department of Biology, Pennsylvania State University, 518 Mueller Lab, University Park, PA 16802, USA, [d]Department of Ecology & Evolutionary Biology, University of California Los Angeles, 612 Charles E. Young Drive South, Los Angeles, CA 90095, USA, and [e]Department of Psychology, Neuroscience & Behaviour, McMaster University, 1280 Main Street West, Hamilton, Ontario L8N 1A8 Canada

Received 29 June 2018; revised 16 October 2018; editorial decision 23 October 2018; accepted 6 November 2018.

The physical environment occupied by group-living animals can profoundly affect their cooperative social interactions and therefore their collective behavior and success. These effects can be especially apparent in human-modified habitats, which often harbor substantial variation in the physical environments available within them. For nest-building animal societies, this influence of the physical environment on collective behavior can be mediated by the construction of nests—nests could either buffer animal behavior from changes in the physical environment or facilitate shifts in behavior through changes in nest structure. We test these alternative hypotheses by examining the differences in collective prey-attacking behavior and colony persistence between fence-dwelling and tree-dwelling colonies of *Stegodyphus dumicola* social spiders. Fences and trees represent substantially different physical environments: fences are 2-dimensional and relatively homogenous environments, whereas tree branches are 3-dimensional and relatively heterogeneous. We found that fence-dwelling colonies attack prey more quickly and with more attackers than tree-dwelling colonies in both field and controlled settings. Moreover, in the field, fence-dwelling colonies captured more prey, were more likely to persist, and had a greater number of individuals remaining at the end of the experiment than tree-dwelling colonies. Intriguingly, we also observed a greater propensity for colony fragmentation in tree-dwelling colonies than fence-dwelling colonies. Our results demonstrate that the physical environment is an important influence on the collective behavior and persistence of colonies of social spiders, and suggest multiple possible proximate and ultimate mechanisms—including variation in web complexity, dispersal behavior, and bet-hedging—by which this influence may be realized.

Key words: **architecture, foraging, human-induced habitat modification, *Stegodyphus dumicola*, web.**

INTRODUCTION

The space that animals live in and move through modulates how easily and how often they encounter other individuals, thereby dictating the number and identity of individuals they compete against or cooperate with (Dunn and Whittingham 2006; Morales et al. 2010; Pinter-Wollman et al. 2011, 2018; Kamath and Losos 2018). The influence of organisms' physical environments might be especially important in complex animal societies, whose success and persistence can depend on coordinated interactions among their members (Queller and Strassman 1998; Clutton-Brock 2009; Pinter-Wollman et al. 2017). Discovering how the collective behavior of animal societies is shaped by their physical environment is not only pertinent to understanding how these societies may have evolved, but also how they function today under the impact of human-induced habitat change (Couzin and Krause 2003; Guttal and Couzin 2010; Pinter-Wollman 2015).

Address correspondence to A. Kamath. E-mail: ambikamath@gmail.com.

The hallmark of many animal societies is the construction of complex structures (e.g., nests, webs, hives) wherein most of these animals' cooperative interactions take place (reviewed in Hansell 1993). By constructing the environments within which they move and interact, nest-dwelling animals may be buffered against changes in their external physical environment (Korb 2003; Laland et al. 2016). Thus, in the face of human-induced habitat change, the collective behavior of such societies may remain relatively unaltered. Alternatively, anthropogenic changes to the physical environment could influence the structure of animals' nests in ways that subsequently shape their behavior (Modlmeier et al. 2014a; Montiglio and DiRienzo 2016; Japyassú and Laland 2017). Human habitat modification thus might be capable of driving shifts in the collective behavior of animal societies, by exposing them to physical environments that may not previously have been common.

In this study, we test these alternative hypotheses by examining the effect of changes to the physical environment via human-induced habitat modification on the collective prey-attacking behavior of *Stegodyphus dumicola* social spiders. For both solitary spiders and social spiders like *S. dumicola*, webs are primarily tools for capturing prey, but also provide the substrate on which communication and interactions (social, reproductive, and predatory) take place (Blackledge et al. 2011; Keiser et al. 2016). Moreover, sociality in spiders has evolved iteratively in association with 3-dimensional nests (reviewed in Avilés and Guevara 2017; Pruitt and Avilés 2018), suggesting that the structure of their webs is important to the functioning of social spiders' societies. Finally, laboratory studies have shown that the structure of the substrate on which social spiders build their nests can affect their collective prey-attacking behavior (Modlmeier et al. 2014a), which in turn may affect their survival and growth (Pinter-Wollman et al. 2017; Pruitt et al. 2018). It is thus possible that human-induced shifts in the physical environments within which social spiders build their webs will affect not only colonies' collective hunting behavior and prey capture success but also their persistence.

Colonies of *S. dumicola* collectively construct nests that are comprised of a 3-dimensional retreat, within which spiders take shelter, and of 2-dimensional capture webs, which radiate from this retreat nest (Wickler and Seibt 1993). Spiders emerge from the retreat to the capture web when they sense vibrational cues from prey that get stuck in the capture web, and then attempt to collectively immobilize and consume the prey (Wright et al. 2017). The nests of *S. dumicola* are naturally located on trees and thorny bushes. Following human activity in these environments, *S. dumicola* nests are also commonly found on human-made structures such as roadside fences (Figure 1). This shift in location represents a substantial change in physical context: fences are 2-dimensional and relatively homogenous environments whereas tree branches are 3-dimensional and relatively heterogeneous.

We examined the collective behavior, prey capture success, and colony persistence of experimental colonies of *S. dumicola* deployed on trees versus on fences in the field. We then repeated the experiment in a controlled greenhouse setting, to confirm that differences observed in the field were driven primarily by the physical environment and not by other subtle abiotic or biotic differences between the 2 habitats.

METHODS

Field experiment

We collected 31 *S. dumicola* colonies from *Senegalia mellifera* trees near Upington, South Africa in October 2017. We used individuals from these colonies to create 30 experimental colonies of each of 2 sizes: 30 individuals and 90 individuals. The number of individuals in a colony affects both colony behavior and success (Keiser and Pruitt 2014), leading us to ask if the effects of the physical environment might also depend on colony size. All individuals in an experimental colony were from the same natural source colony, to preserve natural levels of relatedness and familiarity among individuals within experimental colonies (Seibt and Wickler 1988; Johannesen et al. 2002; Modlmeier et al. 2014b). From each source colony, we created at most 3 large and 2 small experimental colonies. Experimental colonies were housed in 350 ml plastic cups containing 3 *Se. mellifera* twigs arranged in a tripod configuration, on which the spiders built their webs. We quantified the collective foraging behavior of colonies in the cups prior to deployment in the field; foraging behavior assays consisted of placing a small piece of paper in the center of the web, applying a pulsed vibration to the paper with a handheld vibratory device, and measuring the time taken for the first spider to attack the paper (up to a maximum of 3 min) as well as the total number of spiders moving towards the paper at the moment when the first spider reached the paper (following Keiser and Pruitt 2014 and Keiser et al. 2014, who show that these metrics of collective behavior are repeatable). Assays were repeated 4 times over 2 days, with a gap of at least 4 h between assays, to obtain a robust estimate of colonies' predeployment behavior. Colonies were randomly assigned to be deployed on trees or fences, after ensuring that experimental colonies derived from the same source colony were represented in both treatments approximately equally. We conducted t-tests to compare colonies assigned to trees and colonies assigned to fences to ensure that, prior to deployment, there were no differences between the collective behavior of the 2 treatments (mean ± standard deviation for latency to attack: fence-dwelling colonies: 11.8 ± 4.9 s, tree-dwelling colonies: 11.0 ± 8.6 s, $t_{57} = 0.46$, $P = 0.64$; mean ± standard deviation for number of attackers: fence-dwelling colonies: 4.4 ± 1.9, tree-dwelling colonies: 4.7 ± 1.8, $t_{57} = 0.48$, $P = 0.63$).

Colonies were deployed in a paired fashion (each pair comprising 2 large or 2 small colonies) on *Se. mellifera* trees and fence-posts that were between 2 m and 10 m apart from one another. Fences comprised of vertical posts of PVC or wood with wire stretched horizontally between posts. Colonies were deployed by removing the sticks and the attached web from the plastic cup and using a piece of wire to secure the sticks either at a fork in the branches of a tree or at the intersection between a post and the wire on the fence. Colonies were deployed at heights of approximately 1.0–1.5

Figure 1

Stegodyphus dumicola build retreats and 2-dimensional capture webs on (a) trees and (b) fences, 2 very different physical environments. Photographs by (a) Graham Montgomery and (b) Ambika Kamath.

m, at about the same height on the tree and the fence for each pair of experimental colonies. The spiders remained within their web during this deployment process. All colonies deployed on trees and all but one of the colonies deployed on fences established successfully. Establishment was evidenced by individuals remaining within their webs and by the presence of a capture web by the next evening. Subsequently, all established colonies also created one or more retreat nests.

Prey-attacking behavior and success

We assayed collective foraging behavior of these colonies in the field on 2 consecutive days at 1, 2, and 3 weeks after deployment. In field assays, the pieces of paper that were vibrated were placed on the capture web ~10 cm from the colony's retreat. If multiple capture webs were present, we haphazardly picked one for the assay. The multiple retreats of a colony are often connected by their capture web, and all spiders responding to the vibration were counted, regardless of which retreat they emerged from. Additionally, colonies' capture webs were surveyed daily to note the presence of prey. We calculated colonies' prey capture success as the proportion of days on which prey was observed in the capture web prior to colony death or disbandment (see below).

Colony persistence

In our daily observations, we recorded the day on which spiders were no longer observed emerging from within the retreats, due to individuals either dying or emigrating. Colony death or disbandment was further indicated by degradation in the condition of the capture web and consistent lack of capture web repair over several days, and confirmed at the end of the experiment by breaking apart the retreats and searching for live spiders. At the end of 3 weeks, we recorded the number of retreats built by each colony. We collected all of the retreats, counted the number of individuals remaining in each colony, and scored colony persistence as the presence of any retreat with individuals remaining.

Greenhouse experiment

Eleven colonies of *S. dumicola* were collected near Upington and Groblershoop, South Africa, and transported to the University of California Santa Barbara. We created 42 experimental colonies of 30 individuals each from these 11 natural colonies. Spiders were allowed to construct webs in cups as described above. Colonies were fed 2–4 small crickets weekly. Collective behavior was measured twice while the colonies were in cups: 18 days after colony set up and then immediately prior to deployment. Colonies were deployed on a fence constructed of PVC pipes and wire (fence treatment) and on small shrubs of *Acacia cultriformis* (tree treatment) in a greenhouse maintained between 18 °C and 30 °C.

Experimental colonies were assigned to physical environment treatments haphazardly, though we ensured that experimental colonies from the same source colony were approximately equally represented in both tree and fence treatments and confirmed with *t*-tests that the collective behavior of colonies assigned to these treatments did not differ on average prior to deployment (mean ± standard deviation for latency to attack: fence-dwelling colonies: 64.8 ± 41.5 s, tree-dwelling colonies: 65.3 ± 37.9 s, *t*-test: $t_{40} = 0.05$, $P = 0.96$; mean ± standard deviation for number of attackers: fence-dwelling colonies: 2.3 ± 1.4, tree-dwelling colonies: 2.0 ± 1.0, *t*-test: $t_{40} = 0.91$, $P = 0.37$). Due to space constraints in the greenhouse, colonies were deployed in 3 sequential blocks of 7 colonies per treatment ($N = 21$ per treatment in total).

Prey-attacking behavior

Ten days after deployment, colonies' collective foraging behavior was assayed for 4 consecutive days in each of the 2 consecutive weeks (i.e., with a gap of 3 days), following the protocol described above. In the second set of measurements, we exposed the colonies to wind, but found no effect of wind exposure on the collective behavior of these colonies (see Supplementary Information), so all data were pooled for analyses of the effects of physical environment (see below).

Individual movement

In the greenhouse, some spiders moved from their location of deployment into other colonies' webs. These movements were apparent from the silk laid down by the spiders, and were confirmed by counting spiders in each retreat nest after the experiment. We counted the number of colonies that experienced such immigration or emigration for fence-dwelling and tree-dwelling colonies; only colonies that did not have spiders move to or from them (9 tree-dwelling colonies and 20 fence-dwelling colonies) were included in the analyses of collective behavior described below, though results did not change when all colonies were included (results not shown).

Statistical analysis

Statistical analyses were conducted in R v. 3.3.2 (R Core Team 2016; code is available at https://github.com/ambikamath/stegodyphusfencetree). Throughout, we used permutation tests to assess if continuous response variables (latency to attack prey, number of attackers, prey capture success, number of remaining individuals, number of retreat nests) differed significantly between levels of categorical explanatory variables (physical environment [tree vs. fence] and colony size [large vs. small]). We used nonparametric permutation tests instead of parametric mixed effects models because residuals from parametric models on some variables were not normally distributed and we wanted to be consistent in the analysis of all variables.

In each permutation test, we first calculated the mean of each response variable for each level of the explanatory variable and calculated the absolute difference between these means (e.g., difference between the mean latency to attack of spiders from fence-dwelling colonies and tree-dwelling colonies). To test interactions between 2 explanatory variables, we calculated the absolute difference between means of subsets of the data set; subsets were defined based on combinations of levels of the 2 variables, i.e., for variable x and factors A and B with levels A_1 and A_2 and B_1 and B_2, we calculated $|x_{A1B1} + x_{A2B2} - x_{A1B2} - x_{A2B1}|$. For example, we calculated the sum of the mean latency to attack of large tree-dwelling colonies and small fence-dwelling colonies and then subtracted from this the sum of the mean latency to attack of large fence-dwelling colonies and small tree-dwelling colonies. Next, we randomized levels of the explanatory variable(s) across observations, using the function sample() without replacement in R, within each level of the categorical variable that we wished to control for. For example, when controlling for block ID in the greenhouse experiment, explanatory variable levels were randomized across observations within each block; this way, block-level differences were preserved in the randomization. Then, we recalculated the absolute difference in means of the response variables for the permuted data. We repeated this randomization procedure 10,000 times and calculated the *P*-value for the comparison as the fraction of randomizations in which the randomized absolute difference in means was greater than the observed absolute difference in means, i.e., a 2-tailed test. To convey the magnitude of the observed difference in means between levels for each test, we report how much greater the observed difference was than the mean randomized difference in means (denoted as Δx). Values of Δx greater than 100% indicate that the observed absolute difference in means is greater than expected by chance, and values of −100% < Δx < 100% indicate that the observed absolute difference in means is not greater than expected by chance.

We first examined the effect of physical environment (fence vs. tree) on the 2 measures of collective foraging behavior—latency to attack, and the total number of attackers. For the field experiment, we further tested the effects of colony size and the interaction of physical environment with colony size on the 2 behavioral variables while controlling for assay week (1, 2, or 3 weeks after deployment). We also used the same permutation test procedure to examine the effects of physical environment treatment, colony size, and their interaction on the following variables: prey capture success, the number of individuals remaining in each colony, and the number of separate retreat nests built by each colony. We compared the number of fence-dwelling versus tree-dwelling colonies that persisted to the end of the experiment using a Fisher's exact test.

For the greenhouse experiment, we used randomization tests to deduce the effect of physical environment on the latency to attack and number of attackers, controlling for block ID. We used a Fisher's exact test to assess the effect of the physical environment treatment on whether spiders moved either to or from the colony's web (i.e., whether or not the colony experienced emigration or immigration).

RESULTS

Field experiment

Prey-attacking behavior and success

We found that spider colonies on fences attacked prey 38% quicker (Δx = 255%, $P = 0.0043$) and with 90% more attackers (Δx = 646%, $P < 0.0001$) than colonies on trees (Figure 2a,c) in the field.

We did not detect an interaction between physical environment and colony size on the latency to attack prey (Δx = −69%, $P = 0.81$). Spiders from smaller colonies took 34% longer to attack than spiders from larger colonies but this difference was not significant (Δx = 114%, $P = 0.08$). Larger colonies deployed more attackers (Δx = 382%, $P = 0.0001$) than smaller colonies, but this colony size effect was present only on fences (Δx = 412%, $P = 0.0001$) and not on trees (Δx = −7%, $P = 0.46$; physical environment treatment × colony size interaction: Δx = 208%, $P = 0.015$).

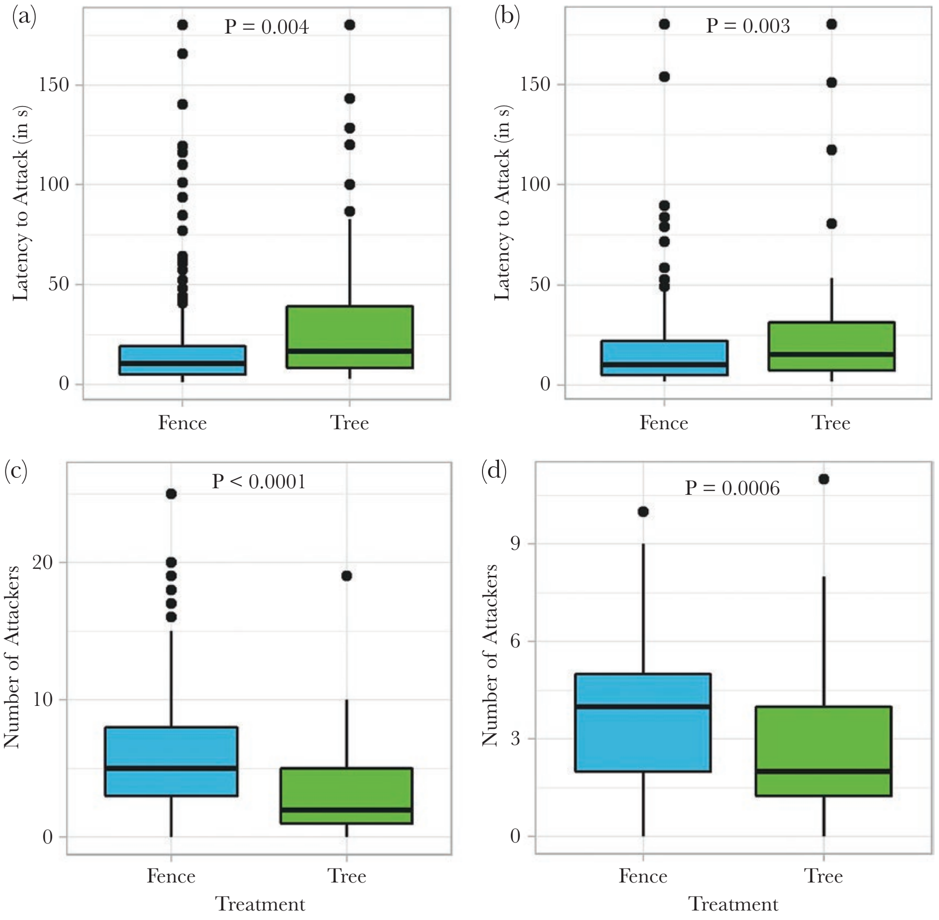

Figure 2
Field (a, c) and greenhouse (b, d) experiments showed similar patterns of differences in the collective prey-attacking behavior of colonies of *Stegodyphus dumicola* deployed on fences and on trees. Colonies on fences tended to attack prey more quickly (a, b) and with a greater number of attackers (c, d), compared to colonies on trees. Here and in the following figure, boxes indicate the lower and upper quartiles; horizontal lines within boxes indicate the median; whiskers extend to the 1.5 interquartile range from the box; and circles indicate outliers.

Physical environment affected the ability of colonies to capture prey in their capture webs. Colonies on fences had prey in their capture webs 37% more often than colonies on trees (proportion of days on which prey was found in the web prior to colony death or disbandment; Δx = 254%, *P* = 0.0045; Figure 3a). Large colonies had prey in their capture webs 36% more often than did small colonies (Δx = 254%, *P* = 0.0036), and there was no interaction between colony size and physical environment on prey found in the capture web (Δx = −99%, *P* = 0.99).

Individual and colony persistence

Spiders in colonies on trees constructed 63% more retreat nests than spiders in colonies on fences (Δx = 302%, *P* < 0.0001; Figure 4a); the number of retreats built did not depend on colony size (measured as the number of individuals in a colony; Δx = 116%, *P* = 0.091), or on the interaction between colony size and physical environment (Δx = 86%, *P* = 0.13). Colonies deployed on fences in the field were 77% more likely to persist than colonies on trees (mean and 95% confidence interval of the odds ratio = 0.0 [0.0, 0.2]; *P* < 0.0001; Figure 3c). Large and small colonies were equally likely to persist (mean and 95% confidence interval of the odds ratio = 0.86 [0.2, 3.5]; *P* = 1). Fence-dwelling colonies contained 3 times as many individual spiders remaining than did tree-dwelling colonies (Δx = 652%, *P* < 0.0001; Figure 3b). We did not detect a difference between large and small colonies (Δx = −97%, *P* = 0.98), nor an interaction between colony size and physical environment (Δx = −90%, *P* = 0.94), on the proportion of individuals that remained at the end of the experiment.

Greenhouse experiment

Prey-attacking behavior

Spider colonies on fences in the greenhouse attacked prey 43% more quickly (Δx = 255%, *P* = 0.003; Figure 2b) and with 36% more attackers (Δx = 302%, *P* = 0.0006; Figure 2d) than colonies on trees.

Individual movement

Tree-dwelling colonies were more likely to experience emigration or immigration into nearby colonies than fence-dwelling colonies (mean and 95% confidence interval of the odds ratio = 24.5 [2.8, 1186.3], *P* = 0.0005; Figure 4b).

DISCUSSION

Our results suggest that the physical environment in which their nests are built can influence the collective behavior and success of *S. dumicola* societies. Thus, the structures constructed by these social spiders do not buffer them against variation in their

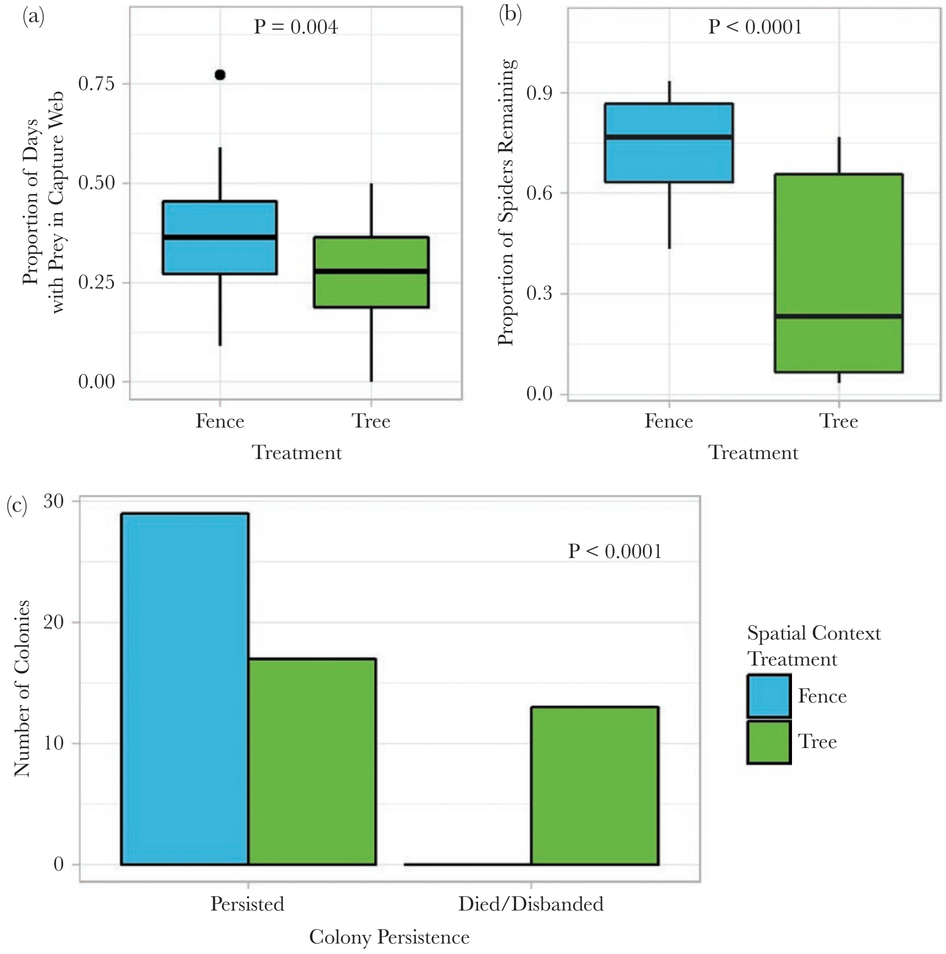

Figure 3

Colonies of *Stegodyphus dumicola* deployed on fences (a) captured prey more often, (b) had a greater number of individual spiders remaining in those colonies that persisted until the end of the experiment, and (c) were more likely to persist than colonies deployed on trees.

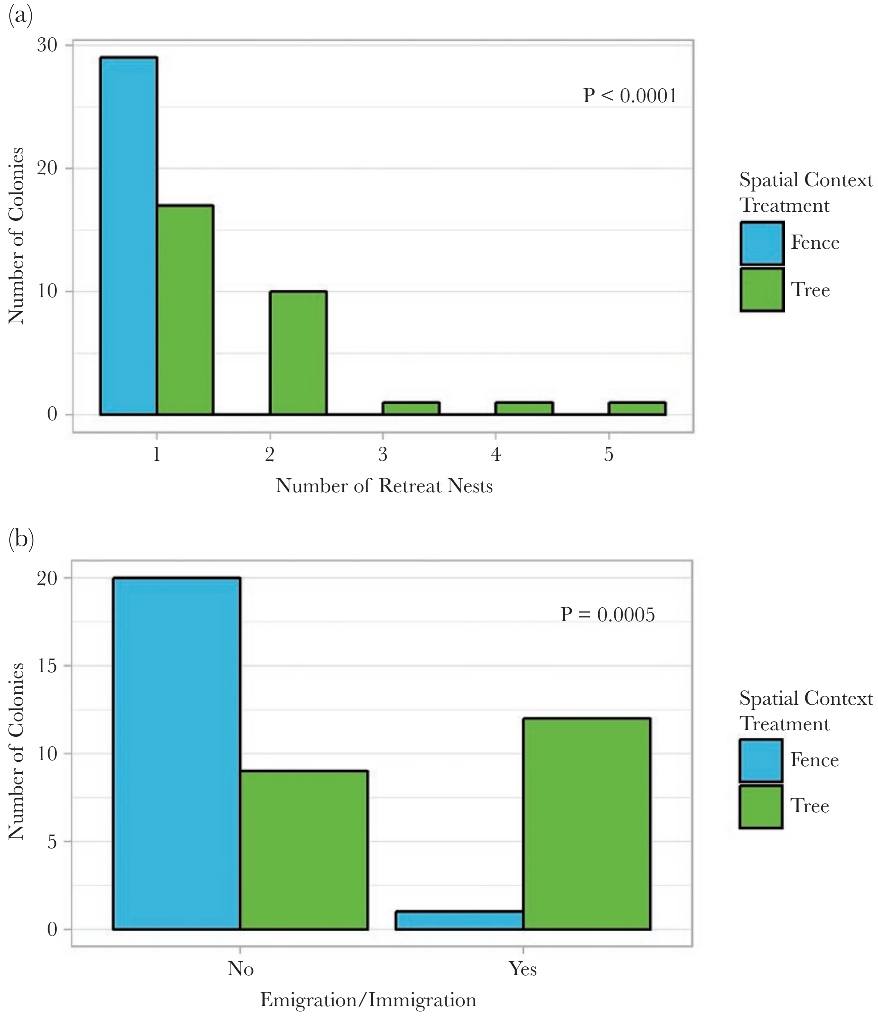

Figure 4
Compared to fence-dwelling colonies, colonies of *Stegodyphus dumicola* on trees were (a) more likely to split into multiple retreat nests in the field and (b) more likely to experience emigration/immigration into nearby colonies in the greenhouse.

external physical environment, including variation induced by human activity.

In particular, spider colonies that built nests on fences attacked prey more quickly and with more attackers than colonies that built their nests in trees. Prey capture—especially the ability to capture large prey—is a time sensitive opportunity that requires a rapid collective response by social spiders (Yip et al. 2008). Furthermore, there is a positive relationship between speed to respond to prey and collective mass gain (Pinter-Wollman et al. 2017). Indeed, consistent with our finding that fence-dwelling colonies attack more quickly and with more attackers, we found that prey was present more frequently in the webs of colonies on fences than colonies in trees. Also consistent with these differences in prey-attacking behavior and prey capture success, we found that fence-dwelling colonies were more likely to persist until the end of the experiment than tree-dwelling colonies; moreover, individuals in fence-dwelling colonies were more likely to survive and remain within the nest compared to individuals in tree-dwelling colonies.

Many species of animals thrive in human-modified environments (reviewed in Ditchkoff et al. 2006; Sol et al. 2013), taking advantage of, for example, increased resource availability in human-dominated areas (Bozek et al. 2007; Merkle et al. 2013). However, the effect we observe in *S. dumicola* is more subtle—here, human-induced changes in the physical structures available for nest construction precipitate shifts in spider behavior that are actually conducive to their increased success. Given that social spiders have built their webs in trees and bushes for the vast majority of their evolutionary history, why or how are *S. dumicola* more successful on fences than on trees? We discuss several proximate and ultimate processes that could plausibly explain this pattern, some of which are suggested or supported by our results and others of which can be ruled out.

First, it is possible that the physical environments of trees and fences impose very different constraints on the structure of the web itself, which in turn constrains or facilitates the spiders' collective behavior in different ways (Nakata 2010; Modlmeier et al. 2014a; Montiglio and DiRienzo 2016; Japyassú and Laland 2017). For example, webs on trees may have more supporting threads, threads at different tensions, or may vibrate more on transverse or radial axes than longitudinally, compared with webs on fences. This, in turn, could lead to lower transmission and greater attenuation of vibrations across the web (Walcott 1963; Masters and Markl 1981; Landolfa and Barth 1996). Such differences in the transmission of vibratory cues could result in spiders taking longer to respond to prey capture cues in tree-dwelling colonies compared to fence-dwelling colonies. More generally, fences are 2-dimensional and relatively homogenous environments whereas tree branches are oriented more 3-dimensionally and are relatively heterogeneous. It is thus possible that social spiders' webs are more complex when built on trees than on fences. For example, tree nests usually have a greater number of capture web sheets positioned at more variable angles, and may therefore have greater variation in thread orientation and connectedness than fence nests. This capture web complexity could readily affect collective behavior. For instance, spiders may take longer to emerge from retreats onto capture webs in tree nests than in fence nests if it takes longer for spiders to navigate a more elaborate web. Our results therefore suggest further research on how the mechanical and structural properties of the environment built by social spiders constrain and influence different aspects of their behavior and consequently their fitness (Pinter-Wollman et al. 2018). A related but distinct hypothesis explaining how web structure influences collective behavior is that different thermal microenvironments might be generated within different types of webs (Jones and Oldroyd 2006). If spiders living in the flatter structures built on fences can warm up more quickly than spiders within the interior of rounder structures built on trees, they could be more active, and would thus be more likely to mount a rapid and sizeable attack on prey (Gunderson and Leal 2016; Abram et al. 2017). Second, fine-scale biotic and abiotic differences between fences and trees that are unrelated to their structural differences may have driven differences in the behavior and success of colonies on fences and trees. However, we found similar behavioral patterns in the greenhouse, where prey availability and other biotic and abiotic factors were more controlled. That said, in the field, colonies on fences deployed 90% more attackers than tree-dwelling colonies, but only 36% more in the greenhouse and it is possible that prey availability contributed in part to the larger differences that we observed in the field. The collective prey-attacking behavior of social spiders can increase in response to increased prey availability (Crouch and Lubin 2000; but see Wright et al. 2016), and the higher prey capture rates and survival of colonies on fences observed here could have been driven by greater prey availability near fences than near trees. Structural differences between fences and trees may therefore interact with fine-scale variation in other abiotic and biotic factors to drive variation in collective behavior that influences individual fitness and group success in turn.

Third, the observed movement patterns of spiders in tree-dwelling colonies—specifically their greater tendency to establish and move between multiple retreats compared to fence-dwelling colonies—could explain some of the observed differences in collective behavior and persistence. Splitting into multiple retreats reduces the number of spiders per retreat, and although these retreats usually remain connected to each other by their shared capture webs, these connections can be destroyed by wind or rain (Purcell and Aviles 2008), effectively dividing a single large colony into several smaller ones. Smaller colony sizes are associated with slower attacks on prey and the deployment of fewer attackers (Keiser and Pruitt 2014) as well as with lower colony persistence (Riechert et al. 1986; Bilde et al. 2007) and slower mass gain (Pinter-Wollman et al. 2017). Thus, colony fragmentation on trees but not fences could explain why spiders in tree-dwelling colonies attacked more slowly and with fewer attackers and were less likely to persist. In effect, colonies in trees but not fences become amalgamations of a large number of smaller, lower-performing colonies. This colony fragmentation may also have masked the effect of the initial size of experimental colonies deployed on trees, potentially explaining why we did not find an effect of colony size on the number of attackers in tree-dwelling colonies or on colony persistence. Finally, individuals' personalities and colony personality composition are known to influence prey-attacking behavior—colonies attack prey faster and with more attackers as the number of bold individuals in the colony increases (Pruitt and Keiser 2014). Splitting into multiple retreats could alter the distribution of personalities within each of these subcolonies. Specifically, bold individuals in tree-dwelling colonies that are split into multiple subcolonies may wield influence over a smaller number of individuals than bold individuals in undivided colonies on fences.

Why might spiders be more likely to establish multiple retreats on trees compared to fences? Short-distance dispersal in social spiders arises from individuals sending out strands of silk and following them if they catch onto a substrate (Pruitt and Avilés 2018). Therefore, dispersal could be more likely on trees because the silk is much more likely to attach to another surface in a complex 3-dimensional environment than in a simple 2-dimensional environment like a fence. This proximate explanation could be tested by observing the short-distance dispersal behavior of spiders in contrasting physical environments. Moreover, this finding further prompts us to ask why, if establishing multiple retreats is detrimental to colony success, has this behavior not been selected against? One testable hypothesis is that in spatially heterogeneous environments, establishing multiple retreats reduces the risk of predation across the whole colony (Van Wilgenburg and Elgar 2007) or otherwise facilitates a form of bet-hedging (Hopper 1999; Starrfelt and Kokko 2012; Childress and Konig 2013), thereby maximizing the likelihood of colony persistence over long time scales (Pruitt 2013). The long-term consequences of the behavioral differences we report will depend on such selective dynamics.

In conclusion, we used field and greenhouse experiments to show that the physical environment in which *S. dumicola* social spiders build their webs influences their collective prey-attacking behavior, their propensity for short-distance dispersal, and the prey capture success and persistence of colonies in nature. Our results demonstrate the importance of human-induced habitat change for revealing variation in animal behavior that may remain hidden in natural conditions, and points to the substantial consequences of the physical environment for the collective behavior and success of animal societies.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

FUNDING

This work was supported by the National Science Foundation Division of Integrative Organismal Systems (grant numbers 1352705, 1455895 to J.N.P., and 1456010 and 1708455 to N.P.-W.); and the National Institutes of Health (grant number GM115509 to N.P.-W. and J.N.P.)

Charles Haddad and the Dawid Kruiper Municipality in Upington, South Africa, provided logistical help. Cameron Bick, Terry Marchiando, and Matthew Petures helped with experimental set up in the greenhouse. Yoel Stuart, Edward Burnell, Alex Gunderson, and two anonymous reviewers made suggestions that improved the manuscript. This work was conducted under research and export permit numbers ODB3130 FAUNA1691 and ODB3129 FAUNA1692.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Kamath et al. (2018).

Handling editor: Louise Barrett

REFERENCES

Abram PK, Boivin G, Moiroux J, Brodeur J. 2017. Behavioural effects of temperature on ectothermic animals: unifying thermal physiology and behavioural plasticity. Biol Rev Camb Philos Soc. 92:1859–1876.

Avilés L, Guevara J. 2017. Sociality in spiders. In: Rubenstein DR, Abbot P, editors. Comparative social evolution. Cambridge (UK): Cambridge University Press. p. 188–223.

Bilde T, Coates KS, Birkhofer K, Bird T, Maklakov AA, Lubin Y, Avilés L. 2007. Survival benefits select for group living in a social spider despite reproductive costs. J Evol Biol. 20:2412–2426.

Blackledge TA, Kuntner M, Agnarsson I. 2011. The form and function of spider orb webs: evolution from silk to ecosystems. Adv. Insect Physiol. 41:175–262.

Bozek CK, Prange S, Gehrt SD. 2007. The influence of anthropogenic resources on multi-scale habitat selection by raccoons. Urban Ecosyst. 10:413–425.

Childress ES, Konig AA. 2013. Polydomus *Crematogaster Pilosa* (Hymenoptera: Formicidae) colonies prefer highly connected habitats in a tidal salt marsh. Fla. Entomol. 96:235–237.

Clutton-Brock T. 2009. Cooperation between non-kin in animal societies. Nature. 462:51–57.

Couzin ID, Krause J. 2003. Self-organization and collective behavior in vertebrates. Adv. Stud. Behav. 32:1–75.

Crouch TE, Lubin Y. 2000. Effects of climate and prey availability on foraging in a social spider, *Stegodyphus mimosarum* (Araneae, Eresidae). J. Arachnol. 28:158–168.

Ditchkoff SS, Saalfeld ST, Gibson CJ. 2006. Animal behavior in urban ecosystems: Modifications due to human-induced stress. Urban Ecosyst. 9:5–12.

Dunn PO, Whittingham LA. 2006. Search costs influence the spatial distribution, but not the level, of extra-pair mating in tree swallows. Behav. Ecol. Sociobiol. 61:449–454.

Gunderson AR, Leal M. 2016. A conceptual framework for understanding thermal constraints on ectotherm activity with implications for predicting responses to global change. Ecol Lett. 19:111–120.

Guttal V, Couzin ID. 2010. Social interactions, information use, and the evolution of collective migration. Proc Natl Acad Sci USA. 107:16172–16177.

Hansell MH. 1993. The ecological impact of animal nests and burrows. Func. Ecol. 7:5–12.

Hopper KR. 1999. Risk-spreading and bet-hedging in insect population biology. Annu Rev Entomol. 44:535–560.

Japyassú HF, Laland KN. 2017. Extended spider cognition. Anim Cogn. 20:375–395.

Johannesen J, Hennig A, Dommermuth B, Schneider JM. 2002. Mitochondrial DNA distributions indicate colony propagation by single matri-lineages in the social spider *Stegodyphus dumicola* (Eresidae). Biol J Linn Soc. 76:591–600.

Jones JC, Oldroyd BP. 2006. Nest thermoregulation in social insects. Adv Insect Physiol. 33:153–191.

Kamath A, Losos JB. 2018. Estimating encounter rates as the first step of sexual selection in the lizard *Anolis sagrei*. Proc R Soc B. 285:20172244.

Kamath A, Primavera SD, Wright CM, Doering GN, Sheehy KA, Pinter-Wollman N, Pruitt JN. 2018. Data from: collective behavior and colony persistence of social spiders depends on their physical environment. Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.3dt11m7

Keiser CN, Jones DK, Modlmeier AP, Pruitt JN. 2014. Exploring the effects of individual traits and within-colony variation on task differentiation and collective behavior in a desert social spider. Behav Ecol Sociobiol. 68:839–850.

Keiser CN, Pinter-Wollman N, Augustine DA, Ziemba MJ, Hao L, Lawrence JG, Pruitt JN. 2016. Individual differences in boldness influence patterns of social interactions and the transmission of cuticular bacteria among group-mates. Proc R Soc B. 283:20160457.

Keiser CN, Pruitt JN. 2014. Personality composition is more important than group size in determining collective foraging behaviour in the wild. Proc Biol Sci. 281:20141424.

Korb J. 2003. Thermoregulation and ventilation of termite mounds. Naturwissenschaften. 90:212–219.

Laland K, Matthews B, Feldman MW. 2016. An introduction to niche construction theory. Evol Ecol. 30:191–202.

Landolfa MA, Barth FG. 1996. Vibrations in the orb web of the spider *Nephila clavipes*: cues for discrimination and orientation. J Comp Physiol. 179:493–508.

Masters WM, Markl H. 1981. Vibration signal transmission in spider orb webs. Science. 213:363–365.

Merkle JA, Robinson HS, Krausman PR, Alaback P. 2013. Food availability and foraging near human developments by black bears. J Mammal. 94:378–385.

Modlmeier AP, Forrester NJ, Pruitt JN. 2014a. Habitat structure helps guide the emergence of colony-level personality in social spiders. Behav Ecol Sociobiol. 68:1965–1972.

Modlmeier AP, Laskowski KL, DeMarco AE, Coleman A, Zhao K, Brittingham HA, McDermott DR, Pruitt JN. 2014b. Persistent social interactions beget more pronounced personalities in a desert-dwelling social spider. Biol Lett. 10:20140419.

Montiglio PO, DiRienzo N. 2016. There's no place like home: the contribution of direct and extended phenotypes on the expression of spider aggressiveness. Behav Ecol. 27:1880–1888.

Morales JM, Moorcroft PR, Matthiopoulos J, Frair JL, Kie JG, Powell RA, Merrill EH, Haydon DT. 2010. Building the bridge between animal movement and population dynamics. Philos Trans R Soc Lond B Biol Sci. 365:2289–2301.

Nakata K. 2010. Attention focusing in a sit-and-wait forager: a spider controls its prey-detection ability in different web sectors by adjusting thread tension. Proc Biol Sci. 277:29–33.

Pinter-Wollman N. 2015. Nest architecture shapes the collective behavior of harvester ants. Biol Lett. 11:20150695.

Pinter-Wollman N, Fiore SM, Theraulaz G. 2017. The impact of architecture on collective behaviour. Nat Ecol Evol. 1:111.

Pinter-Wollman N, Penn A, Theraulaz G, Fiore SM. 2018. Interdisciplinary approaches for uncovering the impacts of architecture on collective behaviour. Phil Trans R Soc B. 373:20170232.

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

Pruitt JN. 2013. A real-time eco-evolutionary dead-end strategy is mediated by the traits of lineage progenitors and interactions with colony invaders. Ecol Lett. 16:879–886.

Pruitt JN, Avilés L. 2018. Social spiders: mildly successful social animals with much untapped research potential. Anim Behav.143:155–165.

Pruitt JN, Keiser CN. 2014. The personality types of key catalytic individuals shape colonies' collective behaviour and success. Anim Behav. 93:87–95.

Pruitt JN, Wright CM, Lichtenstein JLL, Chism GT, McEwen BL, Kamath A, Pinter-Wollman N. 2018. Selection for collective aggressiveness favors social susceptibility in social spiders. Curr Biol. 28:100–105.e4.

Purcell J, Avilés L. 2008. Gradients of precipitation and ant abundance may contribute to the altitudinal range limit of subsocial spiders: insights from a transplant experiment. Proc Biol Sci. 275:2617–2625.

Queller DC, Strassman JE. 1998. Kin selection and social insects. BioScience. 48:165–175.

R Core Team. 2016. R: A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. Available from: https://www.R-project.org/.

Riechert SE, Roeloffs R, Echternacht AC. 1986. The ecology of the cooperative spider *Agelena consociata* in equatorial Africa (Araneae, Agelenidae). J Arachnol. 14:175–191.

Seibt U, Wickler W. 1988. Interspecific tolerance in social *Stegodyphus* spiders (Eresidae, Araneae). J Arachnol. 16:35–39.

Sol D, Lapiedra O, González-Lagos C. 2013. Behavioural adjustments for a life in the city. Anim Behav. 85:1101–1112.

Starrfelt J, Kokko H. 2012. Bet-hedging–a triple trade-off between means, variances and correlations. Biol Rev Camb Philos Soc. 87:742–755.

Van Wilgenburg E, Elgar MA. 2007. Colony characteristics influence the risk of predation of a polydomous ant by a monotreme. Biol J Linn Soc. 92:1–8.

Walcott C. 1963. The effect of the web on vibration sensitivity in the spider, *Achaearanea tepidariorum* (Koch). J Exp Biol. 40:595–611.

Wickler W, Seibt U. 1993. Pedogenetic sociogenesis via the "sibling-route" and some consequences for *Stegodyphus* spiders. Ethology. 95:1–18.

Wright CM, Keiser CN, Pruitt JN. 2016. Colony personality composition alters colony-level plasticity and magnitude of defensive behaviour in a social spider. Anim Behav. 115:175–183.

Wright CM, Lichtenstein JLL, Montgomery GA, Luscuskie LP, Pinter-Wollman N, Pruitt JN. 2017. Exposure to predators reduces collective foraging aggressiveness and eliminates its relationship with colony personality composition. Behav Ecol Sociobiol. 71:126.

Yip EC, Powers KS, Avilés L. 2008. Cooperative capture of large prey solves scaling challenge faced by spider societies. Proc Natl Acad Sci USA. 105:11818–11822.