



Predictors of colony extinction vary by habitat type in social spiders

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Abstract

Many animal societies are susceptible to mass mortality events and collapse. Elucidating how environmental pressures determine patterns of collapse is important for understanding how such societies function and evolve. Using the social spider *Stegodyphus dumicola*, we investigated the environmental drivers of colony extinction along two precipitation gradients across southern Africa, using the Namib and Kalahari deserts versus wetter savanna habitats to the north and east. We deployed experimental colonies ($n = 242$) along two ~800-km transects and returned to assess colony success in the field after 2 months. Specifically, we noted colony extinction events after the 2-month duration and collected environmental data on the correlates of those extinction events (e.g., evidence of ant attacks, no. of prey captured). We found that colony extinction events at desert sites were more frequently associated with attacks by predatory ants as compared with savanna sites, while colony extinctions in wetter savannas sites were more tightly associated with fungal outbreaks. Our findings support the hypothesis that environments vary in the selection pressures that they impose on social organisms, which may explain why different social phenotypes are often favored in each habitat.

Significance statement

Many social animals are susceptible to group extinction events. Identifying the factors that precipitate these events can help us to understand how societies function and evolve. We used a social spider model to evaluate whether the drivers of group extinction events may vary with habitat type. We found that ant attacks were more commonly associated with colony demise at arid sites, whereas fungal outbreaks were associated with collapse in wetter environments. If maintained temporally, these contrasting selection pressures could facilitate the evolution of local adaptation in individual- and colony-level phenotypes and aid in the maintenance of intraspecific trait diversity.

Keywords Colony collapse · Disease · Extinction · Geographic variation · Local adaptation

Introduction

The evolution of sociality changes the ways in which species interact with their environments. Living in groups can confer

the ability to construct larger refuges, subdue more profitable prey, mount amplified defenses against would-be enemies, and increase fitness through alloparental care (Krause & Ruxton 2002, Lubin & Bilde 2007). However, sociality is

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not without costs. Group-living organisms may suffer enhanced resource competition as they struggle to support a larger number of co-occurring conspecifics (Yip et al. 2008, Mayer et al. 2018). They may become more conspicuous to predators (Wrona & Dixon 1991) or be more susceptible to disease (Côté & Poulinb 1995). These costs can accumulate to a critical level at which they outweigh the benefits conferred by sociality, causing a group to collapse or go extinct (Avilés and Tufino 1998).

Site-specific selection, through which discrete areas impose divergent selection on a species, is a relatively common feature in nature that often results in phenotypic diversity (Siepielski et al. 2009, Siepielski et al. 2013, Caruso et al. 2017). For example, spatial and temporal variation in precipitation patterns (Siepielski et al. 2017), prey community structure (Drummond & Burghardt 1983), or interference competition (Riechert 1993) can all generate contrasting patterns of selection on individuals, often resulting in local adaptation. We propose that, like selection pressures predicting the survival or demise of individuals, pressures driving group extinction events might differ according to the environments in which a group resides.

Social spiders provide a convenient means with which to observe the relationship between the environment and group extinctions. Most species of spider are solitary and intolerant of conspecifics; however, social species are less aggressive overall and have higher conspecific tolerance than their solitary counterparts (Lubin & Bilde 2007, Harwood & Avilés 2018). This distinction allows social spiders to coexist in a communal web and work cooperatively on collective tasks, such as foraging (Whitehouse & Lubin 2005), web construction and maintenance (Riechert 1985, Purcell & Avilés 2008), alloparental care (Whitehouse & Jackson 1998), and defense against predator attacks (Henschel 1998, Purcell & Avilés 2008, Yip & Rayor 2011, Wright et al. 2016). Despite these seemingly adaptive collective behaviors, however, many species of social spiders experience high rates of colony extinction in the wild (Aviles 1986, Henschel 1998).

Several hypotheses have been proposed to explain the high incidence of colony extinction events in social spiders. First, the transition to sociality in spiders is met with a transition from outbreeding to inbreeding, which results in low effective population sizes and a reduced ability to respond to changing environmental pressures (Agnarsson et al. 2006, Settepani et al. 2017). Second, the evolution of sociality is associated with a decrease in cross-contextual aggressiveness (e.g., towards conspecifics, heterospecifics, prey, and potential predators/parasites) and increased conspecific densities that together render social spiders susceptible to a diversity of ecological pressures (Pruitt et al. 2012). These pressures include invasion by foreign species of spiders (Cangialosi 1990, Pruitt 2012), increased detection rate by ant predators (Purcell & Aviles 2008, Keiser et al. 2015), increased susceptibility to

starvation and local resource competition (Aviles et al. 2002, Yip et al. 2008, Majer et al. 2018), and an increased propensity to spread socially transmitted microbes (Henschel 1998, Keiser et al. 2018). Different habitats may vary in the severity of these pressures based on local conditions (e.g., prey availability, predator abundance).

In this study, we evaluate whether environments with contrasting precipitation regimes differ in the factors associated with group extinction events. Precipitation has been identified as a key driver of selection across many systems (Purcell 2011, Hoffman & Avilés 2017, Siepielski et al. 2017) and, as we outline below, is a candidate variable that may influence the threats to the survival of social spider groups.

The social spider *Stegodyphus dumicola* (Araneae, Eresidae) occupies both arid and wet regions throughout southwestern Africa in colonies ranging from 1 to 2000 spiders (reviewed in Avilés & Guevara 2017). *Stegodyphus dumicola* colonies in the wild experience mixed success. Though the species is reasonably common, *S. dumicola* experiences high colony extinction rates (Henschel 1998, Pruitt et al. 2018; data herein). The causes of these high mortality rates are potentially manifold, such as a failure to capture sufficient prey (Majer et al. 2018), succumbing to colony attacks performed by ants (Henschel 1998, Keiser et al. 2015), and the spread of fungus through the colony web (Henschel 1998). The high rate of colony extinction in *S. dumicola* renders this species as a convenient model with which to explore associations between habitat type and the correlates of colony extinction. Prior studies on *S. dumicola* have found that the relationship between colony traits and success differs predictably across wet vs. arid sites (Pruitt et al. 2018), hinting that the pressures driving colony success and collapse may differ across environments.

Here we evaluate the following a priori predictions: we predict that colonies at wet savanna sites will capture more prey than colonies at arid sites, because insect abundance and biomass increase in habitats with higher precipitation (Janzen and Schoener, 1968). However, increased insect prey parts within spider webs combined with higher moisture at wet sites may facilitate the growth of fungus. Thus, we predict colony extinctions will be more frequently associated with fungal outbreaks at wet sites than at arid sites. Prior studies at arid sites have demonstrated that predatory ants are a lethal and disruptive force upon *S. dumicola* (Henschel 1998, Keiser et al. 2015, Wright et al. 2017). Although the threat of predatory ants towards *S. dumicola* has not been directly assessed in wet habitats, increased ant abundance in habitats with greater primary productivity suggests that these pressures may be even stronger at wet sites (Kaspari et al. 2000). Accordingly, we predict that higher ant populations at wet sites will increase frequency of attacks by predatory ants, as well as colony mortalities due to ant attack. To evaluate these predictions, we compared the frequency of colony extinction events between

desert and savanna sites and evaluated whether the factors associated with colony extinction differed predictably across these habitat types.

Methods

The data herein were collected as part of a larger study examining site-specific selection on collective behavior and leader-follower interactions in social spiders (Pruitt et al. 2018). Pruitt et al. (2018) evaluated for and confirmed the presence of site-specific selection for social susceptibility at arid sites, using the survivorship data presented in this paper along with behavioral data not used here. The following data on correlates of extinction and risk of various selective agents, which are the unique focus of this paper, have not been published previously. The current paper therefore aims to identify differences in environmental selective forces that may underlie the site-specific selection described in Pruitt et al. (2018). There are no redundant conclusions between this paper and any other work published by our group.

All applicable institutional and/or national guidelines for the care and use of animals were followed.

Collection

We collected whole colonies of *S. dumicola* along roadside fences and *Senegalia mellifera* trees at eight study sites. Sites were distributed across two precipitation transects: one extending north from the Namib Desert towards Angola (810 km), the other extending east from the Kalahari Desert towards Lesotho (981 km) (Fig S1). Each transect contained four sites, two arid desert sites (Kalahari gradient: Upington [−28.403361, 21.071249] and Boegoeberg [−29.037819, 22.027999]; Namib gradient: Rehoboth [−23.209881, 17.092] and Kalkrand [−24.065027, 17.580452]) and two wetter savanna sites (Kalahari gradient: Ladysmith [−38.65655, 29.625249] and Weenen [−28.856239, 30.142306]; Namib gradient: Rundu [−18.299209, 19.407636] and Outjo [−20.233099, 16.354468]). In all, we collected 211 source colonies with populations of mature females spanning from 75 to 512 individuals per colony.

We collected colonies by placing a cloth pillowcase over the entire nest, then either prying the nest loose from fence wires or using garden clippers to separate the retreat from its substrate. We transported colonies in a climate-controlled vehicle to nearby hotels for separation/isolation. We individually dissected colonies by hand, separating each mature female spider into a 59-ml deli cup for a 24-h isolation period prior to assembling experimental colonies. When creating experimental groups, care was taken not mix individuals from multiple source colonies. In social *Stegodyphus*, variation in relatedness and/or familiarity has been demonstrated to alter

colony behavior and performance (Modlmeier et al. 2014, Laskowski et al. 2016).

Experimental colony assembly

We created a total of 242 experimental colonies, each containing 20 mature female spiders. Experimental colonies were housed in 390-ml plastic cups, each containing three *S. mellifera* twigs to facilitate web construction. Several holes were punched into the bottom of each cup to allow for water drainage for instances of rain. Colonies were housed in their group cups for a total of 5 days at a temperature of 22–25 °C before deployment into the field at their respective sites. During this time, colonies were able to acclimate to their new housing as well as build a silken retreat structure. This serves to both disincentivize dispersal from their deployment location and provide structural protection from their environment during colony establishment.

Experimental colony deployment

We deployed our experimental colonies across the eight sites (28–33 colonies per site) using clothespins to attach individual cups to *S. mellifera* trees. Each colony was attached to its own tree (> 3-m distance between deployment trees) to minimize interaction between colonies. *Stegodyphus dumicola* individuals will occasionally disperse to the nearest branch tip following deployment, but most frequently begin building their capture web directly atop the clothespin fixing their cup to the substrate. Allowing a pre-deployment period for the spiders to weave and establish a retreat structure serves to suppress post-deployment dispersion and has been successfully implemented in prior field experiments using experimental colonies of *S. dumicola* (Grinsted et al. 2013, Keiser & Pruitt 2014, Keiser et al. 2015, Wright et al. 2017). Colonies were not deployed onto trees that were actively being patrolled by predatory ants (genera *Anoplolepis* and *Crematogaster*), as these ants have previously been demonstrated to destroy colonies before they can become established (Keiser et al. 2015) and actively rove vegetation in search of prey (Doering et al. 2018). Colonies were deployed in an order that did not conflate one climate type with time of release: (1) wet (Rundu, Nov 2016), (2) wet (Outjo, Nov 2016), (3) dry (Rehoboth, Nov 2016), (4) dry (Kalkrand, Nov 2016), (5) dry (Upington, Dec 2016), (6) dry (Boegoeberg, Dec 2016), (7) wet (Ladysmith, Dec 2016), (8) wet (Weenen, Jan 2017). Colonies were deployed at the same site from which their source colonies were collected.

Colony checks and correlates of extinction

To determine colony survival, colonies were left in their environments for the next 2 months. We then returned to each

colony and determined whether it had survived or had gone extinct. We deemed a colony to have gone extinct if no living members of the society persisted.

To determine the potential causes of colony extinction, in addition to evaluating survival, we noted cues as to whether both surviving and extinct colonies had experienced attack by predatory ants or fungal outbreak. Substantial quantities of *Anoplolepis* spp. ant carcasses in the capture web, nest, and deployment container provided evidence of an attack by ants (Yip & Rayor 2011, Keiser et al. 2015). *Stedodyphus dunicola* do not generally consume *Anoplolepis* as prey, and instead respond in an antipredator fashion by weaving hyperadhesive cribellate silk to stave ants off from the retreat (Henschel 1998, Keiser et al. 2015). Evidence of a fungal outbreak was noted if fungus was sprouting from carcasses of colony members, prey items, and the web (Henschel 1998). To measure the amount of prey captured by the colony, we recorded the number of desiccated prey carcasses within each capture web and nest. Unlike many spider species that discard prey carcasses from their web after consumption, *S. dunicola* instead weave spent prey items directly into the three-dimensional retreat structure of their web. As such, an observer may count the number of prey items captured by the colony.

Statistical methods

We first established that our arid and wet sites experienced quantitatively different rates of precipitation by performing a *t* test on each site's monthly rainfalls over the 5 years preceding the experiment (2013–2017). We grouped Kalkrand (Namibia), Rehoboth (Namibia), Upington (S. Africa), and Boegoeberg (S. Africa) as our arid sites, and grouped Rundu (Namibia), Outjo (Namibia), Ladysmith (S. Africa), and Weenen (S. Africa) as our wet sites. Rainfall data specific to these sites was obtained from World Weather Online.

We used GLMMs to test for associations between colony persistence, factors reasoned to cause colony extinctions in *S. dunicola* (ant attacks, fungal outbreak, no. of prey captured), and habitat type (arid/wet) in R (RStudio ver. 1.1.383) using the package lme4 (Bates et al. 2014). We first compared overall rates of colony extinction between arid and wet sites by constructing a model with site type (arid/wet) as a fixed effect, site ID as a random effect, and colony survival (1/0) as a binary response variable. We used a binomial error distribution with a logit-link function.

To investigate how site type affected prey capture rates, we constructed a model including site type (arid/wet) as a fixed effect, site ID as a random effect, and the number of prey recovered from the colony's web as a response variable. We fitted a Poisson error distribution and log-link function. This model included data only from colonies that both survived the duration of our study and were not attacked by ants. This is because (i) colonies that perished would have had different

and unknown lengths of time in which to capture prey and (ii) ants typically steal prey during attacks on *S. dunicola*, thus obscuring prey capture estimates from those colonies (Henschel 1998).

To test for an association between mortality due to fungal outbreak and site type, we constructed a model with site type as a fixed effect, and site ID as a random effect, and incidence of fungal outbreak (1/0) as a binary response variable. We designated a binomial error distribution with a logit-link function. To focus on mortality-specific incidences of fungal outbreak, this model included data only from colonies that perished.

To test whether ant attacks occurred more frequently at wet sites, we constructed a model with site type as a fixed effect, site ID as a random effect, and evidence of ant attack (1/0) as a binary response. We designated a binomial error distribution with a logit-link function. We included both surviving and extinct colonies in this analysis; including both fatal and non-fatal attack events informs us of the overall frequency of predatory ant encounters. To evaluate whether colony mortality due to ant attack was more prevalent at wet sites, we constructed a model including site type as a fixed effect, site ID as a random effect, and evidence of ant attack as a binary response variable (1/0). We designated a binomial error distribution with a logit-link function. For this model, we used data only from colonies that had perished in order to focus on mortality-specific instances of these attacks.

In a post hoc analysis, we tested whether the number of prey present in a web was associated with fungal outbreaks. For this model, we ran a GLMM with prey number, site type, and their interaction term as fixed effects, site ID as a random effect, and incidence of fungal outbreak as a binary response.

Results

As predicted, we found that our arid and wet site designations reflected quantitatively different precipitation regimes. Monthly precipitation at wet sites was found to be higher than that at arid sites ($t = 6.12$, $p < 0.0001$). Notably, wet sites experienced over double (~ 45 mm per month) the rainfall of arid sites (~ 22 mm per month) during their rainy season of December through March.

We found that colonies at arid and wet sites experienced comparable survival rates ($\sim 55\%$ arid vs. $\sim 44\%$ wet), with a non-significant trend towards colonies surviving slightly better at arid sites (*site type*: z -stat = -1.787 , $df.resid = 239$, $p = 0.0739$).

Among surviving groups that had not been raided by ants (47 colonies or 41% of colonies at arid sites; 48 colonies or 38% of colonies at wet sites, Table 1), colonies at wet sites had higher prey capture rates than colonies at dry sites (*site type*: z -stat = 8.853 , $df.resid = 94$, $p < 0.0001$; Fig. 1). Surviving

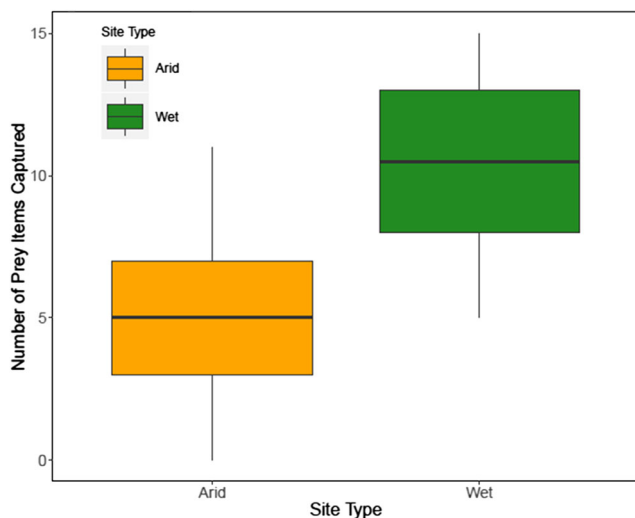
Table 1 Numerical reporting of colony survival, extinctions, and prey capture. Survivorship, mortalities, and correlates of extinction in experimental colonies of *S. dumicola* over the 2-month study period. Extinction percentages indicate the percentage of colony extinctions attributed to each factor

Habitat type	Colonies deployed	Survived	Extinct	Total ant attacks	Ant extinctions	Total fungal infections	Fungal extinctions	Average prey captured
Arid	116	64	52	45	30 (58%)	5	2 (4%)	5.2
Wet	126	55	71	22	15 (21%)	26	23 (32%)	10.3

colonies at wet sites contained an average of 10.3 prey items, whereas colonies at arid sites contained an average of 5.2 prey items (Table 1).

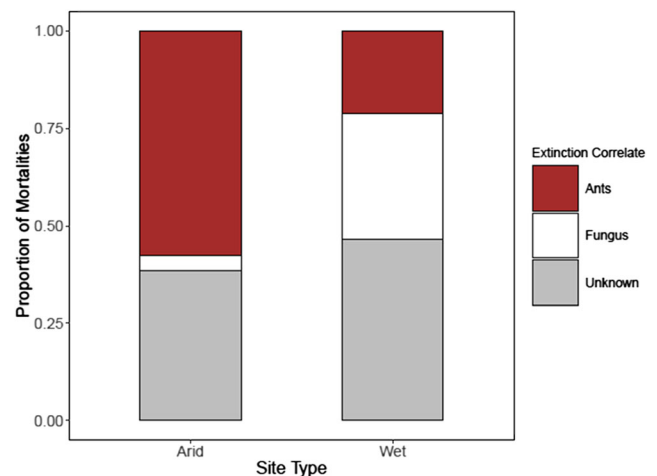
Our prediction that fungal outbreaks would be associated with colony extinctions at wet sites was corroborated by our data. A total of 31 colonies (5 colonies or 4% of deployed colonies at arid sites; 26 colonies or 21% of deployed colonies at wet sites, Table 1) displayed evidence of fungal outbreak. Only 6 of these colonies survived the duration of the study. Among colonies that perished, we detected a significant difference in the frequency of fungal outbreaks across site types (*site type*: z -stat = 3.248, $df.resid = 120$, $p = 0.0012$; Fig. 2). Evidence of fungal outbreak was observed in 32% of the colonies that perished at wet sites and only 4% of colonies that perished at arid sites (Table 1).

We found that prey capture rates were positively associated with fungus across *both* site types, as the fixed effect of prey number was significant (*prey number*: z -stat = 2.367, $df.resid = 237$, $p = 0.01795$; Fig. 3) but the interaction term was not (*site type* × *prey number*: $p = 0.0957$). Therefore, colonies that had a greater number of prey carcasses in the web were more likely to experience fungal outbreaks, regardless of site type (Fig. 3).

**Fig. 1** Number of prey items captured differs between site types. Number of prey items recovered from webs of colonies that survived the full duration of the study and did not display signs of ant attack in arid sites (orange) and wet sites (green). Boxes indicate the lower and upper quartiles; horizontal lines within boxes indicate the median, and whiskers extend to the 1.5 interquartile range from the box

Our prediction that frequency of ant attack would be higher at wet sites was not corroborated by our data. Instead, the frequency of ant attack (including all attack events, survived by the colony or not) was higher in arid habitats than in wet habitats (*site type*: z -stat = -3.630, $df.resid = 239$, $p = 0.0003$). A total of 67 (45 colonies or 39% of deployed colonies at arid sites; 22 colonies or 17% of deployed colonies at wet sites, Table 1) colonies had evidence of ant attack, 45 of which went extinct. Among colonies that perished, we found that the arid site type was associated with evidence of ant attacks (*site type*: z -stat = -4.027, $df.resid = 120$, $p < 0.0001$; Fig. 2). At arid sites, 58% of colony extinction events were associated with evidence of attacks by ants. In contrast, at wet sites, only 21% of colony mortality events were associated with evidence of an attack by ants (Table 1).

Of the 67 colonies that displayed signs of an ant attack, only 2 colonies had *any* prey items remaining in their web. Both prey-containing webs yielded only one prey item each: the elytra of a very large beetle. This result is consistent with prior field observations that *Anoplolepis* ants will consume *S. dumicola*, nest webbing, and remnant prey carcasses during attacks (Henschel 1998).

**Fig. 2** Correlates of extinction vary by site type. Proportion of total colony extinctions associated with ant attacks (red), fungal outbreaks (white), and unknown causes (gray) at arid (left) and wet (right) sites. Colonies containing *Anoplolepis* spp. carcasses were noted to be attacked by predatory ants, while colonies containing puffs of white fungus riddled through the nest were recorded as associated with fungal outbreaks

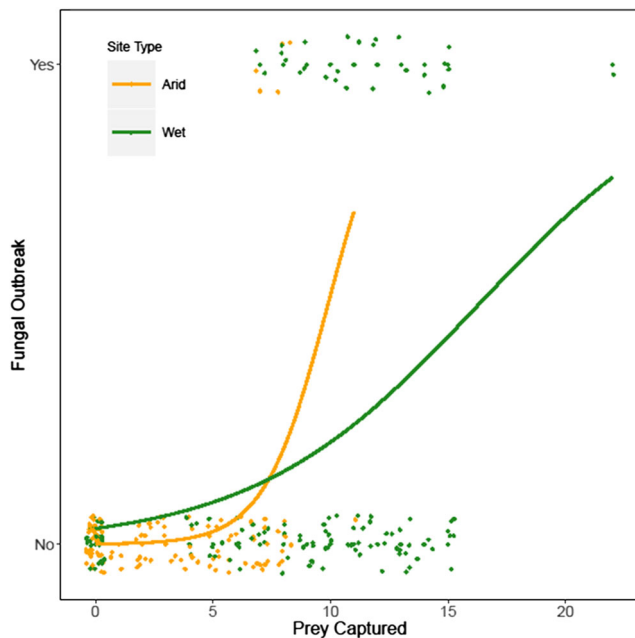


Fig. 3 Incidence of fungal outbreak versus prey capture rate. Relationship between (binary) occurrence of fungal outbreak and prey capture rate at arid (orange) and wet (green) sites. Points are jittered along the y axis to improve visibility. A logistic regression of predicted values for fungal outbreak as a function of prey capture is displayed by site type (arid: orange, wet: green). No significant interaction between site type and prey capture was detected; colonies at both site types experience comparable increasing risk of fungal outbreak with increasing prey capture

Discussion

The study herein leverages a large array of experimental colonies distributed across two deserts and their associated savannahs to evaluate possible drivers of colony extinctions in social spiders. While these data are admittedly only correlative and of a coarse temporal sampling scheme, we detected highly reliable associations between habitat type and likely drivers of colony extinction. We found that ant attacks were the most common correlate of colony extinction events at arid sites, whereas fungal outbreaks were most commonly associated with colony extinction events at wetter savannas. These differences may therefore impose divergent selection pressures on colony attributes at different site types, as has previously been shown in *S. dumicola* (Pruitt et al. 2018), the Amazonian social spider *Anelosimus eximius* (Lichtenstein et al. 2019), and the transitionally social spider *Anelosimus studiosus* (Pruitt & Goodnight 2014).

We did not observe clear differences in overall survivorship/extinction rates in colonies across arid versus wet sites. Thus, both kinds of environments appear equally lethal to colonies, but sources of mortality differ. Colonies were deemed extinct if they contained no living members upon final evaluation. It is admittedly possible that some colonies were mis-classified as extinct, if all living members

dispersed before evaluation. However, multiple assessments were taken during colony deployment to verify that our experimental colonies were appropriately settled. Furthermore, for colonies that perished in association with fungal outbreaks, the carcasses of the spiders were still clearly visible in the ruined nest. This too conveys that these “extinctions” were not merely mass dispersal events that varied by site or habitat type. Finally, there is no evidence that long-distance dispersal from our colonies either is common or varies between arid and wet sites. We therefore reason that our assessments of colony extinctions are consistent across our two site types and represent legitimate colony-wide extinctions.

Our first prediction posited that colonies in wet sites would capture more prey than colonies in arid sites. When examining only surviving colonies, which had equal amounts of time to capture prey, we found that colonies in wet sites indeed had capture rates approximately twice those of colonies at arid sites. This is consistent with data demonstrating that savannas are more productive habitats than tropical deserts (Lieth 1973) and support larger numbers of phytophagous insects (Janzen and Schoener, 1968), which constitute most of the prey for *S. dumicola* (Majer et al. 2018). Prey size was not directly recorded in our observations. However, wetter habitats are generally home to a higher number of smaller, soft-bodied insects compared with deserts, where desiccation risk is more pronounced (Loveridge 1968, Edney 2012). This could skew average prey size across our site types, such that colonies at wet sites might capture smaller prey on average. However, these soft-bodied prey items are not predicted to leave behind as many conspicuous chitinous remains (more characteristic of larger insects), which we used as evidence for prey capture success. Thus, we would predict that our assessment strategy would have underestimated the prey captured by colonies at wet sites relative to arid sites. Yet, we still observed far more prey captured by the webs of colonies at wet sites relative to arid sites.

Consistent with predictions, fungal outbreaks were both more frequent and more commonly associated with extinction in wet sites than in arid sites. One of the likely causes of these outcomes is that entomopathogenic fungus may require more humid conditions to persist and reproduce. This humidity may interact with the higher number of prey items in webs at wet sites to increase the chance of unconsumed prey spoiling and sprouting fungus. Wet sites may also have greater prey diversity with the potential to harbor and transmit fungus to *S. dumicola* colonies. Colonies at wet sites have a higher interaction rate with such prey, as evidenced by their incorporating a larger number of prey carcasses into their webs. Each of these factors has the potential to contribute to increased fungal outbreaks observed at wet sites. Recent metagenomic data from the webs, nests, and cuticles of *S. dumicola* confirm that microbial transmission from prey to spiders is common (Keiser et al. 2019). Furthermore, prior observations of *S. dumicola* colonies infected by fungus note that individuals

“became lethargic and died” (Henschel 1998), indicating that fungal infection can lead to the mortality of these spiders. Alternatively, it is also possible that fungal outbreaks may occur after a colony’s demise. This would give the appearance that a colony had been killed by a fungal outbreak. However, the fact that several colonies were observed to be infected by fungus and still functional lends support to the hypothesis that fungal outbreak precedes colony extinction. Further, were fungal outbreaks merely a byproduct of extinct colonies rotting in a wetter environment, the relationship between increased prey capture and fungal outbreak might have been weaker or non-existent altogether.

At odds with our primary predictions, ant attacks appeared to be both more frequent at arid sites and more likely to lead to mortality for arid-dwelling colonies. Whether ants that prey upon *S. dumicola* are indeed more abundant at arid sites is yet unclear. We reason that an identical number of predatory ants at arid sites could prove more lethal to social spiders than the same number of ants at wet sites. This is because arid deserts, being less structurally complex than wetter savannas, are potentially easier for predatory ants to navigate and explore, leaving little opportunity for social spider colonies to go unnoticed. It is also likely that there are fewer alternative prey at arid sites that might distract predatory ants or satiate them. Deserts are known to limit the time and number of days that ant colonies can forage (Gordon 1991, Pinter-Wollman et al. 2012, Gordon 2013) and their prey preferences (Traniello et al. 1984), due to worker desiccation risk. If this is true in *Anoplolepis*, then this imposition is insufficient to decrease ant-driven lethality to social spider colonies at these sites.

We found that most of the spider colonies attacked by ants had zero prey items in their web. Of the 67 colonies that displayed signs of ant attack, only 2 colonies had prey in their capture webs. Observations of interactions between *Anoplolepis* ants and *S. dumicola* note that attacking ants eat nearly everything in the capture web during their attack (Henschel 1998, Keiser et al. 2015). Additionally, should a colony survive an ant attack (as in 22 of 67 observed attacks in this study), a history of ant attacks is known to decrease colony foraging aggressiveness (Wright et al. 2017). Thus, even non-lethal attacks by ants, if suffered early enough in a colony’s history, could render the group less likely to capture prey later. This could also contribute to the observed differences in prey capture rates across sites, because colonies at arid sites captured fewer prey. These effects are costly, as collective foraging aggressiveness is associated with colony mass gain and colony persistence in this system (Pinter-Wollman et al. 2017, Pruitt et al. 2018, Kamath et al. 2018a).

Roughly 30% of extinctions in arid sites and 40% of extinctions in wet sites did not display evidence of ant attack or fungal outbreak, demonstrating that there are other factors influencing colony mortality. Prior work over a smaller spatial scale (Henschel et al. 1996, Henschel 1998) more exhaustively

documents the various agents of mortality in *S. dumicola*. Potential sources of our undiagnosed extinctions are numerous but include biotic factors such as predatory birds, wasps (Rayor & Uetz 1990, Rayor 1996), and kleptoparasitic or araneophagous spiders (Cangialosi 1990, Rypstra & Tirey 1991), as well as abiotic factors (e.g., stochastic damage to the deployment tree). However, prior work on *S. dumicola* (Henschel 1996) identified predatory ants and fungal outbreaks as the most potent agents of colony extinctions in this system (e.g., predation by ants accounting for 45% of mortalities, compared with predation by birds and araneophagous spiders at 3% each and predation by wasps at 1%), which served as motivation for our focusing on these sources of mortality.

Identifying spatial (between environments) and temporal (between seasons and across years; as in Bengston 2018) variation in selection on collective phenotypes helps us to understand the context-dependent evolution of these traits (Wray et al. 2011, Scharf et al. 2012, Bengston & Dornhaus 2014, Jandt et al. 2014, Jolles et al. 2018, Kamath et al. 2018b). In a prior study, Pruitt et al. (2018) demonstrated the existence of site-specific selection on colony aggression in *S. dumicola*. In this study, we delved further into this system to test for environmental correlates of these extinction events to ascertain what factors might cause site-specific selection on colony behavior. We found that the correlates of colony extinction differed characteristically across site types in *S. dumicola*, with ant attacks being associated with colony extinction primarily at arid sites and fungal outbreaks being associated with extinctions at wet sites. These differences, in turn, may help to explain the differences in selection pressures on colony behavior seen in *S. dumicola* (Pruitt et al. 2018). While we reason that similar site specificity of group extinction drivers could be common in other social taxa, more field data like the kind herein are required to critically evaluate the generality of such findings.

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Author contributions JNP and NPW conceived the experiment. BLM, JLL, CMW, GTC, and JNP performed the experiment. BLM and DNF analyzed the data. BLM, DNF, and JNP wrote the manuscript; other authors provided editorial input.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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