

# Site-specific group selection drives locally adapted group compositions

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**Group selection may be defined as selection caused by the differential extinction or proliferation of groups<sup>1,2</sup>. The socially polymorphic spider *Anelosimus studiosus* exhibits a behavioural polymorphism in which females exhibit either a ‘docile’ or ‘aggressive’ behavioural phenotype<sup>3,4</sup>. Natural colonies are composed of a mixture of related docile and aggressive individuals, and populations differ in colonies’ characteristic docile:aggressive ratios<sup>5,6</sup>. Using experimentally constructed colonies of known composition, here we demonstrate that population-level divergence in docile:aggressive ratios is driven by site-specific selection at the group level—certain ratios yield high survivorship at some sites but not others. Our data also indicate that colonies responded to the risk of extinction: perturbed colonies tended to adjust their composition over two generations to match the ratio characteristic of their native site, thus promoting their long-term survival in their natal habitat. However, colonies of displaced individuals continued to shift their compositions towards mixtures that would have promoted their survival had they remained at their home sites, regardless of their contemporary environment. Thus, the regulatory mechanisms that colonies use to adjust their composition appear to be locally adapted. Our data provide experimental evidence of group selection driving collective traits in wild populations.**

In societies in which individual fitness is tightly linked with the performance of the group, the theory of group selection predicts that evolution will favour traits in individuals that aid in maximizing their group’s success—which, in turn, are predicted to increase individuals’ long-term evolutionary interests<sup>7,8</sup>. Here we define group selection as selection caused by the differential extinction or proliferation of groups<sup>1</sup>. This represents a broad definition that is not in any way adversarial to the importance of kinship selection for social evolution<sup>9</sup>. Although the basic idea of group selection has intuitive appeal, its success as a general explanation of adaptive social evolution has been marred by critiques of its reasoning and usefulness<sup>10–12</sup>. In this paper we provide compelling experimental evidence that group selection drives locally adapted group compositions in wild populations.

The social spider *A. studiosus* exhibits a discrete and heritable (Extended Data Fig. 1) behavioural polymorphism in which individuals display a ‘docile’ or ‘aggressive’ phenotype<sup>5,13</sup>. In nature, colonies are composed of a mixture of related docile and aggressive individuals, and the mixture of types within colonies has large consequences for collective behaviour and colony reproductive success<sup>3,4,14</sup>. We also observe site-specific docile:aggressive mixtures (Fig. 1a), which may reflect local adaptation, such that different sites favour different ideal compositions. Notably, *A. studiosus* exhibits high rates of colony extinction events<sup>3,4</sup> and limited dispersal<sup>4,6</sup>, two attributes that are thought to increase the power of group selection as an evolutionary force<sup>1,2,15</sup> (see Supplementary Discussion 1 for more natural history information).

To determine whether site-specific docile:aggressive mixtures are a result of group selection, we generated an array of artificial colonies of known, variable compositions and deployed them at six field sites: three high-resource sites (Melton Hill, Tennessee; Little River, Tennessee; and Moccasin Creek, Georgia) and three low-resource sites (Norris Dam, Tennessee; Clinch River, Tennessee; and Don Carter, Georgia) (Extended

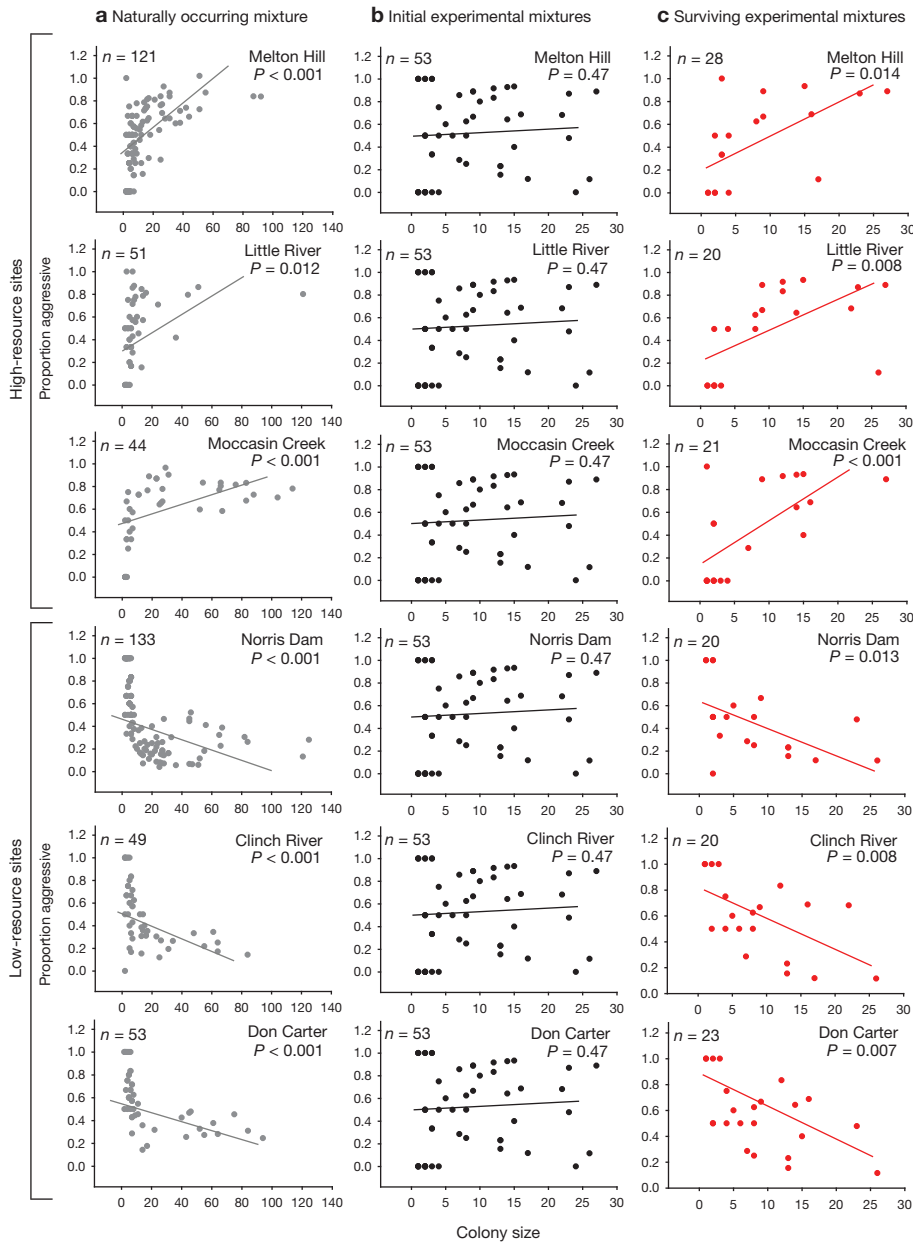
Data Fig. 2). We determined 53 random combinations of colony size (1–27 females) and composition (0–100% aggressive) and deployed an identical array at each site. Thirty-seven colonies were composed of individuals taken from the site where they were subsequently deployed (that is, ‘native’ individuals), and 16 colonies were composed of individuals taken from a paired site of the opposing resource level (that is, ‘foreign’ individuals). Females assigned to experimental colonies all came from the same source colony. This design allowed us to test whether site of origin influenced selection on colony composition and/or colonies’ ability to approximate an optimal composition over time. We deployed these arrays of native and foreign colonies in three paired, reciprocal transplant experiments between high- and low-resource sites: Melton Hill was paired with Norris Dam, Little River with Clinch River (all in Tennessee), and Don Carter with Moccasin Creek (both in Georgia). If group selection is a major selective force that has caused local adaptation in this system, we predict that (1) compositions that approximate the normal mixtures that characterize each site will enjoy greater success, and (2) colonies should only be able to adaptively hone their compositions when composed of native individuals, either because the cues that spiders use to sense their colonies’ ailing compositions or their responses to those cues will be site-specific and locally adapted.

We monitored the success of experimental colonies over the next two generations and noted all instances of colony extinction. We also monitored the composition of 20 naturally occurring ‘local’ colonies at each site. We used these naturally occurring colonies to assess whether our experimental colonies exhibited uncharacteristically low or high extinction rates.

The naturally occurring relationship between colony size and composition differed across sites (general linear model (GLM) site  $\times$  colony size:  $F_{5,280} = 294.27$ ,  $P < 0.0001$ ; Fig. 1a). At our high-resource sites, small colonies were dominated by docile females and the frequency of aggressive individuals increased with colony size. By contrast, at low-resource sites, small colonies were dominated by the aggressive phenotype and the frequency of the docile phenotype increased with colony size (Fig. 1a). The fact that different sites exhibit different relationships between colony size and composition raises the question as to why some compositions are site-specific or whether the observed compositions are locally adapted.

The success of our experimental colonies depended on how well their starting compositions matched the naturally occurring mixture at each site (GLM dissimilarity: likelihood ratio (L-R)  $\chi^2_1 = 52.81$ ,  $P < 0.001$ ). The more similar a colony’s composition was to the naturally occurring local mixture, the higher its probability of surviving. Thus, although there was no significant relationship between colony size and composition in experimental colonies at the start of our experiment (Fig. 1b), there was a significant relationship between colony size and composition two generations later (Fig. 1c). The surviving colonies at each site form a size/composition relationship approximating those of naturally occurring colonies, which differed between high- and low-resource sites (Fig. 1a versus c). Therefore, site-specific group selection, as mediated by colony extinction events, appears to drive the size/composition relationships that characterize each site. Colonies’ reproductive output was also tightly associated with how well they approximated the naturally occurring mixture

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**Figure 1 | Site-specific group selection.** a–c, Scatterplots depicting the colony size versus composition relationship at six riparian sites. a, The naturally occurring, local size/composition relationship. b, The array of 53 experimental colonies of various size/composition combinations deployed at each test site

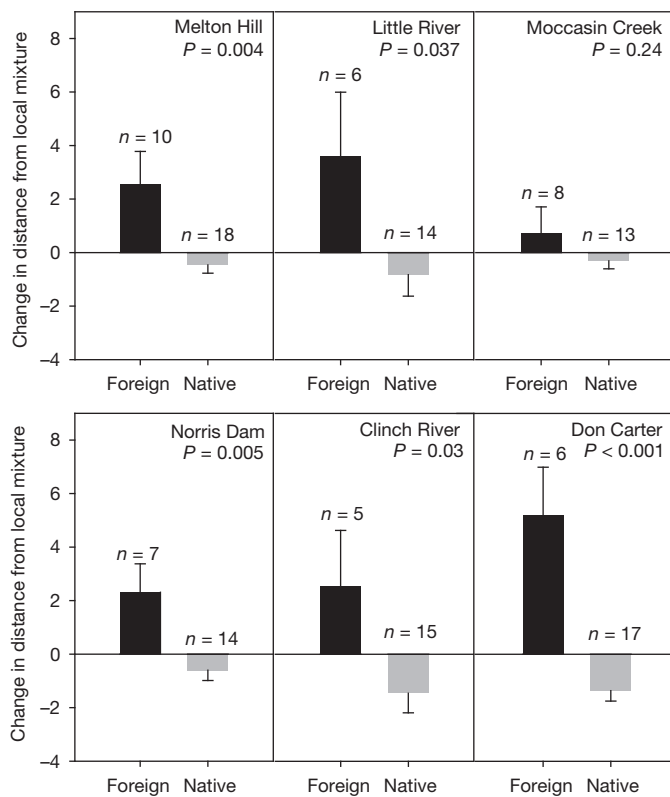
at each site (GLM dissimilarity:  $F_{1,297} = 15.91$ ,  $P < 0.001$ ). Experimental colonies with compositions resembling local colonies produced nearly ten times as many offspring colonies as those bearing moderately dissimilar mixtures, and those with extremely dissimilar mixtures never produced any offspring colonies.

Among the experimental colonies that survived, the compositions of some colonies tended to move closer to the local and successful size/composition relationship while others moved markedly further away. Shifts in colonies' mixtures depended on whether colonies were composed of native versus foreign individuals ( $F$  ratio:  $F_{1,130.7} = 33.35$ ,  $P < 0.001$ ; Fig. 2). Colonies composed of native individuals tended to become more similar to the local mixture, whereas foreign colonies became significantly more dissimilar. Instead, foreign colonies adjusted their compositions to more closely approximate a mixture that would have promoted their survival had they remained at their site of origin (paired  $t$ -test:  $t_{41} = 3.77$ ,  $P < 0.001$ ). In other words, foreign colonies tracked the ideal compositions

(16 points not visible owing to identical size/composition). c, The size/composition combinations of experimental colonies that survived two generations in the field.  $P$  values are the result of univariate regressions. These field experiments were replicated once at each site.

of their home sites regardless of their contemporary environment, and they did this despite having persisted in their new environment for multiple generations. These findings provide compelling evidence that the mechanisms that colonies use to regulate their compositions are themselves locally adapted, presumably because of the survival advantages that they confer to the colony.

Group selection is potentially a powerful and persistent force in *A. studiosus*. Natural populations of *A. studiosus* have characteristic ratios of docile:aggressive individuals, and these ratios affect colony success<sup>3,4</sup>. Here, we demonstrate that the ideal ratios of docile:aggressive individuals vary among sites, and that naturally occurring colonies exhibit ratios that promote colony survival across generations. These results suggest that colonies have evolved to exhibit an ideal site-specific trait mixture, and that the differential survivorship and reproductive success of groups (that is, group selection<sup>1,2,10</sup>) is the driving force. Notably, *A. studiosus* colonies are composed of related individuals<sup>14</sup>, thus colonies differ from



**Figure 2 | Colonies can hone ailing mixtures.** Graph depicting the average change in colonies' dissimilarity from the local mixture: high-resource (top panels) and low-resource sites (bottom panels). Colonies were released at each site and were composed of either 'native individuals' that were collected from the same site where they were subsequently deployed, or 'foreign individuals' that were collected from a paired site of the opposing resource levels. Positive values indicate that colonies became more dissimilar to the local mixture, whereas negative values indicate that colonies became more similar to the local mixture. *P* values for site-by-site comparisons are depicted on the graph (*t*-tests). Bars represent standard error of the mean. These field experiments were replicated once at each site.

each other genetically. This, in turn, can help to explain the apparent marked evolutionary response to group selection in this system. Additionally, our study followed groups for two generations, meaning that all of the original spiders died during the course of the experiment and at the end of the study we were sampling the behaviour of their offspring's offspring. Thus, the patterns shown here should reflect an evolutionary response to group selection, and not only those patterns of group selection that could lead to an evolutionary response. Our observation that groups matched their compositions to the one optimal at their site of origin (regardless of their current habitat) is particularly important given that many respected researchers have argued that group selection cannot lead to group adaptation except in clonal groups<sup>16</sup> and that group selection theory is inefficient and bankrupt<sup>17,18</sup>.

The group selection literature is frequently criticized because it is often not clear whether or how group selection has actually caused the evolution of any trait. Our data here provide evidence that *A. studiosus* has responded to group selection by evolving the capacity to avoid low-performing trait mixtures. Interestingly, this ability was specific to spiders collected and redeployed at their home sites, and the ability was lost when colonies were placed in a novel habitat. If colonies of foreign individuals had been able to adaptively adjust their compositions regardless of their contemporary environment (home versus away) this would have provided evidence that the ability was entirely plastic. Yet, we found the opposite trend: displaced colonies continued to hone their compositions in ways that would have promoted their survival had they remained at their home sites. Thus, we reason that group selection has favoured

colonies' ability adaptively to adjust their composition, and either the cues that colonies use to assess their ailing compositions or the actions colony members take in response are site-specific and genetically influenced (a gene  $\times$  environment interaction). How native spiders are actually able to adjust their composition is unknown, but plausible regulatory mechanisms include developmental plasticity in the docile:aggressive phenotypes, policing of group membership, phenotype-biased dispersal, and/or selective cessation of reproduction. That said, we disfavour the first hypothesis that developmental plasticity in the docile:aggressive phenotypes has a large role, since the docile:aggressive distinction is both highly repeatable ( $r = 0.70$ ) and heritable ( $h^2 = 0.66$ , Extended Data Fig. 1). However, neither estimate approximates 1. Thus, we must acknowledge the possible role that developmental plasticity in these traits may have in this system. Still, we propose that aspects of behavioural plasticity in response to the social environment (for example, selective eviction of fellow group members or cessation of reproduction) are the more likely causes.

Why different sites favour different ideal compositions is unknown, but relevant selection pressures could include social parasitism and egg case cannibalism<sup>4</sup>. The ecological factors associated with extinction differed across the sites in our study (GLM site  $\times$  social parasite abundance: L-R  $\chi^2_1 = 24.41$ ,  $P < 0.001$ ; GLM site  $\times$  proportion of egg cases cannibalized: L-R  $\chi^2_1 = 20.93$ ,  $P < 0.001$ ). Egg case cannibalism was associated with colony extinction at all three low-resource sites but none of the high-resource sites, and the abundance of social parasites (heterospecific spiders) within colonies was associated with extinction at all three high-resource sites but none of the low-resource sites (Extended Data Fig. 3). Thus, the correlates of extinction are tightly linked with sites' resource levels, and this could explain why sites with similar resource levels also exhibit similar size/composition relationships and outcomes of group selection.

Our study extends a strong historical body of work on group selection by conducting careful experimental manipulations on natural populations. First, there are studies that show that laboratory or domestic populations can respond to group selection<sup>19–22</sup>. However, laboratory studies typically have selection imposed by the investigator and are certainly not 'natural' settings. Second, there are studies showing that group selection acts in natural populations or in large mesocosms, for example, work on harvester ants<sup>23,24</sup> or studies on water striders<sup>25</sup>. These studies confirm that we cannot ignore the importance of group selection in nature. However, such studies are based on phenotypic selection and they have never documented variation in group selection across environments. Last, there are studies that show that there are adaptations that appear to be the result of multilevel selection<sup>26,27</sup>. What was missing from this literature until now was an experimental field study that tied all of these elements together. Our study shows group selection acting in a natural setting, on a trait known to be heritable, and that has led to a colony-level adaptation.

**Online Content** Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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**Supplementary Information** is available in the online version of the paper.

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**Author Contributions** J.N.P. designed the experiment, performed the experiment, and wrote the manuscript. C.J.G. assisted with data analyses and writing of the manuscript.

**Author Information** The source data for this manuscript have been deposited in the Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.87g80>). Reprints and permissions information is available at [www.nature.com/reprints](http://www.nature.com/reprints). The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to J.N.P. ([pruittj@pitt.edu](mailto:pruittj@pitt.edu)).

## METHODS

**Collection and laboratory maintenance.** Mid-instar *A. studiosus* were collected along six riparian habitats: Norris Dam, Tennessee (36°13'27'' N 84°5'29'' W); Melton Hill, Tennessee (35°53'7'' N 84°18'0'' W); Moccasin Creek, Georgia (34°50'41.69'' N 83°35'17.11'' W); Little River, Tennessee (35°32'40'' N 84°3'1'' W); Clinch River, Tennessee (35°53'33.46'' N 84°1'4.96'' W); and Don Carter, Georgia (34°23'15.43'' N 83°44'47.26'' W). Colonies from Norris Dam and Melton Hill were collected in March 2010. Colonies from the remaining sites were collected in February 2013. Colonies were collected by placing the colony within a cloth pillowcase and trimming off the supporting branches using pruning snips. Colonies were transported back to the laboratory at the University of Pittsburgh and dissected out by hand. Individual spiders were housed in 59 ml plastic delicatesen cups containing a tangled ball of poultry wiring to facilitate web construction. Spiders were maintained on an *ad libitum* diet of termite workers and fed twice weekly until they reached maturity. Upon reaching maturity, the behavioural phenotype of each individual was determined using the established inter-individual distance test described later. Females were mated randomly to a male of like behaviour type from their same source population, but which was collected from a source colony >5 m distance. The average dispersal distance of this species is 30–40 cm<sup>4,6</sup>.

**Inter-individual distance assay.** Two females of unknown tendency were individually marked with fluorescent powder and placed in the centre of a clear plastic container (13 × 13.5 × 2.5 cm). After 24 h of settling time, we measured the distance between them. All females that exhibited an inter-individual distance greater than zero (that is, they were not in direct contact) were run through a second confirmatory test with a known docile female (that is, one that previously exhibited an inter-individual distance score of zero). This test is necessary to tease apart the two types of females, because aggressive females demand space and chase away docile females. Females that exhibited an inter-individual distance <7 cm in the second confirmatory test were categorized as 'docile' and females that exhibited an inter-individual distance >7 cm were categorized as 'aggressive'. Seven centimetres corresponds to a natural break in the distribution of inter-individual distance measures between the two phenotypes<sup>5</sup>. Inter-individual distance scores are repeatable over individuals' lifetimes, heritable (Extended Data Fig. 1), and highly correlated with several other aggressiveness and boldness measurements<sup>28</sup>.

Although aggressive females demand 7 cm (or more) space in this assay, this does not translate entirely cleanly to the spatial organization of females in natural colonies. Anecdotally, aggressive females seem to position themselves on the outskirts of colonies. And, colonies composed of all or mostly aggressive females tend to have fewer individuals per unit web volume.

**Colony establishment and release.** Females were assigned to experimental colonies within 1 week of their maturation, and painted with a unique pair of coloured dots atop their cephalothorax using fast-drying modelling paint. Experimental colonies were constructed of varying sizes and compositions, ranging from 1–27 females and 0–100% aggressive individuals. Fifty-three mixtures were determined at random using a random number generator in Excel (Microsoft 2010). These same mixtures were deployed at each of our six study sites (total  $n = 318$ ). Thirty-seven of these colonies were composed of individuals taken from the same source site where they were subsequently deployed (native individuals), and 16 colonies were composed of individuals taken from a paired site of an opposing resource. This procedure allowed us to observe whether site of origin influenced selection on colony composition and/or individuals' ability to approximate their optimal compositions over time. Sample sizes reflect a balance of feasibility of replication and our desire to maximize our statistical power. We used three high- versus low-resource site pairs to execute three reciprocal transplant experiments of identical design: Melton Hill (high) with Norris Dam (low), Little River (high) with Clinch River (low) and Moccasin Creek (high) with Don Carter (low).

Colonies were first housed in 473 ml clear plastic cups, each containing a compact ball of poultry wiring to facilitate web construction. After 7 days of web construction, spiders were given an *ad libitum* meal of immobilized 4-week old crickets. Colonies were then allotted another 5 days to construct their webs before being established.

Release localities were selected using pre-existing, naturally occurring colonies as indicators of habitat quality. At each locality, the resident colony was removed and replaced with a randomly selected experimental colony. We then searched the adjacent foliage 4 m around each experimental colony and removed all naturally occurring colonies. We allotted a minimum of 6 m between the placements of experimental colonies. This permitted us to count the number of descendent colonies produced by each experimental colony. Colonies that appeared in the immediate vicinity (<1 m) of an experimental colony were assumed to be descendants of the nearby experimental colony, since 95% of individuals disperse within 2 m of their natal webs.

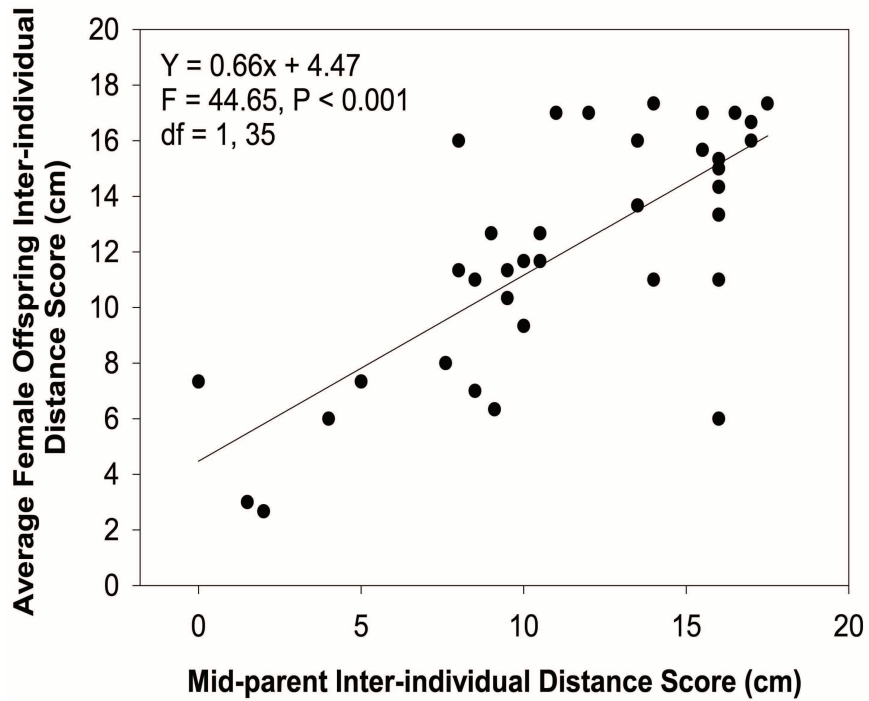
**Colony monitoring.** Colonies were checked every 3–4 months for the next 14–18 months and all colony extinction events were noted. We monitored the colonies at Melton Hill and Norris Dam for 18 months and we monitored the colonies deployed at the other four sites for 14 months. Colonies were deemed to have gone extinct if no living *A. studiosus* could be observed within the colony, the colony lacked fresh silk deposition, and no newly established offspring colonies were observed within a 1 m radius of its original release locality, which could indicate that individuals fled their ailing colonies immediately before their colony collapsed. A 1 m radius is sufficient to track >95% of all dispersing *A. studiosus*<sup>4,29</sup>. Furthermore, dispersal routes of individual females are tracked with relative ease because females deposit a thread of dragline silk as they disperse through the environment, which literally highlights their dispersal routes. In this particular study we failed to observe any incipient colony formation associated with the extinction of our experimental colonies. This further indicates that there were no surviving individuals.

We also recorded the number of foreign spiders (social parasites) within colonies, the number of prey actively being consumed or struggling in a 2 min scan sample, and the proportion of egg cases cannibalized during the height of the reproductive season once for each colony. These metrics were used to test for associations between various ecological factors/pressures and colony survival. At the end of the 14–18-month period, the surviving colonies were re-collected and their size and composition was determined using the protocols described earlier. Observers were blind to colony composition when recording colony vitals.

**Field census of natural colonies.** To ensure that the patterns observed in our experimental colonies resembled that of natural colonies at either test site, 20 natural colonies of varying sizes at each site were selected and monitored over 14–18 months. We haphazardly removed all visible residents (1–28 spiders) using an aspirator in April 2011, determined their aggressive/docile phenotype, and returned them to their source colony within 48 h. We then tracked the survivorship of these colonies over 14–18 months. The rate of colony extinction events in these colonies (20 per site) was compared against our experimentally reconstituted colonies, and against 15 entirely unaltered colonies per site. This allowed us to compare the extinction rates of colonies that experienced differing levels of experimental invasiveness, and to determine whether our protocols generated unnaturally high/low extinction rates.

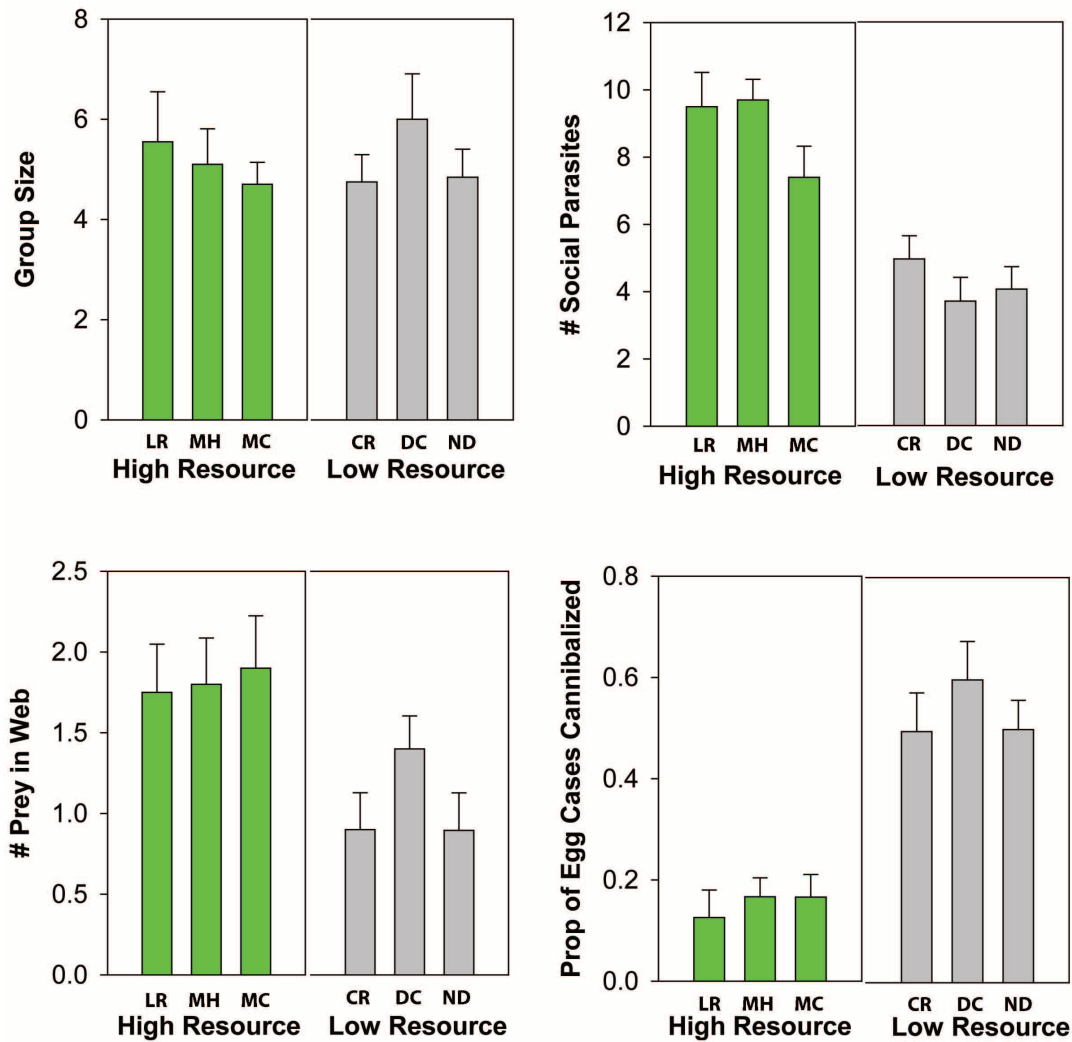
**Statistical methods.** Data were inspected for normally distributed residuals and heteroscedasticity before analysis. To assess whether colonies' size/composition relationship differs among sites, we used a general linear model to predict the number of aggressive females within colonies, with colony size (total number of females), site identifier, and their interaction term as predictor variables, and the number of aggressive females as our response variable. To test whether the determinants of colony extinction differed among sites, we used a multiple logistic regression model with colony size, composition, release site, spiders' site of origin (native versus foreign), colonies' dissimilarity, dissimilarity × release site, composition × colony size, and composition × colony size × site as predictor variables, and survival as a binary response variable. Colonies' dissimilarities were calculated as the distance of each colony from the naturally occurring regression of colony composition (number of aggressive females) on colony size at each site. This distance reflects the dissimilarity of each experiment colony from the naturally occurring composition in demographic space. To test whether colonies composed of native versus foreign spiders differentially shifted their dissimilarity from the naturally occurring size/composition relationship, we used a matched/pair test to compare the same colony at its starting distance to its distance at the end of the study. We then compared the change in distance of colonies composed of native versus foreign individuals using a nested analysis of variance (ANOVA) with individual observations nested within release site and release site designated as a random effect. We also ran separate *t*-tests for each release site independently. Finally, we determined whether colonies of foreign individuals continued to track the mixtures that characterize their home site by using an omnibus paired difference test with release site included as a random effect. We ran all of these analyses four times, first with the proportion of aggressive females as our measure of colony demography, second with the number of aggressive females as our measure of colony demography, third with the average aggressiveness of colony constituents as our measure of colony demography, and fourth with the number of aggressive females as our measure of colony demography but with all singleton colonies dropped from the analyses. Nearly identical patterns of significance were obtained for all three analyses (Supplementary Note 1). All statistics were conducted using JMP 10.0 (SAS Institute).

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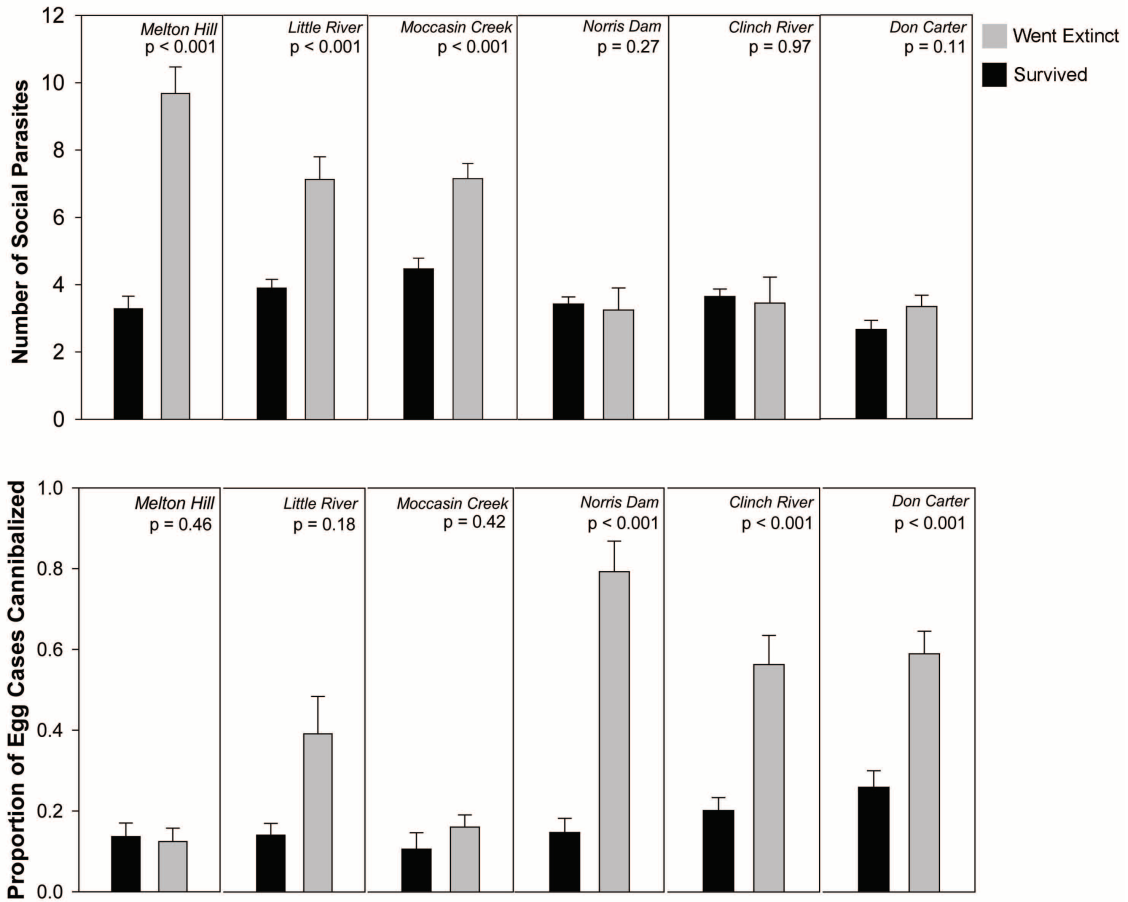
**Extended Data Figure 1 | The heritability of the docile/aggressive phenotype as estimated by offspring on mid-parent regression.** Dams and sires were mated randomly and three female offspring were randomly selected from each brood for assays. The average inter-individual distance score of

the three female offspring was regressed on mid-parent inter-individual distance. The slope of the resulting regression provides the estimate of heritability ( $h^2 = 0.66$ ).



Extended Data Figure 2 | The average group size, number of social parasites, numbers of prey captured in colonies' webs, and the proportion of egg cases cannibalized at the height of the reproductive season for three high-resource sites and three low-resource sites. The sites looked at were

Little River (LR), Melton Hill (MH), Moccasin Creek (MC), Clinch River (CR) Don Carter (DC), Norris Dam (NR). Data presented here represent the averages obtained from 20 randomly selected naturally occurring colonies at each site. Error bars represent standard error of the mean.



**Extended Data Figure 3 | A figure depicting the relationship between colony extinction and two ecological variables: the number of social parasites (heterospecific spiders) and the proportion of egg cases cannibalized at the time of colony extinction. Colony extinction events were**

associated with social parasite presence in high resource populations and egg case cannibalism in low resource populations. Error bars represent standard error of the mean.