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Received: 20 June 2022 | Revised: 15 December 2022 | Accepted: 26 December 2022

DOI: 10.1111/eth.13360

RESEARCH ARTICLE

ethology | WILEY

Population differences in the aggregation and collective foraging behavior of fragmented social spider colonies

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Funding information
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Editor: Marie Elisabeth Herberstein

Abstract

Long-term interactions among individuals are a hallmark of animal societies, but groups rarely remain entirely stable over time. Individuals die or emigrate, or groups become spatially fragmented. Group fragmentation can alter the phenotypic composition of subgroups by separating well-connected individuals or altering sex ratios, which may alter the execution of collective behaviors. Over 10 days, we measured the aggregation behavior and collective prey capture of experimentally fragmented social spider (*Stegodyphus dumicola*) colonies collected from different populations in South Africa and Namibia. Colonies were fragmented for 4 weeks, after which subgroups were allowed to aggregate into a single group over time in a shared novel environment. Namibian colonies aggregated more rapidly than South African colonies. Across both populations, colonies containing individuals with higher average boldness values (faster recovery time after an antagonistic stimulus) attacked prey stimuli with more participants. However, bolder colonies from South Africa attacked prey stimuli faster, whereas attack latency in Namibian colonies was unaffected by colony boldness. These data suggest that fragmentation events, which are a common phenomenon in this species and other animal societies, can influence how individuals interact to accomplish collective tasks. Further, collective behavior and group fusion after fragmentation events can differ among groups from different populations.

KEYWORDS
collective behavior, group fragmentation, polydomy, population differences, *Stegodyphus dumicola*

1 | INTRODUCTION

Social groups are characterized by long-term interactions among individuals, but rarely do social groups remain entirely stable over time (Jacobs, 2010). Groups often become divided into smaller subunits, either temporarily or permanently, as seen in fission-fusion societies of apes (Amici et al., 2008), dolphins (Pearson & Wursig, 2008), or bats (Willis & Brigham, 2004). Arthropod societies that live in colonies can also separate into multiple spatially separated yet socially connected units, a phenomenon referred to as "polydomy" (Robinson, 2014). Polydomy can arise in response to increased population density (Cao, 2013) or interactions with enemies (Dahbi et al., 2008). Polydomy may distribute risk among subunits, can improve foraging organization, and potentially reduce the impact of nest-size limitations (Robinson, 2014). Hypothesized costs of polydomy include the increased energetic costs and risk associated with travelling between groups (Ellis & Robinson, 2014; Handegard et al., 2012; Robinson, 2014).

Group phenotypic composition (e.g., caste ratio, sex ratio, behavioral type mixture) can drastically affect the execution of collective behaviors (Farine et al., 2015). For example, the mixture of proactive and reactive behavioral types in great tits maintains cohesion during foraging (Aplin et al., 2014), variation in individual swimming ability explains leadership dynamics in sticklebacks (Jolles et al., 2017),

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and the mixture of aggressive and docile ants can predict colony defense in acorn ants (Modlmeier, Keiser, Shearer, & Pruitt, 2014). Further, group fragmentation may alter the ability to execute collective behaviors because the phenotypic composition of the subunits may vary from that of the original group. By dividing a group into multiple subunits, the ability to organize group behaviors may be limited, in part, by the isolation of key individuals from large portions of the group (Modlmeier, Keiser, Watters, et al., 2014) or the separation of familiar group-mates (Swaney et al., 2001). Beyond theoretical investigations, little is known about how phenotypic composition in subdivided groups alters group behaviors (Del Mar Delgado et al., 2018). Systems in which groups can be experimentally fragmented and their collective behavior tractably measured can be utilized to address questions about fragmentation, fusion, and group behavior.

Stegodyphus dumicola is a social spider that lives in colonies of tens to hundreds of highly inbred individuals in Southern Africa (Johannesen et al., 2007; Settepani et al., 2017). Colonies are female-biased and females collectively attack prey, co-feed, and cooperatively maintain the web (Avilés, 1997). Social *Stegodyphus* spp. build large webs consisting of a dense communal retreat and one or several two-dimensional capture webs. However, colonies are often found with multiple retreats connected by a shared capture web (i.e., fragmented or polydomous colonies; Henschel, 1998). Colony fragmentation can occur via multiple processes: larger colonies often fragment into smaller nearby subunits (Keiser & Pruitt, 2014); predator attacks are also capable of fragmenting a spider colony into smaller interconnected subunits (Henschel, 1998; Keiser et al., 2015). Finally, the substrate on which spiders build nests can influence the likelihood of fragmentation (Kamath et al., 2019). Collective prey capture in *Stegodyphus* spiders is influenced, in part, by the composition of individual phenotypes present in the colony including personality (Keiser et al., 2014; Keiser & Pruitt, 2014) and internal states such as hunger level (Parthasarathy et al., 2022).

Here, we observe the collective behaviors of experimentally fragmented spider colonies that varied in group phenotypic composition, collected from different source populations in South Africa and Namibia. Our goal here is not to test the effects of colony fragmentation on foraging, as it is already known that fragmented colonies differ from intact colonies in their collective prey capture (Kamath et al., 2019; Najm et al., 2020). Rather, we focus on the effects of group phenotypic composition and population origin on collective behavior in subdivided groups. Using experimentally fragmented colonies in the laboratory, we address three questions: (1) Does colony phenotypic composition alter aggregation after fragmentation? In other words, does a colony's mixture of different behavioral types predict the likelihood and timing of fusion after its separation into multiple subunits? (2) Does colony behavioral composition alter the latency with which fragmented colonies attack prey? (3) Are there population differences in postfragmentation prey capture and group fusion dynamics?

2 | MATERIALS AND METHODS

2.1 | Animal collection

We collected *S. dumicola* colonies in bushes and shrubs along roadsides from South Africa and Namibia in December 2018. The South African colonies were collected along the N10, N14, and R31 highways, while the Namibian colonies were collected along the B1 highway between Mariental and Windhoek (Figure 1a). Colonies were collected by clipping the connecting branches with gardening shears and placing the colony in a 1 L plastic cup. Colonies were then transported to the University of Florida by plane for experiments.

2.2 | Subcolony formation

We haphazardly collected eight *S. dumicola* colonies (four from South Africa and four from Namibia). From these eight wild colonies, we split each colony in half, to obtain two replicates per wild colony, and then fragmented those halves into experimental colonies for a total of 16 experimental colonies. All spiders in the experimental colonies appeared to be adults or penultimate juveniles. The 16 experimental colonies were then split into four smaller subcolonies, each containing 10 spiders, in 350-ml plastic cups with two wooden rods as a substrate for web-construction (Figure 1b). At this time, each subcolony was haphazardly assigned a color designation: blue, green, orange, or yellow. Each spider was given a paint dot on the dorsal abdomen corresponding to their assigned subcolony after boldness assays (see below). Spiders remained in their subcolonies for 4 weeks where they built a retreat and capture webs together and collectively fed on prey. All subcolonies were maintained at ambient lab conditions (~25°C; natural light–dark cycle plus artificial lights between 9:00 a.m. and 5:00 p.m.) and fed one 2-week-old cricket twice per week.

2.3 | Boldness assays

We measured the boldness of each spider immediately after its colony was split into four subcolonies using an established behavioral assay (Lohrey et al., 2009; Riechert & Hedrick, 1990). Boldness was measured as the latency to resume movement after an aversive stimulus. Spiders were placed individually into the center of a petri dish (150 mm diameter) and covered with a small plastic cup for a 60 s acclimation period. Then, we administered to each spider two rapid puffs of air from an infant nasal bulb, which initiated an antipredator huddle response (movement is halted and legs pulled under the body). We recorded the time it took for each spider to move a full body length after the stimulus, waiting up to 10 min. If individual did not move within 10 min, we assigned the maximum value of 600 s. Bolder individuals resume movement more rapidly, shyer individuals resume movement more slowly, though we treated this

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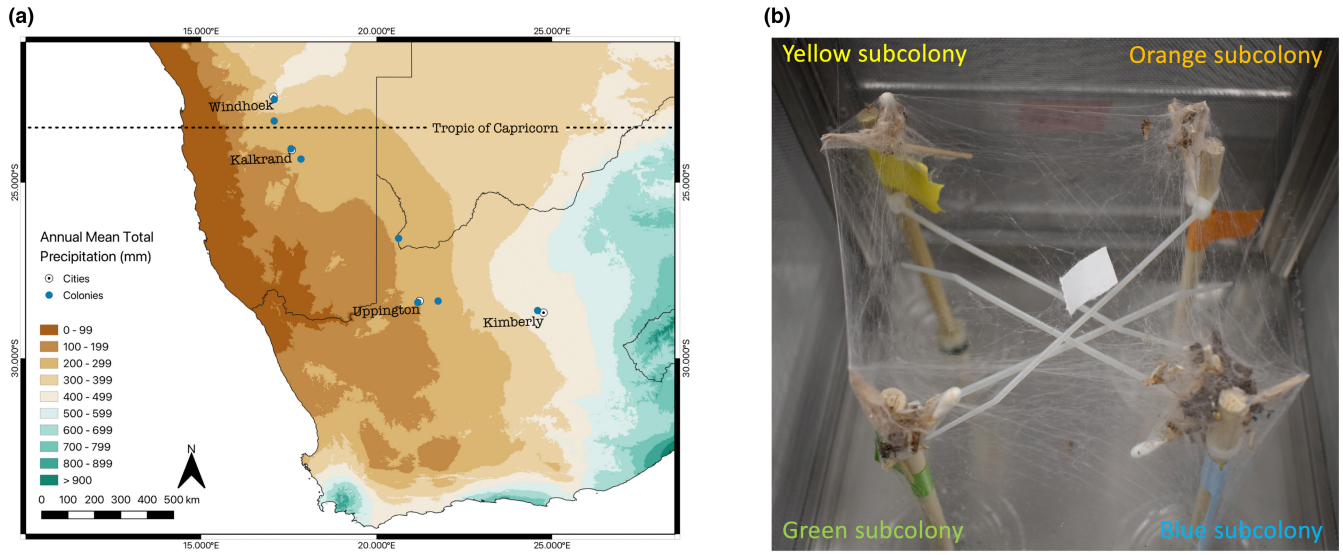

FIGURE 1 Collection map and colony setup. (a) Geographic distribution of the eight wild colonies from Namibia and South Africa, with annual mean total precipitation (https://www.worldclim.org/bioclim; Fick & Hijmans, 2017). (b) Photo depicting experimental colonies post fragmentation and fusion. Between the experimental colonies, zip-ties were used to facilitate shared web-building and the piece of paper was used for simulated prey capture assays.

as a continuous variable rather than separating individuals into bold/shy categories. Although we only measured individuals singly, this has been demonstrated as a repeatable behavioral trait—individuals are consistent in their responses over time and consistently different from each other (Keiser et al., 2014; Parthasarathy et al., 2019). After individual boldness assays, we labeled each spider with their respective subcolony color by painting the dorsal side of their abdomens with a dot of water-based acrylic paint and a small paintbrush. With these data, we calculated the mean boldness value for each subcolony (containing 10 spiders) and each colony (containing four subcolonies). Boldness measures of individuals did not differ between the two populations (Figure S2).

2.4 | Colony aggregation

To test for colony fusion/aggregation after they were experimentally separated, we created polydomous colonies by reuniting each of the four subcolonies into a single 30.5-cm^3 cage (BioQuip®; Rancho Dominguez). We attached each subcolony to the top of a 25.4-cm dowel rod with a zip-tie labeled with the subcolony's color ID roughly 10 cm apart from each other subcolony. An additional zip-tie was attached to each dowel pointing towards the center of the cage to mimic the intertwined branches of an *Acacia* bush, which is their preferred nesting habitat (Rose et al., 2022), and allow for spider movement and web-building between the subcolonies (Figure 1b). We recorded the number of spiders present in each corner roughly 24, 48, and 72 h after they were reunited (March 2nd–March 4th, 2019) and then 10 days later at the close of the experiment. We attempted to record the paint IDs for each spider in each subcolony, but spiders aggregate closely to one another and in directions that make it difficult to observe dorsal ID marks without disturbing the colony. The individual spider ID data were therefore incomplete, and we did not pursue further analysis. Tight aggregations of spiders also made it difficult to get exact counts of individuals in each subcolony. However, individual spiders were rarely entirely covered by nest mates (i.e., body parts like legs, or partial view of an abdomen can be used to count an individual). Observing subcolonies from multiple angles provided better views to count potentially hidden spiders as well. We did our best counting aggregated subcolonies without disturbing them, but on some occasions the total number of spiders counted differed from 40 (the total colony size).

2.5 | Collective prey capture

We measured collective prey capture in each colony once daily for 5 days (March 4th–8th, 2019). To eliminate heterogeneity in prey stimuli, we used a hand-held vibratory device (Maia Toys!) with a plastic zip-tie extended from the vibratory device to make contact with a 2-cm^2 piece of paper placed in the center of each colonies' shared capture web (Figure 1b). The paper was vibrated for 10 min or until the first attack occurred. We recorded (1) the latency until first attack, that is, the time it took for the first spider to bite the paper, and (2) the total number of spiders that emerged from the retreat web at the time of the first attack. One colony was removed from further analyses because it never responded to the simulated prey stimulus.

2.6 | Statistical analyses

To analyze aggregation behavior, we calculated the variance in the number of spiders observed in each subunit. Because colonies were

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divided into four subunits each containing 10 spiders, colonies that never aggregated would have a variance value of 0 (10 spiders in each subunit). Colonies in which spiders have disproportionately moved into one subunit would have a greater aggregation value (higher variance in number of spiders between subunits). We analyzed the average aggregation value for each colony using a repeated measures mixed model (after verifying normality of residuals) with the following independent variables: time point (1 day, 2 days, 3 days, 10 days), colony average boldness value (average of all 40 individuals), population ID, and the interaction term between population and average boldness value.

To analyze collective foraging behavior, we calculated the average latency to attack the prey stimulus and average number of spiders that cooperated in the attack for each experimental replicate. We analyzed colonies' latency to attack and number of attackers using two repeated measures mixed models using the "unequal variance" covariance structure. We included the following independent variables: assay number (Assay #1–#5), colony average boldness, population ID, and two interaction terms: population × average boldness value and population × assay number. For all statistical models, experimental colony ID nested in source colony ID was included as a random effect. All statistical analyses were performed in JMP version 15.0. Tables containing the parameter estimates with standard errors and Beta estimates for interpreting effect sizes can be found in the Tables S1–S3.

3 | RESULTS

Colonies became more aggregated over time, meaning individuals disproportionately moved into a single subunit ($F_{3,20.2} = 9.82$, $p = .0003$; Figure 2). We also detected population differences in aggregation behavior ($F_{1,11} = 7.87$, $p = .02$; Figure 2), where colonies from Namibia were 30% more aggregated in a single subcolony compared to colonies from South Africa, which remained more evenly distributed among subcolonies. The jump in aggregation of South African colonies after day three would have likely been a gradual increase if we monitored them daily for 10 days. We also found that the average boldness value of the 40 spiders influenced aggregation behavior, where bolder colonies were less aggregated on average ($F_{1,11} = 9.07$, $p = .01$). However, a follow-up regression analysis showed that colony boldness explained a small amount of variation in aggregation behavior ($R^2 = .08$).

When attacking simulated prey stimuli, colonies that were bolder on average attacked with more individuals ($F_{1,8.3} = 44.83$, $p < .001$; Figure 3a). We detected no effect of source population on the number of attackers ($F_{1,22} = 0.08$, $p = .78$). Bolder colonies from South Africa, however, attacked simulated prey stimuli faster than shyer colonies, though this trend was not observed in colonies from Namibia (boldness × population interaction term: $F_{1,7.2} = 10.74$, $p = .01$; Figure 3b). Lastly, we found that the number of spiders attacking prey stimuli decreased, on average, across the 5 days of assays ($F_{4,32.8} = 5.37$, $p = .002$), potentially due to habituation to the vibratory stimulus or satiation from daily feedings (Figure S1). The latency with which colonies attacked prey stimuli did not change over the period of the five assays ($F_{4,27.8} = 1.97$, $p = .13$).

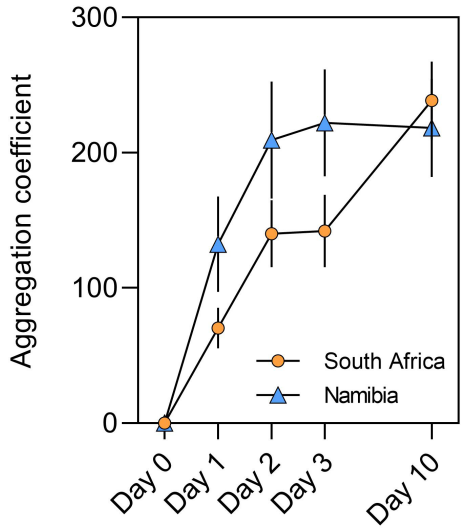

FIGURE 2 Aggregation behavior. Colonies became more aggregated over time, where spiders disproportionately moved into a single subcolony retreat rather than stay separated into different retreats. Colonies collected from Namibia aggregated more quickly than colonies from South Africa. The error bars represent standard errors of the mean, and a break in the *x*-axis represents the longer timespan between observations on day 3 and day 10.

4 | DISCUSSION

Group fragmentation, like fission or polydomy, is a common phenomenon in animal societies, which can influence how individuals interact to accomplish collective tasks. Here, we studied the effects of colony demography and population origin on collective behavior in fragmented groups of the social spider *S. dumicola*. We found population differences in postfragmentation fusion dynamics, where colonies originally collected from Namibia aggregated faster. We also found that colony phenotypic composition may alter the speed at which fragmented colonies attacked prey in the South African social spiders, but not the Namibian spiders. This may have been influenced by fewer represetatives of shyer experimental colonies from Namibia compared to South Africa, though both were constructed haphazardly. Since we conducted all experiments in a standardized lab space, the patterns we observed were not affected by differences in local conditions between populations. Fragmented *S. dumicola* colonies differ from intact colonies in their collective behavior (Kamath et al., 2019), and here we show that the behavior of fragmented colonies can vary among populations and may depend on factors like behavioral composition.

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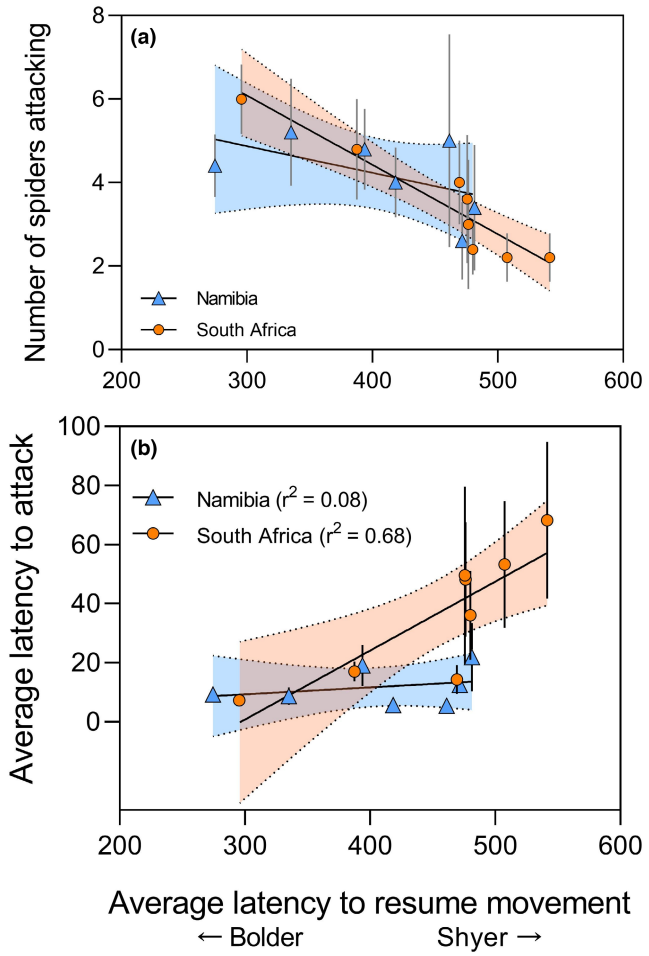

FIGURE 3 Collective foraging in fragmented colonies. (a) Bolder colonies (i.e., shorter average latency to resume movement after aversive stimuli) from both populations attacked the simulated prey with more individuals participating. (b) Bolder colonies from South Africa attacked prey stimuli faster than shyer colonies, though this trend was not observed in colonies from Namibia. Colored bands around regression lines represent 95% confidence intervals, and error bars around single points represent standard errors.

4.1 | Aggregation dynamics in fragmented colonies

Social groups commonly experience fragmentation, also referred to as fission or budding, for a variety of reasons. Some explanations include stochastic events (e.g., tree falls) that disperse spider colonies by destroying nests (Riechert et al., 1986), food availability affecting dispersal events in social spiders (Berger-Tal et al., 2016; Parthasarathy & Somanathan, 2018), stress that induces male dispersal in heart node ants (Cremer & Heinze, 2003), and outbreeding in barbary macaques (Ménard & Vallet, 1993). In this study, even after four weeks of separation, social spider subcolonies from both Namibia and South Africa tended to coalesce into fewer polydomous subunits rather than stay fragmented. Polydomous spider colonies often form more prevalently in older colonies when group size becomes much larger (Bilde et al., 2007), so our experimental fragmentation of relatively smaller colonies (i.e., 40 individuals) may have precluded sustained separation. Hunt et al. (2019) found that *S. dumicola* colonies with higher propensity for aggregation attacked prey faster, which decreases the likelihood that prey escape. This suggests that fragmentation may have important implications for colony success if it affects successful attack rates. Kamath et al. (2019) found that colonies were more likely to become polydomous on Acacia trees compared to fences. Perhaps something about the physical structure of our chambers, which had zip-ties positioned toward the middle of the chamber (Figure 1), facilitated the movement of spiders back into a single group. More studies manipulating aspects of the physical substrate would be helpful in this regard (Modlmeier, Forrester, & Pruitt, 2014; Rose et al., 2022).

4.2 | Foraging behavior in fragmented colonies

Collective prey capture is an important component in group-living predators like social spiders. Phenotypic composition of group members is known to affect collective outcomes (Aplin et al., 2014; Modlmeier, Keiser, Shearer, & Pruitt, 2014), but less is known about how certain group compositions can affect collective behavior differently between populations. Here, we demonstrate that bolder colonies attacked prey faster and with more individuals participating, corroborating several previous experiments (Hunt et al., 2019; Keiser et al., 2014), but we also found that colonies from South Africa and Namibia differed in attack latency and whether boldness affected attack latency. Although Namibian colonies attacked the prey stimuli around three times faster than South African colonies on average, there was a positive relationship between average group boldness and attack latency in South African spiders ($R^2 = .68$) but no relationship between boldness and attack latency in Namibian spiders ($R^2 = .08$). Rapidly attacking prey is important for trap-building predators like spiders to reduce the likelihood of prey escape (e.g., Dangles et al., 2006). Given high genetic differentiation among regions (Smith et al., 2009) due to low gene flow and high inbreeding (Settepani et al., 2017), population-differences in foraging may arise from local adaptation or genetic drift.

Mitochondrial evidence suggests that *S. dumicola* dispersers typically do not travel far (Johannesen et al., 2002), so a lack of emigration/immigration between populations with potentially different selective pressures on prey capture may have resulted in different behavioral strategies between Namibian and South African populations. Potential mechanisms may include differences in prey abundance/diversity and seasonality. Variation in prey species availability and geographic separation can lead to divergence of hunting behavior in predators (e.g., Lillywhite et al., 2002). This may be occurring between Namibian and South African populations, given that those populations mostly reside in tropical and subtropical desert regions, respectively (Figure 1).

Both populations in our study reside on the edges of the same two ecotypes (i.e., Nama Karoo and Kalahari xeric savannah), but differ in several environmental conditions. All Namibian colonies resided at higher elevations than South African ones, where colonies were about 33% higher elevation on average (Table 1). Environmental

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TABLE 1 Abiotic environmental conditions for each wild collected colony.

Colony ID	Population	Latitude	Longitude	Annual precip. (mm)	Precip. seasonality (coefficient of variation)	Annual temp. (°C)	Temp. seasonality (SD × 100)	Elevation	Ecotype
WIN-18-B	Namibia	−22.639	17.085333	350	111.5	19.01	364.95	1736	Kalahari
B1-18-F	Namibia	−23.25	17.083339	250	116.78	19.17	400.43	1412	Kalahari
B1-18-I	Namibia	−24.04	17.56515	212	117.31	19.58	454	1234	Nama Karoo
B1-18-J	Namibia	−24.333	17.8471	219	116.63	20.36	479.27	1200	Nama Karoo
KAL-18-A	South Africa	−26.586	20.628281	211	83.88	20.55	606.33	870	Kalahari
N14-18-B	South Africa	−28.371	21.75421	237	76.4	20.16	586.68	901	Kalahari
UPP-18-A	South Africa	−28.411	21.17684	205	76.02	20.48	578.09	853	Nama Karoo
R31-18-A	South Africa	−28.64	24.59135	442	72.88	18.42	554.89	1130	Kalahari

Note: Table is arranged by increasing latitudes, with the Namibian colonies toward the top and the South African colonies toward the bottom. Environmental data obtained from WorldClim (https://www.worldclim.org/bioclim; Fick & Hijmans, 2017).

conditions appear to be similar between each population, but with the Namibian spiders experiencing higher precipitation variation and South African spiders experiencing higher temperature variation throughout the year (Table 1). This could in part explain why Namibian spiders may be bolder with higher attack latency since they might need to take advantage of each potential prey items that are less available in the much drier parts of the year at their slightly higher elevations. Evidence suggests that *S. dumicola* genetic variants correlated with temperature, DNA methylation correlated with a wide range of climatic variables and microbiome correlated strongly to precipitation variables (Aagaard et al., 2022). On top of some differences in climatic variation, these populations are found at significantly different latitudes, which has been found to broadly affect biodiversity in a diversity of organisms (see latitudinal diversity gradient: Hillebrand, 2004). The Namibian population resides at an average of five degrees of latitude closer to the equator than the South African population does, which could result in a higher diversity of prey items at those populations. With potentially more types of food items available to Namibian colonies, these spiders may be more reactive to prey stimuli.

5 | CONCLUSIONS

Overall, we found differences between populations in colony aggregation behavior and collective foraging and that group composition affected colonies differently depending on their population of origin. Future studies should investigate comparisons between fragmented and unfragmented colonies, aggregation dynamics in the field, and how individual-level movement behavior explains the collective patterns we observe. By comparing behaviors of naturally fragmented and unfragmented colonies, we would better understand if experimental fragmentation methods affected aggregation patterns relative to nonmanipulated colonies. Due to the dense colony silks impeding visual observation, methods such as passive RFID tags (Streit et al., 2003) are required to track individual movement behavior between subcolonies to assess how individual behavior influences aggregation dynamics. Disentangling the effects individual phenotypes have on collective behavior, as well as how those dynamics differ at the population level, is hugely important to understand how animal societies function across heterogeneous landscapes. By integrating this research with fission-fusion dynamics that are common in many animals, we will gain insight into how groups behave as they become divided over time.

AUTHOR CONTRIBUTIONS

Emily S. Durkin: Writing – original draft; writing – review and editing; investigation; conceptualization; supervision; methodology. **Steven T. Cassidy:** Writing – original draft; writing – review and editing; visualization. **Arletys Leyva:** Methodology. **Carl N. Keiser:** Conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; visualization; formal analysis; supervision; resources; methodology.

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ACKNOWLEDGMENTS

We thank Peter Marting and James Malamut for invaluable assistance in collecting spiders. We thank Alice Gau, Gloria Johnson, Tram-Anh Tran, Nicholas Dolezal, Chelsea Gerena, Gloria Johnson, Alex Piriz, Samantha Stein, Joshua Vildor, and Dylan Vega for assistance with colony maintenance and individual behavioral assays. Spiders were collected under the following permits: South Africa Northern Cape Province: FAUNA 0835/2018, Namibia: RPIV00632019. Funding for this research was provided by the University of Florida.

CONFLICT OF INTEREST

None.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on figshare: https://doi.org/10.6084/m9.figshare.20081021.v1.

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How to cite this article: Durkin, E. S., Cassidy, S. T., Leyva, A., & Keiser, C. N. (2023). Population differences in the aggregation and collective foraging behavior of fragmented social spider colonies. *Ethology*, *00*, 1–8. https://doi.org/10.1111/eth.13360

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