

Diverging cooperative prey capture strategies in convergently evolved social spiders

Lena Grinsted¹, Mads F. Schou², Virginia Settepani³, Christina Holm³, Lefang L. Chobolo⁴, Galaletsang M. Dintwe⁴ and Trine Bilde^{3*}: ¹School of Biological Sciences, University of Portsmouth, King Henry Building, King Henry 1 Street, Portsmouth, PO1 2DY, United Kingdom; E-mail: lena.grinsted@port.ac.uk ORCID: <https://orcid.org/0000-0003-3904-3721>; ²Department of Biology, Lund University, Lund, SE-22362, Sweden; ³Department of Biology, Aarhus University, Ny Munkegade 114-116, 8000 Aarhus C, Denmark; ⁴Department of Biological Sciences and Biotechnology, Botswana International University of Science and Technology (BIUST), Plot 10071, Palapye, Botswana

Abstract. Sociality in spiders has evolved independently multiple times, resulting in convergently evolved cooperative breeding and prey capture. In all social spiders, prey is captured by only a subset of group members and then shared with other, non-attacking group members. However, spiders' propensity to attack prey may differ among species due to species-specific trade-offs between risks, costs and benefits of prey capture involvement. We explored whether engagement in prey attack differs among three social *Stegodyphus* species, using orthopteran prey, and found substantial differences. *Stegodyphus mimosarum* Pavesi, 1883 had a low prey acceptance rate, was slow to attack prey, and engaged very few spiders in prey attack. In *S. sarasinorum* Karsch, 1892, prey acceptance was high, independently of prey size, but more spiders attacked when prey was small. While medium-sized prey had higher acceptance rate in *S. dumicola* Pocock, 1898, indicating a preference, the number of attackers was not affected by prey size. Our results suggest that the three species may have different cooperative prey capture strategies. In *S. mimosarum* and *S. dumicola*, whose geographical ranges overlap, these strategies may represent niche specialization, depending on whether their respective cautious and choosy approaches extend to other prey types than orthopterans, while *S. sarasinorum* may have a more opportunistic approach. We discuss factors that can affect social spiders' foraging strategy, such as prey availability, predation pressure, and efficiency of the communal web to ensnare prey. Future studies are required to investigate to which extent species-specific cooperative foraging strategies are shaped by ontogeny, group size, and plastic responses to environmental factors.

Keywords: Group living, social evolution, cooperative hunting

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Cooperative prey attack occurs in a small number of spider species that are found mainly in tropical and subtropical regions of the world (Majer et al. 2015; Aviles & Guevara 2017). These spiders, referred to as social or cooperatively breeding spiders, are similar to other cooperatively breeding animals, such as lions and meerkats, in that adults cooperate in caring for colony offspring, and group members forage and feed together (Lubin & Bilde 2007; Grinsted & Lubin 2019). Although sociality in spiders is phylogenetically rare, this behavior has evolved convergently multiple times within several spider genera (Agnarsson et al. 2006; Lubin & Bilde 2007; Aviles & Guevara 2017; Settepani et al. 2017). While all social spiders display similar cooperative, behavioral traits, we have limited knowledge on whether cooperative strategies in relation to group hunting differ among species. In this paper we explore whether and how cooperation in prey capture differs among social species of the genus *Stegodyphus* Simon, 1873 (Eresidae).

Social spiders cooperate in building nest retreats constructed of silk, and large capture webs that extend out from the main nest and intercept flying insect prey. When prey lands in the web, only a small subset of a colony's members will approach and attack the prey (Settepani et al. 2013). Once subdued, the prey will typically be dragged towards the more protective parts of the nest where it will be shared with a larger number of group members, and multiple spiders will simultaneously feed on the carcass (Ward & Enders 1985; Souza et al. 2007). The decision of an individual spider to approach and attack a prey item is likely based on a number of

factors, such as the spider's proximity to the struggling prey, its species-specific detection range of prey vibratory cues, its hunger state and developmental stage, the presence and behavior of nearby conspecifics, whether certain individuals in the colony specialize in prey capture, and the risk of injury posed by the type and size of prey (Settepani et al. 2013, 2015; Parthasarathy & Somanathan 2019; Chiara & Jeanson 2020; Wright et al. 2020). The degree to which each of these factors influence prey attack behavior of an individual is likely to be highly species-specific due to species-specific trade-offs between risks, costs and benefits of being involved in the actual prey capture event (Settepani et al. 2013). Risks to individual attackers include exposure to predation outside the protective parts of the nest (Rayor & Uetz 1990), as well as injuries received from the prey itself, as prey might defend itself by kicking, biting or stinging (Willey & Jackson 1993; Souza et al. 2007). Costs include energetic costs associated with running, biting and pulling the prey, as well as costs related to injecting venom and digestive enzymes into the prey (Walter et al. 2017). Indeed, spiders that join in feeding on a prey item without having participated in the actual prey capture event will not need to invest venom, and might invest smaller amounts of enzymes than attackers (Ward & Enders 1985; Amir et al. 2000). However, there may also be benefits associated with being attackers, and thereby first to feed on a prey. If the prey is small, the attacker might be able to fully consume it without sharing it (Souza et al. 2007). On a larger prey item that is shared with others, first attackers may be able to choose the most nutritious feeding site on the prey (Mayntz

et al. 2005), and they may be more likely to feed, and may feed for longer, as compared to non-attackers (Ward & Enders 1985; Willey & Jackson 1993).

Cooperative foraging in spiders is most frequently studied in the genera *Stegodyphus* (Eresidae) and *Anelosimus* Simon, 1891 (Theridiidae) (Aviles & Guevara 2017). Both genera contain a number of social species that have evolved independently from an ancestral subsocial state (Agnarsson et al. 2006; Settepani et al. 2017). Subsocial spiders show extended maternal care by sharing prey with or regurgitating food for their offspring, and juveniles have a temporary cooperative stage within their maternal nest after their mother has died, after which they disperse to live and breed solitarily (Yip & Rayor 2014). In all fully social, cooperatively breeding spiders, the dispersal stage prior to mating has been lost entirely, leading to siblings reproducing within colonies, and an obligate inbreeding mating system (Settepani et al. 2017). In *Stegodyphus*, three species are social while the remaining species are subsocial (Kraus & Kraus 1988). This means that studies aimed at identifying costs, benefits and adaptations to sociality and cooperative behavior tend to view the social *Stegodyphus* species and their subsocial sister-species as three comparable replicas for the evolutionary transition to sociality (Grinsted et al. 2014; Settepani et al. 2016, 2017; Majer et al. 2018; Grinsted et al. 2020). All social spider species appear to share convergently evolved traits, such as cooperative brood care, cooperative prey capture, inbreeding, and a female-biased sex ratio (Avilés 1997; Lubin & Bilde 2007), providing an excellent opportunity to perform independent comparative studies aimed at identifying different costs, benefits and adaptations to sociality and cooperative behavior (Grinsted et al. 2014; Settepani et al. 2016, 2017; Majer et al. 2018; Grinsted et al. 2020). In the context of foraging, studies have found that cooperative foraging increases dietary niche width (prey size) in some species, and dietary niche breadth (taxonomic groups) in others (Nentwig 1985; Powers & Aviles 2007; Majer et al. 2018). These studies might suggest that different species employ different cooperative foraging strategies, for example depending on prey size or prey type availability, and the risks associated with hunting. Indeed, we do not know whether different species have evolved similar group hunting strategies, or alternatively, whether variation in environmental conditions favors different hunting approaches, e.g., through behavioral plasticity. Evaluating whether and how cooperative foraging differs among similar, independently derived social spider species may reveal how environmental differences shape cooperative behaviors.

Here, we present an exploratory study addressing the question: Do the three social *Stegodyphus* species differ in the way they engage in cooperative prey capture? Specifically, we investigate the number of spiders in a social group that engage in prey capture during the initial five minutes of prey attack, and how prey size affects the number of attackers. We introduced orthopteran prey (grasshoppers, locusts and crickets) of different body sizes into capture webs of naturally occurring colonies to collect two separate sets of data: (1) acceptance rates (binary measure of acceptance versus rejection) of prey of different sizes, and (2) spider engagement in prey attack over time (only for accepted prey), recorded as (i) the number of colony members engaged in prey attack over

the first five minutes of prey capture, and (ii) the time it took for the first spider(s) to attack. The first set of data was combined with similar data from three subsocial *Stegodyphus* species and used in Grinsted et al. (2020) to ask whether prey size affected prey acceptance in both social and subsocial spiders, including testing for any potential preferences in prey size ranges in each of the six species (Grinsted et al. 2020). The second dataset we use here to explore the complementary but separate question of whether the social *Stegodyphus* species modulate participation in prey capture over time (after prey has been accepted) as a function of prey size.

We predict that after the initial attack, the number of spiders engaged in prey capture will increase over time, as the venom from the first attacker(s) start taking effect on the prey, decreasing the risk of injury to consecutive attackers. Furthermore, we predict a positive effect of prey size on the number of attackers because more spiders may be needed to subdue and drag larger prey back to the protective parts of the nest (Ward & Enders 1985). Such effects would suggest that individual thresholds for participating in prey capture are optimized as to minimize each individual's engagement in risky behavior so that only the number of spiders required for subduing prey of a given size participate, and that prey items of all sizes are worthwhile rewards for the colony members to pursue (Scheel & Packer 1991; Creel & Creel 1995; Souza et al. 2007). Any deviations from these relationships would imply a more complex explanation where the trade-off between reward and risk is less straightforward.

METHODS

Study system and field sites.—Spiders of the genus *Stegodyphus* are found in arid and semi-arid habitats mainly in Eurasia and Africa (Kraus & Kraus 1988; Majer et al. 2013; World Spider Catalog 2021). The genus consists of >20 species of which three are social: *S. dunicola* Pocock, 1898, *S. mimosarum* Pavesi, 1883, and *S. sarasinorum* Karsch, 1892. Sociality has evolved independently in each of the three species, and each species occurs in one of three separate branches within the phylogeny of the genus (Settepani et al. 2017). Social *Stegodyphus* species build communal nests on spiny shrubs, low-hanging branches of trees, and on fences. The nests are compact silky masses from which one or multiple two-dimensional capture webs made of cribellate silk extend (Seibt & Wickler 1988).

Social *Stegodyphus* colonies contain up to several hundreds of individuals. Mating occurs once a year, after which males die and all female colony members (allo-mothers) cooperate in caring for egg cases and hatchlings. At the end of the allo-maternal care stage, juveniles feed on, and kill, the adult females in the colony (gerontophagy) (Seibt & Wickler 1987; Junghans et al. 2017, 2019). This results in a colony structure with no overlapping generations, and all colony members are more or less synchronous with regards to age, developmental stage and body size (Lubin & Bilde 2007; Grinsted & Bilde 2013; Grinsted & Lubin 2019). Adult spiders reach on average the following body lengths: *S. dunicola*: 10.1 mm, *S. mimosarum*: 7.6 mm, and *S. sarasinorum*: 10.6 mm (Grinsted et al. 2020).

We collected data non-destructively with minimal disturbance to the spiders and, hence, did not obtain measures of

Table 1.—Overview of sample sizes and overall species-level prey acceptance rates within 10 min of prey being placed in the capture web. In addition to the presented sample sizes, we also collected data on the number of spiders involved in prey attack in further 14 trials where spiders attacked after the threshold of 10 min had passed.

		Species			
		<i>S. dumicola</i>	<i>S. mimosarum</i>	<i>S. sarasinorum</i>	All species
All introduced prey	N trials (total)	112	63	89	264
	N colonies (total)	41	52	73	166
Accepted prey	N trials (accepted)	69	32	79	180
	N colonies (accepted prey)	37	31	66	134
	Prey acceptance (% trials)	61.6	50.8	88.8	67.1

spider body sizes, precise developmental stages, or colony sizes. Collecting the colonies to measure and count individual spiders is a process that destroys the colony because the dense, silken nest has to be cut open and taken apart. Colony sizes correlate positively with the physical dimensions of their silken nests (Majer et al. 2018) and in this study, we chose nests estimated to be large enough to host as a very minimum 10–20 spiders (and most often >50). As prey attacks mostly involve fewer than 10 spiders (our maximum was 18 spiders involved at T5, or five minutes after attack was initiated; see Methods) the actual sizes of the colonies were unlikely to constrain the number of spiders involved in prey attack. Furthermore, Majer et al. (2018) found that group size did not affect prey sizes caught by the three social *Stegodyphus* species. Published species-specific linear regressions can be used to estimate colony sizes based on nest dimensions, but these equations are not reliable for small- and medium-sized colonies. For example, the linear regression for *S. dumicola* has an intercept of 103.76 and therefore cannot estimate colony sizes of fewer than 103 spiders (Majer et al. 2018). Social spiders, despite their relatively small body sizes, are capable of catching very large prey (many times the size of a single spider), so the exact body sizes of the group members are likely to be of less importance than other factors, such as prey type and prey size, in predicting prey capture success (Drisy-Mohan et al. 2019; Parthasarathy & Somanathan 2019; Grinsted et al. 2020). Furthermore, individual differences in spider body size within colonies does not predict participation in prey capture (Ainsworth et al. 2002; Settepani et al. 2013).

We investigated cooperative prey attack in *S. dumicola* in Otavi, northern Namibia (GPS: -19.595946, 17.367636) in January 2010, in *S. sarasinorum* in Andhra Pradesh in southern India (GPS: 12.775692, 78.296598) from September to November 2010, and in *S. mimosarum* in Palapye, eastern Botswana (GPS: -22.678316, 27.072882) in May and November 2019. Although *Stegodyphus* species are seasonal, having one breeding season a year, substantial variation in developmental stages can be found among colonies found in the same area. Of the colonies that we surveyed, some colonies from all three species contained what appeared to be adult females, but most colonies from all three species appeared to contain large juveniles or subadults.

Prey attack assay.—We located naturally occurring social spider colonies in the field and manually caught prey in the local environment by hand or using sweep nets. We introduced live prey of a range of sizes (2–60mm), representing the range of prey naturally available in their environment (Majer et al.

2018), into the capture webs of the colonies. Prey items belonged exclusively to the order Orthoptera (grasshoppers and crickets) which form part of the natural diet of *Stegodyphus* spiders (Majer et al. 2018; Drisy-Mohan et al. 2019). This prey type was chosen due to the ease of obtaining Orthoptera of a range of body sizes. Majer et al. (2018) found that Orthoptera comprised between 5% and 30% of the diet in various populations of the three social *Stegodyphus* species. Prey body sizes were measured as the length of their body from the tip of the head to the end of the abdomen, excluding any appendages, with digital calipers to the nearest mm, before being placed in the capture web. Body lengths ranged from 3–62 mm (median = 17 mm; mean = 20 mm, see Fig. S1, online at <https://doi.org/10.1636/JoA-S-20-097.s1>). Insect body length correlates strongly with biomass, and thus prey body length is a reliable estimate of prey body size (Hodar 1996).

A trial consisted of introducing a prey item carefully into the capture web of a spider colony using soft forceps. The prey item was placed approximately 10 cm from the dense, silken nest retreat. We first recorded the binary measure of whether or not the prey item was attacked (accepted vs. rejected) within 10 minutes of introducing the prey item. The effect of prey size on binary acceptance rates is presented in Grinsted et al. (2020) while the overall acceptance rates of prey per species is presented here (Table 1). When prey was accepted (i.e., attacked), we started a stopwatch at the time of attack (T0), defined as the point at which the first spider attacked the prey, usually by biting onto an appendage of the prey. Occasionally, two or three spiders attacked simultaneously at T0, so we recorded the number of spiders attacking at T0. We further counted how many spiders were actively engaged in prey attack by biting onto the prey after 1 min (T1), 3 min (T3) and 5 min (T5) after T0. It usually takes a few minutes for the prey to be subdued, for the spider venom to be injected, and for it to affect the prey, so any spiders engaging with the prey within the first 3–5 min would be expected to be involved in the prey capture process (Ward & Enders 1985). Spiders that approach the prey after 5 min might be involved only in feeding, and perhaps transporting the prey, rather than in subduing the prey.

Occasionally, we noticed spiders starting to attack the prey just after the 10 min had passed ($n = 14$ trials) and for these we also recorded the number of spiders attacking at T0, T1, T3 and T5, and included them in the analysis of the number of attackers. These, however, were excluded in the analysis of

time to attack, and also excluded in the calculations of prey acceptance rates.

Some colonies were assayed more than once (40 out of 143 colonies = 28%), but never on the same day, and never more than three times (see Table 1 for a breakdown of sample sizes for both the level of colonies and trials).

Statistics.—We constructed two statistical models, one for the number of attacking spiders, and one for the time it took spiders to attack. First, we modelled the number of attacking spiders using generalized linear mixed models in a Bayesian framework implemented in the package MCMCglmm v.2.26 (Hadfield 2010) in R v.3.5.1 (R Core Team 2020). The number of attackers (response variable) was count data and was therefore modelled as a Poisson distributed trait using a log link-function. The model included the fixed effects of species (*S. mimosarum*, *S. sarasinorum*, and *S. dumicola*), time in minutes (continuous and z-transformed) and prey size in mm (continuous and z-transformed). The lack of independence among recordings from the same trial obtained at different time points was accounted for by including a 2x2 unstructured variance-covariance matrix composed of random intercepts and slopes of individual trials. As some colonies were assayed more than once, we also included colony ID as a random effect.

For both residual and random terms we used the weakly informative inverse-Gamma distribution (scale = 0.001, shape = 0.001, i.e., $V = n, nu = n-1+0.002$, with n being the dimension of the matrix) as priors. Each model was run for 2,500,000 iterations of which the initial 100,000 were discarded and only every 2,500th iteration was used for estimating posterior probabilities. The number of iterations was based on inspection of autocorrelation among posterior samples in preliminary runs. Convergence of the estimates was checked by running the model three times and inspecting the overlap of estimates in trace plots and the level of autocorrelation among posterior samples. We considered a fixed effect to be significant when the 95% credible interval (CI) did not overlap with 0 and the MCMC p -value ($pMCMC$) was less than 0.05. We removed one outlier trial from the dataset which was highly influential on the model output as 34 spiders attacked the prey (the second highest number in the dataset was 18 spiders). Despite being just one of 85 trials with *S. sarasinorum*, inclusion of this trial changed the coefficient of prey size in the model substantially in this species from -0.16 to -0.09 (Table S1, online at <https://doi.org/10.1636/JoA-S-20-097.s1>).

Next, we investigated the time to attack using a similar model structure as presented above, but with the following modifications: The response variable was time to attack in seconds, and the fixed effects were species and prey size as well as their interaction. Time to attack was measured to nearest second and truncated towards zero, and hence, we used the same error distribution as described above. We included Colony ID, but not Trial as random effects, as in this model we only had a single observation per trial (T0).

RESULTS

Overall prey acceptance.—A majority of prey items were accepted in our assays: *S. dumicola* overall accepted 61.6%, *S. mimosarum* 50.8%, and *S. sarasinorum* 88.8% of introduced

prey items (defined as attacked within 10 min of introducing the prey into the capture web, Table 1).

Number of attackers.—As predicted, more spiders tended to engage in prey attack over time in both *S. dumicola* and *S. sarasinorum*. However, this was not the case for *S. mimosarum*, where there was no effect of time on the number of spiders engaged in prey attack (Table 2; Fig. 1; effect of time in *S. dumicola*: Posterior Mean (PM) = 0.20 (CI = 0.1, 0.29), $pMCMC = 0.001$; in *S. sarasinorum*: PM = 0.24 (CI = 0.15, 0.32), $pMCMC = 0.001$; and in *S. mimosarum*, PM = 0.05 (CI = -0.15, 0.25), $pMCMC = 0.63$). In general, for all three species, 1–2 spiders, and on rare occasions 3 spiders, were biting at the time of attack (T0). This number of attackers did not consistently change over time in *S. mimosarum*, whereas for both *S. dumicola* and *S. sarasinorum* between one and four additional spiders (on average) tended to join in over the next five minutes (Fig. 1).

Prey size had differing effects in the three species and so our general prediction, that more spiders would engage in prey attack when prey is larger, was not supported (Table 2, Fig. 1, Fig. S2, online at <https://doi.org/10.1636/JoA-S-20-097.s1>). In *S. dumicola*, more spiders attacked when prey was larger, but this effect was not significant (effect of prey size: PM = 0.14 (CI = -0.04, 0.30), $pMCMC = 0.12$). Opposite to our prediction, the effect of prey size was negative in *S. sarasinorum*, meaning that fewer spiders attacked when prey was larger (Fig. 1; effect of prey size: PM = -0.16 (CI = -0.29, -0.01), $pMCMC = 0.025$; but note that this effect disappears when the single outlier is included in the model, Table S1). In *S. mimosarum*, prey size had no effect on the number of attackers (effect of prey size: PM = -0.02 (CI = -0.28, 0.24), $pMCMC = 0.74$). In pair-wise comparisons where the effect of prey size was contrasted between a pair of species, *S. dumicola* and *S. sarasinorum* were significantly different (Table 2; fixed effect contrast: PM = 0.30 (CI = 0.08, 0.51), $pMCMC = 0.015$).

Time to attack.—*Stegodyphus mimosarum* took significantly longer to attack prey, irrespective of prey size, as compared to the two other species (Table 3; Fig. 2; *S. mimosarum* vs. *S. sarasinorum*: PM = 0.5 (CI = 0.05, 1.27), $pMCMC = 0.04$; *S. mimosarum* vs. *S. dumicola*: PM = 1.02 (CI = 0.31, 1.55), $pMCMC = 0.008$).

Prey size did not affect the time it took for spiders to attack (Table 3; Fig. 2; prey size effect in all three species: CIs of PM overlapped substantially with zero, $pMCMC > 0.16$).

DISCUSSION

Cooperative prey capture associated with spider sociality has evolved independently multiple times (Agnarsson et al. 2006; Johannesen et al. 2007). We explored whether engagement in cooperative prey capture differed between the three social spider species within the genus *Stegodyphus*. Despite general similarities among species, in that a small number of group members attack a prey item and then proceed to share it with other group members (Ward & Enders 1985; Settepani et al. 2013), we found substantial differences among species in their prey acceptance rates, in their latency to attack, and in the way they responded over time and to prey of different sizes, using orthopteran prey. *Stegodyphus mimosarum* tended to engage only one or two spiders throughout the first five minutes of prey attack, independently of prey size, took

Table 2.—Results from Bayesian generalized linear mixed models using the number of attackers as response variable. Model coefficients, represented by Posterior Means (or Posterior Modes for random effects) and their Credible Interval (CI), are on the log-scale as models were fitted with Poisson error and a log link-function. Instead of having a global intercept (i.e., choosing one species as the intercept), an intercept was estimated for each spider species, so the effect of time or prey size could be estimated for each species. This also allowed us to test for differences between pairs of species (contrasts) by subtracting their posteriors and estimating the CI and pMCMC p-value. Variables with a ‘z’ indicates they were z-transformed.

Results from analyses of the number of attackers		
Fixed Effects	Posterior Mean (CI)	pMCMC
<i>S. dumicola</i> * timepoint_z	0.20 (0.1, 0.29)	0.001
<i>S. mimosarum</i> * timepoint_z	0.05 (-0.15, 0.25)	0.633
<i>S. sarasinorum</i> * timepoint_z	0.24 (0.15, 0.32)	0.001
<i>S. dumicola</i> * preysize_z	0.14 (-0.04, 0.3)	0.119
<i>S. mimosarum</i> * preysize_z	-0.02 (-0.28, 0.24)	0.863
<i>S. sarasinorum</i> * preysize_z	-0.16 (-0.29, -0.01)	0.025
<i>S. dumicola</i> * timepoint_z * preysize_z	0.03 (-0.07, 0.14)	0.625
<i>S. mimosarum</i> * timepoint_z * preysize_z	0.03 (-0.16, 0.21)	0.744
<i>S. sarasinorum</i> * timepoint_z * preysize_z	0.02 (-0.07, 0.09)	0.685
Random Effects: Variances		
Random Intercepts: trials	0.306 (0.205, 0.431)	
Random slopes: trials over timepoint_z	0.056 (0.037, 0.084)	
Random Intercepts: colony ID	0.001 (0, 0.097)	
Residuals	0.001 (0, 0.007)	
Contrasts: Comparing the effect of prey size between species		
<i>S. dumicola</i> vs. <i>S. sarasinorum</i>	0.30 (0.08, 0.51)	0.015
<i>S. mimosarum</i> vs. <i>S. sarasinorum</i>	0.17 (-0.13, 0.45)	0.352
<i>S. mimosarum</i> vs. <i>S. dumicola</i>	-0.06 (-0.51, 0.13)	0.302
Contrasts: Comparing the effect of time between species		
<i>S. dumicola</i> vs. <i>S. sarasinorum</i>	-0.02 (-0.17, 0.09)	0.502
<i>S. mimosarum</i> vs. <i>S. sarasinorum</i>	-0.17 (-0.41, 0.01)	0.083
<i>S. mimosarum</i> vs. <i>S. dumicola</i>	-0.14 (-0.36, 0.07)	0.194

relatively long to attack, and rejected a high proportion of prey. In the other two species, a steady increase of attackers was observed over time, irrespective of prey sizes. However, *S. sarasinorum* colonies showed the steepest increase in attackers

when prey was small. Overall prey acceptance rate was extremely high in *S. sarasinorum*. These results indicate that the three species may have different cooperative hunting strategies. Below we hypothesize what the different prey

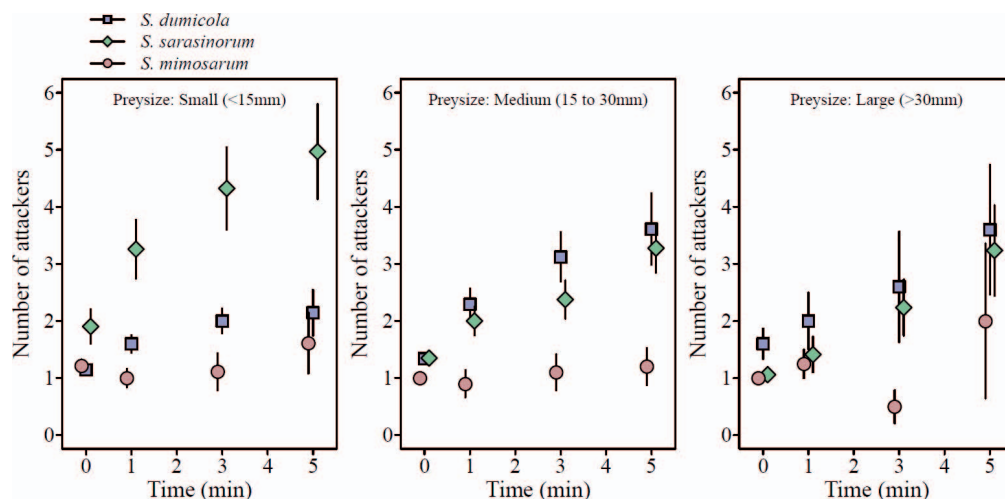


Figure 1.—Mean number of spiders engaging in prey attack over time in the three social spiders *S. dumicola* (blue, square points), *S. sarasinorum* (green, diamond-shaped points), and *S. mimosarum* (red, circular points). Each plot depicts one of three arbitrarily chosen prey size classes in order to give a visual representation of the effect of prey size on the number of attackers (small prey: 2–15 mm body length; medium prey: 15–30 mm; large prey: 30–60 mm). Error bars depict standard errors

Table 3.—Results from Bayesian generalized linear mixed models using the number of seconds it took spiders to attack the prey item as response variable. Model coefficients, represented by Posterior Means (or Posterior Modes for random effects) and their Credible Interval (CI), are on the log-scale as models were fitted with Poisson error and a log link-function. Variables with a ‘z’ indicates they were z-transformed.

Results from analysis of time to attack		
Fixed Effects	Posterior Mean (CI)	pMCMC
<i>S. dumicola</i> * preysize_z	-0.01 (-0.38,0.37)	0.944
<i>S. mimosarum</i> * preysize_z	0.35 (-0.13,0.81)	0.163
<i>S. sarasinorum</i> * preysize_z	0.11 (-0.26,0.41)	0.531
Random Effects: Variances		
Random Intercepts: colony ID	0.001 (0,0.213)	
Residuals	2.134 (1.565,2.567)	
Contrasts: Comparing the effect of prey size between species		
<i>S. dumicola</i> vs. <i>S. sarasinorum</i>	-0.19 (-0.62,0.39)	0.59
<i>S. mimosarum</i> vs. <i>S. sarasinorum</i>	0.26 (-0.33,0.86)	0.429
<i>S. mimosarum</i> vs. <i>S. dumicola</i>	0.41 (-0.25,0.95)	0.248
Contrasts: Comparing species		
<i>S. dumicola</i> vs. <i>S. sarasinorum</i>	-0.17 (-0.69,0.24)	0.344
<i>S. mimosarum</i> vs. <i>S. sarasinorum</i>	0.5 (0.05,1.27)	0.04
<i>S. mimosarum</i> vs. <i>S. dumicola</i>	1.02 (0.31,1.55)	0.008

capture strategies might be, while discussing which factors might shape such strategies. It should be noted that further studies are now needed to test these hypotheses.

Stegodyphus mimosarum.—Irrespective of prey size, very few *S. mimosarum* spiders tended to attack. Only one to two spiders usually engaged in prey attack throughout the first five minutes of prey capture, and in nearly 50% of trials prey failed to be attacked within 10 min of introduction to the capture

web. It also took *S. mimosarum* longer to attack the prey as compared to the two other species. In Grinsted et al. (2020), we found that rejection rate was high across all prey sizes, with no indication that a particular prey size range was preferred or rejected. These results suggest that individual spiders have a low propensity to attack orthopteran prey, irrespective of prey body size, and irrespective of whether a group member has made the first attack. If other prey types elicit low acceptance

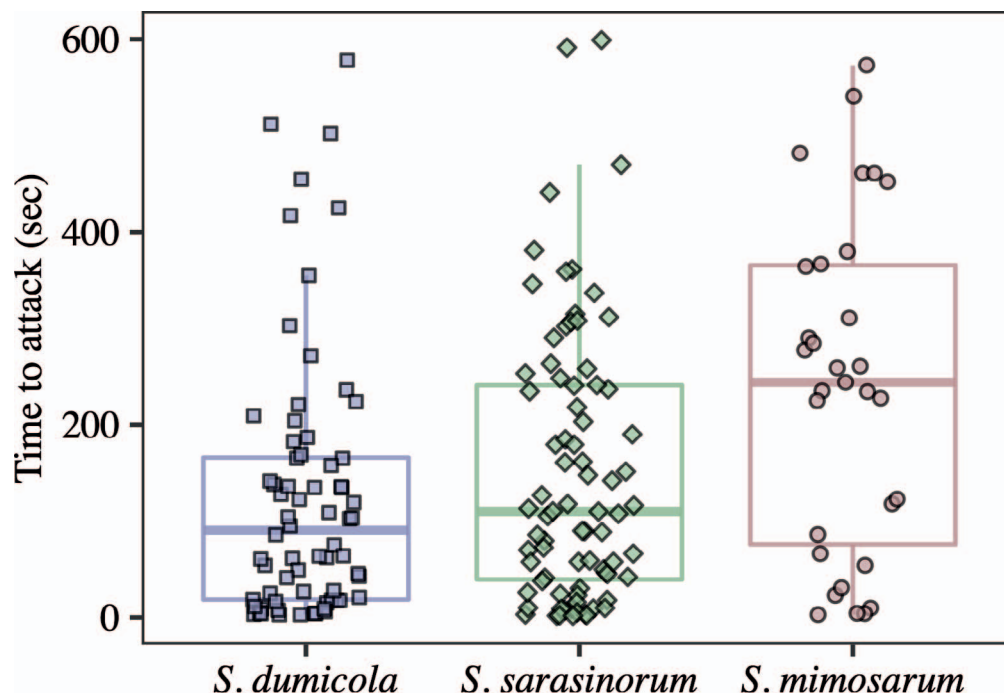


Figure 2.—Box-and-whiskers plot of the time, in seconds, it took for spiders to attack prey items for the three species (box: medians, upper and lower quartiles; whiskers: maximum and minimum values).

rates and a low number of attackers in *S. mimosarum*, this would indicate a generally cautious approach to prey attack in this species. If, on the other hand, low propensity to attack is specific to orthopteran prey, this may indicate niche specialization in this species. As we tested only orthopteran prey in this study, and therefore do not know whether caution extends beyond orthopterans, we will discuss both a cautious approach and the possibility for niche specialization.

Several factors could shape a generally cautious foraging strategy: (1) a high predation risk when venturing outside of the protective parts of the nest; (2) a high prey abundance which would lower the relative value of each prey item; (3) relatively low nutritional demands, e.g., due to a lower metabolic rate, and/or (4) a higher reliance on the web structure to retain and subdue prey in this species as compared to other social species. This would mean that fewer spiders are needed to subdue a prey item, and that fast prey attack is unnecessary. Anecdotally, *S. mimosarum* produces tougher silk than other *Stegodyphus* species (VS personal observation), so future comparative studies of silk properties among the *Stegodyphus* spiders, and the link to sociality, may be worthwhile. We discuss this towards the end of the paper.

Niche specialization could evolve due to *S. mimosarum* and *S. dumicola* having overlapping geographical distributions and having competed for a similar behavioral and ecological niche (Majer et al. 2013). It is possible that *S. mimosarum* has specialized in smaller, less dangerous prey types, such as flies (Diptera) that do not pose a risk of injury from bites and kicks. A study of naturally caught prey and prey availability in the surroundings of the social *Stegodyphus* species suggests that *S. mimosarum* tend to catch the smallest prey of the three social species and that they also have the smallest prey available in their surroundings (median prey sizes: *S. mimosarum*: prey caught = 4 mm, available prey = 2 mm; *S. dumicola*: prey caught = 8 mm, available prey = 3 mm; *S. sarasinorum*: prey caught = 11.5 mm; available prey = 3 mm) (Majer et al. 2018). Furthermore, the proportion of dipterans caught naturally by *S. mimosarum* was relatively high (>30%), while orthopterans formed the smallest proportion of caught prey (~5%) as compared to the other two social species (Majer et al. 2018). The nests of *S. mimosarum* tend to be found higher up in the vegetation than *S. dumicola*, e.g., in tree branches rather than in low bushes (Lubin & Crouch 2003). Here, they are perhaps less likely to encounter orthopterans, which might explain a diet consisting of more dipterans and fewer orthopterans. In addition, *S. mimosarum* has the smallest adult body size of all *Stegodyphus* spiders, perhaps because of shifting selection pressures from a slightly different dietary niche.

Further studies are now needed to test whether the *S. mimosarum* prey capture strategy is cautious in general terms, with low propensities to attack prey of different taxonomic groups, or whether *S. mimosarum* has specialized in a narrower dietary niche allowing differential use of resources between *S. mimosarum* and *S. dumicola* occurring in the same habitat.

***Stegodyphus dumicola*.**—Prey size could not predict the number of attackers, with ~2–4 spiders tending to engage in prey attack over the course of five minutes, irrespective of prey size. However, prey size did affect the prey acceptance rate,

with spiders being more likely to accept medium-sized prey as compared to small and large prey (Grinsted et al. 2020). Indeed, this species was the only of the three social *Stegodyphus* species indicated in Grinsted et al. (2020) to show a preference for a particular range of prey sizes (~15–30 mm). We speculate that this may reflect a more choosy and coordinated strategy where medium-sized prey that can feed more colony members are preferred over smaller prey, with a relatively high number of spiders attacking together, while larger, more dangerous prey may be rejected depending on the hunger state of group members. Such a strategy might reflect niche specialization due to niche competition with *S. mimosarum* and/or a relatively high prey abundance in the environment allowing group members to be more choosy. In conjunction with this, Majer et al. (2018) found that naturally caught prey (median = 8 mm) tended to be larger than the average available prey sizes in the environment (median = 3 mm), although no distinct specialization on a prey size range was identified in this study. Furthermore, prey caught in traps and in webs during field observations of colonies (see section on *S. sarasinorum*) indicate that prey is relatively abundant in the environment of *S. dumicola* (Majer et al. 2018), supporting the suggestion that high prey abundance may lead to choosiness. However, the preference for medium-sized prey might only be true for orthopteran prey, or may vary with ontogeny of the spiders, as group members grow larger over development and may change their prey size preferences. Further studies are needed to confirm whether *S. dumicola* indeed has specialized in a specific size range of prey, whether this prey size preference changes over ontogeny, and whether a prey size preference occurs in other prey types.

***Stegodyphus sarasinorum*.**—A relatively high number of spiders engaged in prey attack in *S. sarasinorum* when prey was small (~3–5 spiders tended to attack prey of <15 mm during the first 5 min) whereas fewer spiders tended to attack medium–large prey (~2–3 spiders attacked during the first 5 min for prey >15 mm). Additionally, this species had very high acceptance rates of prey, irrespective of prey size, showing no preference for a particular prey size range (Grinsted et al. 2020), with >88% of all prey items being attacked within 10 min of prey introduction. We propose that this is a more ‘opportunistic’ prey capture strategy, where individual spiders appear to have a relatively high propensity to engage in prey attack, particularly when prey is small. This might reflect (1) relatively high levels of competition within colonies where individuals compete to monopolize smaller prey items but are slightly less disposed to take on the risk of approaching a larger, more dangerous prey items; (2) a relatively low risk of predation when venturing out of the protective nest onto the capture web; and/or (3) low prey abundance in the environment making each prey item highly valuable.

Studies on naturally caught prey suggest that while *S. sarasinorum* tend to catch prey (median = 11.5 mm) that is substantially larger than the average prey available in their environment (median = 3 mm), most of their prey is <15 mm (Majer et al. 2018). Furthermore, prey trapping data indicated that *S. sarasinorum* had the lowest number of prey available in their surroundings of the three social species (average number of prey caught in traps and in webs during field observations:

S. sarasinorum: 110.6 prey/trap, 6.9 prey/colony, as compared to *S. mimosarum*: 640.0 prey/trap, 9.5 prey/colony, and *S. dumicola*: 537.2 prey/trap, 12.5 prey/colony) (Majer et al. 2018). These observations support the suggestion that an opportunistic foraging strategy might be shaped by relatively low prey availability in the environment. Future studies could explore whether the overall high engagement in prey capture in *S. sarasinorum* is plastic with regards to nutritional needs, e.g., by testing whether an increase in food availability would decrease propensities to engage in prey attack. Additional studies comparing propensities to monopolize small prey items, and the number of disputes emerging from such attempts, could further test for potential differences among species in within-colony competition.

Conclusion and perspective.—In this exploratory study, we identified differences among the three social *Stegodyphus* species in the way spiders engage in cooperative prey attack. We propose that each species has a specific prey capture strategy. For *S. mimosarum* and *S. dumicola* that have overlapping geographical distributions, the specific strategies may be shaped by niche competition. The strategies for these two species may be cautious and choosy, respectively, while *S. sarasinorum* may be more opportunistic. Further studies are now needed to understand whether each species' strategy changes with ontogeny, and to what extent foraging strategies are plastic and affected by prey type or by environmental factors such as prey availability and predation pressure. Future studies will reveal whether the three species converge or diverge even further in their foraging strategies when controlling for developmental stage, spider body size and group size.

An additional avenue to explore is the potential for differences in the physical structure of the capture web among species. Web-building spiders are unique in their ability to create a trap that can be relied upon to ensnare and potentially subdue or weaken a prey item before the spider directly engages with the prey. Through cooperating in web-building, social spiders might be able to increase the capability of their web to ensnare prey, potentially reducing the energy needed to subdue a prey item. This is different from other cooperatively hunting animals, like lions (*Panthera leo*) and wild dogs (*Lycaon pictus*) (Scheel & Packer 1991; Creel & Creel 1995), and other social arachnids such as social pseudoscorpions (*Paratemnoides spp.*) (Zeh & Zeh 1990; Tizo-Pedroso & Del-Claro 2018) that rely on combined physical strength and sometimes coordinated hunting techniques to cooperatively overpower their prey. *Stegodyphus* spiders produce cribellate silk that has strong adhesive properties without the use of glue (Eberhard 1988). The adhesiveness of cribellate silk is affected by the spinning behavior of the spider (Michalik et al. 2019), and the ability of the web to prevent a prey item from escaping may affect individual spiders' propensity to approach intercepted prey. Hence, spinning behavior and the physical properties of capture webs are likely under strong selection and might affect whether foraging strategies are cautious, opportunistic, or choosy.

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SUPPLEMENTAL MATERIALS

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Table S1.—Results from analysis of number of attackers with outlier trial included.

Figure S1.—Distribution of trials according to prey body size in the three social spider species.

Figure S2.—Effect of prey size on the number of attackers in the three species at various points in time during attack sequence.

LITERATURE CITED

- Agnarsson I, Aviles L, Coddington JA, Maddison WP. 2006. Sociality in theridiid spiders: Repeated origins of an evolutionary dead end. *Evolution* 60:2342–2351.
- Ainsworth C, Slotow R, Crouch T, Lubin Y. 2002. Lack of task differentiation during prey capture in the group living spider *Stegodyphus mimosarum* (Araneae, Eresidae). *Journal of Arachnology* 30:39–46.
- Amir N, Whitehouse MEA, Lubin Y. 2000. Food consumption rates and competition in a communally feeding social spider, *Stegodyphus dumicola* (Eresidae). *Journal of Arachnology* doi:10.1636/0161-8202(2000)028[0195:fcracl]2.0.co;2.
- Avilés L. 1997. Causes and consequences of cooperation and permanent-sociality in spiders. Pp. 476–498. *In* The Evolution of Social Behavior in Insects and Arachnids. (Choe JC, Crespi BJ, eds.) Cambridge University Press. Cambridge, United Kingdom.
- Aviles L, Guevara J. 2017. Sociality in spiders. Pp. 188–223. *In* Comparative Social Evolution. (Rubenstein DR, Abbot P, eds.). Cambridge University Press. Cambridge.
- Chiara V, Jeanson R. 2020. Influence of past and current social contexts on hunting behavior in spiderlings. *Behavioral Ecology and Sociobiology* 74(7). doi:10.1007/s00265-020-02870-9.
- Creel S, Creel NM. 1995. Communal hunting and pack size in African wild dogs, *Lycaon pictus*. *Animal Behaviour* 50:1325–1339. doi:10.1016/0003-3472(95)80048-4.
- Drisy-Mohan OM, Kashmeera NA, Sudhikumar AV. 2019. Is cooperation in prey capture flexible in the Indian social spider *Stegodyphus sarasinorum*? *Arachnologische Mitteilungen* 58(1). doi:10.30963/aramit5813.
- Eberhard WG. 1988. Combing and sticky silk attachment behaviour by cribellate spiders and its taxonomic implications. *Bulletin of the British Arachnological Society* 7:247–251.
- Grinsted L, Bilde T. 2013. Effects of within-colony competition on body size asymmetries and reproductive skew in a social spider. *Journal of Evolutionary Biology* 26(3). doi:10.1111/jeb.12072.
- Grinsted L, Lubin Y. 2019. Spiders: Evolution of group living and social behavior. Pp. 632–640. *In* Encyclopedia of Animal Behavior (2nd Edition). (Choe JC, ed). <https://doi.org/10.1016/B978-0-12-809633-8.01040-2>
- Grinsted L, Breuker CJ, Bilde T. 2014. Cooperative breeding favors maternal investment in size over number of eggs in spiders. *Evolution* 68(7). doi:10.1111/evo.12411.
- Grinsted L, Schou MF, Settepani V, Holm C, Bird TL, Bilde T. 2020. Prey to predator body size ratio in the evolution of cooperative

- hunting—a social spider test case. *Development Genes and Evolution* 230(2). doi:10.1007/s00427-019-00640-w.
- Hadfield JD. 2010. MCMC Methods for multi-response Generalized Linear Mixed Models: The MCMCglmm R Package. *Journal of Statistical Software* 33(2):1–22.
- Hodar JA. 1996. The use of regression equations for estimation of arthropod biomass in ecological studies. *Acta Oecologica* 17:421–433.
- Johannesen J, Lubin Y, Smith DR, Bilde T, Schneider JM. 2007. The age and evolution of sociality in *Stegodyphus* spiders: a molecular phylogenetic perspective. *Proceedings of the Royal Society B-Biological Sciences* 274(1607):231–237. doi:10.1098/rspb.2006.3699.
- Junghanns A, Holm C, Schou MF, Overgaard J, Malte H, Uhl G et al. 2019. Physiological adaptations to extreme maternal and allomaternal care in spiders. *Frontiers in Ecology and Evolution* 7. doi:10.3389/fevo.2019.00305.
- Junghanns A, Holm C, Schou MF, Sorensen AB, Uhl G, Bilde T. 2017. Extreme allomaternal care and unequal task participation by unmated females in a cooperatively breeding spider. *Animal Behaviour* 132:101–107. doi:10.1016/j.anbehav.2017.08.006.
- Kraus O, Kraus M. 1988. The genus *Stegodyphus* (Arachnida, Araneae). Sibling species, species groups, and parallel origin of social living. Pp. 151–254. In *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF)* 30. (Kraus O, ed.) Hamburg and Berlin: Verlag Paul Parey.
- Lubin Y, Bilde T. 2007. The evolution of sociality in spiders. *Advances in the Study of Behavior* 37:83–145.
- Lubin Y, Crouch T. 2003. Trial by fire: Social spider colony demographics in periodically burned grassland. *African Zoology* 38:145–151. doi:10.1080/15627020.2003.11657202.
- Majer M, Holm C, Lubin Y, Bilde T. 2018. Cooperative foraging expands dietary niche but does not offset intra-group competition for resources in social spiders. *Scientific Reports* 8, article 11828, doi:10.1038/s41598-018-30199-x
- Majer M, Svenning JC, Bilde T. 2013. Habitat productivity constrains the distribution of social spiders across continents - case study of the genus *Stegodyphus*. *Frontiers in Zoology* 10, article 9, doi:10.1186/1742-9994-10-9.
- Majer M, Svenning J-C, Bilde T. 2015. Habitat productivity predicts the global distribution of social spiders. *Frontiers in Ecology and Evolution* 3(101). doi:10.3389/fevo.2015.00101.
- Mayntz D, Raubenheimer D, Salomon M, Toft S, Simpson SJ. 2005. Nutrient-specific foraging in invertebrate predators. *Science* 307:111–113. doi:10.1126/science.1105493. www.sciencemag.org.
- Michalik P, Piorkowski D, Blackledge TA, Ramirez MJ. 2019. Functional trade-offs in cribellate silk mediated by spinning behavior. *Scientific Reports* 9(1):1–6. doi:10.1038/s41598-019-45552-x.
- Nentwig W. 1985. Social spiders catch larger prey - a study of *Anelosimus eximius* (Araneae, Theridiidae). *Behavioral Ecology and Sociobiology* 17:79–85. doi:10.1007/Bf00299433.
- Parthasarathy B, Somanathan H. 2019. Behavioral responses vary with prey species in the social spider, *Stegodyphus sarasinorum*. *Behavioral Ecology* 30:938-947. doi:10.1093/beheco/arz032.
- Powers KS, Aviles L. 2007. The role of prey size and abundance in the geographical distribution of spider sociality. *Journal of Animal Ecology* 76:995–1003. doi:10.1111/j.1365-2656.2007.01267.x.
- Rayor LS, Uetz GW. 1990. Trade-offs in foraging success and predation risk with spatial position in colonial spiders. *Behavioral Ecology and Sociobiology* 27:77–85. doi:10.1007/Bf00168449.
- R Core Team. 2020. R: A Language and Environment for Statistical Computing. <https://www.r-project.org/>.
- Scheel D, Packer C. 1991. Group hunting behavior of lions - a search for cooperation. *Animal Behaviour* 41:697–709. doi:10.1016/S0003-3472(05)80907-8.
- Seibt U, Wickler W. 1987. Gerontophagy versus cannibalism in the social spiders *Stegodyphus mimosarum* Pavesi and *Stegodyphus dumicola* Pocock. *Animal Behaviour* 35:1903–1905. doi:10.1016/S0003-3472(87)80087-8.
- Seibt U, Wickler W. 1988. Why do family spiders, *Stegodyphus* (Eresidae), live in colonies. *Journal of Arachnology* 16:193–198.
- Settepani V, Bechsgaard J, Bilde T. 2016. Phylogenetic analysis suggests that sociality is associated with reduced effectiveness of selection. *Ecology and Evolution* 6:469–477. doi:10.1002/ece3.1886.
- Settepani V, Bilde T, Grinsted L. 2015. Temporarily social spiders do not show personality-based task differentiation. *Animal Behaviour* 105. doi:10.1016/j.anbehav.2015.04.006.
- Settepani V, Grinsted L, Granfeldt J, Jensen JL, Bilde T. 2013. Task specialization in two social spiders, *Stegodyphus sarasinorum* (Eresidae) and *Anelosimus eximius* (Theridiidae). *Journal of Evolutionary Biology* 26(1). doi:10.1111/jeb.12024.
- Settepani V, Schou MF, Greve M, Grinsted L, Bechsgaard J, Bilde T. 2017. Evolution of sociality in spiders leads to depleted genomic diversity at both population and species levels. *Molecular Ecology* 26(16). doi:10.1111/mec.14196.
- Souza ALT, Gonzaga MO, Vasconcellos-Neto J. 2007. Prey capture behaviour in the social spider *Anelosimus eximius* (Araneae: Theridiidae): Responses to prey size and type. *Ethology* doi:10.1111/j.1439-0310.2007.01384.x.
- Tizo-Pedroso E, Del-Claro K. 2018. Capture of large prey and feeding priority in the cooperative pseudoscorpion *Paratemnoides nidificator*. *Acta Ethologica* doi:10.1007/s10211-018-0288-5.
- Walter A, Bechsgaard J, Scavenius C, Dyrland TS, Sanggaard KW, Enghild JJ, et al. 2017. Characterisation of protein families in spider digestive fluids and their role in extra-oral digestion. *BMC Genomics* doi:10.1186/s12864-017-3987-9.
- Ward PI, Enders MM. 1985. Conflict and cooperation in the group feeding of the social spider *Stegodyphus mimosarum*. *Behaviour* 94:167–182.
- Wille MB, Jackson RR. 1993. Predatory behavior of a social spider, *Stegodyphus sarasinorum* (Araneae, Eresidae) - Why attack first. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 71(11):2220–2223. doi:DOI 10.1139/z93-311.
- World Spider Catalog. 2021. Version 22.5. (14.05.19). doi:10.24436/2. <http://wsc.nmbe.ch>.
- Wright CM, Lichtenstein JLL, Luscuskie LP, Montgomery GA, Geary S, Pruitt JN, et al. 2020. Spatial proximity and prey vibratory cues influence collective hunting in social spiders. *Israel Journal of Ecology and Evolution* 66(1–2). doi:10.1163/22244662-20191062.
- Yip EC, Rayor LS. 2014. Maternal care and subsocial behaviour in spiders. *Biological Reviews*. 89:427–449. doi:10.1111/brv.12060.
- Zeh JA, Zeh DW. 1990. Cooperative foraging for large prey by *Paratemnus elongatus* (Pseudoscorpionida, Atemnidae). *Journal of Arachnology* 18:307–311. JSTOR 3705436.

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