Development Genes and Evolution (2020) 230:173–184
https://doi.org/10.1007/s00427-019-00640-w

ORIGINAL ARTICLE

Prey to predator body size ratio in the evolution of cooperative hunting—a social spider test case

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Received: 18 July 2019 / Accepted: 30 October 2019 / Published online: 25 November 2019

Abstract

One of the benefits of cooperative hunting may be that predators can subdue larger prey. In spiders, cooperative, social species can capture prey many times larger than an individual predator. However, we propose that cooperative prey capture does not have to be associated with larger caught prey per se, but with an increase in the ratio of prey to predator body size. This can be achieved either by catching larger prey while keeping predator body size constant, or by evolving a smaller predator body size while maintaining capture of large prey. We show that within a genus of relatively large spiders, *Stegodyphus*, subsocial spiders representing the ancestral state of social species are capable of catching the largest prey available in the environment. Hence, within this genus, the evolution of cooperation would not provide access to otherwise inaccessible, large prey. Instead, we show that social *Stegodyphus* spiders are smaller than their subsocial counterparts, while catching similar sized prey, leading to the predicted increase in prey-predator size ratio with sociality. We further show that in a genus of small spiders, *Anelosimus*, the level of sociality is associated with an increased size of prey caught while predator size is unaffected by sociality, leading to a similar, predicted increase in prey-predator size ratio. In summary, we find support for our proposed 'prey to predator size ratio hypothesis' and discuss how relaxed selection on large body size in the evolution of social, cooperative living may provide adaptive benefits for ancestrally relatively large predators.

Keywords Social evolution · Group living · Phenotypic plasticity · Predator-prey interactions · Dietary niche

Introduction

Group living and cooperation are associated with a range of fitness costs and benefits. For predators, selective benefits of grouping might include the ability to catch larger prey as a results of cooperative hunting (e.g., lions (Caraco and Wolf 1975), wolves (Nudds 1978) and wild dogs (Creel and Creel 1995)). Social spiders that cooperate in prey capture are able to subdue prey many times larger than an individual spider. This product of cooperation may have been important in the evolution of group living in spiders (Guevara et al. 2011; Majer et al. 2018; Nentwig 1985; Ward 1986). Indeed, it has been suggested that the presence of large insect prey in the environment is essential for the existence of large, social spider colonies that are sessile and depend on prey arrival in their webs (the 'prey size' hypotheses; Aviles et al. 2007; Aviles and Guevara 2017; Majer et al. 2015; Powers and Aviles 2007; Yip et al. 2008). This is because per-capita number of prey caught decreases with group size in social spiders, and so the capture of larger prey is needed to balance out per-capita food intake and sustain a large colony size (Majer et al. 2015; Ward 1986; Yip et al. 2008).

Social spiders have evolved from subsocial ancestors through the loss of a pre-mating dispersal stage (Agnarsson et al. 2006; Johannesen et al. 2007; Settepani et al. 2016). Subsocial spiders show extended maternal care that includes actively feeding the offspring by regurgitation or sharing prey.

This article is part of the Special Issue "Crossroads in Spider Research - evolutionary, ecological and economic significance"

Communicated by Matthias Pechmann

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Subsociality is further defined by juveniles showing a gregarious, social phase in their natal nest after their mother has died (often by matriphagy), during which they cooperate in foraging (Grinsted and Lubin 2019; Lubin and Bilde 2007). This social stage ends when siblings disperse to live solitarily before reaching sexual maturity. In social spiders, however, the dispersal stage is lost and juveniles remain in their natal nest where they continue to cooperate in prey capture, feeding and web maintenance. Eventually, as group members become sexually mature, they mate within the group and females cooperate in brood care. Social spider group sizes commonly reach hundreds, and in some species thousands, of closely related individuals (Avilés 1997; Lubin and Bilde 2007).

Although multiple factors have likely selected for sociality in spiders, such as eliminating the high mortality associated with dispersal and solitary living, and benefitting from increased survival and growth rates of juveniles due to cooperative breeding (Aviles and Tufino 1998; Bilde et al. 2007; Settepani et al. 2017), the access to large prey is likely to play a role at least in facilitating the evolution of spider sociality (Aviles and Guevara 2017; Majer et al. 2018, 2015, 2013a, b). The link between sociality and prey size is well documented and extensively researched within spiders of the genus *Anelosimus* (Theridiidae). This genus contains the highest number of social species of any spider genus: at least seven fully social species (Agnarsson et al. 2006; Aviles and Guevara 2017), at least 16 (and probably many more) subsocial species (Yip and Rayor 2014), and at least one species (and probably more) that can be considered intermediate social where females sometimes form small colonies but where cooperation within the colony is limited (Aviles and Guevara 2017; Yip and Rayor 2014). In the Americas, social *Anelosimus* species are mainly found at low elevation and low latitude while subsocial *Anelosimus* species occur at higher elevations and latitudes, with some overlap between social and subsocial species (Aviles et al. 2007). This distributional pattern corresponds neatly with higher abundance of larger insect prey where social spiders exist, and smaller average prey size where subsocial species occur (Powers and Aviles 2007). Furthermore, within social *Anelosimus* species, larger colonies consistently capture larger prey (Guevara et al. 2011; Nentwig 1985; Yip et al. 2008). The combination of a linear decrease in per-capita number of prey with increasing group size and a concave increase in average prey size results in an optimum per-capita prey biomass obtained at intermediate colony sizes around 500 individuals (Yip et al. 2008).

The well-documented association between sociality and prey size in *Anelosimus* spiders suggests that cooperation mediates access to an otherwise inaccessible resource (large prey); however, whether this applies in general in social spider evolution across genera is not established. Sociality occurs only in eight spider genera, with the highest number of social species, after *Anelosimus*, recorded in the commonly studied genus *Stegodyphus* (Eresidae) and in the little explored genus *Parasteatoda* (Theridiidae) (three species each) (Aviles and Guevara 2017). Although the three social *Stegodyphus* species, like the social *Anelosimus* species, tend to be constrained to geographical areas of high productivity, and therefore presumably areas that sustain a higher abundance of large insect prey (Majer et al. 2013a, b, 2015), the ranges of social *Stegodyphus* overlap extensively with those of their subsocial counterparts (Majer et al. 2018, 2013a, b). Hence, social and subsocial *Stegodyphus* species are not segregated like those of *Anelosimus* by elevation, latitude or average prey size available in the environment. Furthermore, although social *Stegodyphus* spiders might be able to expand their dietary niche as compared to their subsocial congeners, accessing a slightly broader range of prey sizes, both social and subsocial *Stegodyphus* spiders tend to prey on insects that are on average much larger than the average insects available in their environment (Majer et al. 2018). Hence, the access to larger prey per se may not be what facilitates social evolution in this spider genus.

We propose a new hypothesis that we call the ‘prey to predator size ratio hypothesis’. We hypothesise that the capture of large prey is important in social spider evolution but not in the traditional sense that cooperation allows spiders to access a resource, i.e. larger prey, which is inaccessible to non-cooperating individuals. Instead, we propose that the body size ratio of prey to predator is the crucial factor based on the following argument: the common feature for all social spiders is not that they are capable of catching larger prey per se, but that sociality is accompanied by an increased prey size to predator size ratio. This increased ratio can be achieved *either* by an increase in prey size *or* by a decrease in spider size. Note that throughout this paper, we shall let ‘spider size’ refer to the average full body length of adult female spiders. When developing this hypothesis below, we exclude males because females are the cooperative sex in social spiders, involved in all the cooperative tasks in the colony, while males die shortly after mating (Avilés 1997; Lubin and Bilde 2007).

Let us first assume that within a genus of web-building spiders, larger solitary spiders are able to catch larger prey, as larger spiders build larger webs, have larger fangs, and are physically able to subdue larger insects (Nentwig and Wissel 1986; Venner and Casas 2005). This assumption entails that with increasing spider size, the size of prey caught will reach an upper limit, as insect sizes do not increase indefinitely (solitary spiders are shown as a thin curve, ‘sol’, in Fig. 1a, e with its asymptote representing the maximum prey size available in the environment). We further assume that as spiders begin to cooperate and create groups of ever larger sizes (thickness of the curve in Fig. 1a, e correspond to group sizes small, medium and large), the need for a large predator body size is relaxed, as cooperative groups containing smaller spiders will still be able to access the largest prey available (Majer et al. 2018; Powers and Aviles 2007; Ward 1986; Yip et al. 2008).

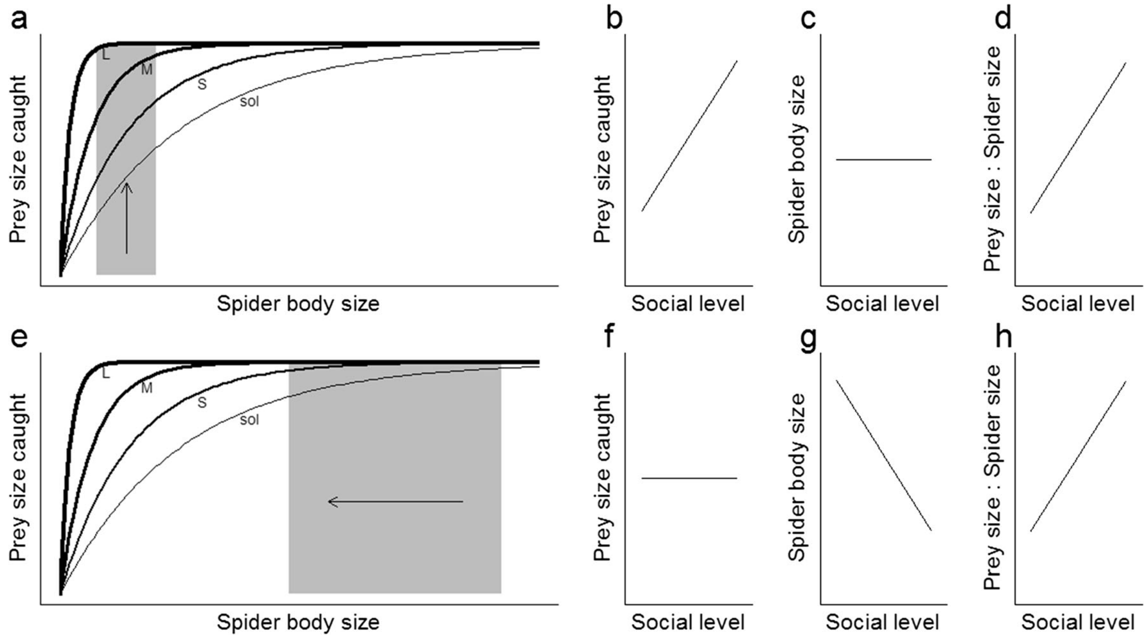

Fig. 1 The 'prey to predator size ratio hypothesis' and its predictions explained. The two identical graphs in **a** and **e** explain how larger solitary spiders are expected to catch larger prey (thin curve, 'sol') up to the maximum prey size available, while groups of increasing sizes (the thickness of the curves indicate group sizes small, medium and large) can access the maximum prey sizes at ever smaller spider body sizes due to cooperative prey capture. The figures in **b**–**d** and **f**–**h** indicate how prey size (**b**, **f**), spider size (**c**, **g**) and the ratio between the two (**d**, **h**) are predicted to vary with increasing social level in each of a genus of relatively small spiders (**a**–**d**) and a genus of relatively large spiders (**e**–**h**). Within a genus of small spiders relative to prey size in their environment (grey area within **a**), the evolution of sociality (vertical arrow in **a**) is expected to be associated with catching larger prey (**b**) without necessarily changing the body size of the spiders (**c**). Within a genus of large spiders that are already able to catch the largest prey available (grey area within **e**), the evolution of sociality (the horizontal arrow in **e**) is expected to be associated with smaller spider body sizes (**g**) while prey sizes remain the same (**f**). This leads to identical predictions relating to the ratio of prey to predator body size for genera of both small and large spiders: the evolution of sociality is expected to be associated with an increased prey-predator size ratio (**d**, **h**)

Now imagine a spider genus with a relatively small spider body size, as is the case for *Anelosimus* (typically between 1.8 and 5.5 mm) (Fernandez-Fournier et al. 2018). If there are selective benefits for a solitary spider to gain access to larger prey, e.g. in an environment where small prey is scarce or competition for large prey is less fierce than for smaller prey, it can either evolve to a larger size or form a group and catch prey cooperatively to utilise that otherwise inaccessible resource. Perhaps this spider is phylogenetically or physiologically constrained from evolving to a large size, and perhaps it is predisposed to cooperative behaviour and group living due to extended maternal care that necessitates tolerance among siblings as they feed together during the brood care phase (Yip and Rayor 2014). In this case, this small species will benefit from transitioning to sociality (Fig. 1a, grey area). In a genus of mainly small spiders with multiple social species, like *Anelosimus*, we would then expect that with an increase in social level we will see (1) an increase of prey size caught (Fig. 1b), (2) no consistent change in spider body size (Fig. 1c), and (3) an increased prey size to spider size ratio (Fig. 1d).

Now imagine instead a genus of relatively large, solitary spiders that are already utilising the available resource, being capable of catching some of the largest prey in the environment (Fig. 1e, grey area). There is no inaccessible, large prey available in the environment that a spider could exploit by forming cooperative groups. However, when social groups do form due to other selective benefits of cooperation, the ability for spiders of a smaller size to continue catching the largest available prey will relax selection on large body size, allowing group living spiders to evolve a smaller body size at which to reach sexual maturation. This is important because cooperative spiders catch fewer prey per spider, and with no real change in the average prey size captured, food intake per spider will be lower for groups as compared to solitary spiders and decrease with group size (Majer et al. 2018; Ward 1986). This form of resource competition will have less of a negative effect if group members mature at a smaller size and therefore have lower nutritional requirements to mature. Smaller adult females in social groups will inevitably mean lower reproductive output per female, as shown in Bilde et al. (2007), but this does not necessarily need to translate to a fitness cost of sociality. This is because the production of fewer offspring decreases resource competition among juveniles within the group (Grinsted et al. 2014). Less competition combined with increased growth and survival of young in social colonies (Bilde et al. 2007) may result in an overall benefit to social spiders of a smaller body size. Hence, in a genus of mainly large spiders with multiple social species, such as *Stegodyphus* (typically between 9.2 and 23.0 mm) (Kraus and Kraus 1988), we would expect that with increased sociality we will see (1) no change in prey size (Fig. 1f), (2) a decreased spider size (Fig. 1g), and (3) an increased prey size to spider size ratio (Fig. 1h)—this final correlation being identical to that of a genus of smaller spiders (Fig. 1d).

We aim to test the assumptions and predictions (as outlined below) of the 'prey to predator size ratio hypothesis'. There is already ample evidence for the predictions that for a genus of relatively small spiders (*Anelosimus*) both the prey size and the prey to predator size ratio increases with the level of sociality (Fig. 1b, d) (Guevara et al. 2011; Nentwig 1985; Powers and Aviles 2007; Yip et al. 2008). Hence, we focused on *Stegodyphus* to test the assumption that in a genus of relatively large spiders both social and subsocial species are capable of catching the largest prey available in their environment (Fig. 1f). We tested this by introducing prey of various sizes to three social and three subsocial *Stegodyphus* species and record the rate of prey acceptance.

Next, we tested the prediction that in a genus of small spiders there will be no association between spider size and social level (Fig. 1c) while in a genus of larger spiders the social species will tend to be smaller than subsocial species (Fig. 1g). To do this, we extracted average body sizes of social and subsocial *Anelosimus* and *Stegodyphus* species from the literature and mapped them onto their phylogenies, testing whether spider size correlated with the level of sociality while accounting for the phylogenetic relationship among species within each genus.

Finally, we tested whether there was support for the predicted relationships between social level and size of prey naturally caught (Fig. 1b, f) as well as the ratio between the prey size and predator size (Fig. 1d, h). To do so, we collated a small dataset from the literature that included not only spider size and social level but also the average prey size actually caught naturally in the webs by both *Anelosimus* and *Stegodyphus* spiders.

Methods

Field assays

Study system and field sites

Stegodyphus spiders occur mainly in Eurasia and Africa (Majer et al. 2013a, b; World Spider Catalog 2019) where they live in arid and semi-arid habitats (Kraus and Kraus 1988). The genus consists of > 20 species of which the majority are subsocial. The three cooperatively breeding species have independently evolved sociality, and each social species has a subsocial species as its sister species (Johannesen et al. 2007; Settepani et al. 2017). For this study, we collected data on the acceptance of prey of various sizes on all three social species (*S. dumicola*, *S. mimosarum*, and *S. sarasinorum*) and three subsocial species (*S. lineatus*, *S. pacificus*, and *S. tibialis*).

Social *Stegodyphus* species live in nests that are dense and compact silky masses built on spiny shrubs or along fences. Each nest has multiple tubular retreats and is surrounded by one or several two-dimensional capture webs that intercepts flying insect prey (Seibt and Wickler 1988). Typically, one or a few spiders attack a prey item after which it is shared with the remaining group members (Grinsted et al. 2013; Settepani et al. 2013). The nests of subsocial species are smaller, funnel-shaped, dense silky structures with a capture web extending from the opening of the funnel, built on the tip of thick grass, low shrubs or on fences (Settepani et al. 2015; Ward and Lubin 1993).

The social *S. dumicola* was studied in Otavi in northern Namibia (− 19.595946, 17.367636) in January 2010. The social *S. mimosarum* was studied in Palapye, eastern Botswana (− 22.678316, 27.072882) in May 2019. The social *S. sarasinorum* and the two subsocial *S. pacificus* and *S. tibialis* were studied in Andhra Pradesh in southern India (12.775692, 78.296598) from September to November 2010. The subsocial *S. lineatus* was studied in the Negev desert in Israel (31.075930, 35.018883) in May 2010 and in April 2019 (additional data was collected in 2019, with prey sizes of 7 to 48 mm, as the 2010 dataset did not cover a large enough range of prey sizes 3 to 26 mm).

Prey acceptance assay procedure

For each of six *Stegodyphus* species, three social and three subsocial species, we recorded the acceptance rates of prey of various sizes. We introduced prey of a range of prey sizes from 2 to 60 mm, representing the range available in their natural environment (Majer et al. 2018), to the capture webs of naturally occurring spider nests in the field. We used *Orthoptera* prey (grasshoppers and crickets) either caught in the local environment of each species, or a locally occurring species that was reared in the laboratory. The order *Orthoptera* was chosen because it forms a part of the natural prey range of these spiders and constitute some of the largest natural prey (Majer et al. 2018), because of their abundance in the habitat, and the easy accessibility of a wide range of sizes.

An assay consisted of introducing a prey item carefully into the capture web of a social or subsocial nest using soft forceps and placed approximately 10 cm from the nest refuge or communal retreat. When at least one spider had attacked the prey (usually by biting onto an appendage of the prey) within 10 min, the trial was recorded as prey accepted. If no spider had attacked within 10 min, it was recorded as prey rejection, as prey were attacked within the first few minutes in the majority of successful prey captures.

Each nest was assayed a maximum of three times, and a nest was never assayed more than once in one day. Sample sizes: social *S. dumicola*, N nests = 41, N assays = 117; social *S. mimosarum*, N nests = 31, N assays = 39; social *S. sarasinorum*, N nests = 76, N assays = 93; subsocial *S. lineatus*, N nests = 71, N assays = 82 (N nests = 43 in 2010, N nests = 28 in 2019); subsocial *S. pacificus*, N nests = 17, N assays = 23; and subsocial *S. tibialis*, N nests = 33, N assays = 44.

Body size data and size of naturally caught prey

We collected body size data for adult females from published papers. Body sizes were represented by average total body length in mm from the tip of the prosoma to the end of the abdomen.

For each of eight *Stegodyphus* species, we found 1–4 average body size measures in the literature: social species: *S. dumicola* (Kraus and Kraus 1988); *S. mimosarum* (Crouch and Lubin 2000; Kraus and Kraus 1988; Seibt and Wickler 1988); and *S. sarasinorum* (Grinsted et al. 2014; Jacson and Joseph 1973; Kraus and Kraus 1988); subsocial species: *S. africanus* (Kraus and Kraus 1988); *S. lineatus* (Kraus and Kraus 1988; Schneider 1997; Ward and Lubin 1993); *S. pacificus* (Grinsted et al. 2014; Kraus and Kraus 1988); *S. tentoriicola* (Kraus and Kraus 1988); and *S. tibialis* (Grinsted et al. 2014; Kraus and Kraus 1988). We further collected an additional body size average for *S. mimosarum* by measuring 56 adult female body lengths to nearest 0.01mm using digital callipers. Prey caught naturally by six species was made available to us from Majer et al. (2018) (all three social species as well as the subsocial *S. africanus*, *S. pacificus* and *S. lineatus*) and we calculated mean prey sizes from this data.

All body sizes of *Anelosimus* spiders were obtained from collated data provided in a single publication (Fernandez-Fournier et al. 2018, see Supporting Information Table S1-1 and references therein). Hence, each *Anelosimus* species ($N =$ 25 of which 21 were placed in the partial phylogeny of *Anelosimus*) was represented by a single average body size. Mean prey sizes caught naturally were also collated and available in Fernandez-Fournier et al. (2018) for nine *Anelosimus* species (the solitary *A. nigriscens*; the subsocial/intermediate social *A. studiosus*, *A. elegans*, and *A. baeza*; and the social *A. guacamayos*, *A. jabaquara*, *A. domingo*, *A. dubiosus* and *A. eximius*).

Social levels and phylogenies

While species are traditionally classified into categorical levels of sociality, e.g. solitary, subsocial and social, in reality some species fall in between these categories. For example, some species can be considered facultative or intermediate social (sometimes referred to as ‘transitional’ between subsocial and social) (Aviles and Guevara 2017). Hence, for some purposes, it may be useful to consider sociality on a continuous scale. Aviles and Harwood (2012) proposed a way of calculating a sociality index for a given species, and we extracted such sociality indexes for 25 *Anelosimus* species provided in Fernandez-Fournier et al. (2018). The sociality index was based on the proportion of the life cycle where spiders live in groups (as opposed to solitarily) and the proportion of nests in a population that contain multiple adult females, or inferred from their level of sociality reported in the literature (solitary, subsocial, intermediate and social) and their phylogenetic position (Fernandez-Fournier et al. 2018). The index ranges from 0.1 to 1 with the approximate values categorised as follows: solitary = 0.1, subsocial = 0.3–0.6, intermediately social = 0.7–0.8 and highly social = 0.9–1.0. In *Stegodyphus*, only three species are fully social and the rest of the species within the genus are considered subsocial (Kraus and Kraus 1988). A continuous measure of sociality is therefore not normally used for *Stegodyphus*. However, for easy comparisons, for plotting purposes and for simple correlations, subsocial and social *Stegodyphus* spiders were here given sociality indexes of 0.3 and 1.0, respectively, according to the continuous scale used for *Anelosimus*.

We used the most recent partial phylogeny of *Stegodyphus* published in Settepani et al. (2017) (provided by J. Bechsgaard). For *Anelosimus*, we used the most recent partial phylogeny (generously provided by I. Agnarsson, unpublished data).

Statistics

Prey acceptance

To test for an association between prey acceptance rate and prey size, and to test for a potential prey size preference for each species, we constructed species-specific logistic regressions (accept = 1, reject = 0) using the R-package lme4 (vs. 1.1-21) (Bates et al. 2015) in (R Core Team 2019). The full models included prey size (mm, scaled to mean = 0 and SD = 1) as a quadratic fixed effect, to allow for a potential intermediate prey size preference. Some nests (91 out of 263) were tested more than once, and we therefore included nest-ID as a random effect. To test for a quadratic effect of prey size, we used likelihood ratio tests to compare the full model (quadratic) to a model with prey size as a linear effect. If the quadratic effect of prey size was nonsignificant, we tested if the linear effect of prey size was significant by comparison to a model where prey size was omitted. In case of a significant quadratic reaction-norm, we estimated the preferred prey size and the 95% confidence interval of the maximum acceptance rate using parametric bootstrapping in the function bootMer ($N = 10{,}000$).

Phylogenetic analyses

To test for a relationship between body size and sociality in the genus *Anelosimus*, we performed a phylogenetic analysis (N average body sizes = 21) with body size as the response variable and sociality index as the sole predictor variable. We used the gls function in nlme (vs 3.1) (Pinheiro et al. 2019) to perform phylogenetic generalized least squares (pgls) regression while accounting for lack of independence due to shared ancestry with Pagel's lambda (λ) correlation structure (i.e. a phylogenetic signal). λ is a scaling parameter that represents the similarity between species that is explained by shared evolutionary ancestry, with 0 being no variation explained by shared evolutionary history and 1 reflecting that all variation is explained by the branch lengths of the phylogeny.

As explained previously, sociality in *Stegodyphus* is typically portrayed as a binary categorical trait (social 1 or solitary 0). To test for a relationship between sociality and body size, we therefore constructed Bayesian phylogenetic mixed models using the R-package MCMCglmm (v. 2.25) (Hadfield 2010). MCMCglmm allows for a binary response variable while accounting for non-independence due to shared ancestry using a random effect structure connecting species to a phylogenetic relationship matrix inferred from the phylogeny (N average body sizes = 19). This model also allows us to use the multiple measures of body size available for some species while accounting for the non-independence of these estimates in an additional random effect of species. In a binary model, the residual variance cannot be estimated and was therefore fixed to one. As the models were fitted with a logit-link function, we specified χ^2 distributed random effect priors as recommended in (Villemereuil et al. 2013) and we used fixed effect priors with mean = 0 and $V = 1 + pi^{2/3}$, which is flat on a probability scale. Convergence of the estimates was checked by running the model four times and inspecting trace plots and their overlap of the MCMC chain and the level of autocorrelation among posterior samples.

We also estimated the phylogenetic signal (measured by λ) separately for body mass and sociality for each of the species using geiger (vs 2.061) (Harmon et al. 2008). To test if λ for each of these traits was different from zero (evidence for a phylogenetic signal) we compared a model where λ was estimated from the original tree, with a model where the tree was rescaled according a λ of zero. The two models were compared with likelihood ratio tests.

Simple correlations

To test for correlations between the level of sociality and the two variables (1) average prey size naturally caught by spiders and (2) the ratio of the average prey size caught to average spider size, we performed simple, non-parametric Spearman's rank correlations. We did this because sample sizes were very low due to the limited number of species for which naturally caught prey was available (N *Anelosimus* species and prey estimates = 9; N *Stegodyphus* species and prey estimates = 6). Hence, the results from these correlations are meant to show simple trends: we stress that phylogenetic relationships are not accounted for in these results.

Results

Prey acceptance

In accordance with the 'prey to predator size ratio hypothesis' we found that all six *Stegodyphus* species were capable of catching some of the largest prey available. Indeed, all three social and all three subsocial species successfully caught prey of sizes spanning the full size ranges available in their natural environment, including large prey (> 30 mm) that are substantially larger than any of the spiders themselves (7.9–18.3 mm) (Fig. 2). For two of the subsocial species (*S. lineatus*, mean body size 11.8 mm, and *S. tibialis*, mean body size 12.8 mm), we even found evidence of a preference for larger prey (Fig. 2d, f; Table 1; *S. lineatus* $\chi^2 = 4.86$, $P = 0.027$; *S. tibialis* $\chi^2 = 4.62$, $P = 0.032$) while the social *S. dumicola* (mean body size 10.1 mm) seemed to prefer prey of an intermediate size of 21.5–28.9 mm (Fig. 2b; Table 1; $\chi^2 = 14.61$, $P < 0.001$). For the remaining three spider species, we found no significant preferences for specific prey sizes, although sample sizes in these species might have prevented us from detecting subtle preferences.

Body size and sociality

As predicted, we found no association between body size and sociality in the genus *Anelosimus* (Fig. 3; Fig. 5b; slope = − 0.50 ± 0.62; $F_{1,19} = 0.65$; $P = 0.429$; $\lambda = 0.67$). We did find support for a phylogenetic signal in both body size ($\lambda = 0.69$; $\chi^2_{(1)} = 12.54$; $P < 0.001$) and in sociality ($\lambda = 0.79$; $\chi^2_{(1)} = 5.61$; $P = 0.019$) in *Anelosimus*. In the genus *Stegodyphus*, we found a close-to significant effect of body size with social species generally being smaller than subsocial species, as predicted (Fig. 4; Fig. 5e; body size = − 0.35, *CI* = − 0.72 to − 0.01, $P_{MCMC} = 0.051$). We found no support for a phylogenetic signal of body size or sociality in *Stegodyphus* (body size: $\lambda = 0$; $\chi^2_{(1)} = 0$; $P = 1$; sociality: $\lambda = 0$; $\chi^2_{(1)} = 0$; $P = 1$).

Sociality level and prey to spider size ratio: simple correlations

As predicted, within the smaller *Anelosimus* spiders, we found positive correlations between social level and both naturally caught prey (Fig. 5a; $S = 16.1$, $P = 0.0026$, $rho = 0.87$) and the ratio of prey to spider size (Fig. 5c; $S = 9.07$, $P < 0.001$, $rho =$

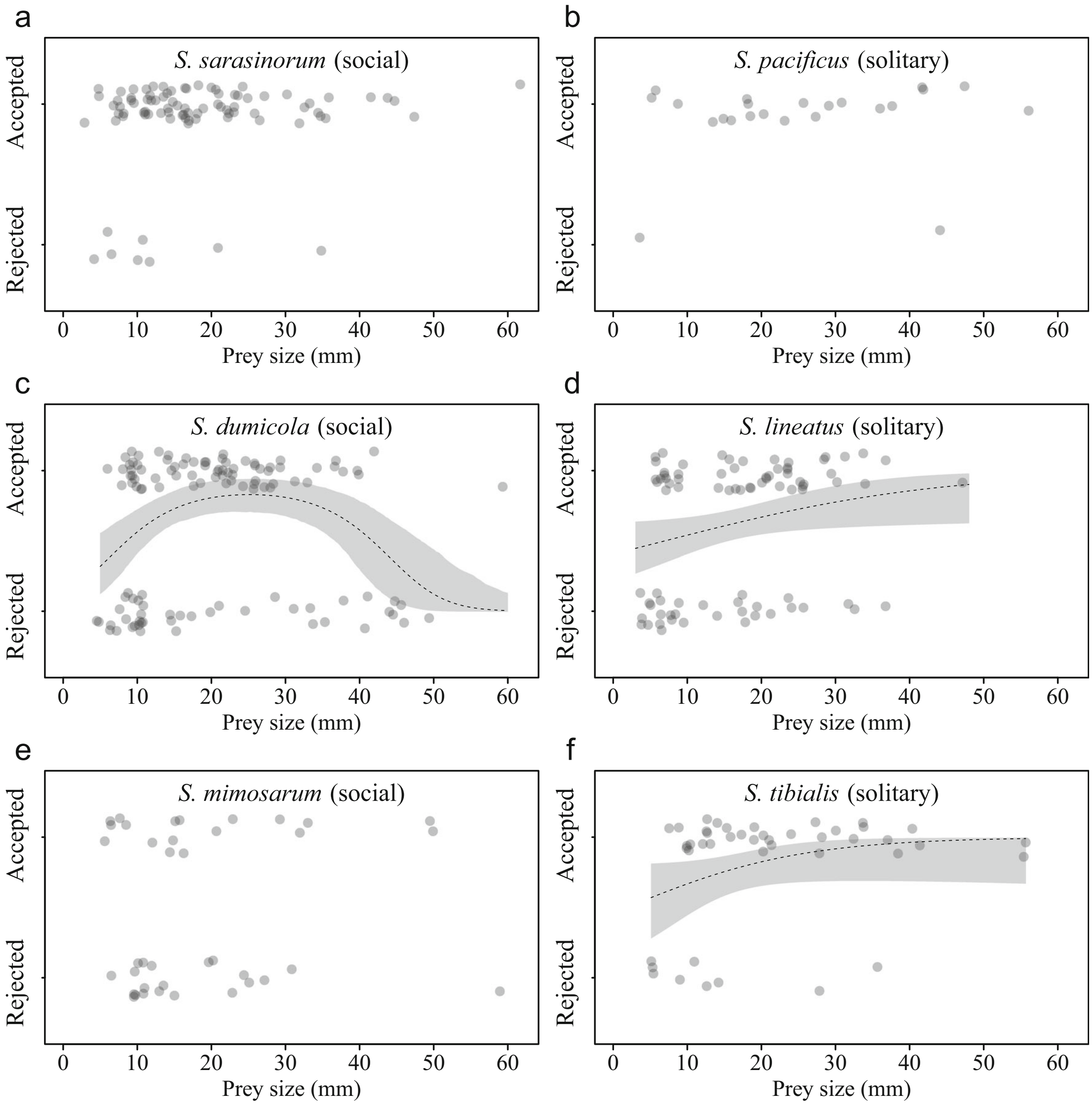

Fig. 2 Prey acceptance rates for six *Stegodyphus* species. **A**ccepted and rejected prey (including random noise to separate data points) plotted against prey size (full body length in mm) for three social, i.e., cooperatively hunting and breeding (**a**, **c**, **e**), and three subsocial, i.e. solitary hunting and breeding (**b**, **d**, **f**) *Stegodyphus* species. Fitted lines and corresponding 95% confidence intervals (curves and grey areas) are shown for the species that showed statistically significant prey size preferences. The 95% confidence intervals for prey acceptance rate were estimated from the minimal adequate model using parametric bootstrapping in the function bootMer ($N = 10{,}000$)

0.92). Also as predicted, within the larger *Stegodyphus* spiders, we found no correlation between social level and naturally caught prey (Fig. 5d; $S = 31.6$, $P = 0.85$, $rho = 0.098$), while we found a positive correlation between social level and the ratio of prey to spider size (Fig. 5f; $S = 4.26$, $P = 0.021$, $rho = 0.88$).

Discussion

We propose a new hypothesis relevant for the evolution of cooperative prey capture in predators—the 'prey to predator size ratio hypothesis'—which we test in two spider genera. This hypothesis proposes that benefits of cooperative hunting include an increased prey to predator size ratio, which can be acquired through one of two routes: (1) the capture of larger prey (while the body size of the predator remains constant) or (2) a reduction in predator body size (while capture of large prey is retained). Cooperative hunting may provide access to an otherwise inaccessible resource in the environment and is a proposed evolutionary driver of group living (Caraco and Wolf 1975; Creel and Creel 1995; Guevara et al. 2011). However, the 'prey to predator size ratio hypothesis' states that the evolution of cooperative hunting does not have to allow predators to catch larger prey per se, instead, cooperation among predators is associated with an increase in the ratio of prey to predator body size. Spiders that are phylogenetically constrained to having small body sizes,

Table 1 Prey size preference results.

	Estimate ± SE	$\chi^2_{(df = 1)}$	*P*	Max. rate (95%CI)
S. sarasinorum				
Intercept	2.27 ± 0.37	–	–	
Prey size	–	2.78	0.095	
Prey size (quadratic component)	–	0.96	0.327	–
S. dumicola				
Intercept	1.47 ± 0.40	–	–	
Prey size	0.61 ± 0.27	–	–	
Prey size (quadratic component)	− 0.81 ± 0.25	14.61	< *0.001*	25.2 (21.5–28.9)
S. mimosarum				
Intercept	− 0.16 ± 0.41	–	–	
Prey size	–	0.44	0.505	
Prey size (quadratic component)	–	0.01	0.968	
S. pacificus				
Intercept	13.01 ± 4.84	–	–	
Prey size	–	0.00	0.975	
Prey size (quadratic component)	–	0.08	0.779	–
S. lineatus				
Intercept	0.54 ± 0.24	–	–	
Prey size	0.54 ± 0.25	4.86	*0.027*	
Prey size (quadratic component)	–	0.97	0.324	–
S. tibialis				
Intercept	1.65 ± 0.49	–	–	
Prey size	1.08 ± 0.61	4.62	*0.032*	
Prey size (quadratic component)	–	1.29	0.256	–

For each species, we assessed whether the prey size preference had a quadratic reaction-norm, a linear reaction-norm or no prey preference in a logistic regression (glmm). Prey size was scaled (mean = 0 and SD = 1) prior to analyses. A quadratic reaction-norm reflects a preference for intermediate sized prey, while a positive linear reaction-norm reflects a preference for the larger prey. The 95% confidence interval of the maximum acceptance rate was estimated for species with a quadratic reaction norm. The three top spp are social, the three lower spp are subsocial.

significant p-values are provided in italics

compared to the body size of potential prey in their surroundings, like *Anelosimus*, are predicted to increase this ratio by increasing their capacity to catch otherwise unavailable, large prey present in the environment (i.e. expanding their dietary niche). Spiders

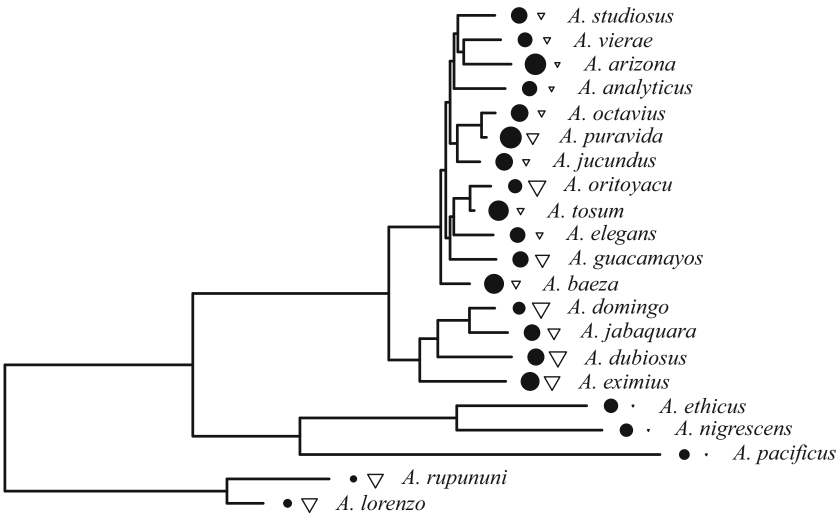

Fig. 3 Body sizes and social level in the phylogeny of *Anelosimus*. **A**verage body sizes (indicated by filled circles; larger circles indicate larger body size) and sociality index (indicated by empty triangles; larger triangles represent higher level of sociality) for each of 21 species mapped onto a partial phylogeny of the genus *Anelosimus*. Average body size and sociality indexes were extracted from the literature while the phylogeny was provided by I. Agnarsson

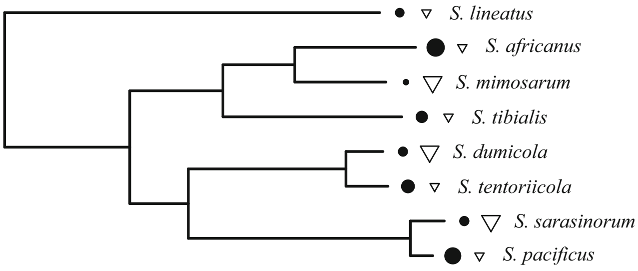

Fig. 4 Body sizes and social level in the phylogeny of *Stegodyphus*. Average body sizes (indicated by filled circles; larger circles indicate larger body size) and level of sociality (indicated by empty triangles; large triangles represent social species while small triangles represent subsocial species) for each of eight species mapped onto a partial phylogeny of the genus *Stegodyphus*. Average body size was extracted from the literature while the phylogeny was provided by J. Bechsgaard

that are relatively large compared to the body size of potential prey, like *Stegodyphus*, can only increase the ratio by instead decreasing their body size (i.e. while maintaining their dietary niche) (Fig. 1). The difference in predictions between the two genera relies on the assumption that large, solitary spiders are already able to catch the largest available prey in the environment. By conducting prey capture assays on three social and three subsocial *Stegodyphus* species in field settings we tested this assumption. We found that, indeed, subsocial spiders within this genus of relatively large spiders were capable of subduing and preying upon some of the largest prey available, just as the social species of much smaller body sizes were (Fig. 2).

We next tested the predictions derived from our hypothesis by collating published data on average body sizes and average prey caught naturally of social and subsocial *Anelosimus* and *Stegodyphus* species. Overall, we found support for our hypothesis: within the genus *Anelosimus* we found, as predicted, that with an increase in the level of sociality there was (1) no associated changes in spider body size, (2) an increase in the size of prey caught naturally (as has been shown before: Guevara et al. 2011; Nentwig 1985; Powers and Aviles 2007; Yip et al. 2008) and (3) an increase in the prey to predator size ratio (Fig. 3; Fig. 5a–c). Within the genus *Stegodyphus*, on the other hand, we found, as predicted, that with an increase in the level of sociality there was (1) a tendency for spiders to be smaller, (2) no consistent change in prey caught naturally and (3) an increase in the prey to predator size ratio (Fig. 4; Fig. 5d–f).

Testing predictions from social evolutionary theory is notoriously difficult in an order where sociality is

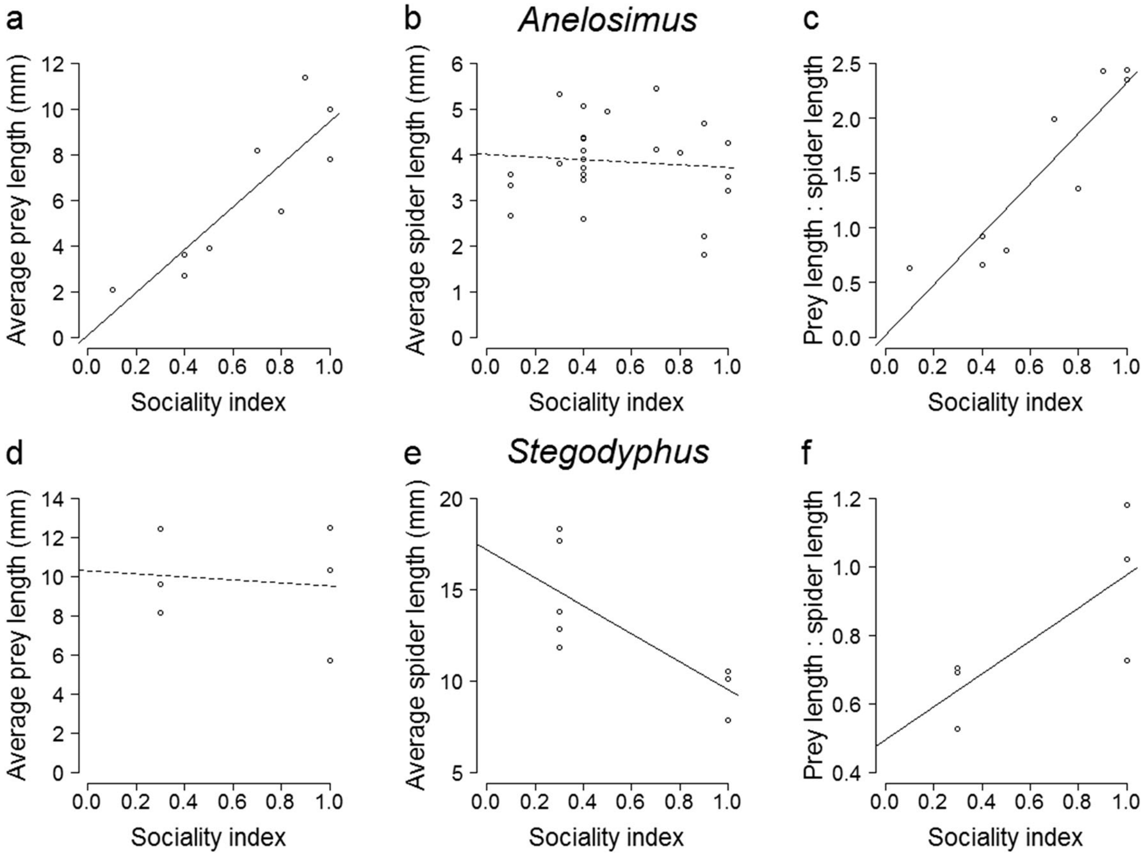

Fig. 5 Overview of all results from testing the predictions of the 'prey to predator size ratio hypothesis'. Prey size (average prey length (mm), **a**, **d**), spider size (average spider length (mm), **b**, **e**) and the ratio between prey size and spider size (**c**, **f**) plotted against the level of sociality (sociality index) for multiple *Anelosimus* species (**a**–**c**) as an example of a genus of smaller spiders, and *Stegodyphus* species (**d**–**f**) as an example of a genus of larger spiders. Full regression lines are shown to indicate significant correlations while stippled lines indicate no significant correlation

phylogenetically rare. In spiders (order Araneae), only five families (out of 120 recognized spider families; World Spider Catalog 2019), encompassing eight genera, contain a total of 19 cooperatively breeding, social species: Agelenidae (*Agelena*: two species), Theridiidae (*Anelosimus*: seven species, *Parasteatoda* (some species previously *Achaearanea*): three species, and *Theridion*: one species), Oxyopidae (*Tapinillus*: one species), Dictynidae (*Mallos*: one species, and *Aebutina*: one species), and Eresidae (*Stegodyphus*: three species) (Aviles and Guevara 2017). This phylogenetic distribution of social spider species naturally limits the available sample size for testing evolutionary transitions to sociality, although sociality has evolved independently multiple times, even within genera (Agnarsson et al. 2006; Johannesen et al. 2007). While the data we present provide support for the predictions of the 'prey to predator size ratio hypothesis', they also suffer from low sample sizes, limiting the power available for phylogenetic analyses. Furthermore, we only present data from a single genus representing large spiders and a single genus representing smaller spiders. Hence, more vigorous testing of our proposed hypothesis is still needed, including data on additional genera, perhaps most relevant *Parasteatoda* and *Agelena* that contain more than one social species each. Including data from multiple populations within each species would also increase power in the analyses, as the total number of social spider species will always be low in these types of analyses.

Perhaps the most intriguing consequence of the 'prey to predator size ratio hypothesis' is the suggestion that sociality relaxes selection on large body size on otherwise relatively large spiders. Solitarily breeding spiders of the family Eresidae, including subsocial *Stegodyphus* have fewer eggs than would be expected based on their body size, obviously related to semelparity and extended maternal care. (Grinsted et al. 2014; Kraus and Kraus 1988; Rezac et al. 2008). Body size correlates positively with number of eggs laid in spiders (Simpson 1995) and within the genus *Stegodyphus* spiders of a larger body size invest in higher numbers of smaller eggs (Grinsted et al. 2014). This suggests that high offspring numbers are generally beneficial in order to compensate for presumed high offspring mortality during development. Hence, the facts that social spiders lay significantly fewer eggs than subsocial congeners (L. Grinsted et al. 2014), and that with increasing group size social *Stegodyphus* spiders experience a decrease in body size, number of eggs per egg sac, and number of egg sacs per female (Bilde et al. 2007; Seibt and Wickler 1988; Ward 1986), are usually considered a fitness cost of sociality caused by competition for resources. Our argument is that the enabling of social spiders to mature at a smaller body size counteracts this effect, and carries with it multiple overall fitness benefits:

Firstly, smaller body sizes and fewer offspring mean less competition for limited resources within a colony as fewer resources are needed for an individual to reach sexual maturity. This might mean that fewer reproductive resources are lost investing into competitively inferior offspring, and less energy is wasted in competitive interactions among group members. As social spider group members are genetically highly related (Settepani et al. 2017), this would mean a reduction in kin competition which should be a selective advantage (Platt and Bever 2009). Secondly, although smaller body sizes are accompanied with the production of fewer eggs per female, social spiders invest in quality over quantity of offspring, producing much fewer but significantly larger eggs than their subsocial congeners (Grinsted et al. 2014). Mortality rates are likely much reduced in social species as compared to subsocial species due to the loss of a risky premating dispersal stage, as well as the large, sturdy, protective nest structure of social colonies providing increased colony level survival (Bilde et al. 2007). This means that an investment into very few, high quality offspring is less of a risky strategy when living socially as compared to solitarily. Hence, producing fewer offspring may not necessarily present a cost. Thirdly, the ability to mature at a smaller size allows for some level of flexibility as a response to unpredictable environmental conditions (Stearns and Koella 1986). For example, according to fluctuations in prey availability females may be able to mature at very small sizes and still successfully raise some offspring with the help from allo-mothers (Junghanns et al. 2017), despite producing only very few eggs. Intriguingly, social spiders occur in relatively more stable environments than their subsocial congeners (Aviles and Guevara 2017; Majer et al. 2018, 2015, 2013a, b), but prey availability is limited as per capita intake and also female body size decrease with increasing group size (Majer et al. 2018). This is in line with selection for smaller body size to reduce resource competition, as mentioned above. Taken together, a smaller adult, female body size may represent a selective advantage for social spiders. We note that it is possible that inbreeding per se leads to smaller body size (Bilde et al. 2005), in which case the driving force behind the reduction in body size in social species could be more complex.

We conclude that our analyses render support for our hypothesis, the 'prey to predator size ratio hypothesis'. We would like to stress that we make no claims as to the relative importance of prey size relative to spider size as a driver of evolution of spider sociality. Many evolutionary drivers will have been involved in favouring cooperation in the few social species present in the spider phylogeny, and these drivers will undoubtedly have played roles of different importance in different taxa, depending on the biology, ecology and life history of each lineage (Avilés 1997; Aviles and Guevara 2017; Grinsted and Lubin 2019; Lubin and Bilde 2007). We simply propose that a larger prey to spider size ratio is a benefit to social spiders, but whether it has been one of the main drivers of the transition to sociality or simply an added component facilitating the maintenance of cooperation after the social transition has occurred will depend on the species or lineage in question. The transition to group living invariably comes with increasing competition for resources. The ‘prey to predator size ratio hypothesis’ suggests that this demand could be met by increasing the prey to predator body size ratio in cooperative hunters. This can be achieved via one of two routes, depending on the relative size of the predators to the potential prey available in the environment: Dietary niche width (prey size) can be expanded through cooperative hunting that mediates access to larger prey; or relative resource demand can be reduced by evolving smaller predator body size while maintaining dietary niche width. We welcome further studies testing the predictions generated from this hypothesis, to assess its generality trough the inclusion of additional taxa and populations.

Acknowledgements We would like to thank Y. Lubin, C. Tuni, M. Majer, I. Musli, I. Hoffman, L. L. Chobolo and G. M. Dintwe for help collecting field data. We thank the Schoeman family in Namibia, the Agastya International Foundation and R. Balakrishnan in India, and Y. Lubin in Israel for additional help and hosting. We also thank I. Agnarsson and J. Bechsgaard for providing us with phylogenies.

Funding information L.G. was supported by The Leverhulme Trust (Early Career Fellowship: ECF-2016-080). C.H. was supported by the European Research Council (ERC StG-2011-282163 awarded to T.B.). Field work was carried out with financing from Drylands Research SSA grant awarded to C.H. (EC contract number: 026064).

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