Is cooperation in prey capture flexible in the Indian social spider *Stegodyphus sarasinorum*?

Ovatt Mohanan Drisya-Mohan, Neisseril Anirudhan Kashmeera & Ambalaparambil Vasu Sudhikumar

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Abstract. Among social spiders, cooperation is a key characteristic behaviour. Cooperation in prey capture increases the probability of successful prey capture and to some extent reduces the individual costs associated with foraging. We assessed spider cooperation in prey capture under natural conditions in relation to the number of spiders in the colony and the type and size of the prey captured by the social spider *Stegodyphus sarasinorum* Karsch, 1892 (Araneae: Eresidae). First, we determined natural prey in the spider webs and found that beetles (Coleoptera) were the most frequent prey followed by grasshoppers (Orthoptera). These two prey types were then used to study the cooperative hunting behaviour of this spider. We investigated prey capture frequency, recruitment and immobilization time when spiders are more active in the mornings and less active around midday. The study revealed that the immobilization time and recruitment time were shorter when hunting beetles, the smaller sized prey, while larger numbers of spiders were recruited in response to grasshoppers, the larger prey. The study concluded that cooperative behaviour in *S. sarasinorum* depends on the size of prey present.

Keywords: cooperative behaviour, immobilization, predatory efficiency, recruitment time

Zusammenfassung. Gibt es flexible Kooperation beim Beutefang der indischen sozial lebenden Spinnenart *Stegodyphus sarasinorum*? Unter sozialen Spinnen gehört Kooperation zum charakteristischen Verhaltensinventar. Kooperation erhöht die Chancen auf erfolgreichen Beutefang und reduziert den individuellen Aufwand, der damit verbunden ist. Wir untersuchten die Kooperation beim Beutefang von *Stegodyphus sarasinorum* Karsch, 1892 (Araneae: Eresidae) unter natürlichen Bedingungen. Zuerst bestimmten wir die Beute in den Netzen und fanden am zahlreichsten Käfer (Coleoptera) vor Heuschrecken (Orthoptera). Diese beiden Beutetypen dienten dann für genauere Studien des Beutefangverhaltens der Art. Die Häufigkeit und die Dauer des Verhaltens (Beuteerwerb und -fixierung) ist am Morgen höher als in der Mittagszeit. Die Dauer war bei den Käfern, der kleineren Beute, kürzer als bei den Heuschrecken, der größeren Beute. Das Kooperationsverhalten von *S. sarasinorum* hängt von der Größe der verfügbaren Beute ab.

Among invertebrates, social life has evolved in two taxa: spiders and insects. In spiders, cooperation is considered a characteristic of a social species (Brach 1975, Jackson 1979, Krafft 1970, Riechert et al. 1986). Among the permanently social spiders, there are approximately twenty species of cooperative spiders distributed across seven families and most of them show remarkable convergent evolution of a suite of traits associated with their social way of life (Lubin & Bilde 2007, Bilde & Lubin 2011). The genera *Anelosimus* and *Stegodyphus* contain both social and subsocial species with multiple independent origins of permanent sociality (Agnarsson 2006, Johannesen et al. 2007). In permanent associations, the individuals share the same web and co-operate in different activities: web construction, prey capture, brood care and web maintenance (Lubin & Bilde 2007).

Organisms foraging in groups experience increased foraging efficiency in comparison to solitary foragers by capturing large or greater numbers of prey, reducing the likelihood of prey escape, hunting risk and lower variability in prey capture (Rypstra 1989). Therefore it decreases the individual consumption rate, which buffers the group against starvation (Caraco et al. 1995) and enables an increase in dietary niche (Guevara & Aviles 2007). Also, resource distribution is a key ecological factor influencing group dynamics (Packer & Ruttan 1988). Hence group living increases the competition for resources with group size (Krause & Ruxton 2002, Majer et al. 2018). Because of this, most species of social spiders live in tropical regions of the world and lowland rain forest where insect size and density is highest, but several sub-social species reach into the Eastern United States and other temperate areas (Powers & Aviles 2007, Guevara & Aviles 2007). New world *Anelosimus* occur in the most productive continental biome i.e., tropical rain forests while the Old World *Stegodyphus* inhabit drier savannah habitats. Low precipitation seasonality supports abundance in social spiders (Majer et al. 2015). *Stegodyphus* species are restricted to areas with relatively high vegetation productivity and insect biomass (Majer et al. 2013).

Social spider nests can contain hundreds or thousands of individuals, who build communal webs to capture insect prey. The communal two or three-dimensional webs that social spiders build function ecologically as single units that intercept prey through their surface (Aviles 1997). Thus the surface area of this webbing exposed to the environment should determine the frequency with which prey items enter the webs (Majer et al. 2018). It is observed that the mean available web surface per individual decreases from solitary to social species (Jackson 1978, Majer et al. 2018). So it can be assumed that in order to increase their rate of energy removal per individual and per web surface unit social spiders must have developed several strategies. For these purposes social spiders could (a) increase the capture ratio of available prey, (b) enlarge their prey size range and capture very large prey that is not available to solitary spiders or increase their prey size range in relation to dietary niche, or (c) reduce capture web production in relation to colony size (Majer et al. 2018).

Cooperation is expected to be of mutual benefit (Downes 1995), either by direct or indirect (kin-selected) benefits like altruism, mutualism, strong reciprocity and group selection (Lehmann & Keller 2006, West et al. 2007). According to the risk-sensitive foraging theory, group hunting occurs in two situations where average prey availability exceeds the minimum necessary for survival (Uetz & Hieber 1997), or where a single prey item is too large to be consumed by a single

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Ovatt Mohanan DRISYA-MOHAN, Neisseril Anirudhan KASHMEERA, Ambalaparambil Vasu SUDHIKUMAR, Centre for Animal Taxonomy and Ecology, Department of Zoology, Christ College, Irinjalakuda, Kerala, India; E-mail: drisyamohan2@gmail.com, kashmeera.n.a@gmail.com, avsudhi@rediffmail.com

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predator. Previous studies described the influence of cooperation on the predatory efficiency of social spiders (Jackson 1979, Krafft 1970, Pasquet & Krafft 1992, Guevara & Avilés 2011, Majer et al. 2018). In *Anelosimus*, there is a tendency for social species to capture larger prey (Nentwig 1985, Avilés et al. 2007, Guevara et al. 2011). For *Stegodyphus* the effects are less strong and with increasing group size, per capita foraging rate decreases (Majer et al. 2018). However, more information is needed on cooperation, predatory efficiency and the nature and size of the prey captured in other species in the genus *Stegodyphus* (Eresidae). In the present study, characteristics of spider cooperation were studied in the Indian cooperative spider *Stegodyphus sarasinorum* (Karsch, 1892), which is one of three permanently cooperative species in the genus *Stegodyphus* (Kraus & Kraus 1988). Individuals live in large cooperatively built colonies with a nest or retreat and a sheet web for prey capture (Jackson & Josephs 1973). The aim of this study was to analyse the efficiency and prey immobilizing characteristics of cooperative prey capture under natural conditions in relation to the type and size of the captured prey.

Material and methods

Study organism and site

Stegodyphus sarasinorum Karsch, 1892 (Eresidae), is a permanent social spider found in India, Sri Lanka, Nepal and Myanmar (Kraus & Kraus 1988, WSC 2019). It makes large complex silk nest of variable sizes on bushes, shrubs, rocky areas and open fields, where flying insects are abundant (Bradoo 1972). The nest is placed in trees and shrubs or sometimes fences, and made by incorporating the structure, leaves, branches, prey remnants and also their own exuviae into the silk nest. The site identified for the study was on the Christ College campus (10.350°N, 76.200°E, 12 m a.s.l., Fig.1a), located in the town of Irinjalakuda in the Thrissur district in Kerala. The study was undertaken during the period of June–September 2017. The observations were made in the field (Fig. 1b-d).

Fig. 1: a. Map of the study area at Christ College, Irinjalakuda (red spots = social spider web colonies); **b.** distribution of colony in *Eugenia uniflora*; **c.** an individual colony of *S. sarasinorum*; **d.** immobilization of the prey

Methods

Natural prey of *S. sarasinorum*. The natural prey was identified by examining prey remnants (wings, cuticle, mouthparts, etc.) from the nest. We sampled 30 nests for the identification of the natural prey types. Observations were repeated 3 times

Tab. 1: Number of prey sampled from the webs of *S. sarasinorum* (prey remnants sampled and fresh prey captured); in brackets: percentage of each order in relation to a total number of prey sampled

	Coleoptera	Orthoptera	Hymenoptera	Hemiptera	Isoptera	Total
Remnants of the prey	48 (40%)	26 (22%)	22 (18%)	18 (15%)	6 (5%)	120
Fresh prey	12 (63%)	5 (26%)	2 (11%)	0	0	19

in one month. The type (order) and size of the prey remnants were noted and identified to the order level with the help of taxonomic keys. We selected two natural types of prey based on their size; a beetle (Coleoptera) and grasshopper (Orthoptera).

Time of activity of spiders. The test periods were chosen by observing and recording the activity of spiders in the field at different times of the day (8 am to 5 pm at each hour). Observations were made during 5 days chosen randomly at the beginning of the test. We noted the different activity of spiders including web weaving, prey capture, feeding, etc. Close observation of the spiders in the field revealed increased weaving and prey capturing/feeding activity at 8.00–8.30 am, while a decrease in these activities was found at around 11.00–11.30 am. From these observations, two periods were chosen: active (8.00–8.30 am) and passive (11.00–11.30 am).

Size of the colony. At the end of the experimental period, all spiders were collected and carefully counted. The average numbers of individuals were 85 per colony (range 20 to 130).

Efficiency, predation and cooperation of *S. sarasinorum*. Grasshoppers were captured with a sweep net (Mean Length = 30 mm, SD = 0.366, n = 72), and beetles with a light trap (Mean Length = 20 mm, SD = 0.311, n = 72). Of the 144 tests, 72 tests were carried out during the inactive period and the remaining 72 tests were conducted during the active period. The test was conducted in 9 colonies over 8 days either with an equal amount of grasshoppers or beetles. We placed larger prey (grasshoppers) and smaller prey (beetles) 15 cm away from the nest entrance and observed the spider-hunting behaviour. The main events of prey capture, the number of spiders recruited, recruitment time and prey immobilization time were recorded.

Statistical analysis. A Wilcoxon rank sum test ('W' is the test statistic) was performed to compare the frequencies of capture for the two prey types (grasshoppers and beetles) in the nine colonies, and also for analyzing immobilization time and recruitment time of two prey types during two different periods. The Spearman's rank correlation coefficient was computed to access the relationship between immobilization time and numbers of recruited spiders for subduing the two different prey types. A significance level of 95% was used to indicate the level of significance in the results. Statistical tests were done using the software R (R Core Team 2018).

Results

Natural prey of *S. sarasinorum*. From the nests of all colonies sampled, remnants of 120 insects were collected, identified (to insect order) and measured (Tab. 1). The median size of the prey was 10 mm and the largest prey item reached 50 mm in length. Coleoptera (40%) and Orthoptera (22%) were the most common prey types, followed by Hymenoptera (18%), Hemiptera (15%) and Isoptera (5%). We collected 19 prey in the process of being eaten (median size = 20 mm; the largest size = 40 mm in length). Coleoptera was the most numerous (63% of total captures). The data show that *S. sarasinorum* catches prey ranging from 10 to 50 mm and a large proportion are Coleoptera and Orthoptera (Tab. 1).

Efficiency, predation and cooperation of *S. sarasinorum*. During the active period (8.00–8.30 am) most of the spiders were occupied outside the nest and some of them fed on prey. But in the passive period (11.00–11.30 am) the number of spiders present outside the nest was less. Whenever prey was placed in the web it created vibrations in the silky threads. These vibrations allow the spider to localize the prey and move asynchronously from the nest towards the prey and entangle the prey by biting different parts of its body. After immobilization, some spiders fed on the prey and some stayed in different parts of the web while others moved into the nest.

It was found that the frequency of reaction to prey did not differ in the 9 cases considered (W = 43.5, p-value = 0.821). Throughout our experiment, we found that the spiders' consumption of a prey item was influenced by vibrations made by the prey and not solely by the differences in the size of grasshoppers and beetles. The immobilization time was higher for grasshoppers than for beetles both in the active (W = 1296, p-value = 2.652 e^{-13}) and passive (W = 1296, p-value = 2.716 e^{-13}) periods (Tab. 2 & Fig. 2). Similarly, recruitment time was longer for grasshoppers than for beetles both in active (W = 1296, p-value = 1.58 e^{-14}) and passive (W = 1296, p-value =1.619 e^{14}) periods (Tab. 2). The spiders always reacted faster to beetles than to grasshoppers (Fig. 2). In the passive periods, there was a tendency towards a positive correlation between the immobilization time and a number of recruited spiders to subdue grasshoppers (Spearman's rank correlation, r_s = 0.288, p-value = 0.087). In the case of beetles, the correlation between immobilization time and the number of recruited spiders, although numerically negative, did not significantly differ from no-correlation (r_s = -0.119, p-value = 0.487). Similarly, in the active periods, both in the case of grasshoppers and beetles immobilization time and number of recruited spiders was not significantly correlated (r = -0.160, p-value = 0.3499; r = -0.064, p-value = 0.706) (Tab. 2).

Tab. 2: Medians of the three different parameters used to explain spider cooperation in prey capture; data presented in relation to spider activity periods and prey types; in bracket: superior and inferior quartiles of the data

	Period		Prey types	
	Inactive	Active	Grasshopper	Beetle
Immobilization time (minutes)	20 (4–60)	10 (2–30)	30 (12–60)	6 (2–15)
No. of spiders recruited	8 (3–18)	9 (6–30)	12 (6–30)	7 (3–16)
Recruitment time (minutes)	8.5 (1–40)	3.5 (1–30)	21.5 (5–40)	1 (1–3)

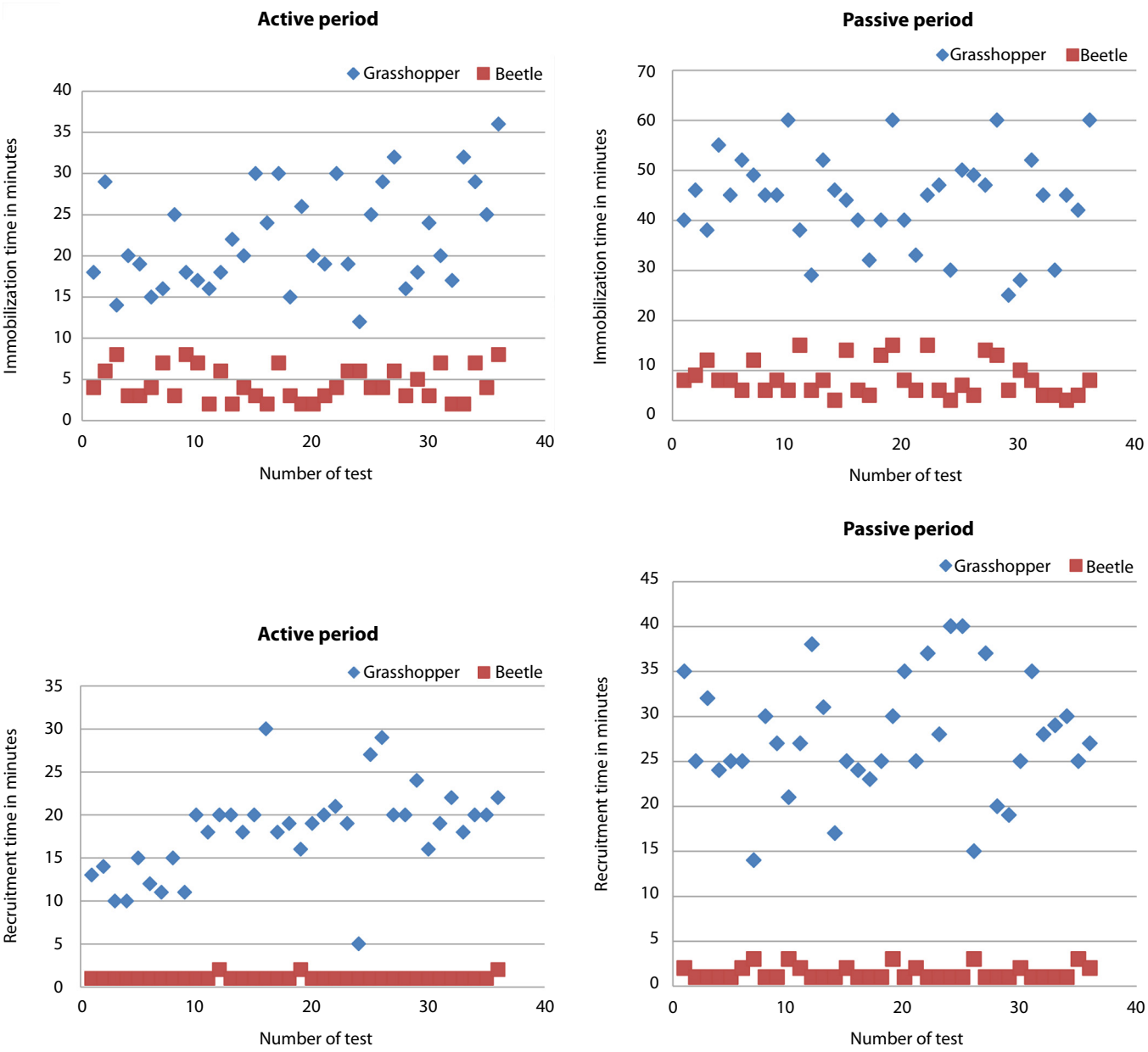

Fig. 2: Immobilization time (minutes) and recruitment time (minutes) of grasshoppers and beetles during the two periods

Discussion

Cooperative social spiders share a communal web and nest where the colonies can extend to group sizes from a few to thousands of individuals (Whitehouse & Lubin 2005). In the case of *S. sarasinorum*, even those who did not participate in the actual prey capture activities may join in the feeding and feed communally (Bradoo 1980). Among the 30 nests analyzed on the Christ College campus, we found that the most abundant prey of *S. sarasinorum* was the order Coleoptera (beetles). The second most abundant prey is Orthoptera, which includes grasshoppers. This finding is similar to Majer et al. (2018), where this social *Stegodyphus* mostly captured the prey from the taxa Coleoptera, Diptera and Hymenoptera and the less abundant prey taxa included Isoptera, Lepidoptera and Orthoptera. Our results confirms that social *Stegodyphus* species forage in relation to available prey rather than on specific prey types. Pasquet & Krafft (1992) studied the cooperative behaviour in another social spider *Anelosimus eximius*. This spider captured a large proportion of Orthoptera and Lepidoptera.

Cooperative prey capture behaviour may function to capture prey that is much larger than the body size of the spider predator (Nentwig 1985, Yip et al. 2008), with several individuals within a group feeding on the prey item simultaneously. *Anelosimus eximius* captures larger prey than spiders of similar size but with a less complex organization (Nentwig & Christenson 1986), and also other social *Stegodyphus* increase dietary niche through cooperative prey capture (Majer et al. 2018). This is also confirmed by our result that *S. sarasinorum* can capture larger sized prey (up to 50 mm) than its own body size (7.5 ± 0.07 mm). Group living and cooperative foraging are hypothesized to expand dietary niche to meet the increasing resource demand of the group and reduce competition, and risk of conflict over the distribution of resources (Ulbrich & Henschel 1999, Majer et al. 2018).

The cribellate web sheets formed by *S. sarasinorum* act as an excellent trap for large insects like locusts, grasshoppers, wasps, beetles, dragonflies, moths and many other kinds of Coleoptera and Hymenoptera, etc. (Bradoo 1972). Once the-

se insects become ensnared in the web, they cannot escape. The struggle of the prey in the web causes web vibrations. The source of vibrations is detected by the vibration receptors located in the legs of the spiders (Walcott & van der Kloot 1959). We did not detect differences in the reaction to prey, suggesting that spiders do not differentiate prey type based on web vibrations.

Pasquet & Krafft (1992) reported that cooperation depends on prey types in *A. eximus*. In *S. sarasinorum* immobilization time and the number of spiders recruited differed between the two prey items in the active and passive periods. The spiders took a longer time to immobilize grasshoppers, as compared to beetles, indicating that larger prey (grasshoppers) requires more effort to subdue. Optimal foraging theory suggests that spiders should invest in the prey that provides the highest energy return. However, social spiders are dependent on the prey that arrives in their webs, and they cannot freely choose a preferred prey type. Our data shows that beetles were more frequent than grasshoppers, and spiders rapidly captured beetles.

Stegodyphus sarasinorum may exhibit two responses to increasing energy needs: it may widen its range of prey by aiming for large-sized insects, and optimize capture efficiency by reducing the time needed to immobilize its prey, which increases its chance of making additional captures. Our study suggests that *S. sarasinorum* uses a different strategy in response to larger prey size, as more spiders were recruited to subdue grasshoppers than beetles during prey capture and prey immobilization. This reflects the fact that grasshoppers are larger and provide more food, and therefore it pays for the spiders to invest more in their capture.

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