

Effect of Kleptoparasitic Ants on the Foraging Behavior of a Social Spider (*Stegodyphus sarasinorum* Karsch, 1891)

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The term kleptoparasitism is used to describe the stealing of nest material or prey of one animal by another. Foraging and food handling behaviors of social spiders increase the vulnerability to kleptoparasitism. Kleptoparasites of the social spider *Stegodyphus sarasinorum* Karsch 1891 were identified based on the observations done in the field. Four species of spiders and two species of ants were observed as kleptoparasites and collected from the nest and webs of this social spider. The ants were found to be the most dominant among them. The influence of a facultative kleptoparasitic ant, *Oecophylla smaragdina* on the foraging behavior of *S. sarasinorum* was studied in laboratory conditions. The experiments suggested that the web building behavior of *S. sarasinorum* was influenced by the exposure to ants. However, exposure to ants caused no significant effect in the prey capture, handling time of prey and prey ingestion behaviors of the spider.

Key words: Social spider, Ecology, Kleptoparasites, Ants, Prey capturing behavior.

BACKGROUND

Kleptoparasitism is a type of feeding behavior, in which one animal steals the food or prey captured by another animal. Kleptoparasites feed on prey which could not be obtained by themselves without time and effort. There are chances for the kleptoparasites to be injured by the host organism (one being stolen from) when the latter defends its prey. Kleptoparasitic behavior is seen in a diverse array of taxa including marine invertebrates (Zamora and Gomez 1996; Morrisette and Himmelman 2000), spiders and insects (Higgins and Buskirk 1988; Field 1992), birds (Brockmann and Barnard 1979), large carnivores (Packer and Ruttan 1988) and primates (Di Bitetti and Janson 2001).

Susceptibility to kleptoparasitism is affected by various characteristics of the organism's behaviors include foraging and food-handling behaviors (Brockman and Barnard 1979; Giraldeau and Caraco

2000). Kleptoparasites depend on high-quality food and it is available to them due to prolonged handling (Giraldeau and Caraco 2000). Lastly, the more conspicuous the hunting and food handling behaviors, the easier it is for the potential thieves to identify the opportunities for exploitation.

Among spiders, web-building spiders are frequent targets of kleptoparasites (Vollrath 1987). Web-building spiders are relatively sedentary, sit-and-wait type of predators and capture prey that is often larger than themselves and that takes time to consume. They usually store many prey items in the web or nest for future consumption (Champion de Crespigny et al. 2001). Social spiders built large sized web and capture large sized prey cooperatively. Due to these behaviors, social spiders are also an attractive resource for kleptoparasites.

A few species of spiders act as kleptoparasites along with insects like some scorpionflies (Thornhill 1975) and ants (Henschel and Lubin 1992; Pasquet et

al. 2007). The spiders which regularly steal food from other species of spiders, *i.e.*, kleptoparasitic spiders, are known to occur in five families. As ants can rapidly recruit a large number of individuals and by patrolling, ants are likely to be the most prominent kleptoparasites (Henschel 1998; Hölldobler and Wilson 1983). Moreover, ants can also become predators, particularly in spider broods (Schneider and Lubin 1997). If kleptoparasitism shown by ants is a sufficiently serious risk to spiders, adaptive responses by spiders should be observed to lower the risk.

Although most of the studies have dealt with the diversity, evolution, and behavior of kleptoparasites, the knowledge about its effect on the web-building and foraging behavior of social spiders are insufficient, due to lack of studies except a few (Cangialosi 1990; Leborgne et al. 2011). A pioneering study conducted by Leborgne et al. (2011), showed that in Eresid sub-social spider, *Stegodyphus lineatus* kleptoparasites negatively influenced the web building behavior and was independent of the success in the spider's previous foraging. According to the accepted theory in spiders, non-territorial permanent-sociality is derived evolutionarily from a sub-social state and is evolutionarily restricted by genetic or ecological factors (Aviles 1997). Since there is a difference between social and sub-social spiders a detailed examination was done on the influence of kleptoparasites on web building as well as foraging behavior of social spiders. So this study was conducted on the social spider, *Stegodyphus sarasinorum*, Karsh 1891 (Araneae: Eresidae) which is commonly known as the Indian cooperative spider. This spider exhibits communal predation and feeding, where individual spiders live in large cooperatively built colonies with a nest or retreat made of silk, and woven using twigs, leaves, food carcasses and a sheet web for prey capture.

The present study identifies the kleptoparasites of *S. sarasinorum* in the natural colonies at Christ College, Irinjalakuda, Kerala, India. The influence of facultative kleptoparasitic ants on web-building and prey capturing behaviors of *S. sarasinorum* was also studied.

MATERIALS AND METHODS

Study Area

The study site was in the Christ College campus ($10^{\circ}21'N$ $76^{\circ}12'E$), located in Irinjalakuda town of Thrissur district, Kerala, India. Colonies of *Stegodyphus sarasinorum* are widely distributed in the campus (Fig. 1) and are found on the branches of plants such as *Eugenia uniflora* (Fig. 2A), *Acacia disparrima*, *Acacia*

sp., *Tamarindus indica*, *Artocarpus heterophyllus* and Nigeria grass (*Pennisetum pedicellatum*).

Kleptoparasites of *S. sarasinorum*

The nests of the spiders were examined in its habitat at different locations of Christ College campus; covering both winter and summer seasons. *S. sarasinorum* thrives on shrubs and the lower branches of tall plants. Kleptoparasites were collected by hand as follows. The specimens were collected by leading them into glass tubes containing alcohol with the help of a brush dipped in alcohol. The collected spiders and non-spider kleptoparasites were preserved in 70% alcohol.

The collected specimens were then taken to the laboratory and examined under Magnus MSZ TR stereo microscope for taxonomic identification. Kleptoparasitic spiders were identified with the help of available literature (Sebastian and Peter 2009; WSC 2018) and kleptoparasitic ants were identified using the catalogue of ants (Bolton et al. 2007) and AntWeb online database (2017, <http://www.antweb.org>). The specimens are housed in the reference collection maintained at the Centre for Animal Taxonomy and Ecology, Department of Zoology, Christ College, Irinjalakuda, Kerala, India (ID – CATE0306).

Effect of exposure of ants on web building behavior of *S. sarasinorum*

S. sarasinorum was collected from Christ College campus. Adult and subadult females were used for this study. Spiders (two groups, 30 spiders each) were introduced into the $45 \times 30 \times 30$ cm enclosures (Fig. 2B) made up of nylon mesh and wooden reapers (Wooden sticks used for making the frame of the enclosure). Twigs and wet cotton were placed in the enclosure which facilitates web building and maintains moisture content in the enclosure respectively. Grasshoppers (*Chortopaga viridifasciata* (0.22 ± 0.008 g), *Oxya hyla intricata* (0.13 ± 0.007 g), and *Neorthacris simulans* (0.28 ± 0.014 g)) were collected from the field and grown in an artificial terrarium ($60 \times 30 \times 30$ cm) and they were used as prey for the spiders. Two similar-sized grasshoppers were given to each group daily in order to homogenize the feeding status (We observed the influence of feeding status and exposure of ants). After 5 days, the first group received two grasshoppers ("fed") while the second group received no prey ("fasted") over the next 4 days.

These two groups were again subdivided into two sub-groups (15 spiders each). The facultative kleptoparasitic ants, *Oecophylla smaragdina* (K) were collected from Christ College campus and 10

individuals each were exposed into one of the fasted and fed sub-groups. Some ants moved on the web and some others moved on the enclosure (Fig. 2C). After 1 hour, ants were removed and all webs both in the K exposed and K unexposed groups were destroyed manually. The experimental setup with spiders alone was kept undisturbed for the next four days except during daily web size measurements. The day 1 measurement was done 24 hrs after the web was destroyed. The process was not invasive as the measurements were taken by opening the lid gently without disturbing the web. For analyzing the surface area of the rebuilt web, we used 30 cm ruler, 180° protractor and dividers to measure the edges and angles and approximated it in to many polygons (Rectangular or triangular structure) to calculate the surface area. The dimensions of the surface

area of the three replicates of the experiment were measured on 4 consecutive days.

Statistical analyses

Welch Two independent Sample t-test was performed to compare the means of the web size built on the first day in the K exposed and K unexposed groups. Two-way ANOVA was conducted for analyzing the significance of the size of the web in the K exposed and K unexposed groups on any of the experimental days and also to compare the relationship between the web sizes built by the fed (K exposed vs K unexposed) and fasted (K exposed vs K unexposed) spider groups on the same. Significance level 95% has been used to indicate the level of significance in the result. Statistical

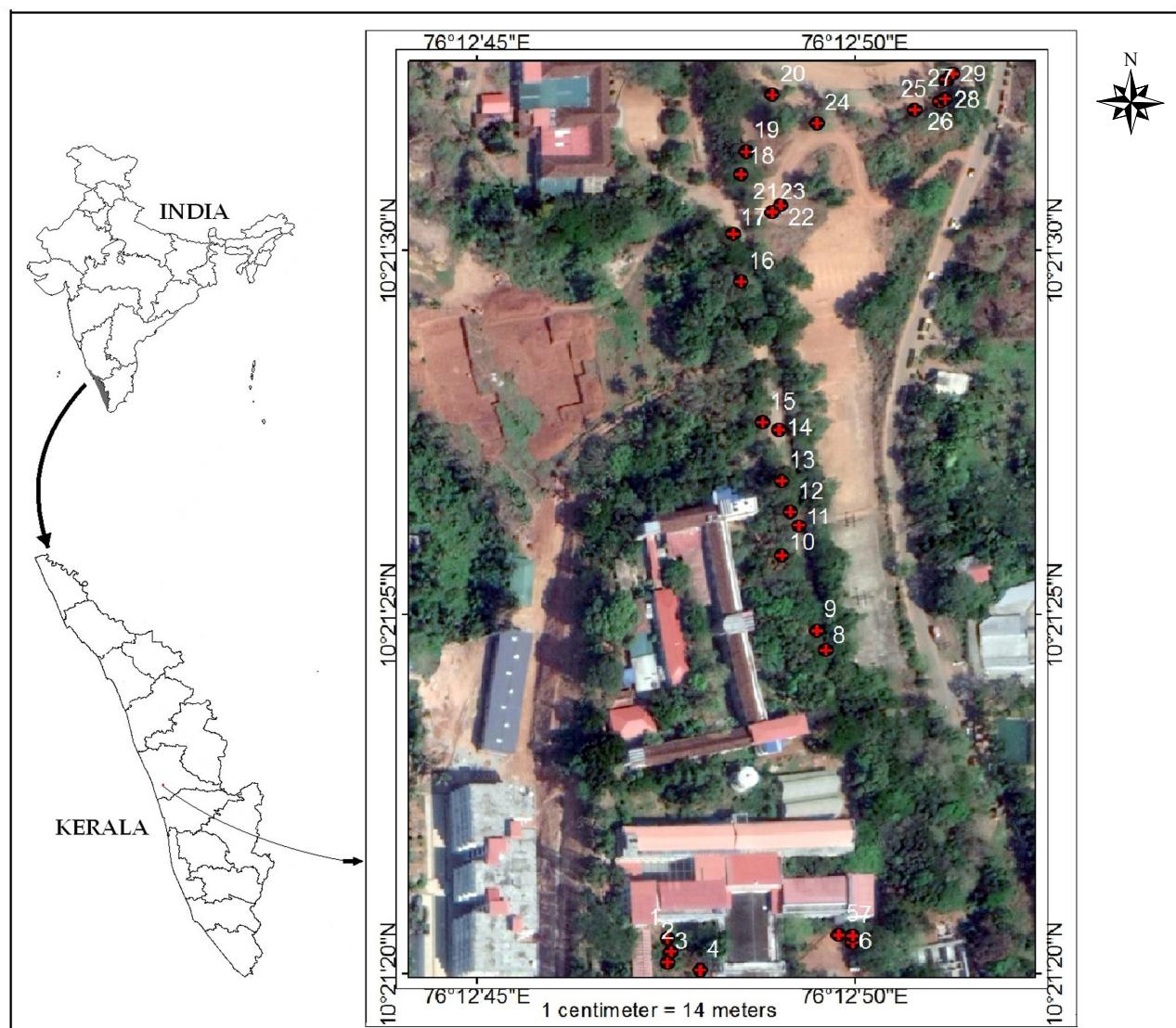


Fig. 1. Map of the study area – Social spider web colonies (Marked as red spot) on Christ College Irinjalakuda.

tests were done using the software R (R Development Core Team 2018). Daily changes in web rebuilding size were measured and analyzed.

Effect of exposure of ants on prey capture ability of *S. sarasinorum*

We collected a second set of spiders for this experiment. The spiders were prepared as before except for the following differences. Spiders were assigned in to two groups (30 spiders each) and fed with two similar sized grasshoppers per week for two weeks until acclimated (The spiders were fed weekly as the influence of ant exposure rather than previous feeding on prey capturing ability was taken into consideration). Spider mass was calculated using electronic balance (Readability-0.001 g) to get the equal-sized groups. The ant *O. smaragdina* (K) was introduced in to the web of one group. After that, each of the weighed grasshoppers

was introduced to both groups (In K exposed group; grasshoppers were introduced one hour after K exposure). The grasshoppers were placed on to the web at a distance of 10 cm from the nest and awaiting its capture. Sometimes in both groups spiders were attracted towards the grasshopper and sometimes the grasshoppers escape from the vicinity of spiders. So we replaced the new grasshopper for the unsuccessful prey capture. We noted the handling time (The time started from the first attack of the spider towards its prey until its immobilization) in three different times of the day (9 am, 1 pm and 5 pm). The difference in the time of the attack in the two groups was calculated. Then the time of prey ingestion was noted in the two groups. The leftover of the grasshopper was taken back exactly after 4 hours and was weighed. The difference between the initial and final weights was calculated (In gram) as the amount which is consumed by the spiders. Three replicates of this experiment were done.

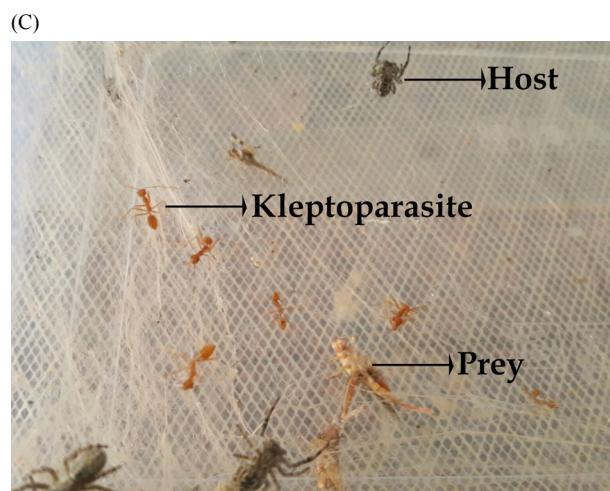


Fig. 2. (A) An individual colony of *S. sarasinorum*. (B) Experimental set-up for the study. (C) Spiders (Host) in captivity- Ant (Kleptoparasite- *O. smaragdina*) exposed.

Statistical analyses

The Spearman's rank correlation was run to access the relationship between prey handling time of each group with the times of the day (9 am, 1 pm and 5 pm). Wilcoxon rank sum test ('W' is the test statistic) was used to analyze the mean ranks of the handling time of two sample populations (K exposed and K unexposed), which whether differed or not. Two-way ANOVA was done in R to find if there was any significant difference in prey ingestion rate of the two groups at different times of the day.

RESULTS

Kleptoparasites of *Stegodyphus sarasinorum*

Before starting the experiments common kleptoparasites of *S. sarasinorum* were observed and collected from the field. Four species of spiders and two species of ants were collected. Collected species include spiders *Argyrodes kumadai* Chida and Tanikawa 1999 (Male and female), *Oxyopes javanus* Thorell 1887, *Phintella vittata* Koch 1846, *Hyllus semicupreus* Simon 1885 and ants *Oecophylla smaragdina* Fabricius 1775 and *Anoplolepis gracilipes* Smith F 1857. *A. kumadai* was collected from the web and others were found inside the nest of *S. sarasinorum* (Fig. 3).

Effect of exposure of ants on web building behavior

From previous studies, it is known that web building is influenced by the previous feeding. This led to the curiosity for examining the influence of ants on the web building capacity. As long as the web remains intact, spiders do not prefer to expand their web. To induce web rebuilding, it may, therefore, be necessary to destroy the webs. So we removed the old web completely from the K unexposed and K exposed fasted and fed groups. The experimental groups of both fed and fasted spiders rebuilt the web from the first day onwards. The rebuilding of the web is a foraging decision. In the first day of K unexposed spider groups, web rebuilding differed in fed ($129.05 \pm 19.82 \text{ cm}^2$) groups than the fasted group ($314 \pm 9.86 \text{ cm}^2$, $t_{(2,93)} = 8.353$, $p = 0.003$, Table 1). Hence, after ant exposure, the web rebuilding was comparatively less in the fed spider ($96.5 \pm 6.87 \text{ cm}^2$) than the fasted spider group ($120.13 \pm 15.14 \text{ cm}^2$, Table 1), though no significant difference was found ($t_{(2,28)} = 1.516$, $p = 0.253$, Table 1).

The size of the web of both K unexposed fed and fasted spider groups were compared during 4 successive

days (Fig. 4). There was a statistical difference in mean web size in K unexposed, between fed and fasted spider groups as determined by two-way ANOVA ($F_{(1,16)} = 252.4$, $p = 3.22e^{-11}$) but there was no statistically significant interaction between the fed and fasted spiders on the 4 experimental days ($F_{(3,16)} = 2.664$, $p = 0.0831$). And also in the case of K exposed fed and fasted groups, significant difference in the size of the web was observed ($F_{(1,16)} = 15.858$, $p = 0.001$) but the interaction between the day and K status was not significant ($F_{(3,16)} = 0.605$, $p = 0.621$, Fig. 5).

Considering the fed spiders, there was no significant difference in the means of the web sizes of K unexposed and K exposed spiders ($F_{(1,16)} = 1.419$, $p = 0.251$) on any of the experimental days ($F_{(3,16)} = 2.119$, $p = 0.138$), whereas the means of the web sizes of K unexposed and K exposed fasted spiders differed significantly ($F_{(1,16)} = 316.2$, $p = 5.81e^{-12}$) (Fig. 6) but there is no interaction between the "day" and "K-status" effects ($F_{(3,16)} = 2.83$, $p = 0.071$).

Effect of exposure of ants on prey capturing behavior

We observed the influence of ants on prey capture, handling time and prey ingestion. It was found that the first reaction to the prey didn't differ in the two cases considered, i.e., K exposed and K unexposed spider groups, both approximately 5 minutes ($W = 9$, $p = 0.87$). All throughout the four experimental days, it was observed that the vibration in the web was the cue that attracted the spider toward its prey and not the presence or absence of kleptoparasites. The three species of prey and their respective weights did not affect the pattern of prey capture in any way, i.e., there was no difference in the frequency of successful prey capture between K exposed and K unexposed groups, 12 cases considered ($W = 12$, $p = 0.18$). When the spider approached the prey, they tightened the silk with the tarsi of the front leg. A single individual always attacked the prey first, but this was often quickly followed by other spiders. The first capture part of the prey item was different; it may be leg, antennae, abdomen or head. The Spearman's rank correlation suggested a positive correlation between the handling time of the K exposed groups and three times of the day ($R_s = 0.608$, $p = 0.03$). However, the K unexposed groups didn't show any significant correlation with the times of the day ($p = 0.071$). The results of the Wilcoxon rank sum test showed that the mean ranks of the handling time in the two groups, i.e., K unexposed and K exposed groups didn't differ significantly ($W = 64$, $p = 0.663$). Even though the K exposed group was found to be positively correlated with the different times of the day, the overall

prey handling time needed for the spiders to immobilize the prey was similar in the two cases considered (Fig. 7). Results of the Two-way ANOVA indicated that there was no significant difference in the mean difference in prey injection activity between the 2 groups ($F_{(1,18)} = 0.07, p = 0.79$). This is independent of “all the three times of the day” ($F_{(2,18)} = 1.25, p = 0.30$).

DISCUSSION

The present investigation enumerated the kleptoparasites of a social spider *S. sarasinorum* and examined the effect of a common facultative kleptoparasite, *O. smaragdina*, on the web building and prey capturing behavior of this spider. Earlier studies

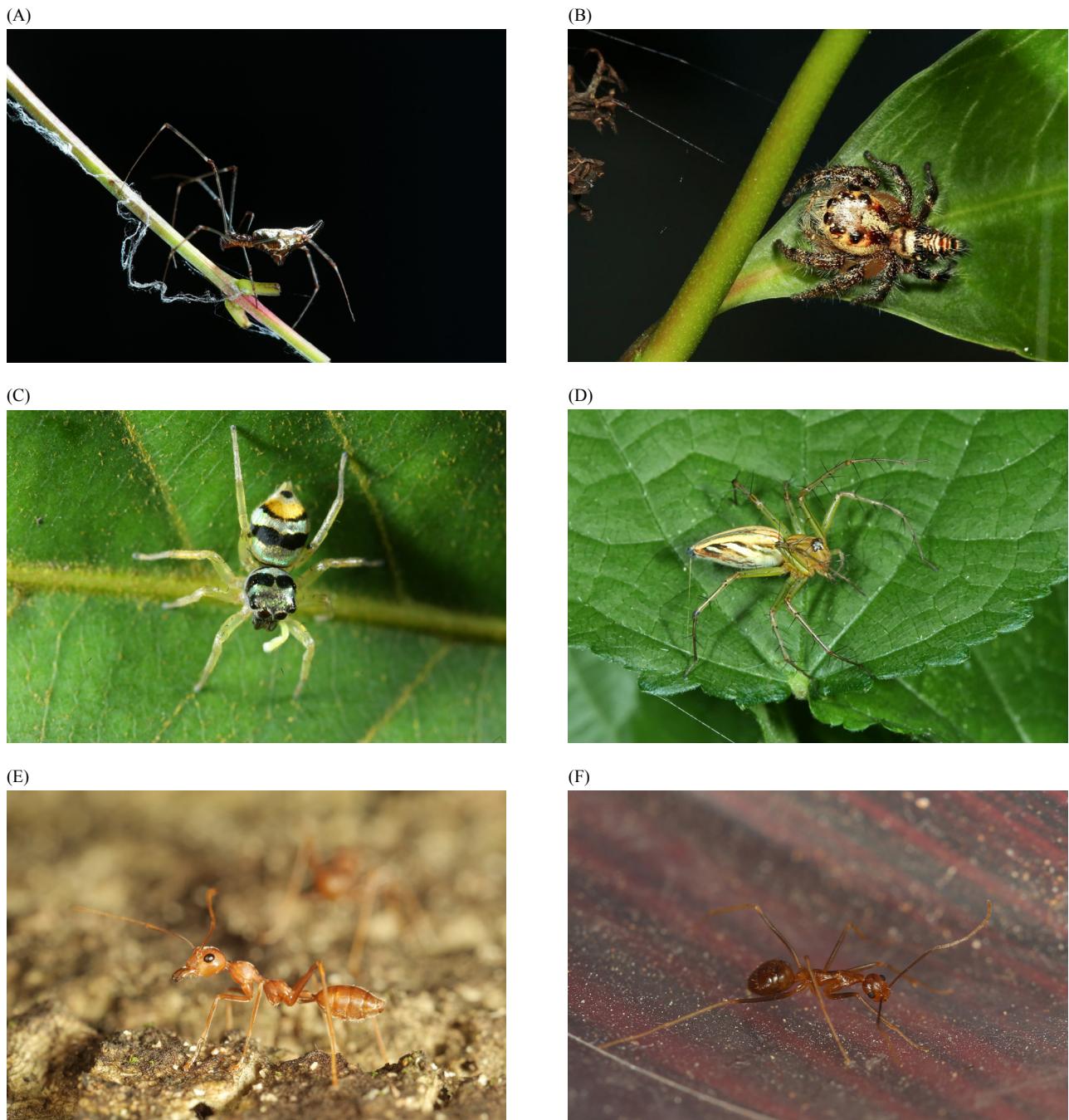


Fig. 3. Kleptoparasites of *S. sarasinorum*. (A) *Argyrodes kumadai* (Dewdrop spider). (B) *Hyllus semicupreus* (Heavy-bodied jumper). (C) *Phintella vittata* (Banded phintella). (D) *Oxyopes javanus* (Lynx spider). (E) *Oecophylla smaragdina* (Weaver ant). (F) *Anoplolepis gracilipes* (Yellow crazy ant). Photo courtesy of: Karunnappilli S. Nafin.

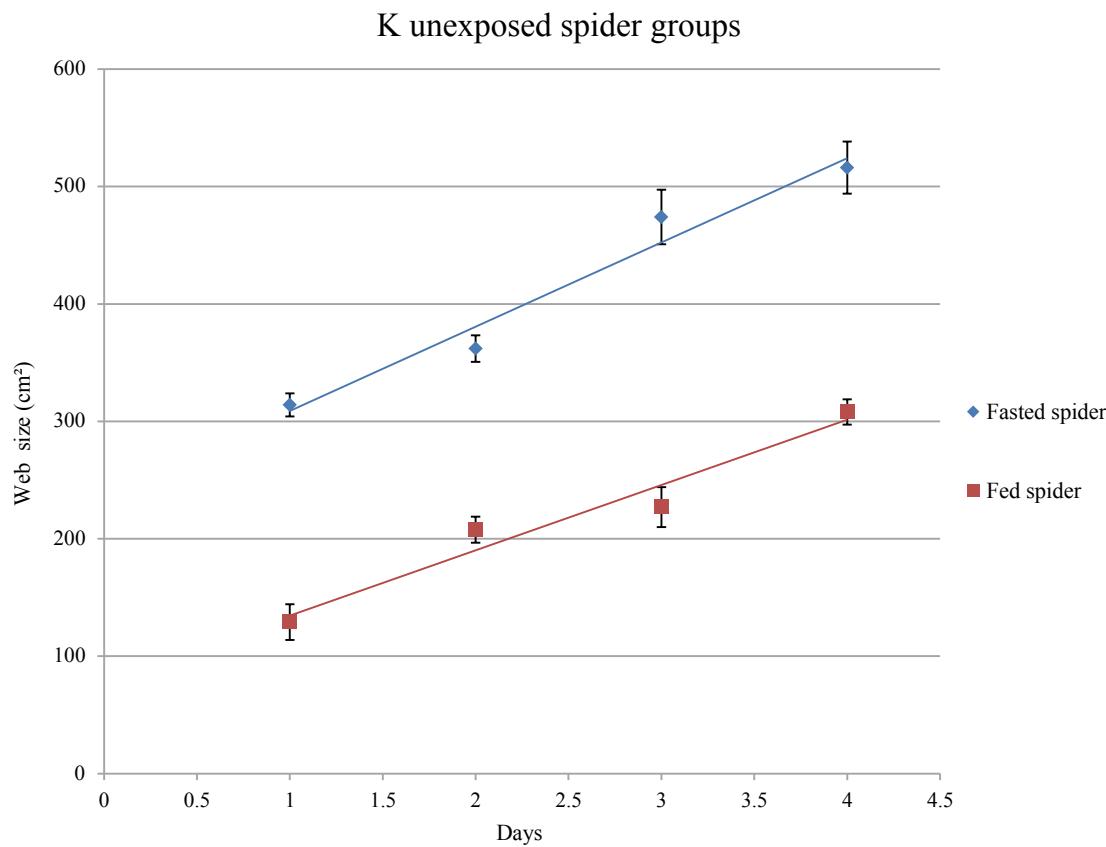


Fig. 4. Web rebuilding ability (Size of the web (cm² ± SEM) of the K unexposed (Kleptoparasite “K” is *O. smaragdina*) spider groups (Fasted ($n = 3$ groups) and Fed ($n = 3$ groups)) during the 4 experimental days. The regression lines, blue line (Fasted spider) has the Intercept $a = 236.94$, Slope $b = 71.812$ and Coefficient of Determination $R^2 = 0.966$ and the red line (Fed spider) has $a = 78.925$, $b = 55.61$ and $R^2 = 0.955$.

Table 1. Size of the web of fasted spiders (K unexposed ($n = 3$ groups) and K exposed ($n = 3$ groups)) and fed spiders (K unexposed ($n = 3$ groups) and K exposed ($n = 3$ groups)) during the 4 experimental days

K unexposed spider groups								
	Fasted spiders				Fed spiders			
Day	I Replicate (cm ²)	II Replicate (cm ²)	III Replicate (cm ²)	Mean web size (cm ² ± SEM)	I Replicate (cm ²)	II Replicate (cm ²)	III Replicate (cm ²)	Mean web size (cm ² ± SEM)
1	298	332	312	314 ± 9.86	100.15	120	167	129.05 ± 19.82
2	343	382.12	360.52	361.9 ± 11.3	182	218.05	232.2	207.75 ± 12.96
3	428	502	492	474 ± 23.2	202	231	248	227 ± 13.43
4	473	547	528	516 ± 22.18	278	304	342	308 ± 18.58
K exposed spider groups								
	Fasted spiders				Fed spiders			
1	92.05	124.34	144	120.13 ± 15.14	90.05	95	104	96.5 ± 6.87
2	208	240	242	230 ± 11.01	159	177	186	174 ± 7.93
3	269	297	328	298 ± 17.03	214.5	284.5	293	264 ± 24.87
4	322	345	359	342 ± 10.78	244.5	297	310.5	284 ± 20.13

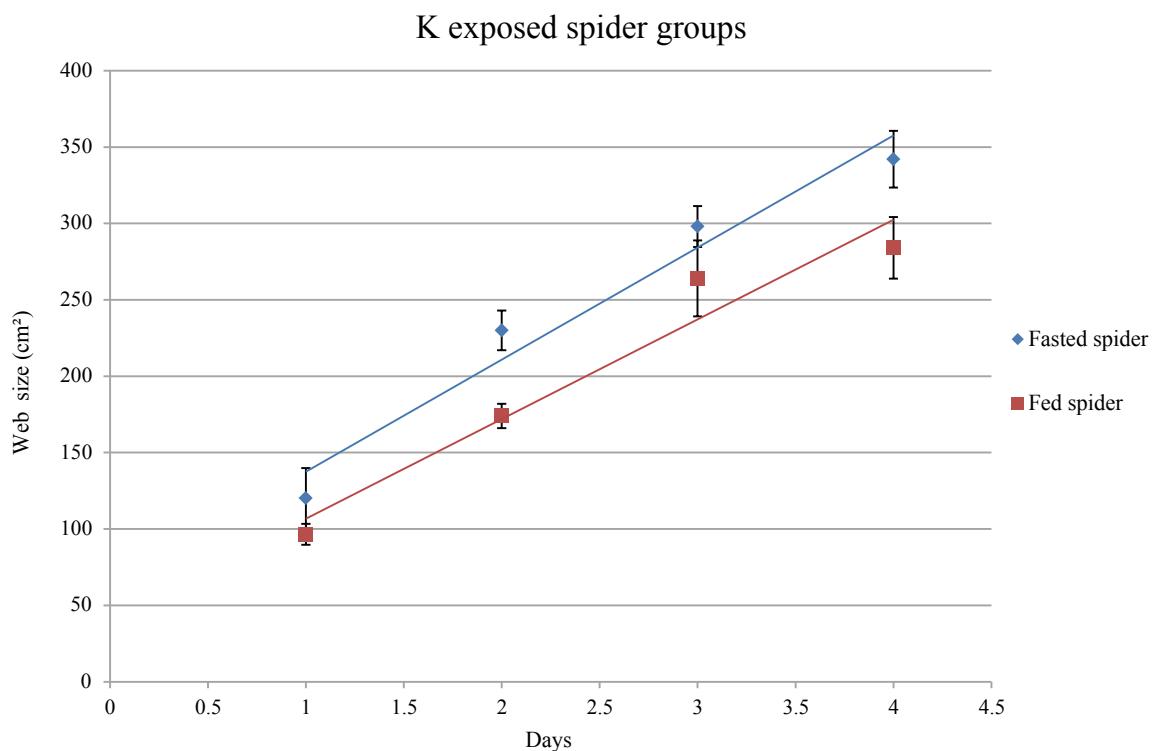


Fig. 5. Web rebuilding ability (Size of the web ($\text{cm}^2 \pm \text{SEM}$)) of the K exposed (Kleptoparasite “K” is *O. smaragdina*) spider groups (Fasted ($n = 3$ groups) and Fed ($n = 3$ groups)) during the 4 experimental days. The regression lines, blue line (Fasted spider) has the Intercept $a = 64.13$, Slope $b = 73.361$ and Coefficient of Determination $R^2 = 0.96$ and the red line (Fed spider) has $a = 41.5$, $b = 65.25$ and $R^2 = 0.948$.

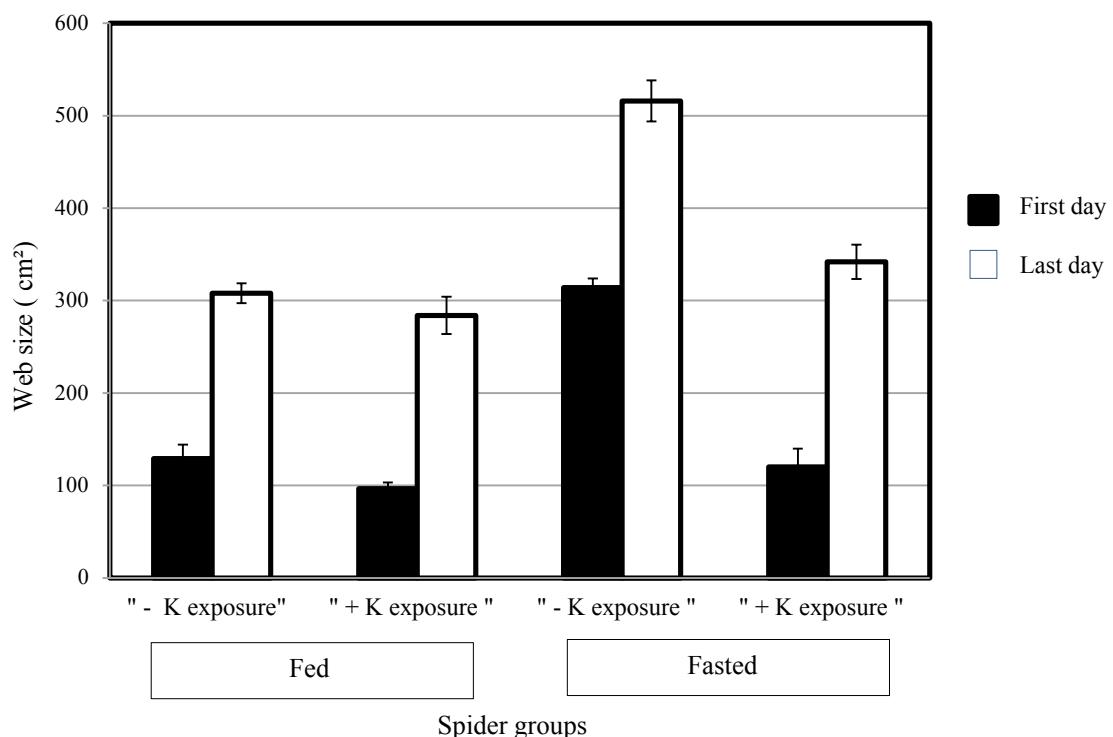


Fig. 6. Size of the web ($\text{cm}^2 \pm \text{SEM}$) built by fed and fasted (K unexposed (“- K exposure”): $n = 3$ groups) and K exposed (“+ K exposure”): $n = 3$ groups) spider groups.

(Bradoo 1967 1971; Bradoo and Joseph 1970) reported that remains of the prey and exuviae of *S. sarasinorum* can serve as the food of other species like Embioptera and Microlepidopteran's larvae. Also Exline and Levi (1962) and Gertsch (1979) explained the behavior of spiders belonging to the genus *Argyrodes*, and their comportment in the webs of other spiders in which they do not seem to build their own webs instead eat the silk of host spiders when the insect availability was limited in the webs of these host spiders (Miyashita et al. 2004). *A. kumadai* is a kleptoparasitic spider in the web of a social spider *S. sarasinorum*. The present study records *A. kumadai* for the first time from India. Kleptoparasitic *Argyrodes* that are known to prey on spiders is usually of the same size or larger than their host (Trail 1980).

Some ants are considered to be kleptoparasites and are active predators of some spiders and beetles (Dorosheva and Reznikova 2006). We investigated the influence of ant on web building and foraging behavior of colonies of *S. sarasinorum*. Following the ant raids, a considerable decrease in the web rebuilding behavior was observed in both fasted and fed groups

of *S. sarasinorum*. In K exposed fasted groups, web rebuilding was delayed in the first 24 hrs compared to the K unexposed fed and fasted groups. Afterwards, web size gradually increased similar to the K unexposed fed groups. But the spiders not exposed to ants were having an overall delay in the pace of web rebuilding after prey ingestion. This result is also compatible with the results of Pasquet et al. (1999) and Leborgne et al. (2011) that immediately after web destruction the food supplemented spiders delayed web rebuilding. A decline in foraging effort in well-fed individuals has also been recognized in other organisms such as scorpions (Skutelsky 1996).

Fed groups have shown delayed web rebuilding and it was dependent on the previous foraging success. This behavior confirmed that feeding and exposure of ant influenced the web rebuilding. But fasted K exposed group also delayed web rebuilding due to exposure to ants than the K unexposed group; this was independent of previous foraging success. So exposure of ant also influenced the web rebuilding ability. Well-fed situation and ant exposure conditions delayed the web

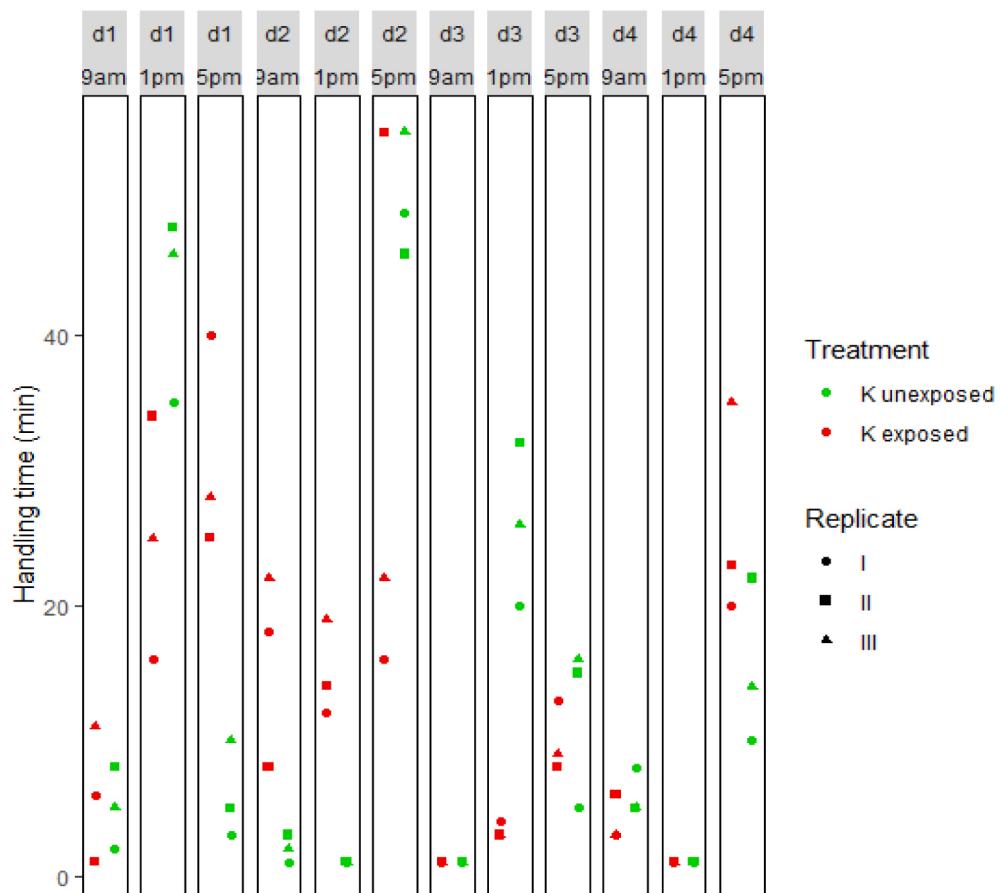


Fig. 7. Handling time (minutes) of both K unexposed (Ku, $n = 3$ groups) and K exposed (Ke, $n = 3$ groups) spider groups recorded during three different times (9 am, 1 pm and 5 pm) of the four experimental days.

rebuilding ability; this is also consistent with the result of the previous work of Leborgne et al. (2011) that ant exposure delayed web rebuilding and was independent of a spider's previous foraging success. In the case of *Stegodyphus mimosarum*, an abundant amount of sticky cribellate silk was produced as a means of defense against ants (Henschel 1998).

In the present study, social spider *S. sarasinorum* did not show any difference in the frequency of response to prey. Previous studies showed that the pattern of prey capture was not influenced by the type or the weight of the prey item (Leborgne et al. 1991). They capture the prey without considering the presence or absence of ants. Willey and Jackson (1993) reported that when the prey appeared, *S. sarasinorum* gained information about prey location by tensing the silk with the tarsi of the front leg and also they left the dead prey uneaten but returned to them later. Even though *S. sarasinorum* feeds communally, its participation in prey capture is not mandatory (Jambunathan 1905). However, their feeding time seems to be dependent on the position in the feeding sequence (Willey and Jackson 1993).

In our study, we analyzed that, ants could influence the handling time of spiders. The handling time of K exposed spiders was shorter compared to handling time during the later periods of the day, i.e., midday and afternoon and it also seemed to increase from morning to evening. This finding is similar to that of Leborgne et al. (2011), where the sub-social spider *S. lineatus* reacted more slowly to the prey in the midday than in the morning and handling time was positively correlated to the times of the day. The prey immobilization time in another social spider, *Anelosimus eximius*, was found to be less in large colonies (Pasquet and Krafft 1991). From the present study, it is evident that in addition to the colony size, prey handling time/immobilization time of *S. sarasinorum* also depends on the exposure of ants to the colony. However, the presence of ants had no observable effect on the prey ingestion rates of *S. sarasinorum* among the three different times of the day. This is substantiated by; Leborgne et al. (2011) that the ingestion rates of sub-social spider *S. lineatus* do not vary in the presence of ant.

CONCLUSIONS

From the present study, it can be concluded that different spiders and particularly ants are frequent invaders of nests of *S. sarasinorum* and hence they act as kleptoparasites. The kleptoparasitic ants have a significant influence on web building. This study helps us to understand that the invasion of nests of the social spider by ants, reduce their web building capacity. The

presence or absence of ants did not have any influence on the feeding behavior of the spider. The study confirms that the effect is not specific to any particular sub-social spider and a set of ant species.

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Author's contribution: AVS designed the study. PK and OMD-M performed the field work. OMD-M executed laboratory work, analyzed the data, and wrote the manuscript. All authors participated in revising the manuscript. All authors read and approved the final manuscript.

Competing interest: OMD-M, PK and AVS declare that they have no conflict of interests regarding the publication of this paper.

Availability of data and materials: Data and collected specimens are available in Centre for Animal Taxonomy and Ecology, Department of Zoology, Christ College, Irinjalakuda, Kerala, India.

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Ethics approval consent to participate: Not applicable.

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