

Habitat selection in Orb weaving spider *Nephila pilipes* Fabricius, 1793 (Araneae: Araneidae): niche complexity determines site selection and distribution of kleptoparasites

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Abstract

It is believed that slight variations in the physical parameters within the microhabitat can lead to significant differences in the populations of both the host and parasite. The golden orb weaver spider, *Nephila pilipes* Fabricius, 1793, serves as a host for various kleptoparasites in its web. This study focuses on examining the abundance of Argyrodinae spiders and their presence in relation to the positioning of the web on roadside vegetation in Kamorta, Nancowry Group of Islands, Andaman and Nicobar Islands, India. We analyzed species abundance using presence or absence data and employed NMDS and PCoA to calculate niche overlap. The total number of specimens collected was assessed using individual rare fractions.

Keywords: Zooplankton, Diversity, Wetlands, Nagaland, North-East India.

Introduction

Orb-web spiders employ a sit-and-wait predation strategy, but there are unanswered questions regarding the key factors influencing prey capture in their circular webs, such as web location and structure. Web location can be influenced by sunlight, wind orientation, and proximity to other webs. Sunlight attracts insects, potentially increasing prey capture success. Wind can blow insects towards the web, impacting prey capture. Proximity to other webs can lead to high competition, although some species mitigate this through the “ricochet effect” (Uetz, 1989; Rao, 2009) This effect occurs when webs are built close together, allowing prey to bounce through multiple webs before being caught, reducing competition costs. Web structure, including size, also affects prey capture efficiency. Larger webs have a higher likelihood of intercepting prey, and spider size may influence capture success due to the correlation with web size (Herberstein and Heiling, 1999; Vasconcellos-Neto *et al.*, 2007).

Studies have demonstrated that aggregation in web-building spiders leads to increased prey capture (Lubin, 1974), even when controlling for prey availability (Uetz, 1988). In such aggregations, individuals reduce their food intake due to higher kleptoparasitic intensity. The evolution of kleptoparasitism in spiders and other invertebrates is influenced by factors such as resource competition, predation risk, and ecological interactions. The study of kleptoparasitism sheds light on animal behaviour evolution and predator-prey dynamics. Brockmann and Barnard (1979) examined kleptoparasitism in birds, encompassing various forms and its evolutionary aspects. Furness (1987) studied kleptoparasitism in seabirds, emphasizing the importance of understanding the ecology and behaviour of kleptoparasites and their prey for comprehending this behaviour's dynamics.

Kleptoparasitism, the behaviour of stealing resources from other individuals, has been the subject of various studies

across different animal species. Hamilton (2002) found that the likelihood of kleptoparasitism is higher when the victim is weaker and when food is abundant. This suggests that unequal competitors are more prone to kleptoparasitic interactions. Vollrath (1979) studied the kleptoparasitic spider *Argyrodes elevatus* and discovered that it actively seeks out the webs of other spider species to steal prey. The study also highlighted the tactics employed by *A. elevatus* to avoid detection by the host spider during the theft. Rypstra (1981) investigated the impact of kleptoparasitism on prey consumption and web relocation in the spider *Nephila clavipes*. The study revealed that kleptoparasitic spiders can significantly reduce the prey consumption of the host spider and induce it to relocate its web. Agnarsson (2002) examined the relationship between sociality and kleptoparasitism in theridiid spiders. The study found that social spiders are less likely to engage in kleptoparasitic behaviour compared to solitary spiders. This suggests that sociality may act as a defense mechanism against kleptoparasites. Su and Smith (2014) investigated the evolution of host use, group-living, and foraging behaviours in kleptoparasitic spiders by constructing a molecular phylogeny. Their findings shed light on the evolutionary relationships within the Argyrodinae

subfamily of the Theridiidae family. Cangialosi (1990) examined the defence mechanisms of social spiders against kleptoparasites. The study revealed that social spiders exhibit more aggression towards kleptoparasites than towards other spiders. Sociality may enhance the spiders' ability to defend against kleptoparasites. These studies contribute to our understanding of the dynamics, evolutionary consequences, and defence strategies associated with kleptoparasitism in various animal species.

Material and Methods

Study Area

The webs analysed for the sampling of microhabitat association between kleptoparasites and orb-web weavers were selected through a random strategy between February 2018 and February 2020 at Kamorta, Nancowry group of Islands, Andaman and Nicobar Islands, India (Figure 1; Table 1). Each web was studied for its microhabitat stratification dynamics and the number of kleptoparasites in each niche category. A single count method was used for the web study while collecting kleptoparasites.

Table 1. Survey locality details

SI No.	Survey Location	GPS Data
	Point 1	8°13'0.87"N 93°32'6.40"E
	Point 2	8°12'0.17"N 93°30'23.25"E
	Point 3	8°11'12.27"N 93°29'17.86"E
	Point 4	8°10'25.55"N 93°28'48.80"E
	Point 5	8°10'29.28"N 93°30'17.53"E
	Point 6	8°11'29.52"N 93°31'26.22"E
	Point 7	8° 6'11.27"N 93°29'43.11"E
	Point 8	8° 5'33.26"N 93°29'42.76"E

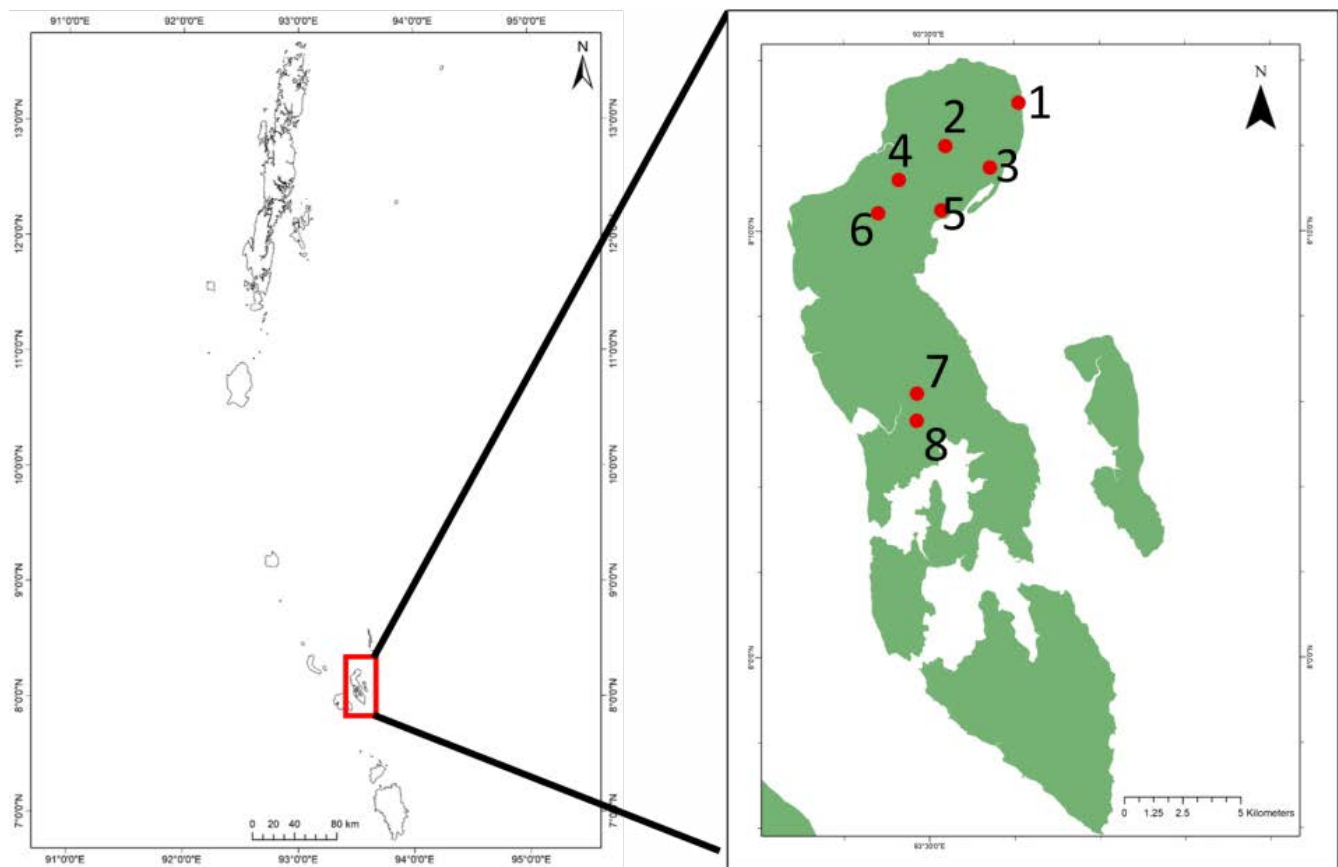


Figure 1. An outline of the survey locality

Collection and analysis of data

The study included active searching for *Nephila pilipes* webs at each visit. (Study period: March and April 2018–2020) Web diameter was measured as the horizontal diameter of the capture spiral. All the webs we found were between 40 and 200 cm from the ground and each was sampled once. For each web, the number of prey items adhered to the webs was counted as the dependent variable. Multiple linear and logit regression analyses to analyse the interplay between web size, isolation, and the presence and number of kleptoparasites. We used non-parametric tests to understand the interplay between habitat patch size, isolation, and the likelihood of patch occupancy by the prey community.

Results

We found 864 kleptoparasites in 119 *Nephila* webs encountered along the transect. When the spider webs were intact the observations showed that 90% of the webs were inhabited by both *Faiditus xiphius* (Thorell, 1887) and *Argyrodes* sp. These

species occurred in about similar frequencies. Occupancy in small webs was lower than expected given non-parametric correlation between web size and kleptoparasite number, which predicted between two to four kleptoparasites for each unoccupied web. The orbs of solitary webs were larger (radius: 1.5 m for *Nephila*), while the orbs of webs that were part of a cluster ranged from 0.15–0.47 m (Table 1). In either case, we found kleptoparasites only in webs larger than 0.04 m². The largest web encountered (90x80 cm, located in the center of a cluster) had the highest number of kleptoparasites (18) (Table 2). Two *Argyrodes* species were identified. The number of kleptoparasites increased with web size ($r^2=0.61$, $F=109.2$, $df=68$, $P<0.001$, $n=70$) (Table 3). Looking at clustered and solitary webs separately, web size explained nearly all the variance in clustered webs ($r^2=0.94$, $F=310.2$, $df=20$, $P>.001$, $n=22$) but much less so in solitary webs ($r^2=0.29$, $F=19.8$, $df=46$, $P>.001$, $n=48$). The homogeneity of the regression line slopes is rejected ($S^2=42.506$, $F=5.861$, $df=1$, $P=0.018$). The difference in variance in kleptoparasitic load in clustered ($S^2=2.1$) and

solitary ($S^2=9.5$) webs is significant ($P>0.01$). There was no difference in the mean number (Table 4) of kleptoparasites per web area between clustered (18.5 kleptoparasites/m,

$SD=13.3$) and solitary (23.1 kleptoparasites/m, $SD=26.4$) webs ($t=0.77$, $df=68$, $P=0.443$).

Table 2. Number of *Nephila pilipes* webs present in response to different habitat structure

Habitat	Number of <i>Nephila</i> Webs	Number of Kleptoparasite	% of Web Intact
Open Forest	22	99	69
Grass Land	24	93	57
Understorey Vegetation	16	184	92.5
Roadside Vegetation	19	122	76.54
Mangrove	5	54	89.6
Agricultural Land	13	109	45
Plantation	37	266	74.8

Table 3. Regression analysis for kleptoparasite occupancy and abundance in host webs for *Argyrodes*

	Multiple		Simple	
	Linear	Logit	Web Size	Distance
Occupancy	$R^2=0.36^*$		$R^2=0.21^*$	$R^2=0.01$
Abundance	$R^2=0.28^*$	$R^2=0.32^*$	$R^2=0.27^*$	$R^2=0.00$

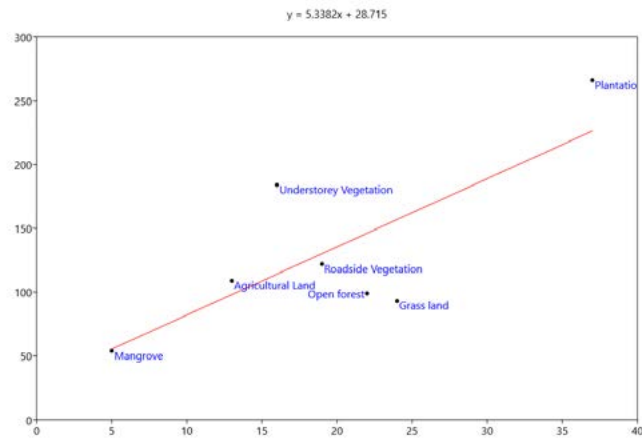
*Indicates significance at $P<0.001$ level

Table 4. Non-parametric tests for understanding the interplay among habitat patch size and isolation on one hand and likelihood of patch occupancy by prey community

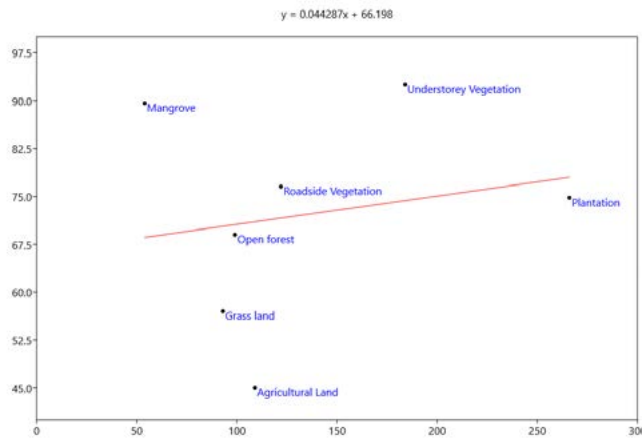
Correlations

			abundance value	relative prey size
Kendall's tau_b	abundance value	Correlation Coefficient	1.000	.786**
		Sig. (2-tailed)	.	.000
		N	20	20
	relative prey size	Correlation Coefficient	.786**	1.000
		Sig. (2-tailed)	.000	.
		N	20	20

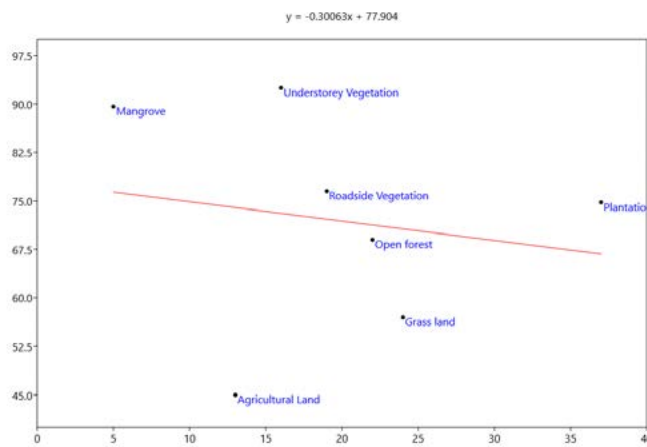
** Correlation is significant at the 0.01 level (2-tailed).



a. Number of Kleptoparsaite~%web intact



b. Number of *Nephila* web~number of kleptoparasite



c. Number of *Nephila pilipes* web~% of web intact

Figure 2 Showing 3 linear models for a. Number of Kleptoparsaite~%web intact; b. Number of *Nephila* web~number of kleptoparasite; c. Number of *Nephila pilipes* web~% of web

(2:0.51)

Table 4 PCoA summary for mean prey at 128 sites

Axis	Eigenvalue	Percent
mean prey	1.63E+05	99.964
mean prey sp. abundance	58.606	0.035863

Discussion

The distribution of kleptoparasites among *Nephila* webs appears to be strongly influenced by patch connectivity. A cluster of webs within a web cluster does not simply function as a single large web; rather, it represents a community of individual webs that may experience multiple extinctions and colonization events by kleptoparasites. Contrary to Elgar’s (1989) conclusions, Grostal and Walter (1999) found results that conflicted with previous findings, suggesting a more random distribution of kleptoparasites. While this study agrees with Elgar (1989) regarding the difference in kleptoparasitic load between clustered and solitary webs, it emphasizes that the distinction lies in stability rather than simply the mean number of kleptoparasites.

Seasonal fluctuations in the population sizes of kleptoparasitic *Argyrodes* and their *Nephila* hosts have been observed by Vollrath (1987) and Higgins and Buskirk (1998). Pooling data from different seasons could mask correlations between kleptoparasite load and web site at smaller time scales. Moreover, if the majority of webs considered were large, Elgar’s (1989) study may have been biased toward larger webs, resulting in a low percentage of webs without kleptoparasites and a high mean number of kleptoparasites per web. Therefore, reanalyzing the data from these previous studies may reveal more general and consistent patterns, with the apparent conflict being more superficial than real.

The structural complexity and longevity of *Nephila* web clusters may partially account for the greater stability of kleptoparasite populations in them compared to shorter-lived solitary webs. Accumulating evidence suggests that kleptoparasites strongly prefer complex, long-lived webs over simpler webs that are frequently dismantled. This

preference is observed not only in *Nephila* webs but also in other spider species such as *Anelosimus*, *Argiope*, *Cyrtophora*, *Diplura*, *Stegodyphus*, and *Tengella* (Elgar, 1993; Miyashita, 2002). Considering the detrimental effects kleptoparasitic *Argyrodes* can have on their hosts, it is tempting to speculate that frequent web renewal may serve as an adaptation against kleptoparasitism. However, determining cause and effect in this context can be challenging due to the influence of various factors on web duration, such as predation by sphecid wasps. Previous studies have demonstrated a correlation between patch (web) size and population size, and the current study reveals an increase in population stability with patch connectivity. These characteristics align with general ecological models, including island biogeography (MacArthur and Wilson, 2016) and metapopulation biology (Hanski, 1999). To further test these models, future studies should incorporate additional factors such as the absolute distances between webs, the number of webs per cluster, the size of barrier webs, the phenology of both hosts and kleptoparasites, and the patterns of migration between host webs. *Nephila* webs are ideal for such investigations due to their relative longevity and the extensive mesh-like structure of their barrier webs, which may facilitate kleptoparasitism (Grostal and Walter, 1999; Miyashita, 2002). Kleptoparasites primarily reside in the host barrier web, providing a safe space beyond the host’s monitoring range when they are not actively foraging. In observed cases of *Nephila* orb reconstruction, the kleptoparasites maintained their association with the specific host. During the rebuilding process, the kleptoparasites stayed in the unchanged barrier web, and no migration was observed. The new orb was connected to the existing barrier web, and once completed, the kleptoparasites rebuilt their association lines. The

barrier web provides a secure substrate for kleptoparasites to monitor the host web, adds a three-dimensional aspect to the orb, potentially facilitating group living, and enables kleptoparasites to remain associated with the host during web reconstruction. The major significances of the study are investments in retreats for the subsequent movement of web-

building spiders, a factor that has been overlooked for a long time. This discovery has broader implications for any species that constructs retreats, particularly those engineering species that modify their environment to enhance their fitness.

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