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SPIDER WEBS AS HABITAT PATCHES—THE DISTRIBUTION OF KLEPTOPARASITES (*ARGYRODES*, THERIDIIDAE) AMONG HOST WEBS (*NEPHILA*, TETRAGNATHIDAE)

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ABSTRACT. Most adult golden orb weavers (*Nephila clavipes*) have kleptoparasites of the genus *Argyrodes* in their webs. The kleptoparasitic load correlates positively with web size. Clustered (interconnected) webs have a more predictable number of kleptoparasites than do solitary webs, but there is no difference in the mean number of kleptoparasites between the two. From the view of the kleptoparasite, host webs are habitat patches or islands. Isolated webs show characteristics of small patches, where web size is a poor indicator of kleptoparasite number and variation is high. The distribution of kleptoparasites in clustered webs, on the other hand, seems to fit the ''ideal free distribution'' where web size nearly entirely predicts kleptoparasitic load. Thus clustered webs, as a habitat patch, are more than merely the combination of their parts. The predictability of kleptoparasite load in clustered webs may be a function of the stability (longevity) of those habitat patches, and ease of colonization, as neighboring webs act as sources.

Keywords: Habitat islands, habitat stability, ideal free distribution, orb web, patch connectivity

Obligatory kleptoparasites of the genus *Argyrodes* Simon 1864 are completely dependent on their host webs (Kullmann 1959; Vollrath 1987; Cangialosi 1990; Miyashita 2001); from the perspective of the kleptoparasite, host webs are thus natural habitat patches, or islands. Unlike islands, however, individual host webs are often interconnected, which adds another dimension to the system. Viewed as habitat patches, host web size and kleptoparasite number should be correlated. The isolation, or clustering, of webs should affect the distribution of kleptoparasites among webs. Interconnectedness should facilitate the movement (immigration and emigration) of kleptoparasites between webs. And, ease of immigration/emigration, together with relative longevity of clustered webs, should result in either higher or more stable kleptoparasite load compared to solitary webs.

This study is intended to examine the general correlation (if any) between *Nephila clavipes* (Linnaeus 1767) host orb size and *Argyrodes* kleptoparasite load, and specifically, if and how the kleptoparasitic load of interconnected (clustered) webs differs from other webs. I ask three main questions: is there a correlation between orb size and kleptoparasite number? Is a cluster of interconnected webs equivalent to a gigantic solitary web? Does the distribution of kleptoparasites in host webs appear to fit the ideal free distribution model, as suggested by Elgar (1993)?

Many authors have studied the biology of kleptoparasitic *Argyrodes* and its interaction with its hosts (see Elgar 1993 for review), yet understanding of the distribution of kleptoparasites among host webs is fragmentary. Cangialosi (1990) showed a strong correlation between social *Anelosimus eximius* (Keyserling 1884) web size and the number of *Argyrodes ululans* O. P.-Cambridge 1880 kleptoparasites residing in them. She attributed this in part to the stability and longevity of the larger colonies. Rypstra & Binford (1995) found that the number of commensal *Philoponella republicana* (Simon 1891) was correlated with web size of its social *A. eximius* host, and that *P. republicana* was more common in social *A. eximius* host webs than in solitary host webs of *Architis* sp. Smith Trail (1980) showed, similarly, that colonies of *Philoponella oweni* (Chamberlin 1924) had higher numbers of *Argyrodes fictilium* (Hentz 1850) kleptoparasites than did solitary *P. oweni* webs. Only a few studies have demonstrated such correlations in *Nephila* Leach 1815 webs. Robinson & Robinson (1973) found that adult *Nephila pilipes* (Fabricius 1793) had more kleptoparasites than did juveniles. Elgar (1989) showed a relationship between host size and kleptoparasitic load (note that host size and orb size are strongly correlated (Witt et al. 1968; Grostal & Walter 1999)), and that clustered webs suffered a higher parasitic load than did solitary webs of *N. edulis* (Labillardière 1799) in Australia. Grostal & Walter (1999) showed a weak correlation between *Nephila plumipes* (Latreille 1804) web size (also in Australia) and kleptoparasite number, but contrary to Elgar (1989), they found no special association between web aggregation and kleptoparasitic load.

This paper reports on *Argyrodes* kleptoparasites in the webs of a fourth *Nephila* species, *N. clavipes* (Linnaeus 1767), in Costa Rica. I look at the data from a different angle (regression variance), and in light of these results I propose a reinterpretation of the results of previous studies.

METHODS

The study was undertaken during the dry season, over a seven day period in February 2001 at Cabo Blanco Absolute Reserve, and three day period in March 2002, in Manuel Antonio National Park, both in Puntarenas Province, on the pacific coast of Costa Rica. Both study sites are in fairly open coastal humid tropical forest. The area has approximately 1400 mm annual rainfall, spread mostly over May–September, but with a dry season between January and April. All observations and data collecting were made from 0900–1700 h.

To assess the distribution of kleptoparasites among host webs, *N. clavipes* webs were located along trails and in the forest within the reserves. For every web encountered, I recorded the owner's size (body length in mm, excluding legs) and developmental status (adult/juvenile based on epigynal appearance), the orb size (height x width of orb in cm) and the number of kleptoparasites occupying each web, including its associated barrier web. Each orb was measured in the same way whether in a cluster or solitary. A web is classified as ‘‘clustered’’ if its structural threads attached to the threads of another *Nephila* web. Solitary webs are any webs that do not physically touch other webs. The distance to the nearest web was not measured exactly, but was never less than one meter. I used linear regression to examine the relationship of web size and kleptoparasite numbers, both for the pooled data and for clustered and solitary webs separately. I used a preliminary model ‘homogeneity of slopes’ test to determine the homogeneity of the regression slopes. As homogeneity was rejected, an ANCOVA was not performed. To test if web size can explain kleptoparasite load equally in solitary and clustered webs I compared the variance of kleptoparasite load in clustered versus solitary webs, using a F-test. I used a t-test to compare the mean numbers of kleptoparasites per orb area between clustered and solitary webs.

I assigned a number to each of the *Nephila* webs encountered, thereby establishing a transect of webs which were then used for observations and experiments. Webs were chosen on this transect by randomly picking numbers, alternatively for the two parts of this study, without replacement (so that no single web could be involved in both experiments). To obtain basic information on the distribution of kleptoparasites *within* host webs, in particular during orb reconstruction, 15 *Nephila* webs were monitored over a 6 day period for a total of 40 observation hours. The data collected was not quantitative, I visited the chosen webs haphazardly, and noted the whereabouts (in barrier web or in orb) and movements of the kleptoparasites, and anecdotal information about the behavior of the kleptoparasites as well as their interaction with the host were also noted. To compare the rates of colonization in clustered and solitary webs, I removed kleptoparasites from 10 solitary and 10 clustered webs. If more than one web was chosen from a particular cluster, I removed the kleptoparasites of only a single web daily, consecutively over the six day period. I counted the number of kleptoparasites in these webs the day after their removal and calculated the difference in re-colonization rates using a two sample t-test.

Voucher specimens from this study are deposited in the arachnological collection of the National Museum of Natural History, Smithsonian Institution.

RESULTS

I encountered 70 *Nephila* webs (48 solitary webs, 22 clustered, in a total of 7 clusters)

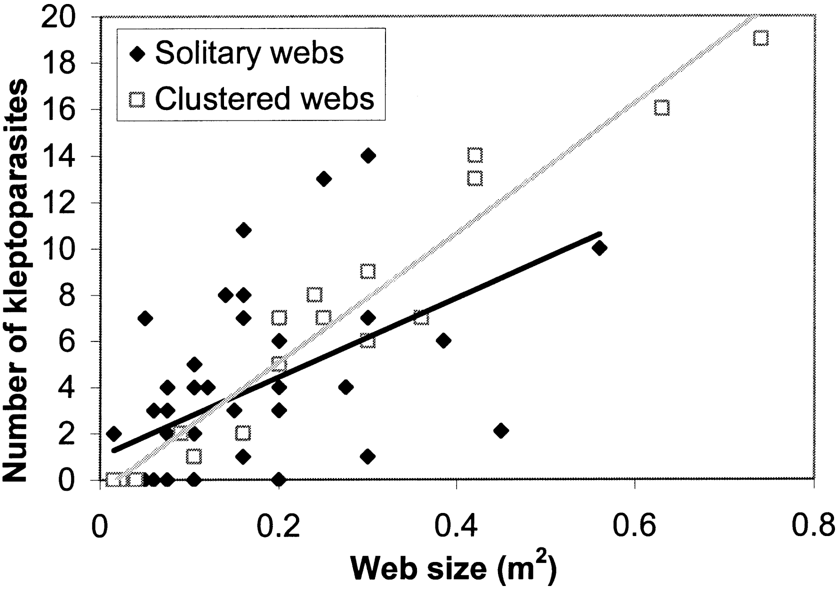

Figure 1.—Kleptoparasite load is correlated with web size in both solitary and clustered *Nephila clavipes* webs in Costa Rica. In clustered webs the number of kleptoparasites is nearly entirely linearly predicted by web size (r^2 = .94). On the other hand, solitary webs have a highly variable number of kleptoparasites (r^2 = .29).

containing close to 300 kleptoparasites. The orbs of solitary webs ranged in size from 0.015–0.56 m^2, while the orbs of webs that were part of a cluster ranged from 0.015–0.77 m^2. In either case, I found kleptoparasites only in webs larger than 0.04 m^2 (i.e. about 20 × 20 cm). The largest web encountered (90 × 80 cm, located in the center of a cluster) had the highest number of kleptoparasites, 18.

Two *Argyrodes* species were identified: *A. elevatus* Taczanowski 1873 of the ‘‘*A. argyrodes*’’ group and *A. caudatus* (Taczanowski 1874), of the ‘‘*A. cancellatus*’’ group (Exline & Levi 1962). Kleptoparasitic load increased with web size, pooling all data ($r^2 = 0.61$, $F = 109.2$, df = 68, $P < .001$, $n = 70$) (Fig. 1). 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 ($F(_2)_{,20,46} = 4.5$, $P < .01$). There was no difference in the mean number of kleptoparasites per web area between clustered (18.5 kleptoparasites/m^2, SD = 13.3) and solitary (23.1 kleptoparasites/m^2, SD = 26.4) webs ($t = 0.77$ df = 68, $P = 0.443$).

The kleptoparasites, when not foraging, spent most of their time in the host barrier web, which provides a haven outside the monitoring range of the host. In two instances *Nephila* orb reconstruction was observed and in both cases the kleptoparasites were observed maintaining an association with that particular host. As *Nephila* rebuilt its orb the kleptoparasites resided in the unaltered barrier web, and no emigration was observed in these two cases. The fresh orb was connected to the old barrier web, and after its completion the kleptoparasites rebuilt their association lines. Most of the kleptoparasites were only ever seen entering a single host web, even if that host web was connected to another. Yet, a few spiders did have silk lines leading to two host webs (counted only once and assigned to the nearest web), and thus could ‘‘monitor’’ more than one web at a time and forage in either (see also Whitehouse & Jackson 1993). All *Argyrodes* instars occurred in host webs, and both species were observed mating in the host barrier web. *Argyrodes* egg sacs were found hanging from the *Nephila* barrier web.

A day after removal of kleptoparasites two of the 10 webs in clusters had three kleptoparasites, five webs had two and three webs had one, while seven of the 10 solitary webs had zero and three had one kleptoparasite, respectively. The re-colonization rates of clustered versus solitary webs differed ($t = 5.737$ df $= 18$, $P < .001$).

DISCUSSION

As in *N. edulis* (Elgar 1989) and *N. plumipes* (Grostal & Walter 1999), the number of *Argyrodes* kleptoparasites correlates positively with web size in *N. clavipes* (Fig. 1). If in clusters, orb size explained nearly all variation in kleptoparasite number whereas if solitary, orb size explained much less of the variation. Although the regression slope of clustered webs is steeper, solitary webs did not have lower mean number of kleptoparasites (unlike *N. edulis*, see Elgar 1989).

Elgar (1993) suggested that the distribution of kleptoparasites among host webs in some cases seems to follow the 'ideal free distribution' (Milinski & Parker 1991). The ideal free distribution model states that for a given population size *k*, there exists a distribution of individuals such that the ''suitabilities'' derived from each habitat are equal and hence stable (Krebs 1994). If all individuals are ''free'' to move to alternate patches, then ''ideally'' each will find the place that maximizes its gain.

The results obtained here suggest that ideal free distribution may only be an appropriate model in the case of clustered webs. It seems that the parasite load for host webs in clusters has an optimal upper limit and the low variance in kleptoparasite numbers suggests that *N. clavipes* webs in clusters are generally near or at that limit. Miyashita (2001) demonstrated that in *Nephila clavata* L. Koch 1878 webs in Japan, the removal of *Argyrodes flavescens* (O. P.-Cambridge 1880) kleptoparasites resulted in a remarkably rapid influx of other individuals of that and another *Argyrodes* species. He interpreted this as evidence for strong inter- and intraspecific competition for limited host web space. Grostal & Walter (1999:557, fig. 4) also concluded that orb diameter imposed an upper limit on kleptoparasite numbers. Furthermore, clustered webs that were cleaned of kleptoparasites in this study regained them more rapidly than did solitary webs.

Kleptoparasites in web clusters can easily relocate to a web that provides more prey (i.e. the ideal free distribution). An ''extinction'' event (disappearance of a kleptoparasite) is short-lived because the neighboring webs act as sources. Web clusters are, in addition, relatively long lived habitat patches, increasing the probabilities of colonization by kleptoparasites. Solitary webs, on the other hand, are more like islands. They may first of all never reach an upper limit because they are relatively short lived, immigration is more stochastic, and they will experience higher rates of extinction (a solitary *Nephila* death will result in total extinction or emigration, whereas a *Nephila* death in a web cluster will result in only partial extinction/emigration from the cluster). Second, some solitary webs have a higher number of kleptoparasites per web area than any one in a cluster. This may be a result of a greater ''risk'' of emigrating from isolated webs and difficulties of finding new ones—isolation makes reaching an ideal distribution harder.

Patch connectivity thus seems to be of great importance in the distribution of kleptoparasites among *Nephila* webs. A web cluster is not merely equivalent to a gigantic solitary web; it is rather a community of distinct webs, each potentially experiencing multiple extinctions and colonizations of kleptoparasites.

Grostal & Walter (1999) found their results to conflict with those of Elgar (1989) and suggested that the distribution of kleptoparasites might be more random than Elgar had concluded. The findings of this study agree with Elgar's (1989) that there is a difference in kleptoparasitic load of clustered and solitary webs. However, the difference seems to be one of stability, therefore comparing simply the mean number of kleptoparasites may not be sufficient to detect those differences. Neither Elgar nor Grostal & Walter considered the regression variance in host web occupation, and thus could not have discovered the patterns reported here. Furthermore, both the current study and that of Elgar were ''snapshots in time'', done over a period of a few days, whereas that of Grostal & Walter took place over different seasons. Vollrath (1987) and Higgins & Buskirk (1998) found large seasonal fluctuations in the population sizes of kleptoparasitic *Argyrodes* and their *Nephila* host. Pooling data from different seasons could easily obscure correlations between kleptoparasite load and web size at smaller time scales. Finally, the current study would predict a greater mean number of kleptoparasites in clustered webs if the majority of webs considered were large (see Fig.1). Elgar (1989) found a very low percentage of webs without kleptoparasites (one out of 92) and a high mean number of kleptoparasites per web (10, versus e.g. 4.2 in the current study) suggesting that his study may indeed have been biased towards larger webs. Thus, reanalysis of the data of these previous studies is likely to reveal more general and congruent patterns, the presumed conflict being more apparent than real.

The structural complexity and longevity of *Nephila* web clusters may explain, at least partially, the greater stability of kleptoparasite populations in them, versus the shorter lived solitary webs. A growing amass of evidence indicates that kleptoparasites greatly prefer complex, long-lived, webs (e.g. *Anelosimus* Simon 1891, *Argiope* Audouin 1826, *Cyrtophora* Simon 1864, *Diplura* C.L. Koch 1850, *Stegodyphus* Simon 1873, *Tengella* Dahl 1901 and *Nephila*), to simpler webs taken down frequently (see Elgar 1993 for review; Miyashita 2002). Given that *Argyrodes* kleptoparasites can significantly and detrimentally affect their hosts (Vollrath 1980; Rypstra 1981; Elgar 1989; Grostal & Walter 1997; Higgins & Buskirk 1998) it is tempting to speculate that frequent web renewal may represent an adaptation against kleptoparasitism. Cause and effect in this case may be hard to tease apart, as many other factors affect web duration (e.g. predation by sphecid wasps). The lack of kleptoparasites in ‘‘daily webs’’ seems nevertheless beneficial and further work might profitably explore the idea.

Nephila webs are not only insect snares, but also discrete habitat islands hosting a dynamic community of kleptoparasitic spiders dependent upon them. Available studies have all shown a correlation between patch (web) size and population size, and the current study shows an increase in population stability with patch connectivity—a cluster of small webs is a more predictable (stable) habitat patch than a large solitary web. These characteristics epitomize general ecological models, such as island biogeography (MacArthur & Wilson 1967) and metapopulation biology (Hanski 1999). In order to test such models, future studies should include additional factors, e.g. absolute distances between webs, number of webs per cluster, barrier web size, phenology of both host and kleptoparasites, and the patterns of migration between host webs. For such studies *Nephila* webs are ideal as both their relative longevity (thus habitat stability) (e.g. Wiehle 1927; Lubin 1983; Foelix 1996), and the extensiveness of their mesh-like barrier webs, may increase kleptoparasitism (Whitehouse 1988; Cangialosi 1990, 1997; Grostal & Walter 1999; Miyashita 2002). The barrier web provides a safe substrate for the kleptoparasites from which to monitor the host web (e.g. Vollrath 1979a, 1979b; Whitehouse 1986; Cangialosi 1990), it makes the orb three dimensional, which may facilitate group living (Krafft 1979; Agnarsson 2002), and it allows the kleptoparasites to stay associated with the host during orb reconstruction.

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