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SHORT COMMUNICATION

Habitat patch size and isolation as predictors of occupancy and number of argyrodine spider kleptoparasites in *Nephila* webs

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Abstract How fully a suitable habitat patch is utilized by organisms depends crucially on patch size and isolation. Testing this interplay is made difficult in many systems by the arbitrariness of defining a "habitat patch", measuring its boarders, and relatively low detection probability of the inhabitants. Spider webs as habitat patches for obligate web kleptoparasites are free from these problems. Each individual web is a highly discrete and readily measured habitat patch, and the detection probability of argyrodine spider kleptoparasites is very nearly 1. Hence, spider webs emerge as simple systems for ecological models such as patch occupancy and metapopulation biology. Recently, I showed that the distribution of kleptoparasites among host webs relates both to web (patch) size as well as patch connectivity. Here, I test the relative importance of patch size versus isolation in explaining patch occupancy and abundance of inhabitants. I find that (1) web size is the better predictor of patch occupancy and abundance. (2) Web size is overall positively correlated with abundance, but predicts it most precisely among interconnected webs and not at all among the most isolated webs. Hence, patch occupancy and inhabitant abundance is explained by a rather complex interplay between patch size and isolation.

Keywords Argyrodes elevates · *Faiditus americanus* · Patch size · Occupancy · Abundance · Patch connectedness · Spider webs · Kleptoparasites · Ideal free distribution

Introduction

Understanding the interplay among habitat patch size and isolation on one hand and likelihood of patch occupancy, and number and diversity of occupants on the other is of increasing importance as habitat fragmentation continues to threaten biodiversity (e.g., Hanski and Simberloff 1997; Nicol and Possingham 2010). In general, patch size and isolation affect both occupancy of individual species and patterns of diversity such that small and isolated patches are least likely to be occupied by any given species and are least diverse (MacArthur and Wilson 1967; Hanski 1999; Drakare et al. 2006; Watling and Donelly 2006; Prugh et al. 2008). Small and isolated patches are expected to have relatively low immigration and high extinction rates (Hanski 1999). Furthermore, species will be absent more frequently from small patches than large patches simply as a function of abundance—the random-sample hypothesis (Andrén 1996).

Determining if small and isolated patches have lower occupancy and/or diversity than expected by the random-sample hypothesis requires sampling of patches of various sizes and degrees of isolation, accurate measurements of habitat patch size, and an accurate estimate of occupancy/abundance of inhabitants (e.g., Sahlin and Schroeder 2010). For many systems, obtaining such data can be challenging for two main reasons. First, defining and measuring the boarders of habitat patches can be arbitrary and is often complicated (e.g., Turlure et al. 2010). Second, the probability of finding a species in a patch, even when

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present, is usually much less than one (Moilanen 2002; Wintle et al. 2004; Kery and Schmid 2004; Pellet et al. 2007). Hence, it is necessary to gain an estimate of the detection probability of a species, adding a confounding variable.

Spider webs as habitat patches for obligate web kleptoparasites are free from these two problems. First, an individual spider web is a highly discrete habitat patch suspended in a matrix of non-habitat. Orb webs, such as those built by the golden orbweaver *Nephila* (Nephilidae) are two-dimensional patches that differ strikingly from the surrounding habitat and can thus be readily measured (e.g., Kuntner et al. 2008a, b). Second, argyrodine spider kleptoparasites range from a couple to several millimeters in size and are usually conspicuously colored, and, in the context of a habitat patch (web) that is rarely larger than 1 m^2, are very easy to locate and count. Hence, the detection probability of argyrodine spider kleptoparasites, that is the probability of detecting them—when present—during a single survey, is very nearly 1. Therefore, this system offers extremely precise estimates of patch size, isolation, and occupancy, and thus also, opportunities to test basic assumptions about their interplay. This system has other benefits as well. Numerous patches (webs) can be surveyed rapidly at low cost. In turn, easy observation invites detailed mark-recapture studies where both host and parasites can be paint-marked allowing understanding of movement (immigration and emigration) of kleptoparasites among host webs in any given area. Preliminary mark-recapture data suggest emigration and immigration can occur rapidly (minimally 12% of individuals moved among webs over a period of 2 days) and that abundance of kleptoparasites is maintained by a balance between immigration and emigration (pers. obs.). One feature of this system that may limit the extent to which webs emulate habitat patches more traditionally modeled in patch ecology is that host webs are relatively short lived. Each *Nephila* may live less than 1–2 year, such that the landscape of available habitat patches can change dramatically through time. Nevertheless, a web site may be in more or less continuous use by different *Nephila* individuals, and the rapid turnover of patches creates a highly mosaic landscape and an excellent context in which to study the interplay of emigration, immigration, and regeneration in explaining habitat occupancy.

While several studies have examined the biology and ecology of spider kleptoparasites (see Vollrath 1987; Elgar 1993 for reviews), few have examined the distribution of kleptoparasites in the context of webs as habitat patches. In general, prior studies have shown a correlation between web size of various host species and number of argyrodine and other spider kleptoparasites (Cangialosi 1990; Rypstra and Binford 1995; Smith Trail 1980; Robinson and Robinson 1973; Elgar 1989; Grostal and Walter 1997, 1999; Agnarsson 2003). Elgar (1989), furthermore, found an association between web (patch) interconnectedness and kleptoparasite number (but see Grostal and Walter 1999).

Recently, I showed that the distribution of kleptoparasites among host webs relates both to web (patch) size as well as patch connectivity (Agnarsson 2003). Web size more precisely predicted the number of kleptoparasites per web in clusters of several interconnected webs than in isolated webs. Here, I test the relative roles of patch size versus isolation in predicting patch occupancy and abundance of inhabitants.

Materials and methods

The study was undertaken along a transect in Bocas del Toro, Isla Colón, Panama, from 17–20 April 2010. Webs of the host, *Nephila clavipes*, were located on vegetation along a transect following the road which crosses the island. Each web was visited twice; however, data analyzed here represent single measurements and counts. For each web, or group of webs, GPS coordinates were recorded. For every web encountered, I recorded the orb size (height × width of orb in centimeters) and the distance to the nearest neighbor web in meters. Exact measurements were taken up to about 20 m; webs with no other webs within sight were assigned distance of 30+ m. When a web was physically connected to another, distance between webs was indicated as 0. Within each web, the presence and number of argyrodine kleptoparasites were noted. The web size and kleptoparasite abundance data are approximately normally distributed, apart from relatively high number of webs in the smallest category, lacking kleptoparasites. I used multiple linear and logit regression analyses to examine the interplay among web size, isolation, and the presence and number of kleptoparasites in the webs. The variables included in the model are web size, distance of web from nearest web, and kleptoparasite occupancy/abundance. Multiple regression was used to test which variable, patch size or isolation, better explained kleptoparasite abundance. I used standard and multiple linear regression to examine the relationship between web size and kleptoparasite occupation and number, and to test if physically interconnected webs and highly isolated webs (arbitrarily defined here as those≥5 m distance from nearest neighbor) showed differences to the general pattern. The variables used were web size and kleptoparasite abundance, and the data were analyzed all together and also partitioned by degree of isolation, analyzing separately interconnected webs (distance to nearest web 0) and “isolated” webs (distance to nearest web 5+ m). Within these rather arbitrary categories, regressions analyses were based on actual measured distances, except for webs in the 30+ m category. The data were partitioned in this manner to test the hypothesis that the occupancy of kleptoparasites in interconnected webs is predicted by the ideal free distribution, whereas the occupancy of isolated webs is not. The general assumption is that webs are uniform patches such that a given area of any given web is qualitatively comparable to any other. Thus, the ideal free distribution should result in a tight correlation between web size and kleptoparasite abundance, while a lack of such fit could be used to reject the ideal free distribution hypothesis.

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

Results and discussion

In total, 864 kleptoparasites were counted in the 119 *Nephila* webs (patches) that were encountered along the transect. About 90% of the webs contained one or more kleptoparasites, which were identified to belong to two species of the subfamily Argyrodinae: *Faiditus americanus* and *Argyrodes elevatus*. These species occur in about equal numbers; numbers represent total counts of kleptoparasites.

This study was designed to test the interplay between, and relative importance of, patch size versus patch isolation in explaining occupancy and abundance of inhabitants, in a system where habitat is discrete and easily measured and inhabiting species have a near 100 % detection probability. In this case of argyrodine kleptoparasites living in *Nephila* orb webs, as also seen, e.g., in aspen-associated saproxylic beetles (Sahlin and Schrodeder 2010), patch size is the better predictor of patch occupancy and abundance than is isolation (Fig. 1a). Only web size was significant in a multiple linear regression analysis, and adding distance (isolation) did not increase predictive value (Table 1).

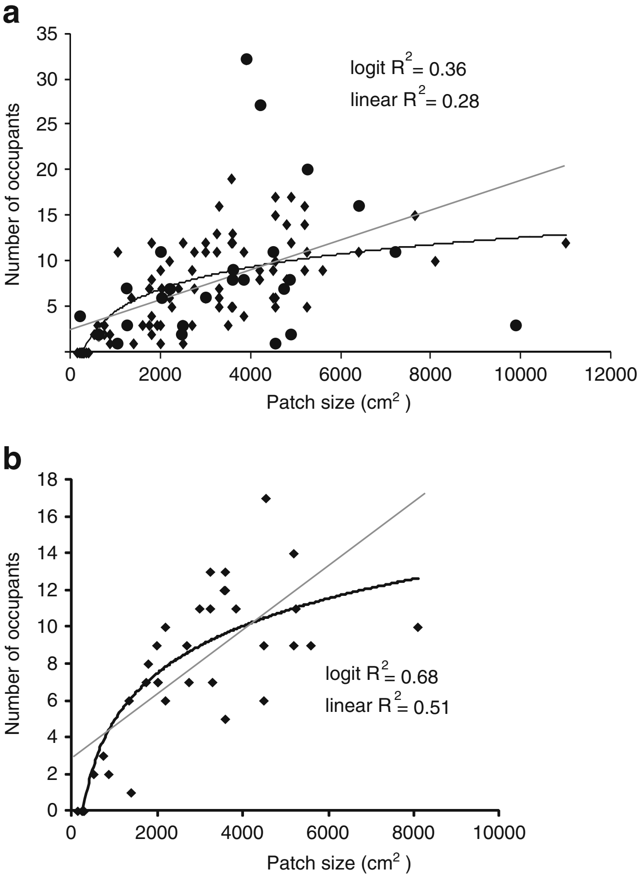

Fig. 1 **a** Regression of web sizes and the abundance of kleptoparasites for all 119 patches, including interconnected and non-interconnected webs. *Circles* indicate isolated webs (≥5 m to nearest web). **b** Regression of web sizes and abundance of kleptoparasites among the subset of interconnected webs from (**a**). *Gray lines* show linear regressions

Occupancy in small webs was lower than expected given linear correlation between web size and kleptoparasite number, which predicted between two to four kleptoparasites for each of the unoccupied webs (Fig. 1a). The random-sample hypothesis (Andrén 1996) would predict smaller patches to be empty more often than large patches simply as a function of size. However, small webs disproportionally lacked kleptoparasites which rejects that hypothesis, implying that the smallest webs are not well characterized as equivalent to a small part of a larger patch. Instead, it suggests some minimum web, or host, size at which stealing from the web is a worthwhile strategy, perhaps when the host is small enough to compete with the kleptoparasites for the smallest insects, which larger hosts ignore. Cangialosi (1997) found that, when hosts are small, the kleptoparasites may prey on the host itself rather than stealing prey from the web. However, she studied a different genus (*Neosphintharus*), while *Argyrodes* and *Faiditus* probably rarely kill the host, and the host was present in all small webs encountered here. An alternative explanation for unoccupied small patches may be that these webs are nearly always young, being predominantly made by small juvenile spiders and thus may not have had time to accumulate colonizers.

Despite the importance of patch size, isolation also plays a role in determining the distribution of kleptoparasites

Table 1 Results of multiple and simple regressions

	Multiple		Simple	
	Linear	Logit	Web size	Distance
Occupancy	R^2=0.23*		R^2=0.21*	R^2=0.01
Abundance	R^2=0.28 *	R^2=0.36*	R^2=0.27*	R^2=0.00

*Indicates significance at P<0.001 level among patches. Web size predicts kleptoparasite abundance in interconnected webs (Fig. 1b) more precisely [$R^2=0.50$ (linear) $R^2=0.68$ (logit), $p<0.001$, df=33] than in webs not interconnected. Agnarsson (2003) found the same comparing larger clusters of *Nephila* to isolated webs; however, here, this pattern holds even though never more than two webs were connected to one another. Furthermore, major outliers—webs with many more or much fewer kleptoparasites than expected given their size—were all webs that were 5 m or more away from their nearest neighbor (Fig. 1), and among these webs, the correlation between web size and kleptoparasite number disappears ($R^2=0.02$, $p>0.05$, df=24).

These effects of isolation are consistent with the idea that, in interconnected webs, kleptoparasite numbers approach the "ideal free distribution" (Elgar 1993; Agnarsson 2003). The ideal free distribution model is based upon the premise that, if all individuals are "free" to move among patches, then "ideally", each will find the place that maximizes its gain (Krebs 1994). This model predicts that habitat patches should be used optimally, and thus, if patches are very similar to one another, as in the case of *Nephila* webs, the abundance of inhabitants should be closely predicted by the size of the patch.

In interconnected web clusters, kleptoparasites can be expected to more readily find and move among alternative patches and thus find "habitats" where competition may be less intense and thereby reduce the effect of local extinctions. Hence, immigration and emigration in interconnected webs likely result in more even distribution of individuals among the available patches. In the more isolated webs (here, those at least 5 m from the nearest web), immigration can be expected to be more haphazard as isolated webs are more difficult to find; global extinction will be more common as there is no nearby source of immigrants, and finally, emigration may also be less frequent as it requires the kleptoparasites to abandon their habitat at risk of not finding another patch. Hence, isolated webs may take longer to accumulate immigrants but may eventually have a higher abundance of kleptoparasites due to lower emigration rates. Means of dispersal probably explain the difference between interconnected and isolated webs. Kleptoparasites can move among interconnected webs by walking but likely use bridging or even ballooning to move among more isolated webs. However, at what exact inter-web distances movement among webs ceases to be fluid remains to be studied.

Obligate web kleptoparasites and their host webs form a convenient system in which to investigate the relative roles of patch size and isolation in explaining the distribution—both occupancy and the abundance—of species among habitat patches. In this model system, habitat is discrete and readily measured, and the detection probability of the inhabitants is approximately 1. This system is, furthermore, very simple, consisting of small but easily observed patches, and typically only one or two species of argyrodine spider species using the patches at any given time. Therefore, empirical data can be readily collected to test basic predictions of ecological models, while eliminating some of the confounding variables (e.g., Pellet et al. 2007). For a few examples, future studies could examine movement among webs using mark-recapture methods, monitor patch landscape and dynamics through seasonal changes, and test how habitat availability affects patch dynamics by comparing landscapes where patches are common versus rare.

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