Which web to invade? Argyrodine kleptoparasites differentiate among architecturally different host webs

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Abstract

Kleptoparasitism, the theft of resources from another organism, is a survival strategy found across the animal kingdom. Many argyrodinae cobweb spiders (Theridiidae) are obligatory kleptoparasites that have largely abandoned web building, relying instead on webs of larger hosts. Theory predicts, and limited prior research indicates, that kleptoparasites are not randomly distributed among host webs, and prior studies indicate that web architecture (size and tenure) and prey availability impact kleptoparasite abundance and host choice. We investigate the distribution of multiple argyrodine kleptoparasite species among three contrasting host types in Madagascar's Analamazaotra National Park: *Nephilingis* (Nephilidae, large nocturnal orb weavers), *Caripetella* (Pisauridae, large nocturnal sheet web builders), and *Anelosimus* (Theridiidae, small cathemeral social spiders constructing three-dimensional tangle webs). Although small in scope, this study is the first to take a real-time snapshot of multi-species endemic communities of spider kleptoparasites and their in-situ distribution across contrasting host webs. We found an unexpectedly high diversity of ten kleptoparasite species that, remarkably, are not conspecific with the five that were previously known from all of Madagascar. Kleptoparasite species composition and abundance varied across the three hosts: some appeared host-specific while others seemed versatile. In general, argyrodine kleptoparasites evidently discriminate among hosts but choose among them with varying degrees of astucity. At the community level, very limited data exist, and based on our study we can only speculate that species assembly into host webs involves a complex interplay between host preference and species competitive hierarchy. Future field research should investigate this system as a community of multiple interacting species to gain a more comprehensive understanding of the rules that may govern the assembly of diverse kleptoparasites into equally variable host webs. Synergistically, laboratory experiments are needed to elucidate key cues facilitating kleptoparasite web detection and choice; likely involving eavesdropping on pheromones intended for the hosts male.

1. Introduction

Species interactions are diverse, ranging from indirect to direct and from mutually beneficial to hostile. Leung and Poulin [1] define a symbiotic relationship as “an intimate interaction between different organisms, where at least one of the parties is obligatorily dependent on the association as a part of its life history". Symbiosis can be mutualistic, where both parties benefit, commensal, where one species benefits and the other is unaffected, or parasitic, where the parasite benefits and the host is harmed [1-4]. Predation and parasitism are prominent forms of antagonistic animal interactions, foraging modes involving the exploitation of innate resources—bodily tissue, fluid, behavior—of the victim. Kleptoparasitism is another exploitative foraging strategy observed among various animals including birds, mammals, insects, and arachnids [5-6]. It involves the theft of extrinsic resources that are of potential value to the host that has secured or produced them. Kleptoparasitism is an intriguing adaptive strategy that requires balancing, among other things, the energy costs of searching for food against the benefits and costs of stealing resources from others [7]. While facultative kleptoparasitism is common [e.g., 6], natural selection has engrained this strategy in some groups, where host-selection may be a more critical foraging decision than the exact nature of the stolen resource. Precious little, however, is known about host choice in many kleptoparasitic organisms like spiders.

Obligate kleptoparasitic spiders have largely abandoned web building, relying instead on symbiosis in the webs of larger hosts to forage in [8-11]. This strategy represents a complex interplay of evolutionary adaptations, ecological dynamics, behavioral decision making, and doubtless, a variety of largely unknown sensory cues [5, 12-13]. The majority of known spider kleptoparasites belong to the subfamily Argyrodinae (Theridiidae, cobweb spiders), a versatile group employing diverse strategies to exploit various host species. Among their hosts are 1) large nephilid orb weavers such as *Nephila*, *Trichonephila*, and *Nephilingis*, that seem to be particularly important/preferred hosts in most subtropical and tropical environments [12], 2) large araneid orb weavers such as *Caerostris*, *Cyrtophora*, and *Gasteracantha*, 3) large sheet weavers including various agelenids, the pisaurid *Caripetella*, the tengellid *Tengella*, and others, 4) social and colonial spiders (mostly Araneidae, Eresidae, and Theridiidae) that build complex silken networks, and 5) some smaller species (notably Theridiidae and Linyphiidae) that are locally abundant [14-21].

Argyrodinae spiders are speciose [13, 22-24] and vary in size, morphology, coloration, and tactics to obtain resources from host webs [5, 11]. These tactics include pilfering small insects ignored by the host, stealing wrapped prey, feeding on digested prey alongside the host, opportunistic predation on the host, its offspring, and eggs, and even the consumption of host web silk [5, 12, 25]. Their hosts are also highly diverse, differing in size, innate aggression (solitary versus communal or social spiders), web architecture, and prey choice. Given this diversity of kleptoparasites and hosts, fundamental ecological foraging and game theories predict that kleptoparasitic species do not distribute randomly among potential host webs [6, 26-28]. Field observations corroborate these fundamental predictions: large, long-lived webs tend to contain kleptoparasites, while they are rarely found in webs of spiders that prefer small prey, and those that have short duration in space and time [5, 12, 28-31]. The few available field studies broadly agree that 1) distribution of kleptoparasites is non-random among hosts, 2) large and predictable webs are favored by kleptoparasites, 3) larger webs have more kleptoparasite individuals and species, and 4) kleptoparasite species range from versatile generalists to relative host specialists [5, 9-12, 28, 32-38]. However, most prior studies focus on a single kleptoparasite or host species [32, 37-39], and none have investigated the in-situ distribution of a species-rich kleptoparasite community among architecturally diverse host webs.

Here, we investigate the real-time distribution of a highly endemic spider community: multiple argyrodine species among three hosts in the small Analamazaotra National Park in Madagascar. The three host species are among the most abundant web builders in the reserve but contrast starkly in web architecture and behavior (Fig. 1, see Methods): We surveyed multiple webs of all three hosts and conducted translocation experiments between *Nephilingis* and *Caripetella* webs to explore kleptoparasite diversity, the assembly of kleptoparasite communities into host webs, and evaluate the evidence for host choice.

2. Materials and Methods

2.1. Study system

The host species belong to three distantly related families and while all build long lasting webs, they differ in web architecture, size, activity patterns, and innate aggression (Fig. 1). *Nephilingis livida* [29] is a large mostly nocturnal nephilid building vertical orb webs that contain sticky silk. The pisaurid *Caripetella madagascariensis* [40] is a large, strictly nocturnal, solitary spider in horizontally domed sheet webs made of dry silk. Spiders of the genus *Anelosimus* are subsocial, cathemeral, and build three-dimensional tangles of dry silk that contain numerous individual spiders. Analamazaotra is home to about 10 highly similar species of *Anelosimus* that we sampled indiscriminately. A few webs of the subsocial pisaurid *Dendrolycosa* were also sampled, highly similar in web structure and content to *Anelosimus*. All three web types have extensive networks of non-sticky structural threads separated from the capture area of the web, where the kleptoparasites accumulate when not foraging.

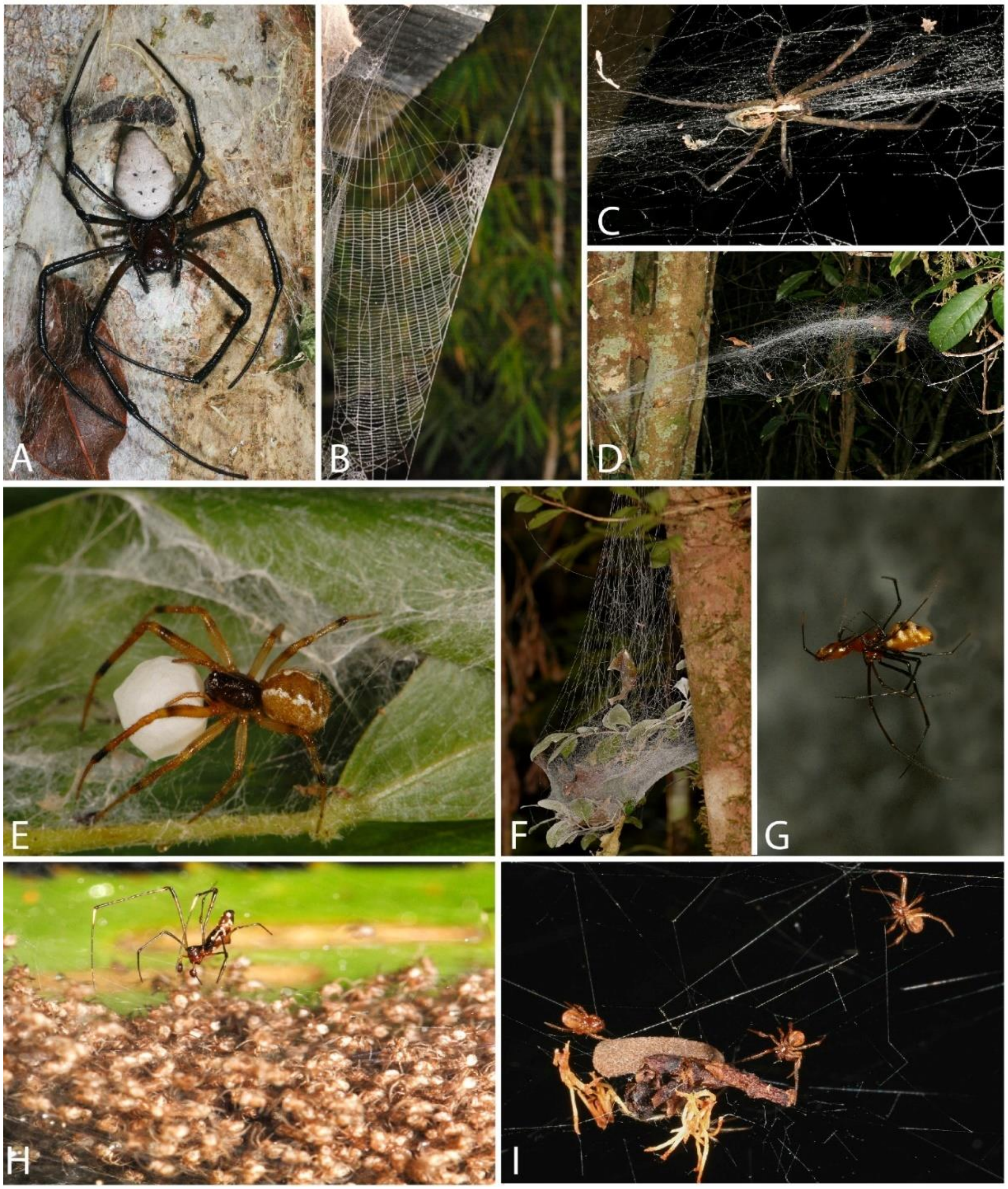

Figure 1: Study system. A-B, *Nephilingis livida* host. A, female. B, vertical orb web. C-D, *Caripetella madagascariensis* host. C, female in web. D, horizontal domed sheet web. E-F, *Anelosimus vondrona* Agnarsson & Kuntner, 2005 host. E, female with egg sac in web. F, social 3D tangle web. G-I, kleptoparasites in action. G, *Argyrodes* sp. 1 from this study, pair in copula in *N. livida* web. H, *Argyrodes* sp. 3 from Montagne d´Ambre, male approaching freshly hatched *N. livida* spiderlings. I, *Argyrodes* kleptoparasites stealing prey from *Nephilingis borbonica* [29] in Réunion. Photographs are not to scale, total length of females (front of carapace to spinnerets) *N. livida* ~20 mm, *C. madagascariensis* ~18-

25 mm, *A. vondrona* ~5 mm, argyrodines ~3-6 mm. Web size (longest axis), *N. livida* orb ~40-80 cm high, *C. madagascariensis* sheet ~30-60 cm wide, *A. vondrona* basket ~10-25 cm width, up to ~30 cm tangle above. Photos A, C, D, I by M. Kuntner, B, E-H by I. Agnarsson.

2.2. Survey of kleptoparasites in host webs

This study was conducted in the small Analamazaotra National Park, a montane rainforest reserve in eastern Madagascar (25.5 km^2, 900-1050 m alt., center ca. 18°56′10″S, 48°25′42″E, Fig. 2), during 21-28 May 2024. Samples were taken of kleptoparasitic argyrodine (Theridiidae) spiders, all presumably endemic to Madagascar, found in three types of host webs: *Nephilingis livida*, *Caripetella madagascariensis*, and subsocial webs, most belonging to *Anelosimus vondrona*, *A. nazariani*, and *A. may*, and a few *Dendrolycosa* sp. (Fig. 1, Table 1). The host species are likewise endemic to Madagascar, except *N. livida* that also occurs on small islands in the northern Indian Ocean [41]. *Caripetella* and various highly similar *Anelosimus* species [42-44] are common in the forest and were mainly collected along the 2.5 km long Indri 1 trail loop that spans the western portion of the reserve (Fig. 2). While *Nephilingis* webs were also sampled within the forest, most samples were taken at the forest edge from the grounds of the Feon’ny Ala cottages (Fig. 2).

The kleptoparasitic spiders were readily visible in webs of *Nephilingis* and *Caripetella* and were captured with manual aspirators (pooters) from ~20 webs of each host and placed in live collection vials. In contrast, in the dense 3D tangle webs of subsocial spiders, kleptoparasites were challenging to detect among the many inhabitants, and the host species cannot be reliably identified in the field. The entirety of 87 subsocial colonies (75 *Anelosimus* and 9 *Dendrolycosa*) were therefore collected in plastic bags and later dissected, with all the web inhabitants preserved in ethanol. Kleptoparasites from *Nephilingis* and *Caripetella* webs were kept alive and used in the translocation experiments described below, before being preserved in ethanol. Taxonomic identification and molecular studies were subsequently performed at the University of Iceland.

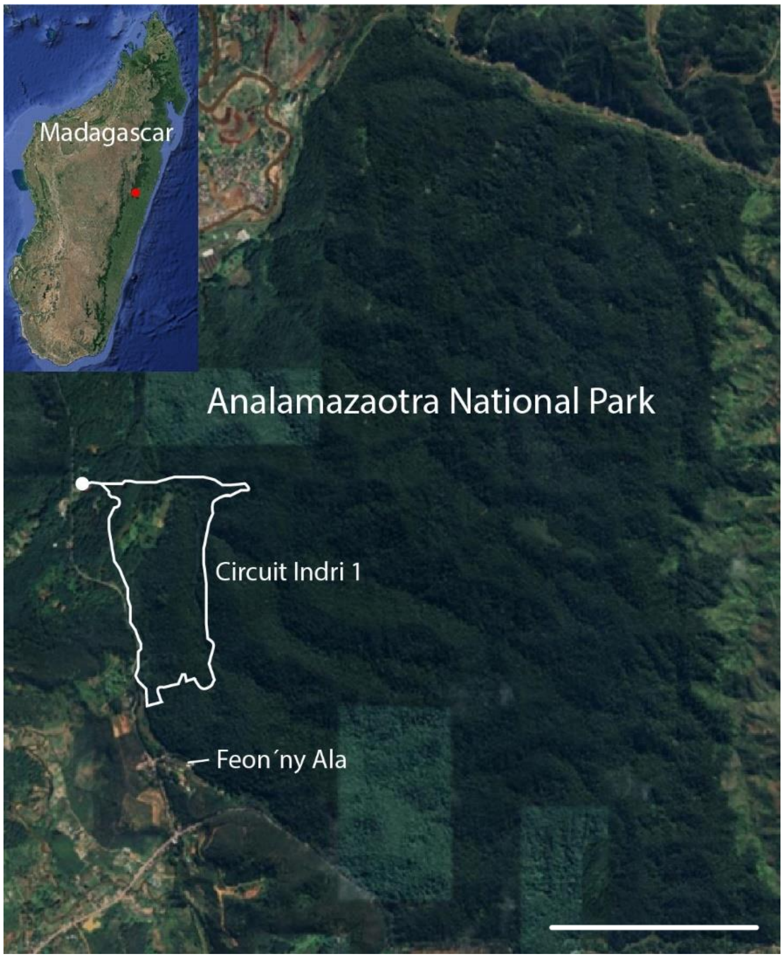

Figure 2: The small Analamazaotra National Park (25.5 km^2), located in eastern Madagascar, see inset map (note that for visibility, the red dot covers a vastly larger area of Madagascar than the reserve). The edges of the park are clearly visible by changes in vegetation, evident by dark green forest cover, surrounded by lighter green vegetation and brownish human developments. The research was done along the approximately 2.5 km Indri trail loop (circuit Indri 1), and on the grounds of the Feon´ny Ala cottages. Scale bar in the lower right corner is 1 km.

2.3. Translocation experiments

To test whether the kleptoparasitic spiders show host-specific or generalist tendencies, a simple field experiment was conducted. Kleptoparasitic spiders from two of the host species, *N. livida* and *C. madagascariensis*, were collected and kept in live vials until they were placed onto the web of the other (*N. livida* kleptoparasites into *C. madagascariensis* webs and vice versa). Kleptoparasitic spiders were placed onto webs that had been cleared of native kleptoparasites, who were used in the reverse experiment. In a total of 17 translocation experiments, four to seven foreign kleptoparasitic spiders were successfully placed onto each cleared host web: 54 native *Caripetella* kleptoparasitic spiders on 10 *Nephilingis* webs and 34 native *Nephilingis* kleptoparasitic spiders on seven *Caripetella* webs. All spiders were placed using their lifeline, inasmuch as possible and depending on access to the web, feet-first to prevent entanglement, onto anchor threads, frame threads, spiral or radius threads, near the outer edges of the web. In the first experiment, the behavior of both the introduced kleptoparasitic spiders and hosts were observed for a period of 45-60 minutes. Our observations were focused on kleptoparasite movement within webs, the nature of which can possibly reflect a kleptoparasitic spider's evaluation of risk [45] and, to an extent, outside the web. Additional behaviors, such as silk deposition, were also noted. Movements of the kleptoparasitic spiders were cataloged into the following categories: 1) stayed on the threads of the host web 2) stayed in the vicinity of host web, either on its own lines connected to the host web or sitting within 5 cm of host web support lines, 3) left host web completely. The translocation experiments were performed during daytime.

2.4. Statistical analyses

To investigate the association between kleptoparasitic species and host web types we used Fisher's Exact Test, appropriate for small sample sizes and low expected values. Given the size of our contingency table, we used a simulation-based approach with one million replicates to ensure accurate p-value calculations.

The contingency table, detailing the distribution of kleptoparasitic species across host web types, was first constructed in Excel (Microsoft, USA) and then imported into RStudio [46] for analysis. To investigate the association between kleptoparasitic species and host web types, we performed statistical tests in RStudio using this table as the dataset. The RStudio code for these analyses is available as supplementary material.

3. Results

3.1. Survey of kleptoparasites in host webs

A total of 316 argyrodine individuals were sampled (Table 1), belonging to a total of 10 putative argyrodine species based on morphology and DNA barcodes. These species were preliminarily assigned to the groups *Argyrodes* (Arg sp. 1-4), *Argyrodes minax*-group (Ami sp. 1-4—tentatively, denoting a group of species similar to ´*Argyrodes*´ *minax*, clearly distinct from other *Argyrodes*, but not well placed in existing genera), *Argyrodella* (Ard sp.1—tentatively, this monotypic genus is only known from the Seychelles), and an additional unknown genus (´Unk´).

Table 1. The distribution and abundance of the ten kleptoparasite species found among the studied three host webs (Arg, *Argyrodes*; Ard, *Argyrodella*; Ami, *Argyrodes minax* group; Unk, unknown). Cell-shading marks the relative abundance of kleptoparasite species for each host web.

Host	**Arg. 1**	**Arg. 2**	**Arg. 3**	**Arg. 4**	**Ard. 1**	**Ami. 1**	**Ami. 2**	**Ami. 3**	**Ami.4**	**Unk**	**Total**
Nephilingis	72 66.1 %	2 1.8 %	0 0 %	0 0 %	1 0.9 %	23 21.1 %	5 4.6 %	5 4.6 %	0 0 %	1 0.9 %	109
Caripetella	0 0 %	0 0 %	13 9.3 %	1 0.7 %	8 5.7 %	78 55.7 %	5 3.6 %	21 15.0 %	13 9.3 %	1 0.7 %	140
Anelosimus	0 0 %	0 0 %	4 6.0 %	0 0 %	0 0 %	32 47.8 %	12 17.9 %	0 0 %	4 6.0 %	15 22.4 %	67

3.2. Translocation experiments

Of the total 54 *Caripetella* native kleptoparasitic spiders introduced onto 10 *Nephilingis* webs, 15 left the web entirely, while 36 stayed in the host web vicinity, less than 5 cm from the support lines, sometimes connected to them with the kleptoparasite own lines, but none stayed on the host capture area. The *Nephilingis* host responded twice towards the introduced kleptoparasitic spiders by attacking and killing them.

Of the total 34 *Nephilingis* native kleptoparasites introduced onto seven *Caripetella* webs, three left the web entirely, 24 stayed on the host capture area, and seven stayed in the vicinity of the host web. The three spiders that left immediately were all large and presumed to belong to *Argyrodes* sp. 1. Many introduced kleptoparasitic spiders were observed moving onto the numerous vertical support threads of the *Caripetella* domed sheet webs. It was not always clear whether the spiders that migrated towards these upper vertical support threads were staying on them or on their own attached silk threads.

No response was recorded towards introduced kleptoparasitic spiders by *Caripetella* hosts.

While few details can be concluded from the translocation experiments, the behavior of introduced kleptoparasitic spiders clearly differs between the different host webs. None of the *Caripetella* native kleptoparasitic spiders introduced onto *Nephilingis* webs stayed on the web itself, while approximately 70% of the *Nephilingis* natives stayed on the *Caripetella* web. In addition, approximately 28% of native *Caripetella* left *Nephilingis* webs entirely, while approximately 9% of native *Nephilingis* left *Caripetella* webs.

3.3. Distribution of kleptoparasitic spiders among host webs.

Fisher's Exact Test with simulated p-values based on one million replicates revealed a significant difference in kleptoparasite species association with the three host web types ($p = 1\times10^{-6}$). These results suggest 1) webs of the three host species represent three different habitats, and 2) at least some kleptoparasite species show strong host-preferences.

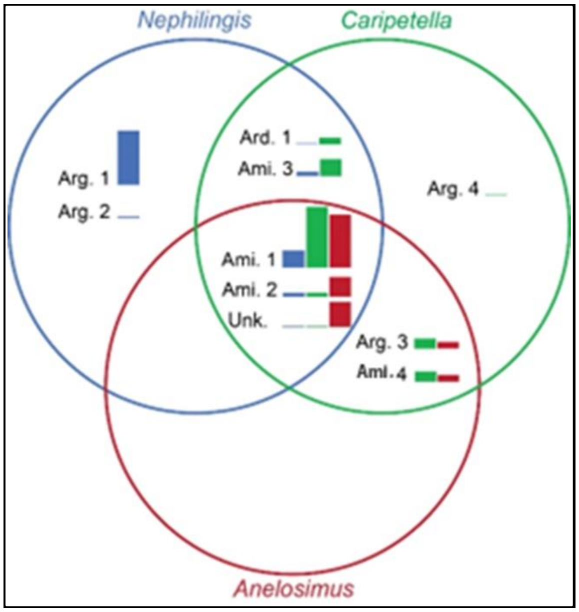

Figure 3. Distribution and overlap of kleptoparasitic species found on different host webs. Arg, *Argyrodes*; Ard, *Argyrodella*; Ami, *Argyrodes minax* group; Unk, unknown.

4. Discussion

4.1. Kleptoparasite diversity and distribution among host webs

This study, conducted in the small Analamazaotra National Park in Madagascar, investigates the distribution of kleptoparasitic argyrodine species among the webs of three host species. As a labor intense but brief student-driven field-course project, the study provides a unique, real-time snapshot of the distribution of an impressively diverse and endemic community of kleptoparasites, across contrasting webs of equally endemic hosts. The hosts include *Nephilingis livida*, a large, mostly nocturnal spider constructing a huge and sticky vertical orb web [47], *Caripetella madagascariensis*, an exclusively nocturnal giant nursery web spider that makes one of the world's largest horizontal domed sheet webs, and the cathemeral *Anelosimus* and *Dendrolycosa* form subsocial spider communities and construct three-dimensional tangle webs, whose numerous inhabitants—a mother and her offspring—are barely larger than the kleptoparasites [41]. Through direct sampling, and simple translocation experiments, we discovered a high diversity of kleptoparasite species and show that while generally versatile, kleptoparasites do distinguish among the different host webs.

Remarkably, at least ten argyrodine species were sampled in the webs of three host species (among a large number of potential local host species), along a 2.5 km linear transect. The study area represents less than 1/200.000th of this vast island, yet we sampled double the diversity of kleptoparasitic argyrodine spiders hitherto known from all of Madagascar. Furthermore, it appears that none of our ten species are among the Madagascar´s currently reported five. This observation underscores both the astounding biodiversity of Madagascar and the high conservation value of protected forests, even tiny patches. While remarkable, this discovery aligns with the reputation of Analamazaotra and the neighboring Mantadia National Parks as rich in spider diversity, e.g., as a world hotspot of the cosmopolitan *Anelosimus* spiders [43-44] and old world *Caerostris* spiders [48].

Kleptoparasite species composition and abundance differed significantly among host webs. Some kleptoparasites appear to be highly selective, for example, the most common kleptoparasite in *Nephilingis* webs, *Argyrodes* sp. 1, was absent in other host webs, and most other species were biased towards a particular host species (Fig. 3). One kleptoparasite species, *Amin* sp. 1, was common in all host webs (though most abundant in *Caripetella* webs), and some occurred in webs of two out of three hosts. While *Caripetella* and *Nephilingis* webs thus represent distinct habitats for kleptoparasites, each occupied by 7-8 argyrodine species, they also support a shared argyrodine community of five species.

Currently, it is impossible to know whether all kleptoparasite species found in a particular host web actively use these as resource sites. Given that some kleptoparasite species occur in low abundance it seems likely that, in search of preferred webs, they may occasionally wander into webs they do not use for resource stealth. This caveat aside, our results suggest that most kleptoparasite species are, to some degree, versatile and capable of utilizing a variety of (perhaps) suboptimal hosts. Notably, relatively few species seem to make use of *Anelosimus* webs. Only five of the ten detected species were found there, and all occurred in low abundance, averaging less than one individual per web. Yet one species, marked ´Unknown´, is almost exclusively found in subsocial webs of *Anelosimus* and *Dendrolycosa*. The relatively small size of *Anelosimus* webs may restrict kleptoparasite abundance, though a comparison between the size of 2D and 3D webs is not straightforward. Beyond that, parasitizing social webs inhabited by numerous, ever active, juvenile spiders not much larger than the kleptoparasites themselves, may require distinct behavioral adaptations compared to living in a web with a solitary giant nocturnal host.

Our translocation experiments provide further support for these patterns. For example, many individuals collected in one host web and introduced into a kleptoparasite-free web of another host, chose to leave. Notably, three *Argyrodes* sp. 1 individuals we could identify with some confidence in the field, were the only ones to immediately leave a *Caripetella* web when introduced. As *Argyrodes* sp. 1 was never found in *Caripetella* webs in nature, indicating the ability of this species to rapidly detect non-preferred host webs. Furthermore, the introduced kleptoparasitic spiders were generally more accepting of *Caripetella* webs than *Nephilingis* webs, reinforcing the prediction that kleptoparasites differentiate among hosts. Most *Caripetella* native kleptoparasitic spiders introduced onto *Nephilingis* webs stayed in their vicinity, although some were not found in *Nephilingis* webs in natural conditions, indicating that this nephilid might serve at least as a facultative host for most of kleptoparasitic species. However, these experiments were preliminary and must be interpreted with caution: they might have been impacted by external variables of an unpredictable rainforest habitat (e.g., wind and rain) and limited by our inability to monitor individual kleptoparasite species in the field. Furthermore, due to time constraints, we were unable to conduct control experiments by reintroducing *Caripetella* kleptoparasites to *Caripetella* webs and vice versa.

Taken together, our evidence supports that argyrodine kleptoparasites are generally versatile, but not randomly distributed or indifferent to host species. While these results may appear somewhat inconclusive, this likely simply reflects the complexity of the system—kleptoparsite species do not neatly fall into square categories such as ´specialist´ and ´generalist´. The current results align well with prior research and allow some general conclusions and promising avenues for future research. Attempting to fit argyrodines into categorical bins, e.g., host generalist vs. specialist, is tempting, but even for relatively choosy kleptoparasites [e.g., 8, 49-50], such boxes have proven to be ill-fitting [11-12, 38, 51-53]. Instead, argyrodines may better be characterized as generally capable of discriminating among host webs, but with varying degrees of astucity or concern. Prior research, focusing mostly on single kleptoparasitic species in isolation, has established that web architecture and prey availability are important factors in individual´s host choice [14, 32-33, 38, 49, 51, 54]. However, in diverse communities of kleptoparasite and host species, underlying mechanisms of host choice are, no doubt, more complex and interactive. Therefore, to understand the distribution of kleptoparasitic species in ecosystems, we need to address host choice at the level of community assembly.

Based on our findings and prior research, we here offer some speculative hypotheses that may serve to guide future research. First, some kleptoparasite species show minimal preference (e.g., *Argyrodes minax* group sp. 1 in this study), perhaps being species that are highly versatile and/or stealthy. Other species astutely choose hosts: For example, *Argyrodes* sp. 1 is the largest kleptoparasite in this study and may specialize on hosts that are the most likely to catch relatively large prey, such as nephilid spiders [55]. An alternative hypothesis, though not mutually exclusive, is that the observed distribution of kleptoparasites results from competition rather than microhabitat specialization. *Argyrodes* sp. 1 may, for example, have competitive advantage due to size and occupy the best habitat patches; Nephilidae appears to be the preferred argyrodine host globally. In a similar lane, the small and delicate ´Uknown´ species may prefer social nests or may be competitively inferior to other argyrodines and thus restricted to smaller and less favorable habitats.

Second, while ´*Argyrodes* sp. 1´ and ´*Argyrodes minax*-group sp. 1´ approximately exemplify opposite ends of the host-choice spectrum, being host-specialists and -generalists, respectively, we hypothesize that other species in this study, and perhaps most argyrodines, likely fall somewhere in between. Thus, deciphering the role of specialization vs competition in shaping kleptoparasite distribution among hosts is an urgent priority. Determining how argyrodine kleptoparasites locate host webs will be a critical segue into testing these hypotheses, as we first need an understanding of the mechanisms of web discovery and kleptoparasite determination of habitat suitability. The extent to which host choice is guided by host specific cues, such as airborne pheromones (that may operate both locally and at a distance, see supplementary data), should offer evidence on specific host choice. Insights into the role of intra-guild competition could, in turn, be gained by examining how kleptoparasites already present in an encountered web, impact further settlement into host webs.

In conclusion, our study shows that argyrodine kleptoparasites are apt at locating host webs and choosing among them. This choice, or more generally, the community assembly of kleptoparasite species into host webs, likely results from an interplay of host-specialization and interspecific competition. We predict that host-specific chemicals (likely pheromones in silk, M. Elgar pers. comm.) inform the kleptoparasites on host choice and speculate that sensory adaptations stemming from an existing system guiding male spiders to conspecific female webs, have played a role in the evolution of web kleptoparasites. This fascinating and accessible study system of giant hosts and tiny thieves occurring in highly distinct habitats—large spider webs—remains poorly investigated while offering a wealth of opportunities for topical research including foraging/game theory, coevolution, diversification, and the role of assembly rules in community structuring. To facilitate such studies, fundamental field research is needed on the diversity and degree of specialization of web kleptoparasites (both in host choice and foraging mode), as are basic laboratory experiments on pheromones and other cues that play a role in kleptoparasite web detection and choice.

Data availability

COI barcoding sequences will be submitted to GenBank (in progress). Other data are available from the authors.

Conflicts of Intersest

The authors declare no conflict of interest regarding the publication of this paper.

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References

1. Leung, T. L. F., & Poulin, R. (2008). Parasitism, commensalism, and mutualism: Exploring the many shades of symbioses. *Vie et Milieu / Life & Environment, 2008, pp.107-115.*
2. Campbell, N. A., & Reece, J. B. (2005). *Biology* (7th ed.). San Francisco, CA: Pearson Benjamin Cummings.
3. Odum, E. P., & Barrett, G. W. (2005). Fundamentals of Ecology (5th ed.). Belmont, CA: Thomson Brooks/Cole.
4. Solomon, E. P., Berg, L. R., & Martin, D. W. (2005). *Biology*. 7th Edition. Belmont, CA: Brooks/Cole-Thomson Learning.
5. Elgar, M. A. (1993). Inter-specific associations involving spiders: Kleptoparasitism, mimicry, and mutualism. *Memoirs of the Queensland Museum*, 33, 411–430.
6. Iyengar, E. V. (2008). Kleptoparasitic interactions throughout the animal kingdom and a re-evaluation, based on participant mobility, of the conditions promoting the evolution of kleptoparasitism. *Biological Journal of the Linnean Society*, 93(4), 745–762.
7. Brockmann, H. J., & Dawkins, R. (1979). Joint nesting in a digger wasp as an evolutionarily stable preadaptation to social life. *Behavioral Ecology and Sociobiology*, 4(4), 283–322.
8. Vollrath, F. (1984). Kleptobiotic interactions in invertebrates. *Annual Review of Ecology and Systematics*, 15, 245–269.
9. Vollrath, F. (1987). Kleptobiosis in spiders. In W. Nentwig (Ed.), Ecophysiology of Spiders (pp. 274–286). Springer-Verlag
10. Grostal, P., & Walter, D. E. (1997). Kleptoparasites or commensals? Effects of *Argyrodes antipodianus* (Araneae: Theridiidae) on *Nephila plumipes* (Araneae: Tetragnathidae). *Oecologia*, 111(4), 570–574.
11. Whitehouse, M. E. A. (2011). Kleptoparasitic spiders of the subfamily Argyrodinae: A special case of behavioural plasticity. In M. E. Herberstein (Ed.),

Spider Behaviour: Flexibility and Versatility (pp. 348–374). Cambridge University Press.

12. Whitehouse, M. E. A., Agnarsson, I., Miyashita, T., Smith, D. R., Cangialosi, K., Masumoto, T., Li, D., Hénaut, Y. (2002). *Argyrodes*: Phylogeny, sociality, and interspecific interactions: A report on the *Argyrodes* symposium, Badplaas 2001. *Journal of Arachnology*, 30(2), 297–306.
13. Agnarsson, I. (2004). Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). *Zoological Journal of the Linnean Society, 141*(4), 447–626.
14. Miyashita, T. (2002). Population dynamics of two species of kleptoparasitic spiders under different host availabilities. *The Journal of Arachnology*, 30(1), 31–38.
15. Vollrath, F. (1979). Behaviour of the kleptoparasitic spider Argyrodes elevatus (Araneae, Theridiidae). Animal Behaviour, 27(2), 515–521.
16. Kuntner, M., & Agnarsson, I. (2010). Web gigantism in Darwin's bark spider, a new species from Madagascar (Araneidae: *Caerostris*). *Journal of Arachnology*, 38(2), 346–356.
17. Leborgne, R., Cantarella, T., & Pasquet, A. (1998). Colonial life versus solitary life in *Cyrtophora citricola* (Araneae, Araneidae). *Insectes Sociaux*, 45(2), 125–135.
18. Hénaut, Y. (2000). Host selection by a kleptoparasitic spider. *Behavioral Ecology and Sociobiology*, 48(3), 288–293.
19. Cruz Da Silva, E. L., & Sierwald, P. (2013). On three monotypic nursery web spider genera from Madagascar with first description of the male of *Tallonia picta* Simon, 1889 and redescription of the type-species of *Paracladycnis* Blandin, 1979 and *Thalassiopsis* Roewer, 1955 (Araneae: Lycosoidea: Pisauridae). *Zootaxa*, 3647(4), 501–528.
20. Lloyd, N. J., & Elgar, M. A. (1997). Costs and benefits of facultative aggregating behaviour in the orb-spinning spider *Gasteracantha minax* Thorell (Araneae: Araneidae). *Austral Ecology*, 22(4), 371–376.

21. McCrate, A., & Uetz, G. W. (2010). Kleptoparasites: A twofold cost of group living for the colonial spider, *Metepeira incrassata* (Araneae, Araneidae). *Behavioral Ecology and Sociobiology*, 64(3), 389–399.
22. Exline, H. & Levi, H. W. (1962). American spiders of the genus Argyrodes (Araneae, Theridiidae). Bulletin of the Museum of Comparative Zoology 127: 75-204.
23. Vanuytven, H., Jocqué, R. & Deeleman-Reinhold, C. (2024). Two new theridiid genera from Southeast Asia (Araneae: Theridiidae, Argyrodinae): males with a nose for courtship. *Journal of the Belgian Arachnological Society* 39(1, supplement): 1-96.
24. *World Spider Catalog.* (2024). *version 25.5.* Natural History Museum of Bern. Retrieved from https://wsc.nmbe.ch
25. Miyashita, T., Maezono, Y., & Shimazaki, A. (2004). Silk feeding as an alternative foraging tactic in a kleptoparasitic spider under seasonally changing environments. *Journal of Zoology*, 263(3), 297–303
26. MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, 100(916), 603–609
27. Gotelli, N. J. (2008). *A Primer of Ecology* (4th ed.). Sunderland, MA: Sinauer Associates.
28. Gregorič, M., Quiñones-Lebrón, S. G., Kuntner, M., & Agnarsson, I. (2024). Exploring resource patch occupancy: Patch size, but not connectivity, explains the abundance of spider kleptoparasites in golden orb webs. *Ecological Monographs*, 94(1), e1523.
29. Vinson, A. (1863). *Aranéides des îles de la Réunion, Maurice et Madagascar*. Librairie Encyclopédique de Roret.
30. Exline, H. (1945). *Spiders of the Genus Conopistha (Theridiidae, Conopisthinae) from Northwestern Peru and Ecuador*. Annals of the Entomological Society of America, 38(1), 505-528.
31. Agnarsson, I. (2003). Spider webs as habitat patches—the distribution of kleptoparasites (*Argyrodes*, Theridiidae) among host webs (*Nephila*, Tetragnathidae). Journal of Arachnology, 31(3), 344-349.

32. Cangialosi, K. R. (1990). *Life Cycle and Behavior of the Kleptoparasitic Spider, Argyrodes Ululans (Araneae, Theridiidae)*. *Journal of Arachnology*, 18(1), 347-358.
33. Eberhard, W. G., Platnick, N. I., & Schuh, R. T. (1993). *Natural history and systematics of arthropod symbionts (Araneae, Hemiptera, Diptera) inhabiting webs of the spider Tengella radiata (Araneae, Tengellidae)*. *American Museum Novitates*, 3065, 1-17.
34. Whitehouse, M. E. A., & Jackson, R. R. (1993). Group structure and time budgets of *Argyrodes antipodiana* (Araneae, Theridiidae), a kleptoparasitic spider from New Zealand. *New Zealand Journal of Zoology*, 20(3), 201–206.
35. Grostal, P., & Walter, D. E. (1999). Host specificity and distribution of the kleptobiotic spider *Argyrodes antipodianus* (Araneae, Theridiidae) on orb webs in Queensland, Australia. *Austral Ecology*, 24(1), 70–80.
36. Tso, I. M., & Severinghaus, L. L. (1998). Silk stealing by *Argyrodes lanyuensis* (Araneae: Theridiidae): A unique form of kleptoparasitism. *Animal Behaviour*, 56(1), 219-225.
37. Hénaut, Y., Delme, J., Legal, L., & Williams, T. (2005). Host selection by a kleptobiotic spider. *Naturwissenschaften*, 92(2), 95-99.
38. Baba, Y. G., Walters, R. J., Miyashita, T. (2007). Host-dependent differences in prey acquisition between populations of a kleptoparasitic spider *Argyrodes kumadai* (Araneae: Theridiidae). *Ecological Entomology*, 32(2), 38-44.
39. Grostal, P. (1999). Five species of kleptobiotic *Argyrodes* Simon (Theridiidae: Araneae) from eastern Australia: descriptions and ecology with special reference to southeastern Queensland. *Memoirs of the Queensland Museum* 43: 621-638
40. Lenz, H. (1886). Beiträge zur Kenntniss der Spinnenfauna Madagascars. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 14, 375–422.
41. Kuntner, M., & Agnarsson, I. (2011). Biogeography and diversification of hermit spiders on Indian Ocean islands (Nephilidae: Nephilengys). *Molecular Phylogenetics and Evolution*, 59(2), 477–488.

42. Agnarsson, I., & Kuntner, M. (2005). Madagascar: an unexpected hotspot of social *Anelosimus* spider diversity (Araneae: Theridiidae). *Systematic Entomology*, 30(4), 575–592.
43. Agnarsson, I., Jencik, B. B., Veve, G. M., Hanitriniaina, S., Agostini, D., Goh, S. P., & Kuntner, M. (2015). Systematics of the Madagascar *Anelosimus* spiders: Remarkable local richness and endemism, and dual colonization from the Americas. *Invertebrate Systematics, 29*(1), 1–19.
44. Agnarsson, I., LeQuier, S. M., Kuntner, M., Cheng, R.-C., Coddington, J. A., & Binford, G. J. (2016). Phylogeography of a good Caribbean disperser: *Argiope argentata* (Araneae, Araneidae) and a new cryptic species from Cuba. *ZooKeys, 625*, 25–44
45. Rosales-García, R., Tapia-McClung, H., Narendra, A., & Rao, D. (2021). Many paths, one destination: Mapping the movements of a kleptoparasitic spider on the host's web. *Journal of Comparative Physiology A*, 207(2), 293–301.
46. RStudio Team (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL http://www.rstudio.com/.
47. Gregorič, M., Agnarsson, I., Blackledge, T. A., & Kuntner, M. (2011). Darwin's bark spider: Giant prey in giant orb webs (*Caerostris darwini*, Araneae: Araneidae). *Journal of Arachnology, 39*(3), 287–295.
48. Gregorič, M., Agnarsson, I., Blackledge, T. A., & Kuntner, M. (2015). Phylogenetic position and composition of Zygiellinae and *Caerostris*, with new insight into orb-web evolution and gigantism. *Biological Journal of the Linnean Society, 115*(1), 58–72.
49. Whitehouse, M. E. A. (1986). The foraging behaviours of *Argyrodes antipodiana* (Theridiidae), a kleptoparasitic spider from New Zealand. *Behavioral Ecology and Sociobiology, 19*(2), 73–79.
50. Su, Y.-C. (2012). *A gang of thieves: Evolution of cooperative kleptoparasitism in the subfamily Argyrodinae (Araneae: Theridiidae)* (Doctoral dissertation). University of Kansas, Lawrence, KS

51. Larcher, S. F., & Wise, D. H. (1985). Experimental studies of the interactions between a web-invading spider and two host species. *Journal of Arachnology, 13*(1), 43–59.
52. Downes, M. F. (1995). Australasian social spiders: What is meant by "social"? *Records of the Western Australian Museum, Supplement*, 52, 25–32
53. Su, Y.-C., & Smith, D. R. (2014). Evolution of host use, group-living and foraging behaviours in kleptoparasitic spiders: Molecular phylogeny of the Argyrodinae (Araneae: Theridiidae). *Invertebrate Systematics*, 28(4), 375–388.
54. Koh, T. H., & Li, D. (2003). State-dependent prey type preferences of a kleptoparasitic spider *Argyrodes flavescens* (Araneae: Theridiidae). *Animal Behaviour, 260(3):227-233*
55. Nyffeler, M., & Gibbons, J. W. (2022). Spiders feeding on vertebrates is more common and widespread than previously thought, geographically and taxonomically. *Journal of Arachnology, 50*(1), 121-134.