The Science of Nature (2026) 113:82
https://doi.org/10.1007/s00114-026-02129-9

CORRESPONDENCE

Gone with the wind: wind-induced web movement reduces kleptoparasite abundance in a golden orbweaver spider

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Received: 24 May 2026 / Revised: 18 June 2026 / Accepted: 23 June 2026

Abstract
Obligate kleptoparasitic spiders (Argyrodinae, Theridiidae) live as thieves in the webs of larger hosts. Web size has long stood above all other variables in predicting how many kleptoparasites occupy a given web, best documented in the large orb webs of golden orb-weavers (Nephilidae). Yet no study has asked whether wind—a ubiquitous force acting on every aerial web—also influences kleptoparasite abundance. Prompted by the observation that exposed, wind-buffeted webs of *Trichonephila inaurata* in the spiny forest of Ifaty, southwestern Madagascar, appeared to carry fewer kleptoparasites than sheltered webs of similar size, we conducted a rapid, intensive survey of 60 webs along two transects in a single afternoon. We quantified wind effect as the maximum lateral sway of the web hub over one minute, controlling for web area. We found a strong negative effect of wind-induced web movement on kleptoparasite number; trumping the positive effect of web size. Wind effect thus emerges as a previously unrecognized axis structuring the distribution of spider kleptoparasites.

Keywords Argyrodinae · Kleptoparasitism · *Trichonephila* · Wind · Web movement · Ideal free distribution · Madagascar

Introduction

Kleptoparasitic animals steal extrinsic resources, like food, from their hosts (Iyengar 2008; Agnarsson 2025). This foraging strategy is found across the animal tree of life, most commonly as an opportunistic complement to own foraging, but is sometimes obligatory (Brockmann and Barnard 1979; Iyengar 2008). Obligate kleptoparasitism typically involves animals that are smaller than their hosts and rely on stealth to go unnoticed (Brockmann and Barnard 1979; Vollrath 1984; Iyengar 2008). Optimal foraging theory predicts kleptoparasites should balance seeking quality 'hosts' while minimizing predation risk and competition. This optimization impacts the spatial distribution of kleptoparasitic organisms. Hence, many kleptoparasites, like spiders, are distributed approximately in accordance with the Ideal Free Distribution, predicting that individuals move among habitat patches (hosts in this case) to maximize individual fitness (Fretwell and Lucas 1969; Reding et al. 2016; Gregorič et al. 2024).

Spider kleptoparasitism—the theft of resources from the webs of larger spiders—is among the most elaborate exploitative strategies known in arthropods. Its textbook exemplar is the theridiid subfamily Argyrodinae, a group of small "dewdrop" spiders whose members glean trapped insects, steal wrapped prey bundles, feed on host silk, and in some lineages attack and consume the host, its offspring, or eggs (Vollrath 1979, 1984, 1987; Elgar 1993; Whitehouse 2011; Agnarsson 2025; Agnarsson and Coddington, submitted). The behavioural repertoire (Vollrath 1987; Whitehouse 2011), host choice and specificity (Larcher and Wise 1985; Cangialosi 1997; Grostal and Walter 1999; Hénaut et al. 2005), impact on host fitness (Rypstra 1981; Grostal and

Communicated by José Eduardo Serrão

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Published online: 08 July 2026

Walter 1997), and use of host webs as a model system for producer-consumer and patch-occupancy theory (Higgins and Buskirk 1998; Agnarsson 2003, 2011; Gregorič et al. 2024) have all received sustained attention. Early studies noted that larger host webs had more kleptoparasites (e.g. Robinson and Robinson 1973) and the scaling of kleptoparasite abundance with web size has been confirmed in several studies, especially in nephilid hosts (Grostal and Walter 1997; Agnarsson 2003, 2011; Kuntner et al. 2019; Gregorič et al. 2024). The relationship is so consistent, and host webs so discrete and easily measured, that individual webs have been adopted as natural "habitat patches" in field tests of patch-occupancy and ideal-free-distribution models (Agnarsson 2011; Gregorič et al. 2024). Among these factors, web size has emerged as the primary explanation of kleptoparasite abundance in spiders: above connectivity, isolation, host size, and host identity.

To our knowledge, no study, hypothesis, or even passing remark has considered whether wind affects kleptoparasite abundance. The omission is striking, the more so because wind demonstrably shapes the architecture and material properties of the webs themselves (Krink and Vollrath 2000; Liao et al. 2009), the very habitat patches the kleptoparasites occupy. Further, wind represents mechanical stress that may make it more difficult for small spiders to shelter and move about in the web, and wind may also make web discovery more challenging by rapidly diluting host pheromones.

During fieldwork in the dry spiny forest near Ifaty, southwestern Madagascar, we encountered dense populations of the golden orb-weaver *Trichonephila inaurata* (Walckenaer 1841) (Nephilidae), persisting in unusually open and wind-exposed conditions. Like in other *Trichonephila*, *T. inaurata* females are giants relative to males, and build large orb webs that capture a variety of prey types (Kuntner et al. 2019). Casual, unstructured inspection of these webs left a clear impression: among webs of comparable size, those swaying most vigorously in the wind tended to carry fewer kleptoparasites than nearby, more sheltered webs. The pattern was suggestive enough to test the hypothesis that greater wind-induced web movement is associated with lower kleptoparasite abundance.

Methods

To test the hypothesis that wind negatively affects kleptoparasite abundance, six observers, working for three hours over a single afternoon, surveyed 60 female (subadults and adults) *T. inaurata* webs spanning a wide range of sizes and degrees of wind exposure. The study was made in a coastal dry spiny forest near Toliara, southwestern Madagascar (23,2089° S, 43,6227° E, alt 3 m) on May 16, 2026, between 14:00–18:00 (Supplementary Figs. 1–2).

Because wind conditions change from hour to hour and day to day, as do prey availability and the activity of the kleptoparasites themselves, our short, intensive snapshot, in which every web is scored within a single narrow time window, holds these conditions approximately constant across the entire sample.

We surveyed webs along two semi-linear transects, running in parallel ~ 10–20 m apart, scoring every encountered web above a minimum size threshold. Webs < 25 cm in diameter were omitted because fewer than 50% of such small webs hold kleptoparasites (Agnarsson and Coddington submitted). For each web, we recorded the maximum width and height of the capture area (cm), the dimensions of any barrier web, the number of argyrodine kleptoparasites present, and wind exposure. Wind exposure was quantified as the maximum lateral sway of the web hub observed over a one-minute period (in cm), estimated using measuring-tape, a simple field proxy that integrates both ambient wind and the web's exposure and compliance. Web capture area was estimated as an ellipse, $A = \pi(w/2)(h/2)$ (Blackledge and Gillespie 2002). The number of argyrodine individuals in webs at the time of inspection were direct counts (Agnarsson 2011). Small and flimsy barrier webs were found only in less than 10 of the webs and were not considered in the model.

Across the 60 webs, kleptoparasite counts were overdispersed (variance/mean = 2.4) with 28% of webs unoccupied. We modeled counts as a function of log web area and hub sway using a negative binomial generalized linear model (log link), which had the lowest Akaike Criterion (AIC = 233.0) among candidate models (Poisson 246.0; zero-inflated Poisson 234.2), as the fitted dispersion ($\alpha = 0.45$) already accommodates the unoccupied webs. The two transects did not differ in web area, sway, or count (Mann–Whitney U, all $p > 0.1$) and were pooled. All analyses were carried out in Python 3.12 (statsmodels 0.14.6; Seabold and Perktold 2010), with coefficient uncertainty assessed by Wald tests and a 5,000-replicate nonparametric bootstrap (Davison and Hinkley 1997).

Results and discussion

As expected, web area had a strong positive effect on kleptoparasite number ($\beta = +0.78$ per natural-log unit of area; $p = 0.008$). Independently of area, hub sway had a significant negative effect ($\beta = -0.096$ per cm; incidence rate ratio = 0.91 per cm, 95% confidence interval 0.85–0.97; $p = 0.003$): each additional centimeter of web sway was associated with roughly a 9% reduction in expected kleptoparasite number, such that a web swaying 10 cm carried about 60% fewer kleptoparasites than an otherwise identical, near-stationary web of the same size (Fig. 1). A nonparametric bootstrap (5000 resamples) placed the probability that the wind effect is negative at 0.999.

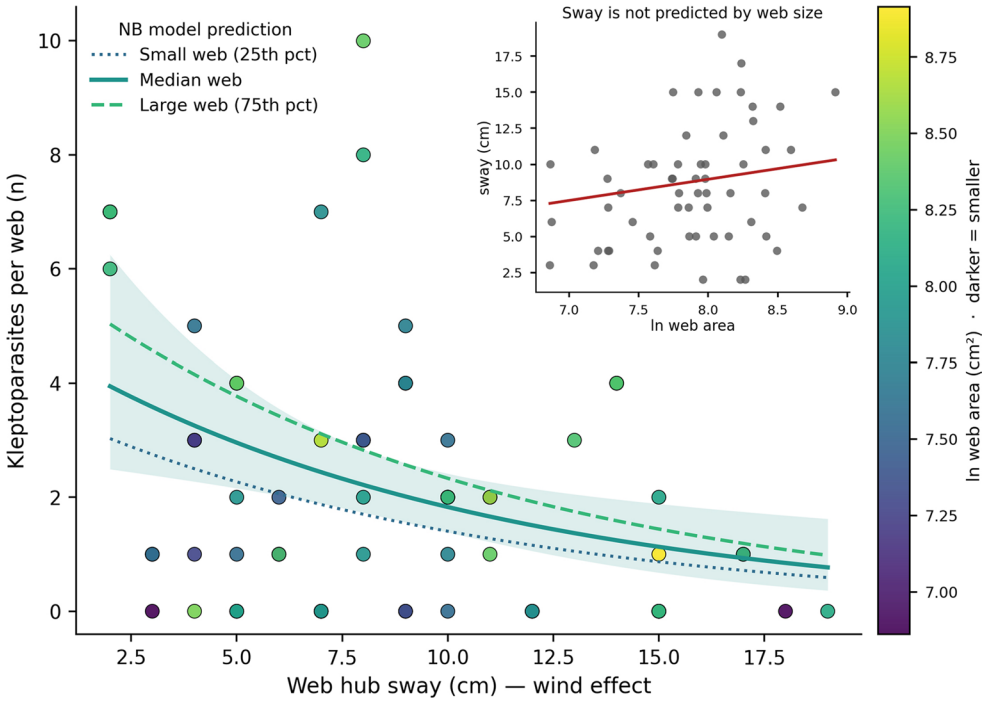

Fig. 1 Kleptoparasite number per web of *Trichonephila inaurata* ($n = 60$) as a function of web hub sway (wind effect). Wind (hub sway) independently reduces kleptoparasite abundance after controlling for web size. Points are individual webs, colored by log web area (darker = smaller). Curves are negative binomial model predictions for small (25th percentile), median, and large (75th percentile) webs; the shaded band is the 95% confidence interval for the median-area prediction. Kleptoparasite abundance declines with wind-induced web movement at every web size and wind has greater effect on abundances than web size. Web sway and web size do not interact ($R^2 = 0.03$, $p = 0.21$)

Wind-induced web movement thus emerges as a second, independent axis structuring kleptoparasite distributions, acting alongside, though slightly trumping in magnitude, the long-recognized effect of web size. Further, wind exposure negatively impacts kleptoparasite abundance similarly across the observed web sizes (Fig. 1). Several non-exclusive mechanisms could generate this pattern: kleptoparasites may actively avoid settling on mobile webs, may be dislodged from oscillating webs more often, may forage less efficiently on a heaving substrate due to impaired locomotion and the disruption of vibrational prey-detection, or mobile webs may themselves capture or retain less prey and so support fewer thieves. A single snapshot cannot distinguish these, and we note the usual caveats of an observational study at one locality: hub sway may co-vary with web height, canopy openness, or host body mass and condition, and "movement" as we measured it conflates wind strength with web compliance. Nonetheless, the effect is large, statistically robust, and recovered after controlling for the dominant known predictor.

Whereas web size and connectivity describe, respectively, the resource value and accessibility of a patch, wind exposure introduces a distinct, abiotic axis of patch quality, a cost that can devalue an otherwise large, prey-rich web. The ideal-free distribution is a purely resource-based framework, but can be extended to incorporate environmental costs, like wind. A direct future test of the impact of wind would be to examine the impact of alternating wind direction on static webs through time, predicting that the cost of wind would move among webs as different wind direction will expose differently angled webs.

Wind therefore deserves a place among the variables considered in the ecology of spider kleptoparasites — and, more broadly, in the patch-occupancy and ideal-free-distribution frameworks for which web-dwelling commensal systems have become a model (Higgins and Buskirk 1998; Agnarsson 2011; Gregorič et al. 2024). That a force as pervasive as wind should have gone entirely unremarked in this otherwise intensively studied system underscores how much basic natural history remains to be done, even in textbook exemplars.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00114-026-02129-9.

Acknowledgements We thank the MICET crew in Antananarivo, Madagascar, who assisted with research permits and we especially thank Razafindratsita Vololontiana "Tiana" and Harin' Hala Rasolondalao "Rin'ha" for help with logistics.

Author contributions IA and MG conceived and designed the study. IA analyzed the data and wrote the manuscript. All authors carried out the experiment and revised the manuscript.

Funding This research was supported by the University of Iceland and the Slovenian Research and Innovation Agency (grants P1-0236, J1-60005).

Data availability Raw data is provided in Supplementary Material S1.

Declarations

Competing interests The authors declare no competing interests.

References

Agnarsson I (2003) Spider webs as habitat patches — the distribution of kleptoparasites (*Argyrodes*, Theridiidae) among host webs (*Nephila*, Tetragnathidae). J Arachnol 31:344–349. https://doi.org/10.1636/s02-21

Agnarsson I (2011) Habitat patch size and isolation as predictors of occupancy and number of argyrodine spider kleptoparasites in *Nephila* webs. Naturwissenschaften 98:163–167. https://doi.org/10.1007/s00114-010-0750-3

Agnarsson I (2025) Spiders as superhosts and secondary kleptoparasites. Front Arachn Sci 4:1544428. https://doi.org/10.3389/frchs.2025.1544428

Agnarsson I, Coddington JA (submitted) Stealing from giants (eds) a comprehensive treatment of obligate kleptoparasitism in spiders

Blackledge TA, Gillespie RG (2002) Estimation of capture areas of spider orb webs in relation to asymmetry. J Arachnol 30:70–77. https://www.jstor.org/stable/3706177

Brockmann HJ, Barnard CJ (1979) Kleptoparasitism in birds. Anim Behav 27:487–514. https://doi.org/10.1016/0003-3472(79)90185-4

Cangialosi KR (1997) Foraging versatility and the influence of host availability in *Argyrodes trigonum* (Araneae, Theridiidae). J Arachnol 25:182–193. https://www.jstor.org/stable/3705643

Davison AC, Hinkley DV (1997) Bootstrap methods and their application. Cambridge University Press

Elgar MA (1993) Inter-specific associations involving spiders: kleptoparasitism, mimicry and mutualism. Mem Qld Mus 33:411–430

Fretwell SD, Lucas HL (1969) On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheor 19:16–36. https://doi.org/10.1007/BF01601953

Gregorič M, Quiñones-Lebrón SG, Kuntner M, Agnarsson I (2024) Exploring resource patch occupancy: patch size, but not connectivity, explains the abundance of spider kleptoparasites in golden orb webs. J Zool 324:244–252. https://doi.org/10.1111/jzo.13212

Grostal P, Walter DE (1997) Kleptoparasites or commensals? Effects of *Argyrodes antipodianus* (Araneae: Theridiidae) on *Nephila plumipes* (Araneae: Tetragnathidae). Oecologia 111:570–574. https://doi.org/10.1007/s004420050273

Grostal P, Walter DE (1999) Host specificity and distribution of the kleptobiotic spider *Argyrodes antipodianus* (Araneae, Theridiidae) on orbwebs in Queensland. J Arachnol 27:522–530. https://www.jstor.org/stable/3706051

Hénaut Y, Delme J, Legal L, Williams T (2005) Host selection by a kleptobiotic spider. Naturwissenschaften 92:95–99. https://doi.org/10.1007/s00114-004-0597-6

Higgins LE, Buskirk RE (1998) Spider-web kleptoparasites as a model for studying producer–consumer interactions. Behav Ecol 9:384–387. https://doi.org/10.1093/beheco/9.4.384

Iyengar EV (2008) Kleptoparasitic interactions throughout the animal kingdom and a re-evaluation, based on participant mobility, of the conditions promoting the evolution of kleptoparasitism. Biol J Linn Soc 93:745–762. https://doi.org/10.1111/j.1095-8312.2008.00954.x

Krink T, Vollrath F (2000) Optimal area use in orb webs of the spider *Araneus diadematus*. Naturwissenschaften 87:90–93. https://doi.org/10.1007/s001140050017

Kuntner M et al (2019) Golden orbweavers ignore biological rules: phylogenomic and comparative analyses unlock the evolution of extreme sexual size dimorphism. Syst Biol 68:555–572. https://doi.org/10.1093/sysbio/syy082

Larcher SF, Wise DH (1985) Experimental studies of the interactions between a web-invading spider and two host species. J Arachnol 13:43–59

Liao C-P, Chi K-J, Tso I-M (2009) The effects of wind on trap structural and material properties of a sit-and-wait predator. Behav Ecol 20:1194–1203. https://doi.org/10.1093/beheco/arp119

Reding I, Kelley M, Rowell JT, Rychtář J (2016) A continuous ideal free distribution approach to the dynamics of selfish, cooperative and kleptoparasitic populations. R Soc Open Sci 3:160788. https://doi.org/10.1098/rsos.160788

Robinson MH, Robinson B (1973) Ecology and behavior of the giant wood spider Nephila maculata (Fabricius) in New Guinea. Smithson Contrib Zool 149:1–76. https://doi.org/10.5479/si.00810282.149

Rypstra AL (1981) The effect of kleptoparasitism on prey consumption and web relocation in a Peruvian population of the spider *Nephila clavipes*. Oikos 37:179–182. https://www.jstor.org/stable/3544463

Seabold S, Perktold J (2010) Statsmodels: Econometric and statistical modeling with Python. In Proceedings of the 9th Python in Science Conference:57–61

Vollrath F (1979) Behaviour of the kleptoparasitic spider *Argyrodes elevatus* (Araneae: Theridiidae). Anim Behav 27:519–521. https://doi.org/10.1016/0003-3472(79)90186-6

Vollrath F (1984) Kleptobiotic interactions in invertebrates. In: Barnard CJ (ed) Producers and scroungers: strategies of exploitation and parasitism. Croom Helm, London, pp 61–66

Vollrath F (1987) Kleptobiosis in spiders. In: Nentwig W (ed) Ecophysiology of spiders. Springer, Berlin, pp 274–286

Walckenaer CA (1841) Histoire naturelle des Insects. Aptères. Tome deuxième. Roret, Paris. https://doi.org/10.5962/bhl.title.61095

Whitehouse MEA (2011) Kleptoparasitic spiders of the subfamily Argyrodinae: a special case of behavioural plasticity. In: Herberstein ME (ed) Spider behaviour: flexibility and versatility. Cambridge University Press, Cambridge, pp 348–386