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ORIGINAL PAPER

Many paths, one destination: mapping the movements of a kleptoparasitic spider on the host's web

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Abstract

Kleptoparasitic spiders live and forage in the webs of other spiders. Using vibratory cues generated by the host spider during prey capture, they leave their resting positions in the upper peripheries of the host web and move towards the centre of the web where they feed along with the host spider or steal small pieces of prey. While the triggers for initiating the foraging raids are known, there is little information about the fine-scale trajectory dynamics in this model system. We mapped the movement of the kleptoparasite *Argyrodes elevatus* in the web of the host *Trichonephila clavipes*. We filmed the movement of the kleptoparasite spiders and quantified the trajectory shape, speed, heading directions and path revisitation. Our results show that kleptoparasitic spider movement is spatially structured, with higher levels of speed at the peripheries and slower in the centre of the web. We found a high level of variation in trajectory shapes between individuals. We found that the majority of heading orientations were away from the hub suggesting that detouring or repeated approaches are an essential component of kleptoparasite movement strategies. Our results of the revisitation rate also confirm this pattern, where locations close to the hub were revisited more often than in the periphery. The kleptoparasite–host spider system is a promising model to study fine-scale movement patterns in small bounded spaces.

Keywords Locomotion · *Argyrodes* · Kleptoparasitism · Trajectory shape · Dynamic time warp

Introduction

Animals move to and between locations of interest to find food, shelter or mates. Foraging movements are mediated by prey availability, suitability of terrain and the animal's perception of cues such as visual, olfactory or vibratory signals. Movement between these locations of interest occurs at different spatial scales: over several hundreds of kilometres [e.g., monarch butterflies, (Reppert and de Roode 2018)], over tens of meters [e.g., ants, (Narendra 2020); amblypygids, (Wiegmann et al. 2016)], and also at the small scale of a few centimetres [e.g., fiddler crabs, (Layne et al. 2003)]. This last group is particularly interesting since the entire behavioural repertoire with respect to movement can occur within a small-scale self-contained system [~ bonsai systems, sensu (Hemmi and Zeil 2005)]. Such bonsai systems are ideal for navigation studies since the behaviour can be recorded in exceptional detail [e.g., learning flights and walks in wasps (Collett and Zeil 1996) and ants (Zeil and Fleischmann 2019)] and the information available to the animals can be reconstructed accurately (Stürzl et al. 2015).

A particularly interesting bonsai system is that of tiny kleptoparasitic spiders that live in the webs of other spiders; they use the host's web as their habitat (Agnarsson 2003) and depend on the host's prey capture abilities for nourishment. There is wide variation in the behavioural repertoire in these spiders, ranging from gleaning, stealing food bundles, feeding with host, silk stealing, attacking the host and catching insects with a net (Whitehouse et al. 2002; Hénaut et al. 2005). Most kleptoparasitic spiders occur in the family Theridiidae, especially in the group Argyrodinae, and these species show a range of specialisations from a completely araneophagic lifestyle to obligatory symbiont on the host (Vollrath 1984). Though

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kleptoparasitism is taxonomically widespread in the animal kingdom, attention has largely been focussed on birds (Iyengar 2008). Among the conditions that give rise to kleptoparasitism, the following three factors are important in the context of locomotion: (1) the host transports or stores the food item, (2) the habitat allows for the transmission of cues and (3) the kleptoparasites can detect these cues (Iyengar 2008). In the kleptoparasite spider system, the host usually carries the prey back to the hub or stores it for later consumption in the web itself and the host's web transmits vibratory cues that are received by the kleptoparasites (Vollrath 1979b).

Kleptoparasitic spider movement is unique and distinct from other arthropods since the spider uses the host's own web as the terrain (Gaffin and Curry 2020). Since they are small in size relative to the host, their own movements produce little or no vibrations that can alert the host to their presence. Their resting position is usually on the outskirts of the host web amidst a tangle of ancillary barrier threads, and their risk increases as they make their way to the centre of the web. However, these spiders can escape an attack from the host by leaving the plane of the host web and dangle with a dragline silk thread, thereby staying out of reach of the host spider (Vollrath 1979a). Kleptoparasitic spiders can use the host web to navigate as well as their own dragline silk. During feeding with the host spider, their greatest risk is when the host spider is wrapping the prey for later consumption.

The kleptoparasitic spider *Argyrodes elevatus* shows two kinds of raiding patterns in the webs of *Trichonephila clavipes* [previously *Nephila clavipes*: Araneae: Nephilidae; Kuntner et al. (2019)]: the kleptoparasites may either head towards the hub when the first prey is caught and wrapped or to the prey caught subsequently (Vollrath 1979a). In these raids, *A. elevatus* attempts to steal food packets away from the host spider, but a third strategy—especially when the prey is too large to be stolen—is to feed with the spider. The trigger for initiating these raids is the characteristic vibration caused by the host spider as it wraps the prey item (Vollrath 1979b).

However, there is no information on the fine-scale structure of the foraging trajectories used by kleptoparasitic spiders to reach the center of the web. For example, do the kleptoparasites seek to minimise travel time by heading to the hub in a straight line, or do they minimise risk using detours and circuitous routes? Do kleptoparasites use similar movement strategies in different parts of the web? In this study, we explored the movement patterns of the kleptoparasitic spiders in their host web at a fine scale. We filmed the movement of the kleptoparasite and the host on the same web after a prey was caught in the web. We asked whether, (a) there are similarities in routes between the kleptoparasitic individuals, and (b) individuals change their movement strategy with respect to their spatial location in the web.

Methods

Study species

Argyrodes elevatus (~ 4 mm, Fig. 1) is a kleptoparasitic spider found inhabiting the webs of several orb-web spiders (Vollrath 1979a). We used *T. clavipes* as the host spider. *T. clavipes* is a large spider (~ 40 mm, Fig. 1) that builds a web composed of a two-dimensional orb web and three-dimensional barrier web in the upper part of the orb (Robinson and Mirick 1971). *T. clavipes* has a wide distribution in the Americas, ranging from the southern United States to tropical and subtropical South America (Ubick et al. 2017). We collected spiders from urban parks and coffee plantations around Xalapa, Veracruz, Mexico. Once a *T. clavipes* web was located, any *A. elevatus* spiders that were inhabiting the web were collected with a paintbrush. Host spiders were collected and housed at the laboratory at the Universidad Veracruzana. The host spiders were fed with house crickets (*Acheta domesticus*) once a week and moved to wooden frame boxes (70 × 70 × 20 cm, with acrylic sides)

Fig. 1 Spider portraits of *Trichonephila clavipes* (host) and *Argyrodes elevatus* (kleptoparasite, red arrow). The kleptoparasite is about to make contact with the prey being consumed by the host spider

for the experiments. The kleptoparasites were placed in individual plastic containers sealed with cotton wool ball for gas exchange and were given water and fed with *Drosophila spp.* flies twice a week.

Foraging trajectories

To elicit kleptoparasite foraging movement, we used a large prey (house cricket). We had previously observed that the kleptoparasite fed with the host at the same time with this type of prey. We introduced one kleptoparasite into the frame containing a host web and allowed an acclimatization time of 24 h before the experiment. We placed a prey at an approximate distance of 10 cm below the hub position (Fig. 2). The host spider captured the prey at its impact location and brought the prey back to the hub of the web, where it proceeded to wrap and consume the prey. Kleptoparasites moved only after the prey capture was completed and during the silk wrapping of the prey. The kleptoparasite movement was filmed at 60 fps until it made contact with the prey. We used a Panasonic camera (LUMIX-DMZ-FZ1000) and filmed perpendicular to the web. See supplementary material S1 for an animation showing a sample kleptoparasite trajectory overlaid on a host web.

We extracted image sequences from the videos and generated positional information (x, y coordinates) of the kleptoparasite, host, prey and hub using the auto-tracker tool of Tracker software (Mather 1991). We analysed the video footage at 1 fps since the kleptoparasite periodically stayed still in the same location for long durations, and this frame rate provided the best representation of the movements without losing crucial information. We translated the host web hub position to the origin and used the accordingly translated coordinates of the trajectories for all subsequent analyses. We interpolated the x,y coordinates of all the trajectories to generate a density map of kleptoparasite activity in the simulated web space. In this representation, areas of higher activity are shown by lighter coloured areas, and areas of low travel are shown with darker colours.

Vector analysis of speed

Using the x, y coordinates of all trajectories, we generated a vector field with speed and direction of movement as the vectors. The vector field is an interpolation based on the

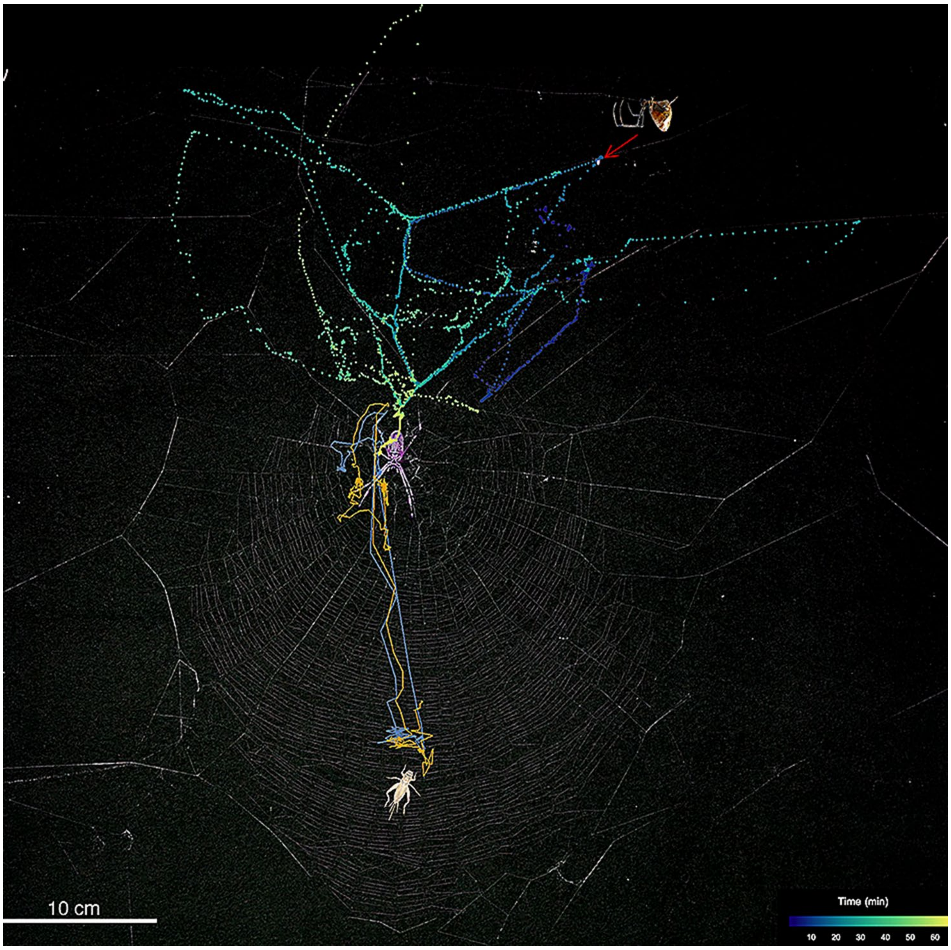


Fig. 2 A sample trajectory of the kleptoparasite overlaid on the host web. The path of the kleptoparasite is colour coded according to the time elapsed. The paths of the host (blue) and the prey location (orange) are shown as solid lines

actual trajectory coordinates. We plotted the vector field and the stream plot separately to visualize speed variation in the web space. In the first, the entire web space was divided into regions where the vectors were represented by arrows coloured according to the average speed of the kleptoparasites at that location and the angle of the arrow corresponds to the direction of motion. In the second, streamlines show the direction of local movement at a particular region in the web space.

Distance profiles for each trajectory were obtained by calculating the Euclidean distance between the kleptoparasite and the hub over time as the kleptoparasite approached the hub. In each distance profile, we quantified the frequency at which the kleptoparasite turned away from the hub.

Given the small size of the spider, we were able to reliably track only one point on the spider. In each video sequence, we used the x, y coordinates of the spider to calculate the heading direction of the kleptoparasite. Using custom-written scripts in Matlab (Version R2020a, Natick, Massachusetts), we calculated this heading direction relative to the hub direction. Circular statistical tests were carried out in Oriana (Version 4.0, Kovach Computing Services, UK).

Trajectory similarity

We compared the similarity in the shape of the trajectories using a dynamical time warping (DTW) based correspondence analysis (Keogh and Ratanamahatana 2005; Fu et al. 2008; Hu et al. 2013; Rao et al. 2019). DTW is a method used to compare two temporal curves by computing the minimal Euclidean distance for any correspondence between sequences and is used as a measure of similarity between two trajectories. We chose the DTW method since it retains shape information during the analysis and is not sensitive to trajectory orientation. For example, trajectories that start and end at different points will be considered highly similar if they follow a similar set of turns and step lengths. Briefly, the warping distance was calculated between the time normalised x,y coordinates of each trajectory pair. Once the DTW distances were computed, we then compared all trajectory pairs with a canonical correspondence analysis. The resulting distance matrix produced values ranging from 0 to 1, where a value of 0 implies that there is no difference in the shape of the trajectories (as seen in the diagonal where a given trajectory is compared with itself), and a value of 1 implies there is no similarity between the trajectories. To compare the relative distances between trajectories of different length, we divided the DTW distance by the length of the correspondence path since two long similar trajectories could have a higher distance compared to short dissimilar trajectories. In addition, we generated an artificial trajectory based on a random walk model with step length equivalent to the median of the real trajectories. This random trajectory was included in the canonical correspondence analysis. All analyses were done in Mathematica Version 12.1 (Wolfram Research Inc. 2020).

Revisitations

We estimated the frequency of repeated visits of the kleptoparasite to the same location on the web as an indicator of the reuse of trajectory segments and path directness. For instance, individuals that approached the hub directly would have fewer repeated visits to the same location. Revisitations were measured as the number of times an individual kleptoparasite re-entered a circle of established radius drawn over the x,y coordinate points. We used a radius of 0.5 cm since this approximates the spider's body length. We used the statistics package *recurse* in R (Bracis et al. 2018) for calculating the revisitations, using the option that moves the circle of chosen radius throughout every point in the trajectory and counts the number revisitations into that circle. We focussed on the locations of the maximum values to quantify areas of repeated revisitations.

Results

As has been reported before, *Argyrodes* spiders spend most of their time waiting in the peripheries of the web but on the upper side and mostly on the barrier webs (Vollrath 1979a). Triggered by the vibrations created by the movement of the host as it wraps the prey, the kleptoparasite makes its way towards the prey using a complex trajectory (Figs. 2, 3a). An analysis of the zones of activity (areas that show high frequency of displacements in space) during foraging (Fig. 3b) showed that overall kleptoparasitic spiders show high levels of activity near the hub but on the upper side as they approach the prey.

Vector analysis of speed

Kleptoparasitic spiders were significantly slower as they approached the hub (Linear regression: $R^2 = 0.04$, $F_{1,25989} = 116.5$, $p < 0.001$). We computed the speed of individual movements and created a vector field of speed of movement (Fig. 3c) of all the trajectories. The resulting stream plot shows that the kleptoparasites were faster towards the peripheries of the web and slowed down as they approached the prey (Fig. 3d). There is a marked slowdown (empty region in Fig. 3d) in speed at the center of the web just above the hub as the kleptoparasite is approaching the prey.

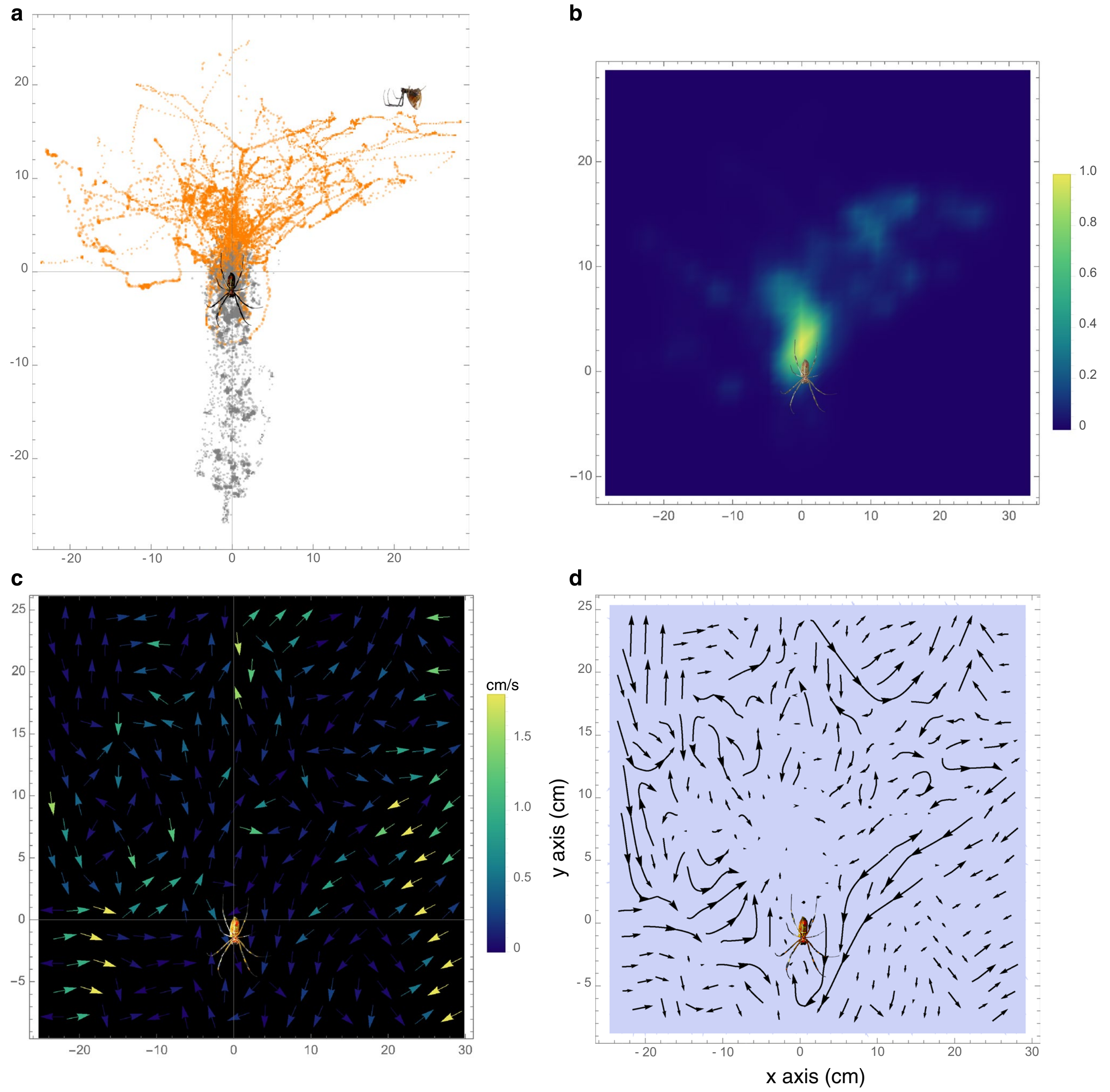


Fig. 3 Summary of movement of kleptoparasites relative to the hub and host. **a** Summary plot of all trajectories of the kleptoparasite (orange dots) and the host (grey dots). **b** Density heatmap of all kleptoparasite positions on the web. All axes are in cm. **c** Vector field plot of kleptoparasite speeds and directions as they approach the hub. Lighter coloured arrows show faster movement. **d** Stream plot of speed. Longer arrows represent local areas of faster movement. All axes are in cm

Distance profiles

Distance profiles showed that the kleptoparasites approached the hub indirectly with frequent detours away from the hub. The kleptoparasites turned away from the hub 6.7 ± 3.4 times (mean ± SD) with the number of turns ranging from 2 to 14. There was a large variation in the fluctuation of distance profiles (see S2 for all trajectories), but we could detect two general strategies (Fig. 4). Some individuals took a more direct route to the hub with fewer retreating turns and others had a number of retreats leading to a highly fluctuating distance profile.

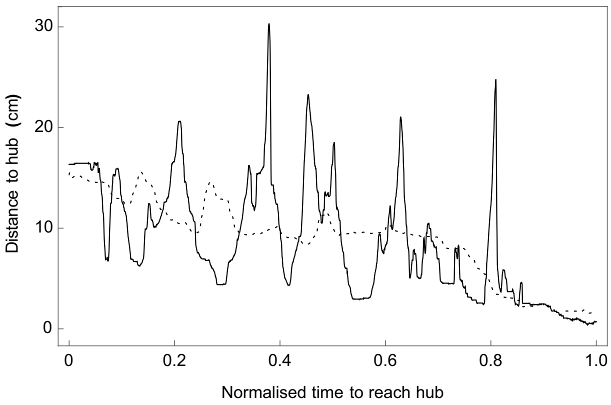


Fig. 4 Example distance profiles of two kleptoparasites as they approached the hub

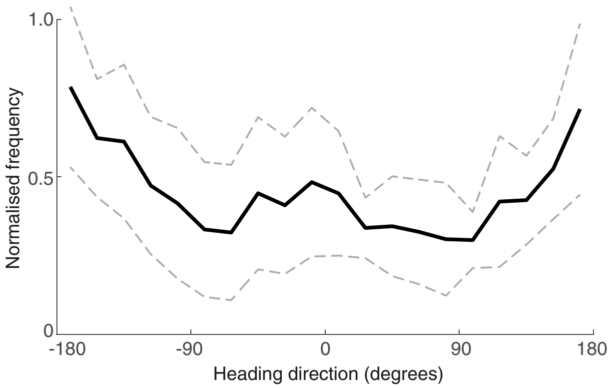


Fig. 5 Summary plot of heading angle of kleptoparasite movements in the host web. Normalised frequency of heading direction relative to the hub direction at 0° is shown. Heading direction was calculated from the *x*, *y* coordinates of the kleptoparasite position between consecutive frames. Means (continuous line) and standard deviation (dashed line) are shown. When the angle is 0º, the kleptoparasite is heading directly towards the hub, and ± 180º corresponds to movement away from the hub

Heading direction

Heading direction of animals was not uniformly distributed (Rayleigh test, $Z = 382.765$, $p < 0.001$). We designated heading direction towards the hub as 0º. The kleptoparasite movements were not consistently oriented towards the hub (*V*-test, $\mu = - 23.69$, $p = 1.0$), but were oriented in directions away from the hub (*V*-test, $\mu = 23.69$, $p < 0.001$) suggesting frequent turns or retreats away from their destination angle (Fig. 5; Supplementary Fig. S3).

Trajectory similarity

Overall, there was little similarity in the shape of the trajectories between individuals, with all trajectories showing a median similarity value of 0.5 (Fig. 6). However, the Dynamic Time warping correspondence distance matrix showed that most trajectories were highly dissimilar whereas a few individual trajectories were similar to others (Fig. 6). For example, the trajectories of individuals 5 and 15 were highly similar whereas the trajectories of individuals 4 and 5 were very dissimilar in shape. The similarity between the random walk trajectory (trajectory18) and other trajectories was comparable to that observed between the real trajectories suggesting that individual trajectories are highly idiosyncratic.

Revisitation

Revisitation of previously traversed paths was seen more often in the hub area (Fig. 7). The rate of revisitation varied widely between individuals (mean: 3.44 revisitations, range 1–65). Trajectories with longer duration did not significantly influence the revisitation rate (linear regression: adjusted $R^2 = - 0.05$, $F_{1,15} = 0.155$, $p = 0.69$).

Discussion

It is useful to consider the foraging movement of the kleptoparasitic spiders as individuals traversing a heterogeneous landscape of fear, with different areas of risk as they approach the center of the host web. In principle, the extreme size difference between the kleptoparasites and their host, coupled with the kleptoparasites' ability to stay out of reach of the host by leaving the plane of the web, suggests that their overall risk is low in this unique system. However, kleptoparasites are dependent on their host for nutrition, and while they may not be directly attacked, they can be accidentally ingested during the prey wrapping stage (RRG, pers. obs.). The kleptoparasite's perception of risk is different in different areas of the web and this is seen in two ways: first, they move at a faster speed at the peripheries of the web and slow down as they approach the center of the web, and secondly, they use frequent turns and retreats to recalibrate their approach.

We used the shape of the whole trajectory to see if the kleptoparasites used stereotypical paths as they made their way to the feeding location. Instead, we found that the trajectories varied immensely between individual spiders. This variation could be due to several factors. First, there is a variation in the starting position of the kleptoparasites. Even though most of the kleptoparasitic spiders start their raiding run from the upper reaches of the web, their initial resting position can differ. Second, each individual spider showed a distinct pattern of retreats away from the hub (see Supplementary Movie S1 for an animated example). In the analysis of heading direction, we found that the majority of

Fig. 6 Similarity in kleptoparasite paths towards the hub as represented by the results of a Dynamic Time Warping-based canonical correspondence analysis of a distance matrix between the shape of the trajectories. Trajectory no. 18 is an artificial trajectory (based on a modified random walk). Values close to 0 represent a high degree of shape similarity and values closer to 1 represent dissimilarity. See text for details

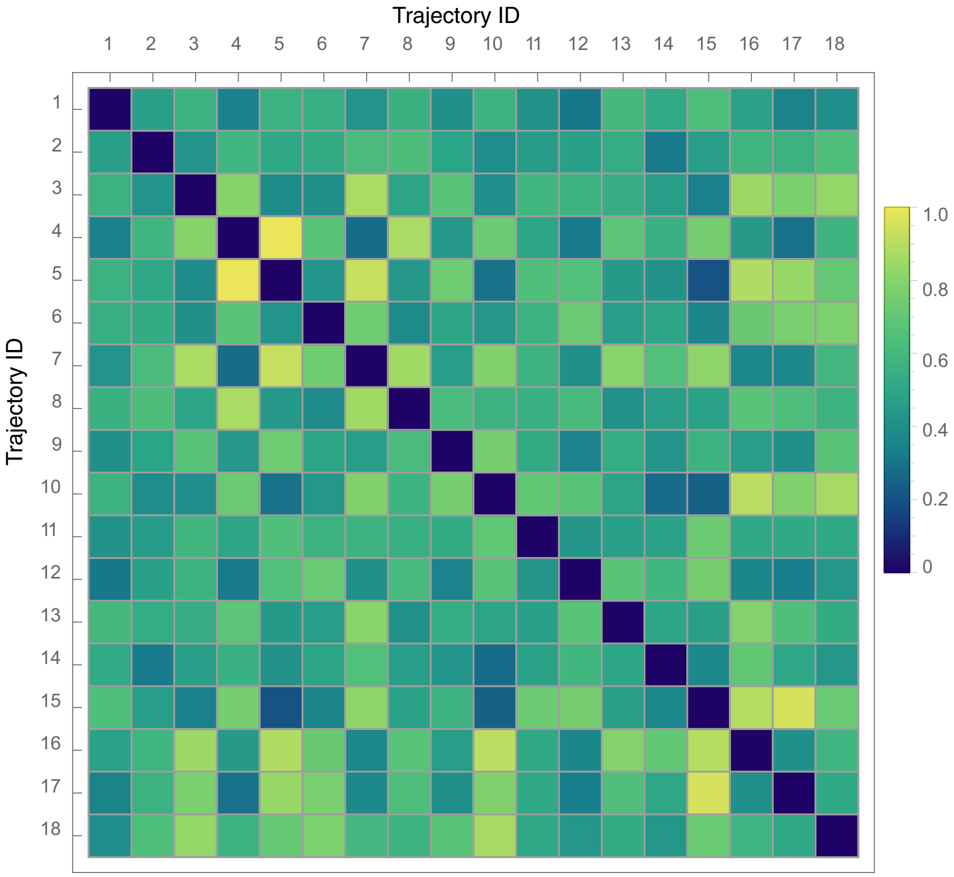
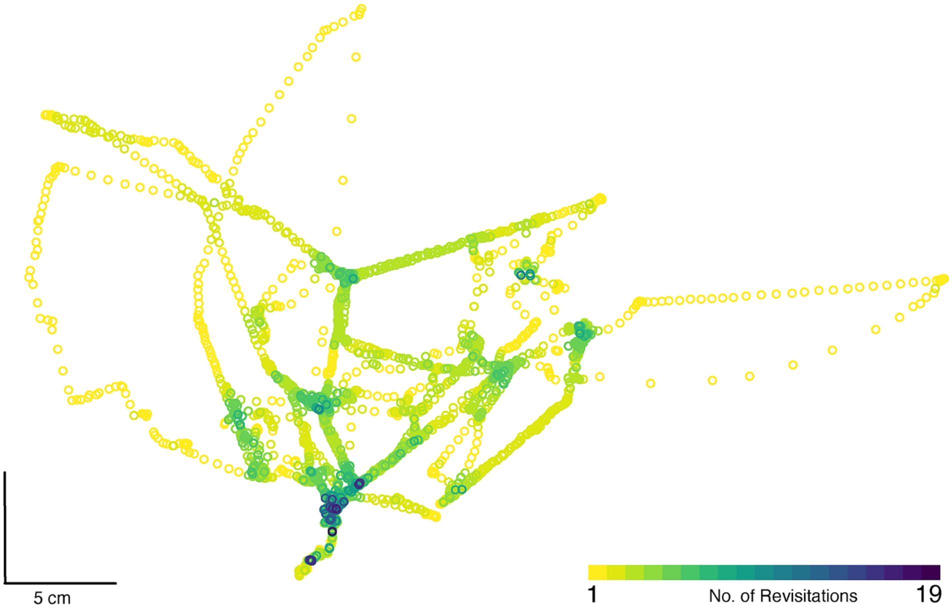


Fig. 7 Revisitation rates in a sample trajectory. Points in darker coloured circles are revisited more often. Web hub position is indicated by a star. See text for details



heading orientations were actually away from the hub suggesting that detouring or repeated approaches are an essential component of kleptoparasite movement strategies. Our results of the revisitation rate also point to the same aspect, where locations close to the hub were revisited more often than in the periphery, suggesting a circling approach, similar to a predator making several passes at a target prey before settling on the final approach. Nevertheless, the distance profiles suggest two types of strategies where there is a more direct approach and another more circuitous approach. We suggest that these two approaches are grounded in a third factor affecting trajectory variability i.e., kleptoparasites may use the micro-movements of the host spider to guide their movements in the web. Since the kleptoparasites are tuned to web vibrations emanating from the host spider's actions (Vollrath 1979b), it is reasonable to assume that their trajectories are dynamic and their approach strategies are modulated by host movement. To confirm this hypothesis, future studies should either measure vibrations directly or use a higher frame rate than the one used here.

In this system, the pattern of slowing down in a high-risk section of the web is markedly different from other studies that have tracked animal movement and related the characteristics of the trajectory to external cues. For example, in elephants, path tortuosity and speed changes in high-risk areas, where the animals are more likely to maintain a straight line and are faster, presumably in response to the risk (Troup et al. 2020). In the kleptoparasite system, since the source of nutrition is linked to the host's activity and to feed along with the host (Whitehouse 1997), the challenge is to evade detection but remain in the area. The kleptoparasitic spiders are capable of moving small prey away from the host or by stealing unnoticed prey stuck to the web, and an analogous system is that of hyenas despoiling a predator of its kill. But when the prey item is large and thus cannot be moved, feeding along with the host is the only option. Other kleptoparasitic spiders in the same genus are known to avoid large prey altogether (Cangialosi 1991).

The kleptoparasite–host spider system is an interesting model to explore issues of locomotion in constrained spaces. In other systems, such as in the tamarins, small-scale navigation is based on a mixture of route-based navigation and attention to local landmarks (Garber and Porter 2014). Male crab spiders use both visual and chemical cues to seek flowers as a navigational strategy during mate searches (Stellwag and Dodson 2010). In the kleptoparasitic spider system, there is a dependence on vibratory cues that guide navigation to and from the centre of the web.

It is known that kleptoparasites can occur in large numbers in a single host web and if many individuals are seeking to feed with the host, there are bound to be aggressive interactions that further allow for variation in approach trajectories as well as increase the chance of depriving the host of its prey (Whitehouse 1997). Individuals are more likely to have aggressive interactions when away from the hub, where predation risk by the host is lower (Whitehouse 1997). Sufficient numbers of kleptoparasitic load can impact the host spider indirectly by diminishing the available food to the host, such that the host spider may abandon the web site to construct a new web, which may be energetically expensive (Elgar 1989).

Though it is unlikely, it is possible that trajectories of the same individual follow similar paths across different instances of feeding. Furthermore, given the changes in speed in different sectors of the web, the kleptoparasite perception of distances in the web may be warped according to their perception of risk. Future studies will allow us to tease apart these interactions.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00359-021-01477-3.

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Author contributions Data collection—RRG. Writing original draft—DR. Writing and revision—DR, RRG, AN and HTM. Analysis—DR, RRG, AN and HTM. Visualisation—DR, RRG, AN and HTM. Conceptualisation—DR. Project administration—DR.

Declarations

Conflict of interest The authors declare they have no conflict of interests. All spiders were released after experiments. Data will be made available on request.

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