Candy-striped spider leaf and habitat preferences for egg deposition

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Abstract
1. Candy-striped spiders (Enoplognatha spp.; Araneae: Theridiidae) are among Britain’s commonest theridiid spiders and are potential immigrant biocontrol agents of many pests in arable fields. Though the presence of these spiders in proximity to agriculture is dependent on the availability of suitable leaves for their egg deposition, their preference for different plant species and habitat types has not been fully investigated.
2. Candy-striped spiders were observed in leaf-rolls during transect surveys of semi-natural habitats (hedgerow, woodland and grassland) adjacent to oilseed rape fields at 10 sites across northeast England in August and September 2021. The local plant community was surveyed and compared against the leaves used by candy-striped spiders via null models.
3. Candy-striped spiders preferentially deposited their eggs in hedgerow, demonstrating relative avoidance of woodland and grassland. They exhibited preference for bramble, common nettle and hogweed leaves, but also used those of dock, ash and blackthorn. Candy-striped spiders appeared to preferentially use leaves with roughly equal length and width and avoided longer, narrower leaves irrespective of their total size.
4. The leaves used by candy-striped spiders are taxonomically broad, but share some morphological commonalities. Candy-striped spiders exhibit some degree of generalism, regularly utilizing suboptimal leaves in sites lacking their preferences. The availability of preferred plants for these spiders in agriculturally proximate semi-natural habitat may enhance their possible contribution to biocontrol.

Keywords
arachnid, Araneae, choice, conservation biocontrol, oviposition, semi-natural habitat

INTRODUCTION

The candy-striped spiders Enoplognatha ovata (Clerck, 1757; Araneae: Theridiidae) and E. latimana Hippa & Oksala, 1982 are among the commonest theridiid spiders in the British Isles. In late summer, candy-striped spiders mate, the male dying soon after, while the female rolls live leaves with silk (Eberhard et al., 2008) in which their characteristic blue egg sac is deposited and then guarded until shortly before the second instar spiderlings emerge from the leaf-roll (Oxford, 1993; Figure 1). The number of mature female candy-striped spiders with egg sacs is thought to vary greatly depending on climate, the availability of suitable habitat, disturbance and other factors, resulting in 4 to 55-fold population fluxes over time (Oxford, 1993). In Britain, populations of up to 2744 E. ovata have been recorded from a...
single broad-leaved vegetation clump (Oxford, 1993) and estimates of up to 0.5 adult or 2 juvenile Enoplognatha spp. spiders were recorded per square metre in a wheat field in arid shrubland (Opatovsky et al., 2016). Populations will, however, likely vary greatly between regions and patches based on habitat suitability. Leaf-rolls such as those constructed for egg deposition by candy-striped spiders confer significant benefits to immature arthropods such as protection from parasitism and egg predation (Kobayashi et al., 2020; Loeffler, 1996; Tvardikova & Novotny, 2012). These structures can, however, introduce additional predation pressure from visually-oriented predators (Danthanarayana, 1983; Kobayashi et al., 2020) or inadvertent vertebrate herbivores through accidental consumption (Tercel et al., 2021).

The presence of candy-striped spider egg sacs in these leaf rolls is predicated on the presence of suitable plant species. In an agricultural context, this means that their potential biological control of crop pests is dependent on the floral community composition of semi-natural habitats adjacent to crop fields. *E. ovata* have long been known to exploit the leaves of bramble, but interactions with those of rosebay willowherb, elm, maple, hazel, ash, beech, willow, oak, may, nettles, umbellifers, *Convolvulus* and various other plants have also been recorded (Bristowe, 1931; Oxford, 1993). These preferences seemingly extend beyond taxonomy and may depend on leaf traits (Zanatta et al., 2022); for example, Stevenson and Dindal (1982) found more juvenile *E. ovata* on curled leaves than on flat, although this was in leaf litter rather than live leaves. The extension of this preference to plant species, and how it factors into egg deposition, is, however, poorly characterized. Although some plant species are known to be used more than others (e.g., common nettle *Urtica dioica* L., bramble *Rubus fruticosus* L.; Bristowe, 1931; Oxford, 1993), the preferences of candy-striped spiders for these in mixed plant communities, and the suitability of alternatives, are poorly understood.

Although theridiids such as candy-striped spiders are often found in or near agricultural crops, they are nonagrobiont spiders (i.e., they do not complete their life cycle in the crop itself) but nonetheless significantly contribute to the web-building spider populations of many agroecosystems (Gavish-Regev et al., 2008; Pluess et al., 2008). *Enoplognatha ovata* has been scarcely studied as a biocontrol agent in Britain, but molecular analysis has revealed that these spiders frequently predate pests such as leafhoppers in British crops (Virant-Doberlet et al., 2011). Globally, other species within the *Enoplognatha* genus have been studied as biocontrol agents of pest beetles (Ranjbar Aghdam, 2013; Tóth et al., 2002) lepidopterans (Luo et al., 2014), aphids (Gavish-Regev et al., 2009) and planthoppers (Chiu, 1979; Ganeshan, 2013). *Enoplognatha* spiders immigrate into crop fields from adjacent habitats and exhibit a high degree of preference toward pests such as aphids (Opatovsky et al., 2012). For candy-striped spiders to enter crops as immigrant biocontrol agents, they first need to be established in adjacent semi-natural habitats, contingent on the provision of suitable habitat and host plants.

By studying the interactions between candy-striped spiders and their host plants and different semi-natural habitats, it is possible to elucidate their preferences, which will have profound implications for their ecology and potential for biocontrol. Such analyses are possible through the lens of network ecology, which is the characterization and assessment of interactions between communities of organisms in complex ecological systems (Bascompte, 2007). Empirical network ecology often uses observations of species interactions in the field to construct interaction networks, which are a powerful means for assessing animal choice in situ (Cuff, Windsor, et al., 2022; Vaughan et al., 2018). The interactions between animals and plants are, however, mostly studied in antagonistic (e.g., herbivory) or mutualistic (e.g., seed dispersal, pollination) contexts, and not in the commensal context of leaf-rolling by largely predatory animals.

In this study, we apply the principles of network ecology and null model-based choice analysis to observations of candy-striped spider leaf and habitat choice in northeast England to improve our understanding of the preferences of these spiders. We test the following hypotheses: (i) candy-striped spiders disproportionately utilize hedgerow habitats for egg deposition given their greater diversity of shrub species; (ii) candy-striped spiders exhibit preference for a small range of common plant species when depositing eggs; and (iii) the plants selected by candy-striped spiders for egg deposition share similar leaf
morphology. By better understanding the microhabitat preferences of these spiders, agricultural management and semi-natural habitat availability can be adjusted to ensure proliferation of these potentially important biocontrol agents.

**MATERIALS AND METHODS**

**Fieldwork**

Fieldwork was carried out as part of a larger European Union Horizon 2020 project, Ecostack, with the aim of constructing ecological networks in oilseed rape crops and their adjacent semi-natural habitats. The sampling described represents a subset of that project which has a broader focus than the data presented herein. Ten sites containing oilseed rape fields with adjacent grassland, hedgerow and woodland (Figure 2) in the northeast of England were surveyed monthly between April and July 2021, with one final sampling round taking place 2 weeks after the oilseed rape crop was harvested (i.e., across late August and early September). Surveys consisted of paired transects ~5 m into the crop and in the adjacent semi-natural habitat (grassland, hedgerow and woodland), totalling six transects per site. Each 25 m transect contained four 1 m² quadrats 5 m apart (i.e., 5, 10, 15 and 20 m into each transect) within which plant species were recorded as proportions of the total quadrat area, and any instances of herbivory or other manipulations of the plants (e.g., leaf rolling, leaf mines, galls) recorded as interactions between invertebrate and plant species. Candy-striped spiders were first observed with egg sacs on 20th July, but given the small number found at this late stage in the July sampling round, and the temporal separation of these surveys from the full round of post-harvest surveys conducted in which candy-striped spiders were commonly found, these July surveys were not included in any analyses. The observations reported and analyses herein are therefore all from the post-harvest surveys which took

**FIGURE 2**  (A) The 10 survey sites in Northeast England. (B) Surveys took place over paired transects (blue lines) for each of the semi-natural habitats. For each semi-natural habitat (grassland, woodland, hedgerow), a parallel transect was surveyed in the adjacent oilseed rape crop. In very few sites where all three semi-natural habitat types were not adjacent to a single field, two proximate fields were used. Figure created using Biorender.com
place in late August and early September, when female spiders are most likely to be with egg sacs (Oxford, 1993). During this time, the crop fields themselves had little to no vegetative cover and thus no observations of candy-striped spider egg sacs were made therein. The spiders were not collected given the perceived ease of identification of candy-striped spiders in the field with suitable arachnological expertise. Although the two most common species of *Enoplognatha* in Britain are morphologically and ecologically similar, their British distribution mostly overlaps in the south of England and Wales (Oxford, 2022a; Oxford, 2022b). *E. latimana* has been reported further north, but uncommonly (Oxford, 2013; Oxford, 2022a; Oxford & Reillo, 1994). It has historically been found in hot and dry environments such as heathlands and sand dunes (Oxford, 1992), although recent records have included those more like the habitats of *E. ovata* (Oxford, 2022a). Most candy-striped spiders in the northeast of England are thus likely to be *E. ovata*, although this cannot be confirmed with certainty in this study without examination of the epigyne. The possibility of *E. latimana* appearing in the surveys thus cannot be ruled out, so the spiders are herein referred to simply as candy-striped spiders (i.e., *Enoplognatha* spp.).

Plants were located by hand searching within quadrats and communities identified morphologically by eye or hand lens by field team members with botanical expertise. Plant community data were recorded at each quadrat and represented as approximate percent-ages of the surveyed quadrat area estimated by eye. Percentages were given either as zeroes (absent) or rounded to values starting at one and increasing in increments of 10 (i.e., 0, 1, 11, 21, 31, etc.); this numeric system was chosen to facilitate representation of the minute contribution of some plants to the total quadrat plant biomass. Where plants were not always identifiable to species level, taxa were aggregated at a higher classification. Grasses were grouped as Graminoid spp. given the difficulty involved in identifying mown or heavily-grazed grasses at many sites, and ferns were resolved as Poly-podiopsida spp. Similarly, thistles (*Cirsium* spp.), hawkweed (*Hieracium* spp.), dead-nettle (*Lamium* spp.), oak (*Quercus* spp.), buttercup (*Ranunculus* spp.), dock (*Rumex* spp.), dandelion (*Taraxacum* spp.), vetch (*Vicia* spp.) and violet (*Viola* spp.) were resolved to genus level.

**FIGURE 3** (A): The three leaves most used by candy-striped spiders for leaf-rolls: Hogweed *Heracleum sphondylium* (left, n = 4), nettle *Urtica dioica* (middle, n = 9) and bramble *Rubus fruticosus* (right, n = 24) leaves. Photos taken by Jordan P. Cuff during surveys. (B) The plant species used by candy-striped spiders for leaf-rolls across the three habitats.
Statistical analysis

All analyses were conducted in R v4.0.3 (R Core Team, 2020). To assess the diversity of spider-leaf interactions detected and the completeness of sampling, coverage-based rarefaction and extrapolation were carried out, and Hill diversity calculated as a robust estimate of species diversity (Chao et al., 2014; Roswell et al., 2021). This was performed using the ‘iNEXT’ package with species represented by frequency-of-occurrence across surveys (Chao et al., 2014; Hsieh et al., 2016). These Hill numbers include the three most widely-used diversity measures: species richness, Shannon diversity and Simpson diversity, each varying in their diversity order, $q$ ($q = 0, 1$ and 2, respectively), which equates to the sensitivity of the measure to relative abundances (Hsieh et al., 2016). Species richness counts interacting species equally, irrespective of their relative abundances; Shannon diversity counts interactions equally, thus representing species proportional to their frequency of interaction; Simpson diversity exclusively pertains to the dominant interactions across the surveys. These were visually represented by plotting the cumulative diversity (according to all three indices) against the number of detections, the cumulative sample coverage (i.e., completeness of sampling) against the number of detections, and the cumulative diversity against the sample coverage. Visual inspection of these figures effectively facilitates assessment of the suitability of sampling effort, and how interaction diversity is structured across the surveys.

In situ spider semi-natural habitat choice was analysed using network-based null models in the ‘econullnetr’ package (Vaughan et al., 2018) with the ‘generate_null_net’ command, visually represented with the ‘plot_preferences’ command and through bipartite networks generated using the ‘bipartite’ package (Dormann et al., 2008).
Four counts of each semi-natural habitat were represented as present to reflect the four quadrats surveyed, and spiders were deemed as interacting with the semi-natural habitat in which they were found at their respective site. An additional choice analysis was run in the same manner for leaf choice, with interactions between spiders and plants defined as spiders having deposited their egg sacs onto the leaf of that plant species, and the plant community data taken from the quadrat surveys described above. The plant preference null models use transect-specific data, so each spider’s plant choices are compared only against the alternatives available in the transect in which it was found. Transects in which spiders were not found were only included in the above habitat preference model, so without any plant community composition data.

RESULTS

General observations

In total, 40 candy-striped spider leaf-rolls were observed across the 120 quadrats in 30 semi-natural habitat transect surveys (0.33 m⁻²).
No spiders were observed in the crop field itself, which hosted little to no vegetative cover given that this survey took place post-harvest. Of these leaf-rolls, 20 contained an intact egg sac, and 19 contained a cluster of spiderlings (the latter typically occurring later in the survey period; this information was not recorded for one observation). Candy-striped spider leaf rolls were observed in the leaves of six plants (Figure 3): bramble Rubus fruticosus (n = 24), common nettle Urtica dioica (n = 9), hogweed Heracleum sphondylium (n = 4), dock Rumex sp. (n = 1), ash Fraxinus excelsior L. (n = 1) and blackthorn Prunus spinosa L. (n = 1). Of the 10 sites visited, candy-striped spiders were found in eight during the August/September surveys (4, 9, 3, 11, 4, 4, 2, and 3 observations at each of the sites). They were, however, recorded at an additional site on common nettle in a hedgerow in late July, and at one of the sites in which they were also found in the post-harvest sampling, again in a hedgerow on common nettle. Spider-leaf interactions were not diverse (Hill-richness = 6.00 ± 4.312; Hill-Shannon diversity = 3.155 ± 0.590; Hill-Simpson diversity = 2.367 ± 0.398) and the surveys identified an estimated 92.69% (±4.7%) of the total spider-leaf interaction diversity (Figure 4).

**Habitat choice analysis**

Candy-striped spiders exhibited preference for hedgerow and a relative avoidance of woodland and grassland (Figure 5). Although most candy-striped spiders were observed in hedgerow (n = 34), some were observed in the other semi-natural habitats (woodland = 4, grassland = 2).

**Leaf choice analysis**

Candy-striped spiders exhibited taxonomically biased density-independent leaf choice across the 24 plant taxa included in the models from plant community surveys (Figure 6). *Urtica dioica, Rubus fruticosus* and *Heracleum sphondylium* were all interacted with more frequently than expected, whereas Graminoid spp. and *Crataegus monogyna* Jacq. were interacted with less frequently than expected. All other interactions occurred at a rate similar to that expected (i.e., not at all, or very little in the cases of *Fraxinus excelsior*, *Prunus spinosa* and *Rumex* sp.).

**DISCUSSION**

Candy-striped spiders exhibited density-independent preferences for a small subset of the local plant community, notably bramble, nettle and hogweed. The former two species are known as common egg-deposition sites for candy-striped spiders (Bristowe, 1931; Oxford, 1993) but hogweed is not frequently recorded, nor are interactions with blackthorn, ash and dock. That these lesser known interactions comprise 17.5% of the total interactions observed indicates that deviation from the most common interactions (bramble and nettle) is frequent, despite overall interaction diversity being low. This range of leaf choices is likely to expand when viewing the global distribution and taxonomy of Enoplognatha spiders (e.g., Miliczky et al., 2014; Milne, 2012).

There were few trait consistencies between the six plant taxa used by candy-striped spiders aside from all having petiolate leaves (Table S2). Almost all six had toothed outlines and even or marginally longer than wide leaves, but compound versus simple leaves and the leaf area were particularly variable between these taxa. The smallest of these leaves, those of blackthorn, particularly contrasted with the much larger leaves of hogweed. This highlights that the size and structure of leaves are not especially critical in the choice of candy-striped spiders, but traits like the length: width ratio may be an important determinant of leaf choice, with equally proportioned leaves seeming to be particularly preferable.

Candy-striped spiders have, however, been known to exploit the long, narrow leaves of rosebay willowherb by sewing two or more leaves together or twisting a single leaf. Importantly, spiders may use suboptimal leaves when there is an absence of suitable options. The only instance of interaction with dock Rumex sp., for example, was in grassland where more commonly selected species such as bramble were less common. That the spiders used so many species with less evenly proportioned leaves may simply relate to the unavailability of such leaves (aside from the recorded interactions, such leaves are only represented in this study by herb Robert Geranium robertianum, the leaves of which are possibly too small, and ivy Hedera helix, the leaves of which may present other challenges through their rigidity and waxy cuticle). The range of leaves with which candy-striped spiders are known to interact is very broad (Bristowe, 1931; Oxford, 1993), but what defines the suitability of these for leaf-rolls is poorly understood. It would be intuitive that these spiders exploit similar leaves for their natal leaf-rolls to those used for foraging, thus further research surrounding the interactions between these plants and the spiders’ prey, and how that might influence leaf selection for egg deposition, may be revealing. Similarly, the microhabitat and microclimatic requirements of juvenile or overwintering spiders may affect site selection, and factors such as leaf density (i.e., penetrability by predators or herbivores), foldability (i.e., ease-of-manipulation into a leaf-roll) and water content (i.e., humid microclimate) may have further implications for the specific leaf choices of these spiders and should be investigated through further study.

Spillover of beneficial invertebrates from semi-natural habitat provides a clear role in the provision of potential immigrant biocontrol agents such as candy-striped spiders (Benhadi-Marin et al., 2020; Blitzer et al., 2012; Gavish-Regev et al., 2008; Sunderland & Samu, 2000; Topa et al., 2010; Zhang et al., 2020), but this study demonstrates that the type of semi-natural habitat (e.g., woodland, hedgerow) and its floral community composition determine suitability. The preference of these spiders for hedgerow and their relative avoidance of grassland and woodland is likely indicative of the suitability of hedgerow for the specific plants used by the spiders and adds to the growing body of evidence regarding the importance of hedgerow habitats for ecosystem service provision in agro-ecosystems (Evans et al., 2013). Other studies have found these spiders most prevalent on road verges and edge habitats backed by walls (Oxford, 1993).
possibly suggesting a preference for edge habitats with shelter from wind or other disturbances. That the spiders were still found in other habitats does, however, suggest that populations of candy-striped spiders could be sustained in most crop-adjacent situations, contingent primarily upon the provision of their preferred plants. Conservation biocontrol via proliferation of natural enemies in semi-natural margin habitats should thus carefully consider the plant species mixture in these habitats, optimizing the benefit to natural enemies and the detriment to potential pests through adjustments to these communities (Windsor et al., 2021).

Throughout the surveys, several candy-striped spider colour morphs were observed (some exemplified in Figures 1 and 3). These morphs and their genetic drivers have been the subject of many studies over the last few decades (Oxford, 1985; Oxford, 2013; Oxford & Reillo, 1993; Reillo & Wise, 1988). It is thought that these polymorphisms are maintained by selective pressure, driven by either predator wariness when confronted with a novel morph or predator search image mismatch (Franks & Oxford, 2009; Oxford, 2005). Importantly, the value of leaf-rolls for candy-striped spiders is also likely based on their protective qualities (Kobayashi et al., 2020; Loeffler, 1996; Tvardikova & Novotny, 2012). Visually-oriented predators that become familiar with the presence of candy-striped spiders in these leaf-rolls may seek them out in the same way that they may seek particular colour morphs (Danthanarayana, 1983; Kobayashi et al., 2020). Behavioural plasticity in leaf choice is likely to be an effective adaptation for avoiding focused predation by visually-oriented predators, whilst also reducing dependence on one plant species.

The relationship between candy-striped spiders and the leaves in which they deposit their eggs is difficult to define. Although leaf-rolling will undoubtedly reduce photosynthetic potential by preventing light from reaching the surface of some leaves, this will likely be negligible at the scale of the whole plant. The spiders do not otherwise negatively impact the plant (e.g., through herbivory) but will likely afford some protection from herbivores, both immediately and upon development of the spiderlings protected by the leaf-roll. The relationship could thus be viewed as mutualistic or at least commensal, rather than parasitic as most leaf-roller relationships tend to be (e.g., Tortricidae moth caterpillars). Leaf-rolls ultimately increase the frequency of interactions, both direct and indirect, linked to their host plant and increase microhabitat diversity (Fukui, 2001), suggesting an important positive effect on local biodiversity. The net impact of leaf rolls on agricultural productivity is thus likely to be positive in the case of candy-striped spiders which may subsequently contribute to conservation biocontrol, but even herbivorous leaf-rollers may yield unobserved net benefits despite their direct herbivory of local plants.

The selection of specific leaves and semi-natural habitats for egg deposition may also relate to foraging by candy-striped spiders. Given the dependence of *E. ovata* on vibrational cues for foraging (Virant-Doberlet et al., 2011), the structure and morphology of leaves and semi-natural habitats may be variably conducive for locating prey and foraging, the outcomes of which may have important implications for agriculture. Although there is evidence for British populations of *Enoplognatha ovata* and other global *Enoplognatha* spp. controlling pest populations, the biocontrol potential of these spiders is poorly characterized and their trophic ecology underrepresented in the literature. Despite evidence existing for the biocontrol potential of many other web-building spiders (Chapman et al., 2013; Cuff et al., 2021; Vink & Kean, 2013), Michalko et al. (2019) found in a global meta-analysis that web-building spiders have a poor, often negative effect on pest suppression. Many such spiders also negate their own biocontrol activity through high incidences of intraguild predation (Cuff, Tercel, et al., 2022; Hambäck et al., 2021; Petráková et al., 2016). Assumptions about the biocontrol efficacy of such spiders are thus contentious, so further research should focus on elucidating the trophic ecology of these spiders to ascertain how regular and effective their interactions with pests may be. This study nonetheless highlights the specific requirements of these spiders in agriculturally-adjacent semi-natural habitats through a network-based analysis of leaf-predator interactions.

The arguably commensal interaction between generalist predators and their natal leaf-rolls exemplifies an underrepresented compartment of invertebrate interaction networks. The analysis of these interactions has elucidated associations between candy-striped spiders and the leaves of plants with which they were not commonly known to interact such as ash, blackthorn and dock, and even a preferential interaction with hogweed. These interactions may differ between years, and across a broader geographical range or wider spectrum of habitat types, thus further study is required to ratify these findings. Management of both internal and external field environments is important for optimally benefiting from spider populations in agriculture (Lang & Barthel, 2008), but such interventions must be directed and purposeful. The optimality of plant mixes for ecosystem service provision goes beyond pollination, depending also on their importance in commensal interactions such as egg deposition that may support generalist predator populations. It is possible to optimize plant mixes in agricultural semi-natural habitats to promote multiple ecosystem services (Windsor et al., 2021), but we must first understand the nature of both direct and indirect interactions between plants and natural enemies. This study provides a direction for management of candy-striped spider populations, but the implications of those spiders and their interaction with these plants for biocontrol require further elucidation.

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**CONFLICTS OF INTEREST**

There are no conflicts of interest to declare.

**DATA AVAILABILITY STATEMENT**

Data and R scripts are publicly available via Zenodo: https://doi.org/10.5281/zenodo.5730392.
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**SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of the article at the publisher’s website.

**Data S1.** Supporting information.