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RESEARCH ARTICLE

Disentangling the visual cues used by a jumping spider to locate its microhabitat

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ABSTRACT

Many arthropod species have evolved to thrive only on the leaves of a particular species of plant, which they must be capable of finding in order to survive accidental displacement, developmental transitions or the changing of the seasons. A number of studies have tested whether such species select leaves to land or oviposit on based on their color, shape or size. Unfortunately, many studies did not control for correlates of these characters, such as the brightness of different colors, the areas of different shapes, and the level of ambient illumination in the vicinity of different sizes of leaves. In the present study, we tested for leaf color, shape and size preferences in a leaf-dwelling jumping spider (*Lyssomanes viridis*) with known summer and winter host plants, while controlling for these correlates. First, color preferences were tested outdoors under the natural illumination of their forest habitat. *Lyssomanes viridis* did not prefer to perch on a green substrate compared with various shades of gray, but did prefer the second darkest shade of gray we presented them with. Of the green and gray substrates, this shade of gray's integrated photon flux (350–700 nm), viewed from below, i.e. the spider's perspective in the arena, was the most similar to that of real leaves. This relationship also held when we weighted the transmitted photon flux by the jumping spiders' green photopigment spectral sensitivity. Spiders did not prefer the star-like leaf shape of their summer host plant, *Liquidambar styraciflua*, to a green circle of the same area. When given a choice between a *L. styraciflua* leaf-shaped stimulus that was half the area of an otherwise identical alternative, spiders preferred the larger stimulus. However, placing a neutral density filter over the side of the experimental arena with the smaller stimulus abolished this preference, with spiders then being more likely to choose the side of the arena with the smaller stimulus. In conclusion, *L. viridis* appears to use ambient illumination and possibly perceived leaf brightness but not leaf shape or color to locate its microhabitat. This calls for a careful re-examination of which visual cues a variety of arthropods are actually attending to when they search for their preferred host species or microhabitat.

KEY WORDS: Habitat selection, Color vision, Salticidae, Visual search, Forest

INTRODUCTION

Many arthropod species have evolved to thrive only within a narrow range of microhabitats, such as the leaves or bark of a specific species of plant, or the leaf litter in a particular type of forest (Gullan and Cranston, 2014). Although some animals spend their whole lives in one microhabitat, others must move to undergo developmental transitions or to survive the changing of the seasons. In addition, accidental displacement is a real risk for animals living on plants, and the ability to relocate one's microhabitat after falling to the ground could mean the difference between life and death (Lowman, 2000).

A number of studies have tested which visual cues arthropods, primarily agricultural pests, use to find their preferred host plant species, with the goal often being to design effective traps to mitigate crop damage (reviewed by Prokopy and Owens, 1983). Although numerous such studies have reported leaf color and shape preferences, many did not control for potential correlates of these traits (e.g. Vaishampayan et al., 1975; Schonherr, 1977; Städler, 1977; Rausher, 1978; Degen and Städler, 1996; Omena and Romero, 2010; Kühnle and Müller, 2011). When testing for color preferences, it is crucial to control for differences in the perceived brightness of different colors by testing the color(s) of interest against various shades of gray or, at the very least, against various perceived brightnesses of another color that reflects light across the same spectral range as the color of interest. Several studies have done this, and provided compelling evidence that certain insects do attend to the color of leaves (Vaidya, 1969; Prokopy and Boller, 1971; Walker, 1974; Harris et al., 1993; Kelber, 1999; Bian et al., 2014).

In contrast to leaf color, we have found only a single study that has reported an innate visual preference for a particular leaf shape while at the same time controlling for leaf area (Degen and Städler, 1997). The few other studies that have controlled for leaf area have found no innate preference for leaf shape (Prokopy et al., 1983; Roessingh and Städler, 1990), so it remains unclear how common it is for arthropods to attend to leaf shape. There is a similar lack of studies of leaf size preferences, but those that do exist have found that insects tend to prefer larger leaves (Ives, 1978; Prokopy et al., 1983; Roessingh and Städler, 1990). How these animals judge one leaf to be larger than another remains untested, however. It could be that arthropods respond to the level of ambient illumination underneath a large leaf (all else being equal, larger leaves cast larger shadows), rather than judging the area, length, width or some other dimensional size measure of the leaf itself.

In the present study, we tested whether a jumping spider (*Lyssomanes viridis*) with known plant substrate preferences and dependencies responds to the color, shape or size of leaves, while controlling for the potentially confounding variables described above. *Lyssomanes viridis* is a translucent green jumping spider that perches on the undersides of leaves. It has been shown to have a chemically mediated preference for, and higher hatching success on, sweet gum (*Liquidambar styraciflua*) leaves during the summer (Tedore and Johnsen, 2015). The contact, but not airborne, chemical cues of this species are attractive to *L. viridis*. These spiders overwinter predominately on the leaves of a broadleaf evergreen species, American holly (*Ilex opaca*), so must migrate to American holly in the autumn, and back to sweet gum in the spring once its

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leaves have re-emerged. A search strategy requiring an individual to sample every plant species by touching it would seem to be rather inefficient, and as *L. viridis* is unable to localize either sweet gum or American holly by olfaction (Tedore and Johnsen, 2015), we expected that the use of visual cues was likely to have been selected for in this species. In particular, we expected that *L. viridis* might use leaf shape to find sweet gum in the spring, and green coloration to find American holly in the autumn and winter.

MATERIALS AND METHODS
Subjects and housing

Immature *Lyssomanes viridis* (Walckenaer 1837) were collected by beating sweet gum trees (*Liquidambar styraciflua*) along the Black Creek Greenway (35°49.3′N, 78°47.1′W) in Wake County, NC, USA, and in Jordan Lake State Recreation Area (35°50.0′N, 78°58.0′W) in Chatham County, NC, USA, in August 2012. Housing conditions were as described previously (Tedore and Johnsen, 2013). Photoperiod was regulated by a timer that followed the natural outdoor photoperiod in the North Carolina Piedmont. Experimental trials were conducted between September and November. Spiders were given four *Drosophila melanogaster* and a light misting of filtered water daily after experimental trials were complete for the day and at least 1 h before the lights were turned off.

Leaf color

To test whether *L. viridis* prefer to perch on green substrates, we printed out a panel of six differently colored 45×25 mm rectangles and affixed it to the outside of the transparent experimental chamber lid, with the colored rectangles facing downwards, into the chamber (Fig. S1). One of the rectangles was green and the remaining five rectangles were various shades of gray. The arrangement of the six rectangles was randomized for each individual. Randomization was accomplished by assigning a number (1–6) to each position and using the random number generator in Microsoft Excel to assign a position to each colored rectangle. The arena (100×100×100 mm) was placed on a black folding table situated outdoors under woodland shade (Endler, 1993) close to midday (between 11:30 h and 12:00 h EST) in mid-October. Radiance spectra directly under the rectangles, situated in the location where the experiments were run, and viewed from below from the spiders' perspective in the arena, were taken with a USB2000 spectrometer (Ocean Optics, Dunedin, FL, USA) calibrated with an LS-1-CAL calibrated light source (Ocean Optics). Radiance spectra were converted to quantum flux (Fig. 1) and multiplied by an opsin template (Govardovskii et al., 2000) peaking at 530 nm, which is where the green photopigment is known to peak in four jumping spider species (DeVoe, 1975; Yamashita and Tateda, 1976; Williams and McIntyre, 1980; Blest et al., 1981; Zurek et al., 2015). We found that the second-darkest gray was somewhat closer than the green, both in integrated quantum flux (350–700 nm) and in quantum flux weighted by spectral sensitivity, to real *I. opaca* leaves plucked and measured in the same place that the colored rectangles were measured (Table 1). This was important because it enabled us to determine which quality of their substrate was more important to the spiders, its wavelength content or brightness.

Spiders were placed on the floor of the experimental chamber and allowed 3 h to wander about and choose which rectangle to cling to. Between trials, for this experiment as well as those described below, the chamber was scrubbed with 70% ethanol, rinsed with tap water, rinsed with 70% ethanol and allowed to air dry.
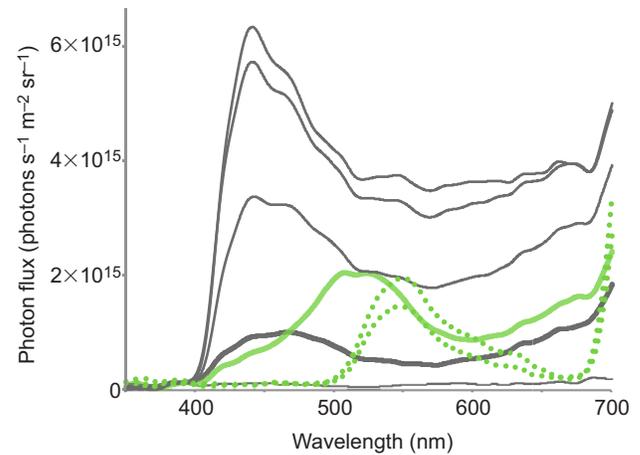

Fig. 1. Photon flux from colored printed rectangles measured in the outdoor experimental arena from the spider's perspective (i.e. from below). Measurements were all taken within 5 min of each other on a clear day. Gray lines denote gray rectangles, the solid green line denotes the green rectangle, and the dotted green lines denote two *Ilex opaca* leaf exemplars. The thick gray line corresponds to the shade of gray that spiders preferred to cling to. Although the spectral content of the green stimulus and green leaves do not match perfectly, both stimuli should stimulate the salticid green photoreceptor more strongly than any other photoreceptors thus far described in jumping spiders (see Yamashita and Tateda, 1976; Zurek et al., 2015). When variation in viewing angle and illumination, as well as genetically and/or environmentally induced traits such as leaf thickness, waxy layer thickness and relative concentrations of chlorophylls a and b and carotenoids are taken into account, it is expected that the artificial green stimulus should fall within the range of natural spectral variation in green leaves (Gates et al., 1965; Breece and Holmes, 1971; Kwolek, 1982; Goncalves et al., 2001; Holmes and Keiller, 2002; Sims and Gamon, 2002; Buschmann et al., 2012).

In this and all subsequent tests, there were always some individuals who did not make a choice and were not perched on any of the stimuli we provided. These individuals were re-run on subsequent days, for up to 3 days, in an attempt to get them to make a choice.

Leaf shape

To test whether *L. viridis* prefer to perch on sweet gum leaf-shaped profiles, we gave them the choice to perch under a printout of a sweet gum leaf shape versus a circle. The sweet gum leaf-shaped stimulus was created by scanning in a real sweet gum leaf and then replacing its color and texture with a homogeneous green. The circle was made the same color. Spiders were run in two different tests: one in which the green circle was the same area as the leaf, and one in which the green circle was made to have the same diameter as the maximum diameter of the leaf. The arena consisted of a

Table 1. Integrated quantum flux values from the leaf color experiment

Color	Quantum flux (10^{16} photons s^{-1} m^{-2} sr^{-1})	Quantum flux×opsin template (10^{16} photons s^{-1} m^{-2} sr^{-1})
Gray 1	4	1
Gray 2	23	7
Gray 3	72	26
Gray 4	113	43
Gray 5	121	47
Green	37	17
Leaf 1	21	10
Leaf 2	16	8

Quantum flux was measured between 350 and 700 nm. The opsin template peaked at 530 nm.

420×290×140 mm plastic container with a clear Plexiglas sheet laid over the top of it. Leaf printouts were laid side-by-side face down on top of the Plexiglas, and which size of leaf was on which side was randomized for each individual (Fig. S2). The arena was illuminated from above by two full-spectrum (including ultraviolet) fluorescent mercury vapor tubes (T8, 32 W, 48 in, Duro-Test Lighting's Vita-Lite, Philadelphia, PA, USA), which were oriented along the long axis of the arena (see Fig. S3 for irradiance spectrum). Each spider was placed on the floor in the center of the arena under a downturned Petri dish and allowed to habituate to the chamber for 10 min. After this period, the Petri dish was removed if the spider was standing on the arena floor, or gently inverted if the spider was perched on the underside of the lid itself. The spider was then allowed to roam freely throughout the chamber for 3 h to choose which leaf to perch under.

Leaf size

To test whether *L. viridis* prefers to perch on larger or smaller leaves, we gave spiders a choice between the printed leaf described in the previous section and the same leaf scaled down to 50% of its original area. The experimental procedure was identical to that described above.

Ambient illumination

To test whether *L. viridis* might be attending to the ambient illumination under larger leaves, rather than the area or some linear dimension of the leaf itself, we again ran the leaf size experiment described above, but this time with a neutral density filter placed over the side of the arena with the smaller leaf. The neutral density filter decreased overhead illumination by 30% (filter no. 298, 0.15ND, Lee Filters, Burbank, CA, USA). As in the above experiments, we first tested whether the spiders that made a choice (i.e. those that settled on either the small or large leaf) still exhibited a size preference. We then analyzed all replicates of trials for all individuals from this and the previous experiment, ignoring whether or not spiders had chosen to perch on one of the leaves. Using the software program SuperMix (Scientific Software International, Skokie, IL, USA), we ran a generalized linear mixed model with a Bernoulli distribution and a logit link function to test whether spiders were more likely to be situated on the side of the arena with the small leaf after the addition of the neutral density filter than they had been before the filter was added. Specifically, the presence/absence of a neutral density filter over the small-leaved side of the arena was input as a fixed effect, with the outcome variable being the size class (large or small) of the leaf on the side of the arena the spider settled on. Individual identity was input as a random effect. We allowed the model to calculate both
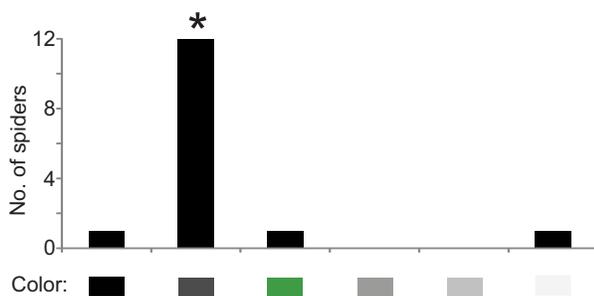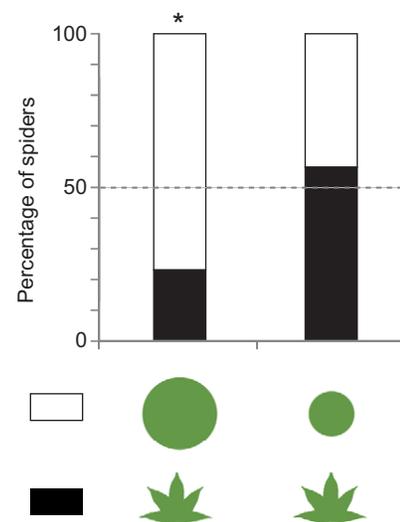

Fig. 3. Percentage of spiders choosing to cling to a sweet gum leaf-shaped stimulus as compared with a circular stimulus. Spiders had no preference when the leaf and circle were of the same area (exact binomial test, N=23, two-tailed P=0.68), but preferred the circle when its diameter equaled the maximum diameter of the leaf (i.e. when the circle's area was larger; exact binomial test, N=26, two-tailed *P=0.0094).

random slopes and intercepts, as well as to test for covariance between the two.

RESULTS

Lyssomanes viridis showed no preference for green over gray substrates, but did prefer the second darkest shade of gray (exact multinomial test, N=15, two-tailed P<0.0001; Fig. 2). Compared with the green and other shades of gray, this shade of gray was the

Fig. 2. Number of spiders choosing to cling to green versus five different shades of gray rectangles. Spiders preferred the second darkest shade of gray to green and all other shades of gray (exact multinomial test, N=15, two-tailed *P<0.0001).
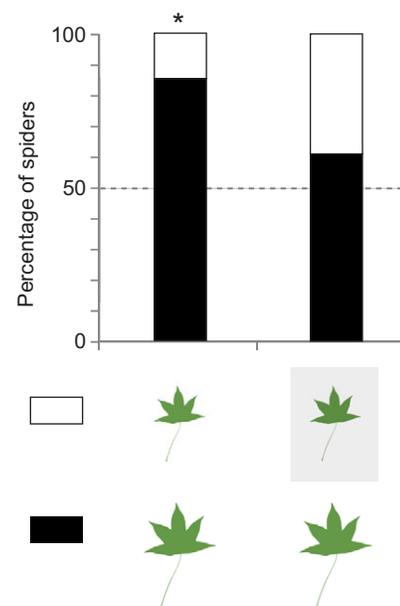

Fig. 4. Percentage of spiders choosing to cling to a larger versus smaller sweet gum leaf-shaped stimulus. When there was no neutral density filter present, spiders preferred the larger leaf (exact binomial test, N=28, *P=0.00091). This preference was abolished when a neutral density filter (shaded rectangle) was placed over the side of the experimental arena with the smaller leaf (exact binomial test, N=23, two-tailed P=0.41).

Table 2. Results of a generalized linear mixed model to test whether spiders were more likely to be situated on the side of the arena with the neutral density filter, regardless of whether the spider settled on the leaf or elsewhere (N=35)

Effect type			Two-tailed P
Fixed	Presence/absence of neutral density filter		0.012
Random	Individual identity:	random intercepts	0.96
		random slopes	0.95
		covariance between intercepts and slopes	0.96

most similar, in 350–700 nm integrated quantum flux, under natural light (i.e. woodland shade), to real leaves. It was also the shade most similar to real leaves in integrated quantum flux when we multiplied quantum flux by a Govardovskii opsin template peaking at 530 nm (Govardovskii et al., 2000) (Table 1).

Spiders showed no preference for the sweet gum leaf-shaped stimulus over the circular one when the two stimuli were of the same area (exact binomial test, N=23, two-tailed P=0.68), and preferred the circular one when it had the greater area (exact binomial test, N=26, two-tailed P=0.0094; Fig. 3). *Lyssomanes viridis* also preferred the larger leaf-shaped stimulus to the smaller one (exact binomial test, N=28, two-tailed P=0.00091). However, when a neutral density filter was placed over the side of the arena with the smaller leaf, this preference was abolished (exact binomial test, N=23, two-tailed P=0.41; Fig. 4). Furthermore, when all replicate trials of both leaf size experiments (including trials in which spiders did not choose a leaf) were run in a generalized linear mixed model, we found that spiders were significantly more likely to be situated on the side of the arena with the small leaf after the addition of the neutral density filter than they had been before the filter was added (N=35, two-tailed P=0.012). The model found no significant effect of individual (random intercepts two-tailed P=0.96, random slopes two-tailed P=0.95, covariance between intercepts and slopes two-tailed P=0.96; Table 2). A similar proportion of individuals chose to perch on one of the leaf stimuli (as opposed to no stimulus) in their first trial of both size experiments: 30% in the experiment without the neutral density filter and 36% in the experiment with the neutral density filter.

DISCUSSION

Our results suggest that *L. viridis* does not attend to the color or shape of leaves, but does have a visually mediated preference for a particular level of ambient illumination and possibly also perceived leaf brightness, which, in our experimental conditions, overrode any potential preference for leaf size. Importantly, if we had not controlled for an effect of leaf size on the ambient illumination in the area surrounding the leaf, we would have concluded that *L. viridis* was capable of judging the relative sizes of leaves using some parameter like relative area or a linear dimension. Although we cannot say for sure that leaf size is not assessed by *L. viridis*, we can say that ambient illumination was the more important factor in determining which leaf they settled under in our experimental conditions.

Because the integrated quantum flux of our green stimulus was somewhat higher than that of the preferred gray stimulus and of real leaves, we cannot say with certainty that color is a cue that *L. viridis* disregards completely. However, it is clear that ambient illumination or brightness of targets is the more important cue when there is competition between illumination/brightness and color.

It is interesting that color and fine spatial vision appear to play little role in helping *L. viridis* locate its preferred plant substrates,
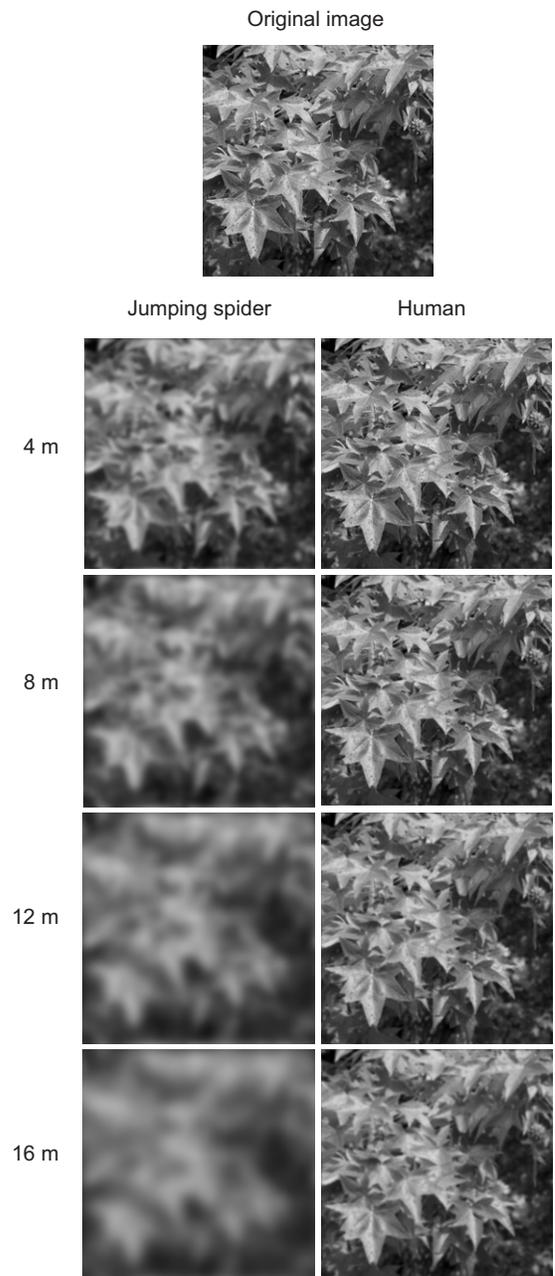

Original image

Jumping spider | Human

4 m

8 m

12 m

16 m

Fig. 5. Simulated visual acuity of a jumping spider versus a human looking at sweet gum leaves from different distances. We used Gaussian blurs with diameters matched to the interreceptor angle of adjacent photoreceptors in the fovea (see Caves et al., 2016, for details). As *L. viridis* appears not to use chromatic cues to identify leaves, we created grayscale images from the green channel of an RGB camera. This channel's transmission spectrum approximates the spectral sensitivity of a photoreceptor with peak sensitivity in the green portion of the spectrum. Original RGB image (not shown) courtesy of Eric Hunt.

given that other jumping spider species are known to have anatomically and physiologically impressive eyes with high visual acuity and the potential for color vision (DeVoe, 1975; Yamashita and Tateda, 1976; Williams and McIntyre, 1980; Blest et al., 1981; Zurek et al., 2015). Instead, it would appear that *L. viridis* must rely heavily on contact chemoreception, especially in the spring, sampling a number of trees before finding the species they depend upon for successful reproduction, i.e. sweet gum (Tedore

and Johnsen, 2015). That said, the visual cues they do use could potentially be more important in autumn and winter than one might initially expect. American holly should have a dark profile against a background of trees having lost their leaves. There are achromatic contrasts between green leaves and leaves undergoing seasonal color changes that spiders may attend to as well. Interestingly, during the winter, we have found *L. viridis* on the occasional broadleaf evergreen vine, which suggests that *L. viridis* may not have a species-specific preference for American holly during the winter per se, but rather a preference for the ambient illumination provided by any broadleaved evergreen species they can find in their habitat, provided it does not have chemical or mechanical properties that are repellent to them. Illumination and brightness preferences may additionally, or alternatively, help spiders find microhabitats that are not subject to rapid thermal changes, as would be experienced in areas receiving direct sunlight. Such preferences may also help protect *L. viridis* from UV damage, as these spiders are translucent and presumably not as well defended against harmful UV rays as other opaque and/or heavily pigmented species. In the field, we do not find *L. viridis* at habitat edges that receive direct sunlight for prolonged portions of the day.

Although we did not test whether *L. viridis* prefer a specific level of absolute illumination or, instead, a specific level of relative illumination scaled to, for example, the most brightly lit area of their habitat, it seems likely that their preference is a relative one. If their preference were an absolute one, these spiders would constantly be on the move, climbing to different parts of the canopy at different times of the day or when a cloud passed over the sun. Still, in future, it would be interesting to test whether and how much *L. viridis* responds to changes in the absolute brightness of its habitat.

As jumping spiders have the finest visual acuity among the arthropods, it is a bit surprising that *L. viridis* does not appear to have evolved a shape- or pattern-based mechanism of locating sweet gum. In contrast, the carrot fly *Psila rosae* has been shown to preferentially land and oviposit on artificial leaves shaped like its host species (Degen and Städler, 1997). In simulations of jumping spider visual acuity at different distances, we have found that the shapes of leaves against a natural background remain discernible at up to 4–8 m away (Fig. 5), so it does not appear that visual acuity should be the limiting factor here. An alternative explanation could be that jumping spiders conceive of shapes in a different way from humans. Dolev and Nelson (2014) found that *Evarcha culicivora*, a jumping spider specializing on mosquitos, did not distinguish between abstract images of intact mosquitos and a similar image in which the legs, body and antennae were disconnected and disarranged. However, they did discriminate between these images and a similar image in which the orientations of the body parts were not preserved. This suggests that jumping spiders identify objects by collections of disconnected oriented edges and do not attend to whether or not a shape is entire. A similar phenomenon seems to exist in honeybees (Zhang et al., 1995; Horridge, 1999, 2006, 2009). If jumping spiders do not perceive objects as entire, but rather as collections of oriented edges, then distinguishing leaf shapes may be a tricky task for them, as leaves occur jumbled together at various orientations and rotations in 3D space. More studies are needed to determine how common leaf shape discrimination is among arthropods, as well as the sensory and cognitive mechanisms behind it.

In conclusion, our study highlights the importance of including adequate controls in studies of visually mediated habitat preference. Although it is tempting to imagine that arthropods, particularly those with anatomically and physiologically advanced eyes, use vision extensively across a variety of different tasks in their daily lives, this is an assumption that needs to be more broadly tested with adequate controls to rule out alternative explanations for habitat-directed behaviors.

Author contributions
C.T. planned and executed the experiments, analyzed and interpreted the results, and wrote the manuscript. S.J. participated in analyzing and interpreting the results and in writing the manuscript.

Supplementary information
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