



Behavioral Ecology (2015), 00(00), 1–10. doi:10.1093/beheco/arv182

Original Article

Flexible color learning in an invertebrate predator: *Habronattus* jumping spiders can learn to prefer or avoid red during foraging

Lisa A. Taylor,^{a,b,c} Zarreen Amin,^a Emily B. Maier,^a Kevin J. Byrne,^a and Nathan I. Morehouse^a

^aDepartment of Biological Sciences, University of Pittsburgh, 4249 Fifth Ave., Pittsburgh, PA 15260, USA, ^bDepartment of Entomology and Nematology, University of Florida, 1881 Natural Area Dr., Gainesville, FL 32611, USA, and ^cFlorida Museum of Natural History, University of Florida, 3215 Hull Rd., Gainesville, FL 32611, USA

Received 23 November 2014; revised 19 September 2015; accepted 15 October 2015.

Understanding the design of prey defenses, such as aposematic colors, involves considering perceptual and cognitive abilities of predators that drive their evolution. Research has focused on avian predators, with little attention to small invertebrate predators. Jumping spiders are abundant and voracious; here, we examined their ability to learn, remember, and generalize color from interactions with aposematic prey. First, we demonstrated that *Habronattus pyrrithrix* can learn to avoid red, aposematic milkweed bugs. Then, we asked whether exposure to either palatable or unpalatable red prey can drive generalized color biases. Spiders were assigned to one of 3 diets that included exposure to 1) distasteful red milkweed bugs (fed milkweed seeds), 2) palatable red milkweed bugs (fed sunflower seeds), or 3) white-eyed *Drosophila* only (control). After exposure, we tested spiders for red biases using artificially colored crickets. In our first color-learning experiment, field-collected adult spiders did not exhibit generalized color biases. However, in a second (similar) experiment with lab-raised juveniles, we found evidence of generalized color learning: Group 1 demonstrated red aversion, Group 2 demonstrated red preference, and Group 3 showed no bias. Finally, we examined persistence of memory and found that learned aversions to milkweed-fed bugs lasted less than 2 weeks if they were not continuously reinforced. We discuss our findings in the context of predator psychology and suggest that jumping spider color generalization may differ from that of avian predators. Such invertebrate predators should be considered more when thinking broadly about the evolution of prey color.

Key words: aposematism, color learning, *Habronattus*, predator psychology, red aversion, Salticidae.

INTRODUCTION

Understanding the design of prey defenses requires consideration of the perceptual and cognitive abilities of the predators that drive their evolution. The importance of predator psychology has been long recognized (e.g., Endler 1978; Guilford and Dawkins 1991) and recently reiterated in the literature (e.g., Miller and Bee 2012; Rowe 2013). Attention to this idea has driven hundreds of studies examining how the psychology of key predators, mainly birds, has shaped the evolution of color in insect prey (reviewed in Ruxton et al. 2004). Yet, many terrestrial invertebrate predators feed on these very same prey items (Hajek 2004). These predators often exhibit color vision (Kelber 2006) and growing evidence suggests that they exhibit sophisticated cognitive abilities (e.g., insects: Giurfa 2013). Although a handful of empirical studies suggest that the psychology of invertebrate predators may play a critical role in

their interactions with colorful prey (e.g., Berenbaum and Miliczky 1984; Losey et al. 1997; Kauppinen and Mappes 2003; Rashed et al. 2005; Hill 2006; Langley et al. 2006; Skow and Jakob 2006), such studies on invertebrates are notably, and surprisingly, absent from broader theoretical discussions of predator psychology (e.g., reviewed in Guilford 1992; Ruxton et al. 2004; Miller and Bee 2012; Rowe 2013). The perceptual and cognitive abilities as well as the foraging behavior and ecology of tiny terrestrial invertebrate predators differ in fundamental ways from those of avian predators, thus providing important opportunities for testing current hypotheses about how colors should (and do) evolve in nature.

The visual systems of terrestrial invertebrates are diverse and often highly specialized (Land and Nilsson 2012); this diversity in morphology and function differs markedly from the relatively conserved visual system shared by all birds (Hart and Hunt 2007). As such, invertebrate predators will likely interact with visual signals from their prey in ways that are distinct from our visual world or that of other vertebrates. For example, among invertebrate predators,

Address correspondence to L.A. Taylor. E-mail: lat12@cornell.edu.

eyes vary widely in their visual acuity as well as their ability to perceive patterns of polarized light (reviewed in Land and Nilsson 2012) and their ability to discriminate color (Kelber 2006). In spiders, most species have 4 pairs of functionally differentiated eyes ranging in visual competency from simple light detection to motion detection to image formation and color discrimination (Foelix 2011). In jumping spiders (Salticidae), the largest forward-facing eyes have a unique mechanism of depth perception that relies on image defocus of wavelength-specific light such that objects illuminated with red light appear closer to an observer than objects illuminated with green light (Nagata et al. 2012); this phenomenon may have implications for how colored objects are perceived.

The foraging behavior and ecology of small invertebrate predators also differs in fundamental ways from those of avian predators in ways that likely affect the selection pressures placed on colorful prey. For example, avian predators peck (and often kill) prey items during the process of learning; this aspect of the predator–prey interaction has led to the often-cited “paradox” for the initial evolution of aposematic coloration: New colorful and chemically defended mutants that emerge in a population are likely to be quickly driven to extinction by naive predators that kill them in the process of learning to associate their colors with chemical defense (reviewed in Ruxton et al. 2004). Many potential solutions to this “paradox” have been proposed with avian predators, only occasionally invoking the idea that predators may catch and release prey without killing it (e.g., Wiklund and Jarvi 1982; Sillen-Tullberg 1985; Wiklund and Sillen-Tullberg 1985; Engen et al. 1986). Unlike birds, tiny invertebrates often attack prey much larger than themselves and very often release chemically defended prey unharmed (e.g., wolf spiders attacking bella moths: Eisner T and Eisner M 1991; jumping spiders attacking milkweed bugs: Hill 2006; jumping spiders attacking fireflies: Gronquist et al. 2006) allowing a new aposematic mutant to immediately benefit from its novel coloration. This difference in the predator–prey interaction may drastically change how colors evolve. Moreover, small invertebrate predators often occur in large numbers and their numbers respond quickly to fluctuations in prey quantity; as such, they have been shown to be extremely important in regulating populations of prey in both agricultural (e.g., Symondson et al. 2002) and natural ecosystems (e.g., Wise 1993). In sum, these understudied predators are likely to be important, as well as fundamentally different, drivers of prey color patterns than avian predators on which most of the predator psychology literature is built.

Jumping spiders (family Salticidae) are promising candidates to expand our understanding of predator psychology and the evolution of prey colors. Salticids have excellent vision, including exceptional

visual acuity for their small size (Williams and McIntyre 1980). In a number of species, behavioral experiments have revealed the ability to discriminate colors in a variety of contexts, including courtship (Lim et al. 2007; Taylor and McGraw 2013), navigation (Hoeffler and Jakob 2006), and, importantly, prey selection (Li and Lim 2005; Taylor et al. 2014). Very recent work has shown that at least 1 genus (*Habronattus*) makes use of intraretinal filter pigments to achieve trichromatic vision (Zurek et al. 2015). Jumping spiders are voracious predators (Jackson and Pollard 1996) and show a remarkable capacity for learning in the context of foraging (reviewed in Jakob et al. 2011), as well as complex decision making during prey choice (e.g., Harland and Jackson 2000; Nelson and Jackson 2012). This taxonomic family includes more than 5500 species (Platnick 2013) many of which are common and abundant in a variety of habitat types (Richman et al. 2005). Salticids are found on every continent except Antarctica (Maddison et al. 2008); thus, they may play a role in shaping the evolution of color patterns of insect prey in many ecosystems. Indeed, salticids have been specifically implicated in driving the evolution of morphological and behavioral defenses in a variety of small invertebrate groups (e.g., flies: Mather and Roitberg 1987; moths: Rota and Wagner 2006; other spiders: Huang et al. 2011; fireflies: Long et al. 2012; butterflies: Sourakov 2013). Previous work has shown that 3 species of salticids (all *Phidippus* sp.) can learn to avoid aposematic prey items (milkweed bugs: Hill 2006; Skow and Jakob 2006; flashing fireflies: Long et al. 2012).

Despite knowing that some jumping spiders can learn to avoid aposematic prey, we know nothing about how interactions with colorful aposematic prey influence the formation of general color biases in foraging. Thus, we chose to evaluate the role of color learning in the jumping spider *Habronattus pyrithrix*, with a particular emphasis on learning of the color red. We have focused here on red for several reasons. First, a series of recent studies have revealed the mechanism by which these spiders see red (Zurek et al. 2015) and have also shown that red is salient to this species in the context of both foraging (Taylor et al. 2014) and mating (Taylor and McGraw 2013). Individuals of both sexes and various age groups attack red and yellow prey items at relatively low rates compared with other colors and these color biases appear to have both innate and learned components (Taylor et al. 2014). This is not surprising; in their natural habitat in Arizona, most of the red food items that they encounter are chemically defended (e.g., milkweed bugs [Lygaeidae], ladybird beetles [Coccinellidae] [Taylor L, personal observation]). Red is also a salient feature of a male’s courtship display; males display brilliant red patches of color on their faces (see Figure 1) to drab females and the presence of this red coloration improves a male’s courtship success (Taylor and McGraw 2013).



Figure 1
Habronattus pyrithrix (a) female and (b) male. Photos by C. Hutton.

The prominence of red ornaments in male courtship offers the intriguing possibility that preferences and/or aversions learned in foraging might spill over and influence how a female responds to red in the context of courtship.

The present study had 3 overarching goals. First, we asked whether *H. pyrrithrix* (Figure 1) can learn to avoid red, aposematic prey. In light of our findings that *H. pyrrithrix* can indeed learn to avoid red aposematic milkweed bugs with experience, a second goal was to examine flexibility in these learned responses by asking whether bug aversions were remembered after 2 weeks without exposure to them. Finally, we went on to examine the role of the color red in the learning process. Specifically, we asked whether differential exposure to either palatable or unpalatable red prey can drive generalized color biases (either preferences or aversions) when encountering the same colors in a different prey item. Because these spiders are voracious generalist predators that will attack a wide variety of prey items in the field, how jumping spiders learn has clear implications for the selection pressures that drive the evolution of color in their prey communities.

METHODS

Study species

Predators

Habronattus pyrrithrix Chamberlin 1924 (Figure 1) is a common jumping spider distributed from southern California and Arizona, USA, south to Sinaloa, Mexico. In Phoenix, AZ, they are found at high densities in leaf litter in natural riparian areas as well as in heavily managed agricultural areas and grassy urban and suburban lawns (Taylor L, personal observation).

Prey

Because we were interested in examining color learning in *H. pyrrithrix*, with a particular emphasis on the color red, we used the large milkweed bug, *Oncopeltus fasciatus*, as a training stimulus. These red and black aposematic bugs are able to sequester cardenolides from milkweed (*Asclepias* sp.) for their own defense; because of their history as a model organism, we have extensive information about their basic biology (reviewed in Feir 1974). In the field, milkweed bugs vary drastically in their toxin content (and, thus, their palatability) (Isman et al. 1977). Importantly, the toxin content of *O. fasciatus*, and thus their palatability to jumping spiders, can be easily manipulated through diet in captivity. Specifically, previous work has shown that if these bugs are reared on sunflower seeds (*Helianthus* sp.), they are palatable to jumping spiders (*Phidippus* sp.) and will be readily consumed; however, if these same bugs are reared on milkweed seeds (*Asclepias* sp.), they will initially be attacked, but subsequently rejected and spiders will learn to avoid attacking these bugs in future encounters (Hill 2006; Skow and Jakob 2006). Given the natural variability in milkweed bug palatability in the field (Isman et al. 1977), such methods allow us to create ecologically relevant prey manipulations that span the range of possible prey types these spiders could encounter and learn from under natural conditions.

Study 1: initial tests of learning, color generalization, and memory

Our first study consisted of 3 components. First, in Experiment 1, we exposed field-collected *H. pyrrithrix* to one of 3 experimental prey communities (i.e., “training diets”) to determine if the spiders

could learn to avoid chemically defended red milkweed bugs. Second, in Experiment 2, on finding that these spiders did learn to avoid red milkweed bugs, we then examined whether they also had learned generalized color biases (preferences or aversions to the color red) from their “training diets” that would carry over across feeding contexts to other types of red prey. Finally, in Experiment 3, we examined whether their learned avoidance of the chemically defended milkweed bugs (demonstrated in Experiment 1) persisted after 2 weeks without exposure to their “training” diets.

Study 1 collection and housing

We collected *H. pyrrithrix* from a single population in Queen Creek, AZ (Maricopa County), (33°13'29"N, 111°35'34"W) between 26 April 2012 and 1 May 2012. We housed spiders individually in clear plastic containers (5.5 cm tall and 2.5 cm in diameter) in the laboratory for use in a related but separate, non-manipulative study of natural color biases, where spiders were given the opportunity to choose between arrays of artificially colored crickets immediately after being collected from the field (see Taylor et al. 2014). During this time, we fed spiders 3 times per week with white-eyed *Drosophila melanogaster*, a prey item selected to avoid inadvertently modifying color biases in these field-collected individuals (for more details on specific rearing protocols, see Taylor et al. 2014). Because the arrays of colored crickets presented to the spiders during this previous experiment were identical and because all colored prey items were equally palatable, we have no reason to think that it created learned color preferences or aversions in these field-collected spiders that would bias the results of the present study. It is also important to note that these field-collected spiders were very likely not color-naïve, but rather came into the lab with natural variation in experience. Although this likely adds additional variation in individual responses to prey items, we are ultimately interested in whether feeding preferences can be shifted in predictable ways, regardless of pre-existing variation present in a natural population.

After the completion of the natural color bias experiment, spiders were housed in larger clear plastic cages (10.16 × 10.16 × 12.86 cm³) for the entirety of the present study. The cages sat on a white paper surface that provided a bright visual background for spiders foraging on the floor of the cages. Each cage had an artificial green plant (approximately 10 cm long, Ashland Fern Collection, Michael's Stores, Irving, TX) that was affixed to the side of the cage to provide enrichment (e.g., Carducci and Jakob 2000), and cages were separated with opaque white barriers so that spiders could not see and interact with neighboring spiders. As discussed above, previous work in *H. pyrrithrix* suggested that the light environment influences the efficacy of color signals, with the color red being more salient to the spiders interacting in natural sunlight (Taylor and McGraw 2013). Thus, we conducted this entire study in a laboratory setting with ample natural light; specifically, fluorescent laboratory lighting was supplemented with natural light from 2 large windows (1.6 × 1.7 m²) immediately adjacent to where the spiders were housed. All choice tests (described below) were run only on sunny days.

Study 1 training protocols

On 23 July 2012, we randomly assigned a subset of the spiders described above ($n = 95$, 58 females and 37 males) to one of 3 treatment groups where they were fed different combinations of prey 3 times per week (more detail on prey quantity is provided below). The control group was fed only white-eyed fruit flies (*D. melanogaster*) that were readily consumed by the spiders. The “toxic red bug”

group was fed white-eyed fruit flies and unpalatable red milkweed bug nymphs (*O. fasciatus*, approximately 3 mm in length, reared on common milkweed seeds, *Asclepias syriaca*); whereas the spiders initially attacked the unpalatable milkweed bugs, they were always rejected (uneaten) and the spiders only consumed the flies. The “palatable red bug” group was fed only palatable red sunflower-fed milkweed bug nymphs (*O. fasciatus*, approximately 3 mm in length, reared on raw sunflower seeds, *Helianthus annuus*) that always were readily consumed by the spiders.

Each feeding consisted of a quantity of edible prey items (i.e., flies and/or palatable sunflower-fed bugs) approximating one-half of the individual spider’s own body mass as this feeding regime results in spiders with body condition indices that fall within the natural range of variation of those collected from the field (Taylor L, unpublished data). In addition, for the “toxic red bug” group we ensured that there were always 3 healthy unpalatable milkweed-fed bugs in the spiders’ cage at each feeding. Because we were interested in manipulating the spiders’ experience with prey, but not their nutritional condition (and subsequent motivation to feed), we monitored body condition (using the residual index in Jakob et al. 1996, a common method of measuring body condition in spiders) throughout the experiment to ensure that our 3 treatment groups of spiders did not differ.

Experiment 1: do *H. pyrrithrix* learn to avoid toxic bugs?

After 2 weeks on the training regimes outlined above, we ran Experiment 1 where we tested the spiders (all of which were mature adults at this stage) to determine if their feeding treatments influenced their likelihood of attacking a palatable sunflower-fed bug. Given their training regimes, we predicted that spiders in the “toxic red bug” group that had 2 weeks of experience with only unpalatable milkweed-fed bugs would assess a palatable sunflower-fed bug using visual cues and avoid attacking it, despite its lack of chemical defense. In contrast, we predicted that spiders in the “palatable red bug” group that had only positive experience with palatable sunflower-fed bugs would readily attack. For this test, we removed spiders from their training cages and placed them individually in clear plastic containers with white floors (5.5 cm tall and 2.5 cm in diameter). After a 2-min acclimation period, a palatable sunflower-fed bug (approximately 3 mm in length) was introduced to the center of the floor of the container. Spiders were monitored for 2 h, and we recorded whether an attack took place (and if so, the time of the attack). After the 2-h experiment, any remaining prey was removed and spiders were returned to their home cages and their training diets were resumed in preparation for Experiment 2.

Experiment 2: first test of generalized color biases

On finding that our “training” diet treatments did indeed influence a spider’s likelihood of attacking a sunflower-fed bug (i.e., spiders exposed to unpalatable bugs learned to avoid them, see Results for details), we went on to examine whether our diet treatments resulted in generalized color biases when attacking a novel prey item (in this case, artificially colored crickets) (Experiment 2). We created colored crickets by adding food dye (Market Pantry Assorted Food Color, Target Corporation, Minneapolis, MN) to the water source of hatchling crickets (*Acheta domesticus*, ca. 3 mm in length) following previously published methods (Taylor et al. 2014). Because crickets are translucent at this developmental stage, drinking colored water causes their bodies to quickly take up the color of the dye (Figure 2a). Red crickets were given red dye (10 drops per 20 mL of water), whereas “control” crickets were given a dilute mixture

of red, green, yellow, and blue dye (one drop each diluted in 4 L of water); this dilute mixture was intended to control for any effect of food coloring while appearing similar in coloration to a natural brown undyed cricket (Figure 2b). After dyeing, we measured the body mass and activity level (percentage of time spent moving) of a subset of each color category to confirm that the presence of the dye did not affect the crickets’ behavior. Our 2 categories of dyed cricket exhibited no differences in body mass or activity level from each other, and furthermore, they did not differ from undyed crickets (Anova, body mass: $F_{2,27} = 1.18$, $N = 30$, $P = 0.32$; activity level: $F_{2,27} = 0.42$, $N = 30$, $P = 0.66$).

One day prior to our generalized color bias test, all “training” prey (milkweed bugs and/or flies) were removed from the test spider’s home cage. At the start of each trial, we simultaneously introduced 4 crickets (2 red and 2 brown) into the center of the white floor of the cage. We monitored the spiders for 2 h and recorded which color was attacked first and the time of attack. Once a cricket was attacked, the trial ended and the other crickets were removed from the cage. If no crickets were attacked in 2 h, we removed all crickets and the spiders were retested on the following sunny day. Conveniently, the data collected in Experiment 2 also allowed us to determine whether our 3 diet treatments differed in overall predatory motivation; we compared the time it took the spiders to make their first cricket attack and compared this among the 3 treatment groups. This allowed us to rule out the possibility that spiders raised with unpalatable milkweed bugs (“toxic red bug” group) developed an overall reduced prey attack rate (rather than learning to specifically avoid milkweed bugs).

Experiment 3: how persistent are learned aversions to toxic prey?

Several jumping spider species have shown flexibility in predatory behavior based on experience (Jakob et al. 2011), but little work has been done to examine how long such learned behaviors last (but see Hill 2006). Thus, in a final experiment (Experiment 3) with this same group of spiders, we went on to test whether spiders retained their prey preferences demonstrated in Experiment 1 after 2 weeks without exposure to any bugs (i.e., after they were removed from their “training diets” for 2 weeks). The spiders in all 3 treatment groups (“toxic red bug,” palatable red bug,” and control) were fed a diet of only white-eyed fruit flies for 2 weeks; as above, each feeding consisted of approximately one-half of the individual spider’s own body mass. All spiders were then tested for their likelihood to attack a palatable sunflower-fed bug, following the methods described in Experiment 1.

Study 2: modified color-learning experiment (a second test of generalized color biases)

In light of findings from the experiments in Study 1 (in particular, that spiders learned to avoid unpalatable milkweed-fed bugs but did not learn to generalize their avoidance of the color red), we went on to conduct Experiment 4 to further examine the potential for learned color generalization. Here, we altered our experimental training regime and again tested for color biases for and against the color red. Our goal in changing our training regime and experimental protocols was simply to increase the opportunity for color learning; we were not aiming to identify the specific features responsible for any differences in our results. There were several differences between Study 1 and 2. First, in contrast to Study 1, which involved field-collected spiders, Study 2 (Experiment 4) involved their first-generation progeny that were reared entirely in the lab

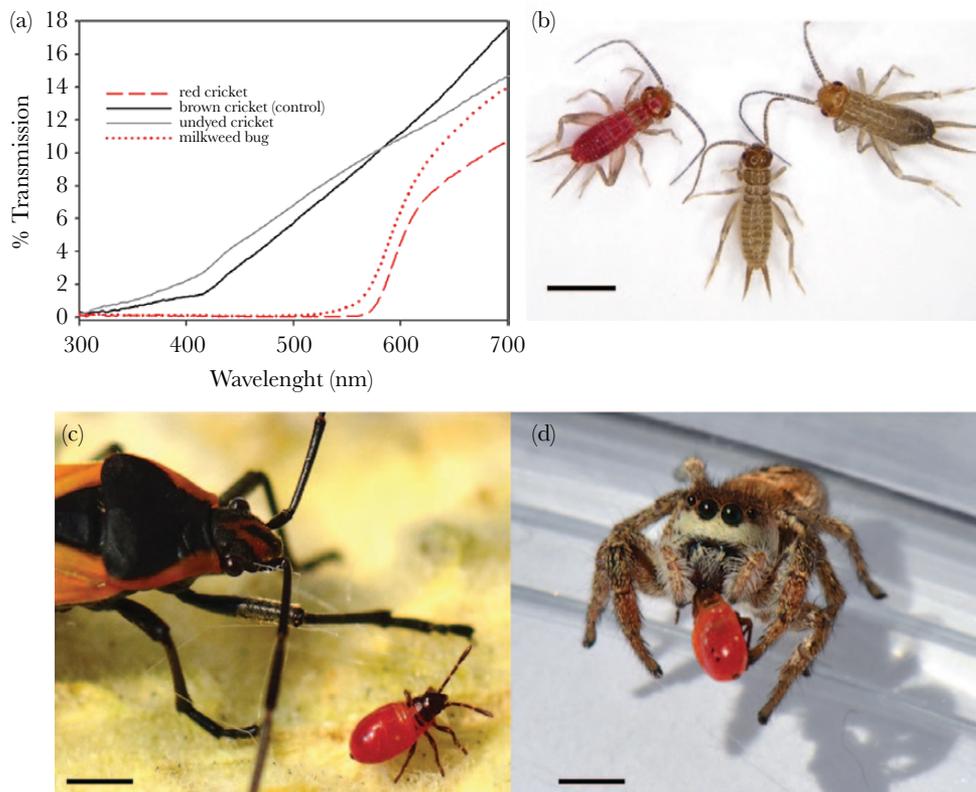


Figure 2

(a) Spectral properties of prey items (colored crickets and milkweed bug nymphs) used throughout the study. Spectral measurements were collected from a 20 μm diameter region of the abdomen with a full-spectrum microspectrophotometer and 75W xenon light source (20/20 PV, CRAIC Technologies, Inc., San Dimas, CA). (b) Artificially colored red (left) and brown/control crickets (right) used in prey color choice experiments. A naturally colored undyed cricket is shown in the center for reference. (c) Milkweed bug adult (left) and nymph (right). (d) Adult female *Habronattus pyrrithrix* feeding on a milkweed bug nymph. Scale bars represent 2 mm.

($n = 52$; 29 juvenile females, 23 juvenile males). We reared these individuals from the egg sacs of 35 field-mated females; to maximize genetic diversity in this lab population, no more than 4 spiderlings from any one clutch were included and those from a single clutch were divided randomly among treatments. On hatching, spiderlings were housed communally in their mother's cage where they were fed a combination of gray and brown springtails (Sminthuridae) and pinhead crickets (*A. domesticus*) until their first molt when they were large enough to capture white-eyed fruit flies (our standard laboratory diet for this study); at this point, they were transitioned to individual cages and all rearing and housing conditions were as described above.

Study 2 training and testing protocols

As small juveniles, spiders in Study 2 were assigned to one of 3 treatment groups that were similar, but not identical, to those in Study 1. As in Study 1, the control group was fed only white-eyed fruit flies, whereas the “toxic red bug” group was fed white-eyed fruit flies and unpalatable milkweed-fed bugs. In contrast to Study 1 where the “palatable red bug” group was given only palatable sunflower-fed bugs, in Study 2 this group was also supplemented with white-eyed fruit flies. The rationale for this change came from close observations of how these spiders were interacting with their prey during Study 1. We wanted to increase the likelihood that these spiders would develop a preference for red prey; this new diet trained them to actively choose the slower-moving flightless sunflower-fed bug nymphs over the faster moving and more difficult to capture flies. In contrast, our feeding regime in Study 1 did not give the

spiders an opportunity to choose the milkweed bugs over another, less profitable, option. As in Study 1, feeding consisted of a quantity of edible prey items (i.e., flies and/or palatable bugs) approximating one-half of the individual spider's own body mass 3 times per week.

We also made a second change to our experimental setup to increase the likelihood of successful training. There is evidence in another jumping spider species (*Phidippus princeps*) that while they can be trained to avoid distasteful milkweed bugs, this association is only retained if spiders are tested in the same environment in which they were trained; negative associations with milkweed bugs learned in one environment were lost if spiders were tested in a novel environment (Skow and Jakob 2006). Our results from Experiment 1 indicate that *H. pyrrithrix* can learn and remember to avoid milkweed bugs, even if they are tested in a different cage than where they received their training (see Results for details); however, it is possible that generalized color biases are more context specific and thus we might expect them to be expressed only if testing conditions are identical to where the spider's training took place. For this reason, in Study 2, we modified our testing regime: Rather than removing stimulus prey prior to the color choice test, we left all prey present for the duration of the test; this meant that flies and/or milkweed bugs were actively moving around in the spiders' cage during the time that they were choosing among the colored crickets. Given the often gregarious nature of aposematic prey (Ruxton et al. 2004), this testing scenario might more closely resemble the conditions where a predator should generalize their color biases in nature. The rest of the protocols followed those described above for Experiment 2 (i.e., colored crickets were introduced to the white floor of the spider's cage and all attacks were recorded).

Statistical analyses

For Study 1, we used Anova to confirm that our diet treatments had no differential effects on body condition. Because the residual body condition index commonly used in spider studies (Jakob et al. 1996) depends on allometry, which differs between the sexes in *H. pyrithrix* (Taylor L, unpublished data), body condition indices were calculated separately for each sex, and studentized values were used in analyses.

For Experiment 1, to determine if the spiders exposed to milkweed-fed bugs were indeed learning to avoid attacking them (compared with spiders exposed to sunflower-fed bugs or no bugs [control group]), we compared likelihood of bug attack during the 2-h trial using binary logistic regression with training treatment, sex of the spider, residual body condition, and the interaction between sex and training treatment as factors in the model. Sex was included in the model because females of this species are typically more voracious than males and thus we might expect higher attack rates from females compared with males (Taylor et al. 2014). Condition was included in the model because we might expect that hungrier individuals (with lower condition values) would be more likely to attack. The interaction between sex and training treatment was included to assess whether males and females were responding differently to the treatment (i.e., whether one sex was better at learning to avoid the bugs than the other). Finally, to rule out the possibility that our treatment groups differed in overall predatory motivation (as opposed to learned avoidance that was specific to milkweed bugs), we used a nonparametric Kruskal–Wallis test to compare the time it took these same spiders to attack their first cricket in Experiment 2.

For Experiment 2, to determine if spiders trained on the different diets developed generalized red preferences or aversions, we used binary logistic regression to determine if diet treatment influenced attack rate on red versus control (brown) crickets. Our prior work demonstrated a lack of sex differences in color-based predation (Taylor et al. 2014) and here we find no evidence for sex differences in learning ($P > 0.05$). Thus, to make effective use of the statistical power provided by our experimental design, we did not include sex as a factor in our model.

Finally, for Experiment 3, to determine if the spiders in the “toxic red bug” group remembered to avoid attacking milkweed bugs, we compared likelihood of bug attack using the same binary logistic regression model described for Experiment 1.

For Study 2 (Experiment 4), to determine if there were differences among the treatment groups in the color of prey first attacked, we used the same logistic regression model described above for Experiment 2. Because we used up to 4 spiderlings from each clutch, we tested for differences in attack latency and color bias among the different clutches; because we found none ($P = 0.53$ and 0.47 , respectively), we did not include clutch as a factor in our model.

To aid in the interpretation of our results, we provide effect sizes (odds ratios and their 95% confidence intervals [CIs]), where appropriate. Odds ratios with narrow CIs encompassing unity (1) indicate the strongest support for the null hypothesis (i.e., no effect) (see Nakagawa and Cuthill 2007). All statistical analyses were performed using JMP 11.1.1.

RESULTS

Study 1

Our 3 training diets (“toxic red bug,” “palatable red bug,” and control) had no differential effect on body condition (Anova, $F_{2,92} = 1.03$, $P = 0.36$). In Experiment 1, spiders exposed to unpalatable milkweed-fed bugs during their training period (i.e., the “toxic red bug” group) learned to avoid them; they were less likely to attack a palatable sunflower-fed bug during Experiment 1 (Table 1, Figure 3a). Interestingly, the spider’s training treatment was the only factor that predicted bug attack; neither sex nor condition had any effect (Table 1). There was no interaction between sex and training treatment, suggesting that the sexes did not respond differently to our training treatments (Table 1). Moreover, we found that the predatory inhibitions that the “toxic red bug” group showed toward milkweed bugs were not a general reduction in predatory motivation as we found no evidence in Experiment 2 that our 3 training treatments differed in the time it took them to

Table 1

Results of logistic regression examining the effect of our training treatments, as well as sex, body condition, and the training treatment × sex interaction, on the willingness of *Habronattus pyrithrix* to attack a palatable sunflower-fed bug in Experiment 1 (immediately following training) and Experiment 3 (after training stimuli had been removed for 2 weeks)

	χ^2	df	<i>P</i>	Odds ratio	Lower 95% CI	Upper 95% CI
Experiment 1: do spiders learn to avoid toxic bugs?						
Whole model test	14.56	6	0.02			
Lack-of-fit test	103.93	88	0.12			
Likelihood ratio effect tests						
Training treatment	13.09	2	0.001	6.37 ^a	1.66	36.32
Sex	<0.001	1	0.99	1.00	0.34	3.38
Body condition	0.35	1	0.55	0.86	0.52	1.41
Training treatment × sex	0.03	2	0.98			
Experiment 3: do spiders remember their learned avoidance of bugs after 2 weeks?						
Whole model test	1.83	6	0.93			
Lack-of-fit test	95.91	73	0.04			
Likelihood ratio effect tests						
Training treatment	0.90	2	0.64	1.73 ^a	0.47	6.87
Sex	0.41	1	0.52	0.72	0.26	2.00
Body condition	0.10	1	0.76	0.92	0.53	1.61
Training treatment × sex	0.98	2	0.61			

Significant *P* values are shown in bold.

^aOdds ratios provided for training treatments compare the “palatable bug diet” versus the “toxic bug diet.” Odds ratios with narrow CIs encompassing unity (1) indicate the strongest support for the null hypothesis (i.e., no effect) (see Nakagawa and Cuthill 2007).

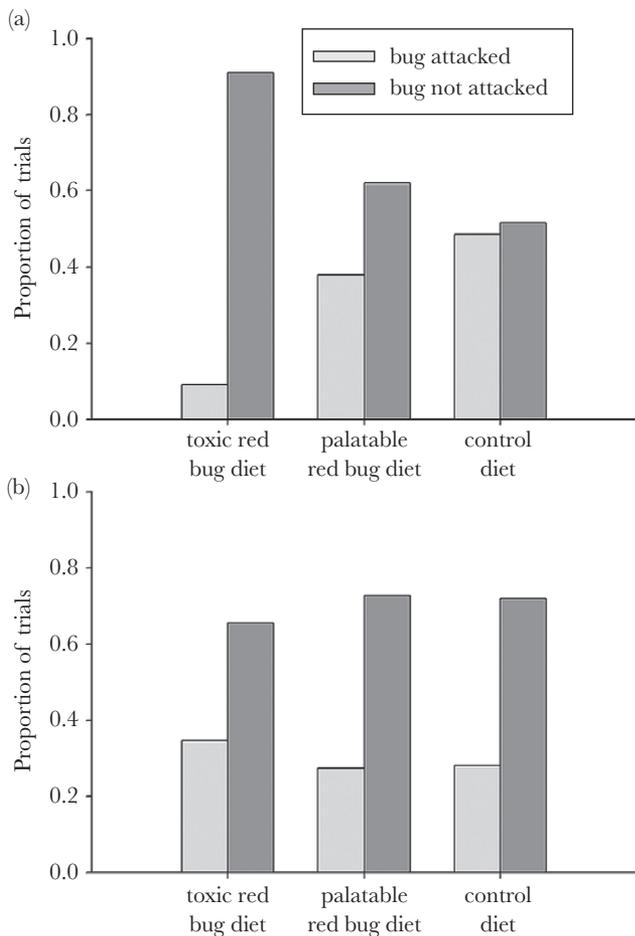


Figure 3

Proportion of trials in which a test sunflower-fed bug was attacked by *Habronattus pyrrithrix* trained on 3 different diet treatments. (a) Immediately following 2 weeks of exposure to training diets, those on the “toxic red bug diet” were less likely to attack the bug (Study 1, Experiment 1). (b) After 2 weeks without exposure to training (i.e., after being removed from their training diets for 2 weeks), there were no differences in propensity to attack among the 3 groups (Study 1, Experiment 3). Also, note the lower overall attack rates in Experiment 3, which may be due to decreased voracity as individuals become acclimated to the lab.

attack their first cricket (Kruskal–Wallis test, $\chi^2 = 1.30$, degrees of freedom [df] = 2, $P = 0.52$).

In Experiment 2, we found no evidence that our training treatments led to generalized preferences or aversions to the color red as there was no difference between the treatment groups in the color of cricket (red vs. control) first attacked (logistic regression, $\chi^2 = 0.50$, df = 2, $P = 0.78$; Figure 4a). The odds ratio comparing the “toxic red bug” diet with the “palatable red bug” diet was 1.33 (95% CI: 0.46, 3.92); thus, being in the “palatable red bug” group increased the odds of attacking a red cricket by a factor of only 1.33, a value not significantly different from unity.

In Experiment 3, after 2 weeks without training, we found no evidence that spiders remembered their aversions demonstrated in Experiment 1 (Table 1, Figure 3b).

Study 2

In Experiment 4 (modified to increase the opportunities for learning and memory), we found that our training diets did indeed lead to generalized preferences and aversions toward the color red. Our

diet treatment groups differed in the color of the crickets that the spiders chose with the “toxic red bug” group showing low attack rates on red, the “palatable red bug” group with high rates of attack on red, and the control group showing intermediate rates of attack on red (logistic regression, $\chi^2 = 7.07$, df = 2, $P = 0.029$, Figure 4b). The odds ratio comparing the “toxic red bug” diet with the “palatable red bug” diet was 7.15 (95% CI: 1.64, 37.42); thus, being in the “palatable red bug” group increased the odds of attacking a red cricket by a factor of 7.15.

DISCUSSION

Here, we show that *H. pyrrithrix* jumping spiders not only learn to avoid red chemically defended prey items (milkweed bugs, *O. fasciatus*) but that, given the right learning environment, exposure to different combinations of prey can lead to generalized preferences or aversions to the color red. Although previous studies with other species of jumping spiders have shown that they can learn to avoid chemically defended prey (Hill 2006; Skow and Jakob 2006) and that they can associate specific colored stimuli (e.g., colored paper or blocks) with either rewards (e.g., Jakob et al. 2007) or punishment (e.g., Nakamura and Yamashita 2000), this is the first to show that spiders can learn generalized preferences and aversions to color. Specifically, a color learned from one predator–prey interaction (foraging on red milkweed bugs) is generalized and applied to interactions with other prey types (foraging on artificially colored red crickets). In addition, consistent with previous findings from other jumping spider species (e.g., Hill 2006), we found that learned responses were relatively transient and flexible; spiders that had learned to avoid chemically defended milkweed bugs did not retain this memory if their training stimulus was removed for a period of 2 weeks.

Implications for the field of predator psychology and the evolution of prey coloration

The fact that jumping spiders can learn color and develop prey color biases that carry over across prey taxa (from milkweed bugs to crickets) has important implications for the selection pressures that shape color patterns in communities of invertebrate prey, particularly because these patterns of color learning differ subtly from those seen in better-studied avian predators. There is a large body of work describing the extent to which avian predators learn to avoid chemically defended insects across a range of taxa (reviewed in Ruxton et al. 2004); even if we just focus our attention on studies examining avian predators and their interactions with red and black aposematic true bugs (order Hemiptera), we find varied levels of color learning and generalization. For example, domestic chicks (*Gallus gallus domesticus*) trained to avoid small red and black seed bug nymphs (Lygaeidae) generalized this aversion to large red and black seed bug nymphs (Gamberale-Stille and Tullberg 1996) and generalization also occurred when chicks were fed bugs of similar shape, but different degrees of red (Gamberale-Stille and Tullberg 1999). Great tits (*Parus major*) transferred learned aversions across 4 species of chemically defended bugs (families Lygaeidae, Pyrrhocoridae, and Pentatomidae); if they learned to avoid one, they subsequently avoided the others (Svádová et al. 2013). Similarly, common quail that learned to avoid one species of red and black bug also transferred this avoidance to red and black bugs in 2 other families (Cercopidae, Lygaeidae, and Pentatomidae; Evans et al. 1987). However, these generalizations are fairly narrow (being transferred from one type of aposematic hemipteran bug to another), and

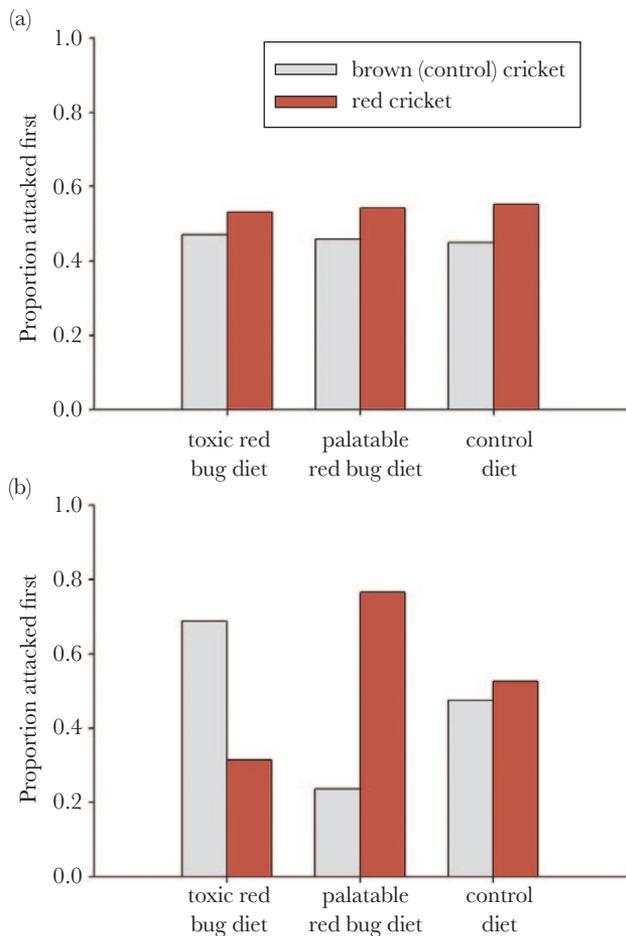


Figure 4

Proportion of trials in which either a red or control (brown) cricket was attacked first by *Habronattus pyrrithrix* trained on 3 different diet treatments. (a) In Study 1 (Experiment 2), we found no evidence of color learning as there were no differences among the 3 training treatments in their color preferences. (b) In Study 2 (Experiment 4) in which our methods were modified to increase opportunities for learning, our training diets did lead to generalized color biases with those on the “toxic red bug diet” showing low attack rates on red and those on the “palatable red bug diet” showing high attack rates on red. Given the differences in experimental protocol used in Study 1 and 2 (see Methods for details), direct comparisons between the two should be made cautiously.

there are also examples of the lack of generalization of such color aversions. Sillen-Tullberg et al. (1982) found that great tits did not generalize aversions between fifth instar nymphs and adults of the milkweed bug, *Lygaeus equestris*, despite their similarity in both shape and color pattern. Vesely et al. (2013) found that wild-caught great tits avoided red and black firebugs but did not avoid similarly sized cockroaches painted to resemble firebugs.

Taken together, the studies described above suggest that avian predators often do develop generalized prey color aversions from their interactions with aposematic red and black hemipteran bugs but that these generalizations are often narrow, and, to our knowledge, there is no evidence that they spill over to other nonchemically defended prey taxa outside of the Hemiptera. In contrast, the spiders in our study showed generalized color aversions (and preferences) that were transferred from aposematic milkweed bugs to artificially colored crickets that are quite different in shape and body form. It may be that differences in visual systems or cognitive

abilities of these 2 different groups of predators are responsible for these different patterns of generalization. As the first study of prey color generalization in spiders, more work is clearly needed to understand how this work fits into the broader predator psychology literature. If spiders, compared with avian predators, do indeed generalize color more broadly across prey taxa with striking differences in morphology, this may help to explain the prevalence of imperfect mimicry in a broad range of organisms (e.g., Kazemi et al. 2014).

Perhaps one of our most intriguing findings is that changes in our experimental protocol seemed to affect whether the spiders expressed generalized prey color preferences and aversions; such color generalization was not seen in Study 1 but was seen in Study 2 (see Figure 4 for a comparison of the 2 studies). Because there were multiple differences between Study 1 and 2, we cannot pinpoint the specific change that was responsible for the different experimental outcomes. However, in the interest of hypothesis generation for future studies, it is valuable to explore potential reasons for these differences. In our initial test of prey color generalization (Study 1, Experiment 2), our testing procedure involved removing stimulus (“training”) prey from the spiders’ home cage prior to testing and we found no evidence that the spiders learned generalized color preferences or aversions. We made 2 strategic changes to our experimental design for our second test of prey color generalization (Study 2, Experiment 4) to increase the likelihood of successful training: 1) Rather than removing stimulus (“training”) prey prior to the color choice test, we left this training prey present to actively move around the spiders’ cage during the test and 2) we provided the “palatable red bug” group with an alternative, but more difficult to capture, prey option to encourage them to develop a preference for the red sunflower-fed bugs. In this second test of prey color generalization, we indeed found that the spiders expressed the expected preferences and aversions to the color red: The “toxic red bug” group showed lower attack rates on artificially colored red crickets (compared with naturally colored brown control crickets), whereas the “palatable red bug” group showed higher attack rates on the red crickets. The idea that subtle differences in experimental context can influence learning has been supported in one other jumping spider species (*P. princeps*); specifically, learned aversions to unpalatable milkweed bugs were not retained when *P. princeps* were tested in a novel environment that was different from where they were trained (Skow and Jakob 2006). More work is clearly needed to examine how environmental context can affect learning and generalization, particularly given the variation these spiders might experience under natural conditions.

There were 2 additional differences between Study 1 and 2 that may have contributed to the differences in learning outcomes. First, spiders in Study 1 were field-collected individuals, whereas those in Study 2 were their first-generation (lab-reared) progeny and thus the 2 groups began the experiments with different experiences. Furthermore, the spiders in Study 1 (all adults) were older than those in Study 2 (all juveniles) when tested; although not previously examined in spiders, age in other invertebrates has been shown to influence the ability to learn new tasks (e.g., Brown and Strausfeld 2009). The fact that subtle differences in our experimental protocols can influence the learning outcomes highlights the challenges of comparing results across studies both within and among species. To fully appreciate how various groups of predators may differ in the selection pressures they place on colorful prey, it would be informative to move toward testing multiple predator taxa in the same study with identical training and testing regimes (e.g., multiple bird

species: Svádová et al. 2010; both vertebrate and invertebrate predators: Fabricant and Smith 2014).

Consistent with previous studies in another species of jumping spider (*Phidippus* sp.: Hill 2006), our results suggest that memory of learned avoidance of aposematic prey is relatively short term when compared with avian predators. Hill (2006) tested jumping spiders that had a variety of encounter rates with milkweed bugs and found that one milkweed bug encounter resulted in avoidance of only a few hours, whereas multiple encounters resulted in aversions that lasted several days. Aversions developed from repeated encounters with milkweed bugs over a 32-day period (similar to our study) were completely forgotten within 10 days (Hill 2006), and in our study with *H. pyrrihrix*, they were forgotten within 2 weeks. Highly flexible memory in jumping spiders might result in color biases that shift seasonally or even as a spider moves from one microhabitat to another. Male *H. pyrrihrix*, in particular, spend a lot of their time moving to find females (Taylor 2012) and so this flexibility might allow them to adjust quickly to new environments. Although little is known about memory of learned aversions in other invertebrates, anecdotal evidence suggests that in praying mantises which consume milkweed bugs, vomit, and then learn to avoid them, aversions can last at least 3 weeks (Berenbaum and Miliczky 1984). In contrast, in birds, anecdotal evidence for a variety of bird species suggests that learned aversions from interactions with live prey can last substantially longer ranging from several months to over a year (reviewed in Waldbauer 1988). Because these rough comparisons range across various types of prey and different experimental contexts, it would be useful to subject different predators to learning and memory tests within the same study for a clearer comparison. However, at this stage, we should begin to think about how the flexible and short-term nature of jumping spider memory might lead to selection pressures on colored prey items that are quite different than those imposed by their bird predators.

Our study focused on the color red, which has unique psychological effects on receivers in various taxa and has thus been argued to be a general signal of intimidation across the animal kingdom (see Pryke 2009). Many animals show an innate avoidance of red in prey choice (e.g., Mastrotta and Mench 1995; Gamberale-Stille and Tullberg 2001; Ham et al. 2006; Skelhorn 2011), and there is evidence that red plays a role in guiding the process of learning to avoid aposematic prey (Marples et al. 1994; Svádová et al. 2009). Given the recent discovery that *H. pyrrihrix* uses unique filter pigment to see red (Zurek et al. 2015) as well the fact that red is particularly salient in the context of both feeding (Taylor et al. 2014) and mate choice (Taylor and McGraw 2013), it makes it an obvious first choice when examining color learning and generalization. An interesting next step would be to determine if *H. pyrrihrix* can also learn other colors to the same degree, as well as how subtle differences in color cues and more natural and variable visual backgrounds might influence color learning.

CONCLUSIONS

Here, we show that *H. pyrrihrix* jumping spiders exposed to naturally occurring prey items can learn generalized preferences and aversions to the color red. The nature of these learned color biases is subtly different from those of the avian predators that dominate the field of predator psychology. As highly voracious (Jackson and Pollard 1996) and ecologically important predators (Wise 1993), jumping spiders should be considered more often when thinking broadly about how predator psychology shapes the evolution of

prey coloration. It may be that their learned color preferences and aversions spill over even more broadly than examined here, to even more distantly related prey and may even affect how they respond to color in other contexts (e.g., mate choice).

FUNDING

This work was supported by funding from the Department of Biological Sciences at the University of Pittsburgh, the Howard Hughes Medical Institute Undergraduate Science Education Program (award no. 52006957), and a Brackenridge Undergraduate Research Fellowship to E.B.M.

M. Brock, C. Cook, and E. Roulette provided helpful comments on a previous version of the manuscript.

Handling editor: Johanna Mappes

REFERENCES

- Berenbaum MR, Miliczky E. 1984. Mantids and milkweed bugs—efficacy of aposematic coloration against invertebrate predators. *Am Midl Nat.* 111:64–68.
- Brown S, Strausfeld N. 2009. The effect of age on a visual learning task in the American cockroach. *Learn Mem.* 16:210–223.
- Carducci JP, Jakob EM. 2000. Rearing environment affects behaviour of jumping spiders. *Anim Behav.* 59:39–46.
- Eisner T, Eisner M. 1991. Unpalatability of the pyrrolizidine alkaloid-containing moth *Utethesia ornatrix*, and its larva, to wolf spiders. *Psyche (Stuttg).* 98:111–118.
- Endler JA. 1978. A predator's view of animal colour patterns. *Evol Biol.* 11:319–364.
- Engen S, Jarvi T, Wiklund C. 1986. The evolution of aposematic coloration by individual selection—a life-span survival model. *Oikos.* 46:397–403.
- Evans DL, Castoriades N, Badruddine H. 1987. The degree of mutual resemblance and its effect on predation in young birds. *Ethology.* 74:335–345.
- Fabricant SA, Smith CL. 2014. Is the hibiscus harlequin bug aposematic? The importance of testing multiple predators. *Ecol Evol.* 4:113–120.
- Feir D. 1974. *Oncopeltus fasciatus*: a research animal. *Annu Rev Entomol.* 19:81–96.
- Foelix RE. 2011. *Biology of spiders.* New York: Oxford University Press.
- Gamberale-Stille G, Tullberg BS. 1996. Evidence for a peak-shift in predator generalization among aposematic prey. *Proc Biol Sci.* 263:1329–1334.
- Gamberale-Stille G, Tullberg BS. 1999. Experienced chicks show biased avoidance of stronger signals: an experiment with natural colour variation in live aposematic prey. *Evol Ecol.* 13:579–589.
- Gamberale-Stille G, Tullberg BS. 2001. Fruit or aposematic insect? Context-dependent colour preferences in domestic chicks. *Proc Biol Sci.* 268:2525–2529.
- Giurfa M. 2013. Cognition with few neurons: higher-order learning in insects. *Trends Neurosci.* 36:285–294.
- Gronquist M, Schroeder FC, Ghiradella H, Hill D, McCoy EM, Meinwald J, Eisner T. 2006. Shunning the night to elude the hunter: diurnal fireflies and the “femmes fatales”. *Chemoecology.* 16:39–43.
- Guilford T. 1992. Predator psychology and the evolution of prey coloration. In: Crawley MJ, editor. *Natural enemies: the population biology of predators, parasites and diseases.* Oxford: Blackwell Scientific. p. 377–394.
- Guilford T, Dawkins MS. 1991. Receiver psychology and the evolution of animal signals. *Anim Behav.* 42:1–14.
- Hajek AE. 2004. *Natural enemies: an introduction to biological control.* Cambridge (UK): Cambridge University Press.
- Ham AD, Ihalainen E, Lindstrom L, Mappes J. 2006. Does colour matter? The importance of colour in avoidance learning, memorability and generalisation. *Behav Ecol Sociobiol.* 60:482–491.
- Harland DP, Jackson RR. 2000. Cues by which *Portia fimbriata*, an araneophagic jumping spider, distinguishes jumping-spider prey from other prey. *J Exp Biol.* 203:3485–3494.
- Hart NS, Hunt DM. 2007. Avian visual pigments: characteristics, spectral tuning, and evolution. *Am Nat.* 169:S7–S26.

- Hill DE. 2006. Learned avoidance of the large milkweed bug (Hemiptera, Lygaeidae, *Oncopeltus fasciatus*) by jumping spiders (Araneae, Salticidae, *Phidippus*). *Peckhamia*. 1:1–21.
- Hoefler CD, Jakob EM. 2006. Jumping spiders in space: movement patterns, nest site fidelity and the use of beacons. *Anim Behav*. 71:109–116.
- Huang JN, Cheng RC, Li DQ, Tso IM. 2011. Salticid predation as one potential driving force of ant mimicry in jumping spiders. *Proc Biol Sci*. 278:1356–1364.
- Isman MB, Duffey SS, Scudder GGE. 1977. Variation in cardenolide content of lygaeid bugs, *Oncopeltus fasciatus* and *Lyaeus kalmii kalmii* and of their milkweed hosts (*Asclepius* spp.) in central California. *J Chem Ecol*. 3:613–624.
- Jackson RR, Pollard SD. 1996. Predatory behavior of jumping spiders. *Annu Rev Entomol*. 41:287–308.
- Jakob EM, Marshall SD, Uetz GW. 1996. Estimating fitness: a comparison of body condition indices. *Oikos*. 77:61–67.
- Jakob EM, Skow CD, Haberman MP, Plourde A. 2007. Jumping spiders associate food with color cues in a T-maze. *J Arachnol*. 35:487–492.
- Jakob EM, Skow CD, Long S. 2011. Plasticity, learning, and cognition. In: Herberstein ME, editor. *Spider behaviour: flexibility and versatility*. Cambridge (UK): Cambridge University Press. p. 307–347.
- Kauppinen J, Mappes J. 2003. Why are wasps so intimidating: field experiments on hunting dragonflies (Odonata: *Aeshna grandis*). *Anim Behav*. 66:505–511.
- Kazemi B, Gamberale-Stille G, Tullberg BS, Leimar O. 2014. Stimulus salience as an explanation for imperfect mimicry. *Curr Biol*. 24:965–969.
- Kelber A. 2006. Invertebrate colour vision. In: Warrant EJ, Nilsson DE, editors. *Invertebrate vision*. Cambridge (UK): Cambridge University Press. p. 250–290.
- Land MF, Nilsson D. 2012. *Animal eyes*. Oxford: Oxford University Press.
- Langley SA, Tilmon KJ, Cardinale BJ, Ives AR. 2006. Learning by the parasitoid wasp, *Aphidius ervi* (Hymenoptera: Braconidae), alters individual fixed preferences for pea aphid color morphs. *Oecologia*. 150:172–179.
- Li DQ, Lim MLM. 2005. Ultraviolet cues affect the foraging behaviour of jumping spiders. *Anim Behav*. 70:771–776.
- Lim MLM, Land MF, Li DQ. 2007. Sex-specific UV and fluorescence signals in jumping spiders. *Science*. 315:481–481.
- Long SM, Lewis S, Jean-Louis L, Ramos G, Richmond J, Jakob EM. 2012. Firefly flashing and jumping spider predation. *Anim Behav*. 83:81–86.
- Losey JE, Ives AR, Harmon J, Ballantyne F, Brown C. 1997. A polymorphism maintained by opposite patterns of parasitism and predation. *Nature*. 388:269–272.
- Maddison WP, Bodner MR, Needham KM. 2008. Salticid spider phylogeny revisited, with the discovery of a large Australasian clade (Araneae: Salticidae). *Zootaxa*. 1893:49–64.
- Marples NM, Vanveelen W, Brakefield PM. 1994. The relative importance of color, taste, and smell in the protection of an aposematic insect *Coccinella septempunctata*. *Anim Behav*. 48:967–974.
- Mastrota FN, Mench JA. 1995. Color avoidance in northern bobwhites—effects of age, sex, and previous experience. *Anim Behav*. 50:519–526.
- Mather MH, Roitberg BD. 1987. A sheep in wolf's clothing: tephritid flies mimic spider predators. *Science*. 236:308–310.
- Miller CT, Bee MA. 2012. Receiver psychology turns 20: is it time for a broader approach? *Anim Behav*. 83:331–343.
- Nagata T, Koyanagi M, Tsukamoto H, Saeki S, Isono K, Shichida Y, Tokunaga F, Kinoshita M, Arikawa K, Terakita A. 2012. Depth perception from image defocus in a jumping spider. *Science*. 335:469–471.
- Nakagawa S, Cuthill IC. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol Rev*. 82:591–605.
- Nakamura T, Yamashita S. 2000. Learning and discrimination of colored papers in jumping spiders (Araneae, Salticidae). *J Comp Physiol A Sens Neural Behav Physiol*. 186:897–901.
- Nelson XJ, Jackson RR. 2012. The discerning predator: decision rules underlying prey classification by a mosquito-eating jumping spider. *J Exp Biol*. 215:2255–2261.
- Platnick NI. 2013. *The world spider catalog, version 13.5*. New York: American Museum of Natural History. Available from: <http://research.amnh.org/iz/spiders/catalog>.
- Pryke SR. 2009. Is red an innate or learned signal of aggression and intimidation? *Anim Behav*. 78:393–398.
- Rashed A, Beatty CD, Forbes MR, Sherratt TN. 2005. Prey selection by dragonflies in relation to prey size and wasp-like colours and patterns. *Anim Behav*. 70:1195–1202.
- Richman DB, Edwards GB, Cutler B. 2005. Salticidae. In: Ubick D, Paquin P, Cushing PE, Roth VD, editors. *Spiders of North America: an identification manual*. American Arachnological Society. p. 205–216. Available from: <http://www.americanarachnology.org>.
- Rota J, Wagner DL. 2006. Predator mimicry: metalmark moths mimic their jumping spider predators. *PLoS One*. 1:e45.
- Rowe C. 2013. Receiver psychology: a receiver's perspective. *Anim Behav*. 85:517–523.
- Ruxton GD, Sherratt TN, Speed MP. 2004. *Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry*. Oxford: Oxford University Press.
- Sillen-Tullberg B. 1985. Higher survival of an aposematic than of a cryptic form of a distasteful bug. *Oecologia*. 67:411–415.
- Sillen-Tullberg B, Wiklund C, Jarvi T. 1982. Aposematic coloration in adults and larvae of *Lygaeus equestris* and its bearing on Mullerian mimicry: an experimental study on predation on living bugs by the great tit *Parus major*. *Oikos*. 39:131–136.
- Skelhorn J. 2011. Colour biases are a question of conspecifics' taste. *Anim Behav*. 81:825–829.
- Skow CD, Jakob EM. 2006. Jumping spiders attend to context during learned avoidance of aposematic prey. *Behav Ecol*. 17:34–40.
- Sourakov A. 2013. Two heads are better than one: false head allows *Calycopis cecrops* (Lycaenidae) to escape predation by a jumping spider, *Phidippus pulcherrimus* (Salticidae). *J Nat Hist*. 47:1047–1054.
- Svářdová KH, Exnerova A, Kopeckova M, Stys P. 2010. Predator dependent mimetic complexes: do passerine birds avoid Central European red-and-black Heteroptera? *Eur J Entomol*. 107:349–355.
- Svářdová KH, Exnerova A, Kopeckova M, Stys P. 2013. How do predators learn to recognize a mimetic complex: experiments with naive great tits and aposematic heteroptera. *Ethology*. 119:814–830.
- Svářdová K, Exnerová A, Štys P, Landová E, Valenta J, Fučíková A, Socha R. 2009. Role of different colours of aposematic insects in learning, memory and generalization of naive bird predators. *Anim Behav*. 77:327–336.
- Symondson WO, Sunderland KD, Greenstone MH. 2002. Can generalist predators be effective biocontrol agents? *Annu Rev Entomol*. 47:561–594.
- Taylor LA. 2012. *Color and communication in Habronattus jumping spiders: tests of sexual and ecological selection*. Tempe (AZ): Arizona State University.
- Taylor LA, Maier EB, Byrne KJ, Amin Z, Morehouse NI. 2014. Colour use by tiny predators: jumping spiders show colour biases during foraging. *Anim Behav*. 90:149–157.
- Taylor LA, McGraw K. 2013. Male ornamental coloration improves courtship success in a jumping spider, but only in the sun. *Behav Ecol*. 24:955–967.
- Vesely P, Luhanova D, Praskova M, Fuchs R. 2013. Generalization of mimics imperfect in colour patterns: the point of view of wild avian predators. *Ethology*. 119:138–145.
- Waldbauer GP. 1988. Asynchrony between Batesian mimics and their models. *Am Nat*. 131:S103–S121.
- Wiklund C, Jarvi T. 1982. Survival of distasteful insects after being attacked by naive birds—a reappraisal of the theory of aposematic coloration evolving through individual selection. *Evolution*. 36:998–1002.
- Wiklund C, Sillen-Tullberg B. 1985. Why distasteful butterflies have aposematic larvae and adults, but cryptic pupae—evidence from predation experiments on the monarch and the European swallowtail. *Evolution*. 39:1155–1158.
- Williams DS, McIntyre P. 1980. The principal eyes of a jumping spider have a telephoto component. *Nature*. 288:578–580.
- Wise DH. 1993. *Spiders in ecological webs*. Cambridge (UK): Cambridge University Press.
- Zurek DB, Cronin TW, Taylor LA, Byrne K, Sullivan ML, Morehouse NI. 2015. Spectral filtering enables trichromatic vision in colorful jumping spiders. *Curr Biol*. 25:R403–R404.