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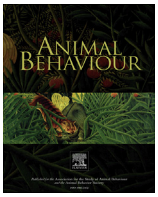

Colour use by tiny predators: jumping spiders show colour biases during foraging

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The evolution of many animal colours is thought to be driven by selection from visually guided predators. Yet research has largely focused on large vertebrate predators such as birds while ignoring smaller, terrestrial invertebrate predators. This is despite clear evidence that small invertebrate predators are important regulators of prey densities in a variety of ecosystems. Jumping spiders are small voracious predators that feed on a wide variety of prey in the field. They are capable of colour discrimination, but little is known about whether they attend to the colour of their prey during foraging. We examined colour biases by offering *Habronattus pyrrithrix* jumping spiders arrays of artificially coloured juvenile crickets. We found that field-collected *H. pyrrithrix* showed populationwide colour biases; across age and sex categories, attack rates were lowest on red and yellow prey (colours commonly used as warning colours) and highest on blue prey. We retested the same individuals after they were housed for several weeks in the laboratory and found that their colour biases had weakened to statistically undetectable levels. We also found that colour preferences in individual spiders were not consistent over time, suggesting that the populationwide colour biases that we observed were not simply driven by consistent preferences of a subset of individuals. Finally, we tested colour preferences in a separate group of naïve, laboratory-raised spiders and found similar biases favouring blue prey, with low attack rates on red, yellow and green. Our study provides the first evidence that both experienced and naïve jumping spiders show colour biases when foraging and suggests that these biases may result from both innate and learned components. We argue that more attention to such understudied predators may provide a more holistic and accurate understanding of the suite of selective pressures that drive the evolution of prey colour patterns, particularly in small invertebrates.

Researchers studying the evolution of animal coloration have made notable progress in recent years towards understanding how predators shape the evolution of colour patterns in their prey (see reviews in Mappes, Marples, & Endler, 2005; Stevens & Merilaita 2009; Stevens & Ruxton, 2012; Stevens, Yule, & Ruxton, 2008). This work has explored the role of innate colour preferences (Gamberale-Stille & Tullberg, 2001; Mastrota & Mench, 1995; Skelhorn, 2011) as well as colour-based learning and memory in dictating predator behaviour during predator–prey interactions (Aronsson & Gamberale-Stille, 2012; Marples, Vanveelen, & Brakefield, 1994; Svádová et al., 2009). Recent advances in visual ecology have further deepened our understanding in this field by providing more precise estimations of colour vision and visual capabilities for a growing number of predator species (Endler & Mielke, 2005; Stoddard, 2012). In addition, researchers have begun to explicitly consider how specific predator visual systems may be influenced by the light environments they function within (e.g. Gomez & Thery, 2004), making it possible to understand how prey colours are shaped by complex predator communities in the field.

While fascinating, most advances in this area have focused on a small subset of ‘key’ predators, typically birds (e.g. all references cited above). While studies have to some extent addressed similar questions in a few other large groups of predatory vertebrates (e.g. fish: Chiao, Wickiser, Allen, Genter, & Hanlon, 2011; frogs: Hatle & Salazar, 2001; primates: Smith et al., 2012), much less is known about how colour is used by terrestrial predatory invertebrates. In a few cases, behavioural experiments have been used to examine food colour preferences in such animals (Harmon, Losey, & Ives, 1998; Langley, Tilmon, Cardinale, & Ives, 2006; Wackers, 1994), yet very few studies have done this using choice tests employing direct manipulations of prey colour (but see Kauppinen & Mappes,

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2003; Rashed, Beatty, Forbes, & Sherratt, 2005; Shelly & Pearson, 1978).

This lack of attention to terrestrial invertebrate predators is surprising, given both the diversity of taxa for which we have evidence of colour vision (e.g. wasps: Peitsch et al., 1992; jumping spiders: Nakamura & Yamashita, 2000; fireflies: Booth, Stewart, & Osorio, 2004; dragonflies and damselflies: Bybee, Johnson, Gering, Whiting, & Crandall, 2012; mantids: Prete et al., 2012) and the wealth of evidence indicating that such predators regulate the densities of prey in both agricultural and natural ecosystems (e.g. Halaj & Wise, 2001; Symondson, Sunderland, & Greenstone, 2002; Tiitsaar, Kaasik, & Teder, 2013; Wise 1993). For example, in a review of over 100 manipulative field experiments in the biocontrol literature, 74% found that a single species of invertebrate generalist predator significantly reduced the abundance of a target pest species (Symondson et al., 2002). Given this diversity and importance, if small invertebrate predators show colour biases during foraging, they are likely to exert a strong influence on the evolution of colour patterns in invertebrate prey (e.g. Losey, Ives, Harmon, Ballantyne, & Brown, 1997). Because of their small size, invertebrate predators may feed on different suites of prey compared with avian predators or on smaller, earlier life stages of the same prey; as such, they may offer novel insights into the evolution of colour in a wide variety of tiny invertebrate prey.

Among these understudied predators, jumping spiders are both highly visual (reviewed in Harland, Li, & Jackson, 2012) and voracious (reviewed in Jackson & Pollard, 1996), making them likely candidates for driving the evolution of colour patterns in small invertebrate prey. Jumping spiders show exceptional visual acuity for their small size (Williams & McIntyre, 1980) and use subtle visual cues and complex decision making to distinguish among different types of prey (e.g. Harland & Jackson, 2000; Jackson, Nelson, & Sune, 2005; Nelson & Jackson, 2006, 2012). Behavioural experiments have shown that jumping spiders respond to colour cues in various contexts, including mating (e.g. Lim, Li, & Li, 2008; Taylor & McGraw 2013), navigation (Hoefler & Jakob, 2006) and standard heat-aversion training experiments (Nakamura & Yamashita, 2000; VanderSal & Hebets, 2007). They can also discriminate colours in the context of foraging (Jakob, Skow, Haberman, & Plourde, 2007; Li & Lim, 2005), but researchers have yet to manipulate prey colours directly across a biologically relevant range of colours to determine whether food colour preferences or aversions exist in this group. In addition, the extent to which learning versus innate preferences may shape colour-based foraging behaviours in these animals is not known. Associative learning during foraging has been reported in jumping spiders (e.g. Jakob et al., 2007), as have innate biases towards specific prey items (e.g. preferences for blood-filled mosquitoes in *Evarcha culicivora*: Jackson et al., 2005). However, whether naïve jumping spiders show specific colour biases prior to experience with palatable and unpalatable prey has yet to be explored.

Information regarding how jumping spiders interact with prey based on prey coloration should have important implications for both the evolution and ecology of prey communities. There are more than 5500 species of jumping spiders (Platnick, 2013), some of which are found at very high densities (Taylor, 2012). Thus, jumping spiders have the potential to be important players in a variety of food webs where colourful prey items are also common. Indeed, large jumping spiders have been argued to be a main predator driving the evolution of ant mimicry in smaller species (Huang, Cheng, Li, & Tso, 2011). Their role in shaping the colours of their prey has yet to be fully considered, but may help to explain features of the colour of a wide variety of terrestrial invertebrate prey.

The goal of the present study was to examine prey colour biases in both experienced and naïve *Habronattus pyrrithrix* (Fig. 1), a highly abundant jumping spider that acts as a major predator in farms, gardens and natural riparian areas in parts of the southwestern United States and Mexico. In the field, these spiders encounter a variety of prey items of various colours (L. A. Taylor, personal observation); the colours red and yellow are typically associated with prey that are chemically defended during multiple stages of development (e.g. ladybird beetles (Coccinellidae): Sloggett et al., 2011; milkweed bugs (Lygaeidae): Scudder & Duffey, 1972; oleander aphids (*Aphis nerii*): Rothschild, von Euw, & Reichstein, 1970; various leaf beetles (Chrysomelidae): Pasteels, Rowellrahier, Braekman, Daloze, & Duffey, 1989). Such chemically defended prey items can cause developmental deficiencies in small invertebrate predators that consume them (e.g. lacewings: Pappas, Broufas, & Koveos, 2007), suggesting an advantage to individuals that avoid these prey items and therefore selection for mechanisms of colour-based prey avoidance. Indeed, we have never observed *H. pyrrithrix* feeding on these red and yellow chemically defended prey items in the field, but rather find them taking a wide variety of other prey items instead (e.g. springtails, flies, green aphids, caterpillars, hoppers, and other spiders, including conspecifics; Taylor, n.d.). These field observations led us to the a priori prediction that field-collected spiders would avoid the colours red and yellow, but it did not give us any reason to make directional predictions about prey of other colours.

Such foraging biases can be the product of pre-existing innate and/or learned preferences and aversions. Innate biases are thought to be advantageous in environments where the phenotypes of palatable and unpalatable prey are predictable over time and/or when the costs of learning outweigh the benefits, while learned preferences should be favoured in environments where prey characteristics are highly variable and/or predators have the opportunity to learn at little or no cost (reviewed in Dukas, 2008). In *H. pyrrithrix*, field populations experience a highly dynamic and diverse prey community over the course of a season. However, unpalatable members of their prey community typically show colours within a restricted colour gamut (e.g. red and yellow; see above). We therefore predicted that any colour biases in foraging behaviours would include elements of both innate and learned components.

Using artificially coloured prey, we first quantified populationwide prey colour biases in field-collected animals and examined how these varied by the sex/life stage of individuals. Second, we examined whether these populationwide colour biases found in freshly collected individuals persisted when spiders were brought into the laboratory and housed on a standard laboratory diet. Third, we examined individuals' food colour choices over the course of the study to determine whether individual spiders were consistent and repeatable in their preferences/aversions to different colours. Finally, we examined the innate colour biases in a separate group of laboratory-raised spiders that had no prior experience with coloured prey.

METHODS

Study Species

Habronattus pyrrithrix Chamberlin 1924 (Fig. 1) is a sexually dichromatic jumping spider found from southern California and Arizona, U.S.A., south to Sinaloa, Mexico (Griswold, 1987). In Phoenix, AZ, they are common and often found in high densities in leaf litter in natural riparian habitats as well as grassy backyards and agricultural areas. Aside from notes of prey records in the field (described above), no work has been done on their foraging behaviour.

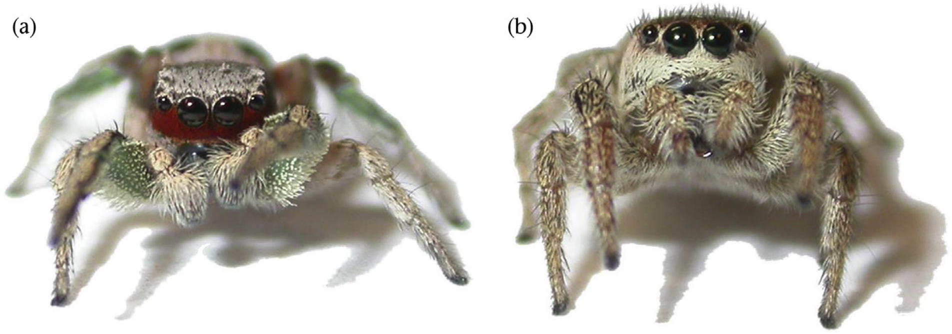

Figure 1. A *Habronattus pyrrithrix* (a) male and (b) female collected from Queen Creek, AZ, U.S.A.

Initial Food Colour Preferences of Wild-caught Individuals

We collected *H. pyrrithrix* ($N = 130$ total; 55 adult females, 44 adult males, 31 juveniles) from Queen Creek, AZ (Maricopa County), U.S.A. (33°13′29″N, 111°35′34″W) between 26 April and 1 May 2012. We housed spiders individually in cylindrical plastic containers (5.5 cm tall and 2.5 cm in diameter) in the laboratory until we ran their initial colour preference tests. We fed spiders in captivity three times per week with white-eyed *Drosophila melanogaster*, a prey item selected to avoid inadvertently modifying colour biases in our population of field-collected individuals; each feeding consisted of a quantity of flies approximating one-half of the individual spider's own body mass (between 1 and 7 flies) as this feeding regime results in hungry spiders (that are motivated to feed) but with body condition indices that fall within the natural range of variation of those collected from the field (Taylor, n.d.). To minimize variation associated with hunger level, we kept all spiders on this laboratory feeding regime for at least 6 days prior to testing (mean ± SE time between collection and first colour preference test = 16.8 ± 0.6 days).

To create artificially coloured prey items for our preference tests, we added food dye (Market Pantry assorted food colour, Target Corporation, Minneapolis, MN, U.S.A.) to the water source of newly hatched crickets (*Acheta domesticus,* ca. 3 mm in length) at least 1 day prior to testing. As these juvenile crickets drink and fill their gut with coloured water, their body appearance quickly changes to the colour of the dye because they are translucent at this stage of development (see Fig. 2; also see Supplementary Fig. S1 for a photograph of coloured crickets as well as the exact concentrations of dye used to create each colour). We created five treatment groups of crickets: red, yellow, green, blue and brown; the brown crickets were a close match to the natural coloration of an undyed cricket (see Fig. 2). We chose these colour groups because they span the range of prey colours that *H. pyrrithrix* may encounter in the field (L. A. Taylor, personal observation). While our manipulations of cricket colour do not separate the effect of differences in prey hue from differences in prey brightness, our current understanding of jumping spider colour vision remains too limited to properly design stimuli that would vary these aspects of visual discrimination independently (see Discussion). We measured the body mass and activity level (percentage of time spent moving) for a subset of these crickets to confirm that the presence of the dye was not affecting the crickets' behaviour. Our colour categories differed only in coloration; there was no difference in body size or activity level among colour categories and no difference between coloured crickets and undyed crickets (ANOVA: body size: $F_{5,54} = 0.58$, $N = 60$, $P = 0.72$; activity level: $F_{5,54} = 0.37$, $N = 60$, $P = 0.87$).

Prior to their initial food colour preference test, each test spider was placed in an enclosed glass chamber in the centre of the preference test arena (Fig. 3), where they were given 2 min to acclimate. During this time, the spider was able to observe the available prey through the clear walls of the chamber. The arena was surrounded by white paper on the bottom and sides, providing a uniform white background and preventing distractions from outside the arena. After the acclimation period, the top of the chamber was removed, allowing the spider to climb up and out of the chamber, view, and approach the available prey from above. A subset ($N = 22$; 18 adult females, 4 adult males) of the field-collected spiders in our study were older individuals that could not climb on the glass walls but were still active foragers (mean prey items fed on per trial ± SE = 3.59 ± 0.55); for these spiders, the vial was flipped over after the 2 min acclimation period so that the spider could be released without the need for climbing. For each spider, we recorded all food items attacked during a 60 min trial. Immediately after a prey item was attacked, another prey item of the same colour was added so that there were always 10 live crickets of equivalent size (two of each colour) available for the spider to choose among. After 60 min, the trial ended and we moved the spider to an individual plastic box (10.16 × 10.16 × 12.86 cm) fitted with a mesh top and an artificial green plant (ca. 10 cm long; Ashland fern collection, Michael's Stores, Irving, TX, U.S.A.) to provide enrichment (e.g. Carducci & Jakob, 2000). Opaque barriers separated these spider cages so that individuals could not see and interact with one another. We

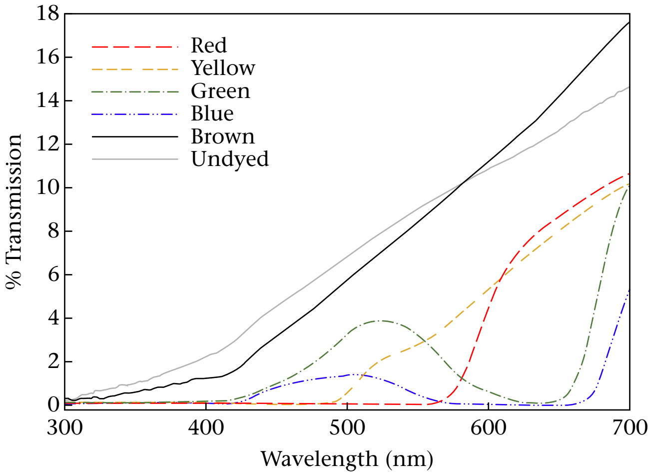

Figure 2. Spectral properties of juvenile crickets fed food dye of different colours (red, yellow, green, blue and brown). The spectral properties of undyed crickets are shown for reference. Cricket spectral measurements were taken from a small region of the abdomen (20 μm diameter) using a full-spectrum 20/20 PV microspectrophotometer and 75W xenon light source (CRAIC Technologies, Inc., San Dimas, CA, U.S.A.).

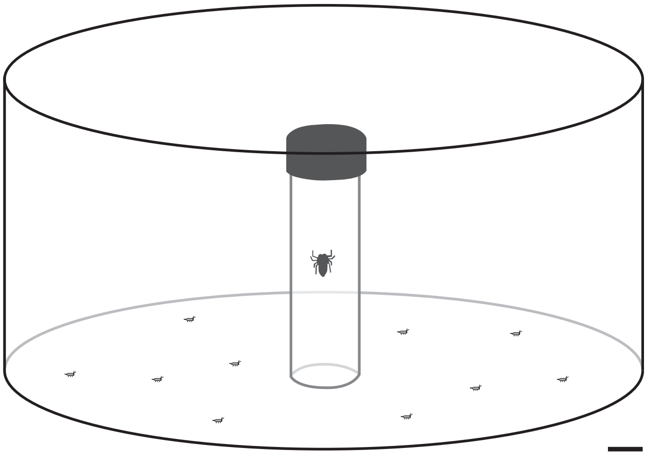

Figure 3. Food colour preference test arena (scale bar represents 1 cm). Test spiders were placed in the sealed clear glass central chamber to acclimate and then were allowed to move up and out of the chamber to attack the prey below. Because a few of the older individuals in our field-collected population had difficulty climbing the sides of the glass chamber (see details in Methods), we modified our set-up prior to testing the naïve, laboratory-raised individuals. In these tests, the acclimation chamber was a small plastic petri dish (1 cm tall and 3.5 cm in diameter), which allowed the spiders to emerge more easily.

housed spiders in these cages for the remainder of the study, except for when they were actively participating in trials.

Throughout the study, fluorescent laboratory lighting was supplemented with natural light from two large windows (1.6 × 1.7 m each) adjacent to where the spiders were housed. All colour choice tests were conducted next to this source of natural light.

Persistence and Repeatability of Colour Preferences

To determine whether the food colour biases shown by field-collected spiders persist in the laboratory and to determine whether individuals showed consistency in their food colour biases over time, we repeated each individual's colour preference tests weekly following the same methods described above. Because spiders did not always attack prey in every trial, we followed this retesting regime with each spider until they completed a total of two 'successful' trials ('successful' trials were those in which the spider captured at least one prey item; $N = 120$ for spiders that completed two successful trials; 54 adult females, 36 adult males, 30 juveniles). The mean ± SE time between their initial collection and their second 'successful' trial was 39.1 ± 1.31 days. During the time between trials, spiders were fed white-eyed fruit flies as described above.

Innate Colour Preferences of Naïve, Laboratory-raised Spiders

To determine whether food colour biases have an innate component, we also examined the colour biases of a separate group of spiders that were raised entirely in the laboratory without prior exposure to colourful prey ($N = 106$ total; 32 adult females, 24 adult males, 50 juveniles). These spiders were the first-generation progeny of the field-collected spiders described above. We reared them from the eggsacs of 35 field-mated females; to maximize the genetic diversity in this sample of spiders, no more than four spiderlings from any one clutch were included. Upon hatching from eggsacs in the laboratory, these spiders were fed communally in their mother's cage with a combination of grey and brown springtails (Sminthuridae) and pinhead crickets (*Acheta domesticus*) until their first moult, when they are large enough to capture white-eyed *Drosophila* (our standard laboratory diet). They were then removed from their nest and housed individually in plastic containers and fed solely with white-eyed *Drosophila* until their colour preference tests were performed; prior to their colour preference tests all rearing conditions were as described above for the field-collected spiders. Colour preference tests were performed as described above with minor modifications to the choice arena (see details in Fig. 3). To approximate the same age structure as the field-collected population, we began the colour preference tests approximately 4 months after the first spiderlings began hatching and continued them over a period of 5 months. Because spiders did not always attack prey in every trial, spiders were retested weekly until they completed a single 'successful' trial (i.e. in which they successfully captured one or more prey items).

At the conclusion of our study, all spiders were transitioned to a separate study on colour learning.

Statistical Analysis

To determine whether our population of field-collected *H. pyrrithrix* showed food colour preferences when first brought into the laboratory, we used ANOVA to examine how prey colour and the sex/stage of the spider (adult male, adult female, juvenile) and their interaction affected prey capture rates. Because most juvenile jumping spiders show no sexual dimorphism (and thus cannot be reliably sexed) until reaching maturity, juveniles of both sexes are typically grouped together for analysis (e.g. Bartos, 2008; Lim & Li, 2006; Nelson, Jackson, & Sune, 2005); we followed this precedent here. Because each individual spider was simultaneously presented with prey from each of the five colour categories, we included spider ID as a random factor, nested within sex/stage. We then used Tukey–Kramer post hoc comparisons to examine differences between colour categories as well as between sex/stage categories. To determine whether any preferences or aversions persisted after spiders were housed in the laboratory (on a constant diet of white-eyed fruit flies), we ran the same analysis on the data for spiders that successfully completed a second colour preference trial.

To determine whether individuals showed consistency in their food colour biases, we examined the repeatability of colour preferences across their two trials. We first calculated the proportion of each colour (relative to the other colours) that an individual attacked during each of the two phases of the study. For each colour, we then examined the repeatability between an individual's two trials using a one-way ANOVA with individual ID as factor (e.g. Boake, 1989; Lessells & Boag, 1987).

To examine innate colour biases, we performed the same analysis described above on the data from the spiders raised entirely in the laboratory without exposure to colourful prey (i.e. ANOVA with prey colour, sex/stage, and their interaction as factors, and spider ID as a random factor nested within sex/stage).

Because our data were not normally distributed, all were rank transformed prior to analysis (following the RT - 1 method in Conover & Iman, 1981). All analyses were conducted using SPSS (Version 20, IBM Corporation, Armonk, NY, U.S.A.).

RESULTS

Individual attack rates across the study varied from 1 to 12 total prey items (including all colours) per trial. When spiders were newly collected from the field, they showed food colour biases. Specifically, there were significant differences in feeding rates among the five colour categories with the highest attack rates on blue and the lowest attack rates on red and yellow (Table 1, Fig. 4a). The sex/stage categories also differed in their feeding rates, with

Table 1
Results of ANOVA examining effects of prey colour, spider sex/stage, and their interaction on the number of prey items attacked during 1 h prey colour preference trials

	df	*F*	*P*
Initial colour preferences of field-collected spiders			
Prey colour	4, 508	6.18	**<0.001**
Stage	2, 127	21.22	**<0.001**
Prey colour*stage	8, 508	0.56	0.810
ID(stage)	127, 508	0.86	0.842
Follow-up preferences of the same field-collected, but laboratory-acclimated, spiders			
Prey colour	4, 468	2.03	0.089
Stage	2, 117	14.86	**<0.001**
Prey colour*stage	8, 468	0.43	0.902
ID(stage)	117, 468	0.57	>0.999
Innate colour preferences of naïve, laboratory-raised spiders			
Prey colour	4, 412	6.70	**<0.001**
Stage	2, 103	1.99	0.142
Prey colour*stage	8, 412	1.20	0.295
ID(stage)	103, 412	1.16	0.158

We ran initial colour preferences tests soon after spiders were collected from the field, and we ran follow-up preference tests on a subset of these same individuals after they had been housed in the laboratory for several weeks. We ran innate colour preference with naïve, laboratory-raised spiders that had never previously been exposed to coloured prey. Significant *P* values are shown in bold.

adult females feeding at higher rates than juveniles and males (Table 1, Fig. 5a). Importantly, there was no significant interaction between colour and sex/stage (Table 1), suggesting that colour biases did not differ between the sex/stage categories.

When spiders were retested after being fed a laboratory diet of white-eyed fruit flies for several weeks, the population no longer showed significant colour biases (although there was a nonsignificant trend, and patterns were qualitatively similar to the results from their first test) (Table 1, Fig. 4b). As in trial 1, females fed at higher rates than males and juveniles (Fig. 5b), but again there was no interaction between colour and sex/stage (Table 1).

Individual preferences/aversions were not repeatable for any of the five colour categories of prey (i.e. ANOVA did not reveal a significant effect of individual identity; Table 2).

For naïve spiders that were raised in the laboratory without any exposure to colourful prey, we also found significant colour biases with attack rates on blue prey higher than attacks on either red, yellow or green (Table 1, Fig. 4c). As in the field-collected individuals, there was no interaction between prey colour and the sex/stage of the spider (Table 1). For these laboratory-raised spiders, the three sex/stage categories did not differ significantly in their feeding rates (Table 1).

DISCUSSION

Here we provide the first evidence that both field-collected (experienced) and laboratory-raised (naïve) jumping spiders show colour biases in prey choice. In field-collected *Habronattus pyrrithrix*, we found evidence of populationwide colour biases with the highest attack rates on blue prey and the lowest attack rates on red and yellow prey. While adult females fed at higher rates than either adult males or juveniles, colour preferences among these different classes did not differ. When we retested the same individuals after several weeks of feeding on white-eyed fruit flies in the laboratory, their colour biases were qualitatively similar, but no longer statistically significant, suggesting that field-based preferences may fade under laboratory conditions. Additionally, we found no evidence that individual spiders have consistent colour preferences or aversions over time, suggesting that the populationwide patterns of prey colour biases found in this study are not simply the product of strong and consistent biases by a subset of individuals. Finally, we found that naïve, laboratory-raised spiders show innate colour biases that are similar to, but subtly different from, those found in field-collected animals, with the highest attack rates on blue, and the lowest attack rates on red, yellow and green. Taken together, these results suggest that colour is a salient feature of prey for these spiders and that these biases, while flexible, appear to originate from a pre-existing innate preference template.

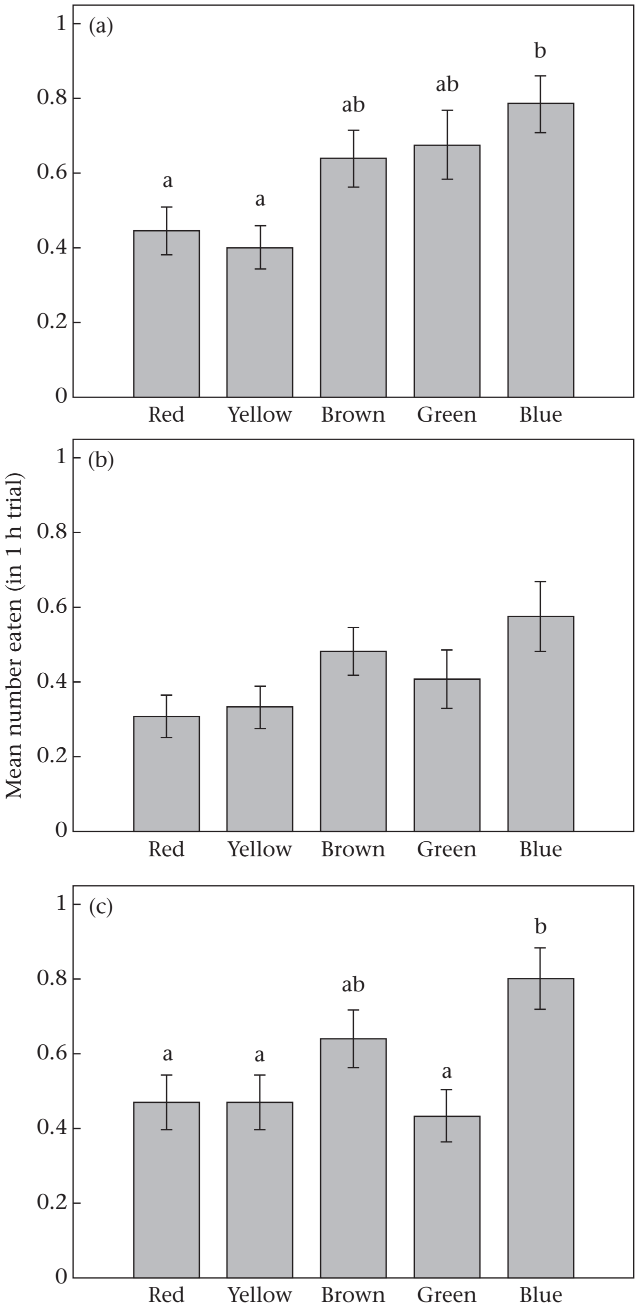

Figure 4. Mean number of prey items of different colours eaten during colour preference tests conducted with (a) field-collected spiders soon after collection, (b) the same field-collected spiders after being housed in the laboratory for several weeks and (c) a separate group of naïve, laboratory-raised spiders that had never previously been exposed to coloured prey.

Our results show that soon after being collected from the field, *H. pyrrithrix* is least likely to attack red and yellow prey items. These results are consistent with our a priori predictions based on observations of the naturally occurring prey in the habitat in which they were collected (see Introduction). As described previously, these spiders are exposed to a wide variety of colourful prey in the field (Taylor, n.d.), and many of the most common red and yellow prey items employ strong chemical defenses (e.g. Pasteels et al., 1989; Rothschild et al., 1970; Scudder & Duffey, 1972; Sloggett et al., 2011; see Introduction). When spiders were brought from the field and housed in the laboratory for several weeks, or when they were raised entirely in the laboratory and had never experienced colourful prey, their colour biases were subtly different, yet attack rates on red and yellow prey were consistently low. While other studies have not examined aversions to specific colours per se, there is evidence that some species have innate preferences for visual attributes of prey (e.g. Jackson et al., 2005; Nelson et al., 2005). We also know that jumping spiders show a remarkable capacity for learning (reviewed in Jakob, Skow, & Long, 2011); of particular relevance to our study, naïve jumping spiders will readily attack red, chemically defended prey items in the laboratory but will immediately discard them and learn to avoid attacking them in future encounters (e.g. Hill, 2006; Skow & Jakob, 2006). Thus, our results from this study, taken together with published reports in the literature, suggest that these spiders may have an innate tendency to avoid the colours red and yellow, but that these tendencies are flexible and reinforced with experience. Future work should continue to disentangle the complex interplay between innate aversions and experience in shaping the behaviour that we see in field-collected spiders.

Table 2
Results of ANOVA examining repeatability of individual colour preferences in *H. pyrrithrix*

Prey colour	*df*	*F*	*P*[*]	Repeatability (*r*)
Red	119, 120	1.13	0.254	0.06
Yellow	119, 120	0.89	0.736	−0.06
Green	119, 120	0.86	0.788	−0.07
Blue	119, 120	0.96	0.587	−0.02
Control	119, 120	0.78	0.914	−0.12

[*] Because our analysis involved multiple tests on the same data set, it may be appropriate to apply Bonferroni correction (5 tests, adjusted significance threshold = 0.01) to maintain an experimentwide α of 0.05. However, with or without Bonferroni correction, we found no evidence of repeatability in colour preferences.

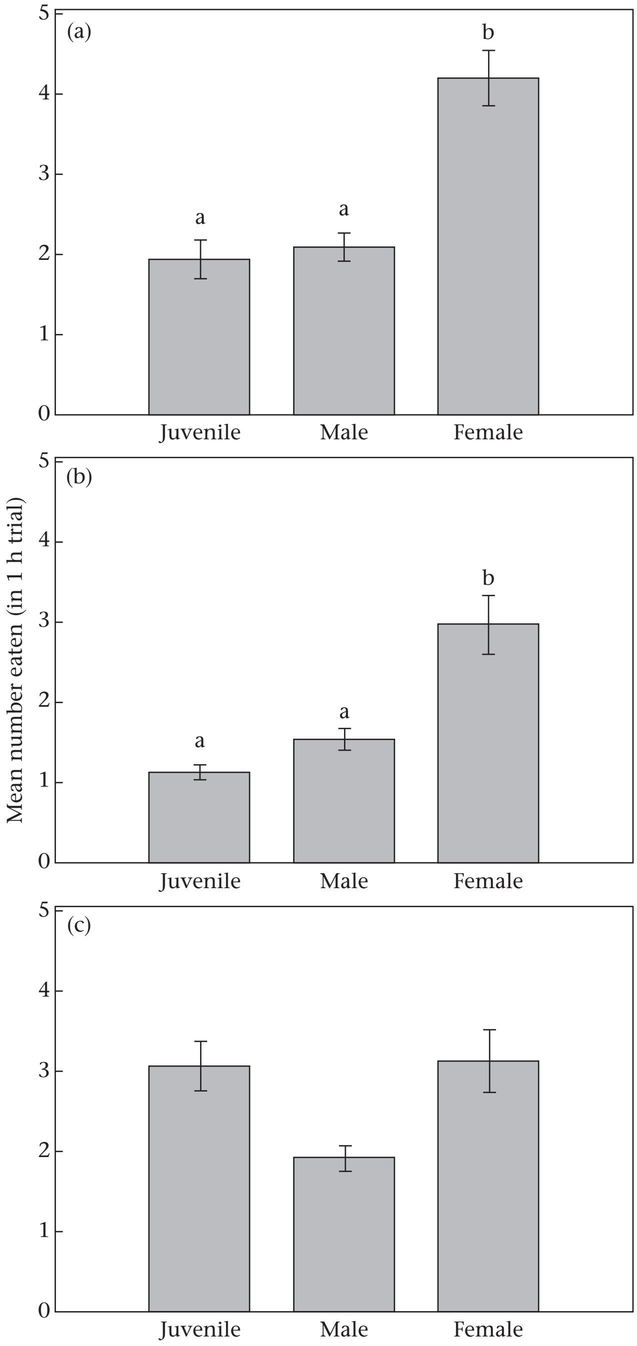

Figure 5. Mean number of prey items eaten by spiders of three different age/sex categories during 1 h colour preference tests conducted with (a) field-collected spiders soon after collection, (b) the same field-collected spiders after being housed in the laboratory for several weeks and (c) a separate group of naïve, laboratory-raised spiders.

Our results also reveal an unexpected, but consistent, preference for blue prey (compared with red and yellow in field-collected animals and compared with red, yellow and green in naïve, laboratory-raised animals). The colour blue is common in many animals that might be suitable prey for spiders (e.g. damselflies, small butterflies, caterpillars; reviewed in Umbers, 2013); however, with the exception of metallic blue chrysomelid beetles, blue prey items at our field site are quite rare (L. A. Taylor, personal observation). In related *Habronattus pugilis* jumping spiders, females show preferences for novelty in mate choice (Elias, Hebets, & Hoy, 2006; Hebets & Maddison, 2005); it may be that the spiders in our study were showing a similar preference for novelty in prey choice. Neophilia has been reported in the context of foraging in other animals (e.g. birds: Heinrich, 1995; slugs: Cook, Bailey, McCrohan, Nash, & Woodhouse, 2000; mice: Bolivar & Flaherty, 2004); this possibility should be explored further in foraging jumping spiders, particularly in relation to their preference for eating blue prey. In addition, the presumed scarcity of blue prey encountered by *H. pyrrithrix* should be explored more broadly in different habitats across their range.

Our study complements previous behavioural work showing that that at least some species of jumping spiders discriminate among different combinations of colours in a variety of contexts (e.g. a range of colour stimuli in heat aversion learning: Nakamura & Yamashita, 2000; VanderSal & Hebets, 2007; red versus blue stimuli in associative learning trials: Jakob et al., 2007; orange versus white in navigation: Hoefler & Jakob, 2006; red versus black in courtship interactions: Taylor & McGraw, 2013; UV versus lack of UV in mating: Lim et al., 2008; UV versus lack of UV in foraging: Li & Lim, 2005). Examination of spectral sensitivities in a handful of species have provided evidence of wavelength sensitivity ranging from UV to red (Blest, Hardie, McIntyre, & Williams, 1981; Devoe, 1975; Peaslee & Wilson, 1989; Yamashita & Tateda, 1976) and recent work suggests substantial variation among species, particularly in the longer wavelengths (I.-M. Tso, personal communication). In other animals, where we have more complete information on visual sensitivities, we can construct visual models that allow us to understand how these animals see colour (e.g. birds: Endler & Mielke, 2005; butterflies: Morehouse & Rutowski, 2010). With only limited data on jumping spiders, and no data on the spectral sensitivities of *H. pyrrithrix*, we cannot yet create choice tests that control for different attributes of colour cues (e.g. hue, chroma, brightness) as spiders see them. Ongoing work in our group aims to directly measure the spectral sensitivities of *H. pyrrithrix* to help us better understand and model its visual system. This work should ultimately allow us to determine which specific aspects of colour these spiders are using in decision making. In the absence of this information, it remains a possibility that these animals used a mixture of chromatic and achromatic cues to distinguish the coloured experimental prey in our study.

In many animals, foraging behaviour varies widely with the age and/or sex of individuals (e.g. monkeys: Rose, 1994; fish: Berglund, Rosenqvist, & Robinson-Wolrath,, 2006; birds: Weimerskirch, Le Corre, Ropert-Coudert, Kato, & Marsac, 2006; bats: Barclay & Jacobs, 2011). In spiders, females often feed at higher rates than males (e.g. Haynes & Sisojevi, 1966; Walker & Rypstra, 2002), a pattern that is consistent with our findings from the field-collected spiders (but not our laboratory-raised spiders). In our experimental trials, mature, field-collected females ate, on average, approximately twice as much as mature males and juveniles. This is not surprising as behavioural observations in the field suggest that male and female *H. pyrrithrix* have different priorities; males spend much of their time wandering (presumably in search of females), while females spend much of their time at rest (presumably waiting for prey while remaining in the vicinity of their eggs) (Taylor, 2012). Many of our field-collected females had mated prior to collection (as evidenced by fertile eggs) while all of our laboratory-raised spiders were virgins; the increased demands of producing eggs following mating may help to explain why our field-collected females showed such markedly higher levels of voracity compared with both males and juveniles. Despite these clear differences in foraging behaviour, the populationwide prey colour biases that we found never differed among the sex/age classes of the spiders. It may be that when it comes to avoiding colourful, chemically defended prey, all spiders benefit from the same innate and/or learned biases regardless of their age or sex.

There is growing evidence that many animals, including spiders, show repeatability in their behaviours across time (e.g. Johnson & Sih, 2005; Sih, Bell, & Johnson, 2004), which led us to consider the idea that perhaps the patterns of populationwide prey colour biases that we observed were driven by strong and repeatable preferences by a subset of individuals, rather than a general pattern shown by the population as a whole. However, we found no evidence that individuals were consistent in their colour preferences between the two trials. This is an interesting distinction because it suggests that even without detectable repeatability in individual-based biases, significant populationwide biases can emerge. In this system, we expect these populationwide biases to be important for driving the evolution of prey colour patterns in nature. It is important to note that our examination of colour-preference repeatability only included two data points per individual; future studies should incorporate more tests per individual to fully characterize subtle patterns of consistency and flexibility in colour preferences (e.g. see recent discussion in Biro, 2012; Edwards, Winney, Schroeder, & Dugdale, 2013).

Our finding that colour preferences differ subtly between freshly field-collected spiders, laboratory-acclimated spiders and colour-naïve spiders has implications for laboratory studies, which often use only laboratory-raised animals (e.g. see Calisi & Bentley, 2009). Prior work has shown that the housing conditions of jumping spiders strongly affect their responses to a variety of behavioural tests (e.g. exploratory, foraging and detouring behaviour: Carducci & Jakob, 2000), and our results hint that experience may also shape food colour preferences, even if they have an innate component. For example, attack rates on green were highest in spiders immediately after being collected from the field; while speculative, this may reflect recent experiences with the abundance of palatable green prey items at our field site (e.g. green aphids, hoppers and caterpillars). Previous work on jumping spider learning has shown that memory of associations learned in laboratory training trials is short term (e.g. Hill, 2006) and context dependent (e.g. Skow & Jakob, 2006), which suggests that any learned preferences or aversions will likely remain flexible throughout the animal's life. All of this supports the idea that, when possible, using field-collected spiders may be most appropriate for studies that aim to understand behaviour in an ecological context. In this study, we wanted to reduce variation associated with hunger level by keeping field-collected spiders on a laboratory diet for at least 6 days prior to their initial testing; yet, had we measured colour preferences directly in the field, we may have found even stronger biases that more accurately reflected their very recent experiences with colourful prey.

Here we provide the first evidence of colour biases during foraging in both field-collected and naïve, laboratory-raised jumping spiders. While this voracious group of predators has been argued to be important in driving the evolution of morphology and behaviour in a variety of small invertebrate groups (e.g. flies: Mather & Roitberg, 1987; moths: Rota & Wagner, 2006; other spiders: Huang et al., 2011; fireflies: Long et al., 2012; butterflies: Sourakov, 2013), their role in shaping the colours of such prey has not been explored. Here we show that these spiders have colour biases with both similarities to and differences from the data on better-studied avian predators from which most of our current understanding of prey coloration has come. For example, some avian predators show a general avoidance of red prey (e.g. Mastrota & Mench, 1995), while others express their red aversions only in certain contexts (e.g. after tasting a bitter substance: Skelhorn, 2011) or even prefer red in some contexts (e.g. foraging for fruit: Schmidt & Schaefer, 2004). Because many avian predators are omnivores (feeding on invertebrates as well as plant material), we might expect them to have subtly different responses to colours than obligate predators like jumping spiders (but see Meehan, Olson, Reudink, Kyser, & Curry, 2009 for a single example of a jumping spider that is not an obligate predator). Moreover, while the invertebrate prey communities upon which jumping spider predators feed may overlap with those fed on by vertebrate predators such as birds (e.g. moths, caterpillars, beetles, grasshoppers), tiny invertebrate predators may exert different selection pressures on these prey if their small size limits them to feeding on smaller, earlier life stages. Alternatively, their small size may limit them to feeding on completely different, smaller species, which are not generally the target of large avian predators. In either case, more emphasis on this guild of tiny predators may reveal consistent or informatively contradictory patterns of predator–prey coevolution occurring in the undergrowth, giving us a more holistic and accurate picture of the suite of selective forces that drive the evolution of colour.

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Supplementary Material

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