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

Lisa A. Taylor [a,b,*], Emily B. Maier [b], Kevin J. Byrne [b], Zarreen Amin [b], Nathan I. Morehouse [b]

[a] *Florida Museum of Natural History, University of Florida, Gainesville, FL, U.S.A.*
[b] *Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA, U.S.A.*

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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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[*] Correspondence: L. A. Taylor, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, U.S.A.
E-mail address: LAT12@cornell.edu (L. A. Taylor).

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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.