

From spiderling to senescence: ontogeny of color in the jumping spider, *Habronattus pyrrithrix*

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Abstract. The diverse colors of animals serve a variety of purposes, from acquiring mates to avoiding predators. Often, color patterns are not static throughout life, but change drastically during development, maturity, and senescence. While recent work has focused on the signaling value of vibrant colors in jumping spiders (Salticidae), we know very little about how colors change as spiders age; such information can provide a context for understanding the functions of and constraints on colorful traits. Focusing on *Habronattus pyrrithrix* Chamberlin 1924, our goals were to examine (1) the microscopic morphology of the colored body regions that males display to females during courtship (i.e., males' red faces, green legs, and white pedipalps), (2) how the colors of these regions as well as dorsal color patterns change during development prior to sexual maturity, and (3) how male condition-dependent red facial and green leg coloration changes as males age beyond sexual maturity. Although the bright white pedipalps and green legs of males appeared only upon sexual maturity, the sexes began to differentiate in facial coloration and dorsal patterning, with males developing red faces and conspicuous black and white dorsal patterning as young juveniles (ca. 2.5 mm in body length, or ca. 45% of their total mature adult body size). Even after maturity, color was not static; a male's green legs (but not red face) faded with age. Results are discussed in the context of potential functions of and constraints on color in salticids, and how they may change throughout an individual's lifetime.

Keywords: Juvenile coloration, Salticidae, sexual dichromatism, sexual dimorphism, sexual selection

Animal colors and patterns can serve a variety of functions. During courtship, they can aid in species recognition or convey information about the quality of an individual as a mate (see reviews in Andersson 1994; Hill & McGraw 2006). They also frequently keep animals hidden (i.e., camouflage) or protected (i.e., aposematism, mimicry) from predators (see reviews in Cott 1940; Ruxton et al. 2004). In many animals, color patterns are not static throughout life, but change dramatically during development, maturity, and senescence, as well as seasonally (Booth 1990). When color patterns differ between the sexes, examination of ontogenetic color change is particularly interesting because the timing and extent of sexual color differentiation can provide clues to the costs and benefits of different color patterns and their functions and constraints across contexts throughout life.

Color change from development to adulthood is typically thought to represent shifts in selection pressures as individuals change in size, mobility, vulnerability to predation, habitat use, or reproductive status (Booth 1990). In animals where bright male colors have evolved via sexual selection, sex-specific color patterns often appear suddenly upon sexual maturity, presumably because they are costly and unnecessary for juveniles (Andersson 1994). When sexually selected colors appear before sexual maturity, they are particularly interesting because they may hint at previously overlooked functional roles (e.g., Kilner 2006; Kapun et al. 2011). When the sexes differ in color due to different ecological selection pressures (e.g., Slatkin 1984), the timing of color pattern divergence can help us understand shifting selection pressures. For example, in the lizard *Eremias lugubris*, adults and older juveniles are tan and cryptic, whereas young juveniles have highly conspicuous markings, mimicking noxious oospister beetles (Huey & Pianka 1977); in this system, subtle and changing functional roles of color would be missed by limiting study to adult stages.

Adult organisms can also change color as they age beyond sexual maturity (Booth 1990). In many birds, colors used to attract mates do not appear immediately upon sexual maturity, but are delayed until after the first breeding season (reviewed in Hawkins et al. 2012). Animals may also decline (more subtly) in color with senescence; colorful pigments or structures contained within dead tissue (e.g., feathers, scales) can fade with age as a product of abrasion, soiling, or photobleaching (Ornborg et al. 2002; McGraw & Hill 2004; Delhey et al. 2006; Kemp 2006). If maintaining colors is costly, age-based fading can have important consequences for signaling, with the ability to maintain bright colors (i.e., the ability to resist tissue/pigment damage) acting as an indicator of quality (e.g., Delhey et al. 2006). Alternatively, color fading may provide direct information about an individual's age (Manning 1985). Such information could help individuals identify more mature, viable mates (reviewed in Kokko & Lindstrom 1996). Alternatively, if older individuals are more likely to carry disease or parasite infection (e.g., Tarling & Cuzin-Roudy 2008) or if they are more likely to accumulate deleterious mutations in their germ-line (Beck & Promislow 2007), age-based color variation might enable individuals to select younger mates. A deeper understanding of how, and ultimately, why colors change with age will enable us to generate informed hypotheses about their potential signal content and evolution.

Jumping spiders (Salticidae) are an excellent group in which to examine ontogenetic color change from development through senescence. In many species, adult males are more colorful than females and display these colors to females during courtship or to other males during competitive interactions (e.g., Peckham & Peckham 1889, 1890; Lim & Li 2004; Girard et al. 2011). In addition, sexual dichromatism in dorsal color that is not displayed during courtship may

reflect different predator-avoidance strategies of males and females (LAT, unpub. data). To date, only three jumping spider species have had their colors quantified using modern color measurement techniques (i.e., spectrophotometry) (*Cosmophasis umbratica* Simon 1903 (Lim & Li 2006), *Phintella vittata* (C.L. Koch 1846) (Li *et al.* 2008a), and *Habronattus pyrrithrix* Chamberlin 1924 (Taylor *et al.* 2011)), and in only one study were juvenile colors measured (Lim & Li 2006). To our knowledge, no study has documented age-based changes in salticid colors as they develop from spiderlings through sexual maturity. Because species descriptions and dichotomous keys typically include details on only adults, with anatomy of mature genitalia required for proper identification (e.g., Ubick *et al.* 2005), the salticid literature includes few, even qualitative, descriptions of juvenile color patterns (but see Nelson 2010 for an exception).

The genus *Habronattus* F.O.P. Cambridge 1901, containing approximately 100 species, is one of the most highly ornamented groups; males are typically elaborately colored whereas females are cryptic (Griswold 1987; Maddison & Hedin 2003). Furthermore, patterns of juvenile coloration also vary across the genus (LAT, pers. obs.). For example, in *H. hirsutus* (Peckham & Peckham 1888) juveniles of both sexes are indistinguishable from one another to the human eye and resemble cryptic adult females until sexual maturity (LAT, pers. obs.). In *H. hallani* (Richman 1973) juveniles of both sexes are indistinguishable from one another but have striking dorsal color patterns unlike either adult males or females (LAT, pers. obs.). In *H. pyrrithrix*, juvenile males and females exhibit color patterns similar to those of sexually mature adults; males have red faces and striped dorsal patterns, whereas females are drab and cryptic throughout their life (LAT, pers. obs.). This diversity in ontogenetic color change suggests that the costs, benefits, and functions of juvenile colors might be just as interesting as those of adults. Additionally, there is evidence that, after reaching maturity, adult male ornamental colors in *H. pyrrithrix* continue to undergo additional age-related changes, which could have important implications for sexual signaling (Taylor *et al.* 2011).

In this study, we focused on *Habronattus pyrrithrix*; males of this species are adorned with red faces, green front legs, and white pedipalps that they display to females during courtship. Our goals were to (1) examine the microscopic morphology of the elaborately colored body regions that males display (i.e., red faces, green legs, and white pedipalps), (2) examine how the colors of these regions as well as dorsal color patterns change during development leading up to sexual maturity, and (3) examine how male condition-dependent red facial and green leg coloration changes as males age beyond sexual maturity. The red facial and white pedipalp colors of *H. pyrrithrix* are contained within modified setae, or scales (e.g., Hill 1979), while the green leg coloration is present on the surface of the cuticle of the femur (e.g., Parker & Hegedus 2003; Ingram *et al.* 2011), which is further adorned with white scales (LAT, pers. obs.). Recent work on *H. pyrrithrix* suggests that adult male facial and leg colors are correlated with body condition in the field (Taylor *et al.* 2011). The red (but not green) coloration is variable among males of the same age and is positively correlated with the quality of a male's diet

(Taylor *et al.* 2011), and the presence of red coloration improves courtship success in certain contexts (Taylor & McGraw 2013); however, we know nothing about the role of red facial coloration in juvenile males. We have hypothesized elsewhere that the conspicuous dorsal coloration in sexually mature adult males (combined with characteristic leg-waving behavior and high movement rates associated with mate searching) provides protection from predators through imperfect mimicry of bees and/or wasps (see Taylor 2012), yet we know nothing about the potential factors that might shape color differences in sexually inactive juveniles. Even after maturity, male colors do not appear to be static (Taylor *et al.* 2011). Throughout the mating season, the scales that produce the colors may undergo natural wear and degradation, which may result in predictable, post-maturity, age-related deterioration of color (e.g., Kemp 2006; Kemp & Macedonia 2006); this may allow females to use color to assess a male's age during courtship (e.g., Manning 1985).

To our knowledge, this will be the first study to quantify ontogenetic color changes throughout development in any of the more than 5000 species (Platnick 2013) of jumping spiders. Standard portable spectrophotometers used in animal coloration studies (reviewed in Andersson & Prager 2006) typically have a minimum reading area of 1 mm (e.g., Lim & Li 2006; Moreno *et al.* 2006; Galvan & Moller 2009); thus, precise quantification of color can only be done on relatively large body regions (>1 mm). Thus, using standard equipment makes the study of minute patches of color on small species of spiders challenging and makes the detailed study of color on particular body regions of juvenile salticids (e.g., faces, legs, pedipalps) impossible. Here we use a custom-designed microspectrophotometer (see Methods and also Taylor *et al.* 2011), allowing us to carefully measure minute patches of color on juveniles and compare colors with those same precise areas on adult spiders.

METHODS

Study species.—*Habronattus pyrrithrix* is found throughout southern California and Arizona, USA, south to Sinaloa, Mexico (Griswold 1987). In Phoenix, Arizona, they are quite common and found at high densities in riparian areas, grassy backyards, and agricultural fields (LAT, pers. obs.). Geographic variation in coloration is common within the genus *Habronattus* (see Griswold 1987) and thus some subtleties of color pattern described in the present study for Phoenix, AZ animals may vary across the species range. Voucher specimens from our study population have been deposited in the Florida State Collection of Arthropods, Gainesville, FL, U.S.A. Additional details on the biology and courtship display behavior of *H. pyrrithrix* are provided elsewhere (Taylor *et al.* 2011; Taylor & McGraw 2013). Most temperate spiders live only one year in the field (see Foelix 2011); to our knowledge, nothing is known about how long *H. pyrrithrix*, in particular, live under natural conditions.

Scale morphology of adult male ornaments (Study 1).—Using five sexually mature adult specimens, we imaged the color patches on the males' red face, green front legs, and white pedipalps that they display to females, using a Leica-Cambridge Stereoscan 360 field emission scanning electron microscope (SEM) (Leica Microsystems, Wetzlar, Germany)

at an acceleration voltage of 2 kV. Prior to imaging, we allowed frozen specimens to air-dry overnight and then mounted the carapace, legs, and pedipalps onto standard SEM stubs using conductive graphite paint.

Ontogenetic color change in juveniles (Study 2).—To examine how male and female coloration changes during juvenile development in the field, we collected spiders ($n = 135$) from a range of developmental stages (i.e., size classes) between May and October 2008 from a single, dense population within an agricultural area in Queen Creek, Arizona, USA (Maricopa County, 33.224744° N, 111.592825° W). This population was chosen because, in contrast with other sites where multiple species are abundant and interact (LAT, unpub. data), the only species of *Habronattus* that we have ever seen at this site in five years is *H. pyrrithrix*. This allowed us to be confident that all spiderlings and juveniles included in the present study were *H. pyrrithrix*. Specifically, we collected spiderlings (before they are able to be sexed, ca. 1.5–2.0 mm in length, $n = 15$), small juveniles (ca. 2.5 mm, $n = 15$ males, $n = 15$ females), large juveniles (ca. 3 mm, $n = 15$ males, $n = 15$ females), subadults (ca. 4–6 mm, $n = 15$ males, $n = 15$ females) and sexually mature adults (ca. 5–7 mm, $n = 15$ males, $n = 15$ females). Immediately after collection, we froze spiders (-80°C) for later color analysis.

Post-maturity age-related changes in condition-dependent male ornaments (Study 3).—To examine how adult male color changes with age post-maturity, we collected 12 gravid adult females in July and August 2008 from the same population described above, brought them back to the lab and allowed them to lay eggs. Spiderlings were housed together until they were large enough to be sexed (ca. 2.5 mm in length), at which point the first three males from each female's egg sac were removed, housed separately in clear plastic containers ($6 \times 6 \times 13$ cm), and fed a constant diet of small crickets (*Acheta domesticus*) three times per week. Spiders ($n = 36$; three from each of 12 egg sacs) were checked daily to determine if they had molted; within each clutch, as males reached their final molt to maturity, they were randomly assigned to one of three different age groups (0, 60, and 120 days post-maturity). These age ranges were chosen because they likely represent the difference in ages of males in the field during the most active part of the mating season at this site (approximately May–August; LAT, pers. obs.). When males reached the appropriate randomly assigned age (0, 60, or 120 days post-maturity), we euthanized them and placed them in the freezer (-80°C) for later color analysis.

Color measurement and analysis.—Body colors were quantified following methods described in Taylor et al. (2011). Briefly, we used a reflectance spectrophotometer (USB2000, Ocean Optics, Dunedin, FL, USA) coupled to a modified Leica DMLB2 fluorescence light microscope with a $40\times$ quartz objective lens (Leica Microsystems, Wetzlar, Germany) and illuminated with a full-spectrum Leica 75 W xenon arc lamp (Leica Microsystems, Wetzlar, Germany). This setup allowed us to quantify the minute color patches of all size classes of these spiders that are too small to measure accurately with standard spectrophotometry equipment. Unfortunately, the optics of the microscope cut out a portion of the UV spectrum, so this instrument only provides spectral data from 375–700 nm. In some jumping spider species, UV

reflectance appears to be important in communication (Lim et al. 2007, 2008; Li et al. 2008b), and thus we must use caution when excluding UV wavelengths from our analyses. However, in a previous study (Taylor et al. 2011), we confirmed that, though reflectance does extend into the UV for the green legs and white pedipalps of *H. pyrrithrix*, there are no UV peaks in either region, so the benefit of using an instrument that allows precise and repeatable measures on minute color patches of these tiny spiders far outweighs the disadvantage of excluding UV.

For Study 2, where we were interested in color changes of the faces, front legs, and pedipalps of males and females that occurred during juvenile development through maturity, we took the average of two reflectance measures of each of these three body regions. The colored areas that we measured on each specimen were 0.25 mm in diameter. For facial coloration, both measurements were taken from the same region of the face (just below the anterior median eyes). For leg coloration, one measurement was taken from the ventral side of each (right and left) femur. For pedipalp coloration, one measurement was taken from the distal segment of each (right and left) pedipalp. From these spectral data, we calculated the single color variable that captured the most sex- and age-related variation for each body region scored. Specifically, because face color among the different sex/age classes varied from white to red, the metric that captured most of this variation was 'red chroma' (i.e., the proportion of total reflectance in the red region of the spectrum, between 600 and 700 nm). Similarly, because the front legs varied from white to green, the metric that captured most of this variation was 'green chroma' (the proportion of total reflectance between 450 and 550 nm). Finally, because the pedipalps varied in coloration from gray to bright white, brightness (total reflectance over the entire spectrum) was the metric that captured most of this variation. For a detailed discussion of the rationale behind selecting relevant color variables, including those used here, see Montgomerie (2006). In addition, we qualitatively characterized the dorsal color pattern of individuals as either (1) tan and cryptic in coloration, similar to the dorsal coloration of adult females, or (2) consisting of black and white stripes and chevrons characteristic of adult males; all individuals examined fit clearly into one of these two categories (see Results). Because these categorizations were based on pattern rather than reflectance properties of the colors, we did not quantify dorsal coloration spectrophotometrically.

For Study 3, where we were interested in more subtle, age-based fading of display colors in adult males, we limited our analysis to the coloration of the red face and green legs, because previous studies showed that these two color patches were correlated with body condition in the field, presenting the possibility that such condition-dependence could be explained in part by the fading of colors as males age (Taylor et al. 2011). We took the average of two reflectance measures from each region and used these spectral data to calculate three color variables that were previously found to be correlated with body condition in the field: (1) the hue of the red face (the wavelength corresponding to the inflection point of the red curve), (2) the red chroma of the face (the proportion of total reflectance between 600 and 700 nm), and (3) the brightness

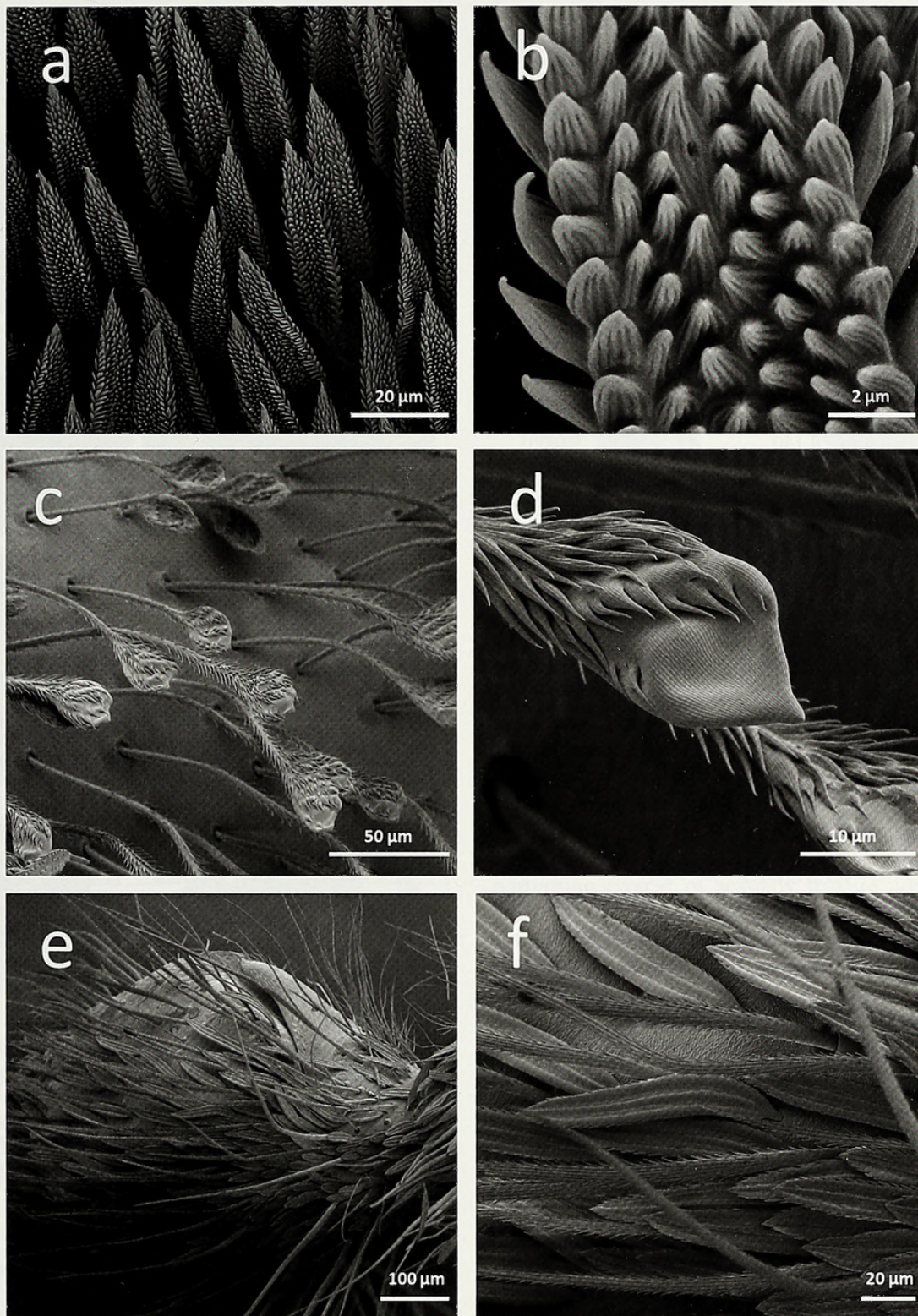


Figure 1.—Morphology of the colored body regions of adult male *Habronattus pyrrithrix*. a–b. Red scales on the face showing ridged protrusions; c–d. White spatulate scales ornamenting the green front leg (femur); e–f. Flat white pedipalp scales.

(mean reflectance) of the green front legs, following the methods described in Taylor et al. (2011). We also determined the relative size of the male's red facial patch; because larger males had larger red faces, we used the residuals of a regression of patch area on carapace width, which provides a 'relative patch size index' that is uncorrelated with body size and has previously been found to be correlated with body condition in the field (Taylor et al. 2011). Three males died

over the course of the study for unknown reasons and were thus excluded from our analyses.

Statistical analysis.—For Study 2, we used analyses of variance (ANOVA) to examine effects of developmental stage (i.e., size class), sex, and their interaction on face color (red chroma), front leg color (green chroma), and pedipalp color (mean brightness). Data did not meet normality and equal-variance assumptions and thus were rank-transformed

Table 1.—Results of ANOVA examining the effect of sex, age (i.e., size class), and their interaction on color metrics associated with the face, legs, and pedipalps during development in *H. pyrrithrix* jumping spiders. Df = degrees of freedom.

Red chroma of face	Df	F	P
sex	1,140	304.96	<0.001
age	4,140	6.30	<0.001
sex × age	4,140	20.27	<0.001
Green chroma of legs	Df	F	P
sex	1,140	0.28	0.60
age	4,140	9.37	<0.001
sex × age	4,140	5.10	<0.001
Brightness of pedipalps	Df	F	P
sex	1,140	1.43	0.23
age	4,140	41.54	<0.001
sex × age	4,140	3.33	0.01

(Conover & Iman 1981) prior to analysis. For Study 3, we used ANOVA to examine the effects of age on the hue, red chroma, and the relative size of a male's red face and on the brightness of his green legs. Because we used three males from each clutch (one assigned to each age category), we included the clutch (i.e., mother's identity) as a random factor in the model. Following ANOVA, we compared the colors among age classes using Tukey-Kramer pairwise comparisons with an alpha level of 0.05. All data from Study 3 met the assumptions of parametric statistics. All statistical analyses were conducted using SAS 9.2 (SAS Institute, Cary, NC, USA).

RESULTS

SEM analyses revealed varied scale structure on the three different colorful body regions of males (Fig. 1). On the red face, we found ridged protrusions covering the surface of each scale (Figs. 1a, b). The green legs were ornamented with long spatulate scales, the flattened ends of which were covered with fine ridges (Figs. 1c, d). The white scales on the pedipalps were similar in size and shape to the red facial scales, but were relatively smooth by comparison (Figs. 1e, f).

In Study 2, we found a significant effect of the age × sex interaction on all three color metrics examined (Table 1), indicating that colors developed differently between the sexes. Although spiderlings of both sexes had sparse red scales around their anterior median eyes (Fig. 2a), development of red coloration on the face was apparent in small juvenile males and increased into adulthood, whereas small juvenile females developed white facial scales (Figs. 2, 3a). Similarly, the conspicuous dorsal color pattern of males was also fully developed in small juveniles (ca. 2.5 mm), whereas spiderlings of both sexes and juvenile females had a cryptic, tan dorsal color pattern similar to adult females (Fig. 4). In contrast, the green coloration of the legs and the bright white pedipalp coloration typical of adult males showed a sudden onset at sexual maturity (Fig. 3b, c).

In Study 3, the green leg coloration of adult males was brighter (lighter) with increasing age ($F_{2,21} = 4.17$, $P = 0.03$; Fig. 5d), but we found no effect of age on any aspect of red facial coloration (hue: $F_{2,21} = 0.37$, $P = 0.69$; red chroma:

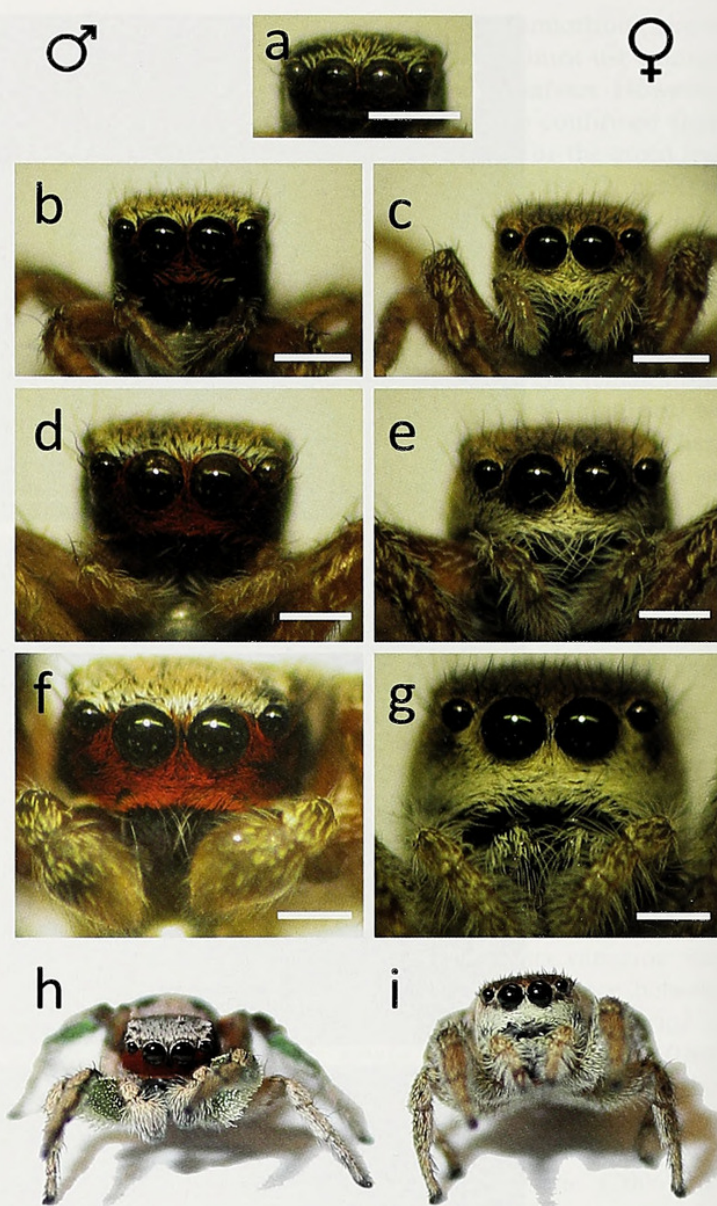


Figure 2.—Ontogenetic changes in coloration in males and females as spiders develop from spiderlings through sexual maturity. a. Spiderling stage (where sexes are indistinguishable); b. Small juvenile male; c. Small juvenile female; d. Large juvenile male; e. Large juvenile female; f. Subadult male; g. Subadult female; h. Sexually mature adult male; i. Sexually mature adult female. Scale bars represent 0.5 mm.

$F_{2,21} = 0.53$, $P = 0.60$; size of red facial patch: $F_{2,21} = 1.97$, $P = 0.17$; Figs. 5a–c).

DISCUSSION

Here we document the scale morphology associated with the three colored body regions in male *Habronattus pyrrithrix* that are prominently displayed to females during courtship. We also show how the colors of these three regions (i.e., red face, green front legs, and bright white pedipalps) develop as individuals grow from spiderlings through sexual maturity. Finally, given that the colors of two of these body regions (i.e., red faces and green front legs) were previously found to be correlated with body condition in the field (Taylor et al. 2011), we examined the possibility of age-related fading of these traits

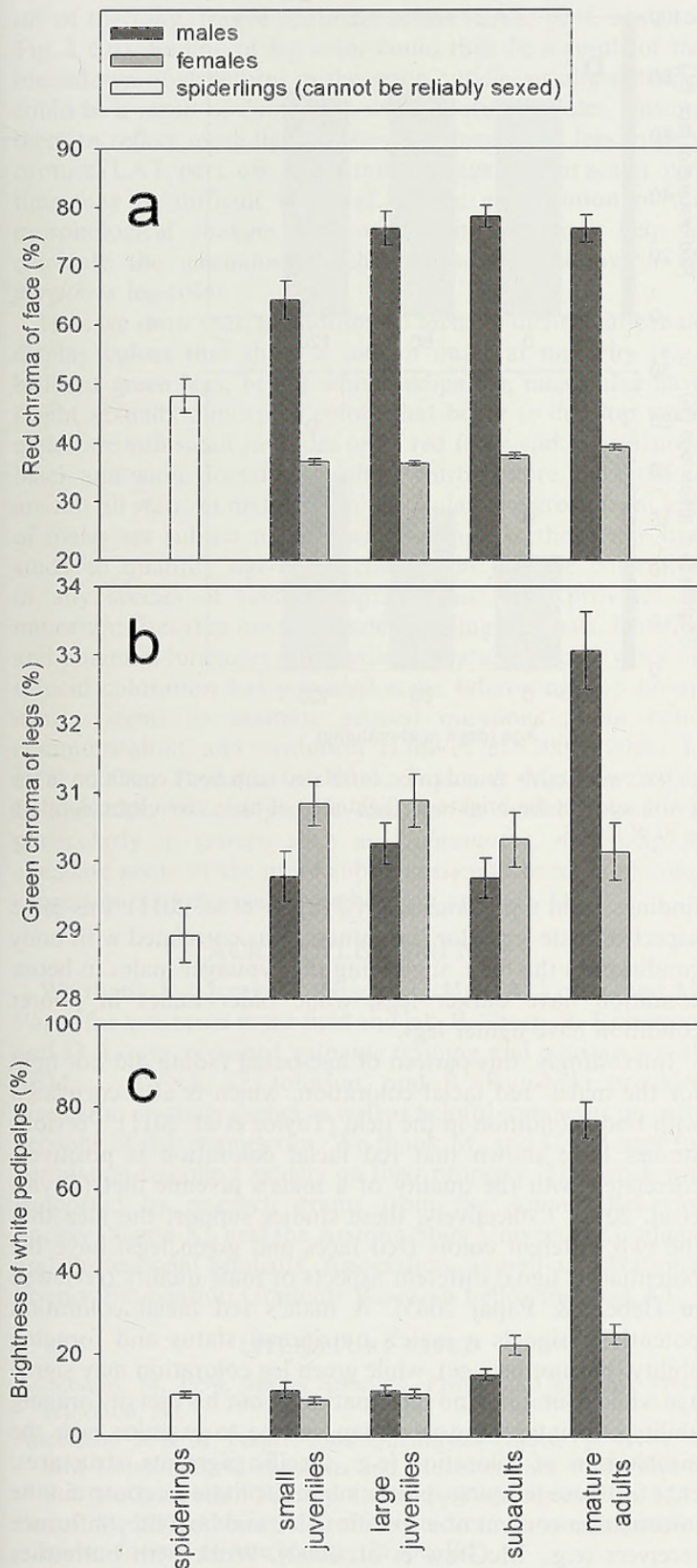


Figure 3.—Ontogenetic changes in coloration in males and females as spiders develop from spiderlings through sexual maturity (mean \pm SEM). a. Facial coloration; b. Front leg coloration; c. Pedipalp coloration.

in adult males and show that green leg coloration, but not red facial coloration, fades (i.e., becomes lighter) with age.

In examining color development, we found that both the bright white pedipalps and green leg coloration of males

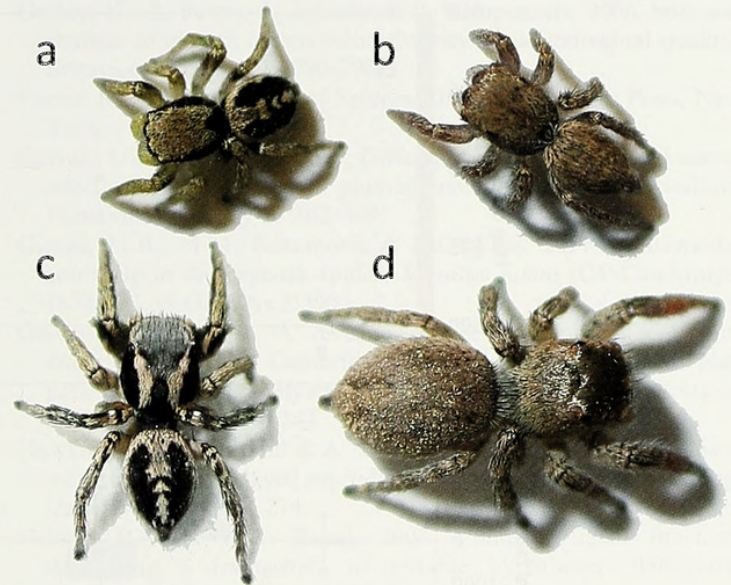


Figure 4.—Sexual dichromatism in dorsal coloration in juvenile and adult male and female *H. pyrrithrix*. a. Juvenile male; b. Juvenile female; c. Adult male; d. Adult female.

appeared only at sexual maturity. This is typical of many animal ornaments used in mating or aggressive competitions over access to mates; moreover, because such colors typically incur costs, it is not surprising that these ornaments are not expressed in juvenile stages (Andersson 1994). In contrast, males and females began to differentiate in red facial coloration and dorsal patterning as young juveniles (ca. 2.5 mm). During these stages, young males began to develop red facial scales and conspicuous black and white dorsal patterning typical of sexually mature adult males. The red coloration of adult males is prominently displayed in courtship and has been shown to improve courtship success in certain contexts (Taylor & McGraw 2013), yet it is unclear whether this coloration might have any functional role for juvenile males who do not engage in courtship. Red coloration has been shown to have important effects on receivers in a variety of taxa (reviewed in Pryke 2009); it could be that juvenile males use their red face for signaling in non-sexual contexts, either with conspecifics, potential predators, or prey. Regarding conspicuous dorsal patterning in adult males, this appears to be linked to higher movement rates associated with mate-searching, compared with cryptic females who spend more time at rest. Presumably, the higher movement rates of males render cryptic coloration ineffective; the pairing of conspicuous body patterns with false antennation (i.e., leg waving behavior) may help adult males avoid predators by imperfectly mimicking wasps and/or bees (Taylor 2012). Again, it is unclear what benefits, if any, this dorsal coloration might provide to young juvenile males. It is possible that, even as juveniles, males and females might face different ecological selection pressures (e.g., different dispersal or movement rates) that may drive such sex-differences in juvenile dorsal patterning (Booth 1990); in future work, such ideas should be examined in more detail. Finally, it is possible that juvenile sexual dichromatism does not have a functional role (e.g., Johnston 1967); it may simply indicate relaxed selection pressure for crypsis, compared with other species in which

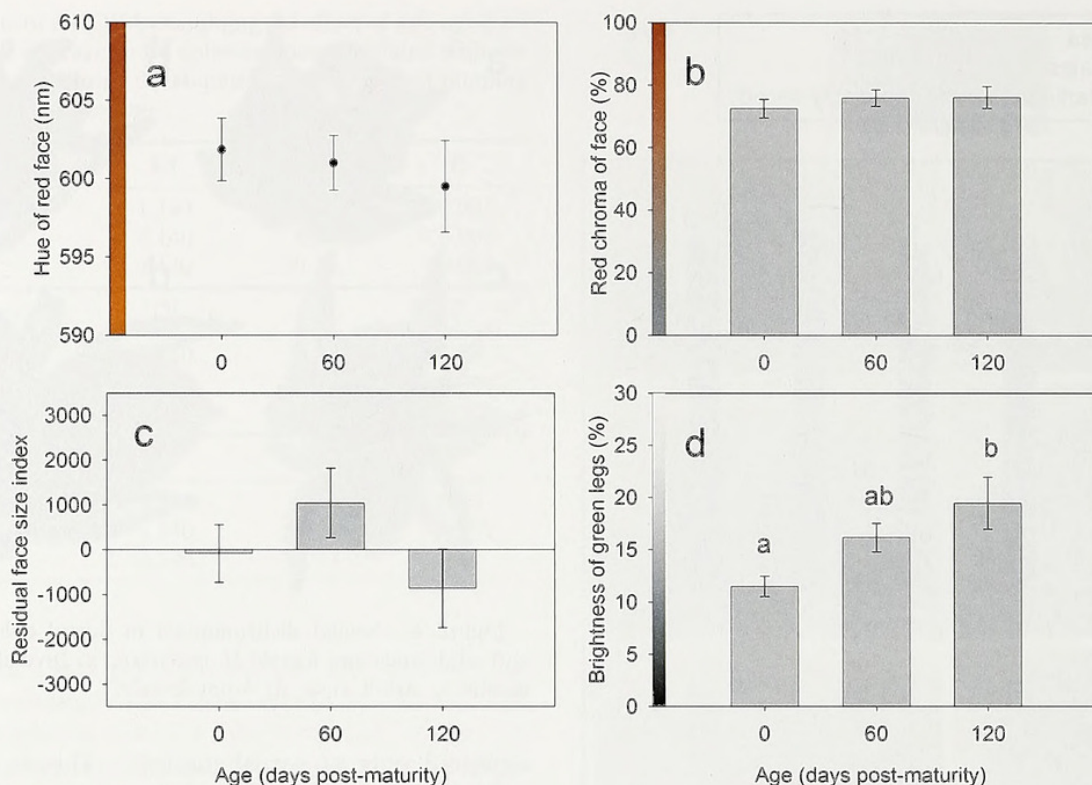


Figure 5.—Effect of adult age (post-maturity) on male display colors that were previously found to be correlated with body condition in the field (mean \pm SEM). Aspects of red facial coloration (a–c) did not change with age, yet the brightness (lightness) of male green leg coloration increased as males aged (d). Different letters indicate significant differences at $P < 0.05$.

males are cryptically colored until maturity. It is interesting, however, that this species is an exception to the general pattern of salticid color development, where juveniles of both sexes typically resemble females in color pattern until reaching maturity (LAT, pers. obs.). To date, studies of any aspect of the biology of juvenile jumping spiders are rare (e.g., Nelson et al. 2005; Bartos 2008), yet they have revealed interesting aspects of life history that would have been missed by simply focusing on adults, as most studies do. *H. pyrrithrix* is a particularly good system in which to examine sex differences in juveniles because, unlike most salticid species, color patterns allow small juveniles to be accurately sexed well before reaching maturity.

In addition to age-related changes that occur during development prior to sexual maturity, our study also uncovered post-maturity, age-based color change. Previous studies have suggested that structural coloration in jumping spiders may be linked to male age (Lim & Li 2007; Taylor et al. 2011), yet both of these studies used comparisons of two groups of spiders, one that had been collected from the field and measured immediately and a second that was field-collected and measured after a certain period of time in the lab. While differences in the two groups may be due to age, we cannot rule out confounding effect of diets and captivity; in both cases, the first group experienced a field-based diet/environment for its entire life while the second group was collected from the field and then switched to a lab-based diet/environment prior to color measurement. Here we remove these confounding effects of diet and captivity to show that, even when spiders are raised entirely in the lab, the green leg coloration of adult males fades (i.e., increases in mean brightness) with age. This is also consistent with correlational

findings from a previous study (Taylor et al. 2011); this same aspect of male leg color (brightness) was correlated with body condition in the field, suggesting that younger males in better condition have darker legs, while older males in poorer condition have lighter legs.

Interestingly, this pattern of age-based fading did not hold for the males' red facial coloration, which is also correlated with body condition in the field (Taylor et al. 2011). Previous studies have shown that red facial coloration is positively correlated with the quality of a male's juvenile diet (Taylor et al. 2011). Collectively, these studies support the idea that the two different colors (red faces and green legs) have the potential to signal different aspects of male quality (reviewed in Hebets & Papaj 2005). A male's red facial coloration potentially signals a male's nutritional status and foraging ability (but not his age), while green leg coloration may signal age while containing no information about his diet or foraging ability. An interesting next step will be to examine how the mechanisms of coloration (e.g., specific pigments, structures, etc.) for these jumping spiders might facilitate or constrain the information content of a specific color and how they influence receivers (e.g., McGraw et al. 2002). Work with butterflies suggests that structural colors are more likely to fade with age than pigmentary colors (Kemp 2006). A better understanding of the detailed mechanisms of color production in *H. pyrrithrix*, including the specific pigments and structure types, will allow us to test the generality of these ideas.

Our examination of the morphology of the males' green legs offer preliminary insight into the mechanisms of age-based fading observed in our study. The green leg coloration is produced in the cuticle, while additional white light is reflected

off of the long, fragile spatulate scales (LAT, pers. obs., see Fig. 1 c,d). Fading of leg color could thus be a result of the breakdown of structures in the green cuticle, or alternatively, could be a result of damage to white spatulate scales, causing them to reflect more light. Males use these front legs in prey capture (LAT, pers. obs.), and thus damage to their scales over time may be difficult to avoid. Closer examination of the morphological changes that occur with age may help to elucidate the mechanisms behind age-based fading in *H. pyrrithrix* leg color.

Here we show that, in addition to sexually dichromatic male display colors that show a sudden onset at maturity (e.g., brilliant green legs, bright white pedipalps), males also have bright sexually dimorphic colors that begin to develop when males are still small juveniles (e.g., red faces and conspicuous black and white dorsal patterning). Furthermore, these colors are not all static at maturity; in particular, the green front legs of males are subject to age-based fading. As this is the first study to quantify age-based changes in juvenile coloration of any species of jumping spider, this work provides an important first step towards understanding the costs, benefits, and potential functions of juvenile coloration. Recent work on salticid coloration has provided some interesting and promising systems to examine general questions about color communication and evolution (Lim et al. 2007, 2008; Li et al. 2008a; Taylor et al. 2011; Taylor & McGraw 2013). Examination of ontogenetic changes in spider coloration, particularly in groups such as *Habronattus*, may help us elucidate some of the more subtle costs and benefits of color expression and change throughout an animal's life.

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LITERATURE CITED

- Andersson, M. 1994. Sexual Selection. Princeton University Press, Princeton, NJ.
- Andersson, S. & M. Prager. 2006. Quantifying colors. Pp. 41–89. In Bird Coloration: Mechanisms and Measurements. (G.E. Hill & K.J. McGraw, eds.). Harvard University Press, Cambridge, MA.
- Bartos, M. 2008. Alternative predatory tactics in a juvenile jumping spider. *Journal of Arachnology* 36:300–305.
- Beck, C.W. & D.E.L. Promislow. 2007. Evolution of female preference for younger males. *PLoS ONE* 2:e939.
- Booth, C.L. 1990. Evolutionary significance of ontogenetic colour change in animals. *Biological Journal of the Linnean Society* 40:125–163.
- Conover, W.J. & R.L. Iman. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *American Statistician* 35:124–129.
- Cott, H.B. 1940. Adaptive Coloration in Animals. Methuen, London, UK.
- Delhey, K., A. Peters, A. Johnsen & B. Kempenaers. 2006. Seasonal changes in blue tit crown color: do they signal individual quality? *Behavioral Ecology* 17:790–798.
- Foelix, R.F. 2011. Biology of Spiders. Oxford University Press, New York.
- Galvan, I. & A.P. Moller. 2009. Different roles of natural and sexual selection on senescence of plumage colour in the barn swallow. *Functional Ecology* 23:302–309.
- Girard, M.B., M.M. Kasumovic & D.O. Elias. 2011. Multi-modal courtship in the peacock spider, *Maratus volans* (OP-Cambridge, 1874). *PLoS ONE* 6:e25390.
- Griswold, C.E. 1987. A revision of the jumping spider genus *Habronattus* F.O.P. Cambridge (Araneae: Salticidae), with phenetic and cladistic analyses. University of California Publications in Entomology 107:1–344.
- Hawkins, G.L., G.E. Hill & A. Mercadante. 2012. Delayed plumage maturation and delayed reproductive investment in birds. *Biological Reviews* 87:257–274.
- Hebets, E.A. & D.R. Papaj. 2005. Complex signal function: developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology* 57:197–214.
- Hill, D.E. 1979. Scales of salticid spiders. *Zoological Journal of the Linnean Society* 65:193–218.
- Hill, G.E. & K.J. McGraw. 2006. Bird Coloration: Function and Evolution. Harvard University Press, Cambridge, MA, USA.
- Huey, R.B. & E.R. Pianka. 1977. Natural selection for juvenile lizards mimicking noxious beetles. *Science* 195:201–203.
- Ingram, A.L., O. Deparis, J. Boulenguez, G. Kennaway, S. Berthier & A.R. Parker. 2011. Structural origin of the green iridescence on the chelicerae of the red-backed jumping spider, *Phidippus johnsoni* (Salticidae: Araneae). *Arthropod Structure & Development* 40: 21–25.
- Johnston, R.F. 1967. Sexual dimorphism in juvenile house sparrows. *Auk* 84:275–277.
- Kapun, M., A. Darolova, J. Kristofik, K. Mahr & H. Hoi. 2011. Distinct colour morphs in nestling European Bee-eaters *Merops apiaster*: is there an adaptive value? *Journal of Ornithology* 152:1001–1005.
- Kemp, D.J. 2006. Heightened phenotypic variation and age-based fading of ultraviolet butterfly wing coloration. *Evolutionary Ecology Research* 8:515–527.
- Kemp, D.J. & J.M. Macedonia. 2006. Structural ultraviolet ornamentation in the butterfly *Hypolimnas bolina* L. (Nymphalidae): visual, morphological and ecological properties. *Australian Journal of Zoology* 54:235–244.
- Kilner, R. 2006. Function and evolution of color in young birds. Pp. 201–232. In Bird Coloration: Function and Evolution. (G.E. Hill & K.J. McGraw, eds.). Harvard University Press, Cambridge, MA.
- Kokko, H. & J. Lindstrom. 1996. Evolution of female preference for old mates. *Proceedings of the Royal Society Biological Sciences Series B* 263:1533–1538.
- Li, J.J., M.L.M. Lim, Z.T. Zhang, Q.Q. Liu, F.X. Liu & J. Chen, et al. 2008a. Sexual dichromatism and male colour morph in ultraviolet-B reflectance in two populations of the jumping spider *Phintella vittata* (Araneae: Salticidae) from tropical China. *Biological Journal of the Linnean Society* 94:7–20.
- Li, J.J., Z.T. Zhang, F.X. Liu, Q.Q. Liu, W.J. Gan & J. Chen, et al. 2008b. UVB-based mate-choice cues used by females of the jumping spider *Phintella vittata*. *Current Biology* 18:699–703.
- Lim, M.L.M. & D.Q. Li. 2004. Courtship and male-male agonistic behaviour of *Cosmophasis umbratica* Simon, an ornate jumping spider (Araneae: Salticidae) from Singapore. *Raffles Bulletin of Zoology* 52:435–448.
- Lim, M.L.M. & D.Q. Li. 2006. Extreme ultraviolet sexual dimorphism in jumping spiders (Araneae: Salticidae). *Biological Journal of the Linnean Society* 89:397–406.

- Lim, M.L.M. & D.Q. Li. 2007. Effects of age and feeding history on structure-based UV ornaments of a jumping spider (Araneae: Salticidae). *Proceedings of the Royal Society Biological Sciences Series B* 274:569–575.
- Lim, M.L.M., M.F. Land & D.Q. Li. 2007. Sex-specific UV and fluorescence signals in jumping spiders. *Science* 315:481–481.
- Lim, M.L.M., J.J. Li & D. Li. 2008. Effect of UV-reflecting markings on female mate-choice decisions in *Cosmophasis umbratica*, a jumping spider from Singapore. *Behavioral Ecology* 19:61–66.
- Maddison, W. & M. Hedin. 2003. Phylogeny of *Habronattus* jumping spiders (Araneae: Salticidae), with consideration of genital and courtship evolution. *Systematic Entomology* 28:1–21.
- Manning, J.T. 1985. Choosy females and correlates of male age. *Journal of Theoretical Biology* 116:349–354.
- McGraw, K.J. & G.E. Hill. 2004. Plumage color as a dynamic trait: carotenoid pigmentation of male house finches (*Carpodacus mexicanus*) fades during the breeding season. *Canadian Journal of Zoology* 82:734–738.
- McGraw, K.J., E.A. Mackillop, J. Dale & M.E. Hauber. 2002. Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *Journal of Experimental Biology* 205:3747–3755.
- Montgomerie, R. 2006. Analyzing colors. Pp. 90–147. In *Bird Coloration: Mechanisms and Measurements*. (G.E. Hill & K.J. McGraw, eds.). Harvard University Press, Cambridge, MA.
- Moreno, J., E. Lobato, J. Morales, S. Merino, G. Tomas & J. Martinez-de la Puente, et al. 2006. Experimental evidence that egg color indicates female condition at laying in a songbird. *Behavioral Ecology* 17:651–655.
- Nelson, X.J. 2010. Polymorphism in an ant mimicking jumping spider. *Journal of Arachnology* 38:139–141.
- Nelson, X.J., R.R. Jackson & G. Sune. 2005. Use of *Anopheles*-specific prey-capture behavior by the small juveniles of *Evarcha culicivora*, a mosquito-eating jumping spider. *Journal of Arachnology* 33:541–548.
- Ornberg, J., S. Andersson, S.C. Griffith & B.C. Sheldon. 2002. Seasonal changes in a ultraviolet structural colour signal in blue tits, *Parus caeruleus*. *Biological Journal of the Linnean Society* 76:237–245.
- Parker, A.R. & Z. Hegedus. 2003. Diffractive optics in spiders. *Journal of Optics A — Pure and Applied Optics* 5:S111–S116.
- Peckham, G.W. & E.G. Peckham. 1889. Observations on sexual selection in spiders of the family Attidae. *Occasional Papers of the Wisconsin Natural History Society* 1:3–60.
- Peckham, G.W. & E.G. Peckham. 1890. Additional observations on sexual selection in spiders of the family Attidae, with some remarks on Mr. Wallace's theory of sexual ornamentation. *Occasional Papers of the Wisconsin Natural History Society* 1:117–151.
- Platnick, N.I. 2013. The World Spider Catalog, Version 13.5. American Museum of Natural History, New York. Online at <http://research.amnh.org/iz/spiders/catalog>
- Pryke, S.R. 2009. Is red an innate or learned signal of aggression and intimidation? *Animal Behaviour* 78:393–398.
- Ruxton, G.D., T.N. Sherratt & M.P. Speed. 2004. *Avoiding Attack: the Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*. Oxford University Press, Oxford, UK.
- Slatkin, M. 1984. Ecological causes of sexual dimorphism. *Evolution* 38:622–630.
- Tarling, G.A. & J. Cuzin-Roudy. 2008. External parasite infestation depends on moult-frequency and age in Antarctic krill (*Euphausia superba*). *Polar Biology* 31:121–130.
- Taylor, L.A. 2012. Color and communication in *Habronattus* jumping spiders: tests of sexual and ecological selection. Ph.D. Dissertation, Arizona State University.
- Taylor, L.A., D.L. Clark & K.J. McGraw. 2011. Condition dependence of male display coloration in a jumping spider (*Habronattus pyrrithrix*). *Behavioral Ecology and Sociobiology* 65:1133–1146.
- Taylor, L.A. & K. McGraw. 2013. Male ornamental coloration improves courtship success in a jumping spider, but only in the sun. *Behavioral Ecology* 24:955–967.
- Ubick, D., P. Paquin, P.E. Cushing & V.D. Roth. 2005. *Spiders of North America: An Identification Manual*. American Arachnological Society.

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