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ORIGINAL PAPER

Condition dependence of male display coloration in a jumping spider (*Habronattus pyrrithrix*)

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Abstract In many animals, conspicuous coloration functions as a quality signal. Indicator models predict that such colors should be variable and condition dependent. In *Habronattus pyrrithrix* jumping spiders, females are inconspicuously colored, while males display brilliant red faces, green legs, and white pedipalps during courtship. We tested the predictions of the indicator model in a field study and found that male body condition was positively correlated with the size, hue, and red chroma of a male's facial patch and negatively correlated with the brightness of his green legs. These traits were more condition dependent than non-display colors. We then tested a dietary mechanism for condition dependence using two experiments. To understand how juvenile diet affects the development of coloration, we reared juvenile spiders on high- and low-quality diets and measured coloration at maturity. To understand how adult diet affects the maintenance of coloration, we fed wild-caught adults with high- or low-quality diets and compared their coloration after 45 days. In the first experiment, males fed high-quality diet had redder faces, suggesting that condition dependence is mediated by juvenile diet. In the second experiment, red coloration did not differ between treatments, suggesting that adult diet is not important for maintaining the color after it is produced at maturity. Diet had no effect on green coloration in either experiment. Our results show different degrees of condition dependence for male display colors. Because red is dependent on juvenile diet, it may signal health or foraging ability. We discuss evidence that green coloration is age dependent and alternatives to indicator models for colorful displays in jumping spiders.

Keywords Diet · Honest advertisement · Nutrition · Ornamental color · Salticidae · Sexual dichromatism · Sexual signaling

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Introduction

In many animals, males are adorned with elaborate ornaments that they display to females during courtship or to other males during competitive interactions (reviewed in Andersson 1994). There are a number of hypotheses that have been proposed to explain the preponderance of such conspicuous, and potentially costly, sexual signals by males. Guilford and Dawkins (1991) provide a useful framework by distinguishing between hypotheses that are content-based and those that are efficacy-based (see also Hebets and Papaj 2005). Content-based hypotheses are those that propose that there is some sort of information being provided by the signal of interest. In the context of courtship, this could include a signal that identifies a courting male as the appropriate species (e.g., Couldridge and Alexander 2002) or provides information about the relative quality of that male as a mate (Andersson 1982). Alternatively, efficacy-based hypotheses propose that there is little or no information present in the signal, but that it has been selected simply as a mechanism to improve signal

transmission or make use of the female's sensory psychology to achieve a specific response. Examples of efficacy-based hypotheses include the use of a signal to attract a female's attention in a noisy environment (e.g., Clark and Uetz 1993), to reduce aggression or cannibalism in a potential female mate (e.g., Forster 1982; Hebets and Papaj 2005), or simply to take advantage of a female's sensory biases (e.g., Basolo 1990) or preferences for exaggerated traits that may have arisen through a Fisherian process (reviewed in Andersson 1994).

Many of these hypotheses are not mutually exclusive—a trait of interest might allow a female to recognize a courting male as the appropriate species and, if the trait is costly, it might also provide her with information about his quality as a mate. Moreover, this same trait may also be selected for its efficacy in initially attracting her attention. Despite their potential overlap, each of these hypotheses generates specific and testable predictions. Of these functional hypotheses, only content-based, indicator hypotheses explicitly predict that the color of interest should be condition dependent. Thus, examining the condition dependence of a trait is a good first step towards teasing apart competing hypotheses for signal function.

Bright coloration has been studied extensively as a costly, quality-indicating trait in many animal taxa (reviewed in Andersson 1994). Indicator hypotheses to explain bright coloration predict that the expression of conspicuous coloration should: (a) be highly variable among individuals in a population, (b) be linked to an individual's condition, and (c) show heightened condition dependence compared with naturally selected (non-display) body colors (Cotton et al. 2004; Dale 2006). There is now a growing body of evidence suggesting that a variety of putative signaling colors show such condition-dependent expression in both vertebrates (fish: e.g., Boughman 2007; reptiles: e.g. Lebas and Marshal 2001; birds: reviewed in Hill 2006) and invertebrates (damselflies: e.g., Contreras-Garduno et al. 2008; butterflies: e.g., Kemp and Rutowski 2007; ambush bugs: Punzalan et al. 2008). Such condition dependence can be mediated through the production costs of color—for example, pigment acquisition or synthesis (e.g., carotenoid coloration in birds: McGraw 2006a) or arrangement and composition of highly precise nanoscale structures (e.g., structural coloration in butterflies: Kemp and Rutowski 2007). Though not well studied, it has also been demonstrated in a few systems that colors are also costly to maintain (e.g., via grooming; Zampiga et al. 2004; Lenouval et al. 2009).

There has been much interest in the evolution and function of the complex courtship displays of male jumping spiders (Family Salticidae) (e.g., Peckham and Peckham 1889, 1890). Many jumping spiders exhibit extreme sexual dichromatism, in which mature males are brightly colored while females and juveniles are dull and inconspicuous (Maddison 1995; Oxford and Gillespie 1998). Males often display their most colorful body regions to potential mates and male competitors (e.g., Peckham and Peckham 1889, 1890; Lim and Li 2004), sometimes in concert with auditory displays (e.g., Maddison and Stratton 1988; Elias et al. 2003). Studies of electrophysiology (e.g., Devoe 1975; Yamashita and Tateda 1976) and behavior (e.g., Nakamura and Yamashita 2000; Lim and Li 2006) suggest that salticids are capable of fine-tuned color discrimination. In some species, visual cues, such as male dancing (Jackson 1981) or the presence of UV light (Lim et al. 2007, 2008; Li et al. 2008) may increase a female's receptivity. In one of the most highly ornamented groups, the genus *Habronattus*, studies of geographically isolated populations suggest that sexual selection is a driving force in the diversification of male display traits (Masta and Maddison 2002). All of this evidence suggests that male color might be a good candidate as a quality signal, yet surprisingly the condition dependence of coloration has only been examined in *Cosmophasis umbratica* (Lim and Li 2007), just one of the more than 5,000 jumping spider species (Platnick 2010).

The goal of the present study was to begin to tease apart the hypotheses for the potential functions of color in male *Habronattus pyrrithrix*, a jumping spider, the adult males of which display a colorfully ornamented red facial patch, green front legs, and bright white pedipalps to females that are a drab gray and brown (Fig. 1). To understand the links between condition and color expression in these spiders, we first used a field study of wild adult male spiders within a single population during the mating season to observationally assess the relationship between body condition and display coloration. We then compared these levels of condition dependence with those of naturally selected body colors that are not displayed to females. We also ran manipulative experiments in the laboratory to explore whether there were causal relationships between display color and diet, a factor likely to affect condition. Because these spiders are generalist predators exposed to a variety of prey types in the field (LAT, personal observation), manipulative experiments can create a variation in diet quality that is biologically relevant (e.g., Mayntz et al. 2005). Furthermore, previous studies with spiders showed that manipulations of diet are effective for manipulating numerous fitness proxies (e.g., growth rate, body condition, survival; Toft and Wise 1999; Mayntz and Toft 2001). In experiment 1, we manipulated juvenile diet to determine nutritional effects on the development of adult male coloration. Because most spiders (including our study species) no longer molt after they have reached sexual maturity (Foelix 1996), males acquire their adult coloration upon their final molt. Thus, this coloration lasts a male

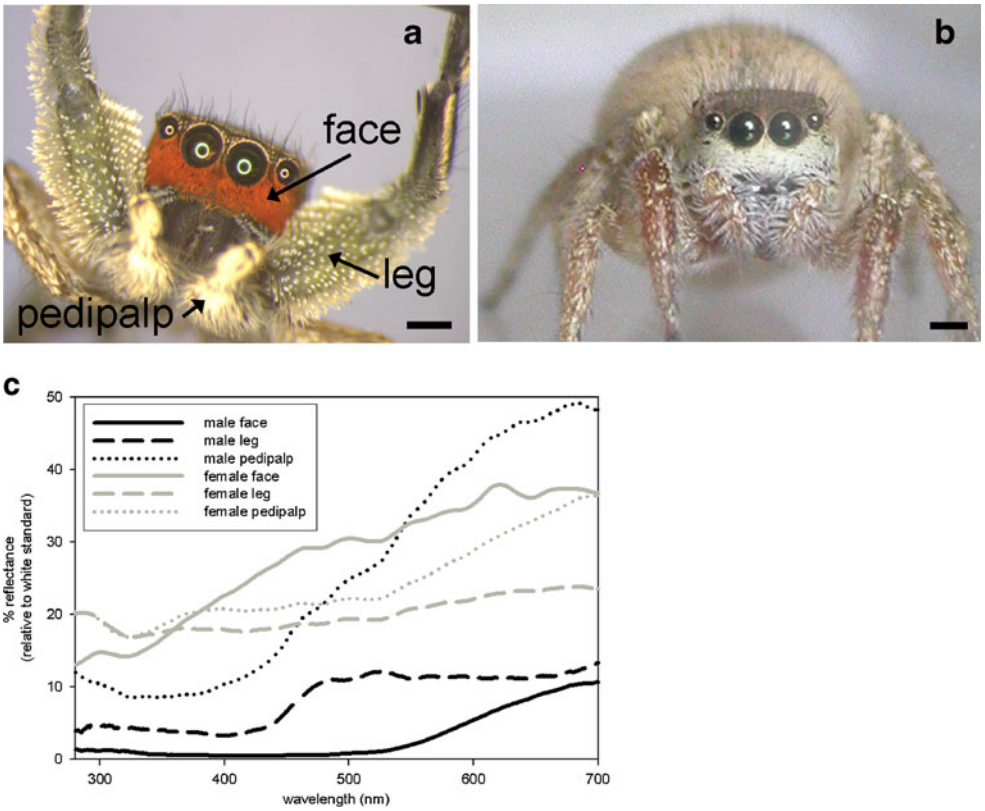

Fig. 1 Sexual dichromatism in *H. pyrrithrix*: **a** adult male, **b** adult female, and **c** representative reflectance spectra for the three potential signaling regions (on males and females) that are the focus of this study. *Scale bars* represent 0.5 mm

through the rest of the mating season and his ability to maintain this coloration may be particularly important. Spider colors are often contained on the surface of the cuticle or within fragile modified body hairs or scales (e.g., Hill 1979) and thus maintenance via grooming and prevention of scale loss, damage, or degradation may be particularly important. In experiment 2, we manipulated the diets of wild-caught adult males (that had already produced their adult colors) to determine if the quality of a male's diet affected his ability to maintain his coloration.

Materials and methods

Study species

H. pyrrithrix Chamberlin 1924 is highly sexually dichromatic. Males are adorned with bright red faces, green front legs, and bright white pedipalps, compared with dull and inconspicuous gray and brown females (Griswold 1987; Fig. 1). The red facial coloration and the white pedipalp coloration are contained within body scales (e.g., Hill 1979), while the green leg coloration is present on the surface of the cuticle of the leg, which is further adorned with white scales (LAT, personal observation). This species is distributed from southern California and Arizona south to Sinaloa, Mexico (Griswold 1987). They are common in the metropolitan area of Phoenix, AZ, where they can be found in high densities in grassy parks, backyards, and agricultural settings as well as leaf litter in more natural areas (LAT, personal observation). As in other species of *Habronattus*, males court females with complex courtship dances (e.g., Richman 1973, 1982), in which their colorful body regions are clearly displayed to females. When viewed from above or from the side, these colors are generally concealed, but during courtship males wave their green legs, expose their red face, and tap their white pedipalps (LAT, personal observation). While they also appear to have a vibrational component to their display (as in some other *Habronattus* species; see Maddison and Stratton 1988), the present study focused only on the colors involved in the visual display. In this study, we focus our discussion on color in the context of female-directed courtship rather than male–male interactions because we rarely observe males interacting with one another in either the field or lab (LAT, personal observation). When males do interact, their displays towards one another are rare and brief, lasting for only a few seconds, compared with displays towards females that can last for hours.

Correlational field study

To determine how color varies with body condition in a natural population of *H. pyrrithrix* during the mating season, we collected 57 adult males from a single population at Schnepf Farm in Queen Creek, AZ (Maricopa

County), USA (33.224744 N, 111.592825 W). The spiders were collected from areas of tall grass either using sweep nets or by hand during three collecting bouts (7 July 2006, $n=30$; 1 August 2006, $n=15$; and 25 August 2006, $n=12$) spanning the most active part of the mating season. Little is known about the synchrony of egg laying and hatching in this species, but we regularly monitor this population and 4 years of data (LAT, unpublished data) suggest that most of the adult males that are active in a given mating season hatched the previous fall and overwintered as juveniles. Immediately upon return to the lab, we weighed each individual to the nearest 0.0001 g with an electronic balance (Mettler-Toledo, Columbus, OH, USA) and photographed each spider once next to a size standard using a Nikon Coolpix 4500 digital camera (Nikon Inc., Melville, NY, USA; image resolution, 2,272×1,704 pixels). We measured the width of the carapace (just behind the posterior lateral eyes) from these photographs using Photoshop software (Adobe Systems Inc., San Jose, CA, USA). Because the carapace width of these spiders is fixed at maturity while the abdomen stretches as an individual gets fatter, we used the residuals of a regression of mass on carapace width as an estimate of body condition (or 'relative fatness') (Jakob et al. 1996). Data from a concurrent study of *H. pyrrithrix* from this same population suggests that this residual condition index is a good predictor of mating success (LAT, unpublished data), so it is likely to be a biologically relevant indicator of condition that is uncorrelated with structural size. After measurements were taken, we immediately placed the spiders in the freezer (−80°C) where they were stored until October 2006 for color analysis (described in detail below).

Captive diet experiments

For the duration of the experiments, we housed spiders individually in cylindrical plastic containers (5.5 cm tall and 2.5 cm in diameter) within an incubator at 28°C on a 14:10 light–dark cycle. For experiment 1 (manipulation of juvenile diet), we monitored the spiders daily for molt, and upon their final molt to sexual maturity we immediately weighed them, measured their carapace width, and froze them (−80°C) for later color analysis (described in detail below). For experiment 2 (manipulation of adult diet), we kept all spiders in captivity on the manipulated diets for 45 days, at which point we weighed, measured, and froze them (−80°C) for later color analysis. The time period of 45 days was chosen for two reasons. First, we wanted the duration of the diet manipulations in the two experiments to be comparable so that we could understand how the same diet manipulations would affect males over different developmental periods; 45 days was our a priori estimate of the length of time that it would take the males from experiment 1 to reach maturity. Secondly, preliminary field data from this population during the previous year indicated that there was a peak in activity of sexually mature males and females that lasted for about 45 days, and so this timeframe corresponded with the most active part of the mating season. Measuring facial coloration on these spiders involved mounting them under a microscope and focusing a full-spectrum light source on their face (described in more detail below), which could potentially blind the spiders and affect their ability to capture prey. For this reason, color measurements were only performed at the end of the diet manipulation experiments (after the spiders were euthanized).

For experiment 1, 28 juvenile male spiders were collected from the same Queen Creek population described above between 24 May and 2 July 2007. While the juveniles of many spider species cannot be reliably sexed until maturity, juvenile male *H. pyrrithrix* can be readily distinguished from females by the presence of sparse red facial scales (LAT, personal observation). Because there was considerable variation in initial body size among juveniles (carapace width = 1.006±0.238 mm (mean±SD)) and because we wanted to ensure that individuals in different size classes were distributed equally across treatment groups, we first grouped the spiders by collection date, paired them by carapace width, and then assigned individuals in each pair randomly to either a 'high-quality' or 'low-quality' daily diet regime (see more below). For experiment 2, we collected 28 sexually mature males from the same population between 24 May and 12 July 2007. We grouped the individuals by collection date and then assigned them randomly to either the 'high-quality' or 'low-quality' daily diet regime. For the adult spiders in experiment 2 (which were mature upon collection), we scored the initial adult body condition at the start of the experiment (as described above for the correlational study). Due to allometric changes as these spiders grow, the residual body condition indices of juvenile male spiders may not be comparable to those of adult males or even to juvenile males of different ages (LAT, unpublished data). Thus, throughout this study, we only used residual condition indices for mature adult spiders.

In both experiments, spiders receiving the 'low-quality' diet were fed daily with wingless *Drosophila melanogaster* reared on basic fruit fly medium only (Carolina Biological, Burlington, NC, USA), as studies with other generalist predator spiders showed this diet to provide enough nutrients for spiders to reach maturity, but with significantly lower growth rates (e.g., Toft and Wise 1999; Mayntz and Toft 2001). In contrast, the 'high-quality' treatment consisted of a daily feeding regime that alternated between week-old crickets (*Acheta domesticus*, approx. 3 mm in length) on one day and then wingless *Drosophila* on the following day. For the high-quality diet group, both the

crickets and flies were reared on basic medium supplemented with protein, calcium, and vitamins (see Table 1 for the specific details of diet formulation and feeding regime). Again, this high-quality diet was chosen because previous studies indicated that similar manipulations increase growth rates in spiders (e.g., Mayntz and Toft 2001; Wilder and Rypstra 2008; Hebets et al. 2008). In addition to manipulating diet quality, our 'high' treatment also received a slightly higher total mass of food (Table 1). During daily feedings, we removed uneaten food from the previous day and replaced it with fresh food. At the end of the experiments, body condition was scored for each individual.

Color analysis

We used reflectance spectrophotometry to measure reflectance from three body regions that males display to females: red face, green front legs, and white pedipalps. We focused on these three body regions as potential signaling colors in this study because they are (1) sexually dichromatic in the spider's visible range, (2) displayed by males to females during courtship (LAT, personal observation), and (3) relatively large, quantifiable, single-color patches (Fig. 1). To test the prediction that these potential signaling colors show heightened condition dependence compared to naturally selected, non-signaling colors (Cotton et al. 2004), we also measured reflectance from two body regions that are not displayed to females and are therefore presumably not involved in sexual signaling: the light gray ventral abdomen, which is unlikely to be visible to females in most natural contexts (LAT, personal observation), and the dark gray dorsal carapace, which is unlikely to be visible to females once a male begins courting (LAT, personal observation).

Depending on the area to be measured, we used one of two spectrophotometer setups: either a standard spectrophotometer or a microspectrophotometer (details of each are described below). Because the color patches on the dorsal abdomen and ventral carapace were relatively large (both approximately 1.6 mm), we were able to take reflectance measures using a standard UV–vis spectrophotometer (USB2000 with PX-2 pulsed xenon light source, Ocean Optics, Dunedin, FL, USA) that can precisely collect reflectance data on areas as small as 1 mm in diameter over the range of 275–700 nm. Reflectance measures were taken in a dark room with the probe positioned perpendicular to the colored surface and were measured relative to a Spectralon diffuse reflectance white standard (Labsphere, Inc., North Sutton, NH, USA).

Because the diameters of the other color patches (red face, green front legs, and white pedipalps) were smaller than 1 mm (ca. 0.4, 0.5, and 0.6 mm, respectively), we were unable to use this same method to accurately and repeatably measure color on these areas. Instead, for these body regions, we used a microspectrophotometer which consisted of a standard spectrophotometer (USB2000, Ocean Optics, Dunedin, FL, USA) coupled to a modified Leica DMLB2 fluorescence light microscope fitted with a ×40 quartz objective lens (Leica Microsystems, Wetzlar, Germany) and illuminated with a full-spectrum Leica 75 W xenon arc lamp (Leica Microsystems, Wetzlar, Germany). Again, reflectance measures were taken in a dark room, relative to the same Spectralon white standard described above and with the probe positioned perpendicular to the colored surface. This setup allowed us to collect precise data within a circular sampling area that was 0.4 mm in diameter. Unfortunately, the optics of the microscope cut out a portion of the UV spectrum and so this instrument only provides data within the range of 375–700 nm for these smaller body regions. In some jumping spider species, UV reflectance appears to be important in signaling (Li et al. 2008; Lim et al. 2008, 2007), so we

Table 1 Feeding regimes of male spiders in juvenile and adult diet manipulation experiments

Experimental diet treatment	Prey species and feeding frequency	Prey diet
High-quality diet	Fed daily, alternating between three wingless *Drosophila melanogaster* on 1 day and three 1-week-old crickets (*Acheta domesticus*) on the following day	High-quality *Drosophila* diet: 3:1:1:1 ratio of Carolina basic fruit fly medium (Carolina Biological, Burlington, NC), high-calcium cricket feed (Fluker Laboratories, Baton Rouge, LA), tropical fish flakes (TetraMin, Blacksburg, VA), and crushed Total cereal (General Mills, Minneapolis, MN)
	Approximate (wet) mass of daily diet=0.480± 0.152 mg (n=10 samples, mean ± SD)	High quality cricket diet: 1:1:1:1 ratio of organic cornmeal (Arrowhead Mills, Melville, NY), high-calcium cricket feed (Fluker Laboratories, Baton Rouge, LA), tropical fish flakes (TetraMin, Blacksburg, VA), and crushed Total cereal (General Mills, Minneapolis, MN)
Low-quality diet	Fed three wingless *Drosophila melanogaster* daily	
	Approximate (wet) mass of daily diet=0.359± 0.069 mg (n=10 samples, mean ± SD)	Low-quality *Drosophila* diet: Carolina basic fruit fly medium (Carolina Biological, Burlington, NC)

must use caution in excluding UV reflectance from our analyses on these small body regions. In pilot studies, to ensure that we were not missing potentially important information in the UV range of the spectrum, we coarsely measured the reflectance on the smaller body regions with the full-spectrum spectrophotometer (without the microscope) described above and we were able to confirm qualitatively that, while reflectance does extend into the UV for the green legs and white pedipalps of males, there are no UV peaks in these spectra (Fig. 1c). Thus, the benefit of using the microspectrophotometer setup to get accurate and repeatable measures in the longer wavelengths (where most of the reflectance and variation are found in this species) far outweighed the disadvantage of not being able to obtain UV data for these small body regions.

For the correlational study, we took three reflectance measurements on each of the following body regions of each spider: face, left leg, right leg, left palp, right palp, ventral abdomen, and dorsal carapace. For the diet manipulation experiments, we took two measurements on each of these regions. All color measurements were completed by the same person (LAT) blind to the treatment group of the specimen being measured. We calculated the overall brightness of the mean spectral curve of each body region, as well as hue and chroma, where relevant. For achromatic regions (gray regions with a flat reflectance), there were no relevant hue or chroma values, and thus we calculated brightness only. For the putative signaling colors, this amounted to seven color variables: (1) hue of the red face (the wavelength corresponding to the inflection point of the red curve), (2) red chroma of the face (the proportion of total reflectance between 600 and 700 nm), (3) brightness of the red face (mean reflectance), (4) green chroma of the front legs (the proportion of the total reflectance between 450 and 700 nm), (5) brightness of the front legs (mean reflectance), (6) brown chroma of the pedipalps (the proportion of the total reflectance between 500 and 700 nm), and (7) brightness of the white pedipalps (mean reflectance) (color metrics reviewed in Montgomerie 2006). For each of the non-signaling regions (abdomen and carapace), which were gray, we calculated brightness (mean reflectance).

Because the face of the spider is a relatively large surface that is only partially ornamented with red scales (unlike the legs and pedipalps in which the entire surface of the structure is covered with scales), we also measured the size of this red patch. We digitally photographed the face of each spider through a Leica MZ 125 stereo microscope at ×50 magnification using a Spot Insight 11.2 digital camera (Diagnostic Instruments, Sterling Heights, MI, USA; image resolution 1,600×1,200 pixels) and Image-Pro Express software (Media Cybernetics, Silver Spring, MD, USA). All photos were taken with the same light and camera settings. We calculated the total area of red scale coverage using Photoshop software (Adobe Systems Inc., San Jose, CA, USA). Not surprisingly, larger spiders (with wider carapaces and thus larger faces) had significantly larger red patches (regression, R^2=0.222, $F_{1,56}$=15.77, P=0.0002). Thus we calculated a 'relative patch size index' from the residuals of a regression of patch area on carapace width (see Jakob et al. 1996 for a description of this method for estimating relative body condition).

Statistical analysis

For the correlational field study, we examined all possible intercorrelations among the color parameters for the putative signaling traits. Because we were interested in broad patterns of intercorrelations rather than the significance of any individual relationship, we did not employ a Bonferroni correction (e.g., Cohen et al. 2008). We then went on to examine the condition dependence of color using linear regression to determine if there were relationships between color traits and body condition. Because the main goal of our study was to assess the condition dependence (and potential signal functions) of each color variable separately, we used univariate, rather than multivariate, tests. Because this correlational data on condition dependence was used to identify potentially important biological relationships that we would explore further with manipulative experiments, we wanted to avoid an excessively high type II error rate (e.g., Moran 2003; Nakagawa 2004), and therefore we again did not employ a Bonferroni correction.

To compare the levels of condition dependence in these display traits with naturally selected traits, we also used regression to assess the condition dependence of the abdominal and carapace colors that are not displayed to females (Cotton et al. 2004).

Because the spiders used in this study were collected during three bouts (from 7 July to 25 August), we examined relationships between collection date and condition using ANOVA and Tukey–Kramer pairwise comparisons (with an alpha level of 0.05). These analyses indicated that condition declined sharply across the mating season (see "Results"). Because condition and collection date were highly correlated, we only included condition in our regression models. This tight relationship between condition and collection date prevents us from being able to tease apart the individual effect of each on color, which was the goal of our diet manipulation experiments.

To assess whether we effectively manipulated condition, we used one-tailed *t*-tests to determine if individuals in the high-quality diet group were in better body condition at the end of the experiments than those in the low-quality diet group. In experiment 1, where the spiders were still

growing and molting over the course of the experiment, we also used a one-tailed *t*-test to determine if the individuals in the high-quality diet group matured with a larger carapace width than those in the low-quality group. In addition, for experiment 2, where adult body condition could be scored both at the start and end of the experiment, we used a one-tailed *t*-test to determine if the change in body condition over the course of the experiment was greater in high- versus low-quality diet treatments. In all of these cases, we used one-tailed tests because we were specifically interested in testing the directional prediction that our diet manipulations were effective (i.e., diet supplementation increased body condition or body size). To ensure that we were not manipulating condition outside of the natural range of variation, we confirmed that the final body condition in each treatment group of our experiments fell within the natural range of variation observed in this population between 2006 and 2008 (LAT, unpublished data).

Color variables that were condition dependent in the field study (hue, red chroma, and size of the red face patch and brightness of the green front legs; see "Results") were compared in the manipulative experiments between animals fed high- and low-quality diets using analyses of covariance (ANCOVA). For experiment 1, there was considerable variation in the initial size of the juvenile spiders (carapace width = 1.006±0.238 mm (mean±SD)), as well as in the total time spent on the experimental diets before reaching maturity (35.8±24.6 days (mean±SD)). Thus, we included these two variables as covariates in the model. In experiment 2, all spiders were on the diet manipulation for the same amount of time (45 days); thus, we included only initial body size (carapace width, 1.77±0.247 mm (mean±SD)) as a covariate. Because of our ability to calculate initial body condition on the adult spiders in experiment 2 (but not in experiment 1—see above), we also ran a second set of analyses on the data from experiment 2 with initial body condition as a covariate. These results were qualitatively similar, and thus only the first set of analyses is presented. Again, for comparison, we ran the same statistical tests on the data for the presumably naturally selected abdominal and carapace coloration. Spiders that died over the course of the experiment (three in experiment 1 and two in experiment 2) were excluded from the analyses.

All data met assumptions of parametric statistics, with two exceptions. For red chroma and relative face patch size data in experiment 1, variances were unequal between treatment groups (Brown–Forsythe test, red chroma: $F=10.61$, $P=0.0035$; relative face size: $F=5.46$, $P=0.029$), and thus a reciprocal transformation was employed to achieve homogeneity. All statistical analyses were conducted using SAS 9.1 and JMP 8.0 for Windows (SAS Institute, Cary, NC, USA).

Results

Correlational study

We found several significant correlations among color parameters of the putative signaling traits (Table 2). In general, variables associated with facial color were positively correlated (with the exception of face brightness), as were variables associated with leg color. In general, red and green color variables were negatively correlated with one another. Variables associated with the pedipalps were not correlated and generally were not correlated with either face or leg coloration.

Field-caught male *H. pyrrithrix* in better body condition during the mating season had redder faces (i.e., higher hue values and higher red chroma values; hue: $R^2=0.144$, $F_{1,56}=9.24$, $P=0.0036$; red chroma: $R^2=0.084$, $F_{1,56}=5.04$, $P=0.0289$; Fig. 2a, b) and more red scale coverage on their faces ($R^2=0.113$, $F_{1,56}=7.02$, $P=0.0105$; Fig. 2d). However, there was no relationship between condition and face brightness ($R^2=0.004$, $F_{1,56}=0.24$, $P=0.6227$; Fig. 2c). Males in better condition also had darker green front legs ($R^2=0.069$, $F_{1,56}=4.07$, $P=0.0486$; Fig. 2f), but there was no significant relationship between condition and green chroma of the legs ($R^2=0.054$, $F_{1,56}=3.15$, $P=0.0813$). There was no relationship between condition and any aspect of pedipalp coloration (brown chroma of pedipalps: $R^2=0.017$, $F_{1,56}=0.96$, $P=0.3301$; Fig. 2g; brightness of the pedipalps: $R^2=0.051$, $F_{1,56}=2.98$, $P=0.0898$; Fig. 2e, h).

For comparison with non-signaling traits, there was no significant relationship between condition and gray abdomen coloration (brightness = 21.386±9.040% (mean±SD), $R^2=0.0120$, $F_{1,56}=0.666$. $P=0.418$) or gray carapace coloration (brightness=11.618±9.309% (mean±SD), $R^2=0.050$, $F_{1,56}=2.896$. $P=0.094$).

Body condition varied among collection bouts ($F_{2,54}=15.73$, $P<0.001$); males collected later in the season (during the last collection date, 25 Aug) had lower body condition indices than the males collected earlier in the season (7 July, 1 Aug).

Experimental studies

In experiment 1, males reared on the high-quality diet matured with a higher body condition index than those on the low-quality diet ($t_{21}=1.737$, $P=0.0484$; Fig. 3a), suggesting that our diet manipulation was effective. Final carapace width was not greater on the high-quality diet than the low-quality diet (high-quality carapace width=2.043±0.0965 (mean±SD), low-quality carapace width=1.973±0.122 (mean±SD), $t_{21}=0.544$, $P=0.295$). Faces were redder (with higher hue and red chroma values) in

Table 2 Pairwise correlations between putative signaling color variables for males in the correlational field study

	Face hue	Face red chroma	Face brightness	Face patch size	Leg green chroma	Leg brightness	Palp brown chroma	Palp brightness
Face hue	–	0.719**	−0.133	0.475**	−0.328*	−0.342**	0.011	0.076
Face red chroma		–	−0.227	0.623**	−0.312*	−0.368**	−0.061	0.140
Face brightness			–	−0.173	0.335*	0.361**	-0.018	−0.140
Face patch size				–	−0.281*	−0.291*	−0.084	0.251
Leg green chroma					–	0.717**	−0.086	−0.294*
Leg brightness						–	−0.143	−0.294*
Palp brown chroma							–	0.166
Palp brightness								–

*$p<0.05$; **$p<0.01$

males from the high-quality diet group compared to the low-quality group (hue: $F_{3,21}=4.61$, $P=0.0436$; red chroma: $F_{3,21}=5.21$, $P=0.0329$; Fig. 4a, b). The relative size of the red color patch was larger in the high-quality diet group compared to the low-quality diet group, but this relationship was not statistically significant ($F_{3,21}=3.83$, $P=0.0638$; Fig. 4c). Brightness of the green legs was unaffected by diet ($F_{3,21}=0.37$, $P=0.550$; Fig. 4d). For comparison with non-signaling traits, diet treatment had no effect on either gray abdominal coloration (high-quality brightness=31.386±18.044% (mean±SD), low-quality brightness=27.384±16.356% (mean±SD), $F_{3,21}=0.19$, $P=0.666$) or gray carapace coloration (high-quality brightness=13.567±7.380% (mean±SD), low quality brightness=11.639±6.998% (mean±SD), $F_{3,21}=0.16$, $P=0.697$). Full ANCOVA tables are provided as "Electronic supplementary material".

In experiment 2, there was no difference in final body condition between the two treatment groups ($t_{24}=0.391$, $P=0.650$; Fig. 3b), nor was there any difference in the change in body condition between the treatment groups over the course of the experiment (change in condition index for high-quality group=0.001±0.003 (mean±SD), change in condition index for low-quality group=0.0008±0.004 (mean±SD), $t_{24}=1.28$, $P=0.893$). Adult diet had no effect on any aspect of red or green coloration (hue of red face: $F_{2,23}=0.23$, $P=0.634$; red chroma: $F_{2,23}=0.59$, $P=0.449$; size of red facial patch: $F_{2,23}=1.83$, $P=0.189$; brightness of green legs: $F_{2,23}=0.43$, $P=0.519$; Fig. 4e–h). Adult diet also had no effect on the non-signaling gray abdomen coloration (high-quality brightness=25.686±12.807% (mean±SD), low-quality brightness=37.759±22.093% (mean±SD), $F_{2,23}=2.65$, $P=0.117$) or gray carapace coloration (high-quality brightness=11.800±7.505% (mean±SD), low-quality brightness=13.658±8.545% (mean±SD), $F_{2,23}=0.22$, $P=0.645$). Again, full ANCOVA tables are provided as "Electronic supplementary material".

Discussion

We used field observational and lab experimental approaches to examine the condition dependence of three separate colored body regions that male *H. pyrrithrix* display to females during courtship: a red facial patch, green legs, and white pedipalps. We compared this with the condition dependence of two colors that are not displayed to females: gray abdomen and carapace coloration. Our correlational field data suggest that aspects of both red facial and green leg coloration (but not white pedipalp coloration) are both variable and condition dependent in a natural population within the most active part of the mating season and that these colors show heightened condition dependence compared with the abdominal and carapace colors not displayed to females. The condition-dependent red and green color variables (but not white pedipalp color variables) were also generally intercorrelated with one another (Table 2), suggesting that these two traits contain information about a male's quality (e.g., Møller and Pomiankowski 1993; Hebets and Papaj 2005).

In addition to assessing condition dependence of color, it is often useful to directly compare the levels of variation among the different color patches to test the prediction that the putative quality-signaling colors are more variable than naturally selected colors (Dale 2006). This was not possible in the current study because the color patches of interest were different colors (red, green, gray) that are quantified on different scales and thus cannot be directly compared (see Dale 2006; Delhey and Peters 2008 for a discussion on the problems associated with comparing variation in different color traits).

To further explore the potential information content of leg and facial colors, we went on to experimentally examine a dietary mechanism underlying their condition dependence and found that juvenile diet affected the development of the adult red facial coloration but had no effect on green leg coloration. Again, in the diet

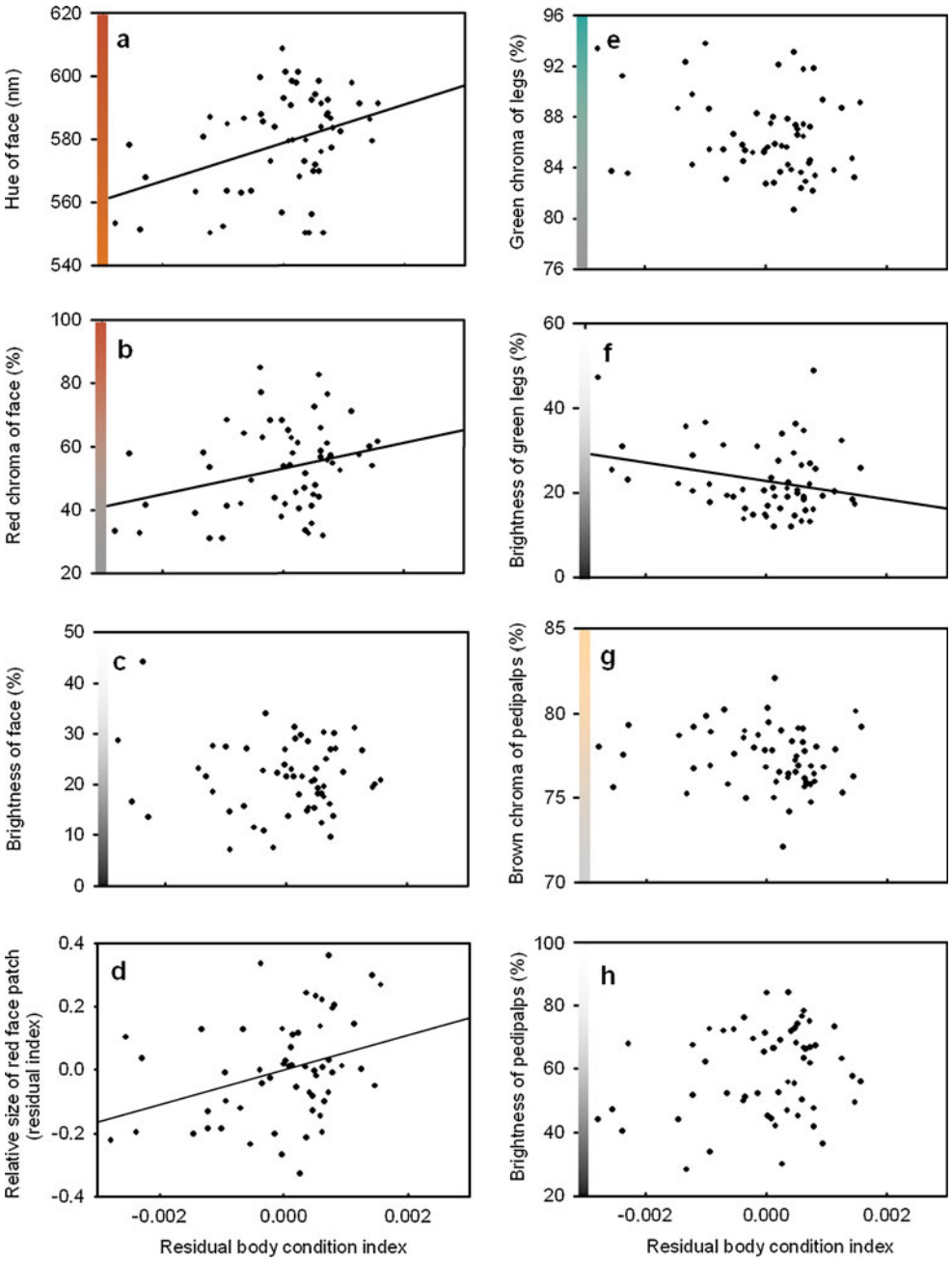

Fig. 2 **a**–**h** Relationships between body condition (residual body condition index) and the different forms of display coloration in wild-caught male *H. pyrrithrix*. *Regression lines* indicate significant relationships between body condition and coloration

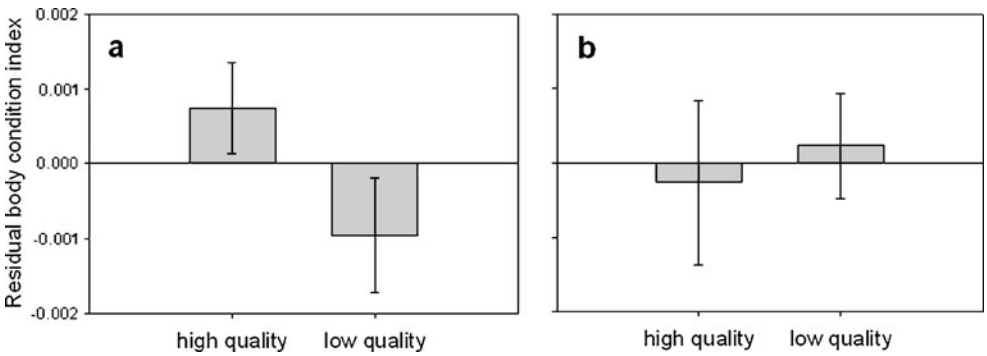

Fig. 3 Effects of diet manipulation on body condition (mean ± SEM). **a** Experiment 1 (manipulation of juvenile diet). **b** Experiment 2 (manipulation of adult diet)

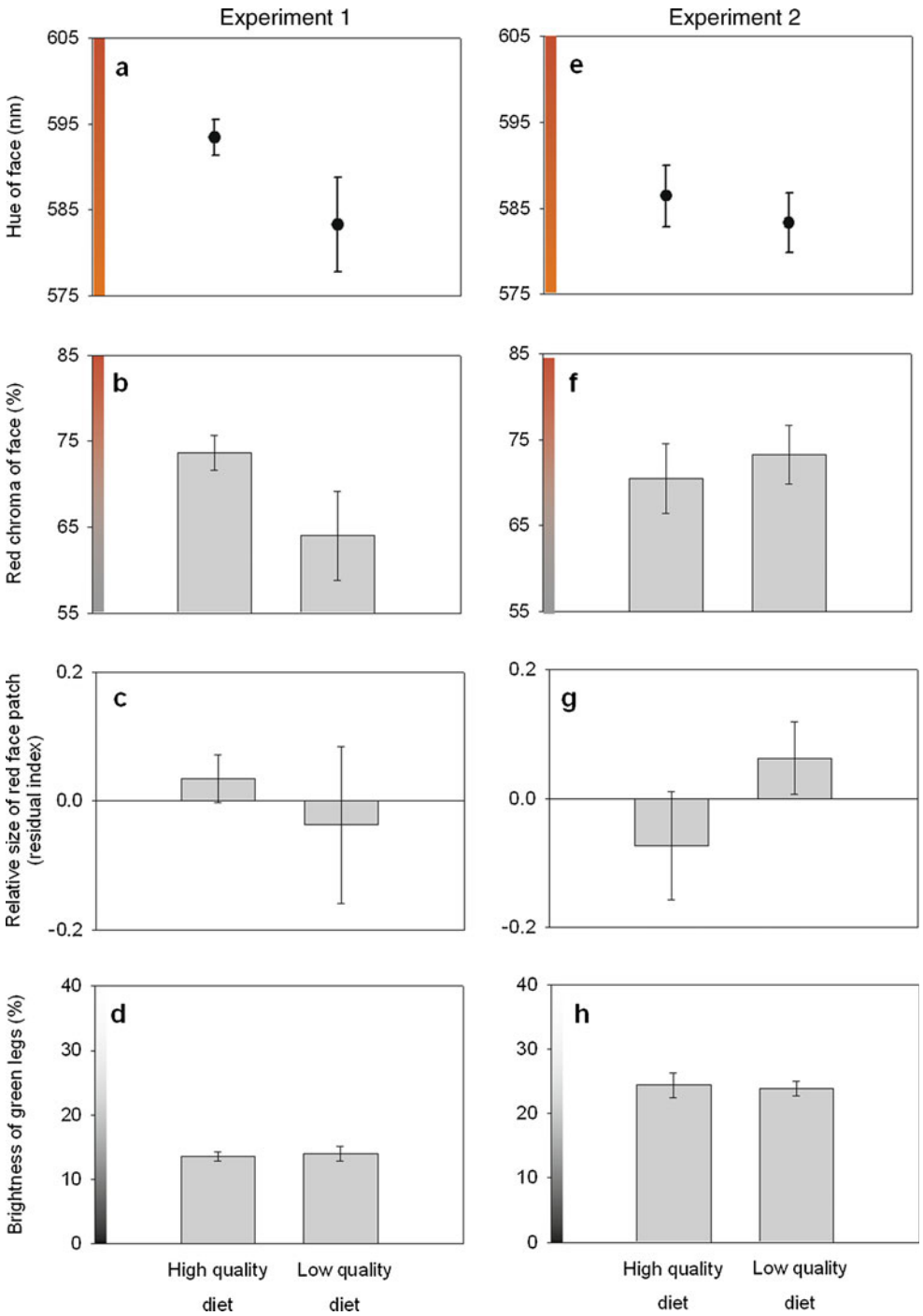

Fig. 4 **a**–**h** Effect of juvenile diet manipulation (*Experiment 1*) and adult diet manipulation (*Experiment 2*) on putative signaling colors in mature male *H. pyrrithrix* (mean ± SEM). As discussed in "Materials and methods", variances were unequal and thus data were transformed in **b** and **c**

manipulation experiment, red coloration showed heightened condition dependence relative to non-signaling colors (abdomen and carapace). However, once this red coloration is produced, manipulation of adult diet did not seem to have any effect on color maintenance. These results suggest that, while facial and leg coloration were both condition dependent and intercorrelated in the field, they may actually contain slightly different information about a male's quality (discussed in more detail below).

The condition dependence of putative intraspecific signaling coloration has only been examined in one other of the more than 5,000 species (Platnick 2010) of jumping spider (*C. umbratica* from Singapore, Lim and Li 2007). Male *C. umbratica* have sexually dimorphic color patterns that are required for eliciting the attention of the opposite sex, and aspects of these colors were found to be dependent on both diet and age (Lim et al. 2007, 2008). However, while our study and theirs both uncovered patterns of condition dependence in coloration, both the experimental

approaches and the details of the findings were quite different (reviewed in more detail below).

Condition and diet dependence of red facial coloration

The red facial coloration of adult males in our experiment was positively correlated with body condition in the field and dependent upon juvenile diet in the lab, and thus this coloration has the potential to be an honest indicator of a male's health and foraging ability. Such patterns of diet dependence are common for many well-studied colorful traits in male animals that are both displayed to and preferred by females (e.g. Kodric-Brown 1989; Hill 1990; Kemp and Rutowski 2007).

Specific to jumping spiders, Lim and Li (2007) found that diet affected the male display coloration in *C. umbratica*; however, they manipulated diet quantity, while we predominantly manipulated diet *quality* (with only subtle differences in diet quantity; Table 1). Furthermore, we found treatment effects on the *development* of male coloration, while Lim and Li (2007) found treatment effects on the *maintenance* of adult coloration. As a result, the putative mechanism for the treatment effects of diet on color was very different in the two studies. Lim and Li (2007) showed that a period of fasting in mature males affected their abdominal coloration, presumably as a result of the colored body scales being more spread out on the stretched abdomens of fatter males. In our study, in contrast, the color patch of interest is on a body region (the face) that does not stretch with feeding as the abdomen does and so any diet-related changes in color in *H. pyrrithrix* will presumably be due to the effects on the development or maintenance of coloration within the individual body scales where it is produced (e.g. Hill 1979) rather than to the mechanical stretching of the body surface. In this way, the control of facial coloration in *H. pyrrithrix* may be much like the control of color production within the wing scales of butterflies (e.g., Morehouse et al. 2007; Giraldo and Stavenga 2008) and the feathers of birds (e.g., McGraw 2006a, b; Prum 2006).

We found no effect of diet on the maintenance of adult male red facial coloration. Interestingly, our diet manipulations had different effects on the body condition of the juvenile spiders (experiment 1) than they did on the adult spiders (experiment 2), despite the fact that the diet manipulations were identical and the two experiments were run in the lab concurrently. The finding that our diet manipulation was more effective at manipulating the condition of juveniles than adults may indeed explain the lack of a treatment effect on the maintenance of adult coloration. If so, this difference in treatment effect on juvenile and adult spiders might suggest that, in the field, juvenile diet may be more likely than adult diet to affect a male's colors. Alternatively, it could also be that because a male's facial coloration is fully produced within body scales prior his final molt, any effect of diet post-maturity is indeed minimal. However, the maintenance of coloration in other animals often requires grooming (e.g., Zampiga et al. 2004; Lenouval et al. 2009), which is also a common behavior in *H. pyrrithrix* (LAT, personal observation). More investigation into the mechanisms of color maintenance post-maturity is clearly warranted in *H. pyrrithrix*.

Condition dependence and potential age-related changes in green leg coloration

Despite the finding that the green leg coloration of males was condition dependent in the correlational field study, neither of our diet manipulation experiments had any effect on its development or maintenance. Due to the patterns of condition dependence that we saw in the field, it would be worthwhile to further explore other environmental and physiological parameters that are linked to condition (such as parasites, health, and age). Males attain their full ornamental coloration at sexual maturity, and 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 changes (e.g., Kemp 2006; Kemp and Macedonia 2006). If so, male color variation might signal viability, in which case we would expect females to choose older males as mates (reviewed in Kokko and Lindstrom 1996). Alternatively, if older individuals are more likely to carry disease or parasite infection (e.g., Tarling and Cuzin-Roudy 2008), we might expect females to choose younger males as mates.

Interestingly, a post-hoc comparison of the results of the two diet manipulation experiments suggests that age may indeed play a role in this coloration. Males in experiment 1 (which were measured immediately at maturity) had much darker leg coloration than the males in experiment 2 (which were at least 45 days post-maturity) (post-hoc *t*-test, $t_{49}=8.30$, $P<0.001$, compare Fig. 4d and h) but showed no differences in aspects of red facial coloration (post-hoc *t*-tests, hue: $t_{49}=0.981$, $P=0.332$, compare Fig. 4a and e; chroma: $t_{49}=0.778$, $P=0.441$, compare Fig. 4b and f; relative size of red patch: $t_{49}<0.0001$, $P>0.999$, compare Fig. 4c and g). These results were similar to those found by Lim and Li (2007), where the color profiles of older males differed from those of younger males and may be typical of invertebrate structural colors (e.g., butterflies: Kemp 2006). In our study species, *H. pyrrithrix*, prey capture specifically involves the green ornamented front legs (LAT, personal observation) and this may lead to natural wear and degradation of the structures that produce the green coloration as males become older.

Although our two experiments with different-aged males were not designed to assess the effect of age on coloration, they were run in the lab concurrently, and specimens from the two experiments were combined and randomized before color measurement; thus, the differences in the green leg coloration of males in the two experiments are likely to be a result of the different ages of the two groups of spiders. We must use caution in this interpretation, however, because the males in experiment 1 spent much of their juvenile development under lab conditions, while the males in experiment 2 spent their entire juvenile development in the field. Clearly, age-related changes in leg coloration should be examined more closely in *H. pyrrithrix*, while eliminating these confounding factors of juvenile diet by using males raised entirely in the lab from eggs.

Functions of jumping spider display coloration

One goal of our study was to begin to disentangle content-based, quality-indicating hypotheses for elaborate male coloration, which explicitly predict condition dependence, from other functional hypotheses that typically do not. Despite the overwhelming support for quality-indicating functions in other taxa (reviewed in Andersson 1994), many have argued that the brilliant and diverse colors of some species of male jumping spiders are likely to function as species recognition signals rather than as indicators of a male's individual quality (e.g., Richman 1977; Crane 1949). Courting male spiders have to deal with the risk of cannibalism, as females of most species are generalist predators that may attack and eat anything that is perceived as a potential prey item. For this reason, immediate and unambiguous species recognition may be more important to male jumping spiders than it is to males of other taxa where the potential costs associated with courtship are not as high. Given the high cost of cannibalism, we might also expect the elaborate colors of males to be more likely to have efficacy-based functions, such as reducing female aggression (e.g., Forster 1982; Hebets and Papaj 2005) or attracting a female's attention from a safe distance (Clark and Uetz 1993).

Here we present correlational and experimental data that support quality-indicating hypotheses for the red facial coloration of male *H. pyrrithrix*. However, these patterns of condition dependence did not hold up for the other two display colors that we examined (green leg color and white pedipalp color). We provide evidence that the green leg color is correlated with condition in the field and may be related to male age. The white pedipalp coloration showed no evidence of condition dependence. These different patterns of condition dependence for each of the different colored regions that males display to females suggest that each may serve different functions or multiple functions (or perhaps no function at all). With an understanding of the patterns of condition dependence for these three colored body regions in male *H. pyrrithrix*, we can now create informed and well-designed behavioral experiments to further test the hypotheses about potential signal functions of these colors both independently and in concert with one another as part of a complex display (e.g., Hebets and Papaj 2005).

Much of our understanding of the functions and control of elaborate coloration in animals comes from a small set of well-studied groups (e.g., birds, fish, butterflies—reviewed in Andersson 1994). Spiders differ in aspects of their biology that might provide additional insights into the evolution of color. Because females are often larger than males and are voracious and potentially cannibalistic generalist predators, courting males have to treat females not only as potential mates but also as potential predators. In addition, in many habitats such as leaf litter and dense vegetation, jumping spiders may face a suite of predators that is quite different from the predators faced by other groups of animals. These two factors are very likely to affect the costs and benefits of being colorful. Given the amazing diversity of colors among jumping spiders (Maddison 1995; Oxford and Gillespie 1998), there is likely to be as much diversity in the way individuals use color as there is for the most thoroughly studied groups of colorful animals. It may be that understudied groups such as spiders will provide novel insights for the field of animal coloration.

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