Coloration indicates body size in *Calopteryx maculata* (Odonata: Calopterygidae)

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ABSTRACT

Calopteryx maculata has become a model system for studying behaviour and reproduction in odonates. Its iridescent coloration is thought to be important in intraspecific interactions but no study has yet measured coloration in a quantitative manner. In a recent study, Fitzstephens & Getty (2000. Animal Behaviour 60: 851-855) showed that lipid levels predict coloration as determined by Munsell chips, such that fat males were blue and lean males were green. In this study we quantified color in *C. maculata* with a spectrometer to test the prediction of Fitzstephens & Getty (2000) using quantitative measures. We found that body size, but not lipid levels, correlates with color. In our study, larger males were green and smaller males blue. Territorial males did not differ from non-territorial males in color, size, or lipid levels. Coloration thus predicts size in male *C. maculata,* but the significance of this in intraspecific interactions remains unclear.

INTRODUCTION

Coloration is an important element of an organism's phenotype, influencing both survival and reproduction. In many species, coloration can directly influence intrasexual competition and female choice (West & Packer 2002; Hill & McGraw 2006). Coloration can also indicate the foraging ability or parasite resistance of an individual, as well as other measures of quality, stamina, and fitness (Hill 1990; Baeta et al. 2008). Insects, and anisopterans and zygopterans in particular, are often brilliantly colored. Wing coloration has been investigated as a signal of male quality in the territorial damselfly genera *Calopteryx* and *Hetaerina*. Wing spots of pigmentation have been linked to mating success, higher immune responses,

higher fat reserves, better survival rates, parasite resistance, and can influence female choice (*C. xanthostoma (Charpentier)*, Siva-Jothy 1999, 2000; *C. haemorrhoidalis* (Vander Linden), Córdoba-Aguilar 2002; *H. americana* (Fabricius), Contreras-Garduño et al. 2006, 2008; *H. titia* (Drury), Córdoba-Aguilar et al. 2007). The function of body coloration is less clear. Since males of some species have extremely bright body coloration, it is possible that body color is an important signal of individual quality or health.

In this study we examined the relationship between body coloration, body size and lipid levels in *C. maculata* (P. de Beauvois). This species is sexually dimorphic and is found along freshwater streams throughout temperate eastern regions of the United States (Corbet 1980; Mullen & Andres 2007). Males have dark, melanized wings and iridescent epicuticles that range from yellowish-green to blue. Females display the same melanized wings but with white stigmata on the tips in addition to a dull brown-black epicuticle. There are two strategies by which males gain copulations. Males can defend oviposition sites and appear to 'charge' females with copulation for access to the site (Waage 1973). These territorial males defend their territories by fighting other males and although contests are usually short in duration, extended aerial contests may occur, which can pose significant energetic costs to males (Waage 1973; Marden & Rollins 1994). Alternatively, both young and old males are often non-territorial and instead seek matings by sneaking onto territories and mating with females (Forsyth & Montgomery 1987; Plaistow & Siva-Jothy 1996).

For *C. maculata* males, energy stores in the form of lipids are critical for successfully acquiring and maintaining a territory (Marden & Rollins 1994; Fitzstephens & Getty 2000). Young males have the largest energy stores and older males have the smallest (*C. xanthostoma*, Plaistow & Siva-Jothy 1996; Fitzstephens & Getty 2000). Defending territories depletes male energy stores, but currently there is no consensus on whether assessment of energy stores is important in either intra or intersexual interactions (Marden & Waage 1990; Marden & Rollins 1994; Plaistow & Siva-Jothy 1996; Fitzstephens & Getty 2000; Schultz et al. 2008). A link between coloration and an aspect of male quality would help determine if color is a functional signal and determinant of male mating success in *C. maculata*.

In *C. maculata*, Fitzstephens & Getty (2000) showed that male body coloration varied with energy reserves, specifically that fatter males were bluer and leaner males were greener. Fitzstephens & Getty (2000) also suggested the mechanism of this variation. Based on transmission electron micrographs of the epicuticle, blue males displayed more compressed epicuticles than green males, suggesting that coloration in *C. maculata* is of a structural nature and can be directly influenced by fat reserves.

Despite the clear results of Fitzstephens & Getty (2000), their measurements of color in *C. maculata* were assessed with Munsell chips, which depend on the human eye and ambient light to match samples with color-saturated chips. In

our work, we replicated the study of Fitzstephens & Getty (2000) using quantitative measurements of color (brightness, chroma, and hue) through spectrometer readings. We compared coloration to multiple measures of lipid content and body size. We expected to confirm their results that fatter males are bluer and leaner males are greener. Instead, we found no correlation between lipid and color and a significant correlation between body size and color such that larger, but not fatter, males were green and smaller males were blue.

METHODS

General methods

This study was conducted on the east and west branches of the Maple River in Pellston, Michigan, within the property of the University of Michigan Biological Station (45°34.358'N, 84°44.703'W). A total of 101 *C. maculata* males were collected from June to August 2009. All males were used for spectral analyses, and 62 of these males were used for lipid analyses. When it was obvious in the field, males were assigned a territorial status upon capture. Territorial males were those actively guarding a region of streamside vegetation, chasing off other males or guarding females. Non-territorial males were chased off by other males, did not restrict their movements to a particular locale and moved further up and down the stream bank (Forsyth & Montgomerie 1987; Fitzstephens & Getty 2000). Males were watched for 2-5 min, and territory status was recorded only if it was clear. We were able to record territory status for 60 of the 62 males used in lipid analyses.

Males were transported to the laboratory in glassine envelopes. Within two hours of capture, they were killed by decapitation. We recorded the fresh weight of the entire body, the abdomen length, and the weight of the thorax and abdomen after the head, wings, and legs had been cut off. Following the methods of Plaistow & Siva-Jothy (1996), we used the entire thorax and abdomen for lipid analysis.

Spectral measurement

We measured reflectance using an Ocean Optics USB2000 UV-VIS spectrometer. This spectrometer was sensitive from 320-700 nm which includes both UV and visible spectra. The spectrometer had a R400-7-SR UV-VIS probe and a PX2 pulsed xenon light source emitting a strobe light flashing at a constant rate (Integration time = 60 ms; Average = 10, Boxcar = 20, Flash Delay = 1 ms). The probe was mounted in a ceramic holder that excluded all ambient light from a standardized measurement area (ca 3 mm², with the probe 1.5 cm away from the work surface) and maintained the probe perpendicular (90°) to the body surface. Every

six samples, we recalibrated the spectrometer against a dark and a white Ocean Optics Spectralon WS-1 standard. Six color readings were taken from each animal: one reading from the thorax and one from S3, S4, S5, S6, and S7. The other five abdominal segments were not large enough to measure accurately.

Spectral data were analyzed with the CLR program (Montgomerie 2008). We retained measures of hue (H1), brightness (B1) and chroma within the blue and green wavelengths (S1B and S1G respectively), as defined by Montgomerie (2006: 101-102).

Lipid analysis

We based our lipid extraction procedure on the method used by Karowe & Martin (1989) but adapted these methods as follows. After the color measurements were taken, the specimens (thorax and complete abdomen) were freeze dried in a Labconco 8 lyophilizer for 24 h and then the dry weight of the sample was measured. The samples was then pulverized in a mortar and pestle, and mixed with a 2:1 chloroform: methanol extraction solution in a Fisher Scientific FS15 sonic bath. Solids were filtered from the extraction solution using Fisherbrand G8 glass fiber filter circles in a Millipore vacuum manifold. We mixed each sample with the extraction solution, inserted them into the sonic bath for 10 min twice, and ran each sample through the sonic bath two more times for 5 min and 1 min respectively, totaling four extractions per sample. All liquids were siphoned off the sample and put onto the filter circles after each removal from the sonic bath. The solids were then dried and weighed to yield the lean weight. Subtraction of lean weight from dry weight yielded lipid weight. Subtraction of dry weight from fresh weight yields water weight. Fat content was calculated separately as a percentage of both dry and wet weights (Marden & Waage 1990; Fitzstephens & Getty 2000). Water weight was calculated as a percentage of fresh weight.

Analyses

Separate principal components analyses (PCA) were performed on the four color measurements for both the thorax and the abdomen. We also performed a PCA on the five size variables: wet weight, dry weight, lean weight, and water weight, all of the thorax and abdomen, and abdomen length. Due to the abundance of measures of insect lipids in the literature, we analyzed lipid as absolute lipid weight (R. Hessler, SP-J unpubl.), as a percent of dry body weight (Fitzstephens & Getty 2000), and as the standardized residuals of lipid on lean body weight (Marden & Rollins 1994). To compare coloration, fat, and size, the retained principal components of color were regressed against fat variables and principal components of size. We compared territory status with color, fat, and size via Mann-Whitney U-tests. Separate regressions between all variables were performed in order to

confirm the PCA results. We chose to report the PC analyses instead of separate regressions for two reasons. First, the PC analyses and separate regressions yielded the same results. Second, the PCA is widely used to reduce noise in large data sets with many variables such as ours (Hotelling 1933).

RESULTS

Male *Calopteryx maculata* reflected strongly in both the blue and green spectral ranges, 400-605 nm, but not in the UV spectral range, below 400 nm (Fig. 1). Across the six measurements (thorax and S3-7), there were significant differences in all measures of color (Friedman test, $p < 0.01$ in all separate tests). We also found a significant difference in percent reflectance between the thorax and the average of the 5 abdomen segments, with the thorax reflecting much less than the abdomen (Wilcoxon signed ranks test, $z = -16.9$, $p = 0.000$). Due to the significant difference in color between the segments, we report the color of the thorax and abdomen – the mean of the readings of the five measured segments – separately. The coloration of the abdomen can be most directly compared to the results of Fitzstephens & Getty (2000).
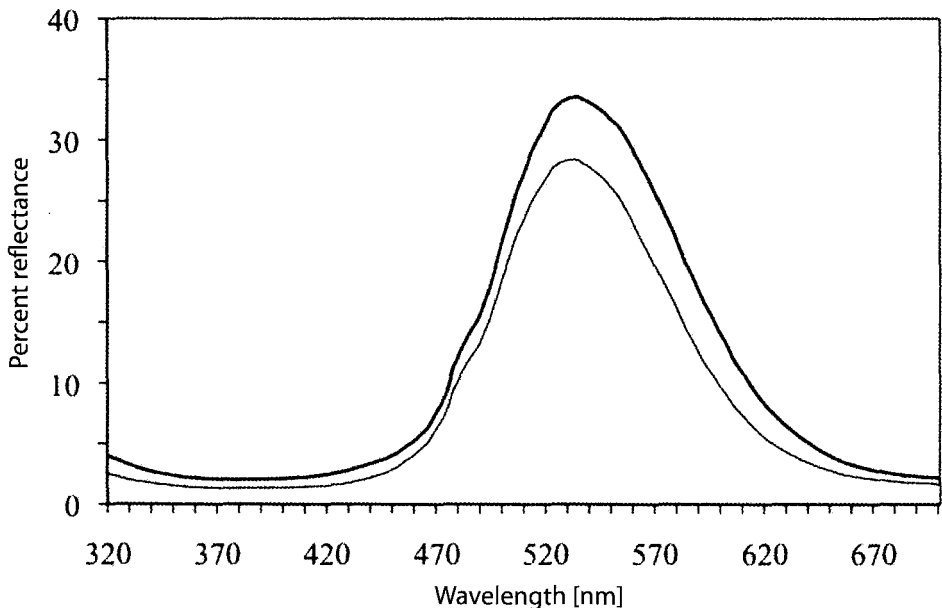

Figure 1: Hue and percent reflectance of the abdomen and thorax in male *Calopteryx maculata*; ▬ abdomen; — thorax.

In the PCA of thorax coloration, only one principal component was retained which accounted for 68.9% of the variation in the four color measurements. Based on the factor loadings, PC1 for the thorax is a measure of greenness (Table 1). In the PCA of abdomen coloration, two principal components were retained that together explained 92.6% of the variation in the four color measurements. PC1 for the abdomen is a measure of the greenness, and PC2 is a measure of overall brightness (Table 2).

In the PCA of size, we retained only one principal component, and it explained 77.1% of the variation in the five size measurements. Based on the factor loadings (Table 2), PC1 of size can best be described as fresh weight, though it describes much of the variation in dry weight and water weight as well.

All measurements of size (abdomen length, fresh weight, dry weight, lean and water weight), both for the entire animal, or just the thorax and abdomen (with the head and legs removed) were strongly correlated with each other ($p < 0.001$ in all separate regressions). Similarly, water weight and lipid levels were larger in larger males ($p < 0.001$ in all regressions). PC1 of size ("fresh weight") also correlated with lipid weight ($F = 18.4, p < 0.0001$).

There was no relationship between any measure of fat – absolute lipid weight, lipid as a percent of fresh or dry body weight, or standardized residuals of lipid on lean body mass – and either thorax greenness (PC1) ($p > 0.144$ for all separate regressions), abdomen greenness (PC1) ($p > 0.136$ for all separate regressions) or abdomen brightness (PC2) ($p > 0.328$ for all separate regressions) (Fig. 2). Without using PC values, the same relationships were evident in correlation matrices and separate regressions of individual color variables and all measures of fat.

Territorial and non-territorial males did not differ by any measured variable. Territory status did not predict lipid weight (Mann Whitney U, $U > 293, p > 0.09$

Table 1. Factor loadings of thorax and abdomen coloration from principal component analysis of color variables in C. maculata. We retained three principal components, two for abdomen coloration, and one for thorax coloration.

Section of body	Color variable	Factor loadings	
		Component 1	Component 2
Thorax	Blue saturation	-0.949	
	Hue	0.935	
	Green saturation	0.877	
	Brightness	0.463	
Abdomen	Blue saturation	-0.956	0.256
	Hue	0.895	-0.380
	Green saturation	0.843	0.370
	Brightness	0.298	0.918

Table 2. Factor loadings of weight and length from principal component analysis of size variables in *C. maculata*. We retained 1 principal component. All weights are in grams and are of the thorax and abdomen only.

Size variable	Component 1
Fresh weight	0.98
Water weight	0.937
Dry weight	0.925
Lean weight	0.878
Abdomen length [mm]	0.627

for all measures of lipid), "fresh weight" ($U = 298$, $p = 0.11$) or any component of color (thorax greenness, $U = 278$, $p = 0.098$; abdomen greenness, $U = 389$, $p = 0.863$; abdomen brightness, $U = 346$, $p = 0.397$).

The size ("fresh weight") of male *C. maculata*, however, did predict color. Greenness of the thorax ($F = 10.8$, $p = 0.002$) and abdomen ($F = 5.4$, $p = 0.023$) were significantly correlated with size (Fig. 3), but brightness was not ($F = 2.5$, $p = 0.12$). Correlation matrices and separate regressions of individual color and size variables also showed these relationships.
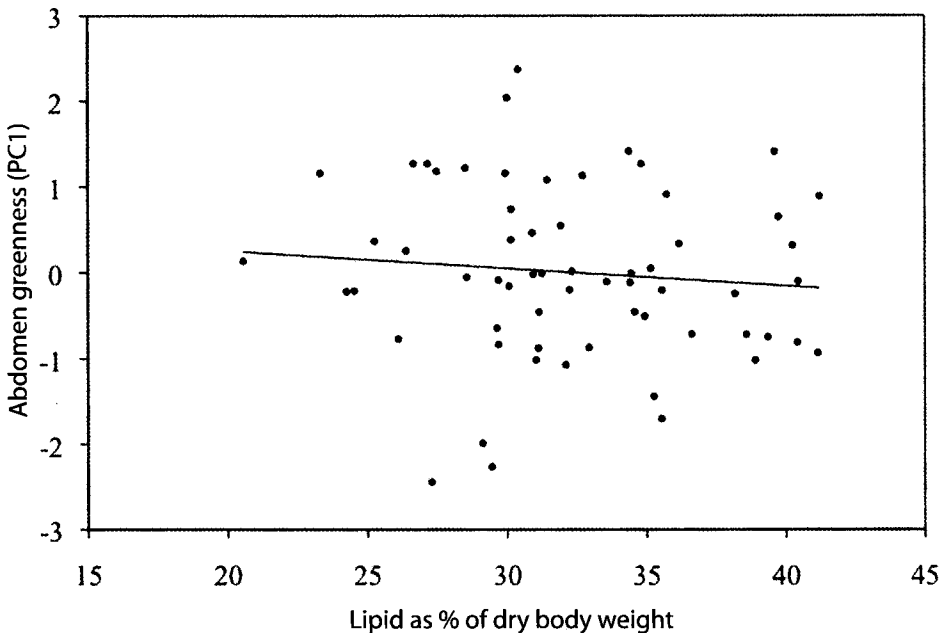

Figure 2: Relationship between lipid as a percent of dry weight and the first principal component of abdomen coloration (greenness) in male *Calopteryx maculata* ($R^2 = 0.01$, $p = 0.447$).
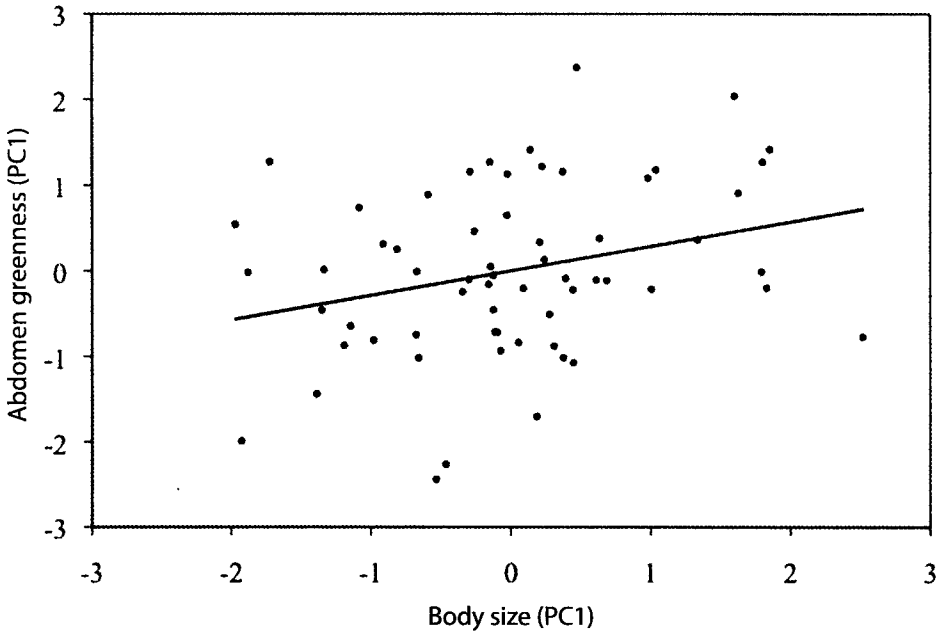
Figure 3: Relationship between the first principal component of size (fresh weight) and the first principal component of abdomen coloration (greenness) in male *Calopteryx maculata* ($R^2 = 0.083, p = 0.023$).

DISCUSSION

In the study by Fitzstephens & Getty (2000), lipid levels correlated with color in the dark-winged damselfly such that fat males were blue and lean males were green. We began this study expecting to confirm these findings with quantitative measures of color, but this is not what we found. In our study, lipid levels did not correlate with any measure of color, either in individual regressions or in comparison with size principal components. Overall size of males did predict color, but in the opposite way predicted (based on lipid levels) by Fitzstephens & Getty (2000). In our sample, larger males were green and smaller males were blue. In individual regressions, all measurements of size correlated with greenness but more importantly, the results of the principal components analysis (Table 1) suggest that the most important independent aspect of size is water weight of males. This finding also fit our qualitative observations during our laboratory work. Once the bodies of the males were freeze dried they visually appeared to us more blue than the males did alive.

Fitzstephens & Getty (2000) found that territorial males in their population were bluer. Although our sample size is smaller than theirs, we found no differ-

ence between territorial and non-territorial males in color, nor in size. Territorial *Calopteryx* males tend to be younger (*C. maculata*, Fitzstephens & Getty 2000), are more likely to win contests (*C. maculata*, Marden & Waage 1990), and have higher mating success (*C. xanthostoma*, Plaistow & Siva-Jothy 1996), but the causal relationship between color and territoriality remains unclear.

Fitzstephens & Getty (2000) proposed a mechanism for the structural basis of color, in which fat compressed the epicuticle of the animal, altering the wavelengths of reflected light. Even if we consider water a substitute for lipids, their proposed mechanism cannot explain our results. Water in tissue should compress the layers of the epicuticle in a manner similar to lipids, however, if water functioned like lipids in their mechanism, we would have found that males with a higher water weight were bluer, not greener as we found. Additional work investigating whether water could function in a manner analogous to lipids and thus have a similar effect on the epicuticle would be insightful.

Fitzstephens & Getty (2000) also report an age effect in which younger males are smaller, fatter and bluer, and older males larger, leaner and greener. As we do not have data on the age of our study animals, we cannot discount the possibility that age influenced fat levels or color in our data. However, even if the large and green males we observed were both large and green due to advanced age, this does not explain the lack of a relationship between fat and color in our data. Although it is possible that the difference between our results and those of Fitzstephens & Getty (2000) is due to methodological differences in the lipid extraction, we used an established extraction procedure (Karowe & Martin 1989) under the supervision of an analytical chemist and have no reason to doubt this methodology or the resultant data.

In addition to the strong relationship between greenness and water weight, we found that coloration differed between the thorax and abdomen and along the abdominal segments. The PC1 of thorax coloration correlated significantly with fresh, dry, lean, and water weights. There was also a significant difference in the percent reflectance of the thorax and the abdomen, with the thorax a little less bright than the abdomen. The brightness of the abdomen did not correlate with any size variable. Since most physiologically available muscle is located in the thorax (Westfall & May 1996: 37-38), there may be an interaction between the amount or weight of muscle tissue and the wavelengths of light the epicuticle of the thorax reflects. It would therefore be informative for future research to measure color and size of the thorax separately from that of the abdomen and compare to thorax coloration. In addition, the courtship display of this species involves the male positioning his thorax toward the female and hovering beside her, such that the male's black wings form a backdrop to the thorax (AS unpubl.). Thorax coloration may therefore impact female perception of these displays.

Despite the fact that the color measurements in Fitzstephens & Getty (2000) were made with Munsell Chips and our color measurements were made with a

spectrometer, this difference is unlikely to explain the difference between their results and ours. Overall coloration in our sample of male damselflies was almost identical to the frequency distribution of color in their sample (Fitzstephens & Getty 2000: fig. 1) with a peak color at around 530 nm. Our color readings were taken at a perdendicular angle to the male's thorax and abdomen segments. Fitzstephens & Getty (2000: 852) viewed their animals "from above, with sunlight coming over the shoulder," which we assume is comparable to our perpendicular angle. Thus, we also do not assume that differences in the methodology of measuring color can explain the differences in our study versus theirs.

We found the same significant positive relationship between lean body and lipid weight as previous research on *C. xanthostoma* (Plaistow & Siva-Jothy 1996). This suggests that a size-corrected measure of lipid is appropriate as the standard measure of fat in *Calopteryx*. Therefore, we analyzed the relationship not only between absolute lipid weight and color, but also of lipid as a percent of dry body weight, and the standardized residuals of lipid on lean body weight. None of these measures had a significant relationship with any measure of color.

The damselflies in our study had more fat and water as a percent of their body weight than previously reported (Marden & Rollins 1994; Fitzstephens & Getty 2000). It is unclear whether this is due to an unusually rich habitat where we worked, or a possible error in measurement. However, the former seems more likely for two reasons. First, it is unlikely that both fat and water weight data were high due to measurement error as they were determined by separate methods. Second, similar data were collected in 2008 at the same field site using a different lipid extraction procedure (R. Hessler, SP-J unpubl.). Therefore, we are confident that our data, though unusually high, are reliable.

In our opinion, the most likely reason for the difference between our results and those of Fitzstephens & Getty (2000) is that the population of *C. maculata* that they studied, at Augusta Creek in southern Michigan, may be fundamentally different than the population we studied in northern Michigan. Both abiotic and biotic factors could differ between the sites and change the relationships between size, fat, and color. One such possibility is gregarine parasites, which are commonly found in odonates (Åbro1971, 1974, 1976), and can influence survival and wing pigmentation (Córdoba-Aguilar et al. 2002; Canales-Lazcano et al. 2004). Parasites can change with habitat; for example, *C. maculata* that occur in streams that are continuous with forest cover can have more parasites than individuals in more fragmented habitats (Taylor & Merriam 1996). Though it is not yet clear how exactly parasites could affect color and fat in *C. maculata*, we do know that in some odonates, parasites can obscure real relationships between physiological factors. For example, unparasitized males of *Libellula pulchella* Drury show a tight relationship between muscle output and territory success, while parasitized males show no relationship (Marden & Cobb 2004). Thus, varying rates of parasitism in *C. maculata* could in part account for the different relationships between size, fat,

and color. Future work at our study site will measure the prevalence of gregarine parasites in our study population.

It is important to consider why it could be adaptive for males to communicate their body size through their coloration. If body size correlates with an aspect of male quality important to females, it would be adaptive for males to advertise this quality through their coloration. However, it is not yet clear if male body size differs according to some measure of quality. Body size does not differ in winners and losers of male-male contests (Marden & Waage 1990; Marden & Rollins 1994), but further research could investigate the relationship between body size and the male's ability to guard or display. Lean body weight has been used as a measure of body size and muscle mass in studies on territoriality in male *C. maculata*, but it has been shown not to correlate with contest success (Marden & Waage 1990) or contest length (Marden & Rollins 1994). However, we cannot rule out the possibility that body size might correlate with the ability of the male to guard ovipositing females (Córdoba-Aguilar & Cordero-Rivera 2005).

An important research question that still remains is how or whether female *C. maculata* detect male coloration, and if so, how or whether they can detect the variation in male coloration demonstrated in this study. Clearly, without this ability, male coloration cannot express any information regarding male quality to females, and the fact that male coloration appears to change to the human eye makes this especially uncertain. Because the purpose of this study was to characterize male coloration and replicate Fitzstephens & Getty's (2000) study, we did not address this question here. However, we suspect that the stereotyped nature of the male display in this species, such that the male hovers facing the female and holds his wings as a backdrop to his thorax, may be an attempt to present his coloration in a consistent light.

Since coloration is used by so many other taxa to communicate male quality, the strong association between body size and coloration described in this paper suggests a link between male body size and some aspect of male quality.

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