

A Color-Mediated Mutualism between Two Arthropod Predators

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Summary

The nature of interactions between animals varies depending on local selection pressure, trophic status of the participants, and evolutionary circumstances [1–6]. Body coloration and other visual signals may also affect animal interactions [7, 8]. Game theory posits that if one species provides a “service” in exchange for a “goods,” a mutualism may ensue [9]. Mutualisms between two predators are rare because of multiple conflicts of interests [3, 10] (but see [11, 12]). We used a nocturnal system traditionally considered kleptoparasitic [12] to determine whether a mutualism ensues because the body coloration of the kleptoparasite is beneficial to the host. Specifically, we tested whether the silver body of the spider *Argyrodus fissifrons* (Theridiidae) attracts prey for the larger, duller spider *Cyrtophora unicolor* (Araneidae), which reciprocates by allowing *A. fissifrons* access to its web. When *A. fissifrons* were removed from *C. unicolor* webs, the webs intercepted fewer prey. Furthermore, covering the silver body parts of *A. fissifrons* also resulted in a reduction in prey interception by *C. unicolor* webs. We thus show that a mutualism between two arthropod predators can be mediated by the coloration of one species enhancing the foraging gains of another.

Results and Discussion

Manipulation of *A. fissifrons* and *C. unicolor* Presence

Experimental removal of *Argyrodus fissifrons* (Figure 1A) from *Cyrtophora unicolor* webs (Figures 1B and 1C) was associated with a significant change in prey composition (homogeneity test: $\chi^2 = 11.046$, $df = 2$; $p = 0.011$). Moths were the principal prey intercepted (~79% of interceptions) when *A. fissifrons* was present, whereas when *A. fissifrons* was absent, ~43% of interceptions were moths. More prey overall were intercepted when *A. fissifrons* were present, regardless of whether or not *C. unicolor* was also present (Table 1). However, when *A. fissifrons* were removed, fewer prey were intercepted regardless of whether *C. unicolor* was present (Figure 2A). We never observed *A. fissifrons* to “steal” any large prey from *C. unicolor*. *A. fissifrons* consumed only the smaller (<7 mm length) prey, whereas *C. unicolor* consumed predominantly larger prey, especially moths (as reported by [13]).

Manipulation of *A. fissifrons* Body Coloration

In the next experiment, we concealed the silver body parts of selected *A. fissifrons* while leaving others exposed. We found

the composition of prey intercepted to differ significantly between treatments (homogeneity test: body parts concealed versus body parts exposed; $\chi^2 = 6.055$, $df = 3$; $p = 0.014$). When *A. fissifrons*' silver body parts were exposed, ~68% of prey intercepted were moths, whereas when *A. fissifrons*' silver body parts were concealed, ~43% of prey intercepted were moths. As in the experiment when *A. fissifrons* were removed from the webs, fewer prey were intercepted overall when *A. fissifrons*' silver body parts were concealed (Figure 2B; Table 2). Moths are too large for *A. fissifrons* to handle, so they are consumed exclusively by *C. unicolor* [13]. Therefore, we compared the moth interception rate between treatments to verify whether the increase in moth interception was due to the presence of *A. fissifrons*. We found that when the silver body parts of *A. fissifrons* were concealed, significantly fewer moths were intercepted (Figure 2C; Table 2). We concluded that (1) *A. fissifrons*' silver body parts are responsible for the increase in prey, especially moth, interception, and (2) *A. fissifrons* does not consume moths, so the resultant enhancement in moth capture exclusively benefits *C. unicolor*.

Spider Body Coloration as Viewed by Moths

Moths are exclusive prey for *C. unicolor*. We therefore assessed the conspicuousness of *A. fissifrons*' silver body parts to moths against the background vegetation. To do this, we calculated the achromatic and chromatic contrast values of *A. fissifrons*' silver body parts, as well as those of *C. unicolor*'s dorsal opisthosoma and the diurnal retreat of *C. unicolor*, as a product of moth photoreceptor sensitivities, using a hawkmoth visual model [14]. We found that the values for *A. fissifrons*' silver body parts were greater than those of *C. unicolor*'s dorsal opisthosoma, which did not differ from those of the diurnal refuge (Figure S1 and Tables S1 and S2). Accordingly, we concluded that the silver body parts of *A. fissifrons* were conspicuous to moths under nighttime illumination levels. There were no significant differences in the achromatic (two-sample t test: $t = -0.227$; $p = 0.826$) or chromatic (two-sample t test: $t = 2.031$; $p = 0.102$) contrasts between the black body parts of *A. fissifrons* and the black paint used to conceal their silver body parts (Figure S2). Painting the silver body parts black therefore effectively prevented them from being viewed by moths.

Moths may use visual cues when undertaking nocturnal activities [14–16]. Thus, our finding that the silver body parts of *A. fissifrons* achromatically and chromatically contrasted against the vegetation background and stimulated moth photoreceptors means that they might be interpreted and used as a cue by moths. We are not certain exactly which cue they resemble. However, models predict that moth photoreceptors can detect starlight [14, 16], and starlight may be used by moths for nocturnal orientation [17]. Perhaps the body of *A. fissifrons*, and other species of *Argyrodus*, reflects light at wavelengths and intensities that resemble starlight, and it is this cue that their coloration imitates to attract moths. Studies comparing the spectral properties and moth photoreceptor detectabilities of starlight and *A. fissifrons*' body parts are nevertheless needed to confirm this proposition.

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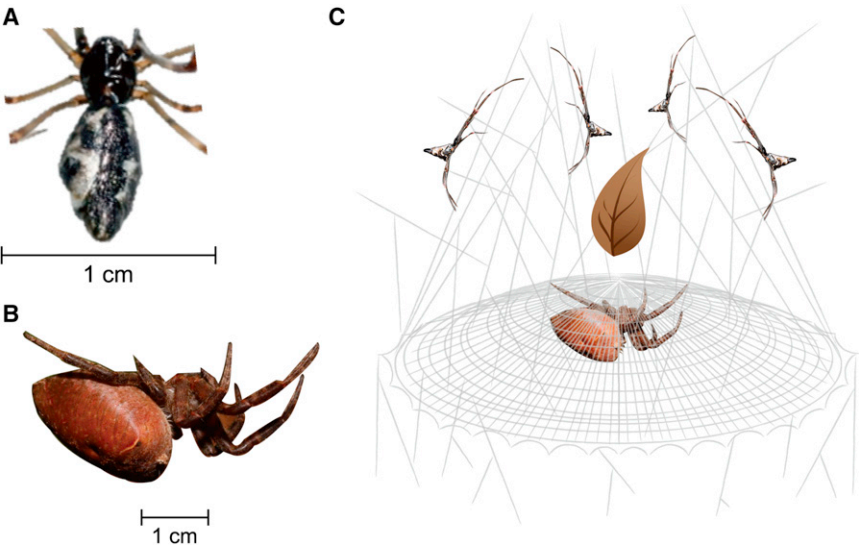


Figure 1. *Argyrodes fissifrons*, *Cyrtophora unicolor*, and *C. unicolor* web
(A and B) Representation of the approximate sizes and colors of adult female *Argyrodes fissifrons* (A) and adult *Cyrtophora unicolor* (B).
(C) Schematic illustration of the three-dimensional web built by *C. unicolor* showing the relative position of the host, the refuge made of dry leaves, and the symbiotic *A. fissifrons* on the web.

Role of Color Signals in Mutualistic Interactions

Color signals may be deployed by animals to attract prey or mates but come at the cost of increasing the conspicuousness of the sender, rendering it more vulnerable to predators [8]. Color signaling thus may be considered a “service” that might be reciprocally partitioned between two or more mutualistic species as long as some “goods” is provided by at least one of the partners [3]. Our study shows a “goods” and “service” exchange promoting a mutualistic interaction between two arthropod predators that is conferred and mediated by one species providing prey-luring body coloration in exchange for the use of a resource supplied by the other, its web.

The body coloration of some nocturnal spiders may be used to lure prey [18, 19], but we are unaware of any previous documentation of spider body coloration being used to enhance the prey capture success of another spider. Visual signals in ectosymbiotic mutualisms are traditionally thought to primarily facilitate partner recognition [20, 21]. Here we show that visual signals in an ectosymbiotic interaction may also serve to attract prey for partner species.

Table 1. Analyses of the Effect of Manipulating Spider Presence					
Treatment	df	Estimate of β	SE	χ^2 Value	p Value
Truncated Poisson Regression					
Intercept	1	-10.339	0.190	67.603	<0.0001
<i>C. unicolor</i> presence	1	0.062	0.245	0.065	0.799
<i>A. fissifrons</i> presence	1	0.713	0.228	9.753	0.002
Interaction	1	-0.203	0.306	0.443	0.506
Inflation Model					
Intercept	1	-2.1186	0.4481	22.3518	<0.0001
Rainfall	1	2.9530	0.6065	23.70998	<0.0001

Results of the zero-inflated Poisson regression, showing a truncated Poisson regression testing the effect of the two symbiotic spiders’ presence on the rate of prey interception of *Cyrtophora* host webs (top) and an inflation model testing the effect of rainfall on excess zeros in prey interception count (bottom). Spider presence and rainfall occurrence were coded as 0 = not present or 1 = present. The predictor variable of excess zeros during rainfall was statistically significant; thus rain affected the number of zero counts in the prey interception data. The β value of the control treatment group was arbitrarily designated as 0 to facilitate comparisons of probabilities of different events.

Is the Interaction between the Two Spiders Truly Mutualistic?

This is the first study to show a “goods” and “service” exchange between two predators. *A. fissifrons* increases prey capture for *C. unicolor* via its body coloration. Nevertheless, to describe the interaction as a mutualism, both partners must benefit [3, 6, 10, 12].

C. unicolor feeds exclusively on the large-bodied, thus energetically valuable, moths that are attracted to the web by *A. fissifrons* [13]. Hence it seems probable that *C. unicolor* experiences greater growth and fecundity when *A. fissifrons* is present. The question that remains unanswered, however, is what benefit *A. fissifrons* reaps from the partnership. We show that, first, *A. fissifrons* gains access to a foraging and reproducing patch, the web, which *C. unicolor* would be reluctant to vacate as long as food is plentiful [22–24]. Because the two species do not compete for food, feeding on the surplus small prey items in *C. unicolor*’s web probably also confers benefits to *A. fissifrons*. Moreover, *A. fissifrons* experiences few antagonistic interactions compared to *Argyroides* that occupy the webs of other hosts [25–27]. Therefore, we are confident in concluding that the system constitutes a mutualism.

Ecological Mosaic Perspective of *Argyroides*-Host Interactions

Argyroides are small (<2 mm body length), colorful spiders that always inhabit the webs of other spiders, usually larger-bodied (>20 mm body length) orb web spiders [24, 27]. Utilizing a host web provides *Argyroides* with benefits such as the capture of food without investing in silk, but their presence is typically thought to have a negative impact or no impact on their hosts [13, 24, 26–28]. These interactions may rapidly switch to mutualistic [29] when the hosts receive benefits such as increased prey capture [11, 12]. Color-mediated mutualisms, however, have not previously been demonstrated between two spiders.

Many symbiotic interactions originally identified as parasitic have become recognized as mutualistic as empirical and permutation studies reveal the complexity of their interactions [30, 31]. Indeed, the *Argyroides*-orb web spider network might not always be kleptoparasitic. *Argyroides* species often exceed the range of their common hosts, so a species may be involved in kleptoparasitic, neutral, or mutualistic interactions with different hosts across its range, depending on the balance of the costs and benefits to the host [12]. Furthermore, the form of any interspecific interactions can rapidly switch in extenuating circumstances [32, 33]. Hence, we expect the nature of the interactions between *Argyroides* and their hosts to respond to local selection pressures. For example, it might

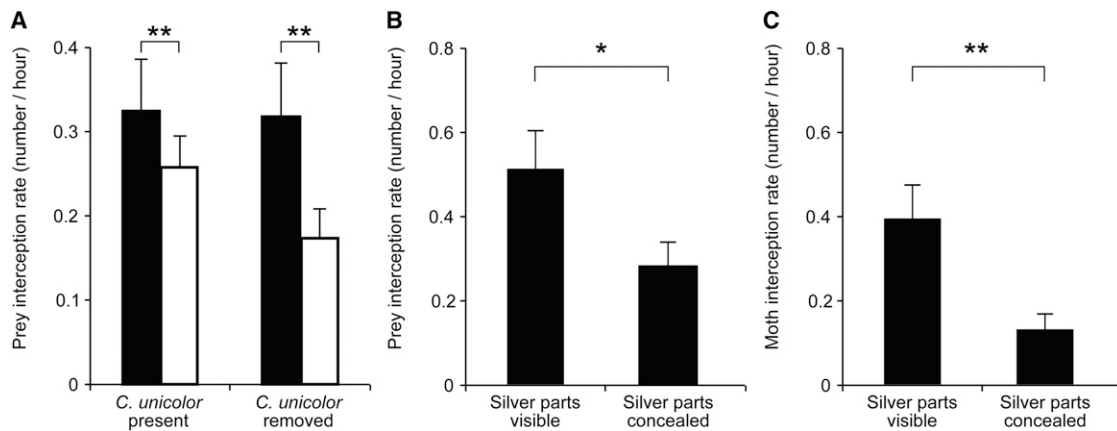


Figure 2. Prey Interception Rates in *C. unicolor* Webs under Different Treatments

(A) Mean \pm SEM prey interception rates in *C. unicolor* webs when *A. fessifrons* were present (black bars) or removed (white bars) and when *C. unicolor* were present or experimentally removed. (B and C) Mean \pm SEM prey (B) and moth (C) interception rates in *C. unicolor* webs with and without the silver body parts of *A. fessifrons* visible. *p < 0.05; **p < 0.01.

be predicted that a greater availability of prey renders *Argyrodes*-host interactions in the tropics more mutualistic than those in temperate regions. Where *Argyrodes* negatively impacts host fitness, we expect the host to show antagonistic behavior toward *Argyrodes*, as documented in some *Nephila-Argyrodes* interactions [23, 26, 27]. On the other hand, we expect there to be minimal antagonism in mutualistic interactions, just as we found for the *A. fessifrons-C. unicolor* system. Because *Argyrodes* spp. occur worldwide, live exclusively on host webs, and have a variety of hosts per species [12, 22, 25], they present as an exceptional model for determining the mosaic nature of interspecific interactions.

Experimental Procedures

Field Experiments

All field experiments were conducted on Orchid Island, Taiwan. For the first experiment, we randomly chose 12–13 *C. unicolor* webs (3–4 per treatment) at the study site each night over nine nights. We removed *A. fessifrons* (n = 25), *C. unicolor* (n = 30), neither species (n = 28), or both species simultaneously (n = 28) from webs. We did a pilot census and found there to be 3.4 ± 0.8 *A. fessifrons* per web (n = 110). We therefore added or removed spiders to ensure that each web contained four *A. fessifrons*.

The body length of all *C. unicolor* used for the experiments was measured, and there were no differences between treatments (t = 1.48; df = 107;

p = 0.20). For each experimental web, the radius of the horizontal orb and height of the tangle web were measured to calculate the web surface using the formula

$$\text{web surface area} = \pi r \sqrt{r^2 + h^2} + \pi r^2,$$

where *r* represents the radius of the orb and *h* represents the height of tangle threads. The prey capture rate of *C. unicolor* webs receiving each of the four treatments was assessed by video monitoring, using video cameras (Sony TRV118, Hi8 HDD) equipped with infrared night viewing scopes, between 2000 hr and 0400 hr. Any rainfall during monitoring was noted for inclusion in analyses.

For the second experiment, we placed four *A. fessifrons* that had either (1) their silver color concealed with paint chromatically matched to their black body parts, or (2) their black body parts covered with an equivalent quantity of black paint (n = 27 for each treatment) onto six *C. unicolor* webs each night over nine nights. *A. fessifrons* used in this experiment were collected from the study site, anesthetized using carbon dioxide, painted, and released in the afternoon (~1700 hr). Prey interception by *C. unicolor* webs was assessed by video monitoring between 2000 hr and 0400 hr. There was no significant difference in the body length of host spiders (t = 1.15; df = 107; p = 0.26) or web surface area (Kruskal-Wallis $\chi^2 = 1.23$, df = 3; p = 0.21) between the treatments.

All video footage was processed in the laboratory. For the first experiment, we viewed 692 hr of video footage: 180 hr for the treatment with *A. fessifrons* and *C. unicolor* both present, 160 hr for the treatment with *A. fessifrons* removed, 182 hr for the treatment with *C. unicolor* removed, and 170 hr for the treatment with both spiders removed. For the second experiment, we viewed 281 hr of footage: 149 hr and 132 hr for the silver parts visible and silver parts concealed treatments, respectively. We recorded all prey items by taxonomic order and counted the number of individuals from each order that were intercepted by the web.

Modeling How the Spider Body Colorations Were Viewed

We collected seven *C. unicolor*, seven *A. fessifrons*, and seven diurnal refuges of *C. unicolor* from our site and measured (using a USB4000 spectrometer and OOIBase32 software, Ocean Optics) the reflectance spectra, across the 300–700 nm wavelength range, for (1) the ventral opisthosoma of *C. unicolor*, (2) the black and silver body parts of *A. fessifrons*, (3) the diurnal refuge of *C. unicolor*, and (4) the black paint used to conceal the silver body parts of *A. fessifrons*. The reflectance spectrum of (5) the background vegetation was that measured at our study site previously [34].

For the following calculations, we used a hawkmoth visual model to represent moths in general. We acknowledge that this may be a misrepresentation, but the hawkmoth model is the only one for which photoreceptor sensitivities in any moth have been reported across the visible spectrum. We calculated the nocturnal color contrast values of (1), (2), (3), and (4) as viewed by moths, the most likely prey of *C. unicolor*, against (5) under full moon illumination. We estimated the quantum catch values of moth

Table 2. Analyses of the Effect of Concealing *A. fessifrons* Silver Body Parts

Treatment	df	Estimate of β	SE	χ^2 Value	p Value
Overall Prey Interception Rate					
Intercept	1	−9.7421	0.2342	67.603	<0.001
Experimental	1	0.108	0.299	4.407	0.0358
Control	0	0	0	—	—
Moth Interception Rate					
Intercept	1	−10.3688	0.2208	67.603	<0.001
Experimental	1	−1.1637	0.3851	6.418	0.003
Control	0	0	0	—	—

Results of negative binomial regressions comparing overall prey (top) and moth (bottom) interception rates of *Cyrtophora* webs in experimental (*A. fessifrons* silver body parts concealed) and control (*A. fessifrons* silver body parts visible) groups. The β value of the control treatment group was arbitrarily designated as 0 to facilitate comparisons of probabilities of different events.

ommatidia when viewing (1)–(5) in turn according to Warrant and Nilsson [35]. All variables used in the model (other than the reflectance spectra above and the full moon illumination spectra, which followed Somanathan et al. [36]) were those reported by Johnsen et al. [14]. The achromatic contrast between the object of interest and the background was calculated using the equation [14]

$$C = \frac{N_{X_1} - N_{X_2}}{N_{X_1} + N_{X_2}},$$

where N_{X_1} is the green photoreceptor (the photoreceptor responsible for achromatic vision) quantum catch value for the object (i.e., spider body part or diurnal refuge) and N_{X_2} is the green photoreceptor quantum catch value for the vegetation background.

To calculate the chromatic contrast values, we determined separate quantum catch values for moth UV, blue, and green photoreceptors (N_{uv} , N_b , and N_g) [14] and used them to calculate their relative quantum catch values (q_{uv} , q_b , and q_g) by the equations

$$q_{uv} = \frac{N_{uv}}{N_{uv} + N_b + N_g},$$

$$q_b = \frac{N_b}{N_{uv} + N_b + N_g},$$

$$q_g = \frac{N_g}{N_{uv} + N_b + N_g}.$$

and

We used the relative quantum catch values of each type of photoreceptor to represent the loci of the object in a color triangle. The chromatic color contrast was calculated as the distance between loci [14].

Statistics

We analyzed the prey interception data from the first field experiment by zero-inflated Poisson regression. The prey and moth interception data from the second experiment fitted a negative binomial distribution (Pearson χ^2 tests, both $p > 0.05$), so we used negative binomial regressions with prey/moth interception counts as the dependent variable and treatment as the independent variable. Web surface area and the period of monitoring were the log-link offset variables. A χ^2 test of homogeneity was used to compare prey composition between treatments in both experiments.

We used ANOVAs and Tukey's honestly significant difference tests to compare the chromatic and achromatic contrast values of *C. unicolor* body coloration with those of the diurnal refuge, and *A. fessifrons* with the vegetation background, to ascertain whether the silver body parts of *A. fessifrons* were more conspicuous to moths than the body of *C. unicolor*. A two-sample *t* test was used to compare the chromatic and achromatic contrast values of the paint used to conceal the silver body parts of *A. fessifrons* with their black body parts. This test was performed to ascertain whether the paint prevented the silver body parts from being viewed by moths.

Supplemental Information

Supplemental Information includes two tables, four figures, and Supplemental Experimental Procedures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2012.11.057>.

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