

A predator's body coloration enhances its foraging profitability by day and night

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Abstract Few predators forage by both day and night. It remains unknown, however, how the costs and benefits of foraging or signaling are partitioned in animals that forage at all times. The orb-web spider *Cyrtophora moluccensis* is brightly colored and forages by day and night. We determined the benefits reaped when it forages by both day and night by estimating the biomass of prey caught in their webs. Additionally, we quantified whether the spider's presence influences the number of prey caught by day and night and whether its colorful body is visible to diurnal and/or nocturnal insects using diurnal and nocturnal insect vision models. We found that approximately five times the biomass of prey was caught in *C. moluccensis*' webs by night than by day. Hemipterans, hymenopterans, and dipterans were predominantly caught by day, while lepidopterans (moths) were predominately caught by night. Accordingly, we concluded that foraging by night is more profitable than foraging by day. We predicted that other benefits, for example, energetic advantages or enhanced fecundity, may promote its daytime activity. Foraging success

was greater by day and night when the spider was present in the web than when the spider was absent. We also found that parts of the spider's body were conspicuous to diurnal and nocturnal insects, possibly through different visual channels. The colorful body of *C. moluccensis*, accordingly, appears to influence its foraging success by attracting prey during both the day and night.

Keywords Body coloration · Color contrast · Diurnal foraging · Nocturnal foraging · Orb-web spider · Visual signals

Introduction

Predators are generally classified as diurnal if they forage by day, nocturnal if they forage by night, or crepuscular if they forage at dawn or dusk. While some cats, dogs, birds, crabs, and spiders may exhibit daytime and nighttime foraging, depending on ecological circumstances (Corbett 1995; Beauchamp 2007; Chuang et al. 2007; Prangle 2008), few terrestrial predators regularly forage at all times. The times when a predator prefers to forage is influenced by a combination of factors, including the activity times of its predators and prey; habitat factors; and the thermal, visual, and other capacities of the predator and/or its prey (Ripple and Beschta 2004; Prangle 2008; Voight and Lewanski 2011).

Characteristics such as the color of a predator can be used for attracting prey, reducing detection by its own predators, or a number of other functions. The nature of these characteristics would be expected to differ according to the time of day at which the predator is active. The form of signals used by predators to attract prey is dependent on the sensory perceptions of the prey and the intensity of the background coloration (Endler 1992; Gawryszewski et al. 2012). By day, visual signals are commonly used by some invertebrate predators, for example spiders, to deceive or lure insect prey (Heiling

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et al. 2003; Tso et al. 2006; Fan et al. 2009; Théry and Casas 2009; Gawryszewski et al. 2012). Nevertheless, the signal-to-background noise ratio is lower at night than during the day, so visual signals successfully used by day are considered less useful by night (Warrant 2004).

The apposition compound eyes of many diurnal insects focus surrounding light onto a single ommatidium for detection and neural propagation within the rhabdom (Hardie 1986). The superposition compound eyes of many nocturnal insects, on the other hand, draw light from several adjacent ommatidia to elicit neural propagation within the rhabdom (Hardie 1986; Bogdanov 2000; Klaus and Warrant 2009). While the amount of light captured by an ommatidium is the same for apposition and superposition compound eyes, there is a difference in the way the neural outputs are linked (Hardie 1986; Klaus and Warrant 2009). It has, accordingly, been suggested that color vision and shape recognition are poorer in nocturnal insects than diurnal insects (Kelber et al. 2003; Roth and Kelber 2004; Warrant 2004; Klaus and Warrant 2009), and, as a result, it might be expected that color signals that are attractive to diurnal insects are not attractive to nocturnal insects. Consequently, invertebrate predators relying on visual lures to attract prey should limit their foraging to either the daytime or nighttime.

Some orb-web spiders forage both diurnally and nocturnally (Herberstein and Elgar 1994; Chuang et al. 2007; Fan et al. 2009). Many of these are also colorful and may use their bodies as signals to attract prey (Tso et al. 2006, 2007; Chuang et al. 2007; Bush et al. 2008; Fan et al. 2009). Accordingly, orb-web spiders are good subjects for testing generalizations about the capacity for predators to forage at different times of day and the effectiveness of visual signals aimed at both diurnal and nocturnal insects (Herberstein and Elgar 1994; Cellabos et al. 2005; Chuang et al. 2007; Fan et al. 2009).

The orb-web spider *Cyrtophora moluccensis* (adult female body lengths ≈ 20 mm), like other members of the genus *Cyrtophora*, builds a ~ 0.3 -m wide horizontal orb web onto which it adds a three-dimensional silk barrier structure that extends vertically upward to ~ 1 m (Lubin 1974, 1980; Berry 1987; Blamires et al. 2012a, 2013). Unlike other members of the genus, which forage at night and spend the day within a retreat constructed from vegetation (Tso and Severinghaus 2000; Peng et al. 2013), *C. moluccensis* forages fully exposed by day and night. At night, it forages predominantly on moths (Blamires et al. 2013). As these are larger prey than those they generally consume by day, nighttime foraging appears to be the more profitable. Adult female *C. moluccensis* have a ventrally and dorsally bright green or red body with scattered yellow or white spots. It is not known, however, whether its body coloration influences the profitability of foraging at different times of the day.

Here, we aimed to ascertain, firstly, the time of the day that foraging is most profitable for *C. moluccensis* by performing

an around-the-clock survey of the biomass of prey intercepted by their webs. We then performed a manipulative field experiment to ascertain whether the presence of *C. moluccensis* on its web affects foraging success during the day and/or night. We then measured the spectral reflectance of selected *C. moluccensis* body parts to ascertain whether they are visible to diurnal and/or nocturnal insects.

Materials and methods

The following experiments were performed at Ape Hill, Kaohsiung City, Taiwan (22° 38' 19" N, 120° 15' 54" E), a secondary forest dominated by mulberry (*Morus* spp.) and elephant's ear (*Alocasia macrorrhiza*) shrubs, over eight consecutive days in August of two consecutive years (2006 and 2007).

Quantification of diurnal and nocturnal prey biomass

We quantified the biomass of prey caught by *C. moluccensis* webs by day and night by marking the web sites of 25 adult females within our study area by fastening numbered colored tape onto nearby vegetation. We estimated the volume of each web, by measuring orb diameter and length of the barrier structure (Tso and Severinghaus 2000; Blamires et al. 2013; Peng et al. 2013), to ensure webs of approximately similar volume were used across treatments. We monitored the number and type of insects caught by *C. moluccensis* webs hourly over a 24-h period over 5 days. The same webs were used repeatedly, and we did not remove spiders from webs to ensure that the webs did not sustain any damage during the experiment. We removed all insects caught by gently reaching into the web without disturbing it, identifying all of them to order and estimating their body length to the nearest millimeter using digital calipers. Prey dry mass (W) was estimated from body length (L) using the allometric relationship (Schoener 1980):

$$W = 0.305L^{2.62},$$

from which the biomass of prey captured by each spider by day and by night was estimated.

Manipulative field experiment

In each year, we randomly selected 16–18 *C. moluccensis* ($n=8-9$ for each treatment) and assigned them to either a spider present (S+) or spider removed (S-) treatment. Before assigning spiders to a treatment, we collected the spiders and measured their body length and width using calipers, thus ensuring spiders of approximately equal body size were used

(spiders with a length or width deviating from the mean by >50 % were discarded) across treatments. Spiders assigned to the S+ treatment were returned to their webs upon completion of measurements. Spiders assigned to the S–treatment were kept in 0.5-l plastic cups with cotton mesh lids until the experiments were completed.

Video cameras with infrared night view scopes (Sony DCR-TRV and DCR-SR series, Tokyo, Japan) were placed approximately 1 m from each web. We incorporated *C. moluccensis* daytime and nighttime foraging into our analyses by monitoring at three time intervals: 0800–1200, 1300–1700, and 1800–2200 h. Two of these time intervals were defined as “daytime” (0800–1200 and 1300–1700 h), while the other (1800–2200 h) was defined as “nighttime”. We stopped recording only in the event of inclement weather. The 2500 h+ of video footage was monitored at Tunghai University, Taichung, Taiwan. All of the video footage was clear enough to identify insects to order. Prey interception was defined as an insect falling into the horizontal orb and remaining for at least 1 s. Occasional camera positional adjustments, battery failure, or other technical issues resulted in unequal hours of footage being available for all treatments, so we defined prey interception rate as the number of prey intercepted by a web per hour of footage. This also accounted for the different number of hours of daytime and nighttime monitoring.

Body coloration measurement

We brought eight female *C. moluccensis* back to the laboratory at Tunghai University. A spectrometer (USB4000, Ocean Optics, Inc.) was used to measure the reflected spectra of five body parts from each spider: (1) the white shoulder points on the dorsum, (2) the white bands on the front end of the dorsum, (3) the orange spots on the dorsum, (4) the yellow stripes on the ventrum, and (5) the green ventral region (Fig. 1a) across the 300–700-nm wave band (see Electronic Supplementary Material Fig. 1 for the spectra for each body part). We calculated the color contrasts of the dorsal and ventral body parts against a tropical forest understory background spectra measured previously at a similar habitat (Tso et al. 2004).

We expected hymenopterans to be the major diurnal prey (bees) and predators (wasps) of *C. moluccensis* (Blamires et al. 2013), so we used a honeybee color vision model (Chittka 1992) to calculate the diurnal achromatic and chromatic contrasts of the various *C. moluccensis* body parts. We considered the honeybee vision model to be applicable to both bees and wasps because bees and wasps have similar types of photosensitive cells, occur in similar environments, and are phylogenetically related (Briscoe and Chittka 2001; Osorio and Vorobyev 2005). We calculated the excitation

values (E_i) of honeybee UV, blue, and green photoreceptors using the equations (Chittka 1992):

$$Q_i = \int_{300}^{700} S(\lambda)D(\lambda)I_s(\lambda)d\lambda$$

and

$$E_i = Q_i/(Q_i + 1)$$

where Q_i is the “quantum catch” of the receptor under investigation (i). $S(\lambda)$ is the sensitivity function of the receptor under investigation. $D(\lambda)$ is the CIE standard illumination function corresponding to average midday sun illumination (D65), and $I_s(\lambda)$ is the reflectance function of the individual spider body parts or background vegetation. We calculated the chromatic contrasts as the Euclidean distance between signal (i.e., one of the five body parts) E_i values, summed across photoreceptors, against the E_i values of the background summed across photoreceptors using the color hexagon model of Chittka (1992). We calculated the achromatic contrasts as the excitation values of the honeybee green receptors when viewing each body part divided by those when viewing the vegetation background (Chittka 1992; Dyer and Chittka 2004).

We expected lepidopterans (moths) to be the major nocturnal prey for *C. moluccensis*, so we used a hawkmoth neuroethological model (Johnsen et al. 2006) to calculate the nocturnal achromatic and chromatic contrast values for the various *C. moluccensis* body parts. We used the reflectance functions of the five spider body parts, the tropical forest understory background spectra of Tso et al. (2004), and the following parameters: (i) moth photoreceptor inclusion angle, (ii) facet lens diameter, (iii) cumulative photoreceptor scoring time, (iv) quantum transduction efficiency, (v) eye fractional transmission, (vi) absorption coefficient of the rhabdom, (vii) absorbance spectra of each photoreceptor, and (viii) tapetal reflection from Johnsen et al. (2006). The mean full moonlight illumination function across the 300–700-nm wave band was that of Somanathan et al. (2008).

The quantum catch values for the spider body parts were plotted on a hawkmoth UV-blue-green visual triangle (Johnsen et al. 2006), and the distance between their Euclidean positions relative to each other were used to calculate their chromatic contrast values. We calculated the achromatic contrasts of the spider body parts when viewed by moths using the equation as follows:

$$C = \frac{N_x - N_{\text{green}}}{N_x + N_{\text{green}}}$$

where N_x is the green photoreceptor quantum catch for the spider body parts and N_{green} is the green photoreceptor

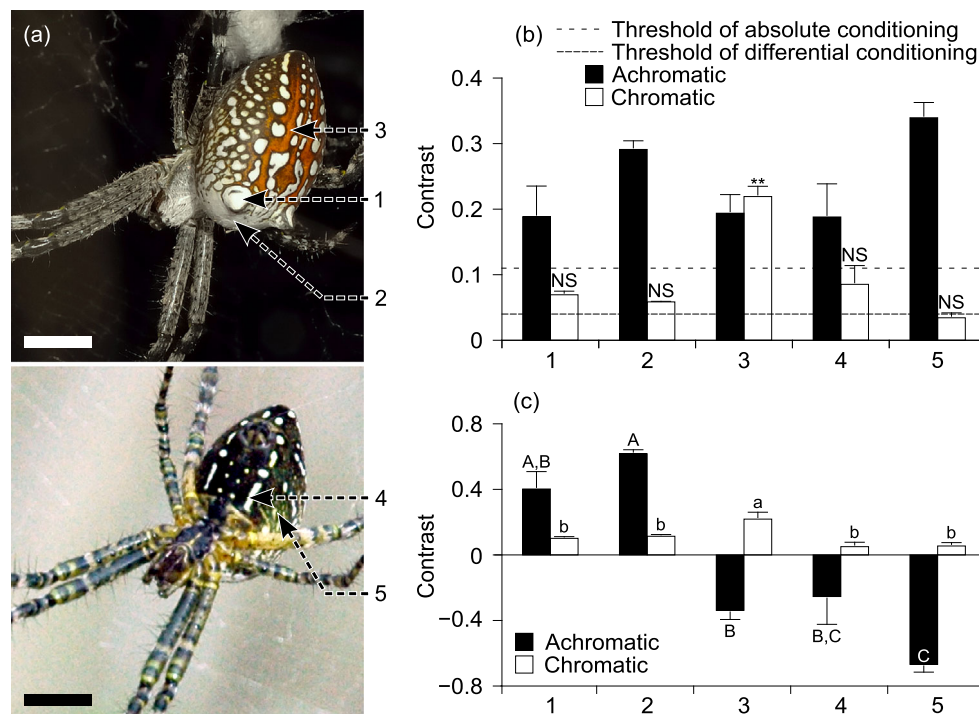


Fig. 1 **a** Photograph of *Cyrtophora moluccensis* (scale bars=10 mm) showing the location and colouration of the white shoulder points on the dorsum (1), the white bands on the front end of the dorsum (2), the orange spots on the dorsum (3), the yellow stripes on the ventrum (4), and the green dorsal region (5). **b** Diurnal and **c** nocturnal color contrasts of different body parts of *C. moluccensis* contrasted against a standard background (measured by Tso et al. 2004) showing mean±s.e. Dashed line with gaps in (b) represents a discrimination threshold of 0.04 hexagon units, the threshold value for differential-conditioned bees, while dashed line without gaps represents a discrimination threshold of 0.11 hexagon units, the threshold values of absolute-conditioned bees (Dyer

and Chittka 2004). Double asterisk indicates the chromatic contrasts were significantly greater ($0.001 \leq P < 0.01$) than 0.11 hexagon units. Because the achromatic contrasts were calculated as the excitation values of the honeybee green receptors viewing each body part divided by those viewing the vegetation background, they have no units, so no comparisons of achromatic contrasts to threshold values in hexagon units are shown. Letters (achromatic contrasts: $A > B > C$; chromatic contrasts: $a > b > c$) in (c) represent the results of a Welch's ANOVA tests and LSD post hoc comparisons. Positive values for achromatic contrasts indicate brighter contrasts than the background, while negative values indicate duller contrasts than the background

quantum catch for the vegetation background (Johnsen et al. 2006; Goyret and Kelber 2012).

Analyses

A permuted Pearson's χ^2 test based on 20,000 replicates was used to compare the number of individuals captured from each identifiable insect order by day and by night. A general mixed linear model with repeated measure design was used to compare the biomass of prey captured by day and by night. Biomass data was log-transformed to achieve normality. The monitor time (day or night time) was a fixed factor, and the individual spider was a random factor.

For the manipulative experiment, the prey interception rate data failed normality and homogeneity of variances tests (Kolmogorov-Smirnov and Levene's tests; $P < 0.05$); thus, parametric procedures such as ANOVA/ANCOVA were not appropriate (Zar 2010). The prey interception data fitted a Poisson model (goodness of fit: $\chi^2_{43} = 38.014$, $P = 0.6870$), so we used a generalized linear mixed model, using a two-factor split-plot design, where spider presence or absence (S−/

S+) is the main between block treatment factor, time of day (day/night) is the main within block treatment factor, individual web is the block (random factor), and recording hours were used as an offset. A χ^2 test of homogeneity was used to compare the composition of prey intercepted across treatments during the daytime and nighttime.

One sample *t* tests were used to compare the color contrast values of the five *C. moluccensis* body parts with honeybee discrimination threshold values of 0.04 and 0.11 hexagon units. These represent the threshold values of differential-conditioned and absolute-conditioned bees, respectively (Dyer and Chittka 2004). We acknowledge that color discrimination may occur at under 0.01 hexagon units in highly conditioned bees (Dyer and Chittka 2004; Dyer and Nuemeyer 2005); however, we used 0.04 and 0.11 as the discrimination threshold values because we considered it unlikely that wild bees and wasps would have the necessary conditioning for extremely fine discrimination (Dyer and Chittka 2004; Dyer et al. 2012).

Unfortunately, no color discrimination threshold values for nocturnal insect photoreceptors have ever been determined, so

the absolute discriminability between body parts in the hawkmoth visual system could not be determined. Instead, the nocturnal achromatic and chromatic contrast values of the five *C. moluccensis* body parts were compared against each other by Welch's ANOVA tests and least squared difference post hoc comparisons of means to assess whether the body parts differed in nocturnal contrast against the vegetation background. We used Bonferroni-adjusted alpha levels (Zar 2010), where appropriate, to account for multiple comparisons.

Results

The prey composition captured by day and night differed ($\chi^2_8=30.856, P<0.0001$). Hemiptera, Hymenoptera, and Diptera were the orders principally intercepted by day, while Lepidoptera were principally intercepted by night (Electronic Supplementary Material Fig. 2). The biomass of prey intercepted by night was approximately five times that caught by day (mean \pm s.e.: night=6.58 \pm 2.45 vs day=1.30 \pm 0.43 mg, general linear mixed model, $\beta=0.1735\pm 0.068 : t_{26}=2.553, P=0.0169$). Webs with spiders (S+ treatment) intercepted significantly more prey than webs without spiders (S- treatment), and both webs intercepted more prey by night than by day, although time of day did not significantly influence the effect of spider presence on prey interception (Table 1; Fig. 2).

Assuming differential conditioning, the diurnal chromatic contrasts of *C. moluccensis*' yellow and green body parts (body parts 4 and 5 of Fig. 1a) were not significantly greater than the honeybee color discrimination threshold of 0.04 hexagon units, while all of the other body parts examined (body parts 1, 2, and 3 of Fig. 1a) were significantly greater than the honeybee color discrimination threshold of 0.04 hexagon units (Table 2; Fig. 1b). Nevertheless, when assuming absolute conditioning, the chromatic contrast of the orange spots on the dorsum became the only body part with a color

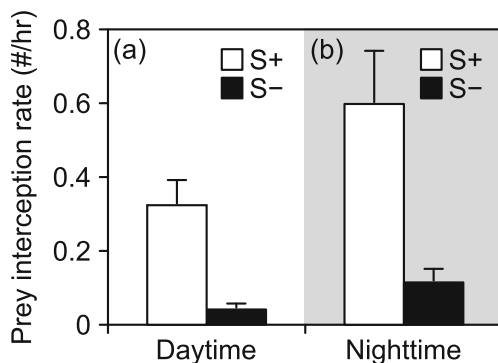


Fig. 2 Prey interception rates (number of prey intercepted per hour of monitoring) showing the mean (\pm s.e.) rate during the **a** daytime and **b** nighttime when the spider was present on the web (S+) and when the spider was removed from the web (S-)

Table 1 Results of a generalized nonlinear model using a two-factor split-plot design

Parameter	Estimate of β	SE	Z value	P value
Intercept	-1.9632	0.1648	-11.912	<0.0001
Spider (S- vs S+)	-1.9029	0.3296	-5.773	<0.0001
Time (nighttime vs daytime)	0.9296	0.2151	4.322	<0.0001
Spider \times time	0.6376	0.4301	1.482	0.1380

Spider presence or absence (S-=absence, S+=presence) is the between block factor, time of day (daytime or nighttime) is the within block factor, the individual web number is the block (random) factor, and hours of video recording is the offset factor. The ratio between probabilities of two certain events was e^β

contrast significantly greater than the honeybee color discrimination threshold of 0.11 hexagon units (Table 2; Fig. 1b).

There were significant differences in the achromatic (one-way Welch's ANOVA: $F_{4,10.93}=174.633, P<0.0001$; Table 3a) and chromatic (one-way Welch's ANOVA: $F_{4,11.49}=4.295, P=0.023$; Table 3b) nocturnal contrasts between the five body parts. The achromatic contrasts varied across body parts, with the white shoulder points on the dorsum and the white bands on the front end of the dorsum having the greatest contrasts. The orange spots on the dorsum and green dorsal region had achromatic contrasts duller than the background, so were not likely to be visible to nocturnal insects through achromatic channels. Least squared difference comparisons (Fig. 1c) revealed that the chromatic contrasts were generally small, with the orange spots on the dorsum having contrast values significantly greater than all of the other body parts. These results suggest that the reason the presence of *C. moluccensis* resulted in an increase in prey interception by day and night is because its body coloration attracts insects at all times.

Discussion

Here we found that (i) a greater prey biomass was caught in *C. moluccensis* webs by night than by day, (ii) when spiders were removed from webs, fewer prey were intercepted by the webs than when spiders were present, (iii) although more prey were intercepted by *C. moluccensis* webs by night, time of day did not affect the influence of the spider's body on prey interception rate, and (iv) the spider's body was visible to both diurnal and/or nocturnal prey. These results suggest that nighttime foraging is more profitable than daytime foraging for *C. moluccensis* and that its body coloration provides a signal that lures prey at all times. It is unlikely that the spider's body enhances prey attraction independent of its coloration, as no previous studies testing the function of spider body coloration has found a prey attracting mechanism for the body itself (Tso et al. 2004, 2006; Bush et al. 2008; Chuang et al. 2007, 2008;

Table 2 The results of one-tailed *t* tests comparing the chromatic contrasts of the measured *C. moluccensis* body parts contrasted against a tropical forest understory background (measured by Tso et al. 2004) using the color hexagon model of Chittka (1992)

		Body parts				
Statistic		1	2	3	4	5
	Mean	0.071	0.061	0.220	0.087	0.036
	SE	0.005	0.002	0.016	0.028	0.007
$H_A: \mu > 0.04$	T_4	5.739**	9.181***	11.590***	1.660	-0.472
$H_A: \mu > 0.11$	T_4	-7.626	-22.015	7.090**	-0.801	-9.877

Numbers correspond to the body parts specified in Fig. 1. We tested whether the contrast values for each body part differed to two hypothetical discrimination thresholds, 0.04 hexagon units ($\mu \leq 0.04$) and 0.11 hexagon units ($\mu \leq 0.11$) to represent the threshold values of differential-conditioned and absolute-conditioned bees, respectively

*** $P < 0.001$; ** $0.001 \leq P < 0.01$; * $0.01 \leq P < 0.05$

Fan et al. 2009; Blamires et al. 2012b; Gawryszewski et al. 2012; Peng et al. 2013).

We found that a greater biomass of prey was intercepted in *C. moluccensis* webs by night than by day, so we concluded that nighttime is the most profitable foraging time for *C. moluccensis*. We acknowledge that biomass estimated from prey body lengths is generally not considered a suitable surrogate for calorific intake (Oxford 2000). Nevertheless, the difference between daytime and nighttime intake was such that we are certain that our conclusion would be the same whether calorific or biomass intake was used as the metric. Studies show that many orb-web spiders, including *C. moluccensis* (Blamires et al. 2013), forage under a greater threat of predation by day than by night (Fan et al. 2009; Blamires et al. 2012b). Hence, it is perplexing why *C. moluccensis* might forage by day at all. Many diurnal spiders overcome the threat imposed by daytime activity by building barricades, decoys, or retreats; using chemical or visual deterrence; or adopting disruptive body coloration (Blackledge et al. 2003; Fan et al. 2009; Tseng and Tso

2009; Tseng et al. 2011). *C. moluccensis* builds a three-dimensional web with an elaborate barricading structure above its horizontally aligned orb web (Lubin 1973, 1974; Blamires et al. 2012a, 2013). We, thus, expect that its web structure enables *C. moluccensis* enough protection to forage throughout the day (Blamires et al. 2013).

Considering we found there to be a fivefold greater biomass of prey intercepted in *C. moluccensis* webs by night than by day, the extra protection from predation endowed by the three-dimensional web alone is unlikely to explain why *C. moluccensis* forages by day. *C. moluccensis* is larger and has a longer reproductive season and produces more egg sacs than most orb-web spiders (Berry 1987), so foraging by day and night might maximize the amount or diversity of prey consumed, which could be important for the attainment of the nutrients required for its growth and reproduction (Toft and Wise 1999a,b; Rickers et al. 2006). Moreover, *C. moluccensis* does not incorporate any sticky silks, which are highly energy-consuming in their construction owing to the associated metabolic investment in salts, glycoproteins, and complex

Table 3 Results of one-way Welch's ANOVA tests and LSD comparisons, comparing achromatic (a) and chromatic (b) nocturnal color contrasts of various body parts of *Cyrtophora moluccensis*

(a)		1 v 2	1 v 3	1 v 4	1 v 5	2 v 3	2 v 4	2 v 5	3 v 4	3 v 5	4 v 5
Mean difference		-0.214	0.755	0.672	1.083	0.969	0.886	1.297	-0.084	0.327	0.411
<i>T</i>		-1.976	6.340	3.377	9.366	16.060	5.200	24.453	-0.473	4.502	2.349
DF		4.418	6.043	6.718	5.539	5.472	4.164	5.960	4.851	7.807	4.624
<i>P</i>		0.400	0.003	0.067	<0.001	<0.001	0.027	<0.001	0.987	0.013	0.275
(b)		1 v 2	1 v 3	1 v 4	1 v 5	2 v 3	2 v 4	2 v 5	3 v 4	3 v 5	4 v 5
Mean difference		-0.001	-0.435	0.004	0.007	-0.434	0.005	0.008	0.439	0.442	0.003
<i>T</i>		-0.147	-7.062	0.129	0.732	-7.077	0.163	1.037	6.352	7.164	0.092
DF		5.259	4.088	4.319	7.797	4.014	4.052	4.920	6.037	4.121	4.442
<i>P</i>		0.999	0.009	0.999	0.942	0.010	0.999	0.830	0.004	0.008	0.999

Numbers correspond to the body parts specified in Fig. 1

peptides (Townley and Tillinghast 2013; Blamires et al. 2014), in its web. Accordingly, once it builds a web, it is not any more energetically costly to forage by day than by night. We recommend further research assess the physiological, building, and reproductive costs and benefits of foraging by night and day to ascertain which explanation applies to *C. moluccensis*.

We found that (i) the presence of the spider increases prey interception rate of *C. moluccensis*' webs and (ii) even under the conservative assumption of absolute conditioning of the bees and wasps encountered (hence, the assumption of a color discrimination threshold of 0.11 hexagon units), the orange spots on the dorsum of *C. moluccensis* are conspicuous to hymenopteran prey by day and lepidopteran prey by night. Thus, the body coloration of *C. moluccensis* appears to function to lure prey by both day and night. If the bees and wasps at our study site had differential or aversive conditioning, for example, by positive or negative nectar reinforcements when exploring different flowers (Dyer and Chittka 2004), their photoreceptors may be more sensitive and they may be able to discriminate among all of the spider body parts measured with the exception of the green and yellow dorsal parts.

If the body coloration of *C. moluccensis* was a lure specifically targeting hymenopterans by day, we would expect more hymenopterans to have been caught during the day than at night. The prey composition data (Electronic Supplementary Material Fig. 2), however, showed that approximately equal numbers of Hymenoptera were captured by day and by night (unidentified prey notwithstanding). This suggests that hymenopterans are lured by *C. moluccensis*' body coloration both by day and night. Our modeling, nevertheless, only tested whether the spider's body coloration lures hymenopterans during the day. Unfortunately, no hymenopteran nocturnal vision models exist to test the conspicuousness of *C. moluccensis*' body to bees and wasps at night. It, nevertheless, seems plausible from our results that its body is conspicuous to hymenopterans by day and night.

We found that the chromatic contrasts of the five *C. moluccensis* body parts differed from each other when viewed by nocturnal insects, although at relatively low levels. Moreover, the nocturnal chromatic contrasts of the white and orange body parts were greater than nocturnal chromatic contrast values measured for nocturnally pollinated white flowers (Chuang et al. 2008). Although there is no published threshold value available to assess the discriminability of each of the body parts at night, our findings suggest that the white and orange body parts of *C. moluccensis* have nocturnal chromatic contrasts higher than those of flowers visited by moths at night. Accordingly, moths may be able to visually discriminate between these body parts and the vegetation background at night. We found that the achromatic contrasts of the *C. moluccensis* body parts, nevertheless, differed to a greater extent than the chromatic contrasts, so nocturnal insect photoreceptor excitation seems likely to be primarily elicited

via achromatic channels. Indeed, other studies show moths to be behaviorally more responsive to achromatic than chromatic cues at night (Johnsen et al. 2006; Goyret and Kelber 2012).

It seems that the visual channel stimulated by *C. moluccensis*' body coloration shifts depending on the time of day and/or the type of insects viewing the body parts. While other studies have suggested that the body colors of orb-web spiders act as prey lures under either daytime (e.g., Tso et al. 2004, 2006, 2007; Chuang et al. 2007; Bush et al. 2008) or nighttime (e.g., Chuang et al. 2008; Fan et al. 2009; Blamires et al. 2012b) illuminations, this study is the first to our knowledge to quantify and compare the foraging consequences associated with spider body coloration during both the day and night.

To summarize, we found that five times the biomass of prey were caught in *C. moluccensis* webs by night than by day. Considering there are more predators of *C. moluccensis* active by day than by night (Blamires et al. 2013), it seems perplexing why *C. moluccensis* forages by day at all. There may be benefits to foraging by day not accounted for in our study, such as energetic dividends or the facilitation of higher fecundity. We found that the body colors of *C. moluccensis* were conspicuous to diurnal and nocturnal insects and the presence of the spider increased prey interception at all times. We, therefore, concluded that the body coloration of *C. moluccensis* improves its diurnal and nocturnal foraging success by attracting prey to its web. Nevertheless, the visual sensitivities of diurnal and nocturnal insects are expected to differ (Warrant 2004), so visual signals aimed at diurnal insects should not be equally received by nocturnal insects and vice versa. Our findings suggest that the insect photoreceptor channel stimulated by *C. moluccensis*' body may shift depending on whether it is viewed by diurnal or nocturnal insects and/or the capacity for many nocturnal insects to see colorful objects may be better than has been assumed.

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