RESEARCH ARTICLE

High contrast yellow mosaic patterns are prey attractants for orb-weaving spiders

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Handling Editor: Ismael Galván

Abstract

1. Many animals improve their foraging success by producing signals that exploit the sensory biases of potential prey, but the specific properties that make these sensory traps effective remain unclear.

2. We combine field experiments with phylogenetic comparative analyses to investigate the visual luring properties of different signal designs in web-building spiders. Our field experiments used cardboard spider models to examine the effects of area of colour patches, colour and pattern on the foraging success of the colourful giant wood spider, *Nephila pilipes*. These experiments revealed that both the colour (yellow) and pattern (yellow and black mosaic) are essential for luring prey in a high ambient light environment.

3. We subsequently used phylogenetic comparative analyses to demonstrate an evolutionary association between prey viewing environment and spider ventral signal among 63 species of orb-weavers from 53 genera.

4. Combined, our data show that (a) the colour of the bright body parts of orb-weavers is essential for both diurnal and nocturnal prey attraction, whereas the pattern and area of colour patches are important for diurnal foraging and (b) the evolution of these visual lures is associated with the viewing environment, specifically ambient light intensity.

5. We conclude that the effectiveness of colour luring might be a major driver of the convergent evolution of yellow mosaic patterns in phylogenetically divergent orb-weavers.

6. Our discoveries indicate that prey colour preferences and signal efficacy play a significant role in the evolution of visually mediated prey-luring systems.

KEYWORDS
colour lure, orb-weavers, signal design, viewing environment, visual lure

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I-Min Tso and Mark A. Elgar contributed equally to this work

1 | INTRODUCTION

The evolution of colour signals is shaped by the visual capabilities and sensory biases of receivers. In this regard, most research has focused on how conspecific receivers shape sexual signals (Taylor, Clark, & McGraw, 2011) or how predators shape the protective colouration of prey (warning signals and camouflage; Stuart-Fox, Moussalli, Marshall, & Owens, 2003). Comparatively, few studies have examined how the sensory biases of prey shape the evolution of predator colour patterns. In particular, colour-based deception is frequently applied in a prey-luring context, where predators exploit the sensory biases of prey (White & Kemp, 2015) to lure or attract the prey to within striking distance. However, the underlying attributes influencing the efficacy of colour lures remain unclear.

Web-building spiders are an excellent system to study the properties of effective prey lures. They are sit-and-wait foragers that rely on a range of strategies to acquire prey. These strategies include modifying the architecture of the web in response to fluctuating prey availability (Blamires, 2010; Blamires, Martens, & Kasumovic, 2018; Blamires & Tso, 2013; Heiling & Herberstein, 2000; Sandoval, 1994; Schneider & Vollrath, 1998), and exploiting different sensory channels to attract prey to the vicinity of the web, for instance by adding odours (Henneken, Goodger, Jones, & Elgar, 2017), colours (Craig, Weber, & Bernard, 1996; Hsiung, Justyn, Blackledge, & Shawkey, 2017), silken decorations (Tan et al., 2010; Walter & Elgar, 2012; Yeh, Blamires, Liao, & Tso, 2015) or prey remains (Bjorkman-Chiswell et al., 2004; Tan & Li, 2009) to their webs, as well as conspicuous colour patterns on the body (Peng, Blamires, Agnarsson, Lin, & Tso, 2013; Tso, Lin, & Yang, 2004). There is remarkable variation in the colour patterns of web-building spiders, and the commonly seen yellow or orange mosaic pattern on the ventral surface of orb-weaver spiders can serve as visual lures to enhance foraging success (Blamires et al., 2011; Chuang, Yang, & Tso, 2007; Liao, Liao, Blamires, & Tso, 2019; Tso, Liao, & Huang, 2007; Tso, Tai, Ku, Kuo, & Yang, 2002; see also White & Kemp, 2015 for a review). However, conspicuous colour patterns may also have a protective function (Tan, Reid, & Elgar, 2016)—aposematic or disruptive—and it is unclear which colour pattern elements are essential for effective prey luring.

Web-building spiders live in a broad range of ambient light conditions, both in terms of when they are actively foraging and where they locate their webs. As ambient light conditions strongly influence the efficacy of visual signals (Endler & Thery, 1996; Seehausen, Van Alphen, & Witte, 1997), the viewing environment could influence the evolution of visual lures (see also Elgar, Allan, & Evans, 1996). The diversity in both morphology and spectral environment of orb-weavers offers an opportunity to investigate this potential association experimentally.

Here, we tested the visual luring properties of different signal designs in web-building spiders using a combination of field experiments and phylogenetic comparative analyses. First, using artificial models, we manipulated the colour, adjacency and area of individual colour patches to reveal which of these attributes of signal design (see Endler, 1992, 2012; Endler & Thery, 1996; Osorio & Vorobyev,

2005 for a review) are the essential elements of orb-weaver spider bodies that exploit prey sensory biases and thus act as lures. Second, we compiled an interspecific dataset describing spider body colouration and natural history characters across a taxonomically broad range of orb-weaving spiders. We analysed this dataset using a phylogenetically controlled comparative approach to determine whether the evolution of spider body colouration is associated with the viewing environment of the targeted prey.

2 | MATERIALS AND METHODS

2.1 | Signal design and prey attraction

2.1.1 | Field experiment

We conducted a field experiment using paper models to manipulate the area and shape of the conspicuous body colouration of *Nephila pilipes* (Figure 1). Golden orb-weaver spiders are active both diurnally and nocturnally. This means their body colouration might be shaped by the combination of different light conditions (day/night) and visual systems of predator/prey species, and hence they represent an excellent species to study deceptive signal efficacy and evolution.
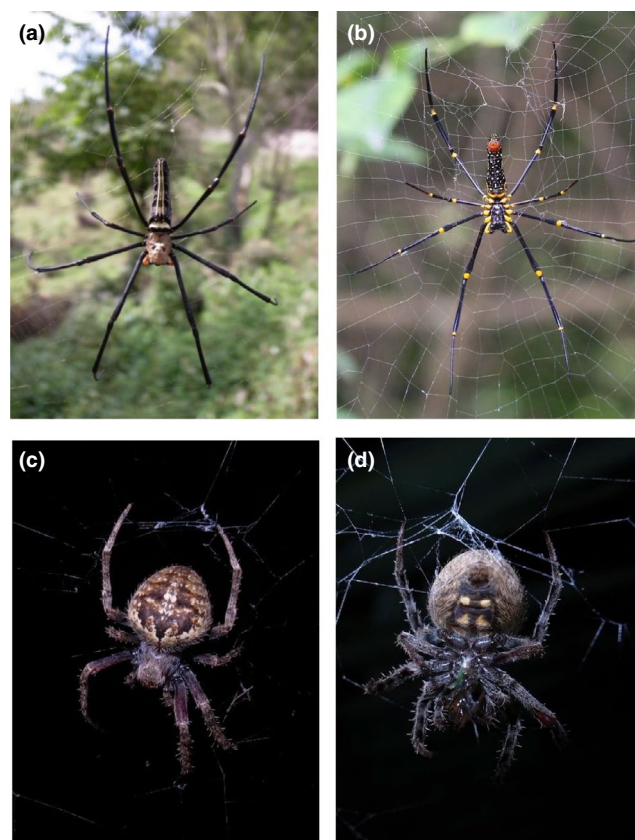
FIGURE 1 The dorsal (a) and ventral (b) views of an adult female giant wood spider *Nephila pilipes*, and the dorsal (c) and ventral (d) views of an adult female *Neoscona* cf. *punctigera*. Photo credits: (a, c and d) Chen-Pan Liao; (b) Ying-Yuan Lo

The field experiment was conducted in Huoyan Mountain (24°06′42.2″N, 121°11′51.1″E), Sanyi Township, Miaoli County, Taiwan, in July and August of 2008 and 2009. The study site was located on a trail through a secondary forest where *N. pilipes* are abundant (about 1–2 females every 10 m along the trail). We haphazardly selected webs of *N. pilipes* at the study site. From preliminary surveys, we found that most individuals of *N. pilipes* (84.48%, 116 individuals censused) built webs on understory shrubs with their dorsal side facing the dense foliage and the ventral side facing the open space. This indicates that the body colouration on the ventral side of spiders might have greater opportunities for prey luring as they are more exposed to the insect viewers. Nevertheless, the perception by predators of the ventral surfaces has been largely neglected (e.g. White & Kemp, 2016, 2017). A drab looking spider on the dorsal surface may have a conspicuous yellow mosaic ventral surface (see Figure 1c,d). There could be an evolutionary benefit to having bright/yellow mosaic patterns on the ventral rather than dorsal surfaces because the web exists as a partial barrier to the spider, presumably to protect it from being easily accessible to predators. Accordingly, our model spiders followed the colouration patterns of the ventral side of *N. pilipes* (Tso et al., 2004).

2.1.2 | Experimental treatments

Five types of spider models were constructed for the field experiment (Figure 2): First, we created standard models to mimic the natural ventral colouration of *N. pilipes* (standard treatment). Second, to test the significance of the chromatic property of the signal, we created models with blue spots rather than yellow spots on the abdomen (blue treatment). The blue and yellow had similar luminance to control for achromatic properties. Third, to evaluate whether the pattern arrangement is an essential element for prey attractiveness, we made models in which the mosaic yellow pattern fused into one single yellow patch (aggregated treatment). The area of the yellow patch in this model was the same as the total area of yellow spots in the standard model. A previous study conducted during the day found that increasing the area of bright yellow not only increased prey attraction rate but also predator attack rate, suggesting that the observed pattern reflects a trade-off between the opposing selection pressures of feeding performance

and predation risk in a diurnal foraging environment (Fan, Yang, & Tso, 2009). However, *N. pilipes* forages during both the day and night, and thus experiences very different degrees of exposure to light, raising the question of whether there is a similar trade-off during nocturnal foraging. We tested this possibility by creating entirely yellow and dark models (yellow and dark treatments). Spider webs without models (web treatment) were also monitored, and data from the web treatment were used as a control to test for the effectiveness of the standard treatment in attracting insects.

We created spider models from cardboard of different texture and cut them into a spider shape, with all eight legs extended. Yellow or blue paper spots were attached to the cardboard models with odourless transparent glue to represent the colouration of un-manipulated and manipulated ventral spots, respectively. We followed the protocol of Tso et al. (2004), to ensure the model spiders resembled real spider body colouration. Briefly, we randomly selected five points for each cardboard model, and measured the reflectance spectra using a spectrometer (S4000, Ocean Optics Inc.) connected to a 450 W Xenon arc lamp, and compared these to spectra obtained from the corresponding body surface of *N. pilipes* (Tso et al., 2004).

2.1.3 | Matching dummy and spider colours based on insect colour spaces

Preliminary surveys conducted prior to the field experiment revealed a variety of hymenopteran and dipteran insects that constitute the primary diurnal prey types of *N. pilipes* (52.34% and 24.30%, respectively), while a number of different species of moths comprised the majority (54.32%) of nocturnal prey. Therefore, four psychophysical colour spaces were applied to determine how the different models and ventral body colouration of female *N. pilipes* were likely to be perceived by insects under different light conditions. First, we computed (a) the bee colour hexagon model (Chittka, 1992). This model was originally derived from the visual physiology of the honeybee, but it is applicable to other hymenopterans given the similar spectral sensitivities across this clade (Briscoe & Chittka, 2001). Due to the uncertainty of colour perception in fly vision (Hannah, Dyer, Garcia, Dorin, & Burd, 2019),

5 cm
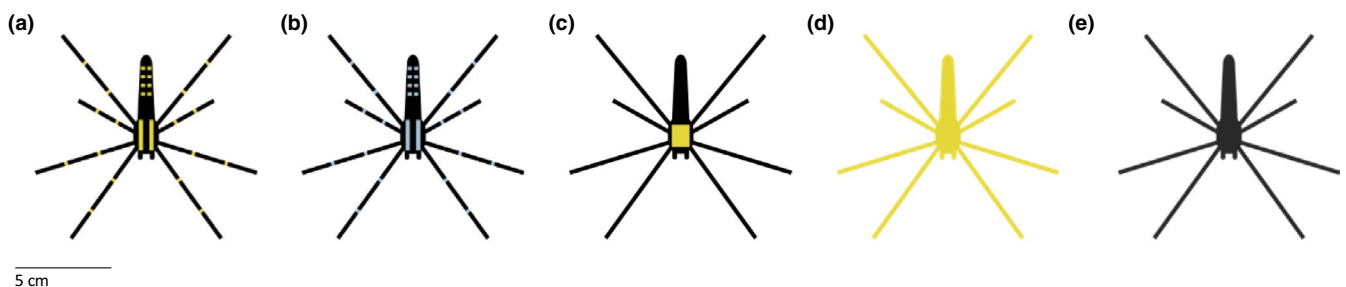
FIGURE 2 Colouration patterns of cardboard models used in the field manipulation. The shape and colour patches mimic that of the ventral side of the giant wood spider *Nephila pilipes*. (a) standard, (b) blue, (c) aggregated, (d) yellow and (e) dark

we modelled two fruit fly colour spaces: (b) fruit fly categorical model (Troje, 1993) and (c) fruit fly tetrahedral model (Endler & Mielke, 2005). Lastly, as moths represent the primary nocturnal prey type of *N. pilipes*, we used the (d) hawkmoth Maxwell triangle model (Johnsen et al., 2006), a neuroethological model developed for nocturnal hawkmoth vision, as representative of nocturnal moths, because hawkmoths are active in a similar ambient light environment. By calculating colour space coordinates using spectra of cardboard and real spider body parts with different models of colour space (see Supplemental Experimental Procedures (i) in Supporting Information for details), we assessed the resemblance between model spiders and real spiders in the visual spaces of relevant receivers. We chose yellow and black paper samples with coordinates in colour spaces that were closest to the yellow and black patches of *N. pilipes* (thereby resembling real spider bodies), and chose blue paper with the lowest achromatic contrast to the yellow patch (i.e. a similar brightness but with a different chromatic property).

2.1.4 | Extracting prey attraction data

We used video cameras to record the responses of prey and insects to the cardboard spider models, with approximately 8 hr of recordings during each period of light exposure (diurnal: 08:00 hr to 16:00 hr; nocturnal: 20:00 hr to 04:00 hr). Before recording, we removed the live spider from her web, randomly chose one type of model spider, and placed it at the central hub of the web. We measured the hub radius, web radius, and number of spirals and radii of the four cardinal directions of the webs. These variables were used to estimate the capture area of each spider web (Herberstein & Tso, 2000), thus ensuring that each model was placed on a similar sized web. Video cameras (Sony DCR-TRV series and Sony DCR-SR series) were placed 1–2 m away from the spider webs, depending on the nearby vegetation. Data used in the subsequent analyses were separately obtained from 656 hr of diurnal and 1,122 hr of nocturnal footage. Of the diurnal monitoring hours, 161 were from aggregated treatments (*n* = 25), 163 from blue treatments (*n* = 24), 177 from standard treatments (*n* = 26) and 155 from web treatments (*n* = 24). Of the nocturnal recordings, 194 were from aggregated treatments (*n* = 29), 198 from blue treatments (*n* = 29), 195 from standard treatments (*n* = 29), 177 from yellow treatments (*n* = 25), 184 from dark treatments (*n* = 27) and 174 from web treatments (*n* = 26). From the footage, we recorded attraction events, which were defined as events where either the prey flew towards or physically contacted the model spiders, or the prey were intercepted by the webs.

For each individual spider model, we calculated the prey attraction rate (number of prey items attracted per hour) by dividing the total number of attraction events by the number of monitoring hours. We include only sequences with more than 4 hr of recording time.

2.1.5 | Data analysis: Field experiment

All of the field data failed Kologorov–Smirnov tests for normality (*p* < .05): prey attraction data were skewed leftward or overdispersed owing to a high proportion of zero values. Therefore, we applied negative binomial regression models for data analyses, where prey interception count was the dependent variable, experimental manipulations (treatments) were used as a fixed independent variable, in which the standard treatment group (model spider that resembles the ventral colouration pattern of *N. pilipes*) was deliberately designated as the reference level in the models to facilitate comparisons of probabilities of different treatments, and the web capture area and the period of monitoring (in hours) were set as offset variables ($\log_e$-link). We also ran power analyses for these models and extracted the effect size (standardized mean difference, SMD). The model fitting was examined using deviance in the goodness-of-fit test. The *G*-test likelihood–ratio test was used to compare the compositions of attracted prey taxa of the spider model treatments. Student's *t* tests were used to compare the chromatic contrast values of the cardboard model spiders against corresponding spider body parts with applicable colour discrimination thresholds in the bee colour hexagon model.

2.2 | Evolutionary association between spider ventral signal and prey viewing environment

2.2.1 | Interspecific comparative approach

We sourced natural history information of web-building spiders to score (a) the degree of exposure of these orb-weavers and thus their opportunity for prey luring and (b) the ambient light condition of orb-weavers that rest on the webs. Specifically, we used phylogenetic comparative analyses to test whether there is an association between (a) the presence of either yellow or white mosaic pattern and the opportunity for prey luring and (b) the presence of either yellow or white mosaic pattern and the ambient light intensity.

2.2.2 | Species selection

A robust genus-level phylogeny of the Araneidae (derived from Dimitrov et al., 2017) with 363 species was used as an initial framework for species selection. The specific species within this genus-level phylogeny were not always identified, so we designated them as the most well-documented species within that genus, based on records in the World Spider Catalog (Platnick, 2016) and Zoological Record database in Web of Science (Reuters, 2012). For example, the genus '*Callobius*' in the original phylogeny is labelled '*Callobius* sp.', which we replaced with '*Callobius claustrarius*' as this is the most extensively documented species of this genus, according to the World Spider Catalog (Platnick, 2016) and Zoological Record database on

Web of Science (Reuters, 2012), and thus most likely to have relevant natural history descriptions.

2.2.3 | Scoring spider colour patterns

We obtained information on ventral body colouration patterns of species represented in the above phylogeny from photographs obtained from field guides (Atkinson, 2017; Huang, 2017; Huber, 2015; Lissner, 2014; Lissner & Scharff, 2017; Nentwig, Blick, Gloor, Hänggi, & Kropf, 2017; Oger, 2017; Tanikawa, 2017; Víquez & Longhorn, 2017; Whyte & Anderson, 2017) and online galleries that are maintained exclusively by arachnologists, arachnological societies, or funded by museums, and thereby minimizing any mislabelling of photographs. We focused our search to online resources that aligned with the geographical distribution of the taxa, since this is likely to improve the reliability of species identification. We included photographs of adult females only because adult males rarely build foraging webs once they become sexually mature (Savory, 1928; but see Hirscheimer & Suter, 1985). Finally, we only included photographs of living spiders, as the colours of preserved spiders typically fade.

We first categorized each species as either with or without either yellow or white body parts. Next, we distinguished between a yellow or white mosaic pattern from a single continuous yellow or white patch if any of the following criteria were met: (a) yellow or white banded legs; (b) yellow or white stripes (including bars and streaks) on the ventral side of the body or (c) mottled (flecked, stippled or spotted) patterns on the ventral side of the body (see Figure 4b for photos of representative species). For species with known polymorphisms, we obtained photographs of all known morphs, and only scored a yellow or white mosaic pattern if all of the morphs met the above criteria. Photos of representative species that were categorized as 'presence of yellow mosaic pattern' and 'presence of white mosaic pattern' are shown in Figure 4c.

2.2.4 | Natural history

For those species for which we had scored colour pattern data, we sourced information about their natural history characters using references listed on the World Spider Catalog (Platnick, 2016) and Zoological Record database on Web of Science (Reuters, 2012). The intention was to quantify the opportunity (or potential) for prey luring. For example, a species that hides within its retreat has no opportunity for prey luring because its body, no matter how colourful, is obscured by the retreat. In contrast, the body colour pattern of species that rest at the hub of the foraging web, which is located in an open habitat, is clearly exposed and thus has an opportunity to lure prey. In our first analysis, we scored for each species the opportunity for prey luring according to three criteria (macrohabitat, microhabitat and refuge, Table 1a), and deemed the species as having little or no opportunity if it scored low opportunity for any of those three criteria (see Table S1). In our second

TABLE 1 Natural history characters used in the comparative analyses to score (a) the opportunity for prey luring and (b) the ambient light condition

Natural history characters	Description	Binary value
(a) Opportunity for prey luring		
Macrohabitat	Semi-closed places, e.g. cave or buildings	Small
	Habitat is in open space, e.g. scrub, woodland	Large
Microhabitat	Concealed locations, such as crevices in rock or outer covering of tree	Small
	Proximity to accessible locations, e.g. building aerial webs distant from obstacles	Large
Refuge	Present, e.g. when the spider hides in a refuge made of silk or dried leaves	Small
	Absent, i.e. the spider rests on the web	Large
(b) Ambient light condition		
Macrohabitat	Overall dark space	Dim
	Habitat is bright, e.g. forest edges, forest gaps	Bright
Microhabitat	Dark, e.g. when the web is built in narrow crack in stones and bark, or beneath litter or logs	Dim
	The web is built away from barriers to exposure to light	Bright

analysis, we excluded species that remained in a refuge, and scored the viewing environment for these species according to two criteria (macrohabitat and microhabitat, Table 1b), and deemed the species as in a dim environment if it scored dim in either of those criteria (see Table S2). These two comparative analyses did not use temporal foraging pattern as a binary measure for the opportunity for prey luring or ambient light environment because there is seasonal variation in the temporal activity patterns of orb-weavers, which is seldom reported and lacks consistency across the literature.

2.2.5 | Phylogenetic comparative analysis

To investigate the association between the presence of yellow/white mosaic pattern and the opportunity for prey luring (Table S1), we pruned taxa with missing colour or illumination values from the phylogeny by Dimitrov et al. (2017), resulting in a sample of 79 genera with 90 species. Next, to test the association between the spider ventral signal and ambient light condition (Table S2), we used a subset of 53 genera with 63 species. Our comparative analysis followed Pagel (1994), which employs transition probabilities between character states along the phylogenetic tree as either independent of or dependent on each other, and then compares the likelihoods of these

two models to detect any correlation between two discrete traits. We used the 'fitPagel' function within the PHYTOOLS (Revell, 2012) package in R (R Core Team, 2018), which depends on R packages APE (Paradis, Claude, & Strimmer, 2004; Popescu, Huber, & Paradis, 2012) and GEIGER (Harmon, Weir, Brock, Glor, & Challenger, 2007). We used the function 'make.simmap' to first fit the continuous-time reversible Markov process for the evolution of the binary traits for each of the four different models (yellow and white mosaic colour patterns with the opportunity for prey luring and ambient light condition), and then simulated stochastic trait evolution using maximum likelihood estimation (Pagel, 1994) and the tip states on the phylogeny. The 'density-Map' function was applied to plot the phylogeny with the posterior density for the mapped characters from stochastic character mapping on the phylogeny.

3 | RESULTS

3.1 | Signal design and prey attraction

The yellow paper used for the model spider has a similar chromatic property as the yellow body parts of *N. pilipes* (see chromatic properties of dummies in Supplemental Experimental Procedures in Supporting Information; Tables S3 and S4). Thus, the colour signals of standard models resembled those of real spiders in the eyes of, presumably, other insects. Blue cardboard spider models had similar or slightly higher luminance but a significantly different chromatic property, whereas aggregated cardboard spider models resembled colour signals of real spiders except for the arrangement of the pattern. The capture area (cm^2) of webs did not differ across treatments in either ambient light environment (diurnal: Kruskal–Wallis test, χ^2 = 0.8924, *df* = 3; *p* = .8273; nocturnal: Kruskal–Wallis test, χ^2 = 6.2059, *df* = 5; *p* = .2867). The

Pearson goodness-of-fit statistics showed that the generalized linear models fitted the prey interception data (daytime: Pearson χ^2 = 103.949, *df* = 95, *p* = .249; night-time: Pearson χ^2 = 170.543, *df* = 159, *p* = .252).

The field experiment demonstrated that both the colour (yellow) and pattern (yellow and black mosaic pattern) are essential for prey luring in a high ambient light environment. Under diurnal conditions, the standard treatment resembling natural ventral colouration of *N. pilipes* attracted significantly more prey than either the blue or aggregated yellow treatments (Table 2a; Figure 3A), suggesting that chromatic properties and pattern, but not luminance, are important in luring diurnal insect prey. Under nocturnal foraging conditions, increasing the area of the yellow colour signal (yellow treatment) did not increase prey attraction (Table 2b; Figure 3B). However, yellow appears to be essential for prey attraction at night as the standard, aggregated and yellow treatments all had higher prey attraction than the blue or dark treatments. The higher prey attraction of the standard models than blue models (both day and night) indicates that the efficacy of yellow for prey attraction is not simply due to high luminance. Under both diurnal and nocturnal conditions, the model spiders resembling the ventral colour pattern of *N. pilipes* (standard treatment) attracted proportionally more Hymenoptera and Lepidoptera, compared with blue models (Figure S2; log-likelihood ratio test: Daytime: *G* = 6.5006, *df* = 2, *p* = 0.039; Night-time: *G* = 10.645, *df* = 3, *p* = 0.014). Standard models also attracted more prey insects than webs without models (web treatment; Table 2; Figure 3A,B). This indicated that the standard models were attractive to prey insects and the colour signal alone was sufficient to lure prey. The standardized mean difference of the model using data collected during daytime was more negative (Table 2a, SMD < −0.008 for all treatments) than the model with nocturnal data (Table 2b, SMD > −0.009 for all treatments), suggesting that the effect of manipulation of visual properties on prey attraction is stronger during bright ambient light conditions.

Treatment	Estimate of ß	SE	Z	p	Standardized mean difference
(a) Daytime					
Intercept	−8.550	0.241	−35.459	<.0001	—
Blue	−1.205	0.415	−2.908	.004	−0.010
Aggregated	−0.921	0.399	−2.308	.021	−0.008
Web	−3.137	0.781	−4.017	<.0001	−0.013
(b) Night-time					
Intercept	−9.137	0.257	−35.512	<.0001	—
Blue	−1.088	0.414	−2.627	.009	−0.007
Aggregated	0.197	0.365	0.541	.589	0.002
Yellow	0.352	0.369	0.955	.340	0.004
Dark	−1.064	0.442	−2.409	.016	−0.007
Web	−2.468	0.653	−3.776	.0002	−0.009

TABLE 2 Results of the negative binomial regression, showing the effect of no visual signal (web without a spider), changing chromatic property (blue), arrangement pattern (aggregated) and colour area (yellow and dark) of the standard model, which resembles the ventral colouration pattern of *Nephila pilipes* on the rate of prey attraction in the field experiments during (a) daytime and (b) night-time

Note: Standard treatment group was deliberately designated as the reference level to facilitate comparisons of probabilities of different events. The ratio between probabilities of two certain events is e^ß.

(A)

(B)
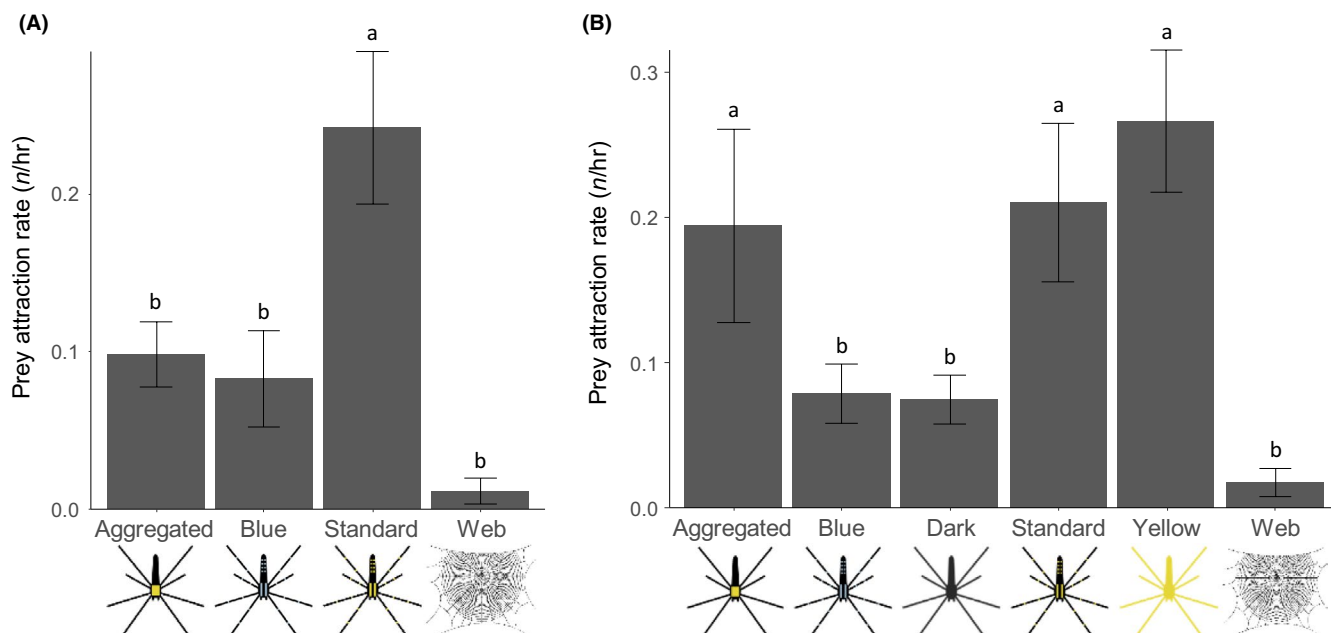
FIGURE 3 Mean (±*SE*) prey attraction rate (number of prey attracted/hour/cardboard model spider) recorded in (A) diurnal and (B) nocturnal field experiments. Letters represent comparisons of prey attraction with the standard treatment, where different letters indicate statistically significant differences

TABLE 3 Test for association between the presence of a yellow/white mosaic colour pattern and the opportunity for prey luring/occurrence in high ambient light intensity in web-building spiders. *L(I)* is the log-likelihood of the model of independent changes between characters; *L(D)* is the log-likelihood of the model of correlated changes

| Models of evolution	*L(I)*	*L(D)*	Likelihood-ratio	*p* value
Substitution rate of the opportunity for prey luring depends on the presence of yellow mosaic colour pattern and vice versa	−87.414	−81.148	12.535	.014
Substitution rate of the opportunity for prey luring depends on the presence of white mosaic colour pattern and vice versa	−104.540	−100.978	7.121	.130
Substitution rate of the ambient light intensity depends on the presence of yellow mosaic colour pattern and vice versa	−66.028	−61.151	9.758	.045
Substitution rate of ambient light intensity depends on the presence of white mosaic colour pattern and vice versa	−73.615	−70.350	6.530	.163

3.2 | Evolutionary association between spider ventral signal and prey viewing environment

Among orb-weaving spiders, there is an evolutionary association between yellow mosaic colour pattern and both the opportunity for prey luring and the ambient light intensity. A yellow mosaic colour pattern was more likely to evolve in species that have an opportunity for prey luring, and, among these species, the colour pattern was more likely to evolve in those species that forage in high ambient light conditions (Table 3, left panel of Figure 4a,b). There was

no significant association between white mosaic colour pattern and the opportunity for prey luring or foraging ambient light intensity (Table 3, right panel of Figure 4a,b).

4 | DISCUSSION

Our field experiments demonstrated that the visual luring properties of orb-weavers are shaped by the chromatic properties of the colour patches on their body. Yellow colouration is effective during both

(a)

(b)

(c)
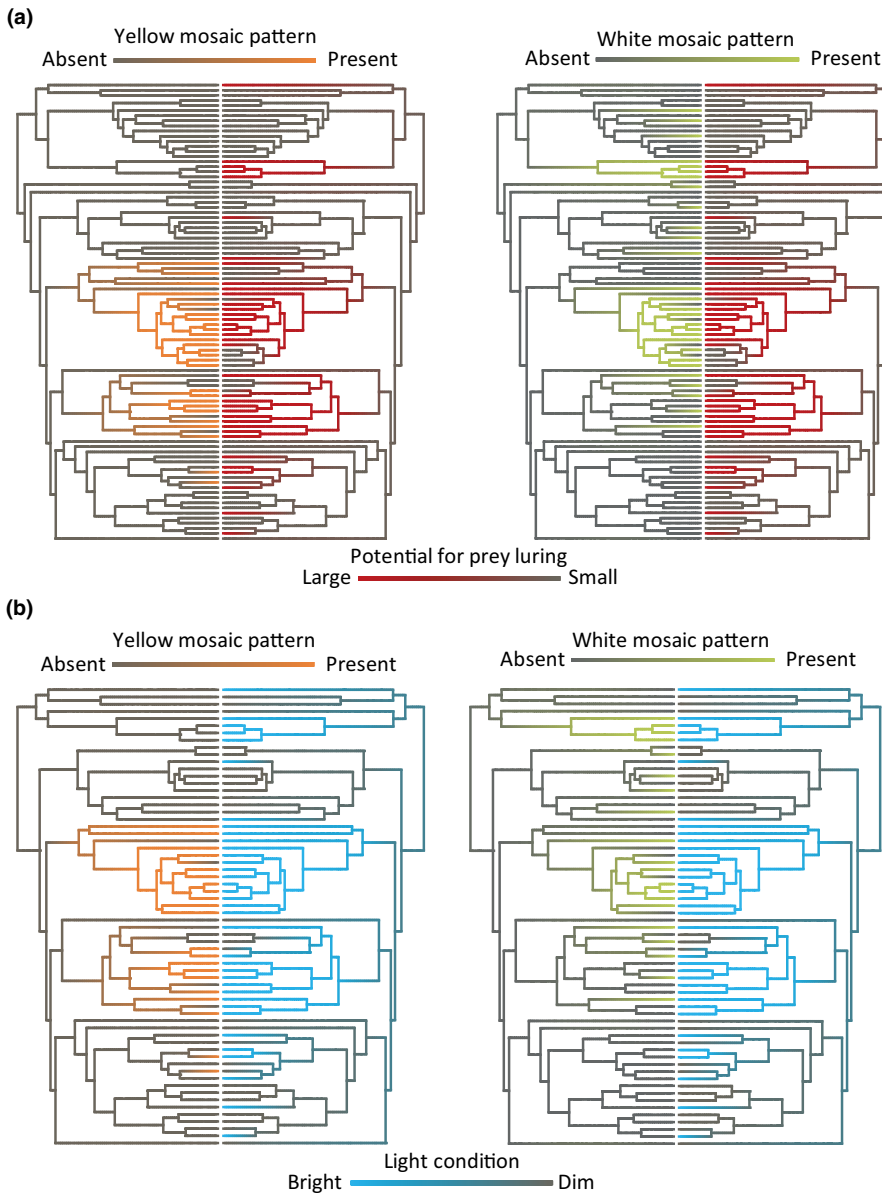
FIGURE 4 The araneid genus-level phylogeny (derived from Dimitrov et al., 2017) with colour gradient bars indicating the posterior density for each mapped character, depicting the evolution of yellow and white mosaic colour patterns with (a) the opportunity for prey luring, and (b) the occurrence of the species in high light exposure. Orange denotes the presence of yellow mosaic colour pattern (left panel), lime green denotes the presence of white mosaic colour pattern (right panel), red denotes the large opportunity for prey luring and blue denotes the bright light condition. (c) Photos of representative species which were categorized as 'presence of yellow mosaic pattern' (left; *Gasteracantha sauteri*), and 'presence of white mosaic pattern' (right; *Zosis geniculata*). Photo credits: Wen-Chun Huang

diurnal and nocturnal foraging and a mosaic of yellow and dark patterning is especially effective under bright light conditions. Surprisingly, aggregating the area of yellow in a single patch reduced prey attraction during the day, and aggregating or increasing the area of yellow had no effect at night. Furthermore, our results show that the efficacy of colouration in prey luring, even under nocturnal conditions, is strongly associated with spectral properties. Our phylogenetic comparative analysis provides evidence that yellow, but not white, mosaic patterns are associated with the foraging ambient light intensity—that is, the viewing context. Combined, our study shows that orb-weaving spiders that forage in high ambient light conditions typically evolve yellow mosaic colour patterns that are highly effective in luring prey.

Our study highlights the heuristic value of combining experimental and comparative analyses. The experimental results indicate that the yellow colour pattern of the body of *Nephila* spiders provides a foraging advantage under both bright (diurnal) and dim (nocturnal) ambient light. This result is consistent with the general association we found between yellow mosaic patterns and the opportunity for prey luring. However, in contrast to the experimental results, the comparative analysis also revealed an association between yellow mosaic patterns and ambient light condition. Nevertheless, the experimental and comparative results may not necessarily be contradictory—the experimental effect size was greater under diurnal than nocturnal conditions (Table 2), so selection may have favoured yellow colour patterns in the majority of *Nephila* because of the foraging benefits under diurnal conditions alone. Clearly, it would be useful to examine the effects of these colour patterns on the webs of spiders that are strictly nocturnal. For example, nocturnal *Neoscona* spiders attract prey with the yellow abdominal spots under dim light conditions, suggesting that the prey luring function of ventral yellow mosaic patterns might not be exclusively applicable in high ambient light environments (Chuang, Yang, & Tso, 2008).

Our results suggest that chromatic properties, specifically yellow colouration, are effective for prey luring, even under nocturnal foraging conditions. The traditional view is that colour preference only applies to the diurnal viewing environment. Notwithstanding the limitations of colour vision in dim light, multiple lines of evidence show that nocturnal animals can discriminate colours under a range of illumination intensities between 1 cd/m^2 (early twilight) and 0.0001 cd/m^2 (starlight intensity) (Kelber & Lind, 2010). Under diurnal conditions, chromatic properties of various floral parts play important roles in the signalling efficacy of flowers to pollinators (Burd, Stayton, Shrestha, & Dyer, 2014; Dyer et al., 2012), where yellow centres or yellow pollen are common attributes of flowers (Lunau, 1995, 2000). Because nectar could represent food resources for insects, the inner parts of many flowers resemble the colour of pollen, with pollinators like Hymenoptera and Diptera innately associating this visual cue with a food reward (Heuschen, Gumbert, & Lunau, 2005; Ushimaru, Watanabe, & Nakata, 2007). Additionally, recent empirical and permutation studies reveal that some nocturnal Lepidoptera also have the ability to discriminate colour under dim light conditions, and innately prefer yellow (Cutler, Bennett, Stevenson, & White, 1995; Kelber, 1997; White, Stevenson, Bennett, Cutler, & Haber, 1994). For example, yellow sticky papers or pan traps can function as better visual lures to dipteran and hymenopteran insects (Alyokhin, Messing, & Duan, 2000; Wu, Chen, & Yang, 2007). We consistently found in our field experiments that naturalistic yellow mosaic (standard) cardboard spider models lured proportionally more pollinators—Hymenoptera and Lepidoptera in daytime, and Lepidoptera in night-time, compared with blue models that had slightly higher luminance but differed substantially chromatically (Tables 2 and 3; Figure S2). Combined, these results suggest that the chromatic property of yellow, rather than its high luminance, is an essential visual element for luring pollinator insects (but see White & Kemp, 2016, 2017).

Previous studies (Edmunds, 1990; Fan et al., 2009) suggest that the area of yellow is constrained by the risk of predation by diurnally active, visually hunting predators. In the colour-luring system of orb-weavers, a larger area of yellow attracts more prey and predators during the day (Fan et al., 2009). Diurnal pollinators, such as honeybees and bumblebees, adopt achromatic vision when stimuli subtend a small visual angle and chromatic vision when a large one is subtended (Giurfa, Vorobyev, Brandt, Posner, & Menzel, 1997; Papiorek, Rohde, & Lunau, 2013). It is possible that entire yellow models subtended a larger angle with a large-sized yellow area and hence could be perceived chromatically from a longer distance and became more attractive to diurnal flying insects (both prey and predators). On the other hand, nocturnal pollinators, such as hawkmoths, prefer inspecting flowers with heterogeneously coloured marks compared with homogeneously coloured ones (Goyret, 2010). This is consistent with our results showing that an increased area of yellow does not increase nocturnal prey attraction. Therefore, unlike diurnal spiders, the yellow mosaic pattern on nocturnal spiders does not represent a compromise between prey attraction and predator avoidance. The effect of both colour and pattern on risk from predators or parasitoids warrants further investigation.

Both colour and pattern are important in luring prey: we found that compared with standard cardboard spider models, the diurnal prey attraction rate was significantly lower for the aggregated treatment, in which the yellow component was a single patch with the same total area. This supports the view that the pattern preference of diurnal prey might be one major driving force for the body colouration of orb-weavers. Studies of diurnal pollinators suggest that a contrasting pattern may be more important in mediating insect attraction than the spectral properties; for example, the elimination of pattern led to a decrease in insect attraction to flowers (Koski & Ashman, 2014). Furthermore, bright and dark colours as well as their combined patterns convey different messages for different species. The conventional view is that high contrast yellow and dark patterns are more likely to be aposematic to advertise the prey's unprofitability to predators (Stevens & Ruxton, 2012), or prevent recognition by disrupting the outline of the body or salient features (Stevens, Winney, Cantor, & Graham, 2009). However, as the resolution of every vision system is limited, a conspicuous colour pattern can be aposematic or disruptive at a short distance, whereas it can merge to appear uniform and cryptic at a long distance, especially for predators (Bohlin, Tullberg, & Merilaita, 2008; Endler, 1978; Marshall, 2000; Tullberg, Merilaita,

& Wiklund, 2005). This distance-dependent effect may not only exist in the context of defensive colouration but also in the colour-luring system of orb-weavers. In almost 1,800 hr of video recording, we only noted three events where wasps (potential predators of orb-weavers) hovered around our cardboard model spiders. These events were all recorded within one treatment group—aggregated models, where the yellow component was merged into one patch. Natural selection is expected to optimize signal design to elicit the maximum possible response from 'intended' receivers, like prey, but avoid detection by 'non-intended' receivers like predators (Endler, 1992). One possibility is that the yellow mosaic colouration pattern of diurnally foraging orb-weaving spiders can simultaneously attract prey and reduce predator detection as a result of distance dependence.

Many web-building spiders in numerous genera have various yellow markings (Platnick, 2016), and this body colouration functions as a visual lure in at least three families (Araneidae, Tetragnathidae and Nephilidae; see White & Kemp, 2015). Our study provides evidence that colour-luring traits are shaped by selection to maximize diurnal and nocturnal prey attractiveness and suggests a general evolutionary association between this trait and ambient light conditions. We conclude that the effectiveness of colour luring might be one major driver of the convergent possession of yellow body colouration in phylogenetically divergent orb-weavers. More broadly, our study highlights that prey colour preferences and signal efficacy play a significant role in the evolution of visually mediated prey-luring systems.

AUTHORS' CONTRIBUTIONS

P.P., S.-W.C., and I.-M.T. conceived the field experiment, while P.P., D.S.-F., E.J.T and M.A.E. devised the comparative analyses. P.P. and S.-W.C. performed the statistical analysis and wrote second language abstract. P.P., S.-W.C., and G.-L.K. designed and conducted field experiment. E.J.T. and S.J.B. helped draft and revise the manuscript for important intellectual content. P.P., D.S.-F., I.-M.T., and M.A.E. took the lead in writing the manuscript, with contributions from all authors. All authors gave final approval for publication.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Peng P, Stuart-Fox D, Chen S-W, et al. High contrast yellow mosaic patterns are prey attractants for orb-weaving spiders. *Funct Ecol*. 2020;34:853–864. https://doi.org/10.1111/1365-2435.13532