



## Sheep in wolf's clothing: multicomponent traits enhance the success of mimicry in spider-mimicking moths



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Predator mimicry occurs when prey resemble their predator to gain protection. We explored the relative importance of the morphological and locomotor signals that spider-mimicking moths use to deceive their jumping spider predators. Two hypotheses explain why animals use multicomponent signals for communication: the 'back-up signal' hypothesis which suggests that multiple traits increase accuracy, and the 'multiple message' hypothesis which suggests that the different traits serve different purposes or target different signal receivers. We conducted predation tests using the putative spider-mimicking moths *Brenthia coronigera* (visual and locomotor mimicry) and *Choreutis hyligenes* (only locomotor mimicry) and a control moth species displaying no mimicry. We found that *B. coronigera* used multicomponent signals, i.e. pattern, display posture and jumping behaviour, to deceive its jumping spider predators, and thus experienced lower predation rates and more time for escaping. Spiders suffered a decreased predation rate when they encountered *B. coronigera*, relative to the other two moth species. Spiders displayed leg-waving behaviour (which is used in courtship and territorial display) to both live and lure *B. coronigera*, suggesting that the spiders considered the moths to be another jumping spider. When the eyespots of *B. coronigera* were erased, the predation rate increased. In addition, the latency of first attacks was significantly longer in live *B. coronigera* moths than in lures fixed in the display posture. This suggests that the eyespots, the 'peacock-like' display position and the jumping movement all add to the similarity with jumping spiders. Our results support the 'back-up signal' hypothesis: that multiple signals can deceive the predators better. Our experimental paradigm enabled us to explore the recognition ability of predators, and gave insight into the ways evolution shapes the mimicry system.

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Animals often misinform others to receive benefit (Mokkonen & Lindstedt, 2016). Mimicry, in which one organism resembles another, is one of the most intriguing examples of deception (Chittka & Osorio, 2007; Ruxton, Sherratt, & Speed, 2004). In many cases of mimicry, evolution is expected to shape both the morphology and behaviour of the prey via predation pressure. Although the integration of appearance and behaviour in Batesian mimicry has been described in the classic paper by Bates (1862), researchers have mainly focused on morphological similarities between organisms (Ruxton, Sherratt, et al., 2004; Ruxton, Speed, &

Sherratt, 2004). However, locomotor mimicry may not be rare, and it might be especially important for mimics that do not perfectly resemble the model visually (Norman, Finn, & Tregenza, 2001). Accordingly, there are interesting cases of behavioural (combined with morphological) imitation in the more recent literature, e.g. ant mimicry by diverse animals (McIver & Stonedahl, 1993), Müllerian mimic butterflies (Srygley, 1994), bee-mimicking flies (Golding & Edmunds, 2000) and octopuses that can mimic diverse animals depending on the situation (Norman et al., 2001).

Multicomponent warning signals may be selected when the signals are equally salient for prey discrimination or when different predators use different traits for recognizing the prey (Kikuchi, Mappes, Sherratt, & Valkonen, 2016). Therefore, multiple displays in animal communication can arise because multicomponent traits increase signalling accuracy (the 'back-up signal' hypothesis) or because multiple cues provide information to different groups of signal receivers (the 'multiple message' hypothesis; Johnstone,

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1996). In this paper, we explore how animals use multicomponent signals for deceiving predators, using a special type of mimicry system, known as predator mimicry (Zaret, 1977) or Batesian–Poultonian mimicry (Pasteur, 1982), where the prey resembles its predator to gain protection. This mimicry can be so successful that predators engage in courtship or territorial displays to their potential prey, showing that they misidentify the mimics as conspecifics (Greene, Orsak, & Whitman, 1987; Mather & Roitberg, 1987; Rota & Wagner, 2006). In contrast to other mimicry systems, prior experience with the prey model for predators is not required.

Predator mimicry has attracted relatively little attention so far. The studies on the wasp-mimicking locust *Scaphura* (Poulton, 1913), *Cichla*-mimicking *Crenicichla* fish (Zaret, 1977) and caterpillars chemically mimicking ants (Akino, Knapp, Thomas, & Elmes, 1999) did not include behavioural tests. The first explored cases were the spider-mimicking tephritid flies and moths (Eisner, 1985; Greene et al., 1987; Mather & Roitberg, 1987; Rota & Wagner, 2006). The flies were shown to mimic their jumping spider predator, although the results on the relative importance of the stripy wing patterns (thought to mimic spider legs) and wing-flicking displays were controversial (Greene et al., 1987; Hasson, 1995; Rao & Díaz-Fleischer, 2012).

Here, we focused on two putative jumping spider mimicking moths (*Brenthia coronigera* and *Choreutis hyligenes*; Fig. 1a, b), both belonging to the family Choreutidae. Both *B. coronigera* and *C. hyligenes* are diurnal and show jumping behaviour when moving on vegetation. In addition, *B. coronigera* shows a specific ‘peacock-like display’ during their active time, raising the forewings and twisting the hindwings to display the eyespots and stripes (which to a human eye look like spider legs), supposedly to mimic their jumping spider predators (Fig. 1a; Aiello & Becker, 2004). We contrasted these two species with the moth *Coryra cephalonica*, which does not have eyespots and does not show jumping behaviour. *Coryra cephalonica* deviates from the common pattern of

*Brenthia* or other putative jumping spider-mimicking insects, and therefore provides a useful control.

However, while some of these moths resemble spiders to human observers, both in appearance and behaviour, several questions remain open. For example, are jumping spiders indeed the intended receivers of these moth displays? Do the displays successfully deter the spiders? The only way to test directly whether the moths’ displays work efficiently for evading jumping spiders is to explore the spiders’ responses in controlled laboratory settings, and to measure the survival rates of moths under precisely defined predation risk from spiders. In experiment 1, we compared the defence capacity of the three moth species against several jumping spider species. In experiment 2, we tested the efficacy of different components of defensive pattern and behaviour in the moth *B. coronigera*.

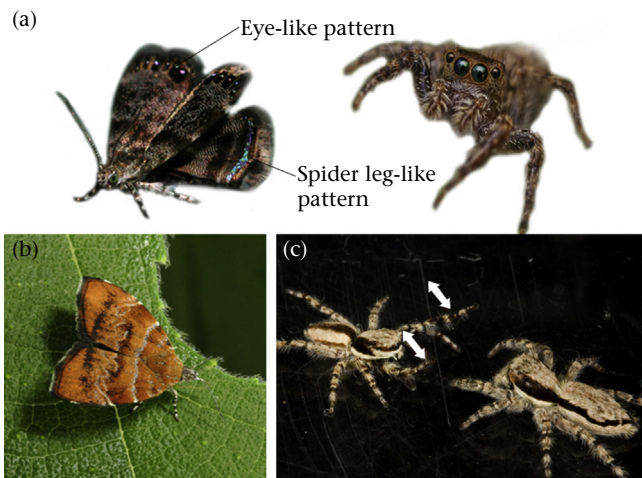
## METHODS

### Study Animals

Larvae of the two putative mimetic moth species (*B. coronigera* and *C. hyligenes*) were collected from their host plants from different localities in Kaohsiung, Taiwan and raised in the laboratory. We chose a dull-coloured moth, *C. cephalonica*, which does not have spider-like displays or behaviour as the control group. Eggs of *C. cephalonica* moths were obtained from the Miaoli District Agricultural Research and Extension Station, Taiwan, and raised in the laboratory on peeled raw rice. Since spiders eat all three moth species without suffering adverse consequences (M-Y Wang, personal observation), we assume the moths do not have any secondary defences. Four jumping spider species, which were both abundant and sympatric with the mimicking moths, were collected from the same habitat as the moths (80 individuals of *Plexippus paykulli*, mean  $\pm$  SE body length =  $7.7 \pm 0.1$  mm, 50 *Hasarius adansoni*, body length =  $7.3 \pm 0.1$  mm, 50 *Menemerus fulvus*, body length =  $6.9 \pm 0.1$  mm, and 50 *Psecus strupifer*, body length =  $7.4 \pm 0.1$  mm, equal numbers of male and female spiders). Spiders were kept in  $5 \times 5 \times 5$  cm plastic containers individually and fed with fruit flies and second to fourth instar cricket larvae every 3 days. Experiments were performed on the spiders’ feeding day before food was given. Spiders were kept under a 12:12 h light:dark cycle at a controlled  $25^\circ\text{C}$  and were kept for more than 1 week in the laboratory before testing. Only mature spiders were used, and all spiders were only used in a single trial. When a moth was not attacked by a spider and moved normally, it was kept to be used in subsequent trials. A total of 56 *B. coronigera* moths (mean  $\pm$  SE body length =  $4.3 \pm 0.04$  mm), 30 *C. hyligenes* moths (body length =  $4.2 \pm 0.03$  mm) and 33 *C. cephalonica* moths (body length =  $7.6 \pm 0.2$  mm) were used. The experiments were approved by the Animal Care and Use Committee of the National Sun Yat-sen University.

### Experimental Apparatus

All experiments were conducted in a  $14 \times 7.5$  cm and 8 cm high plastic container with a nontransparent divider across the middle. The animals were habituated in the opposite sides of the container for 10 min before testing. Experiments started with the removal of the barrier and continued for 30 min or until the spider ate the moth. The time until the first attack, the time to the moth’s death and the duration of the spider’s leg-raising behaviour (Fig. 1c) were recorded. This leg-raising display is often seen in territorial and courtship behaviour both between conspecific individuals and between different species, but not between spiders and their prey (Harland, Jackson, & Macnab, 1999; Jackson, 1982), and thus it



**Figure 1.** (a) Putative spider mimicry of the moth *Brenthia coronigera*, which may be mimicking jumping spiders with its appearance, display posture and locomotion. The photo shows the ‘peacock-like display’ of *B. coronigera* and the spider-like components are labelled. The moth raises the forewings at a  $45^\circ$  angle and twists the hindwings to display the eyespots and stripes (which resemble a spider leg to a human observer). The ventral surface of the hindwing is visible. Eyespots and stripes occur in both the dorsal and ventral parts of the moth’s wings, and during display, the mimetic patterns are visible from both the front and the back of the moth. The moth also performs a jerky jumping behaviour when moving. (b) The putative locomotor-mimicking moth *Choreutis hyligenes*. This moth also performs the short jumping movement, but does not have eyespots or a display posture. (c) The courtship behaviour of the jumping spider *Menemerus fulvus*. The male (left) raises the first pair of legs (white arrows) to the female (right). The display is also used in male–male competition.

indicates successful deception. Experiments were filmed with a JVC GZ-MC200U video camera and performed from April to October 2009–2011. Experiments 1 and 2 were interspersed randomly.

### Experiment 1

We tested the defence capacity of two putative spider-mimicking moths and a dull-coloured nondisplaying control moth (Table 1). Jumping spiders (10 individuals per species per group, i.e. 40 spiders for each moth species and in total 120 spiders) were divided randomly into three moth treatment groups. Survival rate, time to death and the durations of the spiders' leg-raising behaviour were recorded.

### Experiment 2

Here we aimed to separate the mimetic effects of appearance, display posture and jumping behaviour in *B. coronigera* moths (Table 2). Jumping spiders (10 individuals per species per group, in total 40 spiders for each experimental group) were divided randomly into two groups: (1) *B. coronigera* specimens frozen in a display position and (2) *B. coronigera* specimens frozen in a neutral posture. Frozen specimens were made by putting live moths presenting a 'peacock-like' display into a  $-20^{\circ}\text{C}$  freezer for 15 min. The specimens maintained the display behaviour after freezing. The nondisplaying specimens were made from displaying specimens by changing the wing directions with forceps. We tied cotton strings to specimens and moved them slightly every minute during the tests to ensure that the spiders could detect them. To test the effect of eyespots, 30 *P. paykulli* spiders were assigned randomly to two groups: (1) live *B. coronigera* moths whose eyespots had been painted over and (2) live *B. coronigera* moths whose wings had been painted at different random locations as a control. We put the live moths in a  $-4^{\circ}\text{C}$  freezer for 30 s to immobilize them, and removed the scales of the eyespots with small watercolour brushes. The moths could move and fly normally after the manipulation. Time to the first attack and the durations of the spiders' leg-raising behaviour were recorded.

### Data Analysis

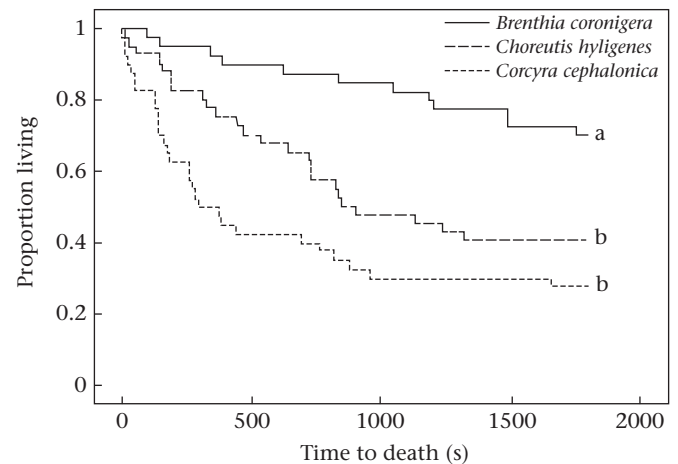
In experiment 1, we used the time to death to estimate the probability of survival past given time points, and compared the resulting survival curves among the three moth species using the Kaplan–Meier model of survival regression analysis. Since the

prepared specimens could not be killed by the spiders, we used the time to the first attack in experiment 2 to calculate 'attack curves'. We compared these, as well as the survival curves of eyespot-painted moths and controls, with a Kaplan–Meier model survival regression analysis. Additional pairwise comparisons were made using the logrank test. We used Pearson's chi-square test followed by post hoc tests (García-Pérez & Nunez-Anton, 2003) to compare the number of spiders that performed leg-raising behaviour in the different groups. All analyses were performed in SPSS 22.0 (IBM SPSS Statistics; IBM Corporation, Somers, NY, U.S.A.).

## RESULTS

### Experiment 1: Only *B. coronigera* Mimics Jumping Spiders

The survival curves of the three moth species were statistically different (Kaplan–Meier:  $\chi^2_1 = 20.80$ ,  $P < 0.001$ ; Fig. 2), and the survival curve of *B. coronigera* was significantly different from those of the other two moths (*C. hyligenes*: logrank:  $\chi^2 = 8.92$ ,  $P = 0.003$ ; *C. cephalonica*:  $\chi^2 = 19.98$ ,  $P < 0.001$ ). All *B. coronigera* moths presented the 'peacock-like display' throughout the experiment and jumped when moving, irrespective of whether spiders were present. The moth *C. hyligenes* had a slightly higher chance of survival than the control moth *C. cephalonica*; however, the difference



**Figure 2.** Kaplan–Meier survival curves for the three moth species. Different letters indicate curves that are statistically different.

**Table 1**  
Moth groups in experiment 1

Moth	Putative mimicry	No. eaten in 30 min	Mean $\pm$ SE time to death (s)	No. of spiders displaying leg-raising behaviour
<i>Brenthia coronigera</i> (N=40)	Appearance, display & locomotor	12	883.1 $\pm$ 162.4 (N=12)	9
<i>Choreutis hyligenes</i> (N=40)	Locomotor	24	548.8 $\pm$ 79.3 (N=24)	0
<i>Corcyra cephalonica</i> (N=40)	None	29	416.0 $\pm$ 106.9 (N=29)	0

**Table 2**  
Moth groups in experiment 2

Moth	Putative mimicry	% Moths attacked	Mean $\pm$ SE attack latency (s)	No. of spider displaying leg-raising behaviour
<i>Brenthia coronigera</i> (N=40)	Appearance, display & locomotor	30	883.1 $\pm$ 162.4 (N=28)	9
<i>B. coronigera</i> specimen with display posture (N=40)	Appearance & display	65	773.1 $\pm$ 110.1 (N=26)	1
<i>B. coronigera</i> specimen with nondisplay posture (N=40)	Appearance	60	390.5 $\pm$ 71.4 (N=24)	0
<i>B. coronigera</i> eyespots painted (N=15)	Display & locomotor	80	244.2 $\pm$ 67.3 (N=12)	2
<i>B. coronigera</i> painted control (N=15)	Appearance, display & locomotor	47	529.3 $\pm$ 76.3 (N=4)	3

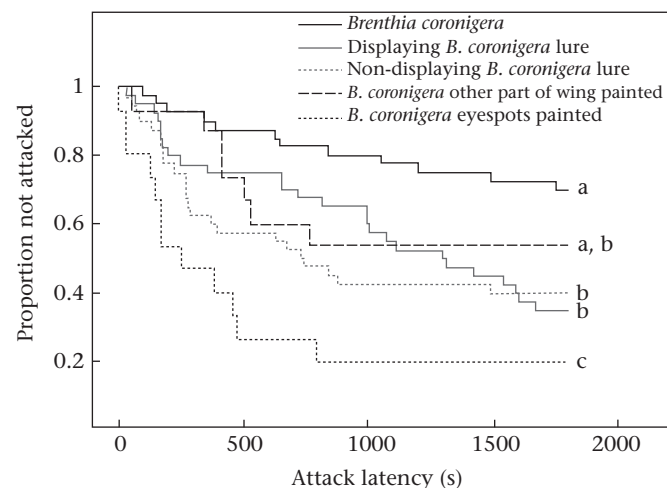


between the survival curves was not significant (logrank:  $\chi^2 = 3.41$ ,  $P = 0.065$ ; Fig. 2). The species of the spider did not have an effect on the survival curves in any of the groups (Kaplan–Meier: *B. coronigera*:  $\chi^2_3 = 6.18$ ,  $P = 0.10$ ; *C. hyligenes*:  $\chi^2_3 = 0.98$ ,  $P = 0.81$ ; *C. cephalonica*:  $\chi^2_3 = 0.75$ ,  $P = 0.86$ ).

Significantly more spiders performed leg-raising behaviour to *B. coronigera* than to the other moths (Pearson's chi-square test:  $\chi^2_2 = 19.46$ ,  $P < 0.0001$ ; Table 1). Spiders only raised or waved their first pair of legs to *B. coronigera* moths, i.e. the moth species that combines spider-like visual signalling with jumping behaviour (Table 1, mean + SE latency of leg-raising behaviour =  $20.6 + 8.6$  s), and five of 40 spiders fled from the moth, indicating that the spiders may have mistaken the moth for another spider. In the spider *P. paykulli*, both sexes waved to the mimetic moths, whereas in the other spider species, only males performed display behaviour. On two occasions, the spiders displayed to the back side of the moth, showing that both the front and back patterns may be effective for deceiving the spider.

#### Experiment 2: All Signal Components Contribute to the Mimicking Effect

The attack curves were statistically different between the five treatment groups (Kaplan–Meier:  $\chi^2_1 = 21.85$ ,  $P < 0.001$ ; Fig. 3). The attack curve for the moth *B. coronigera* was significantly different from the other groups (logrank, compared with displayed lure:  $\chi^2 = 9.30$ ,  $P = 0.002$ ; nondisplayed lure:  $\chi^2 = 9.01$ ,  $P = 0.003$ ; live *B. coronigera* moths with eyespots painted over:  $\chi^2 = 20.51$ ,  $P < 0.001$ ; Fig. 3), meaning that the loss of any component of the mimicry led to reduced survival chances for the moth. The attack curve of the lure *B. coronigera* with display posture was significantly different from the dull coloured nondisplaying *C. cephalonica* moths ( $\chi^2 = 3.85$ ,  $P = 0.05$ ) and the *B. coronigera* moths with their eyespots painted over ( $\chi^2 = 5.67$ ,  $P = 0.02$ ), but not from nondisplaying lure *B. coronigera* ( $\chi^2 = 0.04$ ,  $P = 0.84$ ). When the eyespots of live *B. coronigera* were painted over, the survival curve differed significantly from those of the moths with other parts of the wing painted (Kaplan–Meier:  $\chi^2_1 = 11.78$ ,  $P = 0.001$ ). However, the number of spiders that performed leg-raising behaviour towards eyespot-painted moths was not significantly different from those displaying to live *B. coronigera* (Pearson's chi-square test:  $\chi^2_1 = 0.57$ ,  $P = 0.45$ ; Table 2), which may indicate that some spiders were still deceived



**Figure 3.** Kaplan–Meier survival curves for the spider attacks in five experimental groups. Different letters indicate curves that are statistically different.

by the moths lacking their eyespots. Live *B. coronigera* moths with other parts of the wing painted over had the same survival chances as the nonmanipulated individuals ( $\chi^2 = 0.04$ ,  $P = 0.84$ ; Fig. 3); this indicates that the manipulation itself did not have a significant effect on the moths.

## DISCUSSION

Patterns of insects that appear to mimic jumping spiders, consisting of multiple eyespots and spider leg-like stripes exist in distinct taxa. In addition to those investigated here, these include several Fulgoroidea (planthoppers) species such as *Caliscelis bonellii* (O'Brien, 1967) and nymphs of *Amycle* sp. (Zolnerowich, 1992), Derbidae (Floren & Otto, 2001) and several Lepidopteran species in the Crambidae (grass moths; Munroe, 1991), Choreutidae (metal-mark moths; Aiello & Becker, 2004), Cosmopterigidae, Gelechiidae (twirler moths), Glyphipterigidae (sedge moths), Oecophoridae and Tortricidae (leafroller moths) (Rota & Wagner, 2006), Heliodinidae (sun moths), Immidae and Micropterigidae (M-Y Wang & S-H Yen, personal observation). However, in few of these has the effect on spider behaviour been tested, nor has the efficacy of various components (morphological and behavioural) on survival of prey been thoroughly quantified.

Here we found that jumping spiders preyed less on *B. coronigera* moths that mimicked both the appearance and the locomotion of the spider and displayed the eyespot pattern in a special posture. The putative locomotor-mimicking moth, *C. hyligenes* and the nonmimicking control moth did not differ in their survival chances. Moreover, the spiders displayed courtship/territorial behaviour towards *B. coronigera*. Since these displays are used for communication between and within jumping spider species (Elias, Land, Mason, & Hoy, 2006; Jackson, 1978, 1982; Lim & Li, 2004), but never to animals they identify as their prey (Harland et al., 1999), we suggest that they may misidentify the moths as jumping spiders. Our experiments, which aimed at disentangling the mimetic effects of appearance (eyespots), display posture and locomotion in *B. coronigera* moths, showed that the loss of any component reduces (but does not nullify) the chances of successful mimicry. In particular, eyespots are essential for mimicking jumping spiders. Locomotion mimicry alone resulted in poor protection from predation, but combined with appearance increased the survival rate. Our results therefore support the 'back-up signal' hypothesis, i.e. that multicomponent signals combine to produce efficient mimicry. The relative importance of the individual components depends on predator perception and cognition (Chittka & Osorio, 2007; Cuthill & Bennett, 1993; Gamberale-Stille, Balogh, Tullberg, & Leimar, 2012) and the saliency of the traits (Kazemi, Gamberale-Stille, Tullberg, & Leimar, 2014; Stevens & Ruxton, 2014).

The spiders' leg-raising display is used in both intraspecific courtship communication and inter- and intraspecific territorial displays. It is unlikely that the moths mimic any particular species or sex of spider; instead, they appear to mimic a generalized jumping spider image. Since the diversity of jumping spiders is high, it may be inefficient to mimic a certain species; instead, the model of mimetic moths may be a wide range of general attributes of jumping spiders, such as eyespots, leg-like stripes on wings or the jumping movement. The general resemblance to multiple models and the different sensory and perceptive ability of multiple predators may result in relatively inaccurate, but still efficient, mimicry (Chittka & Osorio, 2007; Dittrich, Gilbert, Green, McGregor, & Grewcock, 1993; Edmunds, 2000; Howse & Allen, 1994).

Male jumping spiders perform leg-waving displays more often than females (Jackson, 1982), and our result is consistent with this in that it was mostly the males that displayed to the mimetic moth.

During both territorial and courtship contests, jumping spiders often spend extensive time signalling back and forth between individuals (Jackson, 1982), and thus moths fooling spiders into engaging in such exchanges may benefit from an increased chance of escaping. In the case of territorial contests between spiders, attacks rarely occur and most contacts end with one individual fleeing from its rival (Jackson, 1982). Still, cannibalism occasionally happens (Jackson & Pollard, 1997), which might explain why eyespots of the moth appear on the top edge of the forewings: they might make the moth look like a bigger spider. In this view, spiders might prefer to err on the safe side: the cost of missing one meal may not be very high for the spider, but mistakenly attacking a (bigger) spider might well be (Mather & Roitberg, 1987).

Even when the spider ate the mimetic moth, the time until the first attack was longer than in nonmimetic groups. This suggests that the aim of the mimicry may not necessarily be limited to scaring off the predator (the intimidation hypothesis; Martin, 2005), but to strive for a longer time in which to escape (the 'satyric mimicry' hypothesis; Chittka & Osorio, 2007; Howse & Allen, 1994). Confusing the spider delays the attack, and the moths can also detect the spiders more easily in their courtship/territorial display position. Our experiments were carried out in a closed container, but in a natural environment the moths can simply fly away, and so their survival rates are expected to be even higher than measured here.

In theory, it is also possible that the spider-like displays might deter other predators (like ants). Jumping spiders have excellent jumping ability and can be difficult to catch as a prey, so the mimetic moths may benefit by resembling them (evasive mimicry, Ruxton, Speed et al., 2004). Alternatively, the eyespot-like displays might attract bites from avian predators to the wings rather than the head (Stevens & Ruxton, 2014), or indeed startle a bird (Martin, 2005), although the moths (and their wing displays) are likely to be too small for either signalling strategy to be efficient with avian predators: their entire wing span is less than 1 cm. Jumping spiders are indeed probably the most important predators of these moths, since they occur in very high densities in the moths' habitat (>10 per square metre; Mason, Jennings, Paul, & Wickman, 1997; M.-Y. Wang, personal observations). Jumping spiders have good spatial acuity (Harland & Jackson, 2000) and colour vision (Nakamura & Yamashita, 2000), which may trigger the evolution of colour pattern in their prey species.

While we cannot exclude the possibility that spider-like displays of insects might in some cases be directed at nonspider predators, we have shown here clear effects of the moths' displays on the responses of jumping spider predators, and a corresponding effect on the survival of the moth under predation pressure from jumping spiders. Further comparative work may elucidate the evolutionary pathways by which some species of insects generate behavioural and morphological traits that mimic their own predators. A fascinating but unexplored possibility is that some insect species with such patterns, which originally evolved in a predation avoidance context, might subsequently come to use them in intraspecific signalling (Spangler, 1988).

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