

## 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,

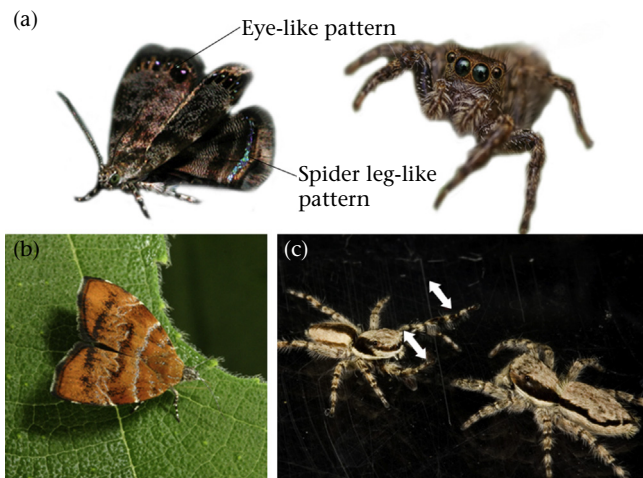
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1996). In this paper, we explore how animals use multicomponent signals for deceiving predators, using a special type of mimicry system, known as predator mimicry (Zaret, 1977) or Batesian–Poultonian mimicry (Pasteur, 1982), where the prey resembles 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



**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° 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.

*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 *Ptocasius 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 °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

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