



A trap and a lure: dual function of a nocturnal animal construction



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Animals that use deceptive visual signals to attract prey often employ colour mimicry or bioluminescence but less commonly self-excreted lures. The conspicuous web decorations and silks of some web-building spiders have been shown to visually lure prey in the daytime. However, it remains unknown whether spider webs can also lure prey at night with these self-produced silks. In this study, we tested this hypothesis by manipulating the coloration of the webs of *Psechrus clavis* and the presence of the web dwellers. We monitored the foraging performance of four treatment groups (spider present, normal web; spider present, blackened web; spider absent, normal web; spider absent, blackened web) and measured the reflectance spectra of spider body parts and web silks. We found that both spider body colour and web silk can lure insect prey at night. Lepidopteran insects comprised the majority of attracted prey. This study is the first to empirically demonstrate that animals can use self-produced substances to visually lure prey in a nocturnal environment and improve foraging success.

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Visual communication is crucial in the lives of many animals, for purposes such as predation, pollination and mating (Goodenough, McGuire, & Jakob, 2009). It is deceptive when a signal from a sender fools or tricks a receiver to the benefit of the sender. For instance, pollinating insects are often attracted by the ultraviolet (UV), blue or green reflection patterns of carnivorous pitcher plants (Joel, Juniper, & Dafni, 1985; Moran, Booth, & Charles, 1999). Certain orchids use visual mimicry to enhance pollination by producing flowers that mimic the appearance of female insects to attract males or mimic the floral shape and colour of certain nectar-rewarding orchids (Gaskett, 2011; Nilsson, 1992; Nilsson, 1983; Roy & Widmer, 1999). In some nuptial gift-presenting species, males use fake gifts to gain mating access to females (Vahed, 1998). Thus, an arms race in visual luring and signal recognition has alternately developed in plants and pollinators as well as predators and prey.

Silk decorations (e.g. stabilimentum) are applied to webs by many species of orb web spiders to attract prey (Elgar, Allan, & Evans, 1996; Li, Lim, Seah, & Tay, 2004; Tso, 1996, 1998; Watanabe, 1999; White & Kemp, 2015). The capture silk of some species has also been reported to lure prey (Craig & Bernard, 1990).

However, most studies on prey attraction have only focused on diurnal spider species. Nocturnal species, in contrast, have been understudied with regard to potential prey-luring abilities stemming from their body coloration, web decorations or web capture silks.

Prey luring in darkness has been mainly reported in bioluminescent organisms, such as the anglerfish, *Melanocetus johnsonii*, which produces bright luminescent signals to attract prey (Widder, 2010; Young, 1983). Interestingly, however, some spider species are capable of attracting prey at night. For instance, the orb web species *Neoscona punctigera*, *Nephila pilipes* and *Leucauge magnifica* can lure nocturnal insects through their conspicuous ventral and dorsal stripes or spots (Blamires et al., 2012; Fan, Yang, & Tso, 2009; Tso, Huang, & Liao, 2007), and nocturnal wandering species *Heteropoda venatoria* and *Dolomedes raptor* have also been reported to lure prey at night by their conspicuous body coloration (Tso, Zhang, Tan, Peng, & Blamires, 2016; Zhang et al., 2015). Nevertheless, it is unknown whether spider webs can lure prey at night, although evidence has shown that the webs produced by some primitive web weavers can reflect UV light to attract flies in the daytime (Craig & Bernard, 1990).

The lace-sheet-weaver *Psechrus clavis* (Psechridae) builds extensive, horizontally oriented sheet webs in shady habitats near the ground (Bayer, 2012; Fig. 1). The web is composed of whitish cribellate silks that are irregularly spaced and visually conspicuous

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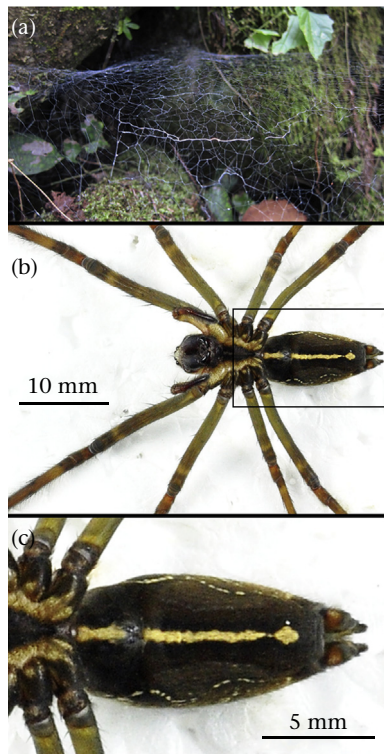


Figure 1. (a) Web of *Psecurus clavis* and (b, c) ventral side of an adult female.

against the background (Bayer, 2012). We hypothesized that the conspicuously whitish web silks act as a prey lure at night. To test this hypothesis, we manipulated the colour of the web and controlled for the presence of the inhabiting spider. We then recorded insects attracted in the field at night using infrared video cameras.

METHODS

Study Site and Spider

We conducted the field experiments in a forest surrounding the Low-Altitude Research Station, Taiwan Endemic Species Research Institute (TESRI), Wu-Shi-Keng, Taichung city, Taiwan (120°6′ 22.45″E, 24°17′ 20.86″N). The study site is situated along a winding trail through a broadleaf forest. There are many large, moss-covered rocks along the sides of the trail with numerous small caves in the spaces between the rocks. Stable and large populations of *P. clavis* were commonly seen building webs along these trails.

Field Experiments

We manipulated the presence of *P. clavis* and the colour of webs to test their effects on the insect attraction rate. We used four treatments: (A) normal web and spider present ($N = 24$), (B) blackened web and spider present ($N = 26$), (C) normal web and spider removed ($N = 29$) and (D) blackened web and spider removed ($N = 22$). In spider-absent treatments, we carefully drove spiders away without damaging their webs. Charcoal powder was used to change the colour of the web. To exclude the potential effects of chemical cues of charcoal powder, we also sprinkled a similar quantity of charcoal powder near the normal web treatments. The amount of charcoal powder that was used was proportional to the web area. Previous studies have shown that the

prey attraction rate of webs is also affected by web area (Herberstein & Tso, 2000) so we also measured the size of each web. Since the web of *P. clavis* has an irregular geometry, we measured the area of the web using the ‘adjusted radii–hub’ formula described in Herberstein and Tso (2000). We assumed the web hub to be located at the intersection of two lines, one being the direction of the spider’s retreat (the retreat has a tube form), the other being perpendicular to the direction of the spider’s retreat. Each radius was measured using a soft tape measure. The body lengths of spiders were measured as well. Webs of different sizes were assigned equally to each of the four treatments and all webs were used only once. Only spiders with intact webs were used in this experiment.

We used infrared video cameras (Sony DCR-SR series, Tokyo, Japan) to monitor prey attraction events of *P. clavis* webs in the four treatments at night (2000–0400 hours). Field monitoring was conducted over 8 nights. About 16 video cameras were used every night, and spiders along the trails were haphazardly chosen. Video footage was analysed in the laboratory at Tunghai University and we recorded the number of insects attracted to each web. We defined an attraction event as when an insect flew directly towards and was intercepted by the web, or flew directly towards and inspected the web continuously from less than 10 cm away for at least 1 min. As we only sprinkled charcoal powder on the upper side of the web, we only noted insects that approached the upper side. Predator attack events were also recorded. In treatments A and B (spider present), we ignored insect attraction events during periods when the spider left the web. Only video footage lasting longer than 3 h was used for data analyses.

A negative binominal regression was used to compare the prey attraction rates (number of prey attracted to a web per hour of monitoring per 100 cm² of web) of four treatments, using web area (per 100 cm²) and recording time (h) as offset terms, attracted prey number as the response variable and the four treatments as explanatory variables. Multiple comparisons between treatments were then performed, and *P* values were adjusted using Holm–Bonferroni methods to control the family-wise error rate. Nagelkerke’s pseudo *R*-squared and Cliff’s *d* were used to quantify the effect size of the model and that between the treatments, respectively. The absolute value of Cliff’s *d* at 0.147, 0.33 and 0.474 was considered negligible, small and medium, respectively, and otherwise considered large (Romano, Kromrey, Coraggio, & Skowronek, 2006). As there were two factors (manipulating spider and web) in this study, the interaction effect of manipulating spider presence and applying carbon powder was examined. An analysis of variance (ANOVA) test with Welch correction and effect size eta-squared (η^2) were used to check whether the web area was different in the four treatments (Zar, 1996). The value of η^2 at ~ 0.01 , ~ 0.06 and ≥ 0.14 was loosely considered small, medium and large, respectively (Cohen, 1988). Spider body size in treatments A and B (spider presence) was also compared with a two-sample *t* test with Welch correction and an effect size Cohen’s *d* to check whether the size of spiders used in these two treatments differed. The value of Cohen’s *d* at 0.2, 0.5 and 0.8 was considered small, medium and large, respectively (Cohen, 1988). We also checked whether there were interaction effects between removing the spider and applying carbon powder. During field experiments the weather was similar every day and there was no rain during the 8 days of field experimentation.

Quantification of Web Silk Coloration

Twelve webs of *P. clavis* were randomly chosen from the study site to measure reflectance spectra using a spectrometer (S4000, Ocean Optics, Inc., Dunedin, FL, U.S.A.). We measured the

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