



The potential role of web-based putrescine as a prey-attracting allomone



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The use of prey-attracting allomones is likely to be an effective foraging strategy for sit-and-wait predators. Despite this, the production and efficacy of such allomones have rarely been documented. Previous investigations into the chemical composition of spider silk have revealed the presence of a number of potential allomone chemicals such as the amide putrescine, a foul-smelling organic compound. Putrescine is attractive to several terrestrial invertebrates, many of which are also typical prey species of spiders, but whether prey attraction is an underlying mechanism promoting its inclusion in web silk is currently untested. Here, we artificially increased the amount of putrescine in the web silk of female *Argiope keyserlingi* and assessed the resulting variation in prey interception of normal versus putrescine augmented webs under seminatural field conditions. We demonstrated that webs misted with a putrescine solution captured significantly more prey than webs misted with a control solution and also found differences in prey capture rates between individuals from different populations. This not only suggests that web-bound putrescine acts as a prey attracting allomone, but also that there is population level variation in the web-based foraging strategies of these spiders.

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Allomones are chemical cues used to transmit information between individuals of different species. They are distinguishable from other interspecific chemical cues, such as kairomones, by being beneficial for the signaller, but detrimental to the receiver (Nordlund & Lewis, 1976). Despite allomones being described from a range of taxa, our knowledge of their efficacy stems largely from those employed defensively by prey species against predators. For example, the earwig *Labidura riparia* releases an allomone that mimics the smell of carrion and thereby discourages predators (Byers, 2015). Other examples of defensive predator-deterrent allomones include toxic or distasteful chemicals released by some species of amphibians (Brodie & Smatresk, 1990; Daly, Spande, & Garraffo, 2005), insects (e.g. stink bugs, Borges & Aldrich, 1992; moths and leaf beetles, Schulz, 1998; see also Whitman, Blum, & Alsop, 1990 and references within) and marine invertebrates (Fontana et al., 1993; Schulte & Scheuer, 1982). Less commonly described are allomones emitted by predators that exploit chemical preferences and thus attract their prey species.

Prey-attracting allomones may be an especially effective foraging strategy for sit-and-wait predators, which do not 'actively'

hunt prey. Sit-and-wait predators are taxonomically widespread, and include trap-building terrestrial invertebrates (Eltz, 1997; Riechert, 1992; Scharf, Lubin, & Ovadia, 2011), reptiles (Andrews, 1979; Porges, Riniolo, McBride, & Campbell, 2003; Secor & Nagy, 1994) and, arguably, carnivorous plants (Englund & Harms, 2001; Harms, 1999). However, the identity and effectiveness of these prey-attracting allomones are rarely investigated. For example, although the exploitation of prey-attracting allomones by carnivorous species was first proposed by Darwin (1875), the action of such allomones has only recently been unequivocally demonstrated. Kreuzwieser et al. (2014) showed that *Drosophila melanogaster* were attracted to volatile organic compounds released by the Venus flytrap, *Dionaea muscipula*, suggesting that the plant attracts *Drosophila* by exploiting a pre-existing preference for these chemicals. Perhaps the best studied example of a prey-attracting allomone involves the bolas spider (particularly *Mostophora* spp.), which produces species-specific female moth sex pheromones that attract male moths searching for a reproductive partner (Gemeno, Yeargan, & Haynes, 2000; Haynes, Yeargan, & Gemeno, 2001; Yeargan, 1994). Once the male moth has been lured to the spider, it is able to trap the moth using a sticky silk ball. This allomone takes advantage of the prey's olfactory bias and yields a fitness benefit for the signaller.

Trap-building sit-and-wait predators may be similarly able to increase the effectiveness of their traps by adorning them with

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prey-attracting allomones. Several components in spider silk may act as allomones and be attractive to prey species (see Schulz, 2013). However, few behavioural studies have attempted to evaluate this role. Additionally, some spider species decorate their webs with insect carcasses or rotting material that is attractive to prey species, either by odours released directly from the debris (Bjorkman-Chiswell et al., 2004; Hénaut, Machkour-M'Rabet, Winterton, & Calmé, 2010) or through the decomposition by odour-releasing yeast (Tietjen, Ayyagari, & Uetz, 1987). Other potential prey-attracting chemicals have been detected in spider silk (Eberhard, 1981; Schulz, 2013), and although the authors suggested they may act as allomones, there has been no behavioural evidence supporting that role. For example, the web silk of the male spider *Pholcus phalangioides* contains the alkene (Z)-9-tricosene, a key component in the pheromones of several insects, including potential prey species such as the house fly, *Musca domestica*. The alkene may act as an allomone when released by the spider, but the necessary behavioural studies required to determine whether it is attractive to prey species have not been undertaken (Xiao, Zhang, & Li, 2010).

The web silk of spiders contains a surprisingly diverse array of chemicals, including salts (Blamires, Hasemore, Martens, & Kasumovic, 2017; Sahni et al., 2014), amides (Townley, Tillinghast, & Neefus, 2006), alkenes (Xiao et al., 2010) and alkaloids (Zhang et al., 2012). Behavioural studies provide strong evidence that some of these spider web-based chemicals are important for mate choice (see Gaskett, 2007), but few studies have investigated alternative functional roles of specific web-based chemicals (but see Zhang et al., 2012). One such chemical is the amide putrescine. This has been found in the silk of a number of spider species including those in the genera *Argiope* (Henneken et al., 2015; Townley et al., 2006) and *Nephila* (Higgins, Townley, Tillinghast, & Rankin, 2001) and is probably a component of the adhesive droplets located on the threads making up the capture spiral of the web (Townley, Bernstein, Gallagher, & Tillinghast, 1991). Many properties of these adhesive droplets vary considerably with different environmental factors including wind (droplet volume; Wu, Blamires, Wu, & Tso, 2013), temperature and humidity (droplet extensibility; Stellwagen, Opell, & Short, 2014), prey type (droplet volume and stickiness; Blamires et al., 2017) and nutrition (salt concentrations and stickiness; Blamires et al., 2017; droplet volume, stickiness and colour; Blamires, Sahni, Dhinojwala, Blackledge, & Tso, 2014). In *Argiope trifasciata*, the amount of putrescine in the silk also varies with diet (Henneken et al., 2015; Townley et al., 2006). Spiders provided with a garlic supplement produced webs that contained more putrescine, suggesting that putrescine's presence in silk may be nutrient dependent (Henneken et al., 2015). Further, nitrogen-containing components such as putrescine are predicted to be expensive for arthropod predators whose prey contain little nitrogen (Fagan & Denno, 2004; Fagan et al., 2002). The presence of putrescine on spider silk is particularly interesting because it has a very distinctive odour (of rotting matter) that can be attractive to flies. In fact, putrescine is a key component of at least two commercial lures targeting tephritid flies (Robacker, 1999). Whether putrescine in the web silk of spiders acts as a prey-attracting allomone has not been demonstrated empirically.

Here, we experimentally manipulated the amount of web-bound putrescine to assess whether it acts as a prey-attracting allomone and thus enhances the foraging success of female St Andrew's cross spiders, *Argiope keyserlingi*. This species of orb-weaving spider is common along the eastern seaboard of Australia. The spiders construct characteristic cruciform-shaped silk decorations (Walter & Elgar, 2012) and readily include flies in their diet (Bradley, 1993; Herberstein et al., 1998).

METHODS

Collection and Housing

To assess variation in foraging strategies between geographically distinct populations we collected 57 subadult and adult female *A. keyserlingi* from five locations (Sydney, Taree, Coff's Harbour, Broadwater and Brisbane) along the east coast of Australia in January 2016 (approximate distances between sites: Sydney and Taree \approx 310 km, Taree and Coff's Harbour \approx 220 km, Coff's Harbour and Broadwater \approx 190 km and Broadwater and Brisbane \approx 250 km). All spiders were collected from semiurban environments (e.g. carparks, roadsides and gardens). Once in the laboratory, individual females were placed in clean Perspex frames that exceeded the size of webs observed in the field (58.5×58.5 cm and 15 cm deep) and maintained at 25 °C under 12:12 h day:night lighting conditions. Females were fed two third-instar crickets, *Acheta domestica*, per week. Webs were misted with water three times a week and females were weighed (mg) prior to commencing the experimental trials. We also measured the length of their front right leg, as an indicator of body size, and subsequently calculated body condition as the residuals of a regression of body weight on leg length following Jakob, Marshall, and Uetz (1996).

Field Assays

We investigated whether putrescine functions as a prey attractant using a paired design that compared the attraction of two separate webs constructed by the same female ($N = 39$ females from four of the five collection sites), which were sprayed with a solution of either putrescine (experimental) or water (control). At the start of the experiment each of the 39 adult females was transferred to a smaller clean Perspex frame (26×26 cm and 10 cm deep) where each was allowed to build a web. After completion of her first web, the female was transferred to a second clean frame in order for her to construct a second web. Females were given a maximum of 5 days to build two webs; webs older than 6 days were discarded. Not all individuals built consecutive webs in the allocated time. As a result, trials consisted of webs built by individuals from four of the five populations and some females contributed webs to multiple trials (number of females building two webs in the allocated time from Sydney = 5, Taree = 6, Coff's Harbour = 5 and Brisbane = 6; number of web pairs from Sydney = 5, Taree = 8, Coff's Harbour = 8 and Brisbane = 9).

After constructing her web, each female was removed and any web decorations were noted. The webs were then transported (in their frames) to a field site in Werribee, Victoria, Australia (37.877456° S, 144.6619° E), a semirural location with a habitat comprising long, unmaintained grass. We randomly allocated the female's first or second webs to experimental or control groups. The experimental treatment involved lightly misting the web three times (equating to approximately 240 μ l of liquid) with a clear and odourless putrescine solution containing 1.1 mg/ml putrescine (1,4-butanediamine; Sigma–Aldrich, St Louis, MO, U.S.A.) in distilled water. The female's other web was allocated to the control treatment, and was similarly lightly misted three times with distilled water only (ca. 240 μ l). Both the water and putrescine solution were similarly taken up by the webs. We ran multiple trials across several days, and to control for any effect of web-building order we ensured that on any given day 50% of the putrescine-sprayed webs were the female's first web and 50% were the female's second web.

The frames containing the spiderless webs were placed in pairs on the ground ensuring a distance of at least 3 m between pairs and 15 cm within each pair. The trial commenced at 0930 hours each morning, and each web was then visually inspected for prey species

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