

Stingless bee response to spider webs is dependent on the context of encounter

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Abstract In the course of their foraging bouts, bees frequently encounter spider webs among the vegetation. The ability to see and avoid these webs is vital for the success of the individual bee's foraging bout. In this study, we report on the response of stingless bees (*Trigona carbonaria*) towards the webs of the St. Andrew's Cross spider (*Argiope keyserlingi*). We studied the ability of bees to avoid webs in different contexts: when bees were on their foraging path or when they were returning to the hive as well as when they were flying North or South. We show that the probability of a bee being able to avoid a web depends on the context of the bee's flight rather than the visual appearance of the web. Furthermore, the presence of the spider seems to alert the bee to the web, resulting in bees being more able to avoid capture. We show, specifically, that the probability of being captured is higher when the bee is returning to the hive compared with when the bee is foraging. The likelihood of avoiding a web is also influenced by the compass direction of the flight, although to a lesser extent. Our results indicate that the context of the predator–prey encounter has a significant influence on a bee's ability to escape interception by a spider web.

Keywords *Argiope keyserlingi* · Orb web · Stabilimenta · Decorations · *Trigona carbonaria* · Visibility · Bee flight · Predator–prey interactions

Introduction

Animals are at their most vulnerable to the attack of predators when they are foraging. Under high levels of predation pressure, animals may forage in groups or reduce their foraging activity in order to reduce the likelihood of an attack. Studies have traditionally focused on predation risk during the act of foraging (Lima 2002), but it is also important to consider the movement of prey en route to the foraging site. In group-living organisms, traveling in a group is advantageous, as the risk of predation can be diluted (Krause and Ruxton 2002). By contrast, solitary foragers such as insects can be prone to high levels of predation from ambush or sit-and-wait predators. For example, pollinators such as bumblebees have a 14% probability of being attacked by spider predators, and we can assume that the total attack probability including other hymenoptera specialists such as bee eaters must be even higher (Dukas 2001).

Prey often face considerable risk whilst moving because their increased exposure allows the predator to precisely target the prey. Prey are generally expected to be ahead in the evolutionary arms race, since the cost of not recognizing a predator is usually fatal to the prey, whilst the cost of not capturing any particular prey item can be overcome by the predator (the 'life-dinner' principle, sensu Dawkins and Krebs 1975, cited in Sih 1984).

Not many studies have considered free moving predators in analyses of how predators influence prey behaviour (Lima 2002). Rather, most studies investigate prey response

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to a predator that is usually kept stationary or abstract without the ability to react to prey movement (e.g. stickleback fish; Milinski and Heller 1978). However, the biological relevance of these assumptions is unclear, as truly stationary predators are rare, with the exception of trap building predators. Less than 1% of all terrestrial predators build traps (Ruxton and Hansell 2008). The most common examples of stationary predators are antlions (the larvae of lacewings), web-building spiders, fungus gnat larvae (Australasian glow worms) and caddis fly larvae (Ruxton and Hansell 2008). Even though these predators are stationary, mobile prey are likely to encounter them under different contexts. For example, in a forest environment, there are a variety of light habitats, ranging from dark areas under the canopy to gaps where the sunlight penetrates. Studies using orb-web spiders have shown that different light environments can influence prey perception of the predator and consequently rates of interception (Craig 1988; Heiling 1999). A prey approaching a spider web from the North would encounter a predator in a slightly different context than one approaching from the South, owing to differences in light environments and intensity of the illumination. Therefore, it may be more realistic to assume that prey move fluidly through a series of contexts wherein the potential predation threat fluctuates accordingly.

In this paper, we explore the predator–prey interactions between a typical stationary predator, the St. Andrew's Cross spider (*Argiope keyserlingi*), and its potential prey, the stingless bee (*Trigona carbonaria*). The St. Andrew's Cross spider builds orb webs in low lying shrubs (Rao et al. 2007; Herberstein 2000), and since individuals show a high level of web site fidelity (Chmiel et al. 2000), they are a true example of a classical stationary predator. However, even though the webs themselves are difficult to detect visually, *Argiope* spiders are known to employ two different prey attraction strategies. Firstly, the spider's abdomen has yellow bands running across the dorsal side and other bright markings on the ventral side. Several studies have shown that colourful markings on spiders have a prey attraction function (Craig and Ebert 1994; Hauber 2002; Hoese et al. 2006; Tso et al. 2006). Secondly, the spider often decorates its webs with extra silk structures, termed decorations or stabilimenta, that are thought to attract insects to the web (Craig and Bernard 1990; Li 2005; Cheng and Tso 2007). The functional significance of decorations has been a source of substantial controversy for many years (Herberstein et al. 2000; Bruce 2006), with other studies demonstrating that decorations function to deter potential predators (Blackledge and Wenzel 2001) or as camouflage (Eberhard 2007, 2008). Irrespective of the functional significance of silk decorations, the visibility of the web is altered since decorations reflect light in the UV wavelength (Craig and Bernard, 1990; Bruce et al. 2005),

which contrasts against a UV-dull green background, thereby rendering the web more visible to insects.

A trap, even one as fine as a spider web, is no longer effective if the prey can recognise it as such. It is quite possible that stingless bees can detect the presence of both spider and web and thereby avoid interception (Craig 1994). However, since stingless bees are sensorially biased towards bright colours, dark centers and striped patterns (Biesmeijer et al. 2005), it is likely that the appearance of the spider and web decoration enhances the likelihood of interception. Stingless bees typically forage for nectar at distances ranging up to 680 m (Heard 1999) and then return to the hive using nest-associated landmarks to home in on their destination (Zeil and Wittmann 1993). In this system, it is possible to ask a series of questions regarding predator–prey interactions under different contexts. More specifically, we asked: (1) does prey response to the predator depend on the perceived threat level? and (2) does prey response to the predator depend on the context of encounter with reference to the flight phase of the bees (i.e. foraging phase and return phase) and the compass direction of flight (i.e. North and South)?

Materials and methods

Study species

T. carbonaria (Hymenoptera, Apidae) are stingless bees native to Australia. *T. carbonaria* are found along the east coast of Australia; its range extends as far north as the tropics and nest in hollow logs (Michener 1961). The bees are quite small (body length of worker bees, 3.9–4.3 mm; Dollin et al. 1997), and typically, colonies contain a single queen and hundreds of workers. Stingless bees of the genus *Trigona* are known to be a common prey of *Argiope argentata* (Craig et al. 2001) and *A. keyserlingi* (Blamires et al. 2008).

A. keyserlingi Karsch, 1878 (Araneae: Araneidae), also known as the St. Andrew's Cross spider, is an orb-web spider with distributions recorded in the eastern coast of Australia (Platnick 2008) in a wide variety of habitats, ranging from rainforest margins to urban gardens. It is locally abundant and typically found on long-leaved bushes such as *Lomandra longifolia* and *Pandanus* sp. (Rao et al. 2007). These spiders build web decorations in the form of zigzag deposits of silk (hereafter referred to as 'silk decorations') stretching outwards from the centre of the web, whilst circular decorations are typically found only in juveniles. A maximum of four diagonal bands (i.e. a cruciate pattern) is seen in this species. In all experiments, we used sub-adult female *A. keyserlingi* spiders, i.e. spiders that were one instar short of adult stage.

Experiment setup

A commercially available hive box (Russell and Janine Zabel Australian Native Bees) was set up on a table in a semi-enclosed green house. The greenhouse had mesh walls and a plastic roof that allowed natural light to filter through in all wavelengths (VP Structures, Australia). Bees were trained to approach a feeder with sugar water (ratio of sugar to water 1:3) that was placed 1 m away from the hive.

Subsequently, we trained bees to fly through an empty wire hoop (10-cm diameter) either en route to the feeder or the hive (Fig. 1). The empty hoop was considered as a control to measure bee activity. For the experiments, we then swapped the empty hoop with hoops containing webs from *A. keyserlingi* spiders. Since decorations rarely extend beyond the hub in this species (Herberstein et al. 2000; Bruce 2006) and since the hub is the most visible area of the web, we used the hub part of the web for all experiments. In order to present the web stimuli in front of a relevant background, we used photographs of *Lomandra* leaves, as these have very similar light reflectance curves to that of actual plants (Hoese et al. 2006). The use of photographs allowed us to control for the variation normally occurring in natural plant colour and composition, which may affect the bees' perception of the webs. Furthermore, in a preliminary experiment (data not presented), we compared the rate of interception of bees with webs against actual *Lomandra* plant background versus a photograph background, and we were satisfied that there were no measurable differences. For the foraging flight, the feeder was placed inside a box with *Lomandra* photographs pasted on it (Fig. 1a). The box had a small opening to allow the bees to land on the feeder. For the return flight, we ensured that the background remained consistent by covering the front of the hive box with *Lomandra* photographs (Fig. 1b).

There were four experimental treatments based on the predicted threat level perceived by stingless bees. Since both spiders as well as web decorations are suggested to exploit the bees' sensory biases (Craig and Bernard 1990; Hauber 2002), we rated the experimental treatments at different levels of threat. From the highest threat to the lowest, the experimental treatments are as follows: (1) Webs with spiders and decorations (Spider & Decs), (2) webs with spiders without decorations (Spider), (3) webs without spiders but with decorations (Decs) and (4) webs without spiders and without decorations (Web). The patterns of decorations used for the experiment were of the cruciate pattern with four bands. Approaching bees were monitored during 1-min trials for each treatment ($n = 15$), and all bees that intercepted the web were counted; each treatment was followed by a control (empty) hoop for 1 min. In the case of control hoops, the number of bees that went through the hoop were counted and used as a covariate. One-minute trial period was chosen as an optimum time period wherein sufficient number of bees intercepted the web, and the probability of learning by individual bees was minimised. The order of the treatments and control was randomised, and there was a delay of at least 10 min between treatments to offset any possible learning effects. The behaviour of the bees did not change during the experiment, suggesting that there was no learning effect as the testing progressed.

Bees encountered webs in two contexts of flight: the flight phase (foraging, return) and direction of flight (North and South). For the foraging phase experiments, we trained bees to go through a hoop as they approached the feeder. The hoop was placed 5 cm in front of the feeder. For the return phase experiments, we placed the hoop 5 cm in front of the hive entrance. For the flight direction treatment, bees were trained to fly either in the North or the South directions (see Table 1 for details). Previous field studies with *A. keyserlingi* showed that the majority of spiders in a

Fig. 1 Schematic representation of the experimental setup with the foraging phase (a) and the return phase (b) of bee flight. See "Materials and methods" for details

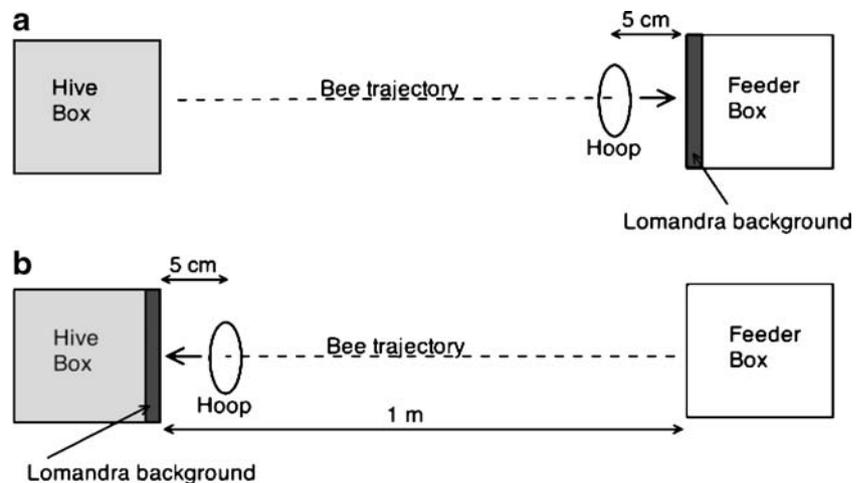


Table 1 Design of experiment

Direction	Flight phase	Treatment	<i>N</i>
North	Foraging	Web	15
		Decs	15
		Spider	15
		Spider & Decs	15
	Return	Web	15
		Decs	15
		Spider	15
		Spider & Decs	15
South	Foraging	Web	15
		Decs	15
		Spider	15
		Spider & Decs	15
	Return	Web	15
		Decs	15
		Spider	15
		Spider & Decs	15

North and South are the compass directions towards which the bees were flying, Flight Phase refers to whether the bees were out foraging or returning to the hive, ‘Spider & Decs’ is spider webs with decoration and with spider, ‘Decs’ is spider webs with decorations but without spider, ‘Spider’ is webs without decorations but with spider, ‘Web’ is webs without decorations or spider. *N* is the number of trials

field population preferred to orient themselves around the South–North axis rather than the East–West axis (Rao et al. 2007). Furthermore, since the illumination and light conditions of a spider facing North may be different from a spider facing South, the direction treatments provide a measure of differing contexts of encounter.

Since the data were normally distributed, we conducted a univariate analysis of variance with the statistical package JMP version 5. The number of bees that hit the web (termed as interceptions) was the dependent variable, the number of bees that went through the empty hoop was used as a covariate in order to account for bee activity, and the independent variables were the spider treatments, the direction of bee flight and flight phase. For the purpose of presentation, all graphs depict interception measures as least-square means, since bee activity was strongly correlated with interception rate in all treatments. All post hoc tests were conducted using the Tukey honestly significant difference (HSD) method, with an alpha of 0.05.

Results

Threat level

Overall, the model was significant, with significant differences in interception rates between treatments (Table 2). The perceived threat level influenced the interception rate

of stingless bees, but differed according to the context of encounter. Foraging bees perceived webs with spiders (irrespective of decorations) as a greater threat and intercepted these webs at a lower rate than stingless bees that encountered webs without spiders (Fig. 2). However, returning bees responded similarly to all treatments (Fig. 2).

Context of encounter

Flight phase

Stingless bees approaching the web whilst foraging intercepted the web at a lower rate than on their return phases ($F_{1,239} = 73.42$, $p < 0.001$). The interaction between flight phase and treatments significantly influenced interception rates ($F_{3,239} = 9.20$, $p < 0.001$). On the foraging phase (Fig. 2), bees were more likely to intercept the web when the webs did not contain spiders (Tukey’s HSD, $Q = 3.06$, $p < 0.05$) than when webs contained spiders. The presence or absence of decorations did not significantly influence interceptions (Tukey’s HSD, $Q = 3.06$, $p > 0.05$). On the return phase (Fig. 2), bees intercepted the web at similar rates for all treatments (Tukey’s HSD, $Q = 3.06$, $p > 0.05$).

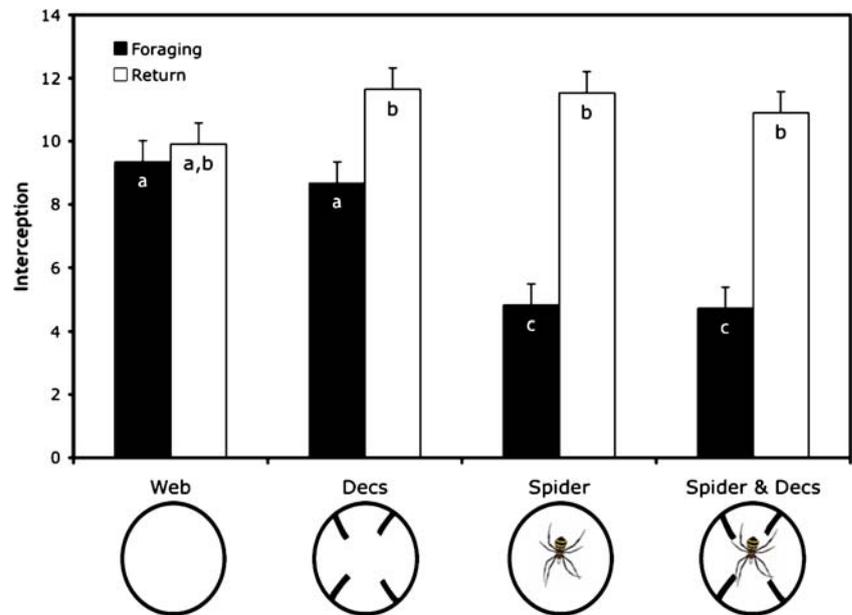
Direction

There was no difference in interception rates for bees that encountered webs whilst flying either North or South ($F_{1,239} = 0.15$, $p = 0.7$). However, there was a significant interaction between the direction of flight and the flight phase ($F_{1,239} = 21.4$, $p < 0.001$). During their foraging phases, North flying bees showed a higher rate of interception than South flying bees in the treatments without spiders (Tukey’s HSD, $Q = 3.46$, $p < 0.05$; Fig. 3). In the treatments with spiders, interception rates between the North flying and

Table 2 Results of the ANOVA showed that stingless bee interception of spider webs was significantly influenced by the flight phase and the type of web encountered ($R^2=0.45$, $F_{16,223}=13.29$, $p<0.0001$)

Effect tests					
Source	Nparam	df	Sum of squares	<i>F</i> ratio	<i>p</i>
Activity	1	1	174.61894	12.9109	0.0004
Direction	1	1	2.00442	0.1482	0.7006
Flight phase	1	1	992.94563	73.4162	<0.0001
Treatment	3	3	230.53856	5.6818	0.0009
Direction × flight phase	1	1	289.42955	21.3998	<0.0001
Direction × treatment	3	3	116.03934	2.8599	0.0378
Flight phase × treatment	3	3	373.38129	9.2023	<0.0001
Direction × flight phase × treatment	3	3	156.47756	3.8565	0.0102

Fig. 2 Stingless bees responded differently to the spider web treatments based on flight phase. The y-axis shows least-square means of interception per 1-min of observation, and bars not shared by the same letter are significantly different



the South flying bees were not significantly different (Tukey's HSD, $Q = 3.46$, $p > 0.05$).

During their return phases, South flying bees showed higher rates of interception than North flying bees in all treatments except the treatment with spider and decorations (Fig. 4), but these rates were not significantly different (Tukey's HSD, $Q = 3.46$, $p > 0.05$). There was also a significant three-way interaction between flight phase, direction of flight and the treatment (Table 2) in predicting the interception of stingless bees.

Discussion

During the course of their foraging bouts, stingless bees are likely to encounter potential predators under different contexts and conditions. In this study, we show for the first time that the context in which a bee encounters a spider web influences its likelihood of being intercepted by the web. Specifically, we show that the rate of prey interception depends on the bee flight phase. Bees are more vulnerable on their way back to the hive than on their way out

Fig. 3 Foraging bees intercepted webs without spiders at a higher rate when they flew North. The y-axis shows least-square means of interception per 1-min observation, and bars not shared by the same letter are significantly different

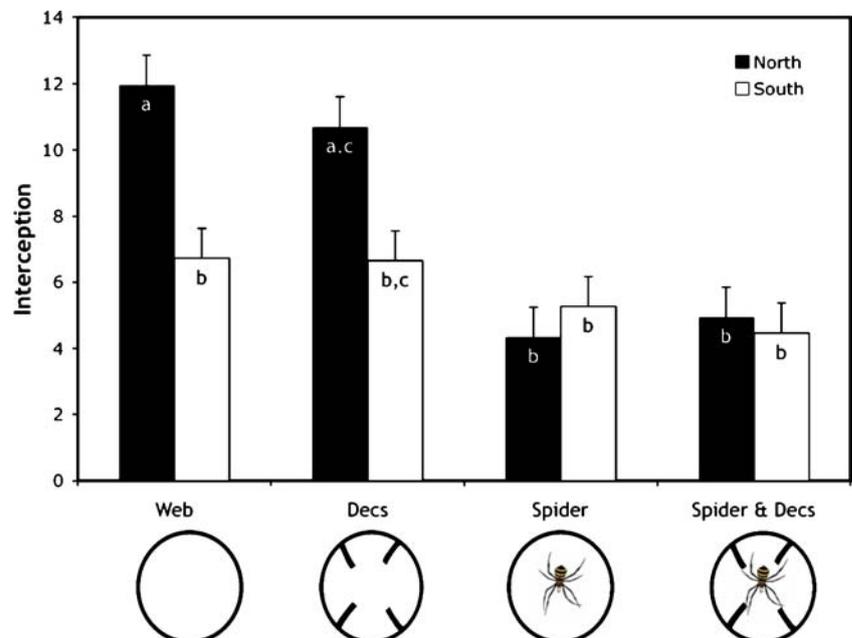
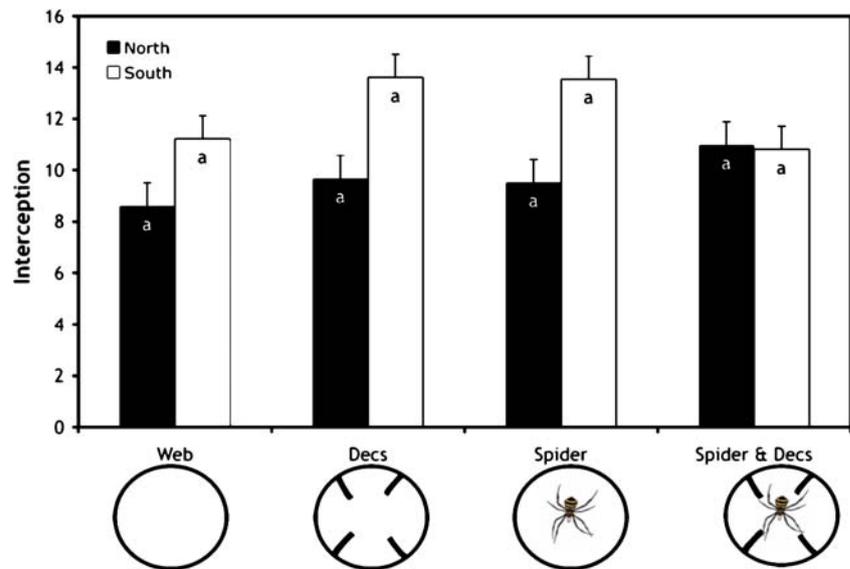


Fig. 4 Returning bees intercepted all treatment at similar rates. The y-axis shows least-square means of interception per 1-min of observation, and none of the bars are significantly different from each other



foraging. We also show that the direction of flight indirectly influences whether bees avoid the web in conjunction with the flight phase. And lastly, the bees are more likely to avoid the web if it is occupied by a spider irrespective of the presence of silk decorations.

Spiders often relocate their webs towards sources of abundant prey (Riechert and Gillespie 1986). *Argiope* spiders generally build their webs in vegetation quite low to the ground (Rao et al. 2007), and stingless bees build their nests in the ground and in hollow logs (Michener 1961). Therefore, it is likely that stingless bees frequently encounter spider webs both whilst foraging as well as whilst returning to the hive.

Interception rates were highest when bees were on their return phase, and this was consistent across all treatments. There are three possible explanations for this difference in rates of interception across flight phases. Firstly, aspects of the stingless bees' flights may be different on their foraging phase when compared to the return phase. Even though we did not measure flight speed, there appeared to be qualitative differences between the flight phases. On their foraging phase, the bees were more exploratory and flew slower since they were actively seeking food. On their return phase, they tended to fly faster and made a beeline back to the hive. Data for differential flight speed during different phases of bee flight are lacking in the literature, since studies typically report average flight speeds (~1.17 m/s in *Trigona*; Inoue et al. 1985). Since the speed of a bee directly affects the assimilation of visual stimuli (Cartwright and Collett 1979), this difference in the flight speed could result in a differential response to the presence of spider webs in their paths. Secondly, when the bees leave the hive, they usually perform an orienteering flight for nest and landmark recognition (Zeil and Wittmann 1993). If

they encounter a web on the way back, this may be an obstacle that was not previously encountered. Hence, their previous experience of a safe path back to the hive may take precedence over the immediate visual input. Thirdly, it is also possible that bees cannot slow down their approach flight without compromising nest location recognition (Theobald et al. 2007) on the return journey despite the presence and recognition of a predator.

In their foraging phase, stingless bees intercepted webs at a higher rate when they were flying North, but only in the treatments without spiders. A previous study showed that *A. keyserlingi* tends to align its web perpendicular to the North–South axis as opposed to the East–West axis (Rao et al. 2007). This alignment was thought to be due to the direction of sunrise in the Southern Hemisphere (Rao et al. 2007; see also Ramirez et al. 2003), but we suggest that by orienting their webs on the North–South axis, spiders may target bees that fly in this direction and thus enjoy higher interception. Furthermore, since bees are known to depend on daylight illumination (Lotto and Chittka, 2005) for contextual cues, objects could have an altered appearance depending on the direction of the bee's flight.

Overall, bees were equally likely to intercept a web with or without silk decorations. This result is contrary to several studies demonstrating the prey-attraction function of silk decorations (Craig and Bernard 1990; Herberstein 2000; Bruce et al. 2001; Li 2005; Cheng and Tso 2007). The present study supports the studies favouring other functions such as predator avoidance and web advertisement (Blackledge 1998; Eberhard 2007; 2008), with the caveat that since there was no difference in interception rates between decorated and non-decorated webs, it implies that prey are equally not deterred by the presence of decorations. However, our study did not set out to test the functional

significance of silk decorations (for a review, see Herberstein et al. 2000; Bruce 2006) and therefore it differs from other studies in three aspects. Firstly, webs were subjected to a steady stream of prey, whereas in the wild, insect interception is stochastic (Venner and Casas 2005; Cheng and Tso 2007). Secondly, the webs we tested were truncated, i.e. we used only the hub of the web, which is the area where decorations are most commonly found (Herberstein et al. 2000; Bruce 2006). Thirdly, there may be species specific differences in prey behaviour towards silk decorations. Whilst sarcophagid flies were attracted to silk decorations (Bruce et al. 2001), *Trigona* bees showed no preference in Y-maze choices (Bruce and Herberstein 2006).

We expected the sensory biases of bees towards striped patterns and bright colours (Biesmeijer et al. 2005) to influence higher interception of spiders with decorated webs. However, we showed that external influences such as direction of flight and flight phase of the prey are also important predictors of the likelihood of interception. In our experiments, the perceived threat level varied across contexts for the stingless bees, as spiders were recognised as a threat when the bees were out foraging but not when returning. In general, stingless bees also show a marked lack of avoidance learning (Craig 1994), and this, coupled with variation in the patterns of silk decorations (Seah and Li 2002; Rao et al. 2007), implies that there is a low probability of a bee associating the presence of decorations with danger. Given that most orb-web spiders are generalist predators, with webs probably designed for large but infrequent prey items (Venner and Casas 2005), it is likely that webs do not target any particular insect prey.

In the design of predator–prey interaction studies, it has often been convenient to restrict the mobility of the predator (Lima 2002). Our study avoided the possibly confounding effect of artificially restricting the mobility of the predator since orb-web spiders are stationary in nature. We also focused on the risk faced by foraging prey en route to the foraging site rather than at the foraging site. Risks that a pollinating insect faces at the foraging site (e.g. predation by crab spiders; Dukas 2001) are very different to the risks faced whilst in flight (e.g. predation by insectivorous birds or orb-web spiders; Dukas 2001). We suggest that the design of future studies in similar systems take into account the fact that prey responses are predicated on environmental conditions and the context of encounter in naturalistic settings.

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