Foraging behaviour and the risk of predation in the black house spider, *Badumna insignis* (Desidae)

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Abstract

Many animals adjust their behaviour according to the presence or threat of predators. However, the foraging behaviour of sit-and-wait predators is typically thought to be inflexible to short-term changes in the environment. Here we investigate the foraging behaviour of the nocturnally active black house spider, *Badumna insignis*. Experiments in which different kinds of prey were introduced into the web during either the day or night indicated that the foraging success of *Badumna* is compromised by behaviours that reduce the risk of predation. During the day, spiders generally remain within the retreat and take longer to reach the prey, which may reduce their foraging success. In contrast, spiders sat exposed at the edge of the retreat at night, and from here could usually reach the prey before it escaped. The spiders were able to escape from a model predator more rapidly if they were at the edge of the retreat than if they were out on the web. These data suggest that the costs to *Badumna* of reduced fecundity through poor foraging efficiency may be outweighed by the benefits of reducing the risk of predation.

Introduction

Animals faced with changes in the risk of predation may adjust their foraging and other behaviours in a variety of ways (Lima and Dill 1990; Lima 1998). For example, animals may invest more time in predator-detection behaviours, change their choice of food items, spend less time in exposed areas, or any combination of these tactics (Lima 1998 for review). Such decisions usually result in less efficient foraging, which may be reflected in lower capture success, selection of less profitable prey, or foraging in areas with fewer available prey items (Lima 1998).

Most studies that examine the influence of the risk of predation on foraging behaviour concern species that actively search for food, rather than those that remain stationary and wait for prey items to come within striking distance (Lima 1998). Web-building spiders are classic examples of these so-called 'sit-and-wait' predators (e.g. Wise 1992), and it is generally assumed that the foraging behaviour of these predators is relatively inflexible to short-term changes in the environment. However, recent research has revealed that web-building spiders adjust their foraging behaviour according to local conditions by modifying the architecture and size of the web (e.g. Elgar *et al.* 1996; Herberstein *et al.* 1999) and their decisions on whether to capture or leave prey items (e.g. Herberstein *et al.* 1998).

While the web is an excellent device for capturing the prey, spiders that remain exposed on the web may be particularly vulnerable to attack by visually hunting predators, such as wasps and birds (Cloudsley-Thompson 1995). Web-building spiders may reduce the risk of predation by building webs only at night (see Elgar 1993; Herberstein and Elgar 1994), remaining concealed at the edge of the web, or even constructing a retreat of either silk or leaves (e.g. Thirunavukarasu *et al.* 1996). Spiders detect when a prey item is intercepted by the web by the vibrations that pass along the silk threads (Foelix 1982), but the efficiency with which they detect these vibrations and respond accordingly may depend upon the location of the spider. Thus, spiders in a retreat and not directly touching the silk threads may take longer to respond to arrested prey than those positioned on the web.

The black house spider, *Badumna insignis* (L. Koch), is an excellent species for investigating how the foraging behaviour of a sit-and-wait predator is influenced by the risk of predation. This

spider constructs an asymmetric, two-dimensional web that stretches outwards from a retreat. The web comprises numerous parallel lines of silk attached to the surrounding substrate. Each parallel silk line is connected by a zig-zag pattern of cribellate silk, which functions to entangle the insect prey. The retreat is located inside a naturally occurring crevice in a tree or building, and connects to the web through a meshed funnel of silk. Some webs have multiple retreat entrances, each with separate funnel connections. The spiders are nocturnal, remaining hidden within the retreat during the day, but are more exposed, with the spiders' legs extending beyond the retreat, during the night.

In this study, we document both the diel activity patterns and prey items of several populations of the black house spider. We conduct several experiments that investigate the response of black house spiders to model predators and to prey items introduced at different times of the day and night.

Materials and Methods

Black house spiders were observed in several populations in southern Victoria during 1995 and 1996. Each population comprised spiders that had built webs in the crevices of separate buildings. The populations were selected on the basis of ease of access and density of webs; two were located in central Melbourne and six in Ballarat. *B. insignis* is typically widespread in the inland arid regions of Australia, but has been introduced into urban areas where it has become established in human habitations. It is possible that some individuals in our study were *B. longinquus*, which is common on the east coast and humid south-east of mainland Australia and in Tasmania. We were unable to identify definitively all of the individuals in the study. Nevertheless, since both species behave similarly in the context of our observations and experiments, the inclusion of both species in the analysis is unlikely to alter our conclusions.

The remains of the prey of *Badumna* are ejected out of the retreat, and can be found below the web or in the web margins. We examined the range of prey caught by these spiders by collecting prey remains that landed on trays placed under the webs at two populations in Ballarat. Although the prey were usually masticated, it was usually possible to identify the remains to the Order level and to distinguish between different species.

Temporal variation in foraging behaviour

The foraging behaviour of *B. insignis* was observed during the night and during the day in trials using two types of prey, blowflies (*Lucilia cuprina*) and cockroaches (*Blatta* sp.). The prey differed in both size and behaviour: cockroaches were larger than flies and struggled more vigorously in the web and appeared to be more difficult for the spiders to subdue.

The webs of 160 spiders from the different populations were individually identified and randomly allocated to one of four treatments that altered the timing and kind of prey introduced into the web. Thus, in each treatment a single prey item (either a fly or a cockroach) was placed 10 cm from the entrance to the retreat during either the day or night. Continuous struggling of the prey was required to ensure consistency among trials; the flies were kept active at night by exposing them to warmth and light, and any prey that ceased struggling was gently touched on the abdomen with a brush, which usually stimulated further movement. A torch was necessary to observe and record the behaviour of spiders at night, but a minimal amount of light was shone directly onto the web.

For each trial, we recorded the time when the prey was introduced into the web, when the spider emerged from the retreat, when the spider commenced moving toward the prey, when the spider reached the prey, when the spider returned to the retreat, and when it finally disappeared into the retreat. Data from trials in which the spider did not appear after 2 min had elapsed following introduction of the prey were excluded from the analysis. Our preliminary trials indicated that spiders that had not appeared by this time were unlikely to respond subsequently.

Predator-avoidance behaviour

We examined the response of black house spiders to predators when the spiders were either adjacent to the retreat entrance or when they were processing a prey item. The 'predator' was a 'wand' in the shape of the plan projection of a flying bird with a 30-cm wingspan. Initially, we waved the wand 10 cm above the web, but in this design the spiders may have responded to either optical cues or changes in air pressure deriving from the movement of the wand. Thus, in a subsequent experiment, we modified whether the wand

generated a change of air pressure by waving it either in front of, or behind, a 50 cm × 50 cm sheet of transparent perspex. For all trials, we waved the predator continuously above the web, and recorded the number of 'passes' before the spider disappeared into the retreat.

Results

Our observations of 40 black house spiders over a period of 10 days revealed that they are most active at night. The spiders were more likely to be visible, at the entrance to their retreats, between 1800 and 0700 hours, and this was also the time when they were frequently observed exposed on their webs (Fig. 1).
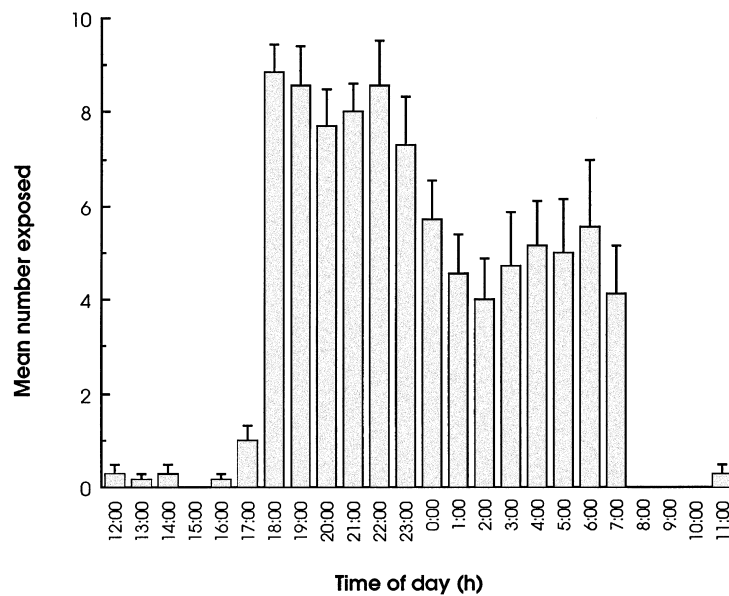

Fig. 1. The mean number of *B. insignis* observed exposed on the surface of the web at hourly intervals across the diel cycle. Data are derived from 40 individuals observed over 10 days. Bars represent ± s.e.

We only observed spiders that initiated foraging from within the retreat: once a prey was caught in the web, the spider emerged from the retreat and grasped the prey with its fangs and chelicerae. The prey was then dragged backwards into the retreat by the spider, which then consumed the prey inside the retreat. The spider disposed of the remains of the prey by taking them to the edge of the web, where they were then dropped. Surveys of the dead invertebrates collected from trays placed at the base of the retreat indicated that the prey consisted primarily of flying and other active insects, and included Coleoptera (six species), Diptera (five species), Lepidoptera (two species), and Dermaptera, Phasmatodea, Orthoptera, Blattodea and Neuroptera.

Temporal variation in foraging behaviour

Black house spiders reached the prey significantly more quickly during the night than during the day ($F_{1,82}$ = 30.72, P < 0.001; Fig. 2). Although there was no significant difference in the time taken to reach flies or cockroaches ($F_{1,82}$ = 1.04, P > 0.3), the magnitude of the difference in the time taken to reach the prey between day and night was influenced by the type of prey
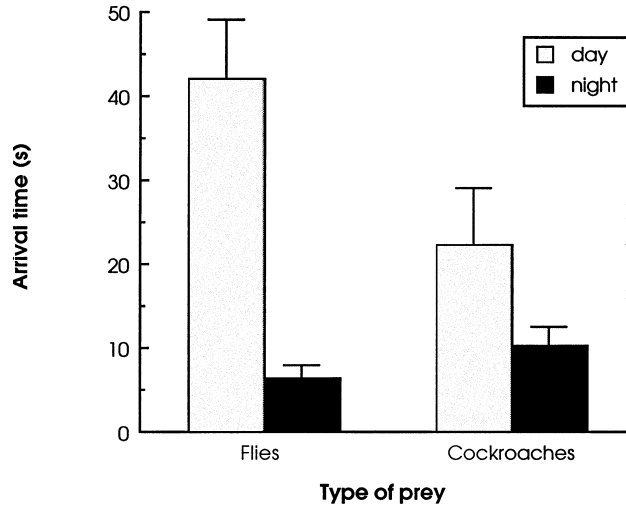
Fig. 2. The mean time for *B. insignis* to reach different prey items during the day or night. Bars represent ± s.e.

Table 1. **The time spent by *Badumna* in four different foraging behaviours when provided with either a fly or a cockroach during the day or night**

mean ± s.e.; *n*, number of trials

Behaviour	Day		Night	
	Bush fly	Cockroach	Bush fly	Cockroach
Time (s) to emerge from retreat	24.7 ± 5.3	13.7 ± 4.7	1.0 ± 0.2	3.4 ± 1.4
	(*n* = 24)	(*n* = 14)	(*n* = 25)	(*n* = 23)
Time (s) waiting at retreat entrance	12.3 ± 3.0	7.1 ± 2.8	2.8 ± 1.1	1.8 ± 0.7
	(*n* = 24)	(*n* = 14)	(*n* = 25)	(*n* = 23)
Time (s) to capture prey	5.5 ± 0.3	1.6 ± 0.3	2.5 ± 0.5	5.0 ± 1.8
	(*n* = 23)	(*n* = 14)	(*n* = 24)	(*n* = 23)
Time (s) to return to retreat	3.9 ± 0.8	51.0 ± 20.7	73.4 ± 16.2	72.1 ± 17.1
	(*n* = 24)	(*n* = 13)	(*n* = 25)	(*n* = 23)
Time (s) exposed on the retreat[A]	9.5 ± 2.0	52.6 ± 20.7	75.8 ± 16.4	77.1 ± 17.7
	(*n* = 23)	(*n* = 13)	(*n* = 24)	(*n* = 23)

[A]This is the sum of the time to capture the prey and return to the retreat

($F_{1,82}$ = 11.62, $P < 0.001$). The time taken to reach the prey comprised three parts: the time between the introduction of the prey and when the spider first becomes visible ('responding'), the time spent waiting at the entrance of the retreat ('waiting'), and the time taken to move from the retreat entrance to the prey item ('capturing'). Spiders that went directly to the prey item spent a negligible time responding and waiting.

Black house spiders took significantly longer to respond to prey during the day than during the night ($F_{1,82}$ = 29.41, $P < 0.001$; Table 1), but this time was not significantly influenced by the type of prey ($F_{1,82}$ = 2.32, $P > 0.1$), or their interaction ($F_{1,82}$ = 2.09, $P > 0.1$). The time spent waiting at the entrance of the retreat was significantly longer for spiders foraging during the day than during the night ($F_{1,82}$ = 45.41, $P < 0.001$; Table 1). This time was not influenced by the type of prey ($F_{1,82}$ = 1.25, $P > 0.7$), but prey type had a significant effect on the magnitude of the difference between day and night ($F_{1,82}$ = 9.01, $P < 0.005$).

The total time that a spider spent exposed on the web was the sum of the time taken to capture the prey and the time spent returning to the retreat with the subdued prey item. Spiders
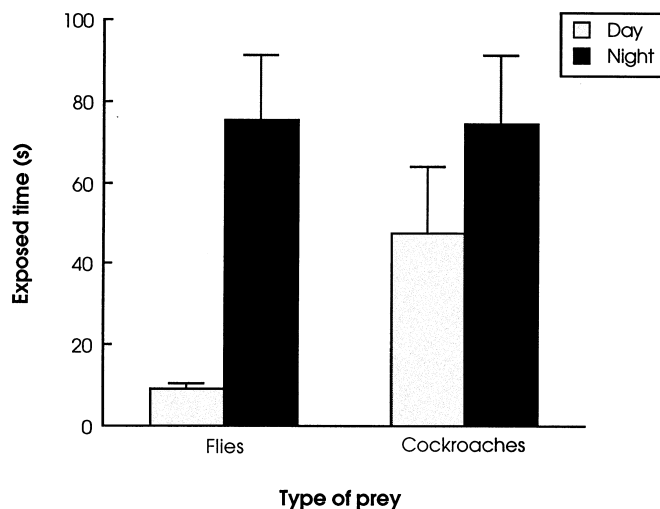
Fig. 3. The mean time that *B. insignis* was exposed on the surface of the web when it was provided with different prey items during either the day or night. Bars represent ± s.e.

remained exposed on the web for significantly longer periods during the night than during the day ($F_{1,82} = 6.87$, $P < 0.01$; Fig. 3), but the type of prey had no significant effect ($F_{1,82} = 2.76$, $P > 0.1$) and there was no significant interaction ($F_{1,82} = 0.72$, $P > 0.1$; Table 1). This pattern arose primarily as a result of the influence of the time of day on the time spiders took to return to the retreat. The time taken to capture the prey was not significantly influenced by either the time of day ($F_{1,82} = 0.17$, $P > 0.6$) or the type of prey ($F_{1,82} = 2.68$, $P > 0.1$), but rather by an interaction between these two factors ($F_{1,82} = 11.98$, $P < 0.001$). Spiders foraging during the day returned to the retreat with their prey significantly more quickly than those foraging at night ($F_{1,81} = 10.46$, $P < 0.002$), and handled flies significantly more quickly than cockroaches ($F_{1,81} = 5.37$, $P < 0.03$). There was no significant interaction between these two factors ($F_{1,81} = 2.75$, $P > 0.1$).

The time taken for the flies to escape from a web that did not have a resident spider was 3.5 ± 0.3 s ($n = 29$), which was similar to that of cockroaches (mean $= 3.3 \pm 0.2$ s, $n = 26$). Interestingly, these times were similar to the time spiders spent waiting adjacent to the retreat during the night.

Predator-avoidance behaviour and foraging efficiency

Spiders at the entrance of their retreats responded more rapidly to a simulated predator attack than those in the web handling a prey item. Spiders waiting adjacent to the retreat rapidly withdrew into the retreat after a mean of 1.4 ± 0.1 attacks, compared with 8.8 ± 0.5 attacks when they were handling a prey item on the web (paired $t = 15.37$, d.f. $= 16$, $P < 0.001$).

The second experiment revealed that the spiders responded to changes in air pressure. When the barrier was absent, the mean number of simulated attacks necessary to elicit a response from the spiders adjacent to their retreats was 1.7 ± 0.4, significantly less than that for spiders handling a prey item (mean $= 9.7 \pm 0.3$; paired $t = 17.8$, d.f. $= 11$, $P < 0.001$). However, when the barrier was present, there was little difference in the response of spiders at the entrance to the retreat (mean $= 7.8 \pm 1.0$) compared with when handling prey on the web (mean $= 9.8 \pm 0.2$; paired $t = 1.96$, d.f. $= 11$, $P > 0.07$).

Discussion

The black house spider is a nocturnally active spider, usually remaining concealed in its retreat during the day and emerging onto the edge of its web during the night. Web-building spiders are vulnerable to a number of wasps and birds (Coville 1987; Cloudsley-Thompson

1995; Elgar and Jebb 1999), and these are usually more active during the day than night. These data suggest that the retreat functions primarily as a safe haven from predators, although we cannot exclude the possibility that the retreat also provides protection from the elements (e.g. Humpreys 1975).

The time that black house spiders spent exposed on the web comprises the time taken to reach the prey item, and the time spent 'handling' the prey. The latter includes capturing, envenoming, and wrapping the prey and then returning to the retreat. The similarity in the time taken to reach the prey during the day or night is not surprising because minimising this time ensures that the prey is captured before it escapes and reduces the risk of predation or exposure to adverse environmental conditions. In contrast, the time spent handling the prey was longer at night than during the day. Shorter handling times may benefit the spider by reducing the risk of predation; but they may also attract several kinds of costs. When a prey item is bitten, the venom typically takes effect after about 30 s when struggling is greatly reduced (authors' observations). Spiders that attempt to return to the retreat with a vigorously struggling prey may experience greater energy expenditure, damage to the web or even risk of injury. Indeed, the spiders take longer to handle the larger and more vigorously struggling cockroaches than the flies. These costs could be avoided at night, when the risk of predation is probably low, by delaying the return to the retreat until after the prey has ceased struggling.

The experiment using a model predator revealed that spiders at the entrance to the retreat responded more rapidly to a simulated attack than did those handling prey in the web. We can not determine unequivocally whether this arises because spiders on the web are less able to detect an aerial threat, or whether they are trading-off the risk of predation against the risk of losing a prey item (e.g. Lima and Dill 1990; Lima 1998). The latter seems more likely, since the experiments also suggest that the spiders respond to differences in air pressure rather than visual cues. Most spiders have relatively poor visual acuity, but their integument contains numerous trichobothria, which can detect fine vibrations and changes in air pressure (Foelix 1982). These stimuli may alert a spider to approaching predators, such as predatory wasps or birds.

While the retreat can provide some protection against predators, remaining within the retreat most likely reduces the foraging success of the spider. Spiders take longer to reach prey items that were introduced into the web during the day than during the night, primarily because they are in the retreat during the day. The time taken for prey to escape from a web is generally less than that to reach it during the day. However, spiders waiting at the edge of the web at night could usually reach the prey before it escaped.

The foraging success of *B. insignis* may therefore be compromised by behaviours that reduce the risk of predation. Remaining within the retreat and handling the prey for shorter periods may reduce the risk of predation, but also reduce foraging efficiency. Although the life history of *B. insignis* is not known, females probably live for several years and therefore could reproduce more than once (Main 1976). Studies of a few spiders suggest that predation rather than food limitation is responsible for most mortality (e.g. Conley 1985; Vollrath 1985; Riechert and Hedrick 1990). For spiders that live a long time, the costs of reduced fecundity through poor foraging efficiency may be outweighed by the benefits of reducing the risk of predation.

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