ORIGINAL PAPER

Attending to detail by communal spider-eating spiders

Robert R. Jackson · Ximena J. Nelson

Abstract Communal predators may often need to make especially intricate foraging decisions, as a predator's success may depend on the actions of its neighbours. Here, we consider the decisions made by *Portia africana*, a jumping spider (Salticidae) that preys on other spiders, including *Oecobius amboseli* (Oecobiidae), a small prey spider that lives under small sheets of silk (nests) on the walls of buildings. *P. africana* juveniles settle near oecobiid nests and then ambush oecobiids as they leave or enter the nest. Two or more *P. africana* juveniles sometimes settle at the same nest and, when an oecobiid is captured, the *P. africana* juveniles may share the meal. We investigated the joining decisions made by naïve *P. africana* juveniles. Experiments were based on using lures (dead spiders positioned in lifelike posture) arranged in a series of 17 different scenes defined by the presence/absence of a nest, the lure types present and the configuration of the lures and the nest. Our findings imply that *P. africana* juveniles make remarkably precise predatory decisions, with the variables that matter including whether a nest is present, the identity of spiders inside and outside a nest and how spiders are positioned relative to each other and the nest.

Keywords Foraging · Predatory tactics · Perception · Decision-making · Communal predation · Araneophagy

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Introduction

It is becoming increasingly apparent that foragers attend to multiple factors, both extrinsic and intrinsic, when assessing where to forage or what to forage on. A basic classification step for a predator is to distinguish prey from non-prey, the European toad, *Bufo bufo*, being perhaps the most celebrated example of a predator for which we have a detailed understanding of how this basic task is achieved. To a large extent, the eyes of *B. bufo* appear to be designed to function as "bug detectors", with "bug" seeming to be anything that meets certain basic criteria related to movement, size, shape and contrast (Lettvin et al. 1959; Wachowitz and Ewert 1996; Ewert 2004). The toad's natural diet may span a wide taxonomic range of arthropod species, but most of the fine distinctions between these different arthropods are irrelevant to the toad for which the most important task may be making a rapid decision to attack or not based on distinguishing bug from non-bug. There are other predators, however, that do considerable classifying of their prey into distinct categories. Predators that adopt conditional predatory strategies in which different taxonomic prey types are targeted with distinctively different innate prey-capture tactics ('predatory versatility': Curio 1976) are of particular interest because a versatile predator's different prey-specific tactics reveal the predator's underlying innate classification scheme (Nelson and Jackson 2011). Here, we take a step further and consider how other variables, including features of the physical environment and other animals that are not the direct target of a predatory attack, might influence a forager's decisions (multi-factor foraging decisions'). Understanding a forager's proficiency at making multi-factor decisions is a step toward understanding the forager's cognitive capacities.

Intra-guild predation (predators preying on other predators) is a context in which multi-factor decisions have been especially often considered, because the interplay between competition and predation may have a sizable influence on community structure (Polis and Holt 1992; Holt and Polis 1997; Donadio and Buskirk 2006). Capacity for making decisions that balance food and safety appears to be widespread among predators (Lima and Dill 1990; Brown and Kotler 2004) large (e.g., mammals: Mukherjee et al. 2009) and small (e.g. insects: Sih 1980). Often the risks in a predator–predator encounters may run in both directions, with each of the two individuals at significant risk of becoming prey for the other (Nelson and Jackson 2011). Predators may often be a risk of injury or death even when the prey encountered is not another predator (Temple 1987; Brodie and Brodie 1999). Multi-factor foraging decisions may also be influenced by factors other than risk of injury or death.

The presence of conspecific neighbours is another factor known to influence predator foraging decisions (Dall et al. 2005). For example, web-building and movement decisions by the spider *Latrodectus hesperus* are influenced by the presence of conspecific neighbours (Salomon 2007, 2009). Here, in research based on a jumping spider, or salticid, we examine whether predators that routinely capture prey in the presence of conspecific individuals ('communal predators') may need to classify situations or scenes paying attention to the location of conspecific predators, as a predator's success may depend on the actions of conspecific neighbours. The salticid we consider as a case study appears to make especially intricate decisions and this, in turn, makes this example interesting in the context of cognitive behaviour being expressed by an animal with a small nervous system.

There seems to be an expectation that the most interesting examples of animal cognition should come from animals with large brains, as conventional wisdom tells us they will have the necessary neural capacity. Yet identifying precisely how and when small-brained animals express these limitations has been notoriously difficult (Chittka and Niven 2009; Eberhard 2011). The honey bee (*Apis mellifera*) is particularly interesting when we consider multi-factor foraging decisions. For example, the waggle dance is a scout bee's primary method for recruiting other workers to a distant food source, but scouts that have detected a serious predation threat at a site stop recruiting other bees to this site (Abbott and Dukas 2009). Sometimes bees may also perform 'stop signals' toward other foragers performing waggle dances directing foragers to areas in which there is predation risk, thus causing these foragers to discontinue recruitment to that location (Nieh 2010).

Turning to spiders, some of the most intricate predatory strategies (Herberstein and Wignall 2011; Jakob et al.

2011; Nelson and Jackson 2011) known have come from research on jumping spiders (Salticidae), and especially *Portia*, a salticid genus known for specialising at eating other spiders (araneophagy) and for deploying large repertoires of prey-specific predatory tactics (Harland and Jackson 2004). For *Portia*, predatory versatility is often linked to aggressive mimicry, 'aggressive mimicry' being a general term used to describe how *Portia*, by using its appendages (legs and palps) and abdomen, makes signals on web silk and, with these signals, manipulates the prey spider's behaviour (Harland and Jackson 2004; Jackson and Pollard 1996). However, the present study is different because previous research on *Portia* has been restricted largely to considering solo rather than communal predation.

In East Africa, the small juveniles (body length 1.5–3.0 mm) of *Portia africana* (Fig. 1a) prey especially often on *Oecobius amboseli* (Oecobidae), a small spider (adult body length 2–3 mm, Fig. 1b) that spins sparsely woven tent-like silk nests (diameter c. 5 mm) on boulders, tree trunks and the walls of buildings, with predation often being communal. Investigating the foraging decisions of *P. africana* juveniles is of particular interest because these are predators that appear to do considerably more than classify types of prey. Our hypothesis is that they also carry out intricate classifying of the situations or scenes in which prey are encountered, with the location and likely next actions of conspecific neighbours being especially important variables.

Except when otherwise specified, we will use the shorter expression 'oecobiid' for *O. amboseli* and '*Portia*' for small juveniles of *P. africana*. The rationale for saying that *Portia* practises communal predation is the previous research showing that two or more of these predators may converge on the same oecobiid nest and, when one predator captures an oecobiid, another may join and feed alongside (Jackson et al. 2008). We hesitate to say what happens is cooperative, as using the term 'cooperative' suggests that two or more animals act in harmony with each other in the achieving of a mutually beneficial outcome (Packer and Ruttan 1988). However, for *Portia*, as for many spiders, often this term might be misleading, with it being more appropriate to characterise feeding together on the same prey as being a consequence of competitors achieving a reluctant truce (see: Amir et al. 2000; Jackson 1979; Kim et al. 2005; Vanacker et al. 2004; Whitehouse and Jackson 1998).

When an insect contacts its nest, the resident oecobiid rushes out and covers the insect with silken threads (Glatz 1967). However, when disturbed by a potential predator, the oecobiid runs away from the nest in a straight line, freezes and then, after a variable, and often lengthy, interval, walks back and enters the nest. The behaviour of a

Fig. 1 Spiders used for testing. **a** *Portia africana* juvenile (body length 2.5 mm). **b** *Oecobius amboseli* adult (body length 2.5 mm)

Portia juvenile during an encounter with an oecobiid can also be characterised as aggressive mimicry because, upon finding *O. amboseli* in a nest, it first settles nearby and then, having remained quiescent for a highly variable interval, begins probing intermittently on nest silk with its palps and intermittently striking the nest with its forelegs. The oecobiid eventually responds by leaving the nest. *Portia* exploits the oecobiid's predisposition to respond in this way either by making a predatory attack when the oecobiid comes out of the nest or, if that fails, by waiting and ambushing the returning oecobiid (Jackson et al. 2008).

Our overarching hypothesis is that *Portia* attends simultaneously to multiple factors when making foraging decisions. We investigate some of these factors here by presenting *Portia* with a series of scenes and determining whether *Portia* attacks a member of the scene, settles within the scene or fails to respond. Our specific hypotheses are that *Portia* attends to whether a nest, whether an oecobiid and whether another *Portia* are in the scene and also to the specific locations and orientation of the scene members.

Methods

All test subjects were F2-generation juveniles (body length, 2.5 mm) of *P. africana* from laboratory culture (standard rearing procedures; for details, see Jackson et al. 2008). As our goal was to address the innate decisions of the predator, we ensured that test spiders and their parents had not experienced prior encounters with oecobiids.

By basing our experiments on the reactions of test spiders to stationary lures (i.e., dead spiders positioned in lifelike posture, sprayed with aerosol plastic to remove odour cues), we avoided confounding variables that can arise when testing with living prey, and we ensured that test spiders were using vision-based cues alone. This was feasible because, although the eyes of most spiders, including oecobiids, are not suitable for discerning the appearance of static objects in precise detail (Land and Nilsson 2002), salticids see with exceptional spatial acuity owing to their unique, complex eyes (Land 1974; Williams and McIntyre 1980), and numerous earlier studies have demonstrated that using motionless lures is a realistic alternative to testing with living prey and living rivals, particularly among *Portia* (e.g., Harland et al. 1999; Harland and Jackson 2001; Nelson and Jackson 2006).

For making lures (for details, see Li and Jackson 1996), we used adult oecobiid females (body length 2.5 mm) collected from the field as needed and *Portia* juveniles (body length 2.5 mm) from the laboratory culture. Measurements of spider body length were accurate to the nearest 0.5 mm. All test spiders were *Portia* juveniles of the same size as the *Portia* juveniles used for making lures. In experiments, the treatments were based on presenting test spiders with scenes; each scene was defined by the configuration and orientation of the lures present on a disc, the spiders used for making the lures, whether one of the spiders was in an artificial nest, and the distance between lures and the nest (Table 1). The disc was the flat surface of a red rubber stopper (hereafter referred to simply as the 'disc', Fig. 2a). For making each artificial nest (diameter 5.0 mm), silk was taken from a nest built by an oecobiid that had been kept in the laboratory without prey for the previous 7 days and then the silk was placed over a lure. The assortment of lures, or lures plus a nest, was always arranged centred on the disc (i.e., when the scene consisted of a single lure or single empty nest, the lure or nest was at

Table 1 Data from testing *Portia africana* juveniles with 'scenes' made from lures (dead spiders mounted in lifelike posture) and silken nests. See text for details. Respond: attack or settle. *Black polygon* lure made from adult *Oecobius amboseli* female (*Oa*). *Grey polygon* lure made from *Portia africana* juvenile (*Pa*). *Radiating lines* nest. *White circles* ('eyes') represent direction in which lure faced. When more than one lure in a scene the centre-to-centre distances of all lures was 8 mm unless stated otherwise

Scene No.	Scene description	Diagram	N	Response (%)	Attacked nest[a] (N)	Attacked already settled spider (N)	Settled (N)	Settled facing nest (if present) (N)	Settled facing settled spider (if present) (N)	Settled in atypical orientation (N)
1	*Oa*. No nest		100	30	NA	30	0	NA	0	0
2	*Pa*. No nest		100	3	NA	3	0	NA	0	0
3	*Pa* and *Oa* facing each other. No nest		100	12	NA	12	0	NA	0	0
4	Two oecobiids facing each other. No nest		100	27	NA[b]	27[b]	0	NA	0	0
5	Empty nest		200	4.5	0	NA	9	9	NA	0
6	*Oa* in nest		200	42	9	NA	75	73	NA	2
7	*Pa* in nest		100	1	0	NA	1	0	NA	1
8	*Oa* facing empty nest		200	20.5	4	37	0	0	0	0
9	*Pa* facing empty nest		200	15	1	0	29	29	0	0
10	*Pa* and *Oa* (in nest), facing each other		200	66	1	0	131	128	3	0
11	Two *Oa* (one in nest), facing each other		100	29	16	3	10	6	3	1
12	One *Portia* and one oecobiid, facing each other. *Portia* in nest		100	20	2	13	5	2	3	0
13	Two *Pa* (one in nest), facing each other		100	6	0	1	5	4	1	0
14	*Pa* and *Oa* (in nest), facing each other. *Pa* 24 mm from nest		200	34.5	4	1	64	61	3	0
15	*Pa* and *Oa* (in nest), facing away from each other (*Pa* facing away from nest)		200	35.5	10	1	60	55	4	1
16	*Pa* and *Oa* (in nest), facing same direction (*Pa* facing away from nest)		100	27	3	1	23	21	2	0
17	*Pa* and *Oa* (in nest). *Oa* facing *Pa*. *Pa* perpendicular to nest		100	74	1	0	73	73	0	0

[a] If two lures without nest, attack directed at lure above

[b] Only type of spider to which attack was directed recorded, not whether to *top* or *bottom* spider
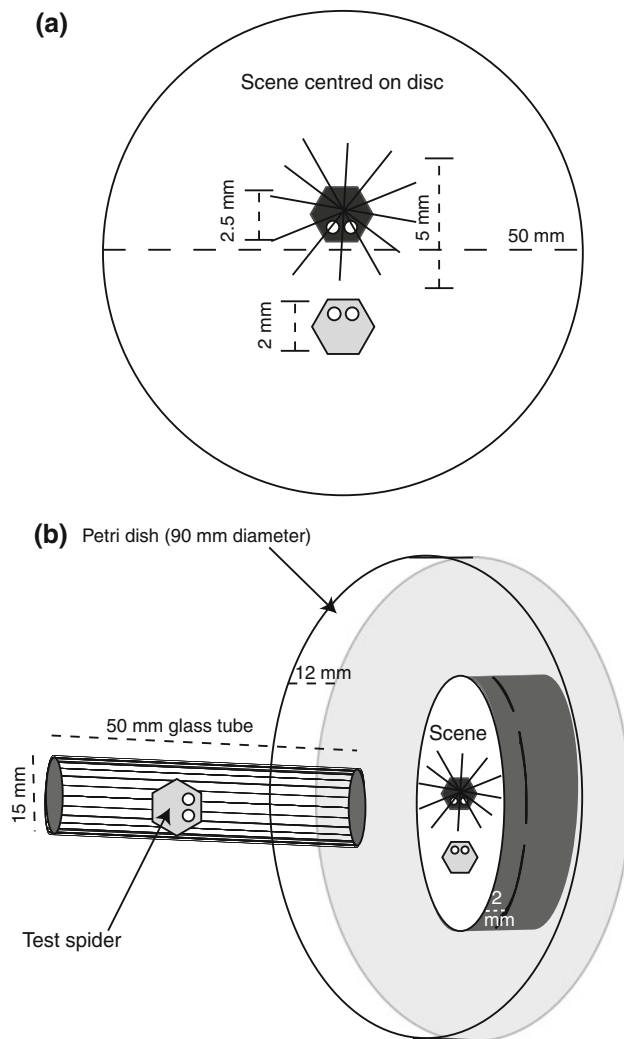
(a)

(b) Petri dish (90 mm diameter)

Fig. 2 Testing apparatus (not drawn to scale) **a** *top view* of disc supporting a scene with a nest and two lures (*Oecobius* inside the nest and *Portia* outside the nest). Dimensions of disc, lures and nest shown. **b** *Perspective view* of testing chamber with rubber stopper, supporting the scene, protruding 2 mm into the Petri dish and aligned opposite the glass tube through which test spiders entered the testing chamber

the centre of the disc; otherwise, the centre of the array of lures and nest was at the centre of the disc).

A test chamber was made by inserting the disc into a hole centred on bottom of a Petri dish so that it protruded 2 mm into the dish (Fig. 1b), such that with the top on the dish, the scene was inside. The dish, along with the scene, was next turned vertical and held in place by clamping the distal end of the disc to a retort stand (lowest point of Petri dish 200 mm above bench).

Before testing began, a test spider was placed in a glass tube (see Fig. 2b for dimensions) with a rubber stopper inserted in each end. After an acclimation period of 5 min, the stopper was removed from the end of the tube farthest from the spider inside and the open end of the tube was

positioned in a hole situated in the centre of the vertically oriented Petri dish. The open end of the tube was flush with the inside surface of the Petri dish and directly across from the centre of the scene.

Tests began when the test spider walked out of the tube and into the Petri dish. Testing was aborted on the rare occasions when test spiders leapt out of the tube, instead of walking out, or did not leave the tube within 30 min. No individual test spider, lure or nest was used more than once, and all tests were conducted between 0800 and 1,200 h (laboratory photoperiod, 12L-12D, lights on 0700 h).

Tests ended and the test outcome was recorded when one of the following occurred: the test spider settled (i.e., the test spider walked on to the disc and, without first attacking a lure or a nest, became quiescent for 2 min), attacked (i.e., without first settling, the test spider leapt, lunged or struck at a lure or a nest) or showed no response (after leaving the tube, 60 min elapsed without the test spider settling or attacking). When the test spider settled, we also recorded its orientation as either toward a lure or the nest (i.e., the test spider was facing no more than 45° away) or atypical (i.e., the test spider was not oriented toward any one of the lures or toward the nest). We also recorded the target whenever attacks were made.

When only a single lure was present in a scene, it always faced downward and, unless stated otherwise, all lures within nests faced downward. When two lures were present without a nest in the scene, they faced each other unless stated otherwise. When a scene included, besides a nest (with or without a lure inside), a lure outside of the nest, the lure outside was referred to as an 'already settled spider'. Already settled spiders were positioned vertically below the nest and, unless stated otherwise, they were facing the nest. Depending on the scene, two distances were applicable (8 and 24 mm). Except when stated as 24 mm, distance was 8 mm. When a nest and one or more lures were present, the relevant distance was from the centre of the lure to the centre of the nest. When two lures, but no nest, were present in a scene, the relevant distance was from the centre of one lure to the centre of the other lure.

Using tests of independence based on Fisher exact tests (FET) and Chi-square tests, we carried out pair-wise comparisons of scenes. Bonferroni adjustments for multiple comparisons were applied and, unless stated otherwise, all results that were significant remained so after adjusting alpha. We used binomial tests where appropriate. Latency to settle and attack was also recorded. However, as there were no significant differences across scenes for either of these variables (settle, $H_{11} = 17.05$, $P = 0.107$, median $= 25.8$ min; attack, $H_{14} = 10.73$, $P = 0.707$, median $= 26.2$ min; Kruskal–Wallis tests), these data are not shown.

Results and discussion

Across all 17 treatments, there were clear differences in the overall responses of spiders considering whether they attacked, settled or did not respond ($H_2 = 14.09$, $P < 0.001$; attack median $= 5$, settle median $= 9$, no response median $= 70$; Kruskal–Wallis test).

Do test spiders distinguish between lure types in the absence of a nest?

Regardless of whether one or two lures were present, test spiders never settled in the absence of a nest, but sometimes they attacked a lure (Scenes 1–4, Table 1). The number of test spiders that attacked a solitary oecobiid lure was significantly higher than the number that attacked a solitary *Portia* lure (Scenes 1 and 2, $P < 0.001$, FET). When two lures were present and facing each other, with one being an oecobiid and the other being a *Portia*, 12 test spiders made an attack (Scene 3, Table 1), with 11 aiming the attack at the oecobiid and only one aiming the attack at the *Portia* ($P = 0.003$, binomial test, $H_2 = 50/50$).

These findings imply that, in the absence of a nest, part of *Portia*'s strategy is to attack when it sees a solitary oecobiid and that its strategy includes no overt response to solitary conspecific juveniles. However, seeing a *Portia* seems to diminish the test spider's inclination to attack at all, as the number of test spiders that attacked either of the two lures when the scene was a *Portia* lure plus an oecobiid lure (Scene 3) was significantly less ($\chi^2 = 9.76$, $P = 0.002$) than the number that attacked a solitary oecobiid lure (Scene 1).

With Scene 4 (2 oecobiids facing each other), we considered as an alternative hypothesis the possibility that reduction in the number of attacks was a consequence of simply seeing two spiders instead of one. Our findings were contrary to this alternative hypothesis, as the number of test spiders that made an attack when presented with Scene 4 was significantly higher than the number that made an attack when presented with Scene 3 ($\chi^2 = 7.17$, $P = 0.007$) and not significantly different from the number that made an attack when presented with Scene 1 ($\chi^2 = 0.22$, $P = 0.638$). Evidently, the inhibitory effect depends on the identity of the second spider.

Is the test spider's behaviour influenced by whether there is a lure inside a nest and by the identity of the lure?

Test spiders settled and attacked significantly more often when the scene was an oecobiid inside the nest (Scene 6) instead of only an empty nest (Scene 5) (Scene 5 and 6 compared: settle, $\chi^2 = 65.64$, $P < 0.001$; attack,

$P = 0.002$, FET). However, findings from using Scene 7 (i.e. when a *Portia* was the spider inside the nest) were not significantly different from findings when using Scene 5 (empty nest) (Scene 5 and 7 compared: settle, $P = 0.084$, FET; no attacks made, Table 1). Comparing Scenes 6 and 7, significantly more test spiders settled when the nest occupant was an oecobiid instead of a *Portia* ($P = 0.024$, FET). These findings imply that it is not just seeing a nest or just seeing a nest occupied by a spider that matters as a cue for settling and that it is, instead, seeing specifically a nest with an oecobiid inside that is critically important for encouraging settling by test spiders.

Does the identity of a lure outside an empty nest influence the test spider's behaviour?

Significantly fewer test spiders settled and significantly more attacked when the scene was an empty nest accompanied by an oecobiid outside (Scene 8) instead of an empty nest alone (Scene 5) (settle, $P = 0.002$, FET; attack, $P < 0.001$, FET). Significantly more test spiders settled when the scene was an empty nest accompanied by a *Portia* outside (Scene 9) instead of an empty nest alone (Scene 5) ($\chi^2 = 11.63$, $P < 0.001$; number that attacked not significantly different, $P = 0.500$, FET). Comparing the two scenes in which there was an empty nest accompanied by a lure outside, significantly fewer test spiders settled and significantly more attacked when the lure was an oecobiid (Scene 8) instead of a *Portia* (Scene 9) (for settle and for attack, $P < 0.001$, FET; Table 1). These findings imply that test spiders are encouraged to settle by seeing that specifically a *Portia* is beside an empty nest.

When there is an oecobiid inside a nest, is the test spider's behaviour influenced by the presence and identity of another spider already settled outside?

The number of test spiders that settled when only an oecobiid-occupied nest was present (Scene 6) was significantly less than the number that settled when an already settled *Portia* was present as well (Scene 10) (settle, $\chi^2 = 31.39$, $P < 0.001$; although fewer attacked ($P = 0.02$, FET), this was not significant after Bonferroni adjustment). When another oecobiid was already settled outside a nest occupied by an oecobiid (Scene 11), the number of test spiders that settled was significantly less and the number that attacked was significantly more than when the scene was an oecobiid-occupied nest alone (Scene 6) (settle, $\chi^2 = 24.83$, $P < 0.001$; attack, $\chi^2 = 16.56$, $P < 0.001$). When the already settled spider was a *Portia* (Scene 10), significantly more test spiders settled and

significantly fewer attacked than when the already settled spider was an oecobiid (Scene 11) (settle, $\chi^2 = 82.44$, $P < 0.001$; attack, $P = 0.001$, FET). These findings imply that a test spider's settling decisions are influenced by seeing another spider already settled at an oecobiid-occupied nest and also imply that the identity of the spider already settled beside a nest occupied by an oecobiid is important, with settling being encouraged by seeing specifically another Portia beside the nest.

When a nest, an oecobiid and a Portia are present in the scene, is the test spider's behaviour influenced by the identity of the spider inside the nest?

When a Portia was inside the nest and an oecobiid was outside (Scene 12), significantly fewer test spiders settled ($\chi^2 = 98.46$, $P < 0.001$) and significantly more test spiders attacked ($P < 0.001$, FET) than when an oecobiid was inside and a Portia was outside (Scene 10). These findings imply that test spiders pay attention to more than just the presence of the three key ingredients that make a scene salient (a nest, an oecobiid and a Portia) and instead also attend to which of the two spiders is inside and which is outside the nest.

When a Portia is already settled outside, is the test spider's behaviour influenced by the identity of the spider inside the nest?

Significantly more test spiders settled when a Portia was beside a nest occupied by an oecobiid (Scene 10) instead of a nest occupied by a Portia (Scene 13) ($\chi^2 = 98.46$, $P < 0.001$; number that attacked not significantly different, $P = 0.446$, FET). These findings imply that the identity of the spider inside a nest is salient to test spiders, with it being specifically the presence of oecobiids in nests that encourages settling.

When there is a Portia inside a nest, is the test spider's behaviour influenced by the identity of another spider outside?

Significantly more test spiders attacked when the spider outside the nest was an oecobiid (Scene 12) instead of a Portia (Scene 13) ($P < 0.001$, FET), but most of the attacks were directed at the oecobiid settled outside the nest (Table 1). However, the number of test spiders that settled when the spider outside the nest was an oecobiid (Scene 12) was not significantly different from the number that settled when the spider outside was a Portia (Scene 13) ($\chi^2 = 1.00$, $P = 1.00$). These findings suggest that a Portia seen inside a nest is largely irrelevant to test spiders.

When the only lure present is a Portia, does the location of the lure matter to the test spider?

The number of test spiders that settled and the number that attacked when the scene was a Portia in a nest (Scene 7) was not significantly different from the number that settled and the number that attacked when the scene was a Portia in the absence of a nest (Scene 2) (settle, $P = 0.500$, FET; attack, $P = 0.123$, FET). However, significantly fewer test spiders settled when the scene was a Portia inside a nest (Scene 7) instead of a Portia beside an empty nest (Scene 9) ($P < 0.001$, FET; number that attacked not significantly different, $P = 0.667$, FET). When the Portia present in the scene was not in a nest, significantly more test spiders settled when an empty nest was present (Scene 9) than when there was no nest in the scene (Scene 2) (settle, $\chi^2 = 16.05$, $P < 0.001$; number that attacked not significantly different, $P = 0.098$, FET, Table 1). These findings are additional evidence that, for test spiders, the presence of a Portia inside a nest is largely irrelevant and additional evidence that test spiders are encouraged to settle by seeing that a spider already settled beside a nest is specifically a Portia.

When there is an oecobiid in a nest, does the presence of another oecobiid outside influence the test spider's behaviour?

Significantly fewer test spiders settled and significantly more attacked when the scene was an oecobiid-occupied nest accompanied by another oecobiid settled outside (Scene 11) instead of the oecobiid-occupied nest alone (Scene 6) (settle, $\chi^2 = 24.83$, $P < 0.001$; attack, $\chi^2 = 16.56$, $P < 0.001$). These findings suggest that seeing an oecobiid exposed outside a nest encourages attacking and discourages settling.

Is test spider behaviour influenced by the distance between a Portia and a nest occupied by an oecobiid?

The number of test spiders that settled when the already settled Portia was far away (24 mm from the nest) (Scene 14) was significantly less than the number that settled when the already settled Portia was close (8 mm from the nest) (Scene 10) ($\chi^2 = 44.92$, $P < 0.001$; numbers that attacked not significantly different, $P = 0.093$, FET). The number that settled and the number that attacked when the already settled Portia was far away was not significantly different from the number that settled or attacked when only a nest occupied by an oecobiid was present (Scene 6) (settle, $\chi^2 = 1.334$, $P < 0.248$; attack, $\chi^2 = 1.184$, $P < 0.276$). These findings suggest that, although a Portia that is already settled is salient to test spiders when close (8 mm), it is largely irrelevant when far away (24 mm).

When the scene is a nest occupied by an oecobiid accompanied by a *Portia* outside and facing away from the nest, is the test spider's behaviour influenced by the orientation of the oecobiid inside the nest?

The number of test spiders that settled or attacked when the oecobiid was facing away from *Portia* (Scene 15) was not significantly different from the number that settled or attacked when the oecobiid faced *Portia* (Scene 16) (settle, $\chi^2 = 1.63$, $P = 0.201$; attack, $P = 0.198$, FET). The orientation of oecobiids inside nests seems to be of no concern to test spiders.

When the scene is a nest occupied by an oecobiid accompanied by a *Portia* outside, is the test spider's behaviour influenced by the orientation of the *Portia* to the nest?

Significantly more test spiders settled when an already settled *Portia* was facing the oecobiid in the nest (Scene 10) rather than facing directly away (pooled data for Scene 15 and Scene 16) ($\chi^2 = 70.16$, $P < 0.001$), but fewer attacked ($P = 0.003$, FET). However, the test spider's decisions when the already settled *Portia* was perpendicular to the nest (Scene 17) were not significantly different from when the already settled *Portia* was facing the nest (Scene 10) (settle, $\chi^2 = 1.72$, $P = 0.189$; attack, $P = 0.446$, FET) and were significantly different from when the already settled *Portia* was facing away from the nest (pooled data for Scenes 15 and 16) (settle, $\chi^2 = 64.79$, $P < 0.001$; attack, $P = 0.051$). These findings imply that test spiders attend to already settled *Portia* that are oriented directly toward a nest or even 90° away from a nest, but they seem to take no interest in *Portia* that are oriented 180° away from the nest, essentially behaving as if they simply were not there.

Orientation of settling

Most (95%) spiders settled when there was a nest in the scene (pooled data from Scenes 5–17; Table 1: 451 out of 475), and none settled in the absence of a nest. The orientation of test spiders when they settled was consistent with test spiders attending to the identity of the spider inside the nest. Pooling all data from testing with scenes in which there was a lure made from a *Portia* positioned in any orientation to, and at either of the two distances from, a nest occupied by an oecobiid, 338 of 351 (96%) of the test spiders that settled were oriented to the nest (Scenes 10, 14–17). However, when the scene was an oecobiid outside and a *Portia* inside (Scene 12), only five spiders settled, and only two of these settled facing the nest. These findings are consistent with settling functioning as preparation to attack an oecobiid that will be leaving the nest.

Targets of attack

Of the 41 test spiders that made an attack when the scene was an oecobiid outside an empty nest (Scene 8), the number that aimed the attack at the oecobiid outside the nest (37) was significantly higher ($P < 0.001$, binomial test, $H_o = 50/50$) than the number that aimed the attack at the nest (4). However, when a *Portia* was outside an empty nest, only one spider attacked, and this was an attack aimed at the nest (Scene 9).

When there were two oecobiids, one in a nest and the other outside (Scene 11), the number of test spiders that aimed an attack at the nest (16) was significantly more ($P = 0.002$, binomial test, $H_o = 50/50$) than the number that aimed an attack at the oecobiid outside (3). When there were two *Portia*, one in a nest and the other outside (Scene 13), only one test spider made an attack, and this was an attack aimed at the *Portia* outside.

When the scene was a *Portia* in a nest and an oecobiid outside (Scene 12), the number of test spiders that aimed attacks at the oecobiid outside the nest (13) was significantly more ($P < 0.001$, binomial test, $H_o = 50/50$) than the number that aimed attacks at the nest (2). However, when an oecobiid was in a nest and a *Portia* was outside (pooled data for Scenes 10, 14–17), the number of test spiders that aimed attacks at the nest (19) was significantly more ($P < 0.001$, binomial test, $H_o = 50/50$) than the number that aimed at the *Portia* (3). These findings are consistent with the hypothesis that oecobiids are being targeted for attack, rather than *Portia*, and that attacks tend to be aimed at nests containing an oecobiid, perhaps because the predatory strategy involving 'startling' the spider to escape the nest and then ambushing it is particularly successful.

General discussion

The variables that matter

One of the first conclusions implied by our findings is that *Portia* is proficient at determining whether the spider it sees is an oecobiid (*O. amboseli*) or a conspecific juvenile. This discrimination is achieved despite the two spiders being of similar size and despite the absence of movement cues. In the absence of a nest, *Portia* often attacked oecobiids, but *Portia* seemed to ignore other *Portia*. However, other findings imply that *Portia*-based predatory decisions on considerably more than simply the identity of the other spider it encounters.

The scene that was most effective at eliciting settling was an oecobiid-occupied nest accompanied by an already settled *Portia* that was close to the nest (8 mm away) and

oriented no more than 90° away from the nest. However, settling was also elicited, although less strongly, by scenes that included only some of these features.

For *Portia* deciding whether to settle, the presence of a nest seemed to be a prerequisite. When the nest was occupied, whether a spider in a nest was an oecobiid or a *Portia* seemed to be important, with an oecobiid in a nest strongly encouraging settling, but a *Portia* in a nest seeming to be irrelevant. When a test spider encountered an oecobiid outside a nest, it often attacked, but seeing a *Portia* outside a nest, even when the nest was empty, seemed to be a cue specifically for settling.

These findings imply that simply seeing two spiders does not suffice as a settling cue. On the contrary, when there are two spiders in a scene, *Portia* attended to both spiders' identities and to both spiders' locations. For a *Portia* deciding whether to settle, it seemed to be important that the spider in the nest was specifically an oecobiid and that the spider outside was specifically an already settled *Portia*.

When deciding whether to settle, the distance between an already settled *Portia* and a nest appeared to be important to *Portia*. Two distances were used in our experiments (8 and 24 mm), but the presence of an already settled *Portia* appeared to be relevant only when close (8 mm from the nest). However, while an already settled *Portia* close to a nest encouraged settling, this was only if the spider was oriented toward or perpendicular to the nest (i.e., the presence of a *Portia* oriented directly away from a nest had no apparent effect on settling decisions).

Innate predatory versatility

These findings reveal some of the decision rules underlying an innate predatory strategy that appears to exploit the antipredator defences of the prey. The test spiders were *Portia* juveniles from laboratory cultures (F2 generation) and standardised rearing ensured that prior experience with oecobiids by test spiders or their parents (learning or maternal effects) were unlikely explanations for our findings. We conclude instead that *Portia* juveniles are innately predisposed to base settling decisions on highly specific features of the scenes they encounter.

This is also an example of predatory versatility (see Curio 1976), as *Portia* attacked during encounters with oecobiids in the absence of nests and settled during encounters with oecobids in nests. Pronounced predatory versatility appears to be characteristic of the genus *Portia* (Harland and Jackson 2004; Jackson and Wilcox 1998). Earlier research has revealed numerous examples of adult *Portia* from several species adopting conditional predatory strategies. In some instances, prey-specific prey-capture behaviour is deployed with the prey types that are salient to

Portia corresponding more or less to scientific (i.e. Linnean) taxonomy. However, there are also examples where the variables determining *Portia*'s tactics do not pertain exclusively to the formal taxonomy. This is illustrated, for example, by *P. labiata* from Los Baños in the Philippines. The Los Baños *P. labiata* preys especially often on spitting spiders (*Scytodes*), and it uses different innate tactics depending on whether or not the spitting spider is carrying eggs (Jackson et al. 2002).

However, the conditional strategy adopted by *P. africana* juveniles seems to be based on exceptionally intricate detail: the identity, location and positioning of two different spiders, one being prey and the other being a conspecific individual. Examples of innate predatory decisions based on attention to a comparable level of detail appear to be rare not only for species in the genus *Portia*, but also for predators general.

Parallels to the strategy of *P. africana* juveniles are known from research on another salticid species, *Cyrba algerina*. Like *P. africana* juveniles, *C. algerina* settles beside nests occupied by oecobiids, intermittently probing or striking the nest and capturing the oecobiid either as it leaves the nest or later when it returns to the nest (Cerveira and Jackson 2011; Guseinov et al. 2004). However, *P. africana* juveniles differ from *C. algerina* by practising communal predation, suggesting that communal predation may favour ability to base foraging decisions on particularly fine detail.

Capacity of small nervous systems

Neurons are constrained to be at least 2 μm in diameter (Beutel et al. 2005). A corollary of this is that bigger animals, such as birds and mammals, can accommodate many more neurons in their sense organs and brains than is possible for small animals, such as arthropods. Salticid brains could easily rest on a pinhead and are believed to contain roughly half a million neurons (M.F. Land, pers. comm.), or half that of a honeybee. Common sense may tell us that nervous system size must impose limitations that will be more severe for arthropods than for birds and mammals, whose brains might consist of several billion neurons, but there is considerable uncertainty when trying to specify what these limitations might actually be (Chittka and Niven 2009; Eberhard 2007, 2011).

Honeybees are possibly the most celebrated example (Srinivasan 2010) of an arthropod that defies the commonsense expectation of small-brain animals being restricted to having minimal capacity for especially complex or cognitive behaviour. However, salticids, and especially the species in the genus *Portia* (Nelson and Jackson 2011), seem to be the bee's arachnid rivals. *Portia* juveniles are a striking example, as these are particularly

small individuals and yet they attend to exceptionally specific details when making predatory decisions.

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