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Interpopulation variation in the risk-related decisions of *Portia labiata*, an araneophagic jumping spider (Araneae, Salticidae), during predatory sequences with spitting spiders

Abstract The extent to which decision-making processes are constrained in animals with small brains is poorly understood. Arthropods have brains much smaller and simpler than those of birds and mammals. This raises questions concerning limitations on how intricate the decision-making processes might be in arthropods. At Los Baños in the Philippines, *Scytodes pallidus* is a spitting spider that specialises in preying on jumping spiders, and *Portia labiata* is a jumping spider that preys on *S. pallidus*. Scytodid spit comes from the mouth, and egg-carrying females are less dangerous than eggless scytodids because the female uses her chelicerae to hold her eggs. Held eggs block her mouth, and she has to release them before she can spit. The Los Baños *P. labiata* sometimes adjusts its tactics depending on whether the scytodid encountered is carrying eggs or not. When pursuing eggless scytodids, the Los Baños *P. labiata* usually takes detour routes that enable it to close in from behind (away from the scytodid's line of fire). However, when pursuing egg-carrying scytodids, the Los Baños *P. labiata* sometimes takes faster direct routes to reach these safer prey. The Los Baños *P. labiata* apparently makes risk-related adjustments specific to whether scytodids are carrying eggs, but *P. labiata* from Sagada in the Philippines (allopatric to *Scytodes*) fails to make comparable risk-related adjustments.

Keywords Salticidae · *Portia labiata* · Scytodidae · *Scytodes pallidus* · Assessment

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Introduction

Application of models from behavioural ecology to real animals will usually depend on an understanding of animal cognition, with perceptual, information-processing, and decision-making abilities being especially relevant to understanding assessment strategies (Yoerg 1991; Belisle and Cresswell 1997; Kamil 1998; Dukas 1999; Shettleworth 2001). Research on intricate and flexible assessment strategies in arthropods is important for clarifying how decision-making and other cognitive abilities might be limited by the size and complexity of the animal's brain.

During conflict with conspecific rivals, animals tend to rely on assessment strategies where the goal can be envisaged as making decisions based on estimates of potential risks and payoffs (Maynard Smith and Price 1973; Parker 1974; Enquist et al. 1990). However, direct detection of risk may often be impossible, and animals usually rely instead on detection of cues that are correlated with particular risks and payoffs (Huntingford and Turner 1987; Bouskila and Blumstein 1992).

Assessment may also be important in predator–prey systems involving different species (Huntingford 1976; Curio 1978; Rowe and Owings 1978; Lloyd 1986; Lima and Dill 1990). Predators are obviously dangerous to prey, and examples are known where prey discriminate between different species of predators (Leger and Owings 1978; Owings and Leger 1980; Seyfarth et al. 1980; Slobodchikoff et al. 1991; Cheney and Seyfarth 1988; Gyger et al. 1987; Greene and Meagher 1998), or even between particular individuals belonging to single species of predator. This includes discerning the likelihood that a predator will attack (Hammerstrom 1957; Buitron 1983; Pettifor 1990), intrinsic variation in how dangerous an individual predator might be should it attack (Rowe and Owings 1978; Curio et al. 1983; Owings and Loughry 1985; Hennessy 1986; Helfman 1989; Loughry 1989; Foster and Ploch 1990; Walters 1990; Rowe and Owings 1996; Swaisgood et al. 1999a) and contextual factors such as where the encounter takes place and the prey's repro-

ductive state (Coss and Owings 1985; Loughry 1987; Swaisgood et al. 1999b).

However, predator–prey interactions may sometimes be risky to the predator as well as the prey (e.g., Owings and Coss 1977; Hennessy and Owings 1988). Some predators have evolved prey-specific prey-capture tactics (Curio 1976), and these may be shaped by the levels and types of risks (chemical defences, ability to harm the predator physically, etc.) from particular species of prey (Forbes 1989; Brodie and Brodie 1990, 1991, 1999; Downes and Shine 1998). Less is known about whether predators rely on cues that reveal intrinsic risk-related variation among individuals within single prey species. Yet the decisions of a predator at this level may be especially instructive when attempting to understand animal cognition.

That scaling factors must constrain the cognitive abilities of animals is widely acknowledged. Smaller animals tend to have fewer, not smaller, neurons (Alloway 1972; Menzel et al. 1984), which means fewer components are available for brains and sense organs, the machinery used for cognitive functions. There is considerable evidence that, even over a small range and among closely related species, brain size influences cognitive ability (Lashley 1949; Jerison 1973, 1985; Eisenberg and Wilson 1978; Clutton-Brock and Harvey 1980; Mace et al. 1981; Lefebvre et al. 1997). That there are drastic limitations on the cognitive capacities that can evolve in animals such as spiders and insects appears to be indisputable because, compared with birds and mammals, most arthropods have much smaller nervous systems. Yet there is little precise information about how severe these limitations might be (see Bitterman 1986; Bernays 2001).

Recent spider studies suggest that size constraints on spider cognition may be less severe than formerly supposed. For example, foraging behaviour, web building, and mating decisions of many spiders are influenced by learning and other types of experience (Grünbaum 1927; Bays 1962; LeGuelte 1969; Lahue 1973; Seyfarth et al. 1982; Sebrier and Krafft 1993; Edwards and Jackson 1994; Sandoval 1994; Whitehouse 1997; Heiling and Herberstein 1999; Nakata and Ushimaru 1999; Morse 1999, 2000a, b; Tso 1999; Chmiel et al. 2000; Rodriguez and Gamboa 2000; Venner et al. 2000), and the level to which salticid spiders rely on problem solving, decision making, and forward planning (Jackson 1977, 1981; Jackson and Wilcox 1990, 1993a, b; Wilcox et al. 1996; Jackson et al. 1998, 2001; Clark et al. 1999; Clark and Jackson 2000; Tarsitano et al. 2000; Jackson and Carter 2001) is unusual even for vertebrates (Wilcox and Jackson 1998, 2002; Harland and Jackson 2000).

Here we investigate whether araneophagic spiders (i.e., spiders that specialise in preying on other spiders) make assessment decisions based on cues that reveal intrinsic risk-related variation among individuals within single prey species. All spiders are predators, and many species routinely take prey comparable to themselves in size (Foelix 1996). However, especially intricate decisions might be important for araneophagic spiders. For a predator that preys routinely on other predators, risk-assessment decisions might often have life-or-death consequences for the predator as well as the prey. As a case study, we investigate a predator–prey system involving two species, each of which is araneophagic and each of which preys on the other. One is a web-building spitting spider (Scytodidae) and the other is a jumping spider (Salticidae).

The eyes of most spiders lack the structural complexity required for acute vision (Homann 1971; Land 1985), but the unique complex eyes of salticids support resolution ability with no known parallel in other animals of comparable size (Land 1969a,b,1974,1985 ; Blest et al. 1990; Land and Nilsson 2001). Almost 5,000 salticid species have been described (Coddington and Levi 1991; Zabka 1993), most of which appear to be cursorial hunters of insects (Richman and Jackson 1992). Having intricate vision-controlled predatory behaviour, most salticids neither build nor use webs (Jackson and Pollard 1996), but there are exceptions, the most striking of which are in the genus *Portia* (Wanless 1978). Besides capturing prey in the open, *Portia* also spins prey-capture webs (Jackson 1985) and they routinely invade alien webs where they take their preferred prey, other spiders (Li and Jackson 1996; Li et al. 1997).

After entering another spider's web, instead of simply stalking or chasing down the resident spider, *Portia* uses aggressive-mimicry signals to manipulate the resident spider's behaviour (Jackson and Wilcox 1998). However, *Portia*'s flexibility includes more than complex, flexible signalling behaviour (Jackson and Wilcox 1993a). When direct routes are unavailable, *Portia* may make deliberate detours (Tarsitano and Andrew 1999), including 'reverse-route detours' (detours that can be completed only by initially moving away from, and losing sight of, the prey (Tarsitano and Jackson 1994, 1997). *Portia* may also take detours by choice even when shorter direct routes are available (Jackson and Wilcox 1993b; Jackson et al. 1998).

Among spiders, spitting is unique to the genus *Scytodes* (Foelix 1996): by forcefully expelling sticky gum from their fangs, these spiders can immobilise their prey from distances of up to 10 body lengths away (Dabelow 1958; McAlistair 1960; Gilbert and Rayor 1985; Nentwig 1985). No other prey of *Portia* has a comparable ability to attack from a distance, and scytodids can gum *Portia* down with their spit. Encounters by *Portia* with spitting spiders are known to be frequent in only one habitat, Los Baños (Lagunas Province, Luzon) in the Philippines. Here *P. labiata* preys routinely on *S. pallidus*, an especially common spitting spider, which is itself primarily a predator of salticids, sometimes including *P. labiata* (Li et al. 1999). This suggests that, during encounters with *S. pallidus*, it might be especially advantageous for *Portia* to make risk-related strategic decisions.

That the Los Baños *P. labiata* is locally adapted to *S. pallidus* has been suggested by comparison with *P. labiata* from Sagada (Mountain Province, Luzon, the Philippines) where *S. pallidus* is not found. The Los Baños *P. labiata*

(sympatric with *S. pallidus*), but not the Sagada *P. labiata* (allopatric to *S. pallidus*), makes consistent use of a particular tactic (soft plucking with palps in signal–detour–leap sequences), and these inter- and intraspecific differences are evident despite the individuals of *P. labiata* studied being reared in the laboratory for two to three generations with no prior experience of scytodids (Jackson et al. 1998). The Los Baños *P. labiata*'s faint signals cause the resident spider to move about in an exploratory fashion. This can be important because it keeps *P. labiata*'s target, the scytodid, out in the open. Other signals are advantageous because they may provoke a full-scale attack. The Los Baños *P. labiata*, but not the Sagada *P. labiata*, avoids making these dangerous signals. The detours taken by *P. labiata* are an especially advantageous way to approach a spitting spider because these indirect paths enable *P. labiata* to reach *S. pallidus* from the rear, opposite the end from which the scytodid's spit is fired. Using its signal–detour–leap tactic, the Los Baños *P. labiata* experiences greater prey-capture success and lesser likelihood of being spat on and killed (Jackson et al. 1998).

Individuals of *S. pallidus* may differ significantly in the intrinsic level of danger they present to *P. labiata*. After oviposition, *Scytodes* females carry their eggs in their chelicerae. As their gum is fired from the chelicerae, egg-carrying females can be envisaged as having 'spiked their own guns' (i.e., blocked the outlet). 'Spiking' is not absolute for egg-carrying *S. pallidus* because they do some-

times lower their eggs from their mouths and spit, but they appear to be reluctant and slow to do so (Li et al. 1999). Here we consider whether the Los Baños *P. labiata*'s decision-making processes have become locally adapted to this variation in the intrinsic risk posed by encounters with different individuals of *S. pallidus*. Having found no evidence in preliminary trials that the signals used by *P. labiata* vary depending on whether *S. pallidus* is eggless or egg carrying, we will consider specifically the detouring decisions of *P. labiata*.

Methods

All spiders were from laboratory cultures that were started from specimens collected at Los Baños (*Scytodes pallidus*, *Phintella aequinosus*, and *Portia labiata*) and Sagada (*Portia labiata*). All individuals of *Portia labiata* were derived from rearing to second or third generation, with no individuals or their laboratory-reared parents having had prior experience with scytodids. *Phintella aequinosus* is a leaf-dwelling salticid on which *S. pallidus* routinely preys in nature (Li et al. 1999).

Standard maintenance, experimental procedures, cage design, and feeding routines were adopted, as detailed elsewhere (Jackson and Hallas 1986). Only critical details are given here. Laboratory-rearing environments (spacious cages containing meshworks of twigs) were 'enriched' in a manner comparable to that described by Carducci and Jakob (2000). Testing took place in a controlled-environment laboratory (light:dark cycle, 12L:12D; lights came on at 0800 hours; temperature constant at 25°C). Maintenance diet for *Portia labiata* consisted of a variety of spider and insect species (Table 1), as comparable varied diets have been shown in earlier

Table 1 Prey used in the laboratory for rearing *Portia labiata*, *Scytodes pallidus*, and *Phintella aequinosus*. All holometabolous insects: adults. All hemimetabolous insects and all spiders: juveniles and adults. Salticids used as prey for *S. pallidus* only. All other prey fed to both *S. pallidus* and *Portia labiata*. *Phintella aequinosus* was fed insects only

Species	Order	Family	Description	Body length (mm)	Origin
Achaearanea sp.	Araneae	Theridiidae	Web-building spider	1–5	New Zealand
Badumna longinqua (L. Koch)	Araneae	Amaurobiidae	Web-building spider	1–8	New Zealand
Tegenaria domestica (Clerck)	Araneae	Agelenidae	Web-building spider	1–5	New Zealand
Zosis geniculatus (Oliver)	Araneae	Uloboridae	Web-building spider	1–5	Laboratory culture (origin: Queensland, Australia)
Cheiracanthium statioticum (L. Koch)	Araneae	Miturgidae	Hunting spider	1–5	New Zealand
Dolomedes minor (L. Koch)	Araneae	Pisauridae	Hunting spider	1–5	New Zealand
Scotophaeus pretiosus (L. Koch)	Araneae	Gnaphosidae	Hunting spider	1–4	New Zealand
Euophrys parvula Bryant	Araneae	Salticidae	Hunting spider	1–7	New Zealand
Jacksonoides queenslandicus Wanless	Araneae	Salticidae	Hunting spider	1–7	Laboratory culture (origin: Queensland, Australia)
Marpissa marina Goyen	Araneae	Salticidae	Hunting spider	1–6	New Zealand
Trite planiceps (Urquhart)	Araneae	Salticidae	Hunting spider	1–8	New Zealand
Micromus tasmaniae (Walker)	Neuroptera	Hemrobiidae	Lacewing	3–4	New Zealand
Ctenopseustis sp.	Lepidoptera	Tortricidae	Moth	4–6	New Zealand
Melancha sp.	Lepidoptera	Noctuidae	Moth	6–8	New Zealand
Brevicoryne brassicae (L.)	Hemiptera	Aphidae	Aphid	1–2	New Zealand
Macrosiphum euphorbiae (Thomas)	Hemiptera	Aphidae	Aphid	1–2	New Zealand
Drosophila immigrans (Sturtevant)	Diptera	Drosophilidae	Vinegar	3–4	Laboratory culture
Drosophila melanogaster (Meigen)	Diptera	Drosophilidae	Vinegar	1–2	Laboratory culture
Macromastix zeylandia Alexander	Diptera	Tipulidae	Crane fly	5–6	New Zealand
Musca domestica (Linnaeus)	Diptera	Muscidae	House fly	4–8	Laboratory culture
Trichocera annulata (Meigen)	Diptera	Trichoceridae	Crane fly	4–6	New Zealand

studies to be optimal for *Portia* (Li and Jackson 1997). Each spider (*Portia labiata*, *Phintella aequinosus*, or *S. pallidus*) was fed to satiation three times a week. The prey used was always about half the estimated body volume of the *Portia labiata*, *Phintella aequinosus*, or *S. pallidus* being fed. The mixed diet of each individual of each species (*Portia labiata*, *Phintella aequinosus*, or *S. pallidus*) consisted of approximately equal numbers of each type of prey.

Hunger level during experiments was standardised: before being used in experiments, all individuals of *Portia labiata*, *Phintella aequinosus*, and *S. pallidus* were maintained without prey for 5 days after the last time of being fed to satiation. All testing began between 0830 and 0930 hours. All individuals of *S. pallidus* and *Phintella aequinosus* used in experiments were adult females (*Phintella aequinosus*, 4–5 mm in body length; *S. pallidus*, 7–10 mm in body length). Each individual of *Portia labiata* that we used was a juvenile that matched (to the nearest millimetre) the length of the individual of *S. pallidus* with which it was paired (see below). Each individual of *Phintella aequinosus* was a virgin female that had matured about 20 days before any test in which it was used.

For the statistical analyses we consulted Sokal and Rohlf (1995). In each instance, $\alpha=0.05$. For tests of independence and for McNemar tests, $df=1$. For Wilcoxon tests, $df=n-1$, where n is the number of paired samples.

In each test we matched a *Portia labiata* with a scytodid female of comparable size (7–10 mm in body length or body length plus length of egg sac). The adult females of *Phintella aequinosus* were without eggs. No individual salticid or scytodid was used in more than one test.

Mated females of *S. pallidus* lay successive egg batches, whereas virgin females of *S. pallidus* remain eggless. In preliminary trials, egg-carrying scytodid females, regardless of whether they were with their first or a later eggsac, rarely spat at or killed salticids, but eggless scytodid females (virgin females, mated females that had not yet oviposited, mated females that were currently without eggs, and mated females from which eggs had been forcibly removed, by using forceps, 2–4 h earlier) readily spat at and killed salticids.

Scytodids for testing were established in webs by placing a leaf (*Psuedopanax* spp.) inside a plastic cage made from a petri dish (diameter 148 mm). The leaf filled about half the surface area of the cage. One adult scytodid female was put in the cage and maintained with prey (vinegar flies, *Drosophila melanogaster*; house flies, *Musca domestica*) for 14–21 days, during which time it built a web that covered most of the leaf. We destroyed silk strands built anywhere in the cage other than on the leaf. All scytodids were adult females without juveniles in their webs. Egg-carrying scytodids were always with their first egg batch, oviposited 5–7 days before the trial (i.e., 7–16 days after the scytodid was placed in a cage). Each scytodid reached maturity in the laboratory about 30 days before being put in the cage. Eggless females were all individuals that had not mated. Egg-carrying females had mated once before being used in experiments.

Experiment 1. Are eggless scytodids more inclined to spit than egg-carrying scytodids?

A salticid (*Phintella aequinosus*) was first held in a vial for 15 s under 100% carbon dioxide, then placed upside down on the centre of a scytodid's web. The petri-dish cage was open and the scytodid was about 50 mm away. The scytodid was quiescent and facing the centre of the web. The 15-s exposure to carbon dioxide rendered the salticid sluggish, but not entirely quiescent. In successful tests, salticids placed on webs immediately righted themselves. Tests were aborted whenever this failed to happen. Tests ended when scytodids spat, *Phintella aequinosus*

left the web, or 10 min elapsed, whichever came first. Latency to spit was recorded as the time elapsing after placing the salticid on the web. Eggless scytodids usually spat during the test (75%, $n=20$), but most egg-carrying scytodids failed to spit at all (3%, $n=30$; test of independence, $\chi^2=28.32$, $P<0.001$).

Experiment 2. Are eggless scytodids more dangerous than egg-carrying scytodids?

During a test, one salticid (a *Phintella aequinosus* or a Los Baños *Portia labiata*) was left for 24 h in a closed petri-dish cage (diameter 148 mm) with a scytodid web and either an egg-carrying ($n=60$ for *Phintella aequinosus* and $n=60$ for *Portia labiata*) or an eggless scytodid ($n=60$ for *Phintella aequinosus* and $n=60$ for *Portia labiata*), after which we recorded any instance in which a spider had died.

More salticids (*Phintella aequinosus* and *Portia labiata*) survived tests with egg-carrying scytodids than with eggless scytodids (Table 2): 77% of the *Portia labiata* survived tests with eggless scytodids whereas 100% of *Portia labiata* survived with egg-carrying scytodids (test of independence, $\chi^2=15.85$, $P<0.001$); 10% of the *Phintella aequinosus* survived with eggless scytodids whereas 87% of the *Phintella aequinosus* survived with egg-carrying scytodids (test of independence, $\chi^2=70.61$, $P<0.001$). Only 10% of the egg-carrying scytodids survived tests with *Portia labiata*, compared to 30% of eggless scytodids (test of independence, $\chi^2=26.03$, $P<0.001$). All scytodids survived in tests with *Phintella aequinosus*.

Experiment 3. Does egg-carrying status of scytodids influence whether *Portia labiata* takes a detour or direct path? Sympatric and allopatric *P. labiata* compared

Each *Portia labiata* was tested twice, on one day with an eggless scytodid and on the next or previous day (decided at random) with an egg-carrying scytodid. With this paired design, the response of each individual *P. labiata* to an egg-carrying scytodid was compared with the response of this same individual *P. labiata* to an eggless scytodid. The design of the test limited the test spider to one of two

Table 2 Findings from experiment 2, showing that more salticids survived tests with egg-carrying scytodids than with eggless scytodids. For each row, $n=60$

Salticid species	Scytodid	Scytodid killed salticid	Salticid killed scytodid	Both spiders survived
Portia labiata	Eggless	14	28	18
	Carrying eggs	0	54	6
Phintella aequinosus	Eggless	54	0	6
	Carrying eggs	8	0	52

Fig. 1 Apparatus used in experiment 3. Not to scale. *Portia* in petri dish before test began. When lid was removed from petri dish, *Portia* chose to take a direct route to the leaf (by leaping) or a detour (by walking to the metal base and then following the arm to the clip)
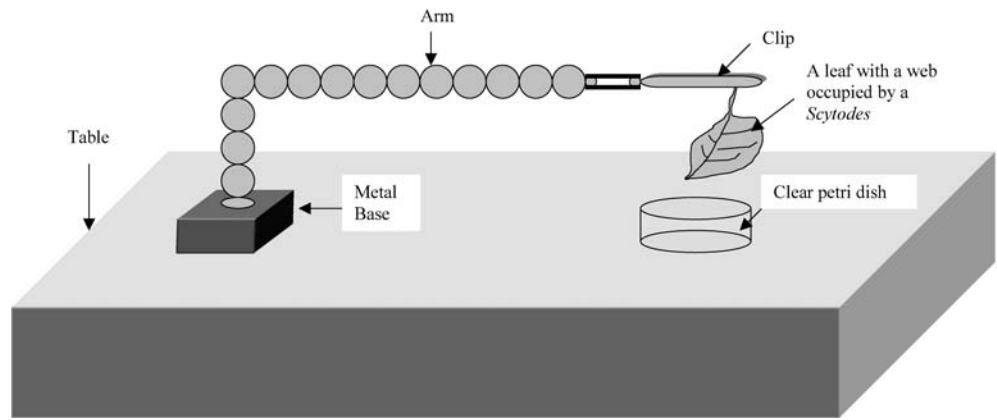
possible responses: leap (direct route) or detour. Most *P. labiata* made a choice (leap or detour) during both tests, and data from individuals that failed to choose during both tests were not analysed.

Before testing began, a leaf on which there was a web occupied by a scytodid was taken from a cage and fastened by a clip to a flexible plastic stand, with the stand being positioned in the open in the centre of a table (Fig. 1). The leaf was angled down from the clip at 45° from horizontal, and the lower end of the leaf was 50 mm above the table top. The web was on the underside of the leaf. There was a transparent petri dish (diameter 35 mm) on the table directly below the leaf (base of stand 300 mm from centre of petri dish). A *P. labiata* (the test spider) was held in the dish for a minimum of 5 min, then the lid was removed to start a test, but only if the *P. labiata* was not on the lid. If the spider was on the lid, testing was postponed until the *P. labiata* moved off. Testing was aborted if *P. labiata* failed to move off the lid within 15 min (timed from when placed in dish). *P. labiata* usually walked slowly out of uncovered dishes and periodically oriented towards the leaf. Testing was aborted if a *P. labiata* moved more than 10 mm from the petri dish without first orienting towards the leaf. Testing with the same *P. labiata* was attempted again on each successive day until a successful test was achieved (maximum required, 4 successive days).

P. labiata could readily leap across the distance between the table top and the leaf. Leaping onto the leaf was recorded as choosing to take a direct route to the leaf. When *P. labiata* walked to the base of the stand, then across the arm and onto the leaf, this was recorded as choosing to take a detour. We allowed 4 h for *P. labiata* to choose either a detour or a direct route to the leaf. During the test, *P. labiata* was watched continuously. If *P. labiata* failed to contact the web within 4 h, moved off the table top before 4 h elapsed, or leapt on to the plastic arm or the clip, this was recorded as failure to choose. Failure to choose was rare (fewer than 5% of the tests). Latency to enter a web was recorded as time elapsing between leaping and first touching the web silk (direct route) or as time elapsing between first contacting the base of the stand and first contacting the web silk (detour). Although the web covered the majority of the leaf, there were always some clear spaces on the leaf surface. When *P. labiata* leapt onto the leaf, it always landed on a clear section and then walked onto the web.

The Los Baños *Portia labiata* more often took detours when tested with eggless scytodids and more often took direct routes by leaping when tested with egg-carrying scytodids (McNemar test for significance of changes, $\chi^2=7.36$, $P=0.007$): (1) 10 took detours with eggless and direct routes with egg-carrying scytodids; (2) only 1 took a detour with an egg-carrying and a direct route with an eggless scytodid; (3) 14 took detours with both; and (4) 2 took direct routes with both. Note that only data from (1) and (2) are used in McNemar tests.

There was no evidence that whether scytodids were carrying eggs influenced whether the direct route or the detour was chosen by the Sagada *P. labiata* (McNemar test for significance of changes, $\chi^2=1.80$, $P=0.180$): (1) 5 took detours with eggless scytodids and direct routes with egg-carrying scytodids; (2) 4 took detours with egg-carrying scytodids and direct routes with eggless scytodids; (3) 6 took detours with both; and (4) 7 took direct routes with both. Only data from (1) and (2) are used in McNemar tests. Regardless of whether scytodids were carrying eggs, the Sagada *P. labiata* took the direct route at a frequency (32%, $n=22$) comparable to how often Los Baños *P. labiata* took the direct route (37%, $n=27$) in tests with egg-carrying scytodids (test of independence, $\chi^2=0.15$, $P=0.703$).

For both the Los Baños and the Sagada *P. labiata*, latencies to enter webs were shorter when direct instead of detour routes were taken (Los Baños *P. labiata*, Wilcoxon signed-rank test, $n=11$, normal approximation, $t=2.9$, two-tailed $P<0.004$, median and range for direct routes 3 min and 1–11 min, median and range for detouring 40 min and 20–113 min; Sagada *P. labiata*, Wilcoxon signed-rank test, $n=9$, normal approximation, $t=2.6$, two-tailed $P=0.009$, median and range for direct routes 3 min and 1–6 min, median and range for detouring 30 min and 25–73 min). Although 14 of the Los Baños *P. labiata* took detours to reach the eggless and egg-carrying scytodids, detour routes to reach eggless scytodids were completed more slowly than detour routes to reach egg-carrying scytodids (Wilcoxon signed-rank test, $n=14$, normal approximation,

t=2.89, P=0.004, median and range for detouring to reach eggless scytodid 57 min and 29–76 min, median and range for detouring to reach egg-carrying scytodid 31 min and 17–53 min). When the Sagada *P. labiata* took detours to reach both types of scytodids, latencies to reach webs were comparable (Wilcoxon signed-rank test, n=4, normal approximation, t=0.63, P=0.529, median and range for detouring to reach eggless scytodid 41 min and 18–44 min, median and range for detouring to reach egg-carrying syctodid 39 min and 14–77 min).

Discussion

Being a salticid-eating spitting spider, *Scytodes pallidus* is an especially dangerous prey for *P. labiata*. Local adaptation was implied by the findings in an earlier study that considered only eggless *S. pallidus* (Jackson et al. 1998). The scytodid-specific prey-capture tactic of the Los Baños *P. labiata* (signal–detour–leap sequences in conjunction with soft palp plucking) is an effective method of minimising risk and capturing this locally abundant, but particularly dangerous, prey spider. The Sagada *P. labiata* does not routinely adopt this tactic and is, compared with the Los Baños *P. labiata*, less effective at capturing *S. pallidus* and more likely to be captured by *S. pallidus*. Our findings here suggest a more intricate level of local adaptation. Individuals of *S. pallidus* differ in the inherent level of risk they pose for *P. labiata* (eggless females of *S. pallidus* are more dangerous than egg-carrying females of *S. pallidus*), and the Los Baños *P. labiata* makes strategic decisions consistent with these risks (taking detours, which are safer but take more time, during encounters with eggless females, but taking shorter direct routes during encounters with egg-carrying females). Evidently, the Sagada *P. labiata* does not make these strategic decisions.

Because we used second- and third-generation spiders that were reared in the laboratory under standardised conditions, maternal effects (Roff 1998; Wade 1998) and other indirect genetic effects (Moore et al. 1998) are unlikely alternative explanations for these findings. However, contextual variables (see McPhail 1985) raise numerous other hypotheses. There is no easy way to rule out the possibility that our findings were consequences of spiders from different habitats being predisposed to respond differently under the standardised conditions in the laboratory. Ruling out contextual variables is notoriously difficult when attempting to show adaptive variation, whether intraspecific or interspecific, in behaviour (Bitterman 1965). Being akin to testing null hypotheses, attempting to identify, and then testing the effects of, all reasonable contextual variables requires a research program, not one or two experiments (Kamil 1998). The present study is a first step in such a research program on Philippines *P. labiata*.

Possibly the Los Baños and Sagada *P. labiata* originally diverged along a cline (see Endler 1977), but these two populations appear now to be disjoint. *P. labiata* requires considerable shelter from direct sunshine, making the large treeless expanses in central Luzon, dominated by rice fields, unlikely avenues for frequent gene flow between Los Baños in Lagunas Province in the south and Sagada in Mountain Province in the north. The Los Baños and Sagada populations of *P. labiata* appear to be, at least currently, examples of behavioural ecotypes rather than ends of a cline.

That spider behaviour may vary geographically within single species is well established (Riechert 1979, 1981, 1991, 1999; Riechert and Hedrick 1990; Jackson 1980; Uetz and Cangialosi 1986). That *Portia*'s predatory and anti-predator behaviour is subject to intraspecific geographic variation is also well established (Jackson and Hallas 1986; Jackson 1992a, b; Jackson et al. 2001). The present study, however, is unusual for spider research because it suggests geographic variation in flexibility: what varies geographically appears to be *Portia*'s propensity for fine tuning of predatory tactics to compensate for variation in the intrinsic dangerousness of individuals of a single prey species. These can be envisaged as at least rudimentary differences in cognitive capacities. Geographic variation in the cognitive capacities of single species has been demonstrated in a wide variety of vertebrates (Huntingford and Wright 1992; Huntingford et al. 1994; Nelson et al. 1996; Thompson 1990, 1999) but rarely considered for arthropods. Yet cognitive capacities may be even more likely to diverge geographically within single species of smaller animals, such as spiders, where adaptive tradeoffs may be especially severe.

Of the 27 Los Baños *P. labiata* tested, only 11 switched tactics depending on whether the scytodid was carrying eggs or not, and it is only these 11 that provide data for McNemar tests of significance of changes. More than half (16 of 27) of the Los Baños *P. labiata* did not switch tactics (14 took detours with both and 2 took direct routes with both). Most individuals took detours with both eggless and egg-carrying scytodids (24 of 27 took detours to reach eggless scytodids and 15 of 27 took detours with egg-carrying scytodids).

It is tempting to suggest that the 15 individuals that used detours when approaching egg-carrying scytodids made an error of judgment because they wasted time when safety did not require the longer detour route. However, when compared with eggless scytodids, egg-carrying scytodids are safer prey, but they are not completely harmless. Perhaps we do not understand fully enough the various factors that enter into the decision-making process that determines whether a particular individual Los Baños *P. labiata* at a particular time will save time and take a shortcut or play it safe and take a detour to reach an egg-carrying scytodid. If we had a sufficient understanding of *P. labiata*'s decision-making processes, then perhaps what initially appears to be an error in judgment would appear optimal for the individual *P. labiata* under highly specific conditions. Moreover, even the individuals of Los Baños *P. labiata* that took detours to reach both types of scytodids appear to have exercised greater caution while approaching eggless scytodids (i.e., they moved more slowly along the detour route when the scytodid at the other end was eggless).

It may be even more tempting to suggest that the three individuals that used direct routes when approaching egg-less scytodids made an error in judgment (i.e., took a bigger risk than was optimal). We might say that the judgments of these three individuals were opposite to what we would have done had we been given the same information. Yet, again, we cannot rule out the possibility that a fuller understanding of decision-making processes would reveal how these seemingly bad decisions are actually optimal.

Perhaps an alternative is that we should simply accept that the Los Baños *P. labiata* often makes decisions that are not optimal, but there may be interesting implications of accepting the notion of a spider making errors of judgment. Automatic, reflex-like, and highly predictable (errorless) behaviour might be more in line with what is usually expected of a spider. The commonsense notion of cognitive decision making might correspond with more intricate information processing that generates less easily predicted behavioural outcomes: we might say that, when deciding what to do next, the animal 'makes up its own mind'. As we enter the twenty-first century, attitudes towards arthropod behaviour have changed considerably if we are now becoming comfortable with the idea that a spider even has a mind to make up.

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