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Solving a novel confinement problem by spartaeine salticids that are predisposed to solve problems in the context of predation

Fiona R. Cross* and

School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand

Robert R. Jackson

International Centre of Insect Physiology and Ecology, Thomas Odhiambo Campus, P.O. Box 30, Mbita Point, Kenya

Abstract

Especially intricate predatory strategies are widespread in the salticid subfamily Spartaeinae. The hypothesis we consider here is that the spartaeine species that are proficient at solving prey-capture problems are also proficient at solving novel problems. We used nine species from this subfamily in our experiments. Eight of these species (two *Brettus*, one *Cocalus*, three *Cyrba*, two *Portia*) are known for specialized invasion of other spiders' webs and for actively choosing other spiders as preferred prey ('araneophagy'). Except for *Cocalus*, these species also use trial-and-error to derive web-based signals with which they gain dynamic fine control of the resident spider's behaviour ('aggressive mimicry'). The ninth species, *Paracyrba wanlessi*, is not araneophagic and instead specializes at preying on mosquitoes. We presented these nine species with a novel confinement problem that could be solved by trial and error. The test spider began each trial on an island in a tray of water, with an atoll surrounding the island. From the island, the spider could choose between two potential escape tactics (leap or swim), but we decided at random before the trial which tactic would fail and which tactic would achieve partial success. Our findings show that the seven aggressive-mimic species are proficient at solving the confinement problem by repeating 'correct' choices and by switching to the alternative tactic after making an 'incorrect' choice. However, as predicted, there was no evidence of *C. gibbosus* or *P. wanlessi*, the two non-aggressive-mimic species, solving the confinement problem. We discuss these findings in the context of an often-made distinction between domain-specific and domain-general cognition.

Keywords

problem solving; cognition; *Brettus*; *Cocalus*; *Cyrba*; *Paracyrba*; *Portia*

*Corresponding author: fiona.r.cross@gmail.com, Telephone: +64 3 364 2987, ext. 7044 Fax: +64 3 364 2590.

Introduction

The extent to which the cognitive processes used by animals are domain-specific instead of domain-general remains poorly understood (Chiappe and MacDonald 2005; Anselme 2012). Domain specificity and modularity are related topics and, although difficult to define (Fodor 1983; Coltheart 1999; Barrett and Kurzban 2006), modularity is usually envisaged in the context of limited computational capacities that make functional specialization advantageous. A related view is that computational power is positively related to brain size (but see Healy and Rowe 2007) and an expectation derived from this view is that modularity, or domain specificity, will be expressed especially strongly by small animals.

However, recent findings from research on insects (e.g. Webb 2012) and spiders (e.g. Jakob et al. 2011) challenge the convention of assuming that there are severe constraints on the expression of cognition by small animals. For research on visual cognition, jumping spiders (Salticidae) are of particular interest because their unique, complex eyes (Land and Nilsson 2012) support highly precise identification of different prey types and other visual objects (Harland et al. 2012). Although salticids are often characterized as being predators of insects, some of the species in the salticid subfamily Spartheinae are known to specialize at preying on other spiders ('araneophagy'), often by invading other spiders' webs (Su et al. 2007).

Species from the genus *Portia* are the most thoroughly studied spartheines (Harland and Jackson 2004). When in another spider's web, *Portia* typically gains dynamic fine control of the resident spider's behaviour ('aggressive mimicry'; Jackson and Cross 2013) by using any one or any combination of its ten appendages (eight legs and two palps) to generate web signals (i.e. vibratory and tension patterns on the silk). As each appendage can move independently and in a variety of ways, the assortment of different signals that *Portia* has at its disposal is virtually unlimited (Jackson and Blest 1982). By repeating signals that elicit an appropriate response from its intended prey and by trying new signals when an appropriate response is not forthcoming (Jackson and Wilcox 1993; Jackson and Nelson 2011), *Portia* achieves a high level of proficiency at adjusting its predatory strategy to the particular prey spiders it encounters. Using this trial-and-error strategy (a 'generate-and-test algorithm'; see Simon 1969), *Portia* preys on a vast array of different kinds of spiders (Jackson and Pollard 1996), including spiders that can prey on *Portia*. It has been proposed that *Portia*'s capacity for flexibly deriving signals by trial-and-error is an important adaptation for successfully targeting other predators as prey (Jackson 1992).

In an earlier study, first steps were taken toward considering whether *Portia*'s proficiency at using trial-and-error is restricted to the context of a predatory strategy (domain specific) or applicable to novel problems (domain general) (see Beecher 1988). *Portia fimbriata* and *Portia orientalis* (formerly *P. labiata*) were presented with a particular problem, how to escape from an island surrounded by water (i.e. a confinement problem). This problem can be envisaged as novel partly because there is no evidence that *Portia* routinely crosses water in nature. However, this problem was all the more novel because test spiders were, at random, helped forward or forced back during the experiments. It is hard to imagine salticids routinely experiencing situations similar to this procedure in nature and yet *P.*

fimbriata and *P. orientalis* successfully adjusted their behaviour in accordance with whether they were forced back to the island or helped forward.

Local adaptation is also relevant, as different populations of single *Portia* species are known to adopt different predatory strategies (Jackson and Pollard 1996). Individuals of *P. orientalis* from two different populations, Los Baños and Sagada (Luzon, Philippines), are known to differ in capacity to solve the confinement problem (Jackson et al. 2006). Los Baños is a low-elevation rainforest habitat where the range of prey-spider species is much wider than in Sagada, a high-elevation pine-forest habitat. Compared with individuals from Los Baños, individuals from Sagada were significantly less inclined to derive signals by trial-and-error (Jackson and Carter 2001) and also less inclined to solve the confinement problem by trial-and-error (Jackson et al. 2006).

Based on these findings, it was proposed that, for web-invading aggressive-mimic spartaeine salticids, being proficient at solving a novel problem by trial-and-error is a spin-off of having evolved proficiency at deploying highly plastic aggressive-mimicry strategies in the context of predation. As a step toward further evaluating this hypothesis, we decided to compare aggressive-mimic with non-aggressive-mimic spartaeine species. For making these comparisons, it was essential to use species we knew were capable of readily moving across water surfaces (i.e. we had to avoid using species that would tend to sink in water or become stuck in the surface film; see Stratton et al. 2004; Suter 2013). Salticidae is a large spider family (about 5,600 described species; Platnick 2014), but the nine species we chose for our experiments are representatives of some of the few salticid genera for which there is evidence of proficiency at crossing water surfaces. For each of these species, water-crossing proficiency appears to be a consequence of specialized predatory strategies (for details about the natural histories, habitats and other characteristics of each species, see references in Table 1). Eight of the nine species we used are araneophagic web invaders from the genera *Brettus*, *Cocalus*, *Cyrba* and *Portia*. These spartaeines do not sink below or adhere to water surfaces, probably as a consequence of having evolved non-wettable cuticle that does not adhere to the wet glue found in the webs built by some of their prey. Seven of these species (*Brettus adonis*, *Brettus albolimbatus*, *Cyrba algerina*, *Cyrba ocellata*, *Cyrba simoni*, *Portia africana*, *Portia schultzi*) also derive effective web-based signals by trial and error, but *Cocalus gibbosus* (Jackson 1990a) has the unique status of being a spartaeine that, despite invading webs, captures resident spiders without making signals. *Paracyrba wanlessi* is even more different, as it is not known for invading webs or for being araneophagic. Instead, *P. wanlessi* specializes at preying on all of the active stages of mosquitoes. As this includes the mosquito's aquatic stages (Abka and Kovac 1996; Jackson et al. 2014), a capacity to contact water surfaces without sinking or adhering appears to have an important function for *P. wanlessi*.

We predicted that, in our experiments, the seven aggressive mimic species would be more proficient than the two non-aggressive-mimic species at using trial-and-error to solve the novel confinement problem.

Materials and Methods

General

Standard laboratory rearing and testing procedures were adopted for all test spiders and only critical details are provided here (for further details, see references in Table 1). Maintenance diet consisted of a variety of spider and insect species for the araneophagic spartaeines. For *P. wanlessi*, the maintenance diet consisted of mosquitoes (adults and larvae of *Anopheles gambiae* s.s. and *Culex quiquefasciatus*) and the adults of a variety of non-biting midge species (Chaoboridae and Chironomidae). All testing was carried out between 0800 hours and 1400 hours (laboratory light-dark cycle 12L:12D, lights on at 0700 hours). No individual spider was tested more than once. Each test spider was 4–5 mm in body length (accurate to the nearest 0.5 mm) and it was either an adult virgin female that had matured 2–3 weeks before tested or it was a juvenile that had moulted 2 weeks earlier and did not moult again for at least 2 weeks. The findings reported here came from experiments carried out in our Kenya laboratory (*P. wanlessi*, the three *Cyrba* species and the two *Portia* species) and in our New Zealand laboratory (*C. gibbosus* and two *Brettus* species).

The apparatus (Fig. 1) was an ‘island’ surrounded by an ‘atoll’ inside a water-filled glass tray. Except for being smaller, square instead of rectangular and made from glass instead of plastic, this apparatus was the same as used in the earlier research on *P. fimbriata* and *P. orientalis* (Jackson et al. 2001, 2006). We added distilled water to the pan, with the water level (18 mm) nearly reaching the height (20 mm) of the island and atoll. Preliminary testing established that, for each of the species we used, individuals that were 4–5 mm in body length could not clear the distance between the island and the edge of the tray simply by leaping.

A plastic tube (diameter 8 mm) extended 60 mm below the tray, its upper end going through a hole in the bottom of the tray and opening in the centre of the island (Fig. 1). The tray was set on a 100-mm high wood frame (painted white), the height allowing space for reaching the lower opening of the tube. When ready to begin testing, we coaxed a test spider into the bottom of this plastic tube. If the test spider failed to walk spontaneously through the tube and on to the top of the island within the next 5 min, we used a ‘plunger’ (a cork, slightly smaller in diameter than the tube, with a stick handle) to gently touch the test spider until it walked out of the top of the tube and onto the island.

Preliminary trials established that test spiders would attempt to leave the island and cross the water either by swimming or by leaping. When leaving the island by swimming, spiders slowly placed their forelegs on the water, pushed off from the island with their rear legs, moved completely out into the water in a spread-eagle posture and then propelled their bodies across the water surface by moving their legs in a stepwise fashion (see Suter 2013). When leaving the island by leaping, spiders landed on the water at a point about halfway across, and then swam the rest of the way. The test spider’s choice (leap or swim) was recorded once all of its legs were on the water and, using this criterion, we could record the spider’s choice unambiguously.

Between trials, we removed the water from the tray, cleaned the apparatus with 80% ethanol followed by distilled water, dried the apparatus, and then put new water in the tray. Lighting was provided by a 100 W incandescent lamp positioned c. 300 mm above the tank. Overhead florescent lamps provided additional ambient lighting.

Experiment 1

Test spiders were assigned at random to two groups, one being spiders for which leaping was pre-determined to be the successful method for reaching the atoll and the other being spiders for which swimming was pre-determined to be the successful method for reaching the atoll. For each species, 40 individuals were assigned to each of the two groups. Any test spider that attempted to cross the water using the behaviour pre-determined to be successful was helped to the atoll. This was achieved by placing a small plastic scoop between the spider and the island and then gently making waves to propel the spider to the atoll. Any spider that attempted to cross the water using the behaviour pre-determined to fail (e.g. a swimming spider in the group with leaping pre-determined to be successful) was returned to the island. This was achieved by placing a small plastic scoop between the spider and the atoll and then gently making waves to propel the spider back. We never touched the spider with the plastic scoop.

Four possible outcomes were defined operationally: 1) both the first and the second choice succeeded; 2) the first choice failed but the second choice succeeded; 3) the first choice succeeded but the second choice failed; 4) neither the first nor the second choice succeeded. The spider always made its initial choice from the island. When the spider's first choice succeeded, its second choice was made from the atoll. As a successful first choice took the spider only part of the way to the edge of the tray, the reinforcement for making the correct choice was only partial success at escaping from the water-filled tray. This meant that a test spider on the atoll had to choose again how to cross the water before it could reach the edge of the tray (i.e. it could repeat its first choice or it could switch). Repetition after a successful first choice was predicted by the trial-and-error hypothesis. A test spider forced back to the island after an unsuccessful first choice had to try again to reach the atoll from the island. It could do this either by repeating its earlier choice or by switching. Switching after an unsuccessful first choice was predicted by the trial-and-error hypothesis.

We aborted testing whenever a test spider, after reaching the top of the island, failed to make its first choice within 10 min or failed to stay on the island for at least 10 s before making its first choice. We also aborted testing whenever a test spider: 1) failed to make its second choice within 10 min after making its first choice and either reaching the atoll or being returned to the island; 2) failed to remain on the island or atoll for at least 10 s before making its second choice; 3) while on the island went back into the hole; 4) while on the atoll attempted to return to the island. The criteria we adopted necessitated aborting no more than 10% of the test spiders of any one species. Spiders in aborted trials were replaced with another spider to maintain the sample size, and were not used again.

Using chi square tests for goodness of fit, we first determined for each species whether there was a bias toward leaping or swimming first. Next, by using chi square tests of

independence, we considered whether the consequence of the first choice influenced the second choice. For each species, $N = 80$.

Experiment 2

Experiment 2 was designed to be a second way of considering our prediction that the seven aggressive-mimic species would be more proficient than the two non-aggressive-mimic species at solving the confinement problem. In Experiment 1, each test spider had only a single opportunity to repeat its initial choice after success or to switch to the other choice after failure. The testing procedure of Experiment 2 was similar, except that the test spider's first choice, regardless of whether it was swimming or leaping, was always pre-determined to fail. Here, we pushed the test spider back to the island until it switched from leaping to swimming or from swimming to leaping. Testing ended if the spider failed to switch after 10 opportunities. The test spider's score was its number of failures before switching, with spiders switching sooner getting lower scores. For example, the test spider was given a score of zero when it switched the next time after its initial failure and a score of 10 was given when it never switched.

We first compared scores within the seven aggressive-mimic species using a Kruskal-Wallis test and within the two non-aggressive-mimic species using a Mann-Whitney U -test. We then compared scores between these two groups, in two different ways, using Mann-Whitney U -tests. The first was a comparison of the pooled scores for the aggressive-mimic species ($N = 105$) with the pooled scores for the non-aggressive-mimic species ($N = 30$). The second was a comparison of the median scores for each of the aggressive-mimic species ($N = 7$) with the median scores for each of the non-aggressive-mimic species ($N = 2$). For each species, $N = 15$.

Results

Each test spider began a trial with no prior experience of the consequences of leaving the island by leaping or by swimming. In Experiment 1 (Fig. 2), we found no evidence that any of the nine species were predisposed to adopt one water-crossing method first more often than the other (i.e. the number of individuals that leapt first was never significantly different from the number that swam first). However, choice of the second water-crossing method varied among the nine species. For the seven aggressive-mimic species (*B. adonis*, *B. albolimbatus*, *C. algerina*, *C. ocellata*, *C. simoni*, *P. africana* and *P. schultzi*), there was a significant relationship between the test spider's second choice and the consequence of its first choice. As predicted, these seven species showed an inclination to repeat water-crossing methods that were successful and to switch when the previously-used method was unsuccessful. Also as predicted, there was no significant relationship between first and second choices made by the two non-aggressive-mimic species, *C. gibbosus* and *P. wanlessi* (Fig. 3).

The findings from Experiment 2 were also as predicted. Scores did not differ significantly within the seven aggressive-mimic species (Kruskal-Wallis test: $H = 4.34$, $P = 0.630$) or within the two non-aggressive-mimic species (Mann-Whitney test: $U_{15,15} = 106$, $Z = 0.25$, $P = 0.804$). The seven aggressive-mimic species usually switched at the first opportunity but

about half of all individuals of the two non-aggressive-mimic species failed to switch even after 10 successive opportunities. The pooled scores (number of failures before switching tactics) for the two non-aggressive mimic species were significantly higher than the pooled scores for the seven aggressive-mimic species ($U_{30,105} = 558$, $Z = 5.38$, $P < 0.001$; Fig. 4). Median scores for the two non-aggressive-mimic species were also significantly higher than the median scores for the seven aggressive-mimic species ($U_{2,7} = 0$, $P = 0.028$).

Discussion

We found no evidence that any of the nine species were biased toward either leaping or swimming when initially leaving the island, but interspecific variation was evident when we considered whether a spider's subsequent choice was influenced by the consequences of its first choice. As predicted, our findings support a conclusion that the seven aggressive-mimic species, and not the two non-aggressive-mimic species, use trial-and-error to solve the confinement problem. Comparable findings from two different experiments give us especially strong support for this conclusion.

When combined with the earlier findings for the Queensland *P. fimbriata* and for the Los Baños *P. orientalis* (Jackson et al. 2001, 2006), nine aggressive-mimic spartaeine species have now been tested for ability to solve the novel confinement problem and each of these nine species succeeded. Only two non-aggressive-mimic spartaeine species have been tested for ability to solve this same problem and both failed.

We proposed that being proficient at solving signal-derivation problems by trial-and-error has, as a spin-off, predisposed aggressive-mimic spartaeines to transfer a similar proficiency to solving novel problems and our findings are as predicted by this hypothesis. However, caution is needed before accepting null hypotheses and we are reluctant to suggest, on the basis of non-significant findings, that *C. gibbosus* and *P. wanlessi* are simply incapable of solving novel problems by trial and error or that these two species have no capacity for operant conditioning. There has been longstanding interest in determining the capacity that insects and spiders express for various categories of learning (Dukas 2008; Bednarski et al. 2012; Liedtke and Schneider 2014), including operant conditioning (Skinner 1938), and we expect operant conditioning to be within the capacity of almost any insect or spider.

Although using trial-and-error to solve the confinement problem in our study can be characterized as at least a rudimentary example of operant conditioning (Staddon 1983), learning based on operant conditioning is usually envisaged as solving a problem and then remembering the solution for some considerable time afterwards. Our current objectives did not include a full consideration of the extent to which spartaeines rely on learning or of how long the spartaeine's memory persists. Instead, we have been primarily interested in the distinction between domain-general and domain-specific cognition.

It has been argued (Johnston 1982; Papaj 1986; Dukas 1998) that, in some cases, animals with special-purpose problem-solving abilities (domain-specific cognition) can become proficient at responding flexibly and adaptively to problems outside the context to which these special-purpose abilities originally evolved (domain-general cognition) (Stephens

1991; Dennett 1996). Testing this hypothesis can serve as a step toward investigating an animal's capacity for innovation or insight (see Reader and Laland 2003; Kuczaj II and Walker 2012), but there is a misleading tendency to envisage domain specific and domain general as two distinct categories. A more useful alternative is to envisage 'domain specific' and 'domain general' as being terms pertaining to different ends of a continuum (e.g. see Jackson and Cross 2011) and our findings suggest that, for understanding the behaviour of aggressive-mimic spartaeines, the domain-general region of this continuum is particularly relevant.

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Fig 1.

Apparatus used for ascertaining capacities of spartaeine salticids to solve a novel confinement problem by using trial-and-error. In a water-filled tray (360 mm $\times$ 360 mm), there is an island (20 mm $\times$ 20 mm) surrounded by an atoll (200 mm $\times$ 200 mm, 10 mm thick). The test spider emerges from a hole (diameter 10 mm) in the island and the makes its first choice (i.e. either it leaps or it swims away from the island). Before testing begins, we determine at random which of the two potential choices will be successful. When the test spider makes the choice we predetermined to be the successful choice, we moved it to the atoll. When the test spider makes the choice we predetermined to be the unsuccessful choice, we returned it to the island. After a successful first choice, the spider can make its second choice from the atoll. After an unsuccessful first choice, the spider must make its second choice from the island

Fig 2.

Number of test spiders that leapt or swam on their first attempt to cross water in Experiment 1

Fig 3.

Results from Experiment 1 (on island surrounded by an atoll in tray of water, test spider given two opportunities to choose its method of crossing the water)

Fig 4.

Pooled data for aggressive-mimic and non-aggressive-mimic spartaeine species (Experiment 2). Test spider was on island surrounded by an atoll in tray of water, and given up to 10 opportunities to switch after leaving the island and failing to succeed at reaching the atoll. Score: number of failures before switching (spiders that switched sooner got lower scores)

Table 1

Spartaeine-salticid species that were used in experiments designed to test for capacity to adopt a trial-and-error routine for solving a novel confinement problem. Locality: site from which spiders used for culturing in the laboratory originated (see References for details)

Test spider species	Locality	Reference
<i>Brettus adonis</i> *	Sri Lanka (Kandy)	Jackson and Hallas (1986a)
<i>Brettus albolimbatus</i>	Sri Lanka (Kandy)	Jackson and Hallas (1986a)
<i>Cocalus gibbosus</i>	Australia (Cairns, Queensland)	Jackson (1990a)
<i>Cyrba algerina</i>	Portugal (Sintra)	Jackson (1990b)
<i>Cyrba ocellata</i>	Kenya (Mbita Point)	Jackson (1990b)
<i>Cyrba simoni</i>	Kenya (Kisumu)	Jackson (1990b)
<i>Paracyrba wanlessi</i>	Malaysia (Kuala Lumpur)	abka and Kovac (1996)
<i>Portia africana</i>	Kenya (Mbita Point)	Jackson and Hallas (1986b)
<i>Portia schultzi</i>	Kenya (Malindi)	Jackson and Hallas (1986b)

* Previously *Brettus cingulatus*