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Portia is a genus of web-invading araneophagic (spider eating) jumping spiders known from earlier studies to derive aggressive-mimicry signals by using a generate-and-test (trial and error) algorithm. We studied individuals of *Portia labiata* from two populations (Los Baños and Sagada) in the Philippines that have previously been shown to differ in the level to which they rely on trial-and-error derivation of signals for prey capture (Los Baños relied on trial and error more strongly than Sagada *P. labiata*). Here we investigated *P. labiata*'s use of trial and error in a novel situation (a confinement problem: how to escape from an island surrounded by water) that is unlikely to correspond closely to anything the spider would encounter in nature. During Experiment 1, spiders chose between two potential escape tactics (leap or swim), one of which was set at random to fail (brought spider no closer to edge of tray) and the other of which was set for partially succeeding (brought spider closer to edge of tray). By using trial and error, the Los Baños *P. labiata* solved the confinement problem significantly more often than the Sagada *P. labiata* in Experiment 1, both when the correct choices were positively reinforced (i.e., when the spider was moved closer to edge of tray) and when incorrect choices were punished (i.e., when the spider got no closer to edge of tray). In Experiment 2, the test individual's first choice was always set to fail, and *P. labiata* was given repeated opportunities to respond to feedback, yet the Sagada *P. labiata* continued to place little reliance on trial and error for solving the confinement problem. That the Los Baños *P. labiata* relied more strongly on trial-and-error problem solving than the Sagada *P. labiata* has now been demonstrated across two different tasks.

Research in animal learning and cognition has focused mainly on using vertebrates as subjects, and the literature typically makes comparisons across large taxonomic groups (Basil, Kamil, Balda, & Fite, 1996; Beer, 1996; Jerison, 1973; Lashley, 1949; McPhail, 1985; Shettleworth, 2003). This research has strengthened our knowledge of cognitive and learning abilities, but the selective pressures that might influence the evolution of these abilities are still poorly understood (Dukas, 1998a; Shettleworth, 1993; Yoerg, 1991). The present paper is unconventional because the animals studied are jumping spiders (Salticidae) instead of vertebrates, and because we consider geographic variation within a single species, *Portia labiata* (Thorell), in the ability to solve a confinement problem.

Important questions remain unresolved concerning the extent to which an animal's various cognitive abilities are single-purpose adaptations tailored for specific functions (Kamil, 1998; McFarland & Bosser, 1993; Stephens, 1991). For example, how often and under what circumstances does the evolution of cognitive skills push animals across a threshold, enabling them to respond flexibly and adap-

tively to problems outside the context in which these skills originally evolved (see Dennett, 1996)? *Portia* may provide especially interesting insights into these questions.

The eyes of most spiders lack the structural complexity required for acute vision (Homann, 1971; Land, 1985), but the level of resolution of salticid eyes has no known parallel in other animals of comparable size (Blest, O'Carroll, & Carter, 1990; Land, 1969a, 1969b, 1974). Almost 5,000 salticid species have been described (Coddington & Levi, 1991; Zabka, 1993), and most of these are cursorial hunters of insects (Richman & Jackson, 1992). Having intricate vision-controlled predatory behavior, most salticids neither build nor use webs for catching prey. Striking exceptions include tropical African, Asian and Australasian salticids in the genus *Portia* (Wanless, 1978). Predatory versatility is pronounced in *Portia*, appearing to exceed that known for any other spiders (Jackson & Pollard, 1996). Besides capturing prey in the open, the species in this remarkable genus also spin prey-capture webs (Jackson, 1985), and they routinely invade alien webs where they capture their preferred prey, other spiders (Li & Jackson, 1996; Li, Jackson, & Barrion, 1997).

Web-building spiders have only rudimentary eyesight (Land, 1985), but their webs are an important part of their sensory system (Foelix, 1996; Masters, Markl, & Moffat, 1986; Witt, 1975). To catch a web-building spider, *Portia* does not simply stalk or chase down its prey. Instead, *Portia* lures the spider over with aggressive-mimicry signals, by manipulating the silk with any combination of its eight legs and two palps (Jackson & Wilcox, 1998; Tarsitano, Jackson, & Kirchner, 2000). *Portia* has an almost limitless repertoire of signals because it can alter the sequences and vary the speed, amplitude and timing of movement of each appendage independently (Jackson & Blest, 1982; Jackson & Hallas, 1986a).

By trial and error, *Portia* flexibly adjusts its signals in response to feedback from its intended prey (Jackson & Wilcox, 1993), thereby appearing to gain dynamic fine control over the resident spider's behavior (Jackson & Pollard, 1996). When using trial and error, *Portia* first presents the resident spider with a kaleidoscope of different signals. Once one of these signals elicits an appropriate response from the resident spider, *Portia* stops varying its signal output and repeats the particular signal that worked. When the prey spider stops responding appropriately, *Portia* goes back to generating a wide range of signals until once again it finds a signal that triggers a favourable response from the resident spider.

Trial-and-error derivation of appropriate web signals is a "generate-and-test" algorithm (Simon, 1969) characterized by an exceptionally large generating capacity. This appears to be an example of flexible problem solving on a level not usually expected in spiders (Mitchell, 1986). *Portia*'s intimate contact with its prey's sensory system and the high level of risk entailed in attempting to gain dynamic fine control over the behavior of another predator (Jackson, 1992a) may be especially important factors favoring the evolution of *Portia*'s flexible problem-solving ability. Ecotypic variation (i.e., genetically based differences between populations) provides evidence in support of this hypothesis.

Behavioral ecotypes were demonstrated in an earlier study (Jackson & Carter, 2001) in which individuals derived from two habitats (Los Baños and Sagada) in the Philippines were compared. Los Baños is a low-elevation tropical

rainforest site where prey (spider) diversity is especially high and where some prey types are especially dangerous (Jackson, Li, Fijn, & Barrion, 1998; Jackson, Pollard, Li, & Fijn, 2002), whereas Sagada is a high-elevation pine-forest site where prey (spider) diversity is considerably lower and the especially dangerous prey from Los Baños are absent. In laboratory experiments, individuals from both populations used trial and error to derive appropriate aggressive-mimicry signals, but the Los Baños *P. labiata* relied on trial and error significantly more often than did the Sagada *P. labiata*. Maternal effects and variation in experience were ruled out as explanations for the findings in the study of ecotypes (Jackson & Carter, 2001) because all individuals tested were from laboratory rearing to second and third generation under standardized conditions.

Here we consider the specificity of the cognitive attribute that varies between the two populations of *P. labiata*. In particular, we compare the performance of individuals from the two populations when presented with a confinement problem, a deliberately artificial situation (which involves crossing water and includes being helped or hindered in doing so) designed for solution by trial and error. Solving this problem by trial and error has already been shown in another species of *Portia* (*P. fimbriata*) from another habitat (Queensland, Australia) (Jackson, Carter, & Tarsitano, 2001). Although *Portia* in nature might sometimes need to cross water, there is no evidence that crossing water is a routine occurrence and the manipulations *Portia* experienced in the confinement experiments (being helped forward or forced back) are almost surely alien to anything *Portia* might routinely encounter in nature.

Although signal derivation is the context in which *Portia*'s ability to adopt trial and error may have evolved, *Portia*'s ability to apply trial and error to a confinement problem (Jackson et al., 2001) suggests that the use of the trial and error algorithm is like a general-purpose learning ability (Beecher, 1988) that can be applied to novel problems (Johnston, 1982). Confronting *Portia* with a confinement problem might be envisaged as investigating a spider's capacity for something akin to innovation or insight (Reader & Laland, 2003).

Here we consider, for the Los Baños and the Sagada *P. labiata*, whether the level of reliance on trial and error varies specifically in the context of signal generation (Hypothesis 1) or whether it is a more general ability to apply the trial-and-error algorithm that varies between the two populations (Hypothesis 2). The experimental design we use has similarities to Thorndike's (1911) confinement-test paradigm in which the goal was to test whether animals can derive methods for escaping from enclosed areas. However, after two modifications, the confinement problem we present to *Portia* has formal similarities to the trial-and-error signal-derivation problem.

First, *Portia* in a web often performs aggressive-mimicry signals while distant from the prey spider. This means that a particular signal might draw in a resident spider stepwise instead of immediately. When this happens, *Portia* experiences only partial success during the steps, with prey capture depending on repetition of the partially successful signals (Jackson & Wilcox, 1993). Partial success is introduced into a confinement-problem paradigm by requiring that *Portia* escape step-wise from confinement.

Second, in the signal-generation study (Jackson & Wilcox, 1993), the signal that would be successful was determined at random before each test began. The confinement tests also require choices (i.e., there are two possible ways by which *Portia* might escape from an enclosed area) where we decide beforehand, at random, which particular choice will succeed.

There were two experiments in this study. In Experiment 1, we determined at random beforehand whether a particular behavior pattern would be successful or not. We then determined whether individuals of *P. labiata* became more likely to repeat a particular behavior pattern (i.e., leap or swim) after partially succeeding at escaping confinement, and whether they became more likely to change to a different behavior pattern after failing. Our objective for this experiment was to ascertain whether the Los Baños *P. labiata* was more inclined than the Sagada *P. labiata* to adopt trial and error after a single experience in the apparatus. In Experiment 2, where the first behavior pattern employed was always predetermined to fail, our objective was to ascertain how many failures it would take before *P. labiata* switched behavior (i.e., whether the Sagada *P. labiata* required more feedback).

General Method

All individuals of *P. labiata* were derived from laboratory rearing to second or third generation. Standard maintenance procedures and terminology were adopted, as detailed elsewhere (Jackson & Hallas, 1986b). Laboratory-rearing environments were "enriched" (spacious cages, meshwork of twigs within each cage) in a manner comparable to that described by Carducci and Jakob (2000). Maintenance diet consisted of a variety of spider and insect species, as this has been shown to be optimal (Li & Jackson, 1997).

All test subjects were juveniles (4-5 mm in body length). Equal numbers of individuals from at least 10 sib-ships were each used only once. All testing took place in a controlled-environment laboratory (laboratory photoperiod 12L:12D; lights came on at 0800 h; temperature constant at 25° C). Before testing, each individual was kept without food for 48 h.

In Experiment 1 (identical to Experiment 1 in Jackson et al., 2001), each individual had one opportunity to escape from confinement. In Experiment 2, each individual was allowed successive opportunities to escape from confinement. The experimental apparatus (Figure 1) was a water-filled rectangular plastic tray in which there was an "island" surrounded by an "atoll". The inner edge of each shorter (210 mm) side of the atoll was 127.5 mm from the closest edge of the island and 127.5 mm from the closest edge of the tray. The edge of each longer (300 mm) side of the atoll was 77.5 mm from the closest edge of the island and 77.5 mm from the closest edge of the tray. The water in the tray came up to the height (20 mm) of the island and atoll. Preliminary testing established that the juvenile stages of *P. labiata* used as test subjects could not clear these distances by leaping.

A plastic tube extended 60 mm below the tray. Its upper end went through a hole in the bottom of the tray and opened in the centre of the island (Figure 1). The tray was set on a 100 mm high wood frame that allowed space for reaching the lower opening of the tube. *P. labiata* was introduced into the bottom of this plastic tube and prodded up onto the island with a plunger (a cork, slightly smaller in diameter than the tube, with a stick handle attached below).

Preliminary testing established that *P. labiata*, like *P. fimbriata*, leaves the island, and attempts to cross the water, either by swimming or by leaping. Although it has been reported that salticids cannot swim (Ehlers, 1939; Foelix, 1996), it is now known that at least a few salticid species have some proficiency at swimming (Stratton, Suter, & Miller, 2004), and *Portia* readily moves across water surfaces without sinking. When leaving the island by swimming, *Portia* slowly places its forelegs on the water, pushes off from the island with its rear legs, moves completely out into the water in a spread-eagle posture and then moves its legs in a stepwise fashion to propel itself across the water surface. When leaving the island by leaping, *Portia* lands on the water (usually at a point about halfway across) and then swims the rest of the way across.

P. labiata's choice (leap or swim) was recorded once all legs were on the water. Using this criterion, the choice recorded was always unambiguous. All trials were carried out between 0830 and 1100 h. Between trials, the island and atoll were cleaned with 80% ethanol and water, and then dried,

and the water in the tray was changed. Lighting was provided by a 200 W incandescent lamp positioned 300 mm above the tank. Overhead florescent lamps provided additional ambient lighting. Statistical analyses are from Manly (1997) and Sokal and Rohlf (1995).
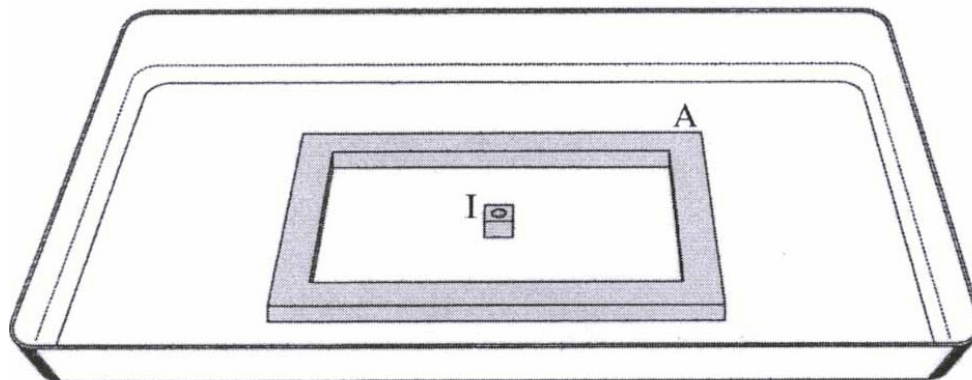

Figure 1. Apparatus used for ascertaining whether Los Baños and Sagada *Portia labiata* use trial and error to solve confinement problem. Spider emerges on island (I) surrounded by atoll (A) in water-filled tray and chooses either to leap or to swim. Choice that will be successful determined at random before testing begins. Successful choice: spider was moved to atoll. Unsuccessful choice: spider was returned to island. After successful first choice, spider makes second choice from atoll. After unsuccessful first choice, spider makes second choice from island. Island: 20 x 20 mm plastic square with hole in centre (entry point for spider). Atoll: 25 mm wide plastic walkway forming rectangle (300 x 210 mm) around island. Tray: 580 x 380 mm.

Experiment 1

Test spiders were assigned at random to two groups: spiders with leaping pre-determined to be successful for reaching the atoll (40 *P. labiata* from Los Baños and 40 *P. labiata* from Sagada) and spiders with swimming predetermined to be successful for reaching the atoll (40 *P. labiata* from Los Baños and 40 *P. labiata* from Sagada). Any test spider that attempted to cross the water using behavior (swimming or leaping) predetermined to be successful was helped to the atoll. Once the spider made its choice, we helped it to reach the atoll by placing a small plastic scoop between the spider and the island, then gently making waves to propel the spider to the atoll. Any spider that attempted to cross the water using behavior pre-determined to fail (e.g., a swimming spider in the group with leaping predetermined to be successful) was pushed back to the island (with scoop placed between the spider and the atoll and gentle waves made to propel it back). The plastic scoop never touched the spider.

Four possible outcomes were defined operationally with no claims being made about a spider's understanding of the outcomes: (1) both the first and the second choice succeeded; (2) neither the first nor the second choice succeeded; (3) the first choice succeeded but the second choice failed; (4) the first choice failed but the second choice succeeded. Whether the consequence of the first choice influenced the second choice was considered by using tests of independence, analyzing separately the data for spiders that leapt first and spiders that swam first. Initial choices were always made from the island. When the first choice succeeded, the second choice was made from the atoll. The reinforcement for making the correct choice was only "partial success" at escaping from the water-filled tray (i.e., a correct first choice got the spider only part of the way to the edge of the tray). This meant that, on the atoll, a test spider had to choose again how to cross the water before it could reach the edge of the tray. It might either repeat its first choice or switch. Repetition 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 might repeat its earlier choice or switch. Switching was predicted by the trial-and-error hypothesis. However, an experiment in the earlier study (Jackson et al., 2001) showed this distinction (whether the second choice was from the island or from the atoll) did not influence the spiders' choices.

After a test spider came up the tube, out of the hole and onto the island, testing was aborted whenever it failed to make its first choice within 10 min or failed to stay on the platform for at least 10 s before making its first choice. The rationale for the 10 s window was to rule out instances in which the spider might have left the island before having time to look around before making a choice. Tests were also aborted whenever a test spider: 1) failed to make its second choice within 10 min after its first choice (i.e., after reaching the atoll or being returned to the island) or 2) failed to remain on the island or atoll for at least 10 s before making its second choice. Only 7% of the tests had to be aborted. Test spiders from aborted tests were not used again. There were no instances in which a test spider on the island went back into the hole or a spider on the atoll attempted to return to the island.

Experiment 2

This was the same as Experiment 1 except that the first choice, regardless of whether it was to swim or to leap, was always pre-determined to fail, and the test spider was given up to 10 successive opportunities to switch (i.e., the test spider was pushed back to the island after each choice until it switched or until it was tested 10 times, whichever came first). The test spider's score was its number of failures before switching. For example, a spider that switched the next time it was tested got a score of zero and a spider that never switched got a score of 10. Scores for Los Baños and Sagada *P. labiata* were then compared using Mann-Whitney U-tests and by running a permutation test.

Results

Experiment 1

First choices (from the island) were about equally often to leap (44 for Los Baños and 47 for Sagada) or to swim (36 for Los Baños and 33 for Sagada) (Los Baños: $X^2 = 0.80$, $p = 0.37$, NS; Sagada: $X^2 = 2.45$, $p = 0.12$, NS; tests of goodness of fit, null hypothesis 50/50).

For the Sagada *P. labiata*, there was no evidence that feedback from the consequence of the first choice influenced the second choice (Table 1). However, findings for the Los Baños *P. labiata* were comparable to the findings for *P. fimbriata* in this same experiment (Jackson et al., 2001). Test spiders that leapt first (Table 2) and succeeded at reaching the atoll usually leapt again, whereas spiders that leapt first, but failed to reach the atoll, usually switched to swimming. Spiders that swam first and succeeded at reaching the atoll usually swam again, whereas spiders that swam first, but failed to reach the atoll, usually switched to leaping.

Table 1
Table 1. Data for Sagada Portia labiata. Results are Analyzed Separately for Leapt First and Swam First.

	Spider leapt first	Spider swam first
Spider repeated successful first choice	21	13
Spider switched when first choice was successful	1	2
Spider switched when first choice was unsuccessful	1	2
Spider repeated unsuccessful first choice	24	16
Test of independence	$X^2 = 0.01$ $p = 0.93$	$X^2 = 0.04$ $p = 0.85$

Table 2

Table 2. Data for Los Baños Portia labiata. Results are Analyzed Separately for Leapt First and Swam First.

	Spider leapt first	Spider swam first
Spider repeated successful first choice	23	17
Spider switched when first choice was successful	3	5
Spider switched when first choice was unsuccessful	13	11
Spider repeated unsuccessful first choice	5	3
Test of independence	$X^2 = 16.93$ $p < 0.001$	$X^2 = 10.81$ $p < 0.001$

The Los Baños *P. labiata* significantly more often made decisions that solved the confinement problem (64 out of 80 tests) than the Sagada *P. labiata* (37 out of 80 tests) (test of independence, $X^2 = 19.57$, $p < 0.001$).

These findings suggest that the Sagada *P. labiata* does not use trial and error for solving the confinement problem. Alternatively, it may be that the Sagada *P. labiata* can use trial and error to solve the confinement problem, but only after more feedback than required by the other species and populations of *Portia*. This alternative hypothesis was considered in Experiment 2.

Experiment 2

Scores for the Los Baños and the Sagada *P. labiata* (Figure 2) were significantly different (Mann-Whitney U-test and permutation test, $p < 0.001$) and, in fact, overlapped only minimally. The Sagada *P. labiata* usually failed to switch at all, whereas the Los Baños *P. labiata* usually switched at the first opportunity.
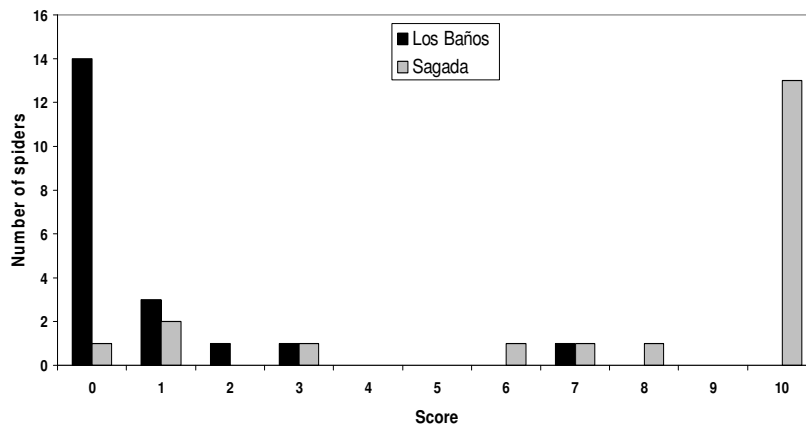

Figure 2. Results from Experiment 2 for Los Baños and Sagada *Portia labiata*, showing scores (number of times spider attempted to reach atoll, either by swimming or by leaping, before switching tactics).

Discussion

Two populations of *Portia*, the Queensland *P. fimbriata* (Jackson et al., 2001) and the Los Baños *P. labiata* (this study), have now been shown to solve a confinement problem by trial and error. We chose this problem because it seems to test *Portia*'s ability to solve problems from a novel, highly artificial context (i.e., a situation that would not be encountered in the field). These two populations of *Portia* (Queensland and Los Baños) switched behavior when prevented from escaping confinement and repeated behavior when they partially succeeded at escaping.

Portia's use of trial and error to solve this confinement problem appears to be at least a rudimentary example of learning (Staddon, 1983), or more technically an example of operant conditioning (Skinner, 1938). At least short-term memory is implied (see Davis & Dougan, 1988) because *Portia* must remember the last decision and its consequence, but we do not know for how long memory traces persist. However, a cognitive issue, problem-solving ability, may be of more interest.

Compared with the solving of the confinement problem, signal derivation apparently relies on a much greater generating capacity (i.e., *Portia*'s choice was always between only two potential methods of crossing an expanse of water, but the number of signals *Portia* may generate in nature appears almost limitless). *Portia*'s predatory strategy is based on web invasion and close interplay with another predator, and a compelling argument might be made for how this strategy might favor especially pronounced problem-solving ability in the context of signal derivation. It has been argued that acquisition of special-purpose problem-solving abilities may sometimes enable animals to respond flexibly and adaptively to problems outside the context in which these special-purpose abilities originally evolved (Dukas, 1998b; Johnston, 1982; Papaj, 1986). In *Portia*, perhaps a predatory strategy that routinely demands fine control over the behavior of dangerous prey has set the stage for the evolution of problem-solving abilities that, as a spin-off, can be readily applied to other situations, including a novel confinement problem.

For the spin-off hypothesis, the Sagada *P. labiata* is of particular interest. The Sagada and the Los Baños *P. labiata* derive signals by trial and error, but the two populations differ because the Sagada *P. labiata* uses trial and error less consistently than the Los Baños *P. labiata* (Jackson & Carter, 2001). In the present study, we found a parallel trend, only more extreme. We found no statistically significant evidence that the Sagada *P. labiata* used trial and error to solve the confinement problem at all even when given as many as 10 successive opportunities to switch choices. Taken at face value, these findings imply that applying trial and error to the confinement problem is a capacity of the Los Baños *P. labiata* that the Sagada *P. labiata* altogether lacks. Acknowledging that other experimental designs might show use of trial and error where the present design failed, the findings still suggest an interesting parallel with the findings from the signal-derivation study (Jackson & Carter, 2001).

It is unlikely that rearing conditions caused the differences between individuals from Los Baños and Sagada in the signal-derivation experiment (Jackson & Carter, 2001) or here in a confinement experiment. For both studies, all subjects were second and third generation spiders reared under standardized conditions, and

no subjects had prior experience of the testing situation. Prior learning, maternal effects (see Roff, 1998; Wade, 1998) and other indirect genetic effects (Moore, Wolf, & Brodie, 1998) were unlikely to confound interpreting the findings.

That the predatory behavior of *Portia* (Jackson, 1992b; Jackson & Hallas, 1986b; Jackson et al., 1998) and various other spiders (Riechert, 1981, 1991, 1999; Uetz & Cangialosi, 1986) varies geographically within a single species has been shown before. However, the signal-derivation study (Jackson & Carter, 2001) and the present study are different because they suggest geographic variation in flexible problem-solving capacities within a single species. However, geographic variation in the flexible problem-solving capacities of a single species has been demonstrated in a wide variety of vertebrates (Huntingford & Wright, 1992; Huntingford, Wright, & Tierney, 1994; Nelson, Whaling, & Marler, 1996; Thompson, 1990, 1999). Capacity limitations are evident even in large animals such as mammals (Desimone, 1998; Dukas, 1999; Dukas & Kamil, 2000, 2001; Rees, Frith, & Lavie, 1997), suggesting that they are especially severe for smaller animals such as spiders.

A prediction we are currently investigating is that processing speed and risk of making errors are lessened when *P. labiata* can rely on less cognitively demanding procedures (see Harland & Jackson, 2000, 2004). For the Los Baños *P. labiata* and in the context of signal derivation, compensation for these costs (processing time and errors) may be more common than for the Sagada *P. labiata*. The Los Baños *P. labiata*'s ability to use trial and error to solve a novel confinement problem can be envisaged as something like innovation.

Portia may show surprisingly flexible behavior for a small animal and an invertebrate. However, the notion that invertebrates are largely inflexible instinct-driven automatons simply does not hold up to close scrutiny (see Cross & Jackson, 2006). For example, recent research with vinegar flies (*Drosophila melanogaster*; Guo & Gotz, 1997), honey bees (*Apis mellifera*; Zhang & Srinivasan, 2004) and butterflies (*Papilio*; Arikawa, Kinoshita, & Stavenga, 2004) illustrate how insects can be trained to discriminate between various visual and olfactory stimuli. There are also examples of social insects that solve maze tasks (Zhang, Bartsch, & Srinivasan, 1996) and use symbolic communication to convey information about the location of food and nest sites (von Frisch, 1967). Foraging, web-building and mating decisions of many spiders are influenced by learning and other types of experience (Bays, 1962; Chmiel, Herberstein, & Elgar, 2000; Edwards & Jackson, 1994; Grunbaum, 1927; Heiling & Herberstein, 1999; Lahue, 1973; LeGuelte, 1969; Morse, 1999, 2000a, 2000b; Nakata & Ushimaru, 1999; Punzo, 2004; Sandoval, 1994; Sebrier & Krafft, 1993; Seyfarth, Hargenröder, Ebbes, & Barth, 1982; Tso, 1999; Venner, Pasquet, & Leborgne, 2000; Whitehouse, 1997), and the level to which salticid spiders rely on problem solving, decision making and forward planning (Clark & Jackson, 2000; Clark, Jackson, & Waas, 1999; Jackson, 1977, 1981; Jackson & Carter, 2001; Tarsitano & Andrew, 1999; Tarsitano & Jackson, 1994, 1997; Tarsitano et al. 2000; Wilcox, Jackson, & Gentile, 1996) is unusual even for vertebrates. Gone are the days when bigger-brained animals such as rats and pigeons were considered the only suitable subjects for research on flexible behavior, and we can count on even more surprises from future invertebrate research.

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