ARTICLE

Reliance on trial and error signal derivation by *Portia africana*, an araneophagic jumping spider from East Africa

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Abstract All species from the jumping spider (Salticidae) genus *Portia* appear to be predators that specialize at preying on other spiders by invading webs and, through aggressive mimicry, gaining dynamic fine control over the resident spider's behavior. From previous research, there is evidence that *P. fimbriata*, *P. labiata* and *P. schultzi* derive signals by trial and error. Here, we demonstrate that *P. africana* is another species that uses a trial and error, or generate and test, algorithm when deriving the aggressive-mimicry signals that will be appropriate in different predator–prey encounters. We discuss the implications of these new findings and the findings from previous work in order to understand the selection factors that drive the evolution of flexibility in aggressive-mimicry strategies.

Keywords Salticidae · Aggressive mimicry · Predation · Cognition · Sensory exploitation

Introduction

Broadly speaking, aggressive mimics are predators that use deceptive signals for gaining control of the behavior of their prey (Wickler 1968; Edmunds 1974). Especially intricate aggressive-mimicry strategies are known for arthropods that invade the webs of spiders (e.g., Wignall

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and Taylor 2010; Nelson and Jackson 2011). Here, we consider the aggressive-mimicry strategy of *Portia africana*, a web-invading jumping spider (Salticidae).

Salticids have eyesight unparalleled in animals of comparable size (Land and Nilsson 2002), and, as might be expected for predators with exceptional eyesight, most of the 5,000 described species in this family (Platnick 2010) appear to be cursorial hunters that, without making use of webs, prey primarily on insects (Richman and Jackson 1992; Jackson and Pollard 1996). The most striking exceptions are African, Asian and Australasian salticids from the genus *Portia*. Although the salticids from this genus feed on insects, their preferred prey are other spiders that they capture by invading webs (Harland and Jackson 2004). Instead of simply stalking or chasing down the resident spider in an invaded web, *Portia* uses its legs and palps to make signals (Tarsitano et al. 2000), and, with these signals, gains dynamic fine control over the resident spider's behavior (Nelson and Jackson 2011). To understand *Portia*'s strategy, it is important to appreciate that the eyes of non-salticid web-building spiders support only rudimentary spatial acuity (Homann 1971; Land and Nilsson 2002). As these spiders rely primarily on the interpretation of web signals (i.e., tension and movement patters in web silk), it is appropriate to envisage the web as an integral part of the web-building spider's sensory apparatus (Witt 1975; Foelix 1996; Barth 2002). This in turn implies that, when practising aggressive mimicry, *Portia* has intimate contact with its prey's sensory world.

Portia preys on many kinds of spiders in many kinds of webs, and this raises questions about the mechanisms by which *Portia* derives the particular signals that will be suitable in different predator–prey encounters. Appreciating *Portia*'s capacity for varying signals is a step toward answering these questions. *Portia* can use almost any

combination of its eight legs and two palps at one time, with the movement characteristics (speed, amplitude and timing) of each appendage also being adjustable (Jackson and Blest 1982; Jackson and Hallas 1986a). However, a critical question remains. What are the mechanisms by which *Portia* derives from this repertoire the different signals needed in different predator–prey encounters?

Our current understanding of *Portia*'s signal derivation mechanisms comes primarily from experiments on *Portia fimbriata* from Queensland and the Northern Territory in Australia, *P. labiata* from Sri Lanka and the Philippines, and *P. schultzi* from Kenya (Jackson and Wilcox 1993; Jackson and Carter 2001). Each of these species first presents the resident spider with a variety of signals. When one of these signals elicits an appropriate response from the resident spider, *Portia* stops varying its signal output and concentrates on repeating the particular signal that worked. If the prey spider stops responding appropriately, *Portia* reverts to varying signals until it again finds a signal that triggers a favorable response.

Population-level differences in the predatory behavior of *Portia* are well known. For example, *Portia fimbriata* has distinctive ecotypic variation in which populations from different areas are locally adapted to local prey. In the Queensland habitat of *P. fimbriata*, another salticid species, *Jacksonoides queenslandicus*, is especially abundant (Jackson 1988) and it is one of the spiders for which this particular population of *P. fimbriata* has a prey-specific predatory strategy. There is also evidence for one species that the level of reliance on trial and error varies between populations. In the Philippines, two populations of *P. labiata* from Luzon were studied (Jackson and Carter 2001), one from a rainforest habitat close to sea level (Los Baños, Laguna Province) and the other from a higher-elevation (1,500 m) pine-forest habitat (Sagada, Mountain Province). In laboratory experiments, reliance on trial and error signal derivation was significantly stronger for the Los Baños than for the Sagada *P. labiata*. Prey diversity experienced by *P. labiata* in the Los Baños site appears to be considerably greater than in the Sagada site, suggesting that prey diversity has been at least one of the selection factors driving the evolution of flexibility in aggressive-mimicry strategies.

An important step toward evaluating this hypothesis is to investigate a wider range of *Portia* species. Here, we investigate *P. africana* from a habitat in western Kenya. Prey diversity in this habitat, as in the Los Baños habitat, appears to be considerably higher than in Sagada. We carried out experiments comparable to those used with *P. labiata* and we predicted that findings for *P. africana* would be more like those for the Los Baños, rather than the Sagada, *P. labiata*.

Materials and methods

General

Except for some minor alterations, the methods we adopt here correspond to two of the experiments carried out earlier using *P. fimbriata*, *P. labiata* and *P. schultzi* (Jackson and Wilcox 1993; Jackson and Carter 2001). All individuals of *P. africana* used as test spiders were adult females (unmated; matured 2–3 weeks prior to being used) taken from a laboratory culture (3rd and 4th generation). Standard maintenance procedures were adopted, as detailed elsewhere (Jackson and Hallas 1986b). Laboratory rearing cages were enriched with a meshwork of twigs. Maintenance diet consisted of a variety of spider and insect species, as earlier studies have shown this to be optimal (Li and Jackson 1997). However, no individual or its laboratory-reared parents had prior experience with the spider species used as prey during experiments and no individual was used in more than one experiment or provided data more than once for any one experiment. For each experiment, the individuals used were derived from at least seven sibships (defined as the progeny of a particular male and female). The number of individuals from each sibship was about equal for each experiment.

Rearing and testing took place in a controlled-environment laboratory (light:dark cycle, 12L:12D; lights on at 0800 hours; temperature constant at 25°C). Test spiders were deprived of food for 48 h prior to testing them in wooden frame cages with removable glass sides (Fig. 1).

By using lures instead of living spiders as prey, we avoided confounding variables that would have come from prey behavior, thereby achieving tighter control of the stimulus provided to the test spider. That using lures was feasible was already known from earlier research showing that responses by *Portia* to lures and living prey are comparable (Li and Jackson 1996; Li et al. 1997).

Lures were made from dead, dried spiders mounted on corks. The spider used for making lures was *Zosis geniculatus* (Olivier) (Uloboridae). We chose this species because it is not present in the western Kenya habitat and preliminary studies showed that *P. africana* readily preys on this species in the laboratory. All individuals of *Z. geniculatus* came from a laboratory culture that originated from specimens collected in Los Baños.

To make a lure, we first immobilized a prey spider under CO_2 and then placed it in 80% ethanol for 60 min. Next, it was mounted in a lifelike posture on the center of one side of a disc-shaped piece of cork (diameter about 1.5 times the body length of the spider), after which the spider and cork disc were sprayed with an aerosol plastic adhesive (Crystal Clear Lacquer, Atsco, Australia). The spider from which

Fig. 1 Wooden frame (interior dimensions, $200 \times 200 \times 30$ mm) cage with removable glass panes used for experiments on trial and error signal derivation by *Portia africana*. To start a test, an open vial containing the test spider was connected to an open hole at the bottom of the cage, and the test spider walked into cage. The cage was held above a table by a clamp and stand. Coil attached to frequency generator placed behind the lure. Spiders not to scale

the lure was made was always a juvenile (body length 5–7 mm). The lure was allowed to dry for about 24 h before being used. In all experiments, the test spider's body length matched (to the nearest millimetre) the lure spider's body length.

The spiders that built the webs used in experiments ('source spiders') were always adult *Z. geniculatus* females. As it is typical for *Z. geniculatus* to build a normal web overnight, each web we used in an experiment was acquired by putting a source spider in a clean cage and then maintaining the spider without prey for 1–2 days. This procedure ensured that the web was free of prey remains. There were rare occasions when a source spider oviposited in its web overnight and in these instances we discarded the webs. The diameter of the web's capture zone (see Foelix 1996) was usually at least 160 mm in all directions. On the rare occasions when smaller webs were built, testing was aborted. No web was ever used in more than one test. Between tests, cages were cleaned with 80% ethanol, followed by distilled water, and then dried in order to remove chemical cues from previous tests. *Z. geniculatus* uses cribellate silk to spin an orb web and, owing to the stickiness of cribellate silk (Foelix 1996), cork discs stayed in place when put on the webs.

Before each test, a test spider was taken from its maintenance cage and kept in a vial for 10 min. The vial was then opened and connected to a hole in the bottom of a web-containing experimental cage. Detail concerning the test spider's behavior (the sequencing of appendage use during signaling) came from analysis of video tapes.

We based our experiments on a randomized paired design, using lure movement as a reinforcement stimulus. We used a coil and magnet to move the lure. A samarium cobalt magnet (1 mm^3) was glued to the side of a cork disc directly opposite the test spider. Using a function generator connected to an amplifier, a 5-Hz sine wave was sent through a coil positioned outside the cage (50 mm from the magnet). Amplitude was set so that the disc moved 2–4 mm. In control tests, the function generator was turned off.

There were two treatments (experimental and control), with the reinforcement stimulus being present in the experimental but not in the control treatment. Both treatments had an acclimation period and a testing period. For the acclimation period, we waited 5 min after the test spider made its first signal and then the testing period began. Before beginning the acclimation period we had chosen a priori, from a random number table, a number from 1 to 5, which would consist of whether the 1st, 2nd, 3rd, 4th or 5th signal made by the test spider during the testing period would be the focal signal. During the experimental testing period, the lure was made to move 1 s after the test spider made the randomly chosen focal signal ('reinforced'), but the lure was not made to move when the test spider made the randomly chosen focal signal during the control testing period. We then recorded in the experimental and in the control treatment whether the subsequent signal made by the test spider was the same as or different from the signal we had chosen to be the focal signal. Tests were aborted on the rare occasions when the test spider made its next signal sooner than 1 s after it made the focal signal and on the rare occasions when the test spider failed to make another signal within 11 s after the focal signal (i.e., within 10 s after reinforcement for experimental treatment and after the equivalent total time for the control treatment).

We did two experiments to determine whether localized movement of a lure encourages test spiders to repeat signals. For Experiment 1, the experimental treatment was always on one day and the control treatment was always on the next or the previous day (whether next or previous determined at random). However, no effort was made to ensure that the particular signal chosen to be the focal signal in the experimental and in the control treatment matched. In fact, at random, they were always different. This efficient procedure allowed for comparing test spider behavior with and without reinforcement only 1 day apart.

For Experiment 2, we relaxed the stipulation that the experimental and the control treatment had to be only 1 day apart so that we could ensure that the actual signal

chosen at random to be the focal signal in the experimental treatment was also the focal signal in the control treatment. We achieved this by altering the rules pertaining to the second trial, while otherwise retaining the methods used in Experiment 1. Firstly, a signal was chosen at random to serve as the focal signal in the first trial (either control or experimental, also chosen at random). However, for a successful second trial (i.e., the other treatment), we stipulated that we would continue only if one of the five signals performed by the test spider during the testing period had been, at random, the focal signal in the first trial. If the first trial had been the control treatment, and if the test spider made this signal as one of its five signals during the testing period in the second trial (i.e., the experimental treatment), then that particular signal, regardless of whether it was the 1st, 2nd, 3rd, 4th or 5th signal performed by the test spider in the experimental treatment, was adopted as the focal signal in the testing period of the experimental treatment (i.e., this particular signal was reinforced). A comparable rule applied if the first trial had been the experimental treatment.

Whenever the first attempt to achieve a successful second trial failed, we attempted the second trial of the pair on successive days until successful. However, when still unsuccessful after 5 days, *P. africana* was fed and then held for another 7-day interval, after which we resumed attempting, on successive days, to complete the second trial. Again, if 5 days elapsed without success, we fed the test spider and waited another 7 days, after which we resumed attempting to complete a second test for another 5 days in succession. Whenever four such repeated 5-day testing sessions failed, the test spider was removed from the experiment.

Results

Our hypothesis was that *P. africana* relies strongly on a trial and error algorithm when deriving signals. In Experiment 1 and in Experiment 2, test spiders repeated the focal signal in the experimental treatment significantly more often that they repeated the focal signal in the control treatment (Fig. 2).

Discussion

The methods in Experiment 1 ensured acquiring data for experimental and control treatment only 1 day apart and the methods in Experiment 2 ensured that the focal signal in the control and in the experimental treatment were the same. Despite the different methods, the findings from these two experiments converged in supporting the hypothesis that
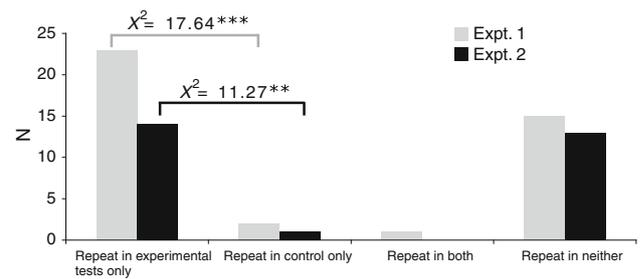
Fig. 2 *Portia africana*'s propensity to repeat a signal chosen at random during the acclimation period compared for the testing period with (experimental) and without (control) reinforcement. Statistical tests are McNemar tests (**$P < 0.001$, ***$P < 0.0001$)

P. africana, when deriving signals, relies strongly on a trial and error algorithm.

At least short-term memory is implied these findings, as *Portia* must have remembered the last signal made and the consequence of making it. This, in turn, implies that trial and error signal generation is at least a rudimentary example of learning (see Staddon 1983; Jakob et al. 2011), or more specifically operant conditioning (Skinner 1938). However, many questions related to learning remain. In particular, *Portia*'s ability to associate particular signals with particular prey remains to be investigated. How long memory traces persist is also currently unknown. The answers to these questions notwithstanding, *Portia*'s signal-making strategy appears to be an example of exceptional flexibility in the context of problem solving.

Theoretical accounts of why especially flexible problem-solving ability may have evolved in *Portia* have emphasized the intimate contact this predator has with its prey's sensory system, the high level of risk entailed in attempting to gain dynamic fine control over the behavior of another predator, and the potential for coevolution (Jackson 1992; Nelson and Jackson 2011). Scaling factors may also be important, as smaller animals tend to have fewer, not smaller, neurons (Bullock and Horridge 1965), which means fewer components are available for sense organs and brains. It may be indisputable that small brain size constrains how complex and flexible an arthropod can become, relative to much larger animals such as parrots and chimpanzees, but a precise understanding of the severity of small-size constraints on arthropod cognitive capacity remains elusive (Chittka and Niven 2009; Srinivasan 2010).

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). In smaller animals such as spiders, where adaptive tradeoffs may be especially severe, cognitive capacities may be even more likely to diverge geographically within single

species or between closely related species (e.g., Heiling and Herberstein 2004). Comparison across ecotypes or species of small animals might, in turn, be especially likely to reveal the particular selection pressures that drive the evolution of the cognitive attributes.

Earlier research (Jackson and Carter 2001) using experiments comparable to those we used in the present study suggested that the diversity of prey spiders and webs encountered by *P. labiata* in the Philippines has shaped the level to which this species relies on trial and error for signal derivation. The diversity of web-building spiders on which *P. labiata* preys in a lowland rain forest (Los Baños) appears to be much greater than that in a high-elevation pine forest (Sagada) and, as predicted, more pronounced reliance on trial and error was revealed when the test spiders were from the Los Baños instead of the Sagada population of *P. labiata*.

Our findings for *P. africana* were remarkably similar to the findings for the Los Baños *P. labiata* (Jackson and Carter 2001). When we compare data from *P. africana* with data from *P. labiata*, considering specifically the numbers of individuals that repeated the focal signal when reinforced, there was no significant difference between *P. africana* and the Los Baños *P. labiata* ($\chi^2 = 0.146$, $P = 0.703$), but *P. africana* was significantly different from the Sagada *P. labiata* ($\chi^2 = 5.679$, $P = 0.017$; Fig. 3).

Our findings for *P. africana*, like the earlier findings for *P. labiata* (Jackson and Carter 2001), suggest that level of reliance on trial and error signal derivation is an innate characteristic subject to local adaptation. Having used 3rd and 4th generation individuals of *Portia* from laboratory rearing under standardized conditions in this study, as in the earlier study (Jackson and Carter 2001), prior experience (see Roff 1998), maternal effects (Wade 1998) and other indirect genetic effects (Moore et al. 1998) are unlikely alternative explanations for the inter-population differences in *Portia* use of trial and error.
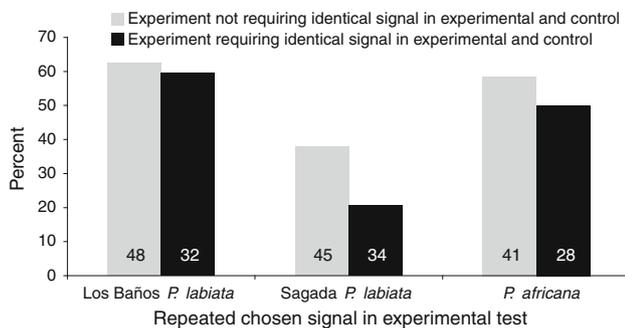
Fig. 3 Comparison of tendencies to repeat chosen signal in reinforced tests. Data for *Portia labiata* (see Jackson and Carter 2001). Data for *P. africana* (see Fig 2; 'repeat in experimental' + 'repeat in both'). *n* within each bar

However, by considering contextual variables (see McPhail 1985), innumerable alternative hypotheses can be formulated whenever attempting to explain inter-population variation in behavior. For example, for reasons unrelated to local adaptation to prey diversity, *Portia* individuals from different populations may be innately predisposed to respond differently to the standardized conditions used in the laboratory. The research on *P. labiata* considered some of these potential contextual variables, and appeared to rule them out. For example, it was shown to be unlikely that the underlying reason for different levels of reliance on trial and error by the two Philippines populations was an innate difference in how the ambient temperature in the laboratory affected the behavior of this species (Jackson and Carter 2001).

Ruling out contextual variables is notoriously difficult when attempting to show adaptive variation, whether intra-specific or interspecific, in cognitive capacity (Bitterman 1965; McPhail 1985; Kamil 1988). Being akin to testing null hypotheses, attempts to identify and then test for the effects of all reasonable contextual variables require an extensive research program, not any one experiment or any few experiments (Kamil 1998). Nonetheless, the data now available for *P. africana* and *P. labiata* have converged to suggest that prey diversity and level of reliance on trial and error signal derivation are closely related. Similarly, Japyassú and Caires (2008) concluded that the plasticity of the foraging behavior of the tetragnathid spider *Nephilengys cruentata* varies less with prey size than prey type.

However, we should also consider how the presence of especially dangerous prey may have influenced the evolution of inter-population differences in the level of reliance on trial and error during signal derivation by *Portia*. When entering a web, *Portia* enters the arena in which the resident spider normally captures its own prey and, in these encounters, *Portia*'s success at gaining fine control over the resident spider's behavior may sometimes determine which of the two spiders lives or dies (Jackson and Pollard 1996). We can predict that, in habitats where especially dangerous prey are more common, flexibility will be more important for *Portia* than in habitats where dangerous prey are less common (see Brodie and Brodie 1999). Consistent with this hypothesis, exceptionally dangerous prey spiders (e.g., scytodids that can spit and glue *Portia* down from a distance; Li et al. 1999) are routinely encountered by *Portia* in the western Kenya site and in the Los Baños site, whereas prey that pose comparable levels of danger are not known at the Sagada site. Further research is needed before we can estimate the relative importance of prey diversity and prey dangerousness as factors influencing *Portia*'s level of reliance on trial and error.

Questions about size constraints should also be taken into account when we consider *Portia*'s level of reliance on

trial and error signal derivation. We might begin with a pair of alternative hypotheses: (1) regardless of habitat, populations of *Portia* have evolved comparable capacity for signal derivation by trial and error; or (2) capacity for signal derivation by trial and error has been subject to local adaptation. Hypothesis 1 would hold if *Portia*'s style of predation has by itself pushed the evolution of trial and error signal-derivation ability in all populations to the ceiling set by size constraints. Hypothesis 2 would hold if the advantages of pronounced capacity for deriving signals by trial and error vary substantially between habitats, but with use of trial and error placing substantial demands on a size-limited nervous system. The idea of adaptive trade-offs is the rationale for hypothesis 2: lesser reliance on trial and error is expected to evolve in habitats where it is advantageous to divert limited nervous system resources to other functions.

A prediction derived from hypothesis 2 is that *Portia* living in habitats where there is a diverse array of prey spiders will rely especially strongly on trial and error signal derivation because, in these habitats, having specific pre-programmed signals would be possible for only a small percentage of the numerous prey species encountered. For *Portia* living in habitats where there are fewer prey species, relying more heavily on pre-programmed signals, rather than trial and error, is predicted. Compared with trial and error signal derivation, reliance on pre-programmed signals for particular prey may be less cognitively demanding because it is based on a more direct processing route from sensory input to motor output (see Toates 1996). We might expect that trial and error derivation, while being more flexible, is likely to be more costly in processing time. This, however, is not a foregone conclusion. It is instead a hypothesis that needs to be tested.

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