REVIEW

# A cognitive perspective on aggressive mimicry

R. R. Jackson[1,2] & F. R. Cross[1,2]

1 School of Biological Sciences, University of Canterbury, Christchurch, New Zealand
2 International Centre of Insect Physiology and Ecology, Mbita Point, Kenya

## Abstract

We use the term 'aggressive mimic' for predators that communicate with their prey by making signals to indirectly manipulate prey behaviour. For understanding why the aggressive mimic's signals work, it is important to appreciate that these signals interface with the prey's perceptual system, and that the aggressive mimic can be envisaged as playing mind games with its prey. Examples of aggressive mimicry vary from instances in which specifying a model is straight forward to instances where a concise characterization of the model is difficult. However, the less straightforward examples of aggressive mimicry may be the more interesting examples in the context of animal cognition. In particular, there are spiders that prey on other spiders by entering their prey's web and making signals. Web invasion brings about especially intimate contact with their prey's perceptual system because the prey spider's web is an important component of the prey spider's sensory apparatus. For the web-invading spider, often there is also a large element of risk when practising aggressive mimicry because the intended prey is also a potential predator. This element of risk, combined with exceptionally intimate interfacing with prey perceptual systems, may have favoured the web-invading aggressive mimic's strategy becoming strikingly cognitive in character. Yet a high level of flexibility may be widespread among aggressive mimics in general and, on the whole, we propose that research on aggressive mimicry holds exceptional potential for advancing our understanding of animal cognition.

## Introduction

We use the term 'aggressive mimicry' for predators that indirectly manipulate the behaviour of their prey by making signals. We can say that these predators communicate with their prey, but it is important to emphasize that this means adopting the first-principles stance on the meaning of communication that was forcefully advocated by Dawkins & Krebs (1978) more than three decades ago. Back then, communication was often characterized as being primarily about the sharing of information (e.g. Smith, 1977), but Dawkins & Krebs (1978) broke with this tradition by emphasizing that communication is fundamentally about indirect manipulation. Communication requires at least two individuals and a signal. One individual (the 'sender') makes a signal to which the other individual (the 'receiver') responds in a way that is beneficial to the sender. Communication is a manipulative endeavour because it is the sender that makes the signal and, therefore, it is how the sender benefits that is of primary importance when trying to explain why the signal is sent. Whether the receiver also benefits is a secondary issue, and not part of what constitutes 'communication'. Manipulation is indirect because, instead of communication being based on the sender physically forcing the receiver to do something in particular, the sender provides a specialized stimulus (i.e. a signal) to which the receiver responds by doing something in particular, with this response being orchestrated by the receiver's own perceptual and motor systems.

By emphasizing manipulation instead of information sharing, Dawkins & Krebs (1978) were breaking away from a prevalent notion that communication is somehow automatically harmonious, with the sender and the receiver sharing the same goals. For making their departure from tradition emphatic, they used an aggressive mimic, the anglerfish, as an example of communication. These large deep-water fish species prey on smaller predatory fish that, in turn, prey on small invertebrates. The anglerfish has fleshy spines extending in front of its mouth and, when it twitches these specialized spines, the smaller predatory fish respond by coming close enough for the anglerfish to attack and eat them. Explaining the smaller fish's response to the anglerfish's signal seems to be straight forward, as the anglerfish's signal appears to resemble the stimulus the small fish would normally get from its own prey (Wilson, 1937; Pietsch & Grobecker, 1978). Using this example from the literature on aggressive mimicry, Dawkins & Krebs (1978) went on to

argue that communication, in general, regardless of whether the sender and receiver are conspecific or heterospecific, should be recognized as instances of the sender's signals indirectly manipulating the receiver's behaviour. By keeping ideas about harmony and mutual benefit out of the definition, Dawkins & Krebs (1978) simplified and focused how we think about communication.

Nowadays, the literature pertaining to situations in which one organism interfaces with the sensory system of another organism includes, besides 'communication', a terminological menagerie: 'sensory trap', 'sensory exploitation', 'sensory drive', 'receiver psychology', 'exploitation of perceptual biases' and so forth (Guilford & Dawkins, 1991; Proctor, 1992; Christy, 1995; Endler & Basolo, 1998; Schaefer & Ruxton, 2009; Bradbury & Vehrencamp, 2011). Of course, there are times when we need terms and we need definitions, but mimicry, communication and cognition are topics that sometimes seem to collapse under the terminological load. Too much emphasis on terms and definitions can predispose us to expect sharply demarcated categories even when we should instead be examining processes that lie along a continuum. We are especially concerned that too much emphasis on terms interferes with appreciating the cognitive character of predatory strategies, and our impression is that having to deal with a multitude of terms obstructs more than it helps when our goal is to explore the relationship between aggressive mimicry and animal cognition. Here, we will minimize the number of terms we use and we promise to introduce no new terms. With our objective here being to consider the instances of how predators communicating with their prey might help us understand animal cognition, 'aggressive mimicry', a convenient term already well established in the literature, will suffice.

All examples of animal communication can be envisaged as animals playing mind games (Krebs & Dawkins, 1984), but the mind game metaphor often seems to be especially appropriate when applied to aggressive mimicry. Here, we will first consider mind games in the context of understanding why the aggressive mimic's signals succeed in controlling prey behaviour. In this context, we reconsider the role of information, but without departing from our stance that indirect manipulation is more fundamental. We are also interested in examining variation in the level of flexibility expressed by aggressive mimics when communicating with their prey and we consider the circumstances that may favour aggressive-mimicry strategies becoming exceptionally cognitive in character.

## Caudal luring by snakes

Despite the anglerfish being a classic example of aggressive mimicry, we actually know little about how and why the anglerfish's signals work. We know considerably more about caudal luring, a predatory strategy practised by more than 50 species of boid, colubrid, elapid and viperid snakes (Neill, 1960; Heatwole & Davison, 1976; Sazima, 1991; Leal & Thomas, 1994; Reiserer, 2002; Hagman, Phillips & Shine, 2008; Reiserer & Schuett, 2008). These snakes appear to be terrestrial analogues of the anglerfish, but in this case, the prey is especially often a lizard. Typically, the signalling snake is coiled and waiting with its tail moving in a characteristic way. These tail movements are sometimes called 'vermiform' because they resemble the wriggling of caterpillars and other worm-like insect larvae that lizards prey on.

For the anglerfish and for the snake, we can propose that success at practising aggressive mimicry is based in large part on the aggressive mimic's prey, another predator, being predisposed to identify its own prey quickly on the basis of simple stimuli. Although the experimental evidence needed for evaluating this hypothesis is not available for the anglerfish, it is available for caudal-luring snakes and apparently there is more to caudal luring than simply being vermiform.

In a particularly elegant experimental study, the snake was the Australian death adder and the snake's prey was the jacky dragon, a lizard (Nelson, Garnett & Evans, 2010). The snake's luring signal was characterized precisely and shown to consist of two components, one based on faster and one based on slower movement. Movement patterns of prey from the habitat of the lizard were characterized and shown to fit a bimodal distribution remarkably similar to the bimodal signal of the snake. Using 3-D animation, the lizards were tested with virtual prey and virtual snake signals, and again there was a remarkable match: the virtual prey and the virtual snake signals to which the lizards were most inclined to approach matched each other and also matched the bimodal distribution of real prey movement patterns and real snake signal patterns. The conclusion suggested by these findings is that the snake's signals have been fine tuned by natural selection to exploit the lizard's fine-tuned prey identification system.

Other research (Hagman et al., 2008) on Australian death adders shows that the snake makes decisions that reveal how it classifies prey. These snakes frequently prey on frogs as well as lizards, but the snake makes luring signals primarily after detecting the presence of a lizard, not a frog. Moreover, using a robotic snake tail, it was shown that the lizards, but not the frogs, were highly predisposed to respond to the typical signal characteristics of the snake. There are other snakes that routinely attract frogs by caudal luring (Reiserer, 2002).Yet, as lizards and frogs are not known for targeting particular prey species, there seems to be little reason to expect that the model of a caudal-luring snake will match a particular prey species of the lizards or frogs (see Pough, 1988).

However, three *femmes fatales* that we consider next show that aggressive-mimicry signals are sometimes specific down to the level of a particular sex of a particular species. These *femmes fatales* also show that aggressive-mimicry signals can work via modalities other than vision and that the receiver of the signal need not be another species.

## Femmes fatales

Our first *femme fatale*, the female bolas spider, is a predator that specializes at eating male moths. Their so-called 'bolas' is a single line of silk with a sticky drop of glue at the end. When a male moth approaches, the spider uses one of her legs to whirl the bolas around in circles and, when contacted by the glue drop, the male moth becomes stuck. The spider then hauls in the moth and eats it (Eberhard, 1977). In this case, the

aggressive-mimicry signal is chemical, and it appears easy to explain why the bolas spider's signal works. It is known that bolas spiders release from their bodies blends of compounds that match specific blends of known compounds used as pheromones by the potential mates (i.e. conspecific females) of the male moths (Stowe, Tumlinson & Heath, 1987; Yeargan, 1994; Gemeno, Yeargan & Haynes, 2000; Haynes *et al.*, 2002).

It might sound straight forward: moth, pheromone, aggressive-mimic spider and fake pheromone. Yet, closer examination reveals something less tidy and more interesting. There are more than 60 bolas spider species belonging to three genera, and there are many moth species serving as potential prey. Remarkably, a single individual bolas spider in a single night can attract male moths belonging to more than one prey species (Yeargan, 1994; Scharff & Coddington, 1997). *Mastophora cornigera* holds the record, as this bolas spider is known to attract the males of at least 19 different moth species (Stowe *et al.*, 1987).

The most thoroughly studied bolas spider is *Mastophora hutchinsoni*. Two male moth species are dominant in this species' diet, and these moths are active in the same habitat, but with peak activity at different times of the night. By releasing analogues of both moth species' pheromones, individual spiders succeed at capturing males of both species in a single night. We might expect the spider to switch between releasing one to releasing the other pheromone analogue at the time of night when a particular moth species is at its activity peak, but the spider's strategy is instead to release both analogues at the same time (Haynes *et al.*, 2002).

Bolas spiders are also known for extreme sexual dimorphism, with male spiders being much smaller than female spiders and also much smaller than the moths on which female spiders feed. This means that male bolas spiders need a different prey, but they do not forsake the use of aggressive mimicry. Along with the smaller juveniles, the adult male *M. hutchinsoni* are chemical aggressive mimics that attract male moth flies (Psychodidae) instead of male moths (Yeargan & Quate, 1996, 1997).

*Euryattus* sp., a jumping spider (Salticidae) from Queensland, Australia, is the victim of our second *femme fatale*. With this example, we seem to have an aggressive mimic that targets its prey by using a signal that has an especially specific meaning for the prey. The nest of a female *Euryattus* is a dead, rolled-up leaf that is suspended from vegetation or from a rock ledge by heavy silk guy lines (Jackson, 1985). Salticids are distinctive spiders because of their unique, complex eyes and, owing to salticid eyesight being based on exceptional spatial acuity (Harland, Li & Jackson, 2012; Land & Nilsson, 2012), these spiders can discern an extraordinary level of detail in visual objects. The male *Euryattus* uses his good eyesight to identify a female's leaf nest and then walks slowly down a guy line and positions himself on the leaf. Next, by suddenly flexing all of his legs at the same time, he shakes the leaf, with this shaking being the courtship signal the male sends to the female inside the nest. The female inside the nest does not see the male, but she responds by coming out to mate if she is receptive, or to drive the male away if she is not. In this case, the *femme fatale*, *Portia fimbriata*, is a female of another sal-

ticid species. When *P. fimbriata* sees a suspended rolled-up leaf, she moves down a guy line and positions herself close to and facing an opening to this leaf, and then she simulates the leaf-shaking signals normally made by male *Euryattus* (Jackson & Wilcox, 1990). This time, when the female *Euryattus* responds by coming out of her nest, the suitor who greets her is a predator, not a courting conspecific male.

## Intraspecific aggressive mimicry

With spiders, mating and predatory strategies have a way of running together because either sex may kill and eat the other (Jackson & Pollard, 1997; Schneider & Andrade, 2011). By blurring the distinction between courtship and aggressive-mimicry signals, our third *femme fatale*, *Portia labiata* from Sri Lanka (Jackson & Hallas, 1986), demonstrates that the prey of an aggressive mimic need not be heterospecific. Courtship sequences usually begin when a male comes into the vicinity of a female *P. labiata* in a web and she is often the first to display, as though she were inviting the male into her web. The male usually obliges, although his approach tends to be hesitant and even the slightest movement made by the female towards him often sends him running. Usually he returns, but slowly. Throughout the interaction, the female continues to display actively, her dominant displays being drumming (pounding on the silk with her two palps) and tugging (sharp pulls on the silk with her forelegs). From time to time, the female moves higher up into the web, after which she turns, faces the male and resumes her display.

The male's displays are visual (e.g. posturing and waving with his legs erect) and vibratory (e.g. a distinctive stepping gait called 'jerky walking'). When within reach of the female, the male switches to tactile displays – tapping and scraping on the female's body with his legs and palps. These tactile displays are performed simultaneously with the male mounting the female by walking over her. Either while mounting or soon afterwards, the female drops on a dragline with the male on board and the pair mates while suspended from a thread. However, hanging from a thread is often, for the *P. labiata* female, also a step in her predatory sequence. Often, while on this thread, the female attacks the male by suddenly and violently swinging around with her fangs extended and with her legs scooping towards the male. When the male's fleeing response is too slow, he becomes the female's next meal. These predatory attacks may come before or during copulation.

'Sexual cannibalism' (Elgar, 1992; Schneider & Lubin, 1998) would be a conventional term for these instances of a *P. labiata* female preying on a conspecific male. However, we wish to avoid simply filing away this example with a familiar label. We will instead emphasize that, for female *P. labiata*, an aggressive mimicry strategy is thoroughly entangled with a mating strategy.

Comparing *P. labiata*'s male–female encounters with the encounters between *P. fimbriata* and *Euryattus* might be instructive. By using signals that simulate *Euryattus* male courtship, females of *P. fimbriata* control the behaviour of female *Euryattus*, and this assists *P. fimbriata* with preying on *Euryattus*. This has close parallels with *P. labiata*, except now

the prey is conspecific. By making specialized signals, female *P. labiata* control the behaviour of male *P. labiata*, and this assists female *P. labiata* with preying on male *P. labiata*. When there is no mating, we might say an unreceptive female has mimicked the signals normally made by receptive females. However, the distinction between receptive and unreceptive females, and between honest and deceitful signals, can be ambiguous because *P. labiata* females sometimes make swinging attacks on males even while mating.

For *P. labiata*, there are various potential ways in which sexual selection might be entangled with predation. If a male is killed after he has initiated mating, then we could consider the possibility that being eaten by the female benefits the male because, in these instances, a consequence of being killed is that he provides the mother of his future offspring with a meal. When an adult female kills a male without first mating with him, entanglement between mating and predatory strategies might still be relevant because, besides gaining a meal, the female also, rather emphatically, rejects the male as a potential father for her offspring. A hypothesis we might entertain is that a female benefits from mating with a male that survives her attack because males that can demonstrate capacity to evade lethal female behaviour contribute good genes to the female's offspring.

However, mature females are not the only females that practise specialized predation on males. Subadult females (i.e. juveniles that are one moult short of maturity) are similar in size to adult *P. labiata* females, but they are physically incapable of mating and yet, like adult females, they actively display at conspecific males. The male responds by entering the web, courting and mounting, and then, while he is on board, the subadult drops on a thread and he performs pseudo-copulation. However, while he appears to be fumbling around and searching for genital openings that are not there, the subadult female, with a twisting lunge, makes a predatory attack and, when successful, the male becomes her prey (Jackson & Hallas, 1986).

The subadult female practises aggressive mimicry by behaving like an adult female and by indirectly controlling the behaviour of her prey, a mature conspecific male. She is physically incapable of mating, and yet we cannot rule out the possibility of entanglement between her predatory and mating strategies. A mating tactic often used by a *Portia* male is to cohabit in a web with a subadult female and then mate with her once she has moulted and become sexually mature. A sexual-selection hypothesis we might propose is that subadults benefit from cohabiting and mating with males that can evade the lethal subadult-female behaviour.

We should emphasize that there is currently no evidence supporting these sexual-selection hypotheses. We should also emphasize that these sexual-selection hypotheses are not simple alternatives to explaining adult and subadult-female behaviour as being examples of aggressive mimicry. Entanglement with mating strategies notwithstanding, we still have predators (adult and subadult females) that use signals to control the behaviour of a specific kind of prey (adult conspecific males). When examining the cognitive implications of this predatory behaviour, *P. labiata*'s mating and predatory

strategy is as relevant as any of the other aggressive-mimicry examples we have considered.

## Information

Anglerfish, caudal-luring snakes and *femmes fatales* are all examples of predators indirectly manipulating their prey's behaviour by providing stimuli to the prey, with the prey's response being advantageous to the predator, but not necessarily to the prey. Adopting a first-principles approach to understanding communication (Dawkins & Krebs, 1978), we can say that all of these are examples of communication and that there is no pressing need to begin with an emphasis on information. However, we should not ignore the things information might explain. 'Information' and 'correlation' are sister concepts and identifying correlations between signals and factors that matter to the receiver can be a critical step towards understanding the receiver's predisposition to respond in some particular way to the signal.

When considering aggressive mimicry as communication, we can substitute the term 'misinformation' for 'information'. This is a way of expressing that the stimulus provided by the signal resembles a stimulus for which the elicited response is usually advantageous to the receiver. The term 'mimicry' predisposes us to expect an easily specifiable model and, for aggressive mimicry, we can envisage 'model' and 'misinformation' as meaning much the same thing. However, there are easily overlooked questions concerning the kind of precision that should be our goal when we specify a model.

For us as scientists, it might be pleasing when we can indicate a mimic's model with taxonomic precision. When we consider the anglerfish and the caudal-luring snakes, we can say the aggressive mimic's model was the prey of the aggressive mimic's prey, but without specifying any particular species. It might be tempting to say that the three *femmes fatales* we considered are more precise aggressive mimics than the anglerfish and the snakes because the models used by each *femmes fatale* are the signals that are used by a particular prey species during male–female interactions (female moths of particular species when the mimic was a bolas spider, male *Euryattus* when the mimic was *Portia fimbriata* and a mature, receptive female *Portia labiata* when the mimic was a subadult female *P. labiata*). However, if our goal is to understand why aggressive mimicry works, it is the prey's own classification system that matters, not formal scientific taxonomy.

Curio (1976) used the expression 'predatory versatility' for predators that deploy a conditional predatory strategy consisting of distinctly different prey-specific prey-capture tactics, with each of these tactics being used for distinctly different prey. In turn, a predator's repertoire of different prey-capture tactics reveals a predator's own prey-classification schemes. Aggressive mimics may be especially predisposed to predatory versatility and it is with *Portia* that we find the most pronounced expression of predatory versatility known for spiders and among the most pronounced for any predators.

Predatory versatility in *Portia* illustrates, in a striking way, the importance of being clear about the classification system

referred to when the labels 'generalist' and 'specialist' are applied to predators. In community ecology, the intended meaning is that a generalist's diet is wide and a specialist's is narrow, although euryphagous and stenophagous are actually more appropriate words for this distinction. Spiders, in general, are often characterized as being primarily euryphagous predators (Wise, 1993), with the underlying notion being that they tend to feed rather indiscriminately on a wide variety of insects and other arthropods, including other spiders. As *Portia*'s natural diet is dominated by spiders, it might be tempting to label *Portia* as stenophagous, and perhaps this is useful in the context of community ecology. However, it is *Portia*'s own prey-classification scheme that pertains to how *Portia* experiences its prey (Jackson & Wilcox, 1998; Harland & Jackson, 2004). *Portia* assigns prey to more distinct categories than is known for any other spider and, in the animal kingdom as a whole, there are few predators known to have behaviour specific to as many different prey categories as is known for *Portia*. When we consider how predators categorize prey, 'euryphagy', not 'stenophagy', is the appropriate label for *Portia*.

## Painted redstarts

Painted redstarts demonstrate that aggressive mimicry can also be based on simulating stimuli that are aversive to prey. These are insectivorous birds that adopt a strategy of flushing small flies out of hiding. They do this by spreading and pivoting their conspicuously patterned tails and wings, thereby creating aversive stimuli to which the flies respond by fleeing. Unfortunately for the flies, moving away from the redstart's tail and wings means entering the foveal field of view of the redstart's eyes where they become easy targets for the predator (Jabłoński & Strausfeld, 2000, 2001; Jabłoński, 2001).

We can say that the redstart's interaction with its prey is based on communication because, by providing a stimulus to which the flies respond, the redstart indirectly manipulates its prey's behaviour in a way that is advantageous to itself and disadvantageous to the prey. However, specifying models for the redstart's signals may appear to be more difficult than it was for the anglerfish, the caudal-luring snakes and the three *femmes fatales*. The best we can do may be to say that the model of the redstart's signal is 'something threatening' for which flying away is normally an appropriate response. Mimicking this model works for the redstart because, when the flight-inducing stimulus comes from a redstart, the redstart's prey renders itself more, not less, at risk of being eaten.

It is interesting that, when discussing the redstart's predatory strategy, the expression Jabłoński (2001) used was 'sensory exploitation' instead of 'aggressive mimicry'. 'Sensory exploitation' (Ryan *et al.*, 1990) and similar terms came into widespread use after 1978. As 'exploitation' and 'manipulation' sound like words for much the same thing, it is easy to envisage how Dawkins & Krebs (1978) might have made good use of 'sensory exploitation' as an alternative term for 'manipulation' when they addressed how communication works.

Our stance is that the redstart is an aggressive mimic and that the redstart also uses sensory exploitation. Although the terms 'aggressive mimicry' and 'sensory exploitation' are often used in a way that suggests a qualitative distinction (e.g. Herberstein & Wignall, 2011), we do not see it that way. We are happy to use these terms interchangeably for redstarts and other predators that indirectly manipulate prey by using signals. All aggressive mimics exploit the perceptual systems of their prey. The primary way the redstart seems to differ from the other aggressive mimics we have reviewed is that we find it more difficult to be concise when we wish to specify a model for the redstart's signal. Yet, with all the examples we have considered, including the redstart, we can specify a model if we try hard enough. It just takes more words to do so in some instances. With our primary interest being animal cognition, the issue of whether a model can be specified concisely is a low priority and we suspect that the more interesting cognitive underpinnings of aggressive mimicry are revealed especially by signals for which models cannot be characterized concisely.

## Cognition

With the examples of aggressive mimicry we have considered so far, mind games and cognition have been relevant primarily in the context of the prey's response to the mimic's signals. Yet it is the signal maker's (i.e. the aggressive mimic's) behaviour that has been most responsible for our interest in investigating aggressive mimicry from a cognitive perspective. Before we shift our attention to the aggressive mimic's behaviour, however, we need to indicate our stance towards the terms 'mind' and 'cognition'.

There are many reasons why cognition has a long history of being a notoriously controversial topic (Dennett, 1996). This includes a tradition of using 'cognition' and 'mental' more or less interchangeably, accompanied by a traditional notion that 'mind' is some sort of separate reality to which people have unique access (Descartes, 1637/1994). Minsky (1986, p. 287) famously expressed an alternative view by saying 'minds are simply what brains do'. Instead of being a definition, this catchy phrase serves as a way of expressing a radical departure from Descartes' view and an active decision not to propose a formal definition. 'What brains do' is accessible to scientific investigation and, if we gain a sufficiently detailed understanding of what brains do, then the impression of needing a formal definition of 'mind' and the notion of there being a purely philosophical problem to address should recede into the background.

Sometimes, 'cognition' is defined simply as 'information processing' (e.g. Shettleworth, 2009). However, when considering the interface between aggressive mimicry and animal cognition, we prefer instead to emphasize representation. Representation has often been envisaged as a key attribute at the boundary between what does and does not qualify as cognitive (Damasio, 1994; Maunsell, 1995; Markman & Dietrich, 2000; but see Epstein, 1982). Vision is the context in which representation is especially often considered by psychologists, and this bias may tempt us to equate representation with something like a picture in the animal's head – a mental picture, or imagery (Neiworth & Rilling, 1987;

Kosslyn, Ganis & Thompson, 2003; but see Pylyshyn, 2003a,b). Yet, we need a concept of representation that will be more basic and not unique to vision, and we do not really have to imply pictures in the animal's head. We are happy to adopt Gallistel's (1989) proposal that representation in the context of cognition functions in a way that is analogous to the way isomorphism functions in mathematics (e.g. the isomorphism between algebraic and graphical computations in geometry). In the case of representation, isomorphism refers to the formal correspondence between external reality (i.e. features of the environment) and the neural processes within an animal (Burge, 2010).

From this perspective, representation is an internal state that functions in conjunction with working memory, where 'working memory' refers to the mechanisms by which priority information is made immediately accessible to other cognitive processes such as selective attention, reasoning and making plans (Postle, 2006; Baddeley, 2012). Specialized working memory may be especially important for aggressive mimics that express flexibility in their use of signals. We have seen flexibility already when, for example, we considered the strategies of bolas spiders that use different chemical signals at different stages in their lives and with different prey. However, it is especially with *Portia* that the cognitive character of aggressive mimicry is strikingly expressed in conjunction with extreme predatory versatility and flexibility.

## Mistress of deception in spider webs

Especially many of *Portia*'s tactics are based on invading the webs of non-salticid spiders and, for understanding these tactics, we need an understanding of the web spider's unusual sensory system. We may be predisposed to think of sense organs as being part of an animal's anatomy, but the web in conjunction with setae and slit sensilla on the spider's body is the primary sense organ of the web spiders on which *Portia* preys (Witt, 1975; Barth, 2001). It is particularly interesting that this sense organ is extended out into the environment because this means that *Portia* can walk directly into it. In another spider's web, *Portia*'s intimacy with its prey's sensory world gives especially literal meaning to the expression 'sensory exploitation'. By invading a web, *Portia* enters into intimate and often dangerous contact with its prey's sensory world – dangerous because the tables may be turned, and *Portia*'s intended dinner may become the diner (e.g. Jackson *et al.*, 2002).

After entering a web, instead of simply stalking or chasing down the resident spider, *Portia* communicates using web signals (Tarsitano, Jackson & Kirchner, 2000), 'web signals' referring to the vibratory and tension patterns *Portia* generates by using any one or any combination of its 10 appendages (eight legs and two palps). Each appendage can be moved independently and in a variety of ways, with the net effect being that *Portia* has at its disposal virtually an unlimited assortment of different signals for potential use when in other spiders' webs (Jackson & Blest, 1982). This is relevant because, instead of targeting only one or only a few web-building spider species, *Portia* appears to be ready to take on almost any

spider it finds in a web, as long as the other spider is similar to *Portia*'s own size. However, each of these prey spiders has its own refined ability to acquire and process sensory information (Barth, 2001). Many variables, including the resident spider's species, sex–age class, feeding state and previous experience (Jackson, 1986; Masters, Markl & Moffat, 1986; Landolfa & Barth, 1996), influence response to signals. Owing to these variables, *Portia* is confronted with the problem of how to select from its large repertoire of web signals the particular signal that will work to its advantage in any particular session with any particular resident spider.

*Portia*'s solution to this problem is based on a remarkable plasticity. During encounters with some of its more common prey, *Portia* is innately predisposed to begin with particular signalling routines, but *Portia* otherwise relies on trial-and-error from the beginning (Jackson & Wilcox, 1993a; Harland & Jackson, 2004). Trial-and-error means that, after going into the web of a spider for which it does not have a pre-programmed tactic with which to begin, *Portia* generates a kaleidoscope of different vibratory signals and, when one of these signals eventually elicits an appropriate response from the resident spider, *Portia* stops varying its signals and instead concentrates on making the signal that worked (Jackson & Wilcox, 1993a; Jackson & Nelson, 2011). However, *Portia* has another problem. Regardless of whether the effective signal was derived by trial-and-error or whether it was instead a signal *Portia* was innately predisposed to use, there is normally no guarantee that the resident will continue to respond appropriately long enough for *Portia* to make a kill. *Portia*'s solution to this problem is to make fine adjustments on the basis of feedback from its prey. If the resident spider switches to inappropriate behaviour, *Portia* finds another effective signal by reverting to trial-and-error (Jackson & Wilcox, 1993a; Jackson & Nelson, 2011).

## Flexible fine tuning of web-invasion strategies

Saying that *Portia*, by trial-and-error, derives a signal that elicits an 'appropriate response' from the resident spider is too simplistic because the meaning of 'appropriate' is not fixed. As long as we think of *Portia*'s strategy as being an analogue of the anglerfish's or the caudal-luring snake's strategy, it may appear easy to specify the meaning of 'appropriate'. For example, when the resident spider is small and not especially dangerous, explaining what happens may seem straightforward. From *Portia*'s perspective, an appropriate response appears to be the resident spider behaving as though *Portia*'s web signal is coming from a small insect ensnared in the web. In these instances, *Portia* can safely lunge at, kill and then eat the resident spider when it comes close (Jackson & Blest, 1982). However, there are many situations in which *Portia* fine tunes the meaning of 'appropriate'.

For example, spiders from the genus *Scytodes* spit a sticky gum on prey and on potential predators (Suter & Stratton, 2005). In the Philippines, *Portia labiata* often preys on a species of *Scytodes* that builds webs on the tops of leaves and this species of *Scytodes* preys especially on salticids (Li,

Jackson & Barrion, 1999). *Scytodes*' spit is a formidable weapon against *Portia*, because a spat-upon *Portia* often remains gummed down long enough for *Scytodes* to finish the job by wrapping *Portia* in silk and injecting venom. The strategy adopted by *P. labiata* includes taking detours during which it initially moves away from and loses sight of the scytodid, and then arrives positioned so that it can approach the spitting spider from behind. Next, *P. labiata* enters the web and approaches while using its palps to make vibratory signals, but in this instance, *P. labiata* derives by trial-and-error signals that do not attract *Scytodes* and instead keep *Scytodes* facing away, thereby minimizing the likelihood of *P. labiata* becoming a target of a spitting attack (Jackson *et al*., 1998).

However, for *P. labiata*, all individuals of *Scytodes* are not the same and *P. labiata* adjusts its predatory strategy accordingly. For example, female *Scytodes* carry their eggs in their mouths and an egg-carrying scytodid has to release her eggs before spitting. Being reluctant to release their eggs, egg-carrying female *Scytodes* are, for *P. labiata*, less dangerous than eggless female *Scytodes* and, consistent with this, *P. labiata* prefers egg-carrying to eggless female *Scytodes* as prey (Li & Jackson, 2003). Moreover, when the female *Scytodes* is carrying eggs, *P. labiata* is more willing to confront the scytodid head-on and make signals that elicit approaching by the scytodid (Jackson *et al*., 2002).

*Scytodes* is not the only dangerous prey targeted by *Portia* and, in general, when approaching a dangerous prey spider, *Portia*'s goal when adjusting its web signals appears to be almost the antithesis of the goal when the resident spider is relatively harmless, because *Portia* seems to be actively avoiding repetition of signals that might encourage a full-scale attack by the prey spider (Tarsitano *et al*., 2000; Harland & Jackson, 2006). When confronting large, powerful spiders in webs, *Portia* often derives signals by trial-and-error that elicit slow approaching in hesitating steps, this being how the resident spider tends to behave when seeming to be uncertain about the source of the web signals it is receiving. Alternatively, *Portia* may move in slowly for the kill while making signals derived by trial-and-error that keep the victim calm and stationary. Calming effects might be achieved by monotonous repetition of a habituating signal, as though *Portia* were putting its victim to sleep with a vibratory lullaby derived by trial-and-error (Harland & Jackson, 2004).

These examples of flexibility in the use of aggressive mimicry suggest that *Portia*, when confronted by different prey, establishes ahead of time different goals and then works towards an intended goal by continual monitoring and adjusting. Although there seem to be analogues of *Portia*'s goal-directed behaviour in other animals, these other animals are most often primates and other vertebrates (Mitchell, 1986; Hauser, 1997; Cartmill & Byrne, 2007).

## Thinking and making plans

*Portia*'s predatory strategy when invading other spiders' webs often bears a particularly interesting correspondence to our commonsense characterization of 'thinking', where an individual perceives a problem, solves the problem mentally, makes a plan and then acts on the plan (Jurado & Rosselli, 2007). For example, *Portia* appears to decide ahead of time the objective that will be adopted when deriving signals by trial-and-error. However, it is when *Portia*'s entry into webs is preceded by detours that we have especially strong experimental evidence that plans made ahead of time are held in working memory.

Besides *Scytodes*, many other spiders elicit detouring by *Portia*, sometimes with the detour paths requiring 20 min or longer to complete, and sometimes with *Portia* losing sight of the prey along the way (Jackson & Wilcox, 1993*b*). Experiments based on these long detours (Tarsitano & Jackson, 1997; Tarsitano & Andrew, 1999; Tarsitano, 2006) have been especially interesting in the context of cognition (Jackson & Cross, 2011). For example, at the beginning of an experiment, *Portia* might be on a platform from which it can see a distant prey spider that cannot be reached directly as well as alternative routes, with only one of these routes leading to the prey. In these experiments, *Portia* consistently follows the correct route to the prey, despite first having to move away from the prey and despite having to complete the detour with the prey no longer in view. Findings from these experiments imply that *Portia* identifies a problem (how to reach the prey), derives a solution, makes a plan and then acts on that plan (Jackson & Cross, 2011), with the problem's solution being derived not by actual trial-and-error in the physical environment, but instead by neural processing that can be likened to running a simulation in a virtual, or mental, space (see Terrace, 1985). Borrowing an expression from Daniel Dennett (1996), *Portia* appears to be a Popperian animal. Like Skinnerian animals, Popperian animals can be said to solve problems by trial-and-error, but the Skinnerian animal does trial-and-error in the outside world while the Popperian animal does the equivalent of trial-and-error in its head. Popperian animals are especially interesting in the context of animal cognition because part of what 'in its head' implies are representations held in working memory (Markman & Dietrich, 2000; Brady, Konkle & Alvarez, 2011). Using everyday language, we could say that, when making plans ahead of time, *Portia* makes up its mind.

## Factors favouring flexible aggressive-mimicry strategies

The cognitive character of *Portia*'s exceptionally flexible strategy seems to beg for an explanation. We propose that part of the explanation is that *Portia*'s success as a raider in other spiders' webs depends on active decision-making, planning and flexibility. This is a setting in which *Portia*'s decisions have immediate life-or-death consequences not only for the resident spider, but also for *Portia*. A more rigid routine might often be fatal. We propose that another part of the explanation is that, when *Portia* enters another spider's web, it enters directly into the arena in which the resident spider captures its prey as well as the resident spider's primary sense organ, this being a setting in which *Portia* has exceptional opportunity to gain a high level of dynamic fine control over the resident spider's behaviour.

We propose that, on the whole, web-invading aggressive mimicry favours exceptionally cognitive predatory strategies. There are opportunities for assessing this hypothesis because, although *Portia* is the most thoroughly studied web-invading aggressive mimic, there are other salticids (Su *et al.*, 2007; Harland *et al.*, 2012), some non-salticid spiders (Jackson, 1992; Herberstein & Wignall, 2011; Jakob, Skow & Long, 2011; Nelson & Jackson, 2011) and even some insects (Wignall & Taylor, 2009, 2010, 2011; Soley, Jackson & Taylor, 2011; Soley & Taylor, 2012) that practise this basic style of predation. Our limited understanding of these other species suggests that our hypothesis about the importance of web-invading strategies will be corroborated.

However, even if we succeed in identifying the sources of natural selection that favour the strikingly flexible, cognitive strategies of web-invading aggressive mimics, another important issue remains unresolved. Regardless of the animal's needs, we can expect that constraints related to the animal's nervous system will impose limitations. Our commonsense may especially predispose us to expect severe size constraints on the computational power of animal brains. Compared with the much larger vertebrate animals used more often in cognitive research, we might expect much less capacity for orchestrating flexible, cognitive strategies by *Portia* and other spiders, as well as insects. However, what counts is the evidence (Eberhard, 2011; Eberhard & Wcislo, 2012), not our intuition.

Among insects, findings from research on honeybees suggest that size constraints may be considerably less severe than many people would expect (Srinivasan, 2010). Among spiders, it is especially the findings from research on *Portia* that suggests the severity of size constraints has been overestimated (Harland & Jackson, 2004). Honeybees are not predators and, for this reason, we might expect the selection pressures responsible for honeybee behaviour to be rather different from those acting on *Portia* and other aggressive mimics. Yet *Portia*'s predatory strategy appears to be among the most flexible described for any predators of any size. That so much of this flexibility is expressed in the context of aggressive mimicry suggests that aggressive mimicry is, in general, particularly conducive to the evolution of interesting expression of animal cognition.

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