

## Specialized exploitation of ants (Hymenoptera: Formicidae) by spiders (Araneae)

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### Abstract

Ants are a dominant resource in the spider's world, and spiders have a variety of ways of exploiting this resource. Two broad domains of exploitation are reviewed, namely specializing on ants for food and specializing on ants for models to mimic. Exploiting of ants as a source of food includes preying on worker ants and also taking food out of the ant's mandibles. Experiments have revealed numerous examples of spiders that specialize on ants by deploying ant-specific prey-capture behaviour. Consistent with other evidence that predatory versatility is widespread among spiders, many of the spiders that specialize at preying on ants sometimes adopt alternative tactics for capturing ants and are also proficient at targeting other prey. The venom, enzymes and sensory systems of spiders can also be specialized for preying on ants. Many spiders adopt Batesian mimicry of ants for protection against predators that readily eat spiders but have an aversion to ants. For these spiders, one of the costs of mimicking ants is attracting the unwanted attentions of spiders that specialize at preying on ants. Sometimes spiders solve this problem by making use of a conditional anti-predator strategy of resembling ants by default but switching to behaviour unlike an ant when ant-eating predators are encountered. Batesian mimicry of ants is sometimes communal (i.e., ant mimics living in groups appear more formidable because of the group's resemblance to a group of ants) and communal Batesian mimicry can then be deployed as a part of an aggressive-mimicry strategy. Ant-averse spiders may abandon their broods when confronted by a swarm of ants and likewise they flee when confronted by a swarm of communal ant-mimics, with the mimics then feeding on the unguarded broods. Other spiders use Wasmannian mimicry based on acquiring the cuticular hydrocarbons of ants as a means of safely mingling with the ants and then robbing the ants of their broods.

**Key words:** Aggressive mimicry, Batesian mimicry, kleptoparasitism, myrmecomorphy, myrmecophagy, myrmecophily, preferences, prey-capture behaviour, review, specialization.

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### Spiders that eat ants

"Ants are everywhere, but only occasionally noticed" (HÖLDOBLER & WILSON 1990). This means noticed by people. People are big and ants are small, and people tend to pay more attention to animals closer to their own size. Spiders are also everywhere, and spiders cannot help but notice ants. Here we will review spiders noticing ants, but it is a biological kind of "noticing" that we will consider. We will explore some of the ways spiders specialize at exploiting these massively abundant insects, but first we need to clarify what we mean by specialized.

We can start with what spiders eat in the field. We might think an ant-eating spider would never go hungry in a world teaming with ants, but there is a problem. Ants can be dangerous because, depending on the ant species, the spider may be confronted with stings, formic acid and other chemical defences (BLUM 1981), it might be confronted with a highly agile insect bearing powerful mandibles (e.g., PATEK & al. 2006) and, as social insects, ants can mobilize communal attacks on would-be predators (MOFFETT

2010). To top it off, many ants are predators that can readily turn a spider into prey (Fig. 1).

More than 40,000 spider species have been named (PLATNICK 2011). For most of these species, there are few if any data on natural diet, but there are sufficient data for reinforcing an impression that most spiders do not make a habit of eating ants (BRISTOWE 1939, 1941, NENTWIG 1987, WISE 1993). This means that seeing a spider eating an ant strikes us as unusual or special. Finding spiders that routinely eat ants might appear even more special, but we mean more than this when we say a spider is an "ant specialist". In the context of predation, "specialist" is useful when reserved only for instances of a predator being especially well adapted at exploiting a particular type of prey (Box 1). Our starting premise is that ants are a dominant potential resource for spiders, and we will review some of the ways in which spiders have become specialized at exploiting this resource.

Box 1: Some important distinctions that need to be made in order to understand the biology of predators.

**Specialization** refers to being especially good at doing something in particular. For example, saying a spider species is a specialized predator of ants is a short way of saying this predator has especially effective ways of targeting ants as prey. Some of the ways in which a spider might express specialization on ants include, for example, deploying specialized prey-capture behaviour, specialized prey-choice behaviour, specialized venom, specialized enzymes or a specialized sensory mechanism. When we say that the prey-capture behaviour of a spider is specialized with respect to preying on ants we mean that this is behaviour that has characteristics that are especially effective at preying on ants in particular.

**Natural diet:** There are other terms that refer to a predator's natural diet, such as polyphagy (eats a variety of prey), monophagy (eats one prey type), euryphagy (includes a wide range of prey types in its diet) and stenophagy (includes only a narrow range of prey types in its diet). However, evidence of monophagy or stenophagy is not on its own evidence of specialization.

**Predatory versatility** refers to predators that are poly-specialists. For example, it is well documented for spiders that a single individual can deploy a large repertoire of distinctively different types of prey-capture behaviour, each type being highly specialized with respect to a different type of prey. These predators are highly polyphagic and the same time highly specialized.

**Preference** refers to a predator's differential motivation to prey on a particular prey type. As such, preference is a cognitive characteristic of the predator that drives prey-choice behaviour. Determining a predator's natural diet might suggest hypotheses about preference and prey-choice behaviour, but these hypotheses should not be accepted as foregone conclusions. Conclusions about preferences and prey choice depend on data from carefully designed experiments.

### Spiders that use silk when preying on ants

First we will consider how spiders capture the ants they eat. Many spiders use silk when capturing prey, the most familiar examples being spiders that build webs (i.e., "web spiders": FOELIX 2011), but web use often entails more than simply eating prey that falls into a snare. For example, there are web-building theridiids that add specialized trip lines to their webs (NENTWIG 1987). These trip lines are strung under considerable tension between the substratum and the bottom of the web, and highly adhesive gum covers the lower portion of each line. An ant that blunders into a trip line gets stuck and struggles. Sometimes the spider rushes down and wraps the ant in silk. Other times the struggling ant breaks the line, which is bad for the ant because now the line recoils, delivering the ant up to the resident theridiid waiting in the web (SHULOV & WEISMANN 1939, SHULOV 1940, MATHEW 1954, NORGAARD 1956, MACKAY 1982, NYFFELER & al. 1988).

"Hunting spider" and similar terms (FOELIX 2011) are used for spiders that make no use of prey-capture webs, but being a hunting spider does not rule out using silk when capturing ants. For example, the prey-capture routine of *Euryopsis*, a hunting-spider genus from the family Theridiidae, is to secure the ant by covering it with viscous thread and then biting on one of the immobilized ant's legs (CARICO 1978, PORTER & EASTMOND 1982).

### Spiders that capture ants without relying on silk

Other spiders capture ants without the assistance of silk, although they sometimes have the assistance of a freshly killed dead ant. With their chelicerae, these spiders carry dead ants in front of their "faces". Inquisitive living ants tap the dead ant and then appear to be none the wiser regarding the presence of a living spider behind the dead ant, leaving the spider at liberty to mingle with its prey, the ants, unharmed (BRISTOWE 1941, MATHEW 1954, OLIVEIRA & SAZIMA 1984, PEKÁR & KRÁL 2002). It might be tempting to think of the dead ant as a mask that hides the appear-

ance of the spider from the ant's eyes, but this can be misleading. It is usually more realistic to think of an ant's world being rendered by chemoreception (HÖLLDOBLER 1971, 1995, MORGAN 2008). The ant is probably deceived primarily by the cuticular hydrocarbons it detects when it contacts the dead ant.

Cuticular hydrocarbons are used by many ants for distinguishing between nest mates and aliens (HOWARD & BLOMQUIST 2005, HEFETZ 2007), and spiders can exploit these chemical-identification systems even without the assistance of a dead ant. The most thoroughly studied example of this is *Cosmophasis bitaeniata*, a salticid spider from Australia that acquires the cuticular hydrocarbons used by weaver ants (*Oecophylla smaragdina*). Chemically disguised as a weaver ant, this salticid enters the ant's nest where it feeds unmolested on the ant's eggs and larvae (ALLAN & ELGAR 2001, ALLAN & al. 2002, ELGAR & ALLAN 2004).

### Predatory versatility

"Predatory versatility" (CURIO 1976) is a term for instances in which an individual predator adopts a conditional strategy. This means each individual deploys a repertoire of distinctly different prey-capture methods according to rules concerning the particular circumstance or the particular prey type encountered (JACKSON 1992, NELSON & JACKSON 2011a).

We can illustrate what this means by taking a closer look at *Zenodorus* (see JACKSON & LI 2001), a genus of salticid spiders. Sometimes these salticids position themselves facing down on tree trunks, remain quiescent and then suddenly lunge down and grab hold of unwary ants walking on the tree trunk below. In the absence of a strategic position from which to launch ambush predation, the salticid resorts to active pursuit (i.e., it approaches rapidly and then leaps on to the ant from 4 - 10 body lengths away). Whether practising ambush predation or active pursuit, the salticid holds on when it attacks small ants, but repeatedly stabs and releases larger ants, with "stabbing"



Figs. 1 - 2: (1) *Odontomachus* ant with unknown salticid prey. (2) Salticid (*Chalcotropis*) with ant prey (*Odontomachus*).

meaning the spider's fangs only briefly penetrate the ant's body. Stabbed ants usually run away, followed by the salticid. Once the successive stabbing attacks render the ant noticeably weakened, the salticid attacks and holds on. Similar attack-and-release routines may be widespread not only among ant-eating salticids (WING 1983, JACKSON & VAN OLPHEN 1991, 1992, LI & al. 1996, 1999, JACKSON & al. 1998, PEKÁR & HADDAD 2011) but also among ant-eating zodariid spiders (HARKNESS 1977, HARKNESS & HARKNESS 1992, CUSHING & SANTANGELO 2002, PEKÁR 2004a, b, 2009, PEKÁR & al. 2008, 2011a), suggesting that ant-eating spiders often need to impair the ant's ability to defend itself.

*Zenodorus* species also make use of webs when preying on ants, but these are not their own webs (JACKSON & LI 2001). They see ants in other spiders' webs (Araneidae, Desidae, Pholcidae, and Pisauridae), slowly approach and then, from the edge of a web, move about, repeatedly orienting so as to fixate its gaze on the ant. When the ant is within a few millimetres of the web edge, the salticid usually leans out and attacks by lunging. Completely entering a web to prey on an ant puts the salticid at risk of becoming the web owner's prey, but the salticid has a solution. It makes use of leaves and twigs that have fallen into the web, the resident spider's prey remains, shed exoskeletons, and other detritus. By leaping from one clump of detritus to another, a vantage point is found from which to lunge out into the web and take hold of the ant. When a detritus pathway is unavailable, the salticid usually leaves the web without attacking the ant.

### Specialized myrmecophagy

Myrmecophagy is a term for *Zenodorus* and other spiders that are especially well adapted for exploiting ants as prey (JACKSON & POLLARD 1996, NELSON & JACKSON 2011a). It is important to emphasize that finding examples of specialized myrmecophagy tells us nothing about adaptive trade-offs or limitations. That specialization with respect to

preying on ants is accompanied by adaptive trade-offs that somehow restrict a spider's proficiency at targeting other prey types is a hypothesis, not a foregone conclusion. Separating trade-off hypotheses from what we mean by specialization, specialized and specialist is essential, as otherwise it is too easy to overlook the importance of actually testing trade-off hypotheses on a case-by-case basis (NELSON & JACKSON 2011a). Saying a jack-of-all-trades is the master of none may appeal to our intuition, but this intuition can be misleading (FRY 1996, WHITLOCK 1996) and often evidence is contrary to the trade-off hypothesis (e.g., DORNHAUS 2008). Many spiders (JACKSON & POLLARD 1996, HARLAND & JACKSON 2004, NELSON & JACKSON 2011a) and other predators are poly-specialists (WEST-EBERHARD 2003; Box 1).

The widespread practice of using the terms "specialist" and "generalist" for specifying a predator's natural diet or for anything that can be determined from field data alone (e.g., FUTUYMA & MORENO 1988, BERENBAUM 1996) is especially misleading. "Monophagy" and "polyphagy" (Box 1) are more appropriate terms for what a predator eats, but these terms have an unfortunate way of suggesting a dichotomy. Envisaging a stenophagy-euryphagy continuum is preferable, where "stenophagy" means to a narrow range and "euryphagy" means to a wide range of prey types in a natural diet (Box 1), but we are still left with a serious, yet rarely acknowledged, issue. Whose classification scheme should we use when deciding where any particular predator fits within a euryphagy-stenophagy continuum? When and why should we refer to prey species, genera, families and so forth? Using formal scientific taxonomy may tell us something interesting in the context of community ecology, but the predator's own classification scheme is something cognitive. When we say a spider "prefers" ants, we are acknowledging that ants are identified by the spider as being especially salient, but determining whether "ant" is a salient category to the spider requires carefully designed experiments (NELSON & JACKSON 2011a).

Similarly, when the term "preference" is used in ecology, it is often implicit, if not explicit, that nothing particularly cognitive is intended. There is nothing objectionable about using cognitively loaded terms as a convenient writing ploy so long as we can reclaim these terms when statements about cognition really are intended. In salticid research, determining the predator's differential motivation to capture different prey types has often been an objective. For this, a cognitive meaning of "preference" is precisely what we need. Likewise, we need a strictly behavioural meaning of "choice", choice being predatory behaviour driven by preferences (MORSE 1980, HUSEYNOV & al. 2008, NELSON & JACKSON 2011a; Box 1). Comparing data on a predator's natural diet with estimates of the availability of different prey types in the field may suggest hypotheses about preference and choice (Box 1). In captivity, observing living predators interact with living prey may also suggest hypotheses about preferences and choices which can then be formally tested.

### The predatory preferences of salticids

Owing to their ability to see with extraordinarily good spatial acuity, their intricate vision-guided predatory behaviour and their frequent expression of pronounced predatory versatility (JACKSON & POLLARD 1996, LAND & NILSSON 2002, ZUREK & al. 2010), salticids are especially attractive subjects for research on specialized preference (Box 1). It is customary to characterize salticids as active, diurnal hunting spiders that rarely, if ever, prey on ants (RICHMAN & JACKSON 1992), but we should bear in mind that more than 5,000 salticid species have been described (PROSZYNSKI 2011) and we have details about the biology of only a fraction of these species. It is also clear that, though they may be a minority, salticids that routinely eat ants (Fig. 2) are at least a large minority. Experimental studies have shown that many of the ant-eating salticid species express pronounced preference for ants as prey (NELSON & JACKSON 2011a), but we should look closely at what we mean by "preference" before we go much further.

Control of confounding variables living prey would bring into experiments is also achievable in salticid research owing to these spiders' capacity to see fine detail and their willingness to respond to dead prey mounted in lifelike posture on cork discs and to virtual prey rendered by computer animation and presented on spider-size monitors (see NELSON & JACKSON 2011a). Converging evidence from a variety of testing protocols has demonstrated strong preference for ants by more than 20 salticid species (NELSON & JACKSON 2011a). Besides choosing an ant significantly more often when it is presented alongside other prey types, these species also accept ants more often than other prey when each prey type is presented one at a time on successive days. Moreover, these spiders drop already captured non-ant prey in order to grab hold of an ant, but almost never drop an ant to grab other prey. Having used second-generation spiders from laboratory rearing under standardized conditions, with no individuals or their parents having had prior experience with ants, these experiments controlled for the influence of individual experience and also for maternal effects (see ROFF 1998). This gives us a strong basis for concluding that these salticids' preferences are innate.

Experiments based on using mounts or virtual prey would be of interest with other ant-eating salticids (SHEP-

ARD & GIBSON 1972, WING 1983, CURTIS 1988, MIYASHITA 1991, ALLAN & ELGAR 2001, PEKÁR & HADDAD 2011) for which we currently do not have an adequate basis for conclusions about innate preference. Innate preference for ants might also be expressed by many non-salticid hunting spiders, including species from the families Aphantochilidae, Corinnidae, Oonopidae, Oxyopidae, Gallieniellidae, Gnaphosidae, Theridiidae, Thomisidae (Hingston 1927, FAGE 1938, SOYER 1943, REISKIND 1969, GENTRY 1974, HELLER 1976, HARKNESS & WEHNER 1977, LEVY & AMITAI 1981, PORTER & EASTMOND 1982, LUBIN 1983, SNEILING 1983, FOWLER 1984, OLIVEIRA & SAZIMA 1984, 1985, CASTANHO & OLIVEIRA 1997, CUSHING 1997, GOLOBOFF 2000), and especially Zodariidae (HARKNESS 1977, JOCQUÉ 1991, HARKNESS & HARKNESS 1992, ALLAN & al. 1996, PEKÁR 2004a, b, 2005, PEKÁR & al. 2005a, b). However, for research on non-salticid spiders, carrying out experiments that control for the confounding variables introduced by using free, living prey appears to be considerably more difficult than it is when using salticids.

Of course, when our objective is not strictly to determine a predator's preferences, staging encounters between predators and living prey are important and sometimes essential. For example, staging encounters with living prey is a critical step toward understanding how prey defend themselves and how predators overcome the prey's defences. An understanding of prey defences and predator countermeasures against these defences can, in turn, suggest ways of improving how preference experiments are designed.

Prey-choice experiments have demonstrated that, even when restricted to relying on vision alone, myrmecophagic salticids have considerable ant-identification proficiency. However, ability to identify ants can be important even for spiders that do not eat ants, as ants (e.g., species from the genera *Camponotus*, *Oecophylla* and *Odontomoachus*) are known to prey on spiders, including tetragnathids and salticids (GILLESPIE & REIMER 1993, HALAJ & al. 1997, JACKSON 1999, NELSON & al. 2004, SANDERS & PLATNER 2007). Experimental findings suggest that vision-based ability to identify and avoid ants is widespread among non-myrmecophagic salticids (NELSON & JACKSON 2006a). In typical experiments, a salticid is inside a chamber with mounts made from ants surrounding one end and mounts made from other arthropods of similar size surrounding the other end. Most salticids avoid the side of the chamber that is surrounded by ants. As the salticids used in these experiments had no prior experience of seeing ants and as the mounts outside the chamber are motionless, we can conclude that these salticids, even when restricted to cues coming from the static appearance of the ant, have an innate capacity to identify ants.

### Specialized use of the physical environment when preying on ants

Besides needing to be cautious when concluding a predator expresses preferences, we also need to be cautious when concluding a predator does not express preferences (e.g., PEKÁR & HADDAD 2011), as illustrated by research on *Aelurillus m-nigrum*, a salticid from Azerbaijan (HUSEYNOV & al. 2008). The natural habitat of this species is open sandy ground with sparse vegetation. Findings from laboratory experiments show that expression of this species' prey-capture and prey-choice behaviour is intimately re-

lated to specialized use of physical-environment features. *Aelurillus m-nigrum*'s motivation to attack ants is considerably elevated when in the presence of sand and in the presence of a small stone. Using the stone as a perch, the salticid detects and identifies prey and then it moves on to the sand to capture it. In the absence of these physical features, initial experiments failed to demonstrate statistically significant choice of one prey over another. However, when the relevant physical features are present during experiments, distinctive preference for ants was evident. Taking a wider perspective, these findings illustrate the perils of over-interpreting statistical non-significance. In instances like this, doing a power analysis will be of little use, as the problem is with the experimental design, not with the sample size (NAKAGAWA & FOSTER 2004).

The biology of *Aelurillus m-nigrum* also illustrates the importance of distinguishing between natural diet and preference (HUSEYNOV & al. 2008). Unusually many prey records are available for *A. m-nigrum* and this species' diet seems to be skewed toward the euryphagic, rather than the stenophagic, end of the continuum. Only about a third of the prey recorded from the field were ants, the remainder being other Hymenoptera along with representatives of another nine arthropod orders. Yet, on basis of its prey-capture and prey-choice behaviour, "ant specialist" is an appropriate term for *A. m-nigrum*. We could say this is a disparity between a salticid's fundamental and its realized niche (HUTCHINSON 1957), but it is more straightforward, and it more directly pertains to behaviour, when we say the disparity is between a spider's preference and its natural diet.

#### Other ways of specializing on ants

Preference and prey-capture behaviour are only two out of many ways a predator might specialize at preying on a particular type of prey. For example, the webs of some ant-eating spiders are routinely found in close proximity to ants nests, suggesting that these spiders may make specialized web-site choices that function as means of specializing on ants as prey (HÖLLDOBLER 1970, PORTER & EASTMOND 1982, CLARK 1996). Venom may also contain ant-specific characteristics. This is suggested by data on paralysis latency (i.e., the time elapsing between prey being bitten by the spider and the prey becoming quiescent). Some ant-eating zodariid spiders may also be metabolically specialized at feeding on ants. This may include selectively feeding on different parts of the prey's body (the head and thorax of the ant) as a mechanism for achieving a balanced diet which ultimately leads to improved fitness traits, such as faster growth and survival time, or it may include venom use especially effective at paralyzing ants or even particular ant subfamilies (PEKÁR 2005, PEKÁR & al. 2005a, b, PEKÁR & al. 2008, PEKÁR 2009, PEKÁR & TOFT 2009, PEKÁR & al. 2010).

Yet another way of specializing is to have sensory systems that are especially sensitive to chemical cues from their ant prey. The most thoroughly studied example is *Habronestus bradleyi*, an Australian zodariid that preys especially on *Iridomyrmex purpureus* (ALLAN & al. 1996). During territorial disputes, *I. purpureus* (THOMAS & al. 1999) and various other ants (DUFFIELD & al. 1977, BLUM 1981, TÜRKER 1997a, b) release 6-methyl-5-hepten-2-one. For the ant, this compound functions as an alarm pheromone. However, besides attracting nest mates, 6-methyl-5-hepten-2-

one is an airborne cue that attracts the spider (i.e., the ant's pheromone is the spider's kairomone: see BROWN & al. 1971).

*Habrocestum pulex*, a myrmecophagic salticid from North America, has a specialized ability to identify ant-derived contact-chemical cues from ants (CLARK & al. 2000), but with a proviso that these cues should be on soil. When given a choice between walking over clean soil or soil that has housed ants, *H. pulex* spends significantly more time on ant-treated soil, but there is no evident discrimination between clean blotting paper and blotting paper over which ants have walked. Ant-derived olfactory cues are also salient to this salticid. When given a choice in a Y-shaped olfactometer between clean air (control) and air coming from a cage containing ants, or 6-methyl-5-hepten-2-one, *H. pulex* moves toward the odour significantly more often than toward the control. Other effects of ant-derived chemical cues on this salticid include the triggering of an agitated walking style, posturing with body elevated and perching on stones or other objects.

#### Cross-modality priming of selective visual attention

Ant-derived chemical cues also have a distinctively cognitive effect on *Habrocestum pulex*. After smelling ants, *H. pulex* becomes selectively attentive to visual cues from ants (CLARK & al. 2000). Another way of saying this is that the ant's odour prepares *H. pulex* to see ants. In the literature on predatory strategies, interest in selective attention has been associated primarily with research on search images. Lukas TINBERGEN (1960) is usually given primary credit for interest in this topic and he used expressions like "learning to see" instead of referring explicitly to selective attention, but a modern rephrasing of what Tinbergen meant would be that experience by a predator with a particular prey type primes the predator to be selectively attentive to specific identifying features of this particular prey. It may be easy to deflect or ignore the cognitive implications of the term "preference", but selective attention is a topic that can hardly be anything other than cognitive. There was a time when the cognitive implications of Tinbergen's search-image hypothesis fostered considerable controversy (see KENNEDY 1992), but the expression "search images" is now widely used, and frequently misused. Too often Tinbergen's hypothesis is misconstrued as being about predators shifting their preferences from one prey type to another. However, search images are fundamentally about selective attention and selective attention is distinctively different from preferences (BOND 2007, SHETTLEWORTH 2009).

However, the research on *Habrocestum pulex* departs from conventional search-image research because, with *H. pulex*, we have evidence of cross-modality priming of selective visual attention. Conventional search-image studies pertain to same-modality priming of selective visual attention. Another difference is that conventional search-image studies pertain to instances in which the predator experiences the prey repeatedly and in this way acquires the search image by perceptual learning (DAWKINS 1971, GOLDSTONE 1998). However, whether the underlying mechanism pertains to the triggering of something innate or instead pertains to something acquired by perceptual learning is a separate question about a search image, not a part of the definition (see JACKSON & LI 2004, CROSS & JACKSON 2009, 2010a, b). Perceptual learning cannot ex-



Figs. 3 - 5: (3) *Myrmarachne melanotarsa*, an ant-mimicking salticid "tending" to Homoptera, as does its model, *Crematogaster* sp. (4) Female of *Myrmarachne bakeri*, an "imprecise" ant mimicking salticid. (5) Female of an undesciptioned *Myrmarachne* from the Philippines, probably a mimic of *Tetraponera*.

plain what was shown for *H. pulex*. Despite no prior experience of seeing ants, *H. pulex* responded to ant odour by becoming selectively attentive to the appearance of ants. The most straightforward conclusion for *H. pulex* is that, when this salticid detects chemical cues from ants, it calls up an innate visual search image for this particularly salient prey.

#### Spiders that use ants as a food source without preying on the ants

Theft is an alternative to preying on ants. Returning to an example we looked at earlier, *Cosmosphaxis bitaeniata* is a salticid that snatches ant larvae and eggs from the man-

dibles of workers (ALLAN & ELGAR 2001). This can be envisaged as theft, but the predator is still eating ants. However, sometimes salticids acquire something other than ant flesh when theiving. BHATTACHARYA (1936) may have been the first to describe how this works. In India, he observed juveniles of *Menemerus bivittatus* grabbing food from out of the mandibles of fire ants, *Solenopsis geminata*. More detail is available from the shores of Lake Victoria in Kenya, where *M. bivittatus* and another two species from the same genus (*M. congoensis* and *M. africanus*) snatch food away from worker ants belonging to two genera, *Crematogaster* and *Camponotus* (JACKSON & al. 2008a). In typical sequences, the salticid positions itself beside an ant

column, repeatedly fixating its gaze on different individual ants and then moves in close to a worker that is carrying prey. After manoeuvring about so that it is head on, the salticid uses its chelicerae to grab hold of the prey and then rapidly pulls the prey out of the ant's mandibles. Having secured the prey, the salticid moves away from the ant column to feed.

By practicing the stalk-and-leap routines typical of many other salticid species (JACKSON & POLLARD 1996), these three *Menemerus* species also prey frequently on free prey (JACKSON & al. 2008a), but not on ants. For *Menemerus*, active pursuit of live prey and theft appear to be a distinct alternative foraging tactics, with the objects taken from the workers' mandibles usually being dead midges (Chaoboridae and Chironomidae).

That a salticid would need an ant's help overpowering inoffensive, soft-bodied midges may seem farfetched and, as midges are exceedingly abundant in the vicinity of Lake Victoria (BEADLE 1981), it is unlikely that a salticid would have much trouble finding them. However, for a salticid, the choosing and capturing of a living midge may be far from effortless. For example, time considerations may be important because success for *Menemerus* during stalk-and-leap sequences often depends on slowly moving close enough to gauge an accurate leap, with these stalking sequences typically taking several minutes, compared with the few seconds needed to intercept an ant (JACKSON & al. 2008a).

The impression of unlimited midge prey may also be misleading. Many of the midges around Lake Victoria, covering vegetation, tree trunks and walls are, in fact, dead. Besides an abundance of midges, there is also an abundance of spiders. Dead midges are often held in place in life-like postures owing to stray lines of spider silk, and a gentle breeze will often animate a dead midge, making it twitch and jiggle about as though it were alive. Salticids often stalk these dead flies, leaping on them when close and then almost immediately releasing them (JACKSON & al. 2008a). However, immediate release and moving away from a dead midge is rare when the fly is taken from the mandibles of an ant. By robbing ants, the salticid may be relying on the ant to select midges that are still fresh enough to be palatable.

### **Batesian ant mimicry**

Spiders are at the mercy of many predators, not just ants, and many of the spider's non-ant predators may be averse to eating ants. Aversion to ants, in turn, is something a spider can exploit by resembling ants (myrmecomorphy: ROBINSON 1969, EDMUNDS 1974, CLOUDSLEY-THOMPSON 1995, CUSHING 1997). However, we should think about whose perspective we mean when we say a spider is myrmecomorphic. We might misclassify a myrmecomorphic spider as being an ant (Figs. 3 - 5), but conclusions about non-human predators being deceived by a spider's resemblance to an ant require experimental evidence. That animal eyes vary considerably in their capacity for spatial acuity, colour vision and other functions is only part of the problem because, besides sensory input, a large part of what we mean by "seeing" depends on processing of information delivered by the animal's eyes (CUTHILL & BENNETT 1993, GREGORY 1998, PALMER 1999, LAND & NILSSON 2002).

Fossil evidence illustrates that, among spiders, myrme-

comorphy goes deep into the past (WUNDERLICH 2000). More than 300 extant spider species, belonging to 13 families, are known to be myrmecomorphic (PLATNICK 2011), and it is estimated that, within the spiders, there have been at least 70 instances of independent origin of myrmecomorphy (MCIVER & STONEDAHL 1993). The majority of myrmecomorphic species are salticids and there is considerable evidence that myrmecomorphy by salticids deceives predators (e.g., PALMGREN & al. 1937, ENGELHARDT 1971, CUTLER 1991, EDMUNDS 1993), with the most extensive experimental evidence being based on using ant-averse mantises and especially ant-averse salticids as the predators (NELSON & JACKSON 2006a, NELSON & al. 2006a, HUANG & al. 2011). If we adopt a liberal definition, we can say these findings imply that myrmecomorphic salticids are Batesian mimics of ants.

We say "liberal" because, for the classic examples of Batesian mimicry, the mimic is a palatable species that deceives predators by advertising like an aposematic prey species, "aposematic" being a term for species that are unpalatable to predators and also communicate to potential predators that they are unpalatable (JORON & MALLET 1998, RUXTON & al. 2004). It could be argued that the term "aposematic" is not totally appropriate for most ants. Although ants have defences that repel many would-be predators and they are also distinctive in appearance, it is unlikely that the ant's general appearance (e.g., its slender body, narrow waist, erratic style of locomotion and distinctive way of waving its antennae) evolved as a mechanism by which ants advertise their identity to predators. However, hypotheses about the origin of the ant's general appearance are irrelevant to the predator.

Experiments using myrmecomorphic salticids have shown that ant-averse predators respond to these salticids as though they were ants and the most straightforward expression to use is "Batesian mimicry" when drawing conclusions about the benefits the mimic gains from resembling ants (NELSON & JACKSON 2011b).

What we know about myrmecomorphic salticids is unconventional in other ways when compared with the more traditional literature on Batesian mimicry where the predator is typically a bird and the predator acquires its aversion to the aposematic prey by learning (BROWER 1958, DARST 2006). In salticid research, the predator is more often another arthropod and learning is usually ruled out because predators used in experiments have no prior experience with the ants or the ants' mimics (NELSON & JACKSON 2011b). There may be a general lesson here. For the literature on Batesian mimicry, the emphasis on learning may be excessive, making it too easy to overlook the likely prevalence of Batesian mimicry based on innate aversion (see CALDWELL & RUBINOFF 1983, CALEY & SCHLUTER 2003).

### **Sexual dimorphism and compound mimicry**

Myrmecomorphy is known from 15 salticid genera (CUSHING 1997, WESOLOWSKA 2006), with *Myrmarachne* being the largest. The species from this genus are also notable for their striking sexual dimorphism. The chelicerae of *Myrmarachne* females are angled downward at right angles to the body and are not especially large (Figs. 3 - 5), but *Myrmarachne* males have enormously elongated chelicerae (Figs. 6 - 8) that extend forward (WANLESS 1978, POLLARD 1994, EDWARDS & BENJAMIN 2009). Experimental



Figs. 6 - 8: (6) Male of an undescribed *Myrmarachne* sp. from the Philippines, probably a mimic of *Tetraoponera*. Note enlarged chelicerae typical of male *Myrmarachne*. (7) Male of *Myrmarachne bakeri*, an imprecise mimic, showing enlarged chelicerae. (8) Male of *Myrmarachne assimilis*, a mimic of the Asian weaver ant *Oecophylla smaragdina*, showing enlarged chelicerae.

findings suggest that *Myrmarachne* males, with their enormous chelicerae, mimic a very specific model.

Ants use their mandibles to carry lots of things, including food, eggs, larvae and other workers (HÖLLDOBLER & WILSON 1990). We can call an ant worker with something in its mandibles "encumbered". In experiments, ant-averse salticids avoid both encumbered and unencumbered ants, and they also avoid both sexes of *Myrmarachne* (NELSON & JACKSON 2006b, NELSON 2012). We call *Myrmarachne* males "compound mimics" because the male's model seems to be not simply an ant but a combination of an ant and something in the ant's mandibles (i.e., an encumbered ant). For myrmecophagic salticids, encumbered ants are safer prey and unencumbered ants are more dangerous, and myrmecophagic salticids have a preference for these safer ants. The *Myrmarachne* male's predicament appears to be that, by resembling encumbered ants, it has inadvertently become more attractive to myrmecophagic salticids.

Compound mimicry is especially refined in *Myrmarachne plataleoides* males. This salticid species mimics Asian weaver ants, *Oecophylla smaragdina*, and the *M. plataleoides* male has a black spot positioned on the top of the distal end of the basal segment of each of its long chelicerae (WANLESS 1978). In *O. smaragdina* colonies, there are major workers that forage and minor workers that care for the eggs and larvae inside the nest. Major workers commonly carry minors from one sub-nest to another by holding the smaller ant's abdomen in their mandibles. While being carried, the minor worker often holds its legs against the side of its body (HÖLLDOBLER & WILSON 1990).



With "eyespot" on their long chelicerae, *M. plantaleoides* males are remarkably similar in appearance to these worker-ant duos.

#### The myrmecomorphic salticid's defences against myrmecophagic salticids

Costs as well as benefits should be considered for a full understanding of Batesian mimicry (see HOLEN & JOHNSTONE 2004) and trading one predator for another appears to be one of the costs for myrmecomorphic salticids (i.e., myrmecomorphy repels ant-averse predators but attracts myrmecophagic predators, NELSON & JACKSON 2006b, NELSON & al. 2006b). This problem is not suffered passively by *Myrmarachne*, as Batesian mimicry can be turned off when resembling an ant is disadvantageous (NELSON & al. 2006c). However, for understanding how this is done, more than static appearance needs our attention. We should also consider motion and behavioural resemblance between mimic and model (see SRYGLEY 1999, GOLDING & al. 2001, THÉRY & CASAS 2009, PEKÁR & JARAB 2011).



Fig. 9: A group of *Crematogaster* ants and *Myrmarachne melanotarsa* (see Fig. 3 for close up) swarming a salticid nest complex in Kenya. Left: male *M. melanotarsa* flanked by a female. Right: mostly ants with a female *M. melanotarsa* on the far right.

When active, ants and *Myrmarachne* tend to be in continual motion on zigzagging paths. This is strikingly different from the stop-and-go gait adopted by more typical of salticids (JACKSON & POLLARD 1996). Moreover, *Myrmarachne* has slender (antenniform) forelegs that are held in a posture that resembles an ant's antennae and *Myrmarachne* waves these legs in a way that resembles how an ant waves its antennae (REISKIND 1977, CECCARELLI 2008). Typical salticids use their forelegs for walking and, during encounters between conspecific individuals, for displaying. These displays, which include specialized posturing or waving of the forelegs (JACKSON & POLLARD 1997), render a salticid's appearance decidedly unlike the appearance of an ant.

Similar displays are adopted by *Myrmarachne* during encounters with conspecific individuals, and also when stalked by myrmecophagous salticids. When displayed at by *Myrmarachne*, myrmecophagous salticids that had been stalking normally desist. *Myrmarachne* also displays preemptively at myrmecophagous salticids that have not yet begun to stalk and this appears to dispel the myrmecophagous salticid's inclination to begin stalking (NELSON & al. 2006c). Evidently *Myrmarachne*'s strategy is to be dishonest (i.e., use Batesian mimicry) by default, but switch to honest communication when resembling an ant is disadvantageous. That prey may defend itself by honestly advertising to predators is nothing new (HASSON 1991), but a Batesian mimic actively revealing its true identity to its models' predators is an unusual example of truth in advertising.

#### Salticids that practise communal mimicry

Ants are social, but most salticids are solitary hunters (JACKSON & POLLARD 1996). Yet there are examples of salticids aggregating, with the largest salticid aggregations being reported from the Lake Victoria region of Kenya and Uganda. These East African species build clusters of nests interconnected by silk ("nest complexes"). These nest complexes can be occupied by 50 or more individuals (JACKSON 1986, 1999). Several salticid species often share the

same nest complex and ants are never far away in this region. An unidentified species of *Crematogaster* is especially often found in the vicinity of nest complexes. *Myrmarachne melanotarsa*, one of the species living in nest complexes, mimics *Crematogaster* (WESOLOWSKA & SALM 2002) and, being an aggregating salticid that mimics a social insect, *M. melanotarsa* adds a previously unappreciated perspective to our understanding of *Myrmarachne*-ant relationships.

*Crematogaster* and many other ants (CARROLL & JANZEN 1973) feed on honeydew, the sugary waste of scale insects (coccids) and other sap-feeding homopterans (BUCKLEY 1987, VÖLKL & al. 1999). *Crematogaster* typically moves from place to place in columns, with *M. melanotarsa* often joining the marching ants, arriving at the honeydew and feeding alongside the ants (JACKSON & al. 2008b) (Fig. 3). *Myrmarachne melanotarsa* also feeds on the broods of the non-myrmecomorphic salticids in nest complexes (i.e., these salticids' eggs and small juveniles), sometimes with the help of ants. When a swarm of ants moves across a nest complex (Fig. 9), females of the non-myrmecomorphic salticids in nest complexes often flee and *M. melanotarsa* exploits these salticids' predisposition to flee from ants. Experiments using mounts made from ants and from *M. melanotarsa* show that the non-myrmecomorphic salticids living in nest complexes are especially prone to flee when they perceive the presence of a group of *Crematogaster*, a group of *M. melanotarsa* or a mixed group in the vicinity. After fleeing from *Crematogaster*, the nest-complex silk and the silk around egg sacs usually suffice as barriers that keep eggs and small juveniles out of harm's way, but a swarm of *M. melanotarsa* is different because, being a spider, *M. melanotarsa* has little difficulty negotiating the silk and preying on the unguarded brood.

The non-myrmecomorphic salticids are not so prone to abandon nest complexes when they perceive a single *Crematogaster* or a single *M. melanotarsa* (NELSON & JACKSON 2009a) and this suggests that resembling a group of

ants is a critical part of this ant mimic's predatory strategy. With *M. melanotarsa*, we have a predator that appears to be, when in a group, a mimic of specifically a group of ants and also an unusual example of a predator that deploys Batesian mimicry as a means of practising aggressive mimicry.

### Aggressive mimicry

"Aggressive mimicry" (or Peckhamian mimicry) is one of the many terms used in the literature on mimicry (WICKLER 1968, EDMUNDS 1974, VANE-WRIGHT 1980, RUXTON & al. 2004), this being a literature that seems to be subject to ever expanding terms for making ever finer distinctions. All the while, real-world examples have a habit of not fitting seamlessly into the categories we define and name. We see this with "aggressive mimicry". This term is often used for most any example of predator using mimicry as a predatory ploy, but we should have our eyes open to the diversity of predatory strategies that get lumped together this way. Comparing *M. melanotarsa* to *C. bitaeniata* is an example. Both of these salticids practise deceit. However, *C. bitaeniata* deceives weaver ants to prey on the ants' broods, whereas *M. melanotarsa* deceives ant-averse salticids to prey on these salticids' broods. For *C. bitaeniata*, deception pertains to the chemical cues that matter to ants. For *M. melanotarsa*, resemblance pertains to vision-based cues by which other salticids identify ants. It would be futile to look for separate terms for each and every distinction like these, but there is another distinction that appears to pull the meaning of "aggressive mimicry" in opposite directions: active eliciting of specific responses from the deceived victim and the opposite, namely not provoking specific overt responses.

In the most straightforward examples of spiders practising aggressive mimicry, the prey has been web spiders or male moths. The web spider approaches the predator as though it were a small insect ensnared in a web and the male moth responds by approaching the predator as though it were a conspecific female (YEARGAN 1994, HAYNES & al. 2002, HARLAND & JACKSON 2004). Like these other aggressive mimics that elicit specific overt responses, *M. melanotarsa*'s strategy is to stand out and, under false pretences, elicit an overt response, except that the overt response elicited by *M. melanotarsa* is alarm and fleeing (NELSON & JACKSON 2009b). Alarm evidently depends on mimicking a group of ants, which makes it appropriate to call *M. melanotarsa* a Batesian mimic as well as an aggressive mimic. However, the strategy adopted by *C. bitaeniata* is almost the antithesis of the strategy adopted by *M. melanotarsa* and the strategies adopted by the spiders that deceive male moths and web spiders. There is no clear evidence that *C. bitaeniata*, for example, attracts the ants it robs. *Cosmophasis bitaeniata* is instead more like a wolf in sheep's clothing that relies on blending in with the crowd and keeping its victims calm.

"Wasmannian mimicry" is an alternative term that might be used for predators like *C. bitaeniata*. As with many terms, Wasmannian mimicry has been subject to shifting meaning (RETTENMEYER 1970, KISTNER & JACOBSON 1975, HÖLLDOBLER & WILSON 1990), but this is a term that could probably be used, with minimal distortion of previous usage, for instances of a predator's ploy when using mimicry being to gain acceptance by the group it exploits

and, on the whole, avoid eliciting overt response. As with most terms in the mimicry literature, we should expect examples that blur across the boundaries, but it could be useful to have one term for when any given example is close to the end of the continuum where the predator uses mimicry for actively eliciting responses (aggressive mimicry) and another term for when any given example is close to the end of the continuum where the predator avoids active eliciting of responses (Wasmannian mimicry).

### Precise and imprecise mimics

It has been argued that, while resembling the model is highly advantageous for the Batesian mimic, the company of the mimic can be disadvantageous to the model, with this conflict leading to coevolutionary chases (GAVRILETS & HASTINGS 1998). However, the pressure on the model might usually be considerably weaker than the pressure on the mimic (NUR 1970) and a phylogenetic analysis suggests that, while the evolution of *Myrmarachne* has been strongly influenced by selection favouring close resemblance to model ants, the ants have experienced negligible selection pressure favouring divergence away from their mimics (CECCARELLI & CROZIER 2007).

Setting aside the question of whether the mimic influences evolutionary change in ant populations, an appealing hypothesis about the mimic remains. Through learning or else by natural selection over evolutionary time, perhaps the potential predators of myrmecomorphic spiders become ever better at distinguishing between mimic and model, in turn favouring myrmecomorphic spiders becoming ever more similar to the model ant (see TURNER 1987). This hypothesis encourages us to expect precise matching between the appearance of Batesian mimics and their models, and yet numerous examples of imprecision are known (REISKIND 1970, PEKÁR & KRÁL 2002, PEKÁR & al. 2005a, NELSON 2010).

No clear consensus has emerged, but a variety of hypotheses have been proposed for explaining the apparent success of imprecise mimics (e.g., Figs. 4, 7). For example, improved match to the model's appearance might be of little use when the model is especially noxious and especially abundant relative to the mimic, as the mimic's potential predators can be expected to generalize and not attend to fine-detail discrepancies between mimic and model (LINDSTRÖM & al. 1997, PILECKI & O'DONALD 1971, SHERRATT 2002). All the same, we should carefully consider the criteria we use when deciding whether a mimic is precise or imprecise. For example, a mimic we call "imprecise" on the basis of static appearance might be more correctly called "precise" when we consider behavioural mimicry (PEKÁR & JARAB 2011).

Another hypothesis is that a point may be reached at which further improving the precision in the mimic's matching to the model is no longer advantageous because the potential predator lacks the perceptual capacity required for making finer discrimination between mimic and model (DUNCAN & SHEPPARD 1965, CHITTKA & OSORIO 2007). In this context, the speed at which a predator needs to make mimic-model discriminations and decide how to respond may be an especially important, but often overlooked, factor (see INGS & CHITTKA 2008, CHITTKA & al. 2009). Another consideration is that, when modelling the evolution of Batesian mimicry, a routine simplification has been to

consider a single guild of predators. However, when ant-eating and ant-averse predators are considered as different guilds interfacing with the mimic, the advantages of imprecise mimicry become more evident (PEKÁR & al. 2011b).

HOWSE & ALLEN (1994) suggested that many examples of imprecise mimicry might instead be Satyric mimicry, this being a term for prey that defends itself by confronting predators with ambiguous stimuli and thereby causing the predator to pause long enough for the prey to flee. This interesting hypothesis, which might be readily tested using salticids as predators, has been largely neglected in the mimicry literature.

For understanding the apparent success of imprecise ant mimics, some more basic issues also need our attention. For example, more clarity about what we mean by "imprecise" would help. Is it that imprecise mimics only poorly resemble some particular ant as its model or is it more appropriate to think of imprecise mimics as being generalized mimics of a variety of ants as a group rather than having any particular ant species as a model (EDMUNDS 1978, 2000, 2006, PEKÁR & KRÁL 2002).

However, the most important issue pertains to whose perceptual world we are talking about. We should also be open to the possibility that a mimic we, as people, perceive as being precise or imprecise may not correspond to what non-human predators perceive as being precise or imprecise. On the whole, the discrimination abilities of the myrmecomorphic spider's potential predators may be poorly understood, but there is a particularly interesting exception. *Portia fimbriata* is a salticid that prefers other salticids as prey (LI & JACKSON 1996) and practises "cryptic stalking", this being the name given to a distinctive prey-capture routine *P. fimbriata* adopts specifically when targeting a salticid as prey (JACKSON & BLEST 1982). Experiments show that *P. fimbriata*, even when restricted to using vision alone, reacts to ants as something to avoid and reacts to salticids as prey to be pursued using cryptic stalking (HARLAND & JACKSON 2004, NELSON & JACKSON 2006b), but there is an interesting exception.

The exception is that *Portia fimbriata* avoids myrmecomorphic salticids instead of adopting cryptic stalking (HARLAND & JACKSON 2001, NELSON 2012), but with a proviso. When the myrmecomorphic salticid is a species that, to people, appears to be a precise ant mimic, *P. fimbriata*'s response is avoidance instead of cryptic stalking, but *P. fimbriata*'s response to imprecise ant mimics occasionally includes cryptic stalking. Apparently *P. fimbriata* is deceived by the precise, but less so by imprecise, ant mimics.

### Directions for future research

Our starting premise was that ants are a major resource in the spider's world. It is apparent that various spiders have adopted a variety of ways of exploiting this resource. We considered two broad domains of exploitation, namely specializing on ants for food and specializing on ants for models to mimic. It is satisfying to see how much we know, but it is a short step from this appreciation of what we know to wishing we knew more. We will finish with a wish-list for future research.

We need a better understanding of what spiders actually eat in the field. Our impression is that only a minority of spiders have a routine of eating ants, but data are scarce. For determining the natural diets of spiders, we

are still relying primarily on what we are lucky enough to see. With modern molecular methods (SYMONDSON 2002, GREENSTONE & al. 2005, KING & al. 2008) becoming more widely used, our understanding of what spiders eat in the field may soon let us more objectively discuss how rare or common it is for spiders to eat ants. All the same, we will need more than data on what spiders eat in the field when our larger goal is to understand how spiders specialize at exploiting ants.

Besides knowing that a spider eats ants in the field, we need experiments that are carefully designed for determining whether ants are a distinct, salient prey category for the spider. One step in this direction is to formulate and investigate hypotheses about ant-specific preferences. Removing living prey from the experimental design is particularly advantageous when testing prey-preference hypotheses. These experiments have been carried out primarily with salticids as the predators and it may appear to be considerably more difficult to design experiments with living prey absent when the predator is a spider that does not rely on seeing detail at the level known for salticids. However, a difficult goal does not mean an insurmountable one. For instance, it is likely that many spiders rely strongly on specific chemical cues from prey and a fuller understanding of these chemical cues might readily become the basis for designing experiment in which the uncontrolled variables from living prey are removed when investigating the preferences of non-salticid spiders.

However, for research on preferences, staging encounters with living prey remains important, especially when observing these encounters gives us details about predator and prey behaviour. These details become the rationale for specific hypotheses about preferences and lead us to the specific ways experimental design should be refined for later research on preferences. Refinements might often include including variables related to prey behaviour or specific responses by the prey to the predator. Advances in animation and robotics technology (KRAUSE & al. 2011) suggest that, in the foreseeable future, it will become increasingly more realistic to design preference experiments in which living prey are replaced by simulated prey that behave and respond to the predator under the control of the experimenter.

Another step toward determining whether ants are a distinct, salient prey category for a predator is to determine whether the predator adopts ant-specific prey-capture behaviour and the first step toward understanding a spider's prey-capture behaviour is by staging encounters with living prey. Research on araneophagic spiders, and especially araneophagic salticids, has illustrated that prey-capture behaviour can be based on a remarkable level of rapid fine tuning in response to details about the prey (HARLAND & JACKSON 2004, NELSON & JACKSON 2011a). Many different variables are known to matter to araneophagic spiders when making prey-capture decisions. To name a few, these include the prey's size, sex and location, whether or not a female prey is carrying eggs and the location of other conspecific predators. Araneophagic spiders especially often base prey-capture decisions on the prey's behaviour and prey response.

It has been argued that the araneophagic spider's capacity for a remarkable level of flexibility when making prey-capture decisions is, in part, something that evolved in the

context of targeting especially dangerous prey, namely other spiders (NELSON & JACKSON 2011a). Myrmecophagic spiders also target prey that can be particularly dangerous, namely ants, yet the details we know about the prey-capture decisions made by myrmecophagic spiders lags considerably behind the level to which we know these details about araneophagic spiders. Closing this gap should be a high priority for future research.

However, prey-specific prey-capture behaviour and preferences are only part of what we should be considering when investigating how spiders practise specialized exploitation of ants as prey. For example, hypotheses concerning spiders making use of ant-specific venom can be investigated using modern methods based on a better understanding of the biochemistry of the venom and the physiology of the prey. Experiments based on paralysis latency after spiders encounter prey leave venom volume as an uncontrolled variable and it is known that spiders can control the volume of venom injected into prey (MALLI & al. 1999, WULLSCHLEGER & NENTWIG 2002, WIGGER & al. 2002, HOSTETTLER & NENTWIG 2006). Experiments based on injecting known volumes of venom or venom components into different prey types would be particularly useful, but this would require methods that are currently feasible only with especially large spiders, and myrmecophagic spiders do not tend to be especially large. However, considering the pace at which we are seeing advances in the miniaturization of equipment, having access to the technology required for working with known volumes of venom and venom components would seem likely in the foreseeable future.

Other technological input will also advance our understanding of mimicry. We need more objectivity when characterizing the static appearance of myrmecomorphic spiders and how closely this matches to the appearance of putative models. Use of modern methods will also advance our understanding motion and behavioural mimicry (HOESE & al. 2008, NELSON & al. 2010). Besides objective characterization of the resemblances behind mimicry, we also need interactive experiments for testing hypotheses about the role of specific characteristics of the mimic. For example, using computer animation, experiments can be based on varying mimic features (static appearance, motion and behaviour) and presenting these virtual mimics to living predators.

For future research on spiders that specialize on ants, as for research on specialization in general, one of the highest priorities should be to insist on the critical formulating and testing of trade-off hypotheses. There are some bad habits to break. When discussing "specialization", much more care should be given to specifying what we know as opposed to what has not been investigated. When formulating hypotheses concerning specialization leading to trade-offs, the rationale for each hypothesis should be examined carefully. For morphological specialization, finding a convincing rationale for trade-off hypotheses may often appear straightforward, as we tend to think about structures being inalterable or at least only slowly altered. The notion of an animal slotting in different morphology when faced by different circumstances or different prey usually seems unlikely, but we know that spiders can slot in different behaviour when faced by different circumstances or different prey. This kind of flexibility is what we normally mean by predatory versatility, conditional predatory strategies and polyspecialization (WEST-EBERHARD 2003, NELSON & JACKSON 2011a).

Knowing there is pronounced expression of predatory versatility sits uncomfortably with how trade-off hypotheses often seem to be carried along when specialized behaviour is discussed in the literature. Of course, spider behaviour is a product of the spider's nervous system and there must be a limit to the computational power of any nervous system. The question comes down to the level at which limitations become evident. Our intuition might be that animals with spider-size nervous systems will be subject to especially severe computational limitations and yet the evidence we have is contrary to this expectation (CHITTKA & NIVEN 2009, CHITTKA & SKORUPSKI 2011, EBERHARD 2011). Demonstrating that a predator is specialized, especially when we mean specialized in behaviour, is distinctively different from demonstrating that trade-offs have imposed limitations on the predator.

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