

A review of the ethology of jumping spiders (Araneae, Salticidae)

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Introduction

Ethology is the study of behaviour. Jumping spiders (Salticidae), because of their complex behaviour and unique, complex eyes, have been (among spiders) disproportionately well-represented in ethological studies. We will review five areas of salticid ethology: predatory strategies, courtship, maternal behaviour, silk utilisation and mimicry. First, however, it will be useful to present some background information on the characteristic that makes salticids so unique among spiders.

Most spiders have simple eyes and poorly developed vision, but salticids have acute vision (Drees, 1952). The unusual and highly evolved visual system of salticids, extensively studied by neurobiologists (Forster, 1982a; Blest, 1985; Land, 1985), is probably the most important characteristic of this family. Because no other spider family has comparable eyes, the evolutionary relationship of salticids to other spider families is unclear.

Our understanding of salticid eyes is derived, to a large degree, from the ground-breaking work of Homann (1928, 1971) and Land (1969a,b), and major extensions of this work from David Blest's laboratory (e.g. Blest & Carter, 1987). The salticid antero-median (AM), or principal, eyes are responsible for acute vision. Three pairs of secondary eyes, the antero-lateral (AL), postero-median (PM) and postero-lateral (PL) eyes, are primarily movement detectors. In most salticids, the PM eyes are minute and vestigial, but these eyes are large and functional in a few primitive species. It is the AM eyes, however, that are especially unusual.

All eight eyes have fixed cuticular lenses, but the AM eye tubes are long and have six pairs of muscles attached to them. The salticid uses these muscles to co-ordinate precise and complex rotational and side-to-side movements of the eye tube, important in tracking moving prey and in recognising shapes. However, the AM eye tube is not capable of accommodation; it cannot move forwards and backwards to change focal length.

The structure of the AM eye retina also distinguishes these eyes. The retina is tiered: light coming from the lens system passes successively through layers 4, 3, 2 then 1. The tiered structure is crucial in enabling the salticid to compensate for chromatic aberration. In essence, the AM eye is a miniature telephoto system, much like a Galilean telescope. First, because the retina is at the rear of a

long eye tube, the AM eye has a long focal length. More remarkably, there is a second (diffracting) lens at the rear of the eye tube, just in front of the retina, which increases the magnifying power of the lens (Williams & McIntyre, 1980). The AM lens system and retina combine to give salticid eyes extraordinary resolving power and allow the salticid to perform phenomenal feats of visual discrimination (Jackson & Blest, 1982a). The resolving power of salticid eyes has no doubt been an important factor in the evolution of complex visually mediated behaviour, including prey capture, agonistic display and visual courtship.

The AM eye retina also enables salticids to perceive colour, with sensitivity ranging from red to ultraviolet (Peaslee & Wilson, 1989). The ability to see colour probably was important in the evolution of one of the most distinctive characteristics of salticids as a group: these spiders are often outlandishly colourful. The salticid's colourful markings are especially evident during courtship, suggesting that colour is important in intraspecific communication in this family.

Predatory strategies

Jumping spiders are, for the most part, diurnal hunters, which is not surprising for a group with such a highly developed visual system. Forster (1982b) analysed in detail how visually hunting salticids usually catch their prey. Typically, the salticid first orients by swivelling its cephalothorax around to bring the AM eyes to bear on the prey. Next, the salticid aligns its abdomen with its cephalothorax and begins to stalk slowly, almost cat-like, towards the prey. When close to the prey, the salticid pauses, lowers its body and fastens a dragline to the substrate, then leaps on the prey.

Salticids resemble web-building spiders in being able to detect and precisely locate prey at a distance (Enders, 1975). Web-builders do this by accurately interpreting vibrations coming across the web from the ensnared prey. Salticids, in contrast to the web-builders, do not depend on a silk structure erected in the environment. Salticids, instead, use sight to gain accurate information about potential prey.

Remarkably, a salticid does not have to take a straight-line path to reach its prey. It can take a circuitous route (detour) to its prey, sometimes temporarily losing sight of the prey (Hill, 1979). Detouring, suggesting remarkable problem-solving abilities for a spider, is currently a topic of intensive research by Michael Tarsitano at the University of Canterbury.

Some salticids are apparently active searchers (Enders, 1975), spending much of their time walking and stopping periodically to look around. If they come near prey, they actively pursue it. Other species spend more time visually scanning the environment from one place, then actively stalking prey that comes near. *Phaeacius*, a Sri Lankan salticid that sits motionless while facing downwards on tree trunks, has taken sit-and-wait predation to an extreme. This salticid rarely stalks its prey; instead, it prefers simply to lunge down on prey that walks in front of it (Jackson & Hallas, 1986a).

Ant-eating salticids also use unusual and specialised prey-capture techniques. Most salticids exclude worker ants from their diets, but *Corythalia canosa* (Walckenaer), *Habrocestum pulex* (Hentz) and *Pystira orbiculata* (Keyserling) routinely eat ants [Edwards *et al.*, 1974; Cutler, 1980; Jackson & van Olphen (1991)]. Ant-eating salticids have prey-specific predatory behaviour for catching ants. *Corythalia canosa*, for example, circles around in front of the ant, then lunges over the insect to grab it behind the head. Ant-eating salticids, however, do not appear to be limited to eating ants. For example, they are also efficient predators of flies, which they catch using the standard predatory behaviour outlined by Forster (1982b), and attack from any direction.

Web-invasion is another unusual predatory tactic of certain salticids. Some salticids are known to leap into, or walk across, webs to catch web-building spiders (araneophagy) or insects (kleptoparasitism) ensnared in the webs (e.g. Robinson & Valerio, 1977). *Phidippus audax* (Hentz) has been observed attacking *Tetragnatha* orb-weavers in this manner (Richman, unpubl. observation). Four genera, *Brettus*, *Cyrba*, *Gelotia* and *Portia*, however, are more specialised web-invaders (Jackson & Blest, 1982b; Jackson & Hallas, 1986a,b; Jackson, 1990b and in press). These salticids go slowly on to the alien web and manipulate silk with their legs and palps, making vibratory signals. The web-owner spider sometimes responds to these signals by approaching as if the signal came from a small ensnared insect. Instead of getting a meal, the web spider becomes the aggressive mimic's meal. As with the ant-eating species, web-invading salticids do not limit predation to one type of prey. The web-invading salticids are also efficient at using other predatory tactics against other types of prey. For example, *Portia fimbriata* (Doleschall) from Queensland, Australia, has a specialised way of stalking and catching other (ordinary) salticids, which involves a slow, mechanical, stalking motion (Jackson & Blest, 1982b). The behaviour of web-invaders, like that of ant-eaters, suggests, in the Salticidae, the notion that the jack-of-all-trades is the master of none does not apply (Jackson & Hallas, 1986c).

Courtship

Courtship is another context in which salticid behaviour tends to be complex. Peckham & Peckham (1889, 1890) were the first to make a systematic study of salticid courtship, emphasising the importance of intersexual selection as a factor in the evolution of salticid behaviour. During the Peckhams' time, and for most of this century as well, intersexual selection was not well understood; yet intersexual selection is now one of the most important topics in ethology. Recent studies (e.g. Jackson, 1981) support the Peckhams' contention that intersexual selection has shaped the evolution of salticid courtship by forcing males to overcome female resistance by performing more complex dances and by being more strikingly ornamented.

Researchers are also interested in using information about courtship to understand salticid phylogeny and classification. Crane (1949), in a well-known and exten-

sive comparative study of salticid display, examined broad phylogenetic trends. She did not, however, propose a phylogenetic classification system based on behaviour. She divided jumping spiders into three broad behavioural groups: runners, hoppers and intermediates. These groups often crossed phylogenetic lines and were referred to by her as stages. More recently, Richman (1982) showed that salticid displays, if used with care, are useful characters in systematics.

Individual salticid displays are often elaborate. For example, *Habronattus hallani* (Richman) males run sideways, then jump at the end of the run, displaying their iridescent femora; *Habronattus coecatus* (Hentz) males creep slowly towards the female with front legs raised, suddenly raising then lowering their third pair of legs from time to time as they advance. *Hentzia palmarum* (Hentz) males approach the female in a zigzag path while tilting their abdomen to the side and spreading their chelicerae apart (Richman, 1982). Each salticid species tends to have repertoires of numerous discrete displays, this being another source of complexity. For example, *Corythalia canosa* has a repertoire of about 30 major displays that can be combined in diverse ways (Richman, 1982; Jackson & MacNab, 1989). There also appears to be considerable variation between species, not only in the details of each species' display repertoire, but also in repertoire size. For example, *Platycryptus undatus* (DeGeer), an exceptionally cryptic North American salticid, appears to have a considerably smaller repertoire of displays than does *C. canosa* (Richman, 1982).

All salticids use visual displays during courtship (i.e. special behaviours that function to provide a special visually perceived stimulus to a conspecific of the opposite sex). This is not surprising in a spider family with such acute vision. However, acute vision has not limited salticids to visual communication. On the contrary, multi-channel communication is common in the Salticidae, and this is an important factor contributing to the complexity of salticid display.

Many salticids perform tactile displays when the male and female come into contact with each other before mating, the repertoire of these displays sometimes being large and complex (e.g. Jackson & Harding, 1982). Several salticids communicate by stridulating (Edwards, 1981; Gwynne & Dadour, 1985; Maddison & Stratton, 1988a,b). Also, pheromones are known to be important for many species (Crane, 1949; Richman, 1982; Pollard *et al.*, 1987; Jackson, 1987). Besides volatile pheromones perceived by olfaction, salticids commonly use pheromones associated with silk and perceived by contact chemoreception.

There is yet another common mode of communication in the Salticidae: vibratory signals transmitted across silk (e.g. Jackson & MacNab, 1989). Although web-building spiders from other families are well known for communicating with vibratory signals on silk (Robinson, 1982), silk-borne signals are surprising in the salticids, hunting spiders with acute vision. Yet salticids, like all spiders, use silk, even if they do not normally build webs. In particular, most salticids spin a cocoon-like nest as a resting, moulting and oviposition site. The male of many salticid

species performs vibratory courtship on the silk of the female's nest and, if successful, enters the nest to mate with the female. The male does not have to be able to see to perform this type of courtship (Jackson, 1977). Indeed, nests are often built in places with little light, such as under rocks.

The same individual that courts with vibratory displays adult females he finds in nests will use visual displays if he finds an adult female outside her nest. He uses yet another tactic if the female he finds inside her nest is subadult: first he courts her using vibratory displays, then he spins a second chamber on her nest and cohabits until he can mate with her in the nest after she matures (Jackson, 1982).

There is an interesting parallel between predatory and courtship behaviour in the Salticidae. In both cases, salticids often have conditional strategies (i.e. they use discretely different tactics in different circumstances). In the conditional mating strategies, different tactics are used depending on the location and maturity (or even receptivity) of the female; in the conditional predatory strategies, different tactics are used depending on the type of prey. The study of conditional strategies is an important current area of research in zoology (e.g. Dominey, 1984), and salticids seem to be a group in which conditional strategies are especially well developed (Jackson & Wilcox, 1990).

Closely related to courtship displays are male-male confrontations or agonistic displays. These visual displays are similar to courtship, but have added aggressive aspects that make them distinct (e.g. Crane, 1949; Richman, 1982; Jackson & MacNab, 1989). We lack space for a thorough discussion of male-male aggressive displays, which do not appear to occur in all salticid species. These are apparently lacking, for example, in most of the species of *Habronattus*, but occur in such varied genera as *Corythalia*, *Phidippus*, *Hentzia* and *Menemerus* (see Richman, 1981 for a review of the literature to that date).

Maternal behaviour

Courtship and mating are followed by oviposition, and maternal care of eggs and recently hatched juveniles appears to be widespread, if not universal, in the Salticidae. Salticids spin silken eggsacs and stay with these, presumably guarding them. Exactly *what* salticid females guard against and *how* they guard the eggs is unclear (Eberhard, 1974), but the maternal female could probably deter many egg predators and parasitoids.

The most common type of salticid eggsac is, more or less, a spherical mass of eggs wrapped in dense silk and embedded in the interior of a cocoon-like nest. However, other designs are known. For example, lyssomanine salticids stand in the open on leaves (usually on the underside) over eggs that are only loosely covered with silk, and the eggs are usually widely spaced under the silk (Richman & Whitcomb, 1981; Jackson, 1990a).

A European species, *Marpissa rumpfi* (Scopoli) [= *M. muscosa* (Clerck)], stacks three to five flat eggsacs one on top of the other inside a nest (Holm, 1940). *Holcolaetis*

stands in the open over a flat papery eggsac on tree trunks (Wanless, 1985). *Euryattus* chooses a dead, rolled-up leaf as an oviposition site and hangs the leaf up on a tree trunk or a rock face by several heavy guylines (Jackson, 1985a). *Pellenes nigrociliatus* (L. Koch) does something similar, only this species chooses a snail shell instead of a leaf (Mikulska, 1961). *Thiania* seals a pair of green leaves together with strong silk rivets and oviposits in the tight space between the leaves (Jackson, 1986).

Silk utilisation

Besides using silk to make nests and eggsacs, all salticids trail a dragline behind them when they walk. If the salticid loses its footing in the vegetation, it can return to its starting point by climbing up the line. As an alternative to a cocoon-like nest, some salticids rest at night hanging from draglines (Carroll, 1977) and some drop on draglines when feeding (Robinson & Valerio, 1977).

Salticids also use silk for dispersal by using a behaviour known as ballooning. While standing at the edge of vegetation or hanging from a dragline (Eberhard, 1987), the salticid is carried away on the wind when air currents catch hold of strands of silk from the spinnerets.

Some salticids even build pre-catching webs. *Pellenes arcigerus* (Walckenaer) (Lopez, 1986) and *Spartaeus* (Jackson & Pollard, 1990) build sheet webs. *Spartaeus* primarily catches moths in its web, but the predatory behaviour of *Pellenes arcigerus* has not been studied. *Portia*, besides invading alien webs (as noted earlier), also builds an unusual funnel-shaped aerial web, and uses this web to catch other spiders (Jackson & Hallas, 1986b). *Euryattus*, besides hanging up a dead leaf as an oviposition site (see above), also spins a flimsy space web; primarily the juveniles build these webs (Jackson, 1985a). *Simaetha* spins a dense space web, often embedding a cocoon-like nest within the web, or it may just build a nest (Jackson, 1985b). *Simaetha* has another unusual habit; it often builds its web within the communal webs of *Badumna candida* (L. Koch), a social amaurobiid in Australia, and gleans trapped insects off the sticky web of these social spiders.

Web-building in the Salticidae is unexpected. The salticids are a group renowned for their well-developed eyes and generally thought of as a classic example of hunting spiders. Perhaps web-building in salticids is a relic of the evolution of this family from web-building ancestors (Jackson, 1985c).

Mimicry

We have reviewed one type of mimicry already — aggressive mimicry in which a predator tricks its prey by making deceptive signals on a web. Batesian mimics are prey species that deceive their predators, and this type of mimicry may be common in salticids. Ant mimicry is the best known (Edmunds, 1978; Reiskind, 1977).

Many salticids are remarkably similar to ants in morphology and in locomotory behaviour. Ants are avoided by many predators of spiders, suggesting that the ant-like salticids are Batesian mimics (Edmunds, 1974). Data are

scarce to support this supposition, but Engelhardt (1971) showed that birds fail to distinguish between ants and an ant-like salticid, *Synageles venator* (Lucas).

Besides ant-like salticids, there are also wasp-like and beetle-like species. *Phidippus apacheanus* Chamberlin & Gertsch, for example, is remarkably similar to velvet ants (mutillid wasps) in both general appearance and locomotory behaviour (Edwards, 1984; Richman, unpubl. obs.). *Agassa cyanea* (Hentz) resembles flea beetles and has been collected in the company of flea beetles (Richman, unpubl. obs.). Numerous salticids, including species in at least four genera (*Agassa*, *Sassacus*, *Cylistella* and *Coccorchestes*) resemble chrysomelid beetles.

Batesian mimicry is a reasonable hypothesis to account for the wasp mimicry because wasps have potent stings. The advantage of beetle mimicry is not as clear, but the hard exoskeleton and the prevalence of noxious tastes in some beetle species lends credence to the notion that Batesian mimicry has been important in the evolution of beetle-like Salticidae.

Orsima formica Peckham & Peckham from Borneo is apparently a "generalized, reverse insect mimic" (Reiskind, 1976). This salticid waves its abdomen and spinnerets in a fashion to resemble the head of an ant or beetle. That is, this salticid uses its rear end to mimic the front end of an insect.

There is another way the tables can be turned; sometimes the insect tricks the salticid. Certain fruit flies have markings on their wings that resemble a salticid performing a threat display. A salticid that sees the fly's wing displays back, as if it had seen a rival, giving itself away to the fly (Whitman *et al.*, 1988). An even more remarkable mimic of this type is a recently discovered fulgorid plant-hopper nymph that bears a close resemblance to a jumping spider when viewed from the rear (G. Zolnerowich, pers. comm.). These are unusual instances in which prey species mimic a predator to gain protection from the same predator mimicked.

Concluding remarks

This review has been, by necessity, selective both in the topics we covered and the examples we used for each topic, but the interested reader can find other examples and topics in the references we have cited (see also Richman, 1981).

Salticids have a combination of traits that make them unique subjects for ethological study. These traits include, among other things, the specialised salticid visual system, the complexity of salticid behaviour, a tendency of these spiders to evolve conditional strategies and interspecific diversity in behaviour. Although much research has been done already, our impression is that the potential of these animals for ethological research is not as widely appreciated as it should be.

Acknowledgements

This is Journal Article 1579, New Mexico Agricultural Experiment Station, Las Cruces, New Mexico.

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