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OUTLOOK

When it looks and walks like an ant

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Summary
Some jumping spiders (family Salticidae) bear a striking resemblance to ants, a dangerous type of prey, both in terms of their appearance and in terms of how they move. Recent research has taken important steps toward determining whether predators categorize these spiders as ants on the basis of the way they move.

Keywords Biological motion · Categorization · Cognition · Predation · Spiders

By individuating, identifying, and categorizing objects, an animal can tame the potential its visual system has of delivering an otherwise unmanageable influx of distinguishable stimuli, but these cognitive processes need to be structured into a classification system that corresponds adaptively to the world in which the animal lives. When classifying, an animal can rely on the static features of objects (e.g., colour, shape, size), but another intriguing possibility to consider is whether an animal can also categorize specifically on the basis of the movement patterns of objects. For this, we need experimental methods that separate movement-related features from static features. As Johansson (1973) demonstrated more than 4 decades ago, this can be achieved by using point-light displays, which is an especially elegant way to present strictly motion-related cues to the subject. Although Johansson's subjects were human, point-light displays were subsequently used with nonhuman animals (Dittrich, Lea, Barrett, & Gurr, 1998). For animals in their natural environments, movement-pattern categorization might often be of exceptional importance, but our impression is that behavioural ecologists are largely unaware of the potential that point-light displays have as a method for testing this hypothesis.

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As illustrated by jumping spiders (Salticidae), predator–prey interactions offer an especially interesting context in which to investigate the categories that matter to animals in their natural environments. Salticids are especially suitable experimental subjects because they have exceptionally good eyesight and a capacity to classify prey into many different categories, including a capacity to identify ants as being dangerous prey-size arthropods that are best avoided (Jackson & Cross, 2011). *Myrmarachne*, a genus of salticid spiders, is particularly interesting in this respect because people often misidentify these spiders as being ants; more importantly, many ant-averse predators are deterred by *Myrmarachne*'s appearance. Avoiding ants is understandable because these insects come armed with a battery of defences, including capacities for stinging, spraying formic acid, and biting with strong mandibles. Compounding these risks, ants are rarely found alone; when attacking one ant, a predator is in danger of being mobbed by other ants from the neighbourhood.

In casual conversation, 'ant' usually means the adults of a particular insect family (Formicidae), with members of the worker caste being the most abundant. More than 12,000 ant species and more than 200 *Myrmarachne* species have been given scientific names and, while they are not all identical in appearance, professional taxonomists understand that the workers of these ant species are exemplars of a single category ('ant'). People can easily misidentify *Myrmarachne* species as being more exemplars of this same category, and, when this happens, 'ant mimic' is a convenient label for *Myrmarachne*. We can propose that the defining features for the category 'ant' include having six slender legs and two slender antennae, as well as having a slender body segmented into a distinct head, thorax, and abdomen, with a slender waist, called the pedicel, located between the thorax and abdomen. Although spiders have a cephalothorax (sometimes called a 'prosoma') instead of a separate head and thorax, *Myrmarachne*'s cephalothorax is unusually slender, with a constriction at the front end that gives a strong impression of there being a separate head and thorax. *Myrmarachne* also has a habit of elevating its slender first pair of legs and angling them forward in a way that makes them resemble an ant complete with six legs plus two antennae.

We need data from experiments when our goal is to understand how salticids distinguish between ants, *Myrmarachne,* and 'ordinary' salticids, where 'ordinary' means the salticid species that do not mimic ants. While most salticids probably avoid ants ('myrmecophobia'), there are almost 6,000 described salticid species and, within this large family, there are species that specialize at eating ants ('myrmecophilia'). Most salticids might eat another salticid when the opportunity arises, but, on the whole, experimental evidence suggests that myrmecophilic as well as myrmecophobic salticids respond to seeing *Myrmarachne* as though they were seeing an ant. Importantly, however, most of these studies were carried out by presenting salticids with stationary lures made from dead ants and from dead *Myrmarachne* that could not be touched, smelled, or interacted with. This gives us a limited perspective because ants, *Myrmarachne,* and other salticids are rarely stationary when seen by predators. Moreover, people often comment on how *Myrmarachne*'s style of locomotion resembles an ant's.

This suggests that a version of the 'duck test' (when it looks, quacks and walks like a duck, then it probably is a duck) might apply when people assign *Myrmarachne* to the category 'ant' (when it looks and walks like an ant, then it probably is an ant). Two recent studies (Nelson & Card, 2016; Shamble, Hoy, Cohen, & Beatus, 2017) are steps towards understanding whether *Myrmarachne*'s natural predators might adopt a similar rule. In both studies, the motion patterns of *Myrmarachne* individuals were compared to the motion patterns of a variety of ants and a variety of ordinary salticids. Shamble et al. (2017) used *M. formicaria*, a *Myrmarachne* species from Europe which is now established and common in North America, whereas Nelson and Card (2016) used four *Myrmarachne* species from the fauna of Australia. For the predator in their experiments, Shamble et al. (2017) used *Phidippus audax*, a myrmecophobic salticid, whereas Nelson and Card (2016) used *Sandalodes bipencillatus*, a myrmecophilic salticid.

The two studies have their different strengths and weaknesses. The descriptive work of Shamble et al. (2017) was sensational, as it was based on using a battery of high-speed cameras. For example, how *M. formicaria* positions and moves its forelegs during walking bouts was documented: *M. formicaria* walks on eight legs, not six, and only raises and waves its forelegs during the brief pauses between steps. However, we do not know whether the way ants move their antennae or the way *M. formicaria* moves its forelegs matters to myrmecophobic and myrmecophilic predators. For determining this, we would need experiments in which antenna and foreleg movement is manipulated as a variable, independent of the other variables. Shamble et al. (2017) carried out experiments, but these were not designed to determine whether *M. formicaria*'s 'antennal illusion', noticeable to people, is noticeable and salient to *P. audax*.

In both studies, there was a primary interest in whether predators categorize *Myrmarachne* as ants on the basis of locomotory pattern. Both studies included experiments during which the predator viewed animation, but the experiments of Nelson and Card (2016) came closer to addressing this question because, unlike Shamble et al. (2017), they varied motion pattern in animation while keeping morphology constant. However, as the animation with the ant-like locomotion also moved more, Nelson and Card's (2016) findings could be accounted for by a hypothesis that solely the amount of time moving, instead of the moving pattern itself, mattered to the predator.

While neither study included experiments that adequately addressed whether predators can make discriminations on the basis of strictly motion-related details, the experiments that have been done so far are encouraging. In both studies, the primary objectives pertained to locomotory mimicry and, using animation, we now know that salticids respond to animations of moving ants and of *Myrmarachne*. This suggests that, as a next step, point-light animations could be used in experiments for determining whether salticids categorize prey on the basis of strictly motion-related cues.

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