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REVIEW

A road map of jumping spider behavior

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Abstract. The largest family of spiders, jumping spiders (Salticidae), is known for performing complex visually mediated predatory and courtship behavior. As cursorial predators, they rely on their sensory systems to identify objects at a distance. Based on these assessments, salticids perform flexible and target-specific behavioral sequences which demonstrate a high level of cognitive processing. Recent studies have highlighted the role of other sensory modalities in these processes, such as chemoreception and mechanoreception, and elucidated the visual cues used for object identification, including motion, color, contrast, and shape-based cues. Until recently, sensory modalities other than vision were largely overlooked, but current advances in technology now allow us to probe their sensory and cognitive capabilities, as well as how these are shaped by experience. In this review, I provide an overview of current knowledge of salticid behavior and the sensory systems underpinning this behavior, and highlight areas in need of further research. This review focusses on our understanding of salticid communication, parental behavior, personality, antipredator behavior, and diet, as well as habitat selection. I argue that a historical vision-based focus on a small number of species due to their coloration or their unusual behavior provides a springboard for a deeper understanding of the general cognitive and sensory attributes that have evolved in this lineage, of which we yet have much to learn.

Keywords: Multimodal communication, sexual selection, chemical ecology, predator-prey interaction, sensory ecology.

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Spiders diverged from insects about 400 mya (Vollrath & Selden 2007). The family Salticidae, whose most recent common ancestor with other spiders was about 41—50 mya (Bodner & Maddison 2012) and which only radiated widely about 35 mya (Maddison 2015), is a relatively recent radiation among the order Araneae. This has not precluded their expansion: there are more salticid species than all species of mammals. Salticids represent about 15% of all spider genera and species (World Spider Catalog 2022), and perhaps half of them remain undescribed. A key reason for the success of these small spiders (typically < 1 cm) is their remarkable vision, which has allowed them to become proficient active hunters and has enabled them to inhabit almost all habitats on Earth, from high mountains to littoral zones. It is, in fact, their hunting and final pounce on prey, like miniature leopards, that leads to their name, Salticidae: jumping spiders.

Like most spiders, salticids feed through extra-oral digestion, where the spider bites and injects venom into its prey to subdue it, and then bathes it in digestive enzymes before sucking up the liquefied product (Walter et al. 2017). Salticid respiration, like that of several other spider families (but not all), is through the combined use of internal branching tubes (tracheae) and book lungs (Fincke & Paul 1989; Schmitz & Perry 2001). Comprised of folds of cuticular lamellae, book lungs provide a large surface area for gaseous exchange from the air to the oxygen-carrying hemolymph, which freely circulates around the body in direct contact with the tissues it supplies. Both book lungs and tracheae open to spiracles, which can be opened to the atmosphere using a valvular system (Gullan & Cranston 2005). Beyond this, aspects of salticid physiology, as well as their role in agroecosystems and in pest control, surpass the scope of this review. Here, my aim is to provide a broad overview of salticids, specifically focusing on salticid behavior and the sensory systems that mediate behavior. In so doing, I will also highlight areas in need of further study.

As cursorial hunters, with few exceptions (notably among *Portia* Karsch, 1878), salticids do not spin webs, but build cocoon-shaped silken retreats (Fig. 1), often on the undersides of leaves or rocks, to sleep and lay eggs (Jackson 1978; Vieira & Romero 2008; McGinley et al. 2015a). Typically diurnal (Soley et al. 2016; Tork 2019), salticids leave the nest to hunt and find potential mates, for which they rely on their sensory systems, especially their vision, which sets them apart from most other spiders.

The diverse sensory systems of spiders have been described as “masterpieces of ‘engineering’” (Barth 2002) and salticids truly exemplify this, having high-resolution vision, the ability to detect vibrations through air or ground (mechanoreception), and chemoreception. Indeed, the surge of studies of salticid sensory systems and behavior in the 21st century has led to a rapid expansion of bio-inspired engineering based on salticid biology. For example, the salticid visual system has inspired camera systems designed to deal with depth focus issues and miniaturization while maintaining exceptional resolution (Tonet et al. 2008; Guo et al. 2019), and their hunting behavior (search and stalk) has led to mathematical optimization techniques (Peraza-Vázquez et al. 2022). The speed and pivotal flexibility of salticid jumps (due to the hydraulic mechanism used for the leg extension phase of the jump) is used to develop lightweight robots needed for tasks involving high pressure and fast motion (e.g., hydraulic pistons) and for safe-grasping tasks, including interactions with humans (Faraji et al. 2016; Zhu et al. 2018; Göttler et al. 2021a,b).

Vision (below) is the best studied of the sensory modalities used by salticids, yet they use chemoreception to detect both volatile chemical compounds from the environment (olfaction) and chemical cues through direct contact (contact chemoreception), much like our senses of smell and taste. Although little is known about how they accomplish this (see Fischer 2019; Müller et al. 2020), behavioral evidence demonstrates

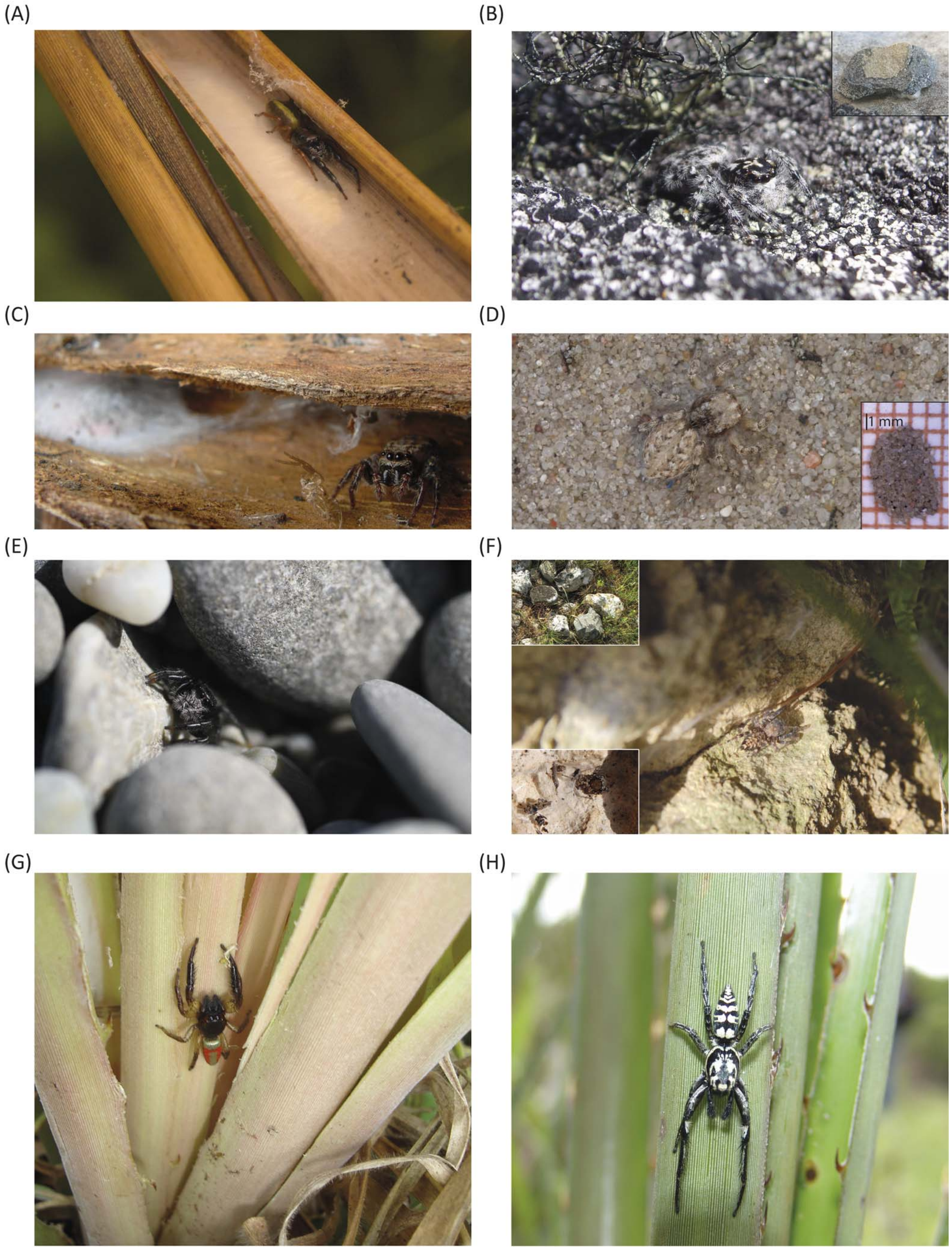

Figure 1.—Salticid use of microhabitats. (A) Female *Trite planiceps* Simon, 1899 and eggs (yellow) inside rolled-up leaves of a *Phormium tenax* New Zealand flax plant in which it almost exclusively lives (Photo: Andrew Pratt). (B) Undescribed alpine scree salticid from New Zealand depicting background matching (Photo: Laura Young); inset: nest with spider on eggs (Photo: Robin Long). (C) Female *Servaea incana* (Karsch, 1878) outside nest of other female sitting on eggs (pink) within *Eucalyptus* bark. (D) *Yllenus arenarius* Simon, 1868 on sandy beach habitat, depicting background matching; inset: nest, with sand glued to outer wall (Photos: Maciej Bartos). (E) Male *Marpissa marina* (Goyen, 1892) in pebble beach habitat. (F) Juvenile *Cyrba algerina*; top inset: rocky patch habitat; bottom inset: juvenile emerging from nest (Photos: Ana Cerveira). (G) *Psecas chapoda* female and (H) male live almost exclusively in *Bromelia balansae* (Photos: Paula Munhoz de Omena).

that salticids can use chemoreception for prey detection and identification (Jackson et al. 2002, 2005) and make use of pheromones for intraspecific communication regarding sex, maturity, and virgin *versus* mated status of conspecific individuals (Gaskett 2007; Nelson et al. 2012a). Additionally, salticids use vibrations through the ground (seismic signals) for courtship communication (Elias et al. 2003, 2004) and potentially also detect predators through airborne acoustic stimulation, or ‘hearing’ (Shamble et al. 2016).

VISION

In any given visual system, many visual functions—such as temporal resolution (ability to resolve changes in light intensity over time, or 'motion'), spatial acuity (ability to resolve fine detail), contrast sensitivity, and color vision—compete with each other in terms of eye ultrastructure, and only relatively large eyes can do all of these tasks well. Salticids have three to four pairs of tiny eyes (typically 50–500 μm) (Nelson & Jackson 2012a; Goté et al. 2019), each adding specific capabilities (e.g., wide field of view, high spatial acuity, motion sensitivity, color vision) to the whole (Land 1971; Williams & McIntyre 1980; Zurek et al. 2015), as due to their small size it is not possible for salticids to realize all of these traits in a single pair. Instead, salticids have divided the tasks of larger, more versatile eyes into multiple more specialized eyes (Harland et al. 2012). These form a modular visual system that achieves the performance of large eyes by integrating information across different pairs of eyes (Zurek et al. 2010; Menda et al. 2014; Jakob et al. 2018).

The key trade-off that any eye faces, and which is exacerbated in small eyes, is that of sensitivity (the amount of light an eye is able to capture and process, leading to the ability to see in dim light) versus spatial acuity. As each photoreceptor samples a specific part of the image, spatial acuity depends on photoreceptor width and the inter-receptor spacing of the retinal mosaic. If receptors are small, densely packed and optically isolated, the image is sampled in detail, and the eye will have high spatial acuity (Land 1981, 1985a). However, at low light levels, only a small number of photons reach individual photoreceptors, so small photoreceptors perform poorly (Land 1981, 1985a; Laughlin 1990; Warrant & McIntyre 1993). In contrast, large photoreceptors can capture enough photons to form an image, but considerable detail will be lost (Warrant & McIntyre 1993). Thus, high spatial acuity is light-hungry—requiring small photoreceptors able to capture enough photons within a short timeframe, while larger photoreceptors allow for less detail to be gathered in less light due to increased photon capture ability. This trade-off—in favor of spatial acuity (Su et al. 2007)—is thought to be why salticids tend to be diurnal (Land 1985a; Tork 2019), although there is considerable variation in the light levels at which different species operate. Details regarding the interspecific variation of the resolution/sensitivity trade-off in salticids can be found in Cerveira et al. (2021).

Salticid vision has been extensively described by Harland, Li and Jackson (2012), so here I provide an overview necessary for understanding their vision-based behavior. Of the (typically) four pairs of camera-type eyes of salticids, three pairs (anterior lateral, posterior medial, and posterior lateral eyes) are known as secondary eyes, and one large forward-facing pair is known as the principal, or anterior medial eyes. Salticid eyes are structurally different from those of vertebrates, and indeed, the secondary and principal eyes are also structurally different from each other, mirroring their specific functional tasks.

Despite the principal eyes typically measuring less than 500 μm, they provide visual detail rarely matched by any other animal. Salticid spatial acuity can be as high as 0.04°, allowing the individuals to discern objects 0.12 mm apart at a distance of 200 mm (Land 1969a, 1981, 1985a; Williams & McIntyre 1980; Blest et al. 1990; Nelson & Jackson 2012a; Morehouse 2020; Cerveira et al. 2021). Given their tiny eye size, this compares favorably with our own acuity of 0.007° (Kirschfeld 1976). Salticids achieve this due to the structure of the eyes, which consist of the corneal lens, a long eye tube, and a boomerang-shaped retina with a diverging pit (which magnifies the image) lying at the end of the eye-tube (Land 1969a). All-in-all, the structure of the principal eyes lets them act like miniature Galilean telescopes. Although they only have a field of view of 3–5°, they compensate through the use of muscles attached to the eye tube that move the retina side-to-side and up-and-down by as much as 35°. These muscles can also rotate the retina on its axis and, by intricate combined rotary and displacement movement of the retinae, the salticid can perform detailed visual scanning of objects of interest (Land 1969b).

A unique characteristic of principal eyes is the layered structure of their retinae, in which the photoreceptors are arranged in four tiers, each lying on a different focal plane, with the most distal layer having the highest density of photoreceptors, producing the sharpest image (Land 1969a). This layered structure might support depth perception (Nagata et al. 2012) and color vision. Depending on species, color vision can be di, tri, or tetrachromatic (De Voe 1975; Blest et al. 1981; Nagata et al. 2012; Zurek et al. 2015; Glenszczyk et al. 2022). It is thought that most salticids are dichromats, with ability to see in UV (which humans do not see). The difference of adding a single 'color' to the spectrum through the addition of a further peak wavelength makes a large impact on the range of visible colors. This is illustrated in Fig. 2, where the same image is shown as seen in human trichromatic vision and simulated Daltonic vision (protanopia, or red-green color blindness), a common condition in humans where red and green cannot be disambiguated. Even in salticids that have multichromatic vision, not all colors are resolved equally well. This is because differential refraction of wavelengths occurs when light enters the cornea, so different wavelengths are focused on different layers of the retina (chromatic aberration), and it is only the distal layer (which focusses shorter wavelengths) that supports the highest acuity vision. This has led to the suggestion (Land 1969a; Nagata et al. 2012) that salticids can use their tiered retina for absolute depth perception through monocular mechanisms, specifically through chromatic aberration and/or image defocus. Current evidence suggests that depth is assessed through image defocus by the comparison of a non-focused image on one layer to a focused image on another layer within the same eye (Nagata et al. 2012; Aguilar-Arguello et al. 2022).

The three smaller pairs of secondary eyes have fixed retinae, have wide fields of view, and are arranged around the side of the cephalothorax, providing almost a 360° field of view (Land 1985b). The role of the secondary eyes is usually – and mistakenly – assumed to be limited to motion detection. As defined histologically (Eakin & Brandenburger 1971), optically (Land 1985a; Cerveira et al. 2021), and behaviorally (Zurek et al. 2010; Zurek & Nelson 2012), the anterior lateral and posterior lateral secondary eyes have remarkable spatial acuity in their own right. Furthermore, at least in *Hasarius adansoni* (Auduoin, 1826), evidence suggests that the posterior medial eyes, while seemingly unable to form focused images, express UV and blue sensitive visual pigments (Terakita & Nagata 2014), which may possibly aid in phototactic orientation. Additionally, the forward-facing anterior lateral pair also provides a large region (c. 30°) of binocular overlap, leading to the speculation that this region mediates depth perception (Land 1985a,b), and may be used for stereopsis. Although this seems likely, there currently is no evidence to support this, possibly due to the difficulty of performing such experiments, as they require having the spiders behave with their principal eyes covered, which they are loathe to do. It is their role as motion detectors, however, that is best understood, and it is in this light that we can truly appreciate the importance of the secondary eyes in the modular system as a whole. Indeed, these eyes play a pivotal role in regulating behavior.

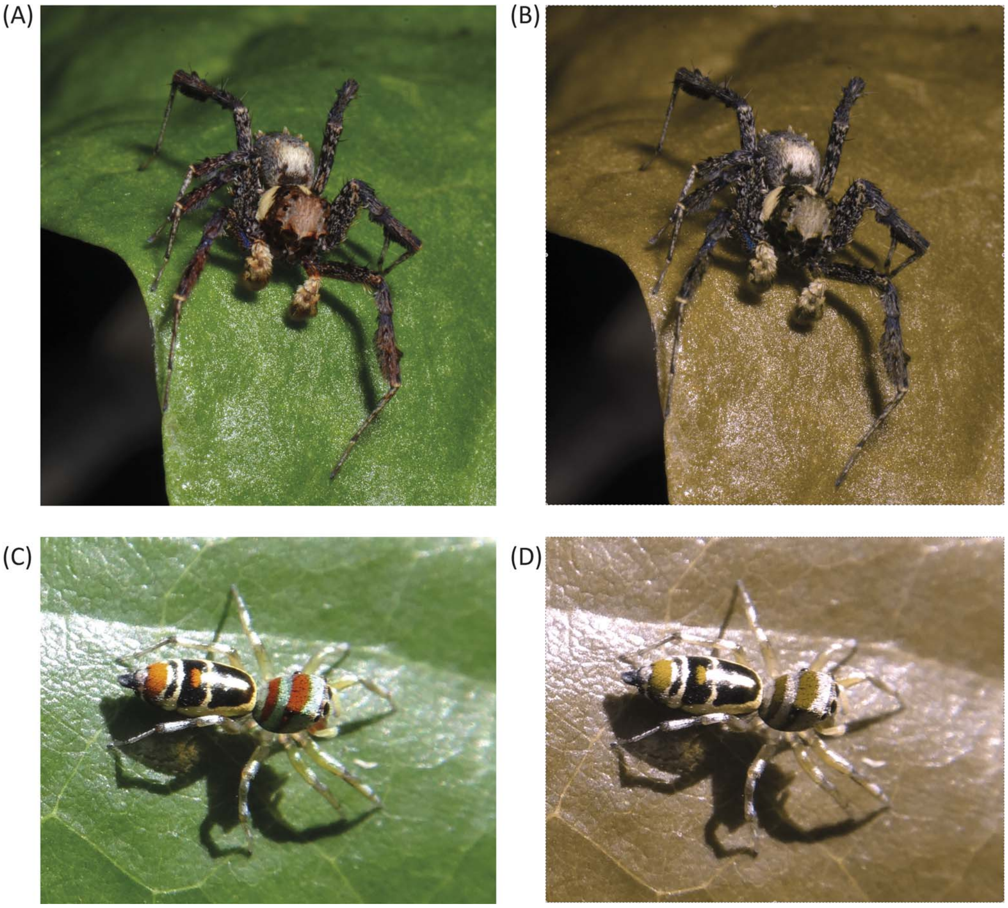

Figure 2.—The effect of the addition or removal of a single peak in wavelength, from trichromatic (A, C) vision to dichromatic vision (B, D). In (A, B) a 'drab' spider (*Portia fimbriata*) and in (C, D) a colourful spider, *Cosmophasis bitaeniata* (Keyserling, 1882). Note how in *P. fimbriata* under dichromatic vision the 'blue' patches on legs stand out, while to a dichromat (which most salticids are believed to be) the colourful impact of *C. bitaeniata* is all but lost. *Portia fimbriata* photo: Matthew Walters.

In salticids, a target detected by the secondary eyes evokes an optomotor turning response to bring the object of interest into the field of view of the principal eyes, which then process the details (i.e., distance, color, size, shape, orientation) of the object that is being viewed (Land 1969a,b, 1971, 1974; Duelli 1978; Forster 1979; Komiya et al. 1988; Harland et al. 2012; Nagata et al. 2012; Zurek & Nelson 2012; Jakob et al. 2018). The secondary eyes thus mediate orientation turns in response to visual stimuli in their field, and as such they coordinate visual input with body movement to bring the target into a frontal field of view for closer inspection. The secondary eyes also play a role in quickly categorizing moving objects and in the initiation of appropriate responses, such as escape or prey capture (Forster 1979; Zurek et al. 2010; Spano et al. 2012; Jakob et al. 2018; de Agrò et al. 2021), mediating not only detection, but also tracking target movement (Zurek & Nelson 2012). By 'deciding' what to respond to, and preferentially eliciting orientation turns to a subset of stimuli for accurate classification by the principal eyes and subsequent behavioral response (Forster 1979; Zurek et al. 2010; Zurek & Nelson 2012; Humphrey et al. 2018; Jakob et al. 2018; Bruce et al. 2021; de Agrò et al. 2021), the secondary eyes should be classified as the first level decision-makers of salticid visual behavior.

To visualize salticid vision we must imagine a small, moveable field of view supporting exceptional spatial detail and color, embedded within a 360° panoramic greyscale image with noticeably less detail. Perhaps we could conceptualize this as being outside in dim moonlight: in our periphery (which hypothetically extends to 360°) we detect rough shapes, and then we switch on a bright point-source torch and illuminate the small, now colorful, area toward which we point (while the periphery remains spatially elusive and monochromatic); we 'paint' our picture by scanning the environment with our flashlight. And, if we want to act on what we have seen in detail, we presumably must remember what we have scanned to decide, for example, whether we are facing a potential predator, prey, or mate.

INTRASPECIFIC BEHAVIOUR

Intersexual communication.—Salticids use elaborate species-specific multimodal displays for courtship and for assessment of rivals (Jackson & Pollard 1997; McGinley et al. 2015a). Most salticids are sexually dimorphic, with males typically being the more colorful sex. Intersexual displays are usually initiated by males toward females, which tend to display minimally while watching male displays (Jackson & Pollard 1997). Because of this, research has been heavily biased toward female choice, but mutual mate choice does exist (Cross & Jackson 2009a) and males are known to select larger, earlier-maturing females, which they detect based on vision and contact chemoreception of their silk nests (Hoefler 2007). Courtship displays involve waving often colorful body parts in coordinated and flexible dance movements (Jackson & Pollard 1997; Elias et al. 2012; Echeverri et al. 2017), vibratory/seismic signals (Girard et al. 2011; Elias et al. 2012), and pheromonal signaling (Nelson et al. 2012a; Cerveira & Jackson 2013).

Salticid color signaling is among the most varied in any animal group and includes possessing both pigment-based and structure-based color (including UV) to enhance reflectance and iridescence (Land et al. 2007; Stavenga et al. 2016) and even fluorescence (Painting et al. 2017a). These colors are thought to be used for mate choice, on the assumption that potential mates assess male quality based on color attributes, which can signal male fighting ability (Lim & Li 2013) or condition (Lim & Li 2007; Taylor et al. 2011), and also female condition (Painting et al. 2017a). An example of the flamboyance of salticid signaling can be found in *Cosmophasis umbratica* Simon, 1903. Male *C. umbratica* have two UV reflective patches (Lim & Li 2006), and behavioral work suggests that are used by females to assess males, as also found for *Phintella vittata* (CL Koch, 1846) (Li et al. 2008). In *C. umbratica*, UV signals are also used by males to assess rival males (Painting et al. 2016). Removal of the male UV signal alters rival male behavior from aggressive to courtship displays, and female behavior toward males changes from 'watching' to aggressive displays. This suggests that UV may be a species-specific male-recognition signal (Painting et al. 2016) honestly reflecting body condition (Lim & Li 2007). In turn, females have a UV-induced green fluorescing patch on their palps, which seems to be used by males to recognize females (Lim et al. 2007). However, like many other salticid studies, female choice for both *C. umbratica* and *P. vittata* was based on the time that females spent watching displaying males, which is not necessarily a reliable indicator of eventual mate choice and copulation (Chan et al. 2008; see Jackson & Pollard 1997 for a review of salticid copulation behavior).

A recently highlighted problem with many studies is that displays are assumed to flaunt the colors to watching females (Glenszczyk et al. 2022). However, a lack of understanding of the spectral properties of the eyes of the salticid viewing the dance, which can vary from UV-green dichromacy to tetrachromacy, has led to numerous potentially erroneous assumptions about the functional significance of their coloration in mate choice (Glenszczyk et al. 2022). In rare cases, such as in *Habronattus pyrrithrix* (Chamberlin, 1924) (Echeverri et al. 2017), studies confirm that dances are aligned to exhibit coloration visible to the potential mate; in other instances, studies confirm that they are not (Girard et al. 2018; Glenszczyk et al. 2022). The vast majority of cases remain untested, but may explain why condition-dependent coloration does not necessarily predict mating success (see Taylor et al. 2011, 2014). Thus, the function of these 'mate-choice' colors presents a challenging, but intriguing puzzle. For example, luminance and contrast may play a key role, as many colorful patches are flanked by light-absorbing, unusually low reflectance 'super black' areas (McCoy et al. 2019). Recent work suggests that contrast may be the most important signal component leading to mating success in some species (e.g., Girard et al. 2018), highlighting the role of multimodal signaling in mating success.

We know little about the role of chemosensory signaling in salticids or in spiders more generally, and the mechanisms for chemoreception in spiders have been notably difficult to discern. Hairs distributed on the legs and pedipalps, called tip-pore sensilla, are thought to have both a chemosensory role and a mechanosensory role (Müller et al. 2020). These hairs have an open pore at the tip which allows soluble chemicals to reach chemoreceptors within the shaft. The presence of chemoreceptive cells in the tip-pore sensilla can explain contact chemoreception (akin to our sense of taste). It is possible that these sensilla also detect airborne chemical signals (akin to our sense of smell), yet how volatile chemical information is processed remains unclear (Müller et al. 2020). However, electrophysiological and behavioral experiments have shown that spiders are capable of detecting volatile chemical signals (e.g., Fischer et al. 2021).

As noted, behavioral evidence of chemoreception is relatively abundant (see Gaskett 2007), including in salticids. Males of most of the few salticid species tested are responsive to both contact chemicals (pheromones deposited on silk draglines) and airborne odors of conspecific females, although females rarely respond to male odor (Nelson et al. 2012a). Contact pheromones on draglines may be used as long-distance signals, while airborne pheromones may act as a cross-modal 'primer' for the spider to search for visual attributes suggestive of a conspecific (Tedore & Johnsen 2013), although not all species tested (e.g., *Habronattus pyrrithrix;* Humbel et al. 2021) appear to be responsive to airborne chemical cues. Intriguingly, although most salticids (including *H. pyrrithrix*) belong to the salticoid clade, almost all species with published responses to pheromones (e.g., Nelson et al. 2012a; Cerveira & Jackson 2013) belong to a different clade of Old World, typically more sedentary species, where perhaps reliance on chemical cues plays a more important role in conspecific location (Nelson et al. 2012a; Humbel et al. 2021). However, given the lack of testing to date, this is largely speculation.

Spider mechanoreception is best understood from Friedrich Barth's excellent studies on the wandering spider *Cupiennius salei* (Keyserling, 1877) (Trechaleidae). This body of work (see Barth 2002, 2004) has elucidated mechanoreceptive organs that appear to be used by most, if not all spiders (including salticids, Hill 1977, 2010), and which are singularly sensitive to disturbances in airflow or to substrate vibrations. These mechanoreceptors consist of different types of hairs and 'slit sensilla', which are cuticular slits in the exoskeleton of the legs. Thousands of tactile hairs on the body of the spider bend in response to tactile pressure (or loading), while trichobothria are medium flow rigid hairs found on the legs and which are especially sensitive to disturbances in air. Slit sensilla are grouped in rows of different lengths within 'lyriform organs' and are strain sensors. Compressing with the slightest mechanical pressure and able to detect a wide range of amplitudes, slit sensilla function both as proprioreceptors and as exteroreceptive detectors of vibratory signals (Schaber et al. 2012). The sensitivity of these mechanoreceptive organs is among the highest of any known biological sensor (Barth 2004); for example, with energy levels approaching those of thermal noise, deflections of the trichobothria cover a frequency range of c. 10–1000 Hz (Barth 2002, 2014).

Although only recently described as a communication channel, salticid use of vibrational or seismic signaling is relatively well understood. Males of many species, including *Habronattus* F. O. Pickard-Cambridge, 1901 (paradise spiders), *Cosmophasis* Simon, 1901, and *Maratus* Karsch, 1878 (peacock spiders), perform abdominal 'thumps' and palp or leg drumming on the ground during courtship displays (Elias et al. 2005, 2012; Girard et al. 2011; Zeng et al. 2019) and these can exhibit geographical variation. Mountaintop populations of *Habronattus pugillis* Griswold, 1987 have intraspecific regional differences in the complexity of seismic signaling, perhaps due to rapid signal diversification (Elias et al. 2006a,b), which aligns with the generally rapid diversification among salticid traits, especially among *Habronattus* (e.g., Hedin et al. 2020; Bougie et al. 2021).

In terms of function, seismic displays have been assumed to provide a further channel of communication to the female, perhaps indicating body condition or as a backup for visual signals (Zeng et al. 2019). In some instances, such as in *Habronattus dossenus* Griswold, 1987, the seismic component of the display is crucial for mating success (Elias et al. 2005), while in others the seismic component may be used to gain attention, and novelty might be favored (Elias et al. 2006b). In other cases, such as in *Cosmophasis umbratica* (Zeng et al. 2019) and *Maratus volans* O. P.-Cambridge, 1874 (Girard et al. 2011, 2018), the seismic signal appears to be relatively immaterial for mating success, but may complement visual signals, perhaps under low-light conditions, or trigger the female to turn toward the male to watch his display. This highlights how little we really understand of the roles of the different sensory signaling systems used by salticids.

Intrasexual communication.—Male-male and female-female agonistic displays are common, even among juveniles. Like intersexual displays, these are often complex and flexible (McGinley et al. 2015a) but are readily differentiated from intersexual displays. Evidence suggests that at least male displays, which tend to be more complex than those of females, are used to assess the resource-holding potential (RHP) of a rival, with size-matched pairings more likely to escalate interactions than mismatched pairings, especially among large spiders (McGinley et al. 2015b). This is achieved through a combination of self-assessment and mutual assessment, and is largely vision-dependent, although in species that use vibratory signaling, this is also used (Taylor et al. 2001; Elias et al. 2008; McGinley et al. 2015a; Tedore & Johnsen 2015; McGinley & Taylor 2016). In mismatched contests, findings suggest that maximum contest escalation is predicted by the size of the smaller spider (self-assessment), rather than the size difference between the spiders, but mutual assessment also plays a key role (Taylor et al. 2001; Elias et al. 2008; McGinley et al. 2015a). Furthermore, external sources of information—such as the odor of a potential mate escalates interactions in a nuanced manner. In 'traditional' species with female mate choice, the odor of different-sex spiders escalates fights only among males, but in 'non-traditional' species such as *Evarcha culicivora* Wesołowska & Jackson, 2003, that exhibit mutual mate choice, both sexes escalate interactions with the odor of a different-sex individual (Cross & Jackson 2009a).

Same-sex fights among females appear to be both less ritualized and more likely to end in death than those of males (Elias et al. 2010). It is believed that female agonistic interactions are driven not by the perceived strength of the rival or RHP, but instead by the perceived value of a resource (e.g., paucity of suitable reproductive areas), whereby the cost of not fighting is higher (e.g., inability to reproduce) than that of losing against stronger rivals (Elias et al. 2010). This hypothesis leaves unresolved why non-reproductive (e.g., subadult or juvenile) females also fight (e.g., McGinley et al. 2015a). In these cases, the resource may not be access to a nesting site, but to food. For example, in the spider-eating genus *Portia*—the genus in which odor cues have been most extensively investigated with respect to same-sex interactions—the odor of spider prey primes females of *P. fimbriata* (Doleschall, 1859) to escalate fights (Cross & Jackson 2011). The role of chemical cues in *Portia* interactions is complex. Chemical cues associated with draglines provide *P. labiata* (Thorell, 1887) females (but not *P. fimbriata* or *P. schultzi* Karsch, 1878) with information regarding the fighting ability of unseen rival females, with draglines of previously-winning individuals avoided compared with those of previously-losing individuals (Clark et al. 1999). Overall, studies to date suggest that self-assessment may be the dominant characteristic of female-female interactions. For example, in *Phidippus clarus* Keyserling, 1885 size differences among females do not predict contest outcome, as they can in males (Elias et al. 2008); instead, proximity to molt and nest residency have strong effects on outcome (Elias et al. 2010). However, it is possible that differential assessment of the costs and benefits associated with molting vulnerability and having a nest can account for these differences, rather than it being self-assessment *per se*.

Parental behaviour.—As mentioned, males typically (although not always) instigate courtship, and regardless of female mate choice, their mating success is much higher with virgin females. Once mated, the female spins a reproductive nest, which is more densely built than non-reproductive nests and includes several layers of silk, including around the eggs (Bartos 2002; Mooney & Haloin 2006; McGinley et al. 2015a). Species appear fairly consistent in that the female typically lays a single clutch of eggs about one month after copulation, and 2–4 weeks after that the spiderlings emerge from the eggs, remaining in the nest until they have molted at least once (Eberhard 1974; Jackson 1978), although in *Apricia bracteata* (L. Koch 1879) maternal care is considerably longer and more than one clutch is often found (Rienks 2000). Typically, if a female lays a second clutch of eggs, it is only after dispersal of the previous clutch.

The guarding female (Fig. 1A,C) rarely leaves the nest and requires higher predation threat to abandon her nest than non-guarding females, actively defending her offspring against predators such as ants, mantispids, or spiders (Eberhard 1974; Rienks 2000; Mooney & Haloin 2006; Nelson & Jackson 2008; Vieira & Romero 2008; McGinley et al. 2015a). Defense mechanisms against ants or mantispids include building flap-like doors at both ends of their nests (Rienks 2000; Nelson & Jackson 2009a). Salticids, too, readily eat the eggs of other spiders, and some ant-mimicking salticids such as *Myrmarachne melanotarsa* Wesołowska & Salm, 2002 even use their resemblance of ants to frighten salticid females out of their egg-containing nests in order to eat the eggs (Nelson & Jackson 2009b).

Although typically solitary, some species, such as *Myrmarachne assimilis* Banks, 1930, build nests connected to each other by silk, and this is especially common among reproductive females, a 'crèching' behavior most likely as defense against predation by ants (Nelson & Jackson 2008). Indeed, it seems likely that egg predation is a key driver selecting for rare instances of sub-social or social nesting behavior in salticids (Rienks 2000; Jackson et al. 2008; Nelson & Jackson 2008, 2009b; see Yip & Rayor 2014 for elaboration on spider sociality and spider parental behavior).

HABITAT SELECTION

Salticid habitat choice is driven both by availability of food (Romero & Vasconcellos-Neto 2005a; Meehan et al. 2009; Nelson et al. 2021) and provision of shelter from predators (Romero &

Vasconcellos-Neto 2005b). While most salticids live in open, brightly lit habitats, many live and hunt for their prey in dimmer microhabitats like the under surfaces of broad leaves in the forest, in leaf litter, shallow caves, under rocks, and even in the internodes of fallen bamboo (Blest 1985; Jackson & Hallas 1986; Zabka & Kovač 1996; Soley et al. 2016; Cerveira et al. 2019, 2021). Salticids are often very picky about the habitat type in which they are found; scree-spiders will be found only on scree slopes (pers. obs.), while others might choose sandy (Bartos 2002) or pebbly (Jackson et al. 1990) beaches (Fig. 1). Narrowly defined microhabitats often include specific plant taxa, or even species, such as New Zealand flaxes (Taylor & Jackson 1999) and bromeliads (Romero & Vasconcellos-Neto 2005a), and both olfactory and visual cues are used by spiders to locate host plants (de Omena & Romero 2010; Nelson et al. 2012b).

Salticid-plant associations commonly include instances in which the spider ingests nectar or pollen from the flower (Jackson et al. 2001; Chen et al. 2010; Painting et al. 2017b). Although no known spider can survive solely on a plant-based diet, phytophagous feeding by salticids is especially common, accounting for c. 60% of known phytophagous feeding in spiders (Nyffeler et al. 2016). Nectar provides spiders, especially juveniles, with important nutritional benefits that might be difficult to obtain through hunting which, although an innate behavior, improves with experience (Edwards & Jackson 1994; Nelson et al. 2005; Nelson & Jackson 2013). Further, by feeding on, or altering the behavior of, phytophagous insects that cause harm to the plant, nectivorous spiders may also provide the plant with indirect benefits (Ruhren & Handel 1999; Romero & Vasconcellos-Neto 2004; Romero et al. 2006). The surprisingly large proportion of spiders that feed on plant nectar (Jackson et al. 2001; Taylor & Pfannenstiel 2008; Chen et al. 2010: Nyffeler et al. 2016) suggests that further work is required to understand the role that spiders play in plant biology, and concomitantly how plants might affect spider biology. For example, juveniles and adults of the mosquito-eating salticid *Evarcha culicivora* are innately attracted to specific components of the floral scent of *Lantana camara*, the plant on which they are often found (Cross & Jackson 2009b; Nelson et al. 2012b), but juvenile attraction to the plant volatiles depends on hunger level. Hungry juveniles are more responsive than sated ones, but there is no effect of hunger on adult responses, suggesting that attraction to *L. camara* may have different functions for *E. culicivora* depending on its age (Nelson & Jackson 2013). Further complicating things, the plant compounds to which *E. culicivora* is attracted affect its predatory decision-making (Nelson et al. 2021).

In addition to *E. culicivora*, some other remarkably close associations are known. For example, *Bagheera kiplingi* Peckham & Peckham, 1896 feeds almost exclusively on Beltian bodies, the nutrient-enriched leaf tips of *Vachellia* (previously called *Acacia*) shrubs, making it an obligate resident of these plants (Meehan et al. 2009), while *Psecas chapoda* (Peckham & Peckham, 1894) (Fig. 1G) lives almost exclusively within *Bromelia balansae* (Romero & Vasconcellos-Neto 2005a,b; Vieira & Romero 2008).

DIET AND PREDATORY BEHAVIOUR

Spiders, including salticids, are important predators of other spiders, including conspecifics (Taylor et al. 2019). As they compete for the same prey, they are also intraguild predators (Nyffeler 1999; Saqib et al. 2021). Most salticids are ‘generalist’ predators that hunt a variety of prey – mainly insects – of similar size to themselves, but are also capable of hunting much larger prey, including documented instances of predation on lizards and frogs (Nyffeler et al. 2021). In contrast, several ‘specialist’ species, discussed below, have behavioral preferences and specialized hunting tactics for a narrow range of prey.

Predatory behavior in salticids is innate, but prey capture success improves with experience/age (Edwards & Jackson 1994). Being a generalist salticid does not mean that prey selection is indiscriminate, and both visual and odor cues are used. Despite the broad range of prey consumed, salticids make assessments of different prey types, including prey escape risk, and adopt prey-specific hunting tactics (known as alternative or conditional hunting tactics) corresponding to different prey (Edwards & Jackson 1994; Bartos 2007). Motility, wing presence, shape, size, cues from the head (e.g., eyes), and direction of locomotion are all used to make decisions about how to approach and attack prey, with attacks directed toward the head, and with situations in which prey are distracted (e.g., grooming) exploited by the approaching predator, similar to ‘smokescreen behavior’ described below (Edwards & Jackson 1994; Bartos 2007; Bednarski et al. 2012; Bartos & Minias 2016).

Prey aversion – for example to potentially toxic prey – is less well-studied, but generalist salticids do avoid certain potential prey. For example, they typically have an innate aversion to ants (Nelson & Jackson 2006a) and can learn avoidance to toxic prey (Skow & Jakob 2006; Taylor et al. 2016). Best studied among *Habronattus*, salticids can show innate and learned color biases to prey, often avoiding certain aposematic colors, such as red and yellow (Taylor et al. 2016; Powell et al. 2019). Aversions to color-based signals can sometimes be triggered, or primed, by prey defensive odors, as found in *Habronattus trimaculatus* Bryant, 1945 (Vickers & Taylor 2020). As found in *H. brunneus* (Peckham & Peckham, 1901), color-biases also exhibit geographical variation, possibly as a consequence of different prey composition available to different populations of a given species (Powell et al. 2019).

A number of salticid species have very specific innate preferences for distinct prey types. These are often ants (which usually evoke fleeing responses in most salticids) or other spiders, including specialization specifically on other salticids, as in *Portia fimbriata*. Indeed, these preferences can be extreme: as its preferred prey are blood-fed female mosquitoes in the genus *Anopheles* (Jackson et al. 2005), *Evarcha culicivora* is possibly the pickiest animal on Earth. How specialized predators identify their prey is discussed in general terms below under ‘Cognition’, but the following detailed examples provide insight into the sensory processing involved in prey-choice decision-making.

Evarcha culicivora can identify its preferred prey through vision or through olfaction (Jackson et al. 2005), and each of these modalities facilitates searching in the other sensory modality (priming) to locate the target more quickly. Details of the prey odor cues used for identification are unclear, but visually, *E. culicivora* bases its decisions on a combination of prey resting posture (which identifies the mosquito as *Anopheles*, as it has a specific resting posture), how engorged the abdomen is (as a cue to being blood-fed), and how setose the antennae are (females have barer antennae) (Nelson et al. 2005; Nelson & Jackson 2012a). Furthermore, by feeding on blood-fed female *Anopheles*, sexually-mature *E. culicivora* acquire an odor that renders them more attractive to the opposite sex (Cross et al. 2009; Cross & Jackson 2009c, 2010), suggesting that prey preference here may be driven, at least in part, by sexual selection.

Salticids that specialize in eating especially dangerous prey, like spiders and ants, often employ strategies that minimize risk to themselves during the hunt. For example, ant-eating spiders often approach their prey from behind, and, having pounced on the ant, hold down the head, thus avoiding contact with their strong mandibles (Jackson & Nelson 2012). Similarly, like *Portia* (reviewed in Jackson & Cross 2011), the spider-eating *Cyrba algerina* (Lucas, 1846) (Fig. 1F) exhibits complex predatory behavior, including trial-and-error derivation of web-based signals as a form of aggressive mimicry with which to lure a web-spider gently towards the awaiting hunter without eliciting a predatory response from the web-spider. *Cyrba algerina*, also like *Portia*, additionally makes use of 'smokescreens' (Cerveira et al. 2003), in which the spiders move toward their web-spider prey, but not toward insects caught in webs, during periods in which the resident's web is disturbed (e.g., by wind). To identify prey, *C. algerina* uses visual (Cerveira et al. 2019) and odor-based cues (Cerveira & Jackson 2011), but exhibits marked and nuanced geographical variation in responses. Cerveira & Jackson (2011, 2022) compared *C. algerina* populations in which the non-salticid prey spiders *Oecobius machadoi* Wunderlich, 1995 (Oecobiidae) and *Zelotes thorelli* Simon, 1914 (Gnaphosidae) are common, to another *C. algerina* population in which these prey spiders are absent. They found that *C. algerina* from sites devoid of *Oecobius* Lucas, 1846 or *Zelotes* Gistel, 1848 exhibited no preference for odor over a blank control (Cerveira & Jackson 2011, 2022). However, *C. algerina* from sites where *O. machadoi* Wunderlich, 1995 is present are attracted to the odor of sympatric *O. machadoi*, but not to allopatric *Oecobius amboseli* Shear & Benoit, 1974. Furthermore, prior experience mediates responsiveness toward locally abundant prey, as naïve lab-reared *C. algerina* are not attracted to the odors of *Oecobius* or *Zelotes* (Cerveira & Jackson 2022). This demonstration of local adaptation and geographic variation in kairomone use is not unique: a similar situation is known among Queensland *Portia fimbriata* responding to its salticid prey *Jacksonoides queenslandicus* Wanless, 1988 (Jackson et al. 2002). Given that spider-eating spiders respond to very specific odors of their preferred, yet potentially dangerous prey (Jackson et al. 2002; Cerveira & Jackson 2011), responsiveness to specific prey-derived chemosensory cues may be driven by the level of danger posed to the predator by its prey.

ANTIPREDATOR BEHAVIOUR

The response of salticids toward their own predators is possibly the least studied aspect of their behavior, and the work that has been done is all based on vision, although given their use of odor-based information in intraspecific and predatory interactions (above), it is quite possible that this is also used to detect predators. Salticids typically respond to threat from a static predator by initially freezing before retreating (Rößler et al. 2021), while a looming object (e.g., Spano et al. 2012) is more likely to evoke a quick fleeing response, and these responses appear to be innate (Nelson & Jackson 2006a; Rößler et al. 2021). As in hunting, it is apparent that salticids also rely heavily on specific cues, especially the presence of eyes, shape, and possibly size disparity, among others, when identifying predators (Rößler et al. 2021).

Other than fleeing visually located predators, the most obvious defensive strategies to escape predation are crypsis and mimicry (see framework proposed by Robledo-Ospina & Rao 2022). Most salticids (especially females, which are also typically more sedentary than males) tend to be cryptically-colored, and this is likely to avoid detection by visual predators, including other salticids and wasps (Taylor et al. 2019). Ant mimicry is found in hundreds of salticid species (Cushing 1997), especially among the exclusively ant-mimicking genus *Myrmarachne* MacLeay, 1839. This type of mimicry has been demonstrated numerous times as Batesian mimicry against ant-averse predators, including other salticids, mantises, and wasps (Edmunds 1993; Nelson & Jackson 2006a,b, 2008, 2009c; Durkee et al. 2011; Huang et al. 2011; Jackson & Nelson 2012; Nelson 2012; Uma et al. 2013; Nelson & Card 2016). Ant mimicry may be less effective against other predators, such as birds (being significantly larger and better able to survive ant attacks) (Gunnarsson 2007), ants (which rely more heavily on chemical cues than on vision; but see Uma et al. 2013), and other less-visual predators, such as assassin bugs (Jackson et al. 2010). The relatively common phenomenon of beetle and pseudoscorpion mimicry (see Maddison 2015) has, unfortunately, never been studied. While it might be assumed that this mimicry is for defense, pseudoscorpions and beetles are unusual candidates for Batesian mimicry.

In a related defense tactic, some salticid species use the presence of nearby ants as a deterrent to would-be predators, or as a "protector species." This requires the benefits to the ant-associating salticids, such as *Phintella piantensis* Barrion & Litsinger, 1995 and the communal species *Menemerus* spp. Simon, 1868, *Pseudicius* spp. Simon, 1885, *Myrmarachne melanotarsa*, of obtaining indirect protection from the ants to outweigh the costs of ant-predation on them or on their eggs (Jackson et al. 2008; Nelson & Jackson 2014). It is known that at least some of these species adopt specific strategies to reduce their risk of exposure to ants, both behaviorally, and in nest construction (Nelson & Jackson 2009a).

An evident barrier against predators is the nest. In areas of high ant density and consequently high risk of ant predation (e.g., Nelson et al. 2004; Jackson et al. 2008), nests are often unusually densely built, and instead of having openings at either end of the cocoon-like structure, may have flaps as 'doors' (Rienks 2000; Nelson & Jackson 2009a). As mentioned above, the unusual behavior of building nests together also protects eggs and young from ant predation, as found in *Myrmarachne assimilis* (Nelson & Jackson 2008), and this benefit may select for communal nest-building among salticids (Jackson et al. 2008). However, the role of nests in escaping predation, either as a physical barrier against predation or to escape detection, requires further understanding (e.g., Michalik et al. 2019). For example, some assassin bugs that prey on salticids appear to 'target' communal nest-building salticids and can easily pierce through the silk with their needle-like sucking mouthparts to impale and feed on the eggs or spider/s within (Jackson et al. 2010), suggesting that the nests themselves might be used by these bugs to locate potential prey.

COGNITION

Salticids are known for their cognitive behavior, defined as how information is acquired and mediates behavior through evaluative processes, such that decision-making is the cognitive process interfacing assessment and discernible behavior (Blumstein & Bouskila 1996).

Comparative studies suggest that salticid cognitive ability is graded (Tarsitano & Jackson 1992; Cross & Jackson 2016; Aguilar-Arguello et al. 2019, 2020, 2021), with the genus *Portia* considered the salticid equivalent of Einstein. As *Portia* behavior has been reviewed elsewhere (e.g., Jackson & Cross 2011; Aguilar-Arguello & Nelson 2021), I will only lightly touch on *Portia* and more generally discuss other lesser-known salticids with comparable cognitive attributes.

Studies on *Portia* and other spider-eating salticids, such as *Cyrba* Simon, 1876 and *Brettus* Thorell, 1895, have consistently found them capable of using trial-and-error reinforcement-based learning. This behavior is exhibited in a flexible manner to derive and maintain effective hunting strategies to safely lure web-spiders toward the hunting salticid, but the frequency of its use is species-dependent and also population-dependent within species, possibly due to variation in the types of prey available (Jackson 2002; Jackson & Cross 2011; Jackson & Nelson 2011). Whether this is mirrored in overall learning ability or brain area volume remains to be determined. However, recent advances in micro-CT scanning technology mean that now it is possible to image salticid brain regions (Steinhoff et al. 2017, 2020), finally making study of the centers of learning in salticids tractable. This is evidenced by a recent study (Steinhoff et al. 2018) on *Marpissa muscosa* (Clerck, 1757) showing that in contrast to spiders reared in solitary environments, early development in physically or socially-enriched environments leads to greater volume in the arcuate body region of the brain, an area which receives higher-order visual input and contains locomotory fibers (Menda et al. 2014), demonstrating developmental plasticity.

Habronattus dossenus Griswold, 1987, *H. pyrrithrix*, *Phidippus princeps* (Peckham & Peckham, 1883), *P. regius* CL Koch, 1846, *Hasarius adansoni*, and *M. muscosa*, among others, associate color, shape or seismic cues with a stimulus (Nakamura & Yamashita 2000; Jakob et al. 2007; VanderSal & Hebets 2007; Taylor et al. 2016; de Agrò et al. 2017), showing that salticids are capable of both associative learning and association reversal, as well as conditioning (Jakob et al. 2007; Liedtke & Schneider 2014). Nevertheless, it can be difficult to establish a protocol that works for salticid learning experiments (Jakob & Long 2016), and to date, memory retention studies have not been especially successful, with retention lasting up to two weeks with reinforcement (Taylor et al. 2016). Although numerical ability has been found in salticids (Nelson & Jackson 2012b), difficulties in training salticids may account for why this has so far only been described in juvenile *Portia africana* Simon, 1886, which lend themselves through their natural behavior to such studies. When hunting, juvenile *Portia africana* sometimes sit-and-wait in groups outside prey spider nests, and their decision about whether to settle by a nest is based, among other things, on the number of conspecifics already there (one spider is preferred to zero, two, and three). Establishing a protocol whereby numerical ability in a wider variety of salticids could be tested would be especially informative about whether this is a more generalized ability.

Evolution.—Numerous hypotheses have been proposed to explain the evolution of advanced cognition in animals, but they broadly fall into two categories: those pertaining to sociality (i.e., sociality facilitates advanced cognition) and those pertaining to ecological drivers, including that selection for advanced cognition is increased in animals living in more complex environments or facing challenges in obtaining food (e.g., patchy spatiotemporal distribution, or hunting risky prey). Although there are some social salticids (see 'Parental behavior'), little is known about them, so I will focus on ecological aspects of cognition (see Aguilar-Arguello & Nelson 2021).

Environmental complexity affects individual cognitive capacity through developmental plasticity: salticids reared in physically enriched cages have greater exploratory behavior (Carducci & Jakob 2000; Liedtke et al. 2015). Animals use one or more of several mechanisms to move about their environment, with these often involving the combined use of external and internal cues for navigation (Cheng 2006). For example, visual landmarks used for orientation can also be used to calibrate internal/idiothetic compass-like mechanisms (e.g., path integration: an internal representation of the position of the individual with respect to a fixed origin) (Cheng 2006).

Salticids often inhabit complex three-dimensional environments and can use landmarks to return to their nests (Hoefler & Jakob 2006), but their navigational prowess is best exemplified by the use of indirect routes, or detours. As cursorial predators, when moving through the environment salticids are unlikely to use permanent paths, so they must make decisions about routes leading toward a specific goal (e.g., prey, nest, mate). However, detouring is an elaborate cognitive process, as it implies assessing several alternatives and planning a route, which can consist of several subsections. Additionally, it involves an element of forward-planning (e.g., Tarsitano & Andrew 1999; Aguilar-Arguello et al. 2019, 2020). For example, having seen a mosquito (the primary objective) on a distant leaf of *Lantana camara*, *Evarcha culicivora* must choose which selection of branches (secondary and tertiary objectives) is required to approach it for attack. Because when it moves towards the secondary (or tertiary) objective, it commonly turns both its gaze and direction of movement away from the goal, *E. culicivora* must retain an internal representation of the relative position of the mosquito at all times as it moves from objective to objective to reach its goal (Tarsitano & Jackson 1992; Tarsitano & Andrew 1999). This suggests the use of both external (landmarks or goal/prey) and idiothetic (relative position) cues. Despite this complexity, several salticid species take detours (Tarsitano & Jackson 1992; Cross & Jackson 2016). Studies show that salticids can remember the position of the goal from detour initiation, can use detours that initially move the spider away from the goal, and can determine which routes do or do not lead to the goal. However, many questions remain, such as whether salticids account for distance or risk when making route evaluations (e.g., Aguilar-Arguello et al. 2019, 2020), whether species that evolved in more complex habitats perform better, whether variation in visual spatial acuity accounts for variation in behavior (e.g., Tarsitano & Jackson 1992), or whether animals that prey on especially dangerous items—which may require more careful and cognitive approaches to obtain the prey without harming themselves are better at detouring tasks.

As many salticid species have diets that involve hunting prey that can easily kill the would-be predator, it is possible that these species have evolved sophisticated processes for assessment and decision-making. This may include how to approach prey, but also detailed assessment of prey, or even predators. For example, males of the ant-mimicking genus *Myrmarachne* have enlarged chelicerae compared with females, and these make them appear like an ant carrying something (possibly another ant) in its mandibles. In prey-choice tests, Nelson & Jackson (2006b) found that specialist ant-eating salticids, which are also fooled by *Myrmarachne*, chose lures made of ants with something in their mouthparts over ants with their mandibles exposed, and chose male over female *Myrmarachne*, presumably because they were assessed as being safer prey. The idea that salticids that specifically target dangerous prey, like spider-eating *Portia* or ant-eating salticids, are 'smarter' does not fully explain salticid patterns. *Evarcha culicivora* makes assessments as least as complex (Nelson & Jackson 2012a; Dolev & Nelson 2014) as those required by ant and spider-eating salticids, but it eats harmless mosquitoes.

The alternative that prey specialization might favor cognition requires further evaluation, but as the processes underlying predator and prey evaluation among generalists and specialists appear to be similar (but see Dolev & Nelson 2016), this may also not fully explain the observed patterns. This highlights the question of how salticids recognize objects. While salticids use motion-based cues, and are attuned to local and global biological motion (Bednarski et al. 2012; Bartos & Minias 2016; Nelson & Card 2016; de Agrò et al. 2021), they are also capable of identifying static objects, often through local cues or features (in some cases even independent of their global configuration as long as relative angle positioning of the specific features remains intact), but also through more global whole-object or multi-trait spatial relationship strategies, which can include the relative angles of traits (Harland & Jackson 2002; Nelson & Jackson 2012a; Dolev & Nelson 2014, 2016; de Agrò et al. 2017). Nevertheless, accurate visual assessment takes time, and there is a trade-off between assessment speed and accuracy, suggesting cognitive limitations to rapid and accurate assessment (Aguilar-Arguello et al. 2019; Nelson et al. 2021). While much prey and predator identification appears to be innate (e.g., Dolev & Nelson 2014; Rößler et al. 2021), salticids can also form search-images of relevant objects (e.g., prey) with a single exposure (Jackson & Li 2004).

Salticids show considerable promise to explore ecological hypotheses pertaining to the evolution of cognition due to the myriad complexity differences among habitats that they live in, and due to the presence of both generalist and specialist predators that often tackle 'challenging' prey. Furthermore, aspects of social living and rearing environments can be investigated, making salticids uniquely poised for studies pertaining to the selection pressures that drive for cognitive ability. I suggest that there is something rather unique about vision, as this sense alone allows for accurate assessment *in real time* of objects at a distance, potentially enabling animals to assess, with less risk to themselves, other group members, foraging locations, or potentially dangerous prey. In turn, this real time assessment at a distance may facilitate both prey specialization and expansion of home ranges, leading to advanced spatial cognition.

PERSONALITY

All animals have intra-individual variation in their responses, but for many, there is consistency within individuals, and this average behavioral type can be considered its personality (Sih et al. 2004). Selection acts on all aspects of behavior, including variable expressions of behavior and personality types. There is a growing body of evidence that personality traits exist among salticids, and that these are affected both by genetic factors and the spider's experience during development, in that spiders reared in more socially or physically-enriched environments, irrespective of their parentage, are more exploratory (Leidtke et al. 2015). Furthermore, irrespective of genetic factors, early social (but not physical) enrichment improves associative learning ability and reduces aggression in adult *Marpissa muscosa* (Liedtke & Schneider 2017). How selection acts on these traits is not straightforward: in *Siler semiglaucus* (Simon, 1901), aggressive males are more often chosen by both docile and aggressive females and are more likely to win male-male contests (Kwek et al. 2021), leaving few opportunities for less aggressive male behavioral types. However, female choice was measured as gazing time, and, as mentioned above, this does not necessarily predict mating success.

Recent studies have sought to determine how behavioral types affect spider decision-making in complex functional situations. For example, having established aggressive/docile personality types and levels of intra-individual variation in individual spider-eating *Portia labiata* and its salticid prey (*Cosmophasis umbricata*), Chang et al. (2017a) demonstrated a behavioral interaction that predicts predation outcomes. Specifically, aggressive *Portia* are better at capturing unpredictable prey (with high levels of intra-individual variation) than predictable prey, compared with more docile *Portia*, which are more effective at capturing predictable prey. These interaction-based results between predator and prey behavioral types nicely illustrate the complexity of considering selection on personality types in the absence of different functional contexts. This difficulty is further illustrated by other studies in which aggressive *Portia labiata* make quicker decisions about attacking web-building prey than docile *Portia*, but both behavioral types 'correctly' opt for their preferred, i.e, larger, prey type (Chang et al. 2017b). This suggests that decision-making accuracy is not affected by decision speed, but this is contradicted by a follow-up study in which, when faced with more difficult tasks involving losing sight of the potential prey spider, aggressive *Portia* tend to make mistakes, in contrast to more docile *Portia* (Chang et al. 2018).

Being able to be lab-reared in groups or in isolation, and with known parental lineage, makes salticids an exceptional group in which to investigate the interaction of personality types, genetic factors ('nature'), rearing experience ('nurture'), intra-individual variation, and how these play out in different functional contexts. Coupled with the recent ability to image brain areas in salticids (Steinhoff et al. 2017, 2020), this dramatically expanding area is likely to provide important insights into these complex issues.

CONCLUSIONS

Characterized by great diversity, salticids are the most successful evolutionary lineage of spiders, and as such play a key ecological role as important arthropod predators. Nevertheless, studies of their predatory behavior have largely been confined to a few groups (most notably *Portia* spp. and *Evarcha culicivora*), particularly among the specialized predators. However, their ecological role is driven by the vast majority of generalist predator species that have been significantly less studied. As roaming hunters, understanding their trophic role is of general interest, as it may provide an indirect mechanism to quantify global insect decline due to cascading effects on their prey: in collecting trips in the southern hemisphere in the past two decades, I have experienced dramatic declines in salticid abundance (including in species previously easily found which are now not found at all in many areas in which the habitat superficially appears to be the same), suggesting that food abundance may be affecting salticid numbers.

Much of the work on salticids has been on colorful species, but most salticids are cryptic (often matching the background of the habitat in which they live, Fig. 1) and it is important that the function of coloration in non-colorful species and/or sexes be investigated. Assumptions, for example, that females are choosy and that color-based signals indicate male condition, are largely derived from the avian literature and have rarely been experimentally corroborated. As diverse as each of these groups is, salticids and birds have dramatically different visual systems and life-histories, and care should be taken when extrapolating from one group to another. In saying this, salticids also provide an incredibly tractable and diverse system in which to explore the generality of some of the hypotheses proposed in taxa such as birds and fish. These opportunities include investigating the role that color plays in sexual selection and speciation, or the role of signals in species identification, to name but a few.

Salticid sensory systems are remarkable, especially given the relatively small number of neurons that necessarily underpin them. Researchers have established a large and fascinating literature on their visual system but have somewhat passed over other sensory systems. This is especially true of chemoreception. We have yet to properly understand the preponderance and function of airborne and tactile chemoreception; we also know little about the location or physiological mechanism of the chemoreceptors responsible. Additionally, we know about mechanoreception in terms of the use of seismic signaling, but, unlike other spider groups, we know very little of its use to inform the spider about its environment, or about the receptors involved. Further sensory modalities/channels may remain undiscovered: it was only recently that airborne 'hearing' was shown (accidently) to elicit neural responses (Shamble et al. 2016).

Technological advances have only recently allowed us to scan salticid brain regions, and to investigate aspects of salticid communication not visible to the human eye, including UV and seismic signaling. These advances make it clear that the secret life of salticids is just beginning to be revealed. A key area that will grow with our understanding of their sensory life will be the richness of their cognitive life. Understanding salticid cognition, sensory systems, physiology and behavior is not simply of interest to biologists, but also provides important new perspectives into advances in bio-engineering.

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