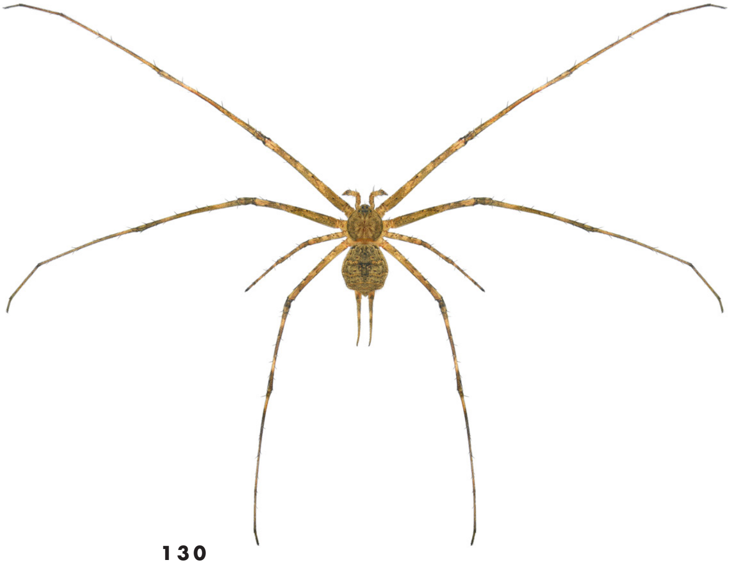


CONTENTS

↑ A spider on a leaf has to contend with differentiating vibrations across the surface of the leaf, and discriminating between leaf movement due to wind or a potential predator, such as a bird.

↗ Spiders can be very cryptically colored on bark, with a flat body, making some trunk-dwelling, ambush-hunting spiders near impossible to detect. The spider, however, will notice any movement of air, or possibly prey odor, as it sits still and waits.

Chemoreception

The ability to detect information from chemicals is known as chemoreception and is often performed via two channels: Olfaction discerns airborne chemicals, while chemotactile information, or taste, requires physical contact between the sensing organ and the chemical in question.

Chemoreception is thought to be the most ancient of the sensory abilities in animals, yet, paradoxically, it is one of the least understood. This is especially true for spiders, where behavioral evidence for the use of olfaction and chemotactile information abounds, but where an understanding of the mechanisms used to detect chemical information, especially airborne chemicals, are sorely lacking. In fact, we are still unsure about where many of the chemical sensory receptors, or chemoreceptors, actually are.

Spiders use chemical information in one of two ways. The first is straightforward signaling for communication, where the recipient of the signal adaptively changes their behavior upon detecting the signal of a member of the same species, and this was the intended outcome from the sender's point of view. Chemical signals like this are known as pheromones and often include sex-based information informing the recipient of the sex and age of the emitting spider.

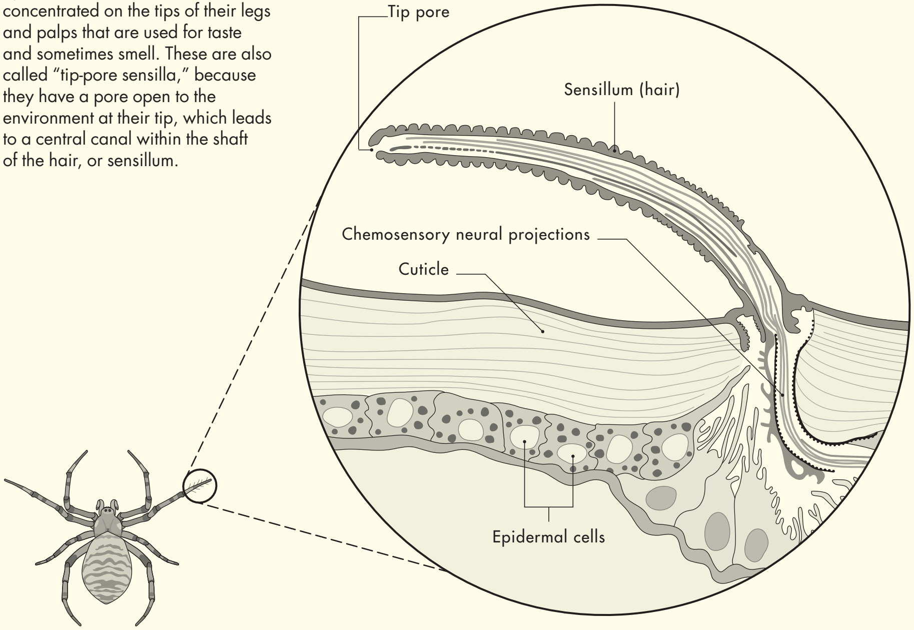
However, spiders can also adaptively change their behavior upon detecting a chemical that was not intended to do so by the emitter, which is often not a member of their own species. This can be thought of as eavesdropping on chemical information. These are called cues and include, for example, the ability to detect the chemical cues that might give away the presence of nearby potential prey. From the prey's point of view, this is not a signal; it was evidently not intended to elicit searching behavior in the receiver, but being able to detect this is highly advantageous from the point of view of the receiver, which may end up nicely engorged with food.

↑ *Scytodes* spitting spiders (see page 128) are nearly blind but seem to have an uncanny ability to detect the presence of prey or danger through smell and "taste" (contact chemoreception). On detecting potential prey—typically other spiders—they expel silk to snare the potentially deadly prey from a distance.

← Wandering spiders (Ctenidae) typically have more mechanoreceptive hairs than web spiders, suggesting that detecting airflow and ground-based vibrations are particularly important to them, but they also have chemoreceptive hairs, allowing them to perceive chemical compounds of interest.

Chemoreceptors in sensilla

Spiders have curved, blunt hairs concentrated on the tips of their legs and palps that are used for taste and sometimes smell. These are also called "tip-pore sensilla," because they have a pore open to the environment at their tip, which leads to a central canal within the shaft of the hair, or sensillum.



SIGNALS IN SCENT

All spiders seem to respond to chemotactile pheromones, but the use of olfaction seems to be more limited. Chemotactile signals are often deposited on silk, which is almost universally used by spiders. Web-builders use silk for construction of the web (among other uses), while burrowing spiders often line their burrows with silk and may leave silken trip lines extending out of the burrow, alerting the spider inside of any potentially edible thing that might walk over the silk near their burrow. Finally, spiders that do not build webs, but instead wander around the environment (wandering spiders) typically deposit walking draglines as safety anchors as they walk. Silk is therefore a good indicator of the presence of a spider, and if signals are deposited on that silk, another spider might be able to glean important information about its owner.

Behavioral evidence suggests that spiders can obtain a level of information from chemotactile signals and cues that are difficult for humans to comprehend. For example, spiders can determine the size and hunger level of another spider. It might seem odd to be able to figure out if a nearby spider is hungry, but in spiders, which are intraguild predators of each other, it pays to know the level of threat posed by a nearby potential predator, even if that same individual may also be a potential mate. More mundane chemotactile information, such as whether a spider is a member of their own species, and the sex, virgin-mated status, and maturity level (an indicator of whether it is sexually mature or about to become sexually mature) of the spider seems to be commonplace among spiders of many types. For males in search of females, this is important information: They prefer virgin females, in part because this increases their chances of paternity and in part because they might not survive the interaction for another try. However, females, especially sedentary females such as web-builders, also face the problem that they may remain undetected and therefore unmated, and they increase their effort to lure a mate by increasing pheromone production as time runs out for them.

← Funnel web spiders build a dense silk-lined burrow, here in heather, which can be over 8 in (20 cm) deep. They will hide at the bottom until they detect the presence of something worth emerging for.

→ If you reach out to a spider, and it doesn't run away immediately, it will likely also reach out toward you with a hairy foot—all the better to "smell" you with.

DEFENSIVE CLUES

Spiders also use chemotactile cues from other species of spiders to determine threats, in addition to cues from members of their own species to determine the presence and size or condition of rivals. Yet, despite all of this behavioral evidence, details of the compounds that are used for signaling, and how and where these are detected, remain largely elusive.

Nevertheless, progress is being made. The chemical compounds of some spider pheromones, often comprised of acids and lipids, have been identified, and from the evidence available, they seem to be more diverse than those of insects. Although we still don't know where exactly the chemosensory structures that mediate olfaction are, there are thousands of chemotactile sensilla on the palps and tips of the legs. This might explain why spiders often daintily touch items with their appendages before walking on them. Try having a spider walk on your hand: It will reach out a leg and touch you before most likely turning away, which suggests that you don't taste too good! These same organs may also detect smell, which explains why many spiders will stop their activity and wave their first or second pair of legs around, possibly smelling something of interest in the environment, as a snake or a lizard does when it flicks its tongue out. Perhaps the spider approaching your hand raised its legs toward you but didn't even touch you—in which case you probably didn't smell too good either.

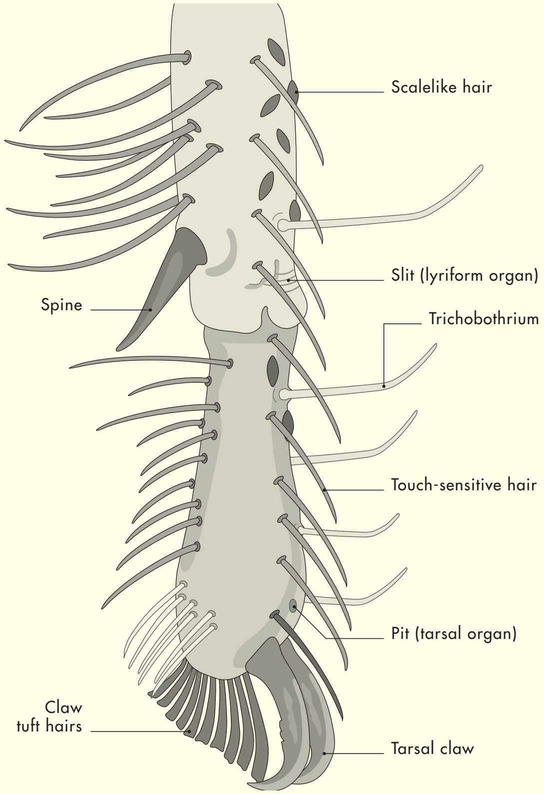
Mechanoreception

One of the first words that pops into people's minds when describing spiders is "hairy." They are indeed hairy, and many of these hairs are used to interpret the world around them in dizzying detail, simply by the fact that they can bend—or if they are stiff hairs, be deflected in their entirety.

In spiders, stimuli that can cause a mechanical change, such as deflection, bending, or pressure, are detected by a range of organs, including tactile hairs, slit sense organs, and articulated stiff hairs known as trichobothria. Mechanoreception, largely mediated by hairs, is the sense most widely used by spiders, and the range of sensory organs employed gives an indication of the importance of mechanoreception to survival.

Hairy feet

Spiders have sensory feet that are capable of detecting the slightest touch, puff of air, or even smell, depending on the type of hair responding to the stimulus.



GOOD VIBRATIONS

Let's start with web-builders. Sitting either at the hub of the web or in a retreat attached to the web, these spiders rely not on vision but on vibrations to detect their surroundings. The thin strands of silk making up the web vibrate with the wind and shake if the web is struck. The shaking of the interconnected strands of silk, coupled with the geometry of these intersections, informs the spider about where the web has been intercepted. The amplitude, or strength, and frequency of the vibrations tell the spider about the size and strength of the struggling prey. As the prey tires from its struggles, this, too, will be transmitted through the silk as a change in amplitude and frequency in the vibrations, thus telling the spider about when it is safe to approach. Similar information can be obtained by burrowing spiders, such as some trapdoor spiders (which have an openable lid covering the burrow entrance), which extend radiating strands of silk from within their burrows (where they reside safely out of view from predators) to the outside. Here, any insect walking by the undetected burrow will trigger vibrations in the given silken trip line it has walked over, thus telling the spider within not only that something is out there, but because of the individual strand of silk along which most of the vibrations are humming, also its location. Once again, the strength of those vibrations may tell the spider, much like the web-builder, how large and potentially dangerous the animal outside is. All of this information is detected by slit sensilla and mechanosensory hairs that bend and deflect with the vibrations passing along the silk.

↑ Silken strands of vibration sensors extend like Medusa's hair from a trapdoor spider's burrow.

← Up close, we can see that a spider's leg has one or more tarsal claws, with which they can grasp onto silk strands, and is exceedingly hairy. Many of these hairs provide the spider with sensory information.

Movement that causes hairs to respond to vibrations along silk is also present in other media, such as air. Hearing requires hairs sensitive enough to bend or deflect with the movement of air particles that are compressed by sound, creating waves of compressed and decompressed molecules of air. For a given tone, there will be a characteristic wavelength between the peaks of each cycle of compression and decompression of particles. Hairs of different length or stiffness respond (for instance, deflect) best to specific wavelength frequencies, as in our inner ear: This is the basis of our tonal hearing—a high-frequency shriek is discernible from a low-frequency rumble. Recent work suggests that without ears, but instead using mechanosensory hairs, spiders also detect airborne sound, either directly, as in jumping spiders and ogre-faced spiders that can discern prey and predators 6 ½–10 ft (2–3 m) away through specific sound frequencies (tones) associated with their flight behavior, or in the case of web-builders, once again though the silk. In this case, the silk is so sensitive that the web itself pulses with sound at a distance and is thus detectable to the spiders, essentially transforming the web from a direct vibration sensor responsive to items contained within it, to a large antenna capable of detecting and localizing sound produced by a potential predator or prey from at least 33 ft (10 m) away.

GROUNDING ENERGIES

Yet another medium capable of transmitting vibrations is the ground. Anyone who has felt an earthquake will be well aware of this. Earthquakes contain a phenomenal amount of energy, while the pitter-patter of another spider or beetle walking about is another matter altogether, and these require very sensitive organs to be detected. Yet, organs sensitive enough to detect these tiny movements can also trigger appropriate responses in their owner. It is not as though smaller organisms somehow have better sensibility due to being small: This is constrained by biological needs, chemistry, and physics, and does not scale according to size. In fact, our understanding of some physics is challenged by spider sensory systems. Known as seismic vibrations, these substrate-borne movements can lead wandering spiders to potential mates, prey, or even rivals. Specific "drumbeats" can also be used as signals:

for example, by courting wolf spider males trying to impress females with the virility of their beat.

There are slightly different forces involved in vibrations transmitted through the air or the substrate, and consequently spiders use different sensory organs to detect them. Slit sense organs are found in some configuration (sometimes in groups, sometimes singly) throughout the body. These are tiny slits in the exoskeleton that respond to mechanical stimulation, due to the slight deformation of the cuticle that occurs when there is a seismic vibration or when there is strain in the exoskeleton during movement. Groups of these (known as lyriform organs) are often found on the leg joints, suggesting that they have an important proprioceptive role.

FLEXIBLE HAIRS

Bendable tactile hairs, of which spiders have tens of thousands, are hollow and respond to both very small and very large forces without breaking. These hairs respond to direct pressure, and so are crucial to proprioception, but also to direct vibrations, such as those passed along a strand of silk. In contrast, the narrow, stiff trichobothria are very sensitive to airflow, like that caused by a flying predator such as a wasp, or a potential prey such as a fly. Much like the arrangement of the hairs in our inner ear that give us our ability to distinguish between tones, the spider's tactile hairs often occur in rows, with each hair in a given clump being of a particular length. Because of the properties of fluid mechanics, beyond the scope of this book, long trichobothria respond well to airflow of low frequency, while short trichobothria respond best to high frequency, with mid-length hairs acting accordingly. Consequently, by having hairs of varying length, the spider can clearly discern a wide range of frequencies, some of which will indicate danger and others nearby prey. Using high-powered microscopy, we can see that in some species, such as *Cupiennius salei* (see page 56), these hairs have tiny filaments poking out of them. These dramatically extend the range of frequencies and sensitivity of the trichobothria, arguably making them the most sensitive organ so far discovered.

↑ A net-casting or ogre-faced spider can detect sound from prey flying nearby and rapidly deploy its expandable leg-held web to snare the prey.

↖ The spider will interpret the movements caused by this fly struggling on the web through the different types and energy characteristics of the vibrations down each stand of silk. This helps the spiders to determine the fly's location, its size, and how tired it is.

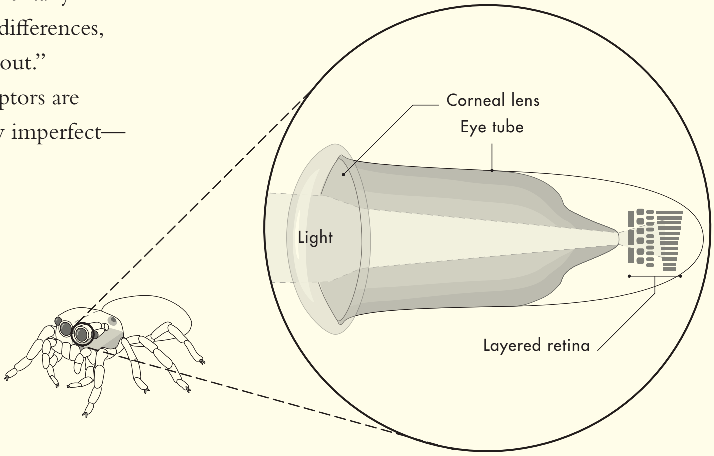
Vision

Unlike the compound eyes of insects, which look like a mirror ball of individual lenses, spider eyes have a single lens, like our own, and are known as simple or camera eyes. The camera eye lens faces the environment. Light entering the lens gets channeled onto the retina, which contains the cells that respond to light, the photoreceptors.

Photoreceptors are neural cells, and contain light-sensitive rhabdomeres that absorb light from the environment and provide the brain with visual information on shape, contrast, color, and motion. Unlike our eyes, which can swivel independently of our head to "face" the object of interest, spider lenses are part of the exoskeleton and are unable to move.

Spider eyes come in two flavors: principal and secondary. The principal eyes are formally called the anterior median eyes because they are often in the front and middle of the face. When spider lineages lose a pair of eyes, the principal eyes are usually the ones that are lost. The remaining three pairs, also named because of their relative position around the head (anterior lateral, posterior lateral, and posterior median eyes), are the secondary eyes. A number of things differentiate the principal and secondary eyes, and this starts right at the beginning: They arise from developmentally distinct tissue, leading to large structural differences, such as the secondary eyes being "inside out."

In the secondary eyes, the photoreceptors are positioned with the dense—and optically imperfect—cell bodies "facing" the light, while the long light-collecting portion of the cell (containing the rhabdomeres) is deeper inside the head, farther from the light entering the eye. This counterintuitive arrangement is not uncommon: It is the same situation with our own eyes. The principal eyes of spiders are the right way around, and because there is less scatter of photons of light due to intervening cell bodies (as in the secondary eyes), for optical reasons this is generally a better arrangement. Furthermore, the photoreceptors in the principal eyes are typically small and much more densely packed than in secondary eyes, allowing the principal eyes to see well, with excellent resolution or spatial acuity. In most cases, the principal eyes also mediate color vision.



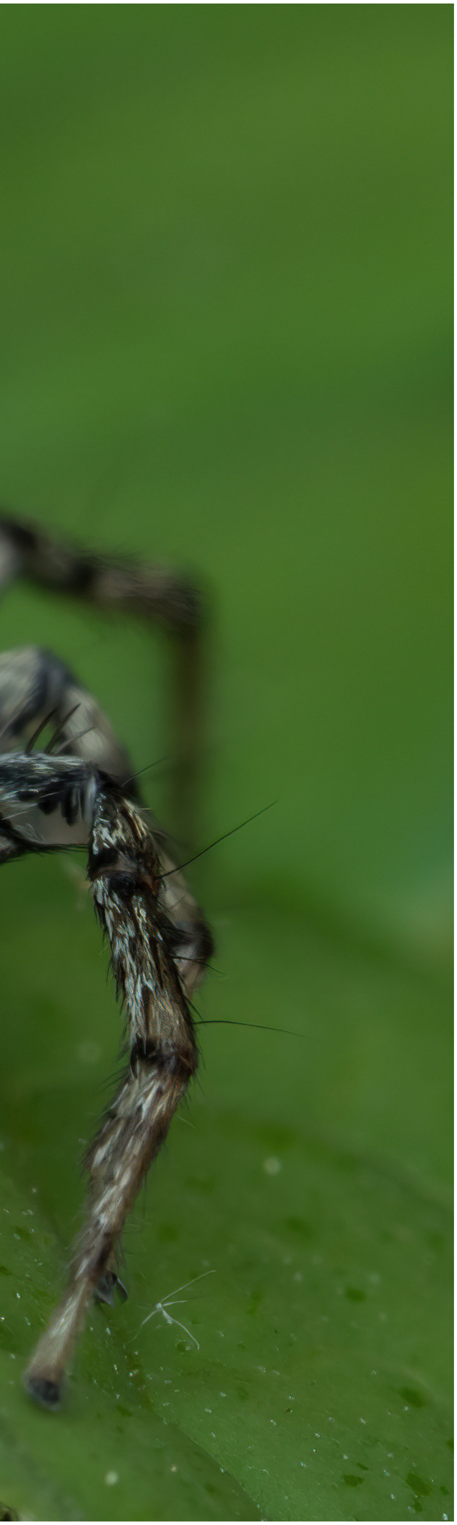
Principal eye

Morphology of the principal eyes of jumping spiders, depicting a long eye tube that acts as a telescope, at the end of which sits a retina with layers of photoreceptors.

↑ Most spiders have four pairs of "camera-type" eyes, and their arrangement or positioning on the head is a key indicator of the spider's taxonomic grouping, while the size and number of the eyes gives away the importance of vision to each spider group.

ULTRAVIOLET SIGHT

Many spiders can see in color, but it is a different color spectrum to our own. Color vision is possible because different photoreceptor types are sensitive, or respond, to different wavelengths of light, which correspond to different colors. Central nervous system processing of the information provided by these different photoreceptor types compares these responses, much like mixing primary paint colors to produce a perceived output color spectrum. In a hypothetical example, if you get equal responses of photoreceptors sensitive to yellow as to blue, you would perceive the color as green. Our vision is typically trichromatic, in that we have three classes of photoreceptors sensitive to three wavelengths of light, corresponding roughly to blue, green, and red. Most mammals are dichromats and can only compare the outputs of two classes of photoreceptors, severely restricting the color palette that they are able to see. Spiders that see in color exhibit the variation we come to expect: They can be dichromatic, trichromatic, and even tetrachromatic. However, one of the colors they are all able to see is ultraviolet (UV), which humans cannot.



REFLECTIONS ON TAPETA

With some exceptions, the secondary eyes do not support color vision, but can be especially good for detecting motion, contrast, and objects in low light. The secondary eyes of many families have a tapetum, a thin layer lying behind the retina that reflects light like a mirror back into the eye for the rhabdomeres to have a second chance at trying to extract photons from the available light. This is an excellent way of spotting nocturnal spiders: If you go out at night with a flashlight, and tiny globes at ground level reflect back at you, they are most likely wolf spiders and the light shining back is reflecting off their tapeta. Other families, such as net-casting or ogre-faced spiders and jumping spiders, do not have tapeta, possibly because the reflection of the light back into the eyes causes some optical problems when the aim is to provide the best possible spatial resolution.

RETINAL DIFFERENCES

Another major difference between the principal and secondary eyes is that the retinae of the secondary eyes is fixed—they can't move—but in many families the retinae (not the lenses) of the principal eyes are movable. This affords those spiders the ability to turn their gaze on something without giving away their presence by having to move their cephalothorax or body. These retinal displacements are best developed among jumping spiders, where a series of muscles enable horizontal, vertical, and torsional movements of the retinae, which are used to track and carefully assess objects of interest within the field of view afforded by the movements of the retinae. Retinal movement of the principal eyes is especially important to spiders that rely heavily on vision, because it is these eyes that are typically responsible for high resolution and color vision.

What this shows is that the two types of eyes work together, each performing their own specific and dedicated functions. In general, the secondary eyes provide the spider with motion-based information across a wide peripheral view, which tells the spider that there may be a mate, food, or danger nearby. This information is than used to guide the spider to orient its body, or if possible, its principal eye gaze (via retinal movements) toward the source, allowing these eyes to investigate the object in glorious detail.

← The large forward-facing eyes of jumping spiders indicate that they are visual predators. Compare this, for example, to grazing animals: Their eyes are positioned to the sides so that they can better see around them and escape their carnivorous predators, which in turn have forward-facing eyes to stalk and track prey.

LATRODECTUS HESPERUS

Western black widow spider

Web womanizer

SCIENTIFIC NAME	*Latrodectus hesperus*
FAMILY	Theridiidae
BODY LENGTH	Females ½–⅗ in (12–16 mm), males ¼ in (6 mm)
NOTABLE ANATOMY	Red hourglass shape on shiny black body in females
MEMORABLE FEATURE	Potentially venomous bite to humans

Much feared by humans due to their neurotoxic venom, "widow" spiders in the genus *Latrodectus* use chemical information, or pheromones, to glean crucial insight into potential mates. Like most spiders, the tiny *Latrodectus hesperus* males seek out their nine-times-larger female counterparts for reproduction. The male can discern between species based on odor; and based on contact with the silk-borne female pheromones present on a female's web, they can distinguish between females of different ages, hunger level, geographical subpopulation, and virgin/mated status.

WEB OF INFORMATION

Female widow spiders are more likely to produce eggs fertilized by the first male with which she mates, creating strong selection for males to seek out and court virgin females. This is especially true because, although less frequently than their "widow" name implies, females sometimes attack and kill males before, during, or after copulation. If they survive the interaction, after mating, male *Latrodectus* sometimes destroy the female's web. This unusual behavior may impede—at least for a time—the female's ability to attract further males by limiting sex pheromone emission. This may also suit females, as mated females can manipulate the amino acid-derived sex pheromones on the silk to control mating attempts by males. Mated female silk contains a different chemical profile from unmated female silk and elicits no courtship from males, thus communicating their lack of receptivity to males once their sperm stores are full, and saving the male the risk of potentially being eaten.

REDUCE DANGER AND MAXIMIZE PATERNITY

A female's recent feeding history is woven into her web, both in the web's silken architecture and in the chemical profile of the silk, and males pay attention. Mating with a well-fed female in good body condition is beneficial because she produces more eggs than a hungry female, so this information is useful for a courting male. Furthermore, as males may become their mate's next meal even before copulation, it can pay to know how hungry the female is: A well-fed female is less likely to attack a potential mate and engage in sexual cannibalism. Sure enough, males are more likely to court on the webs of well-fed females than starved females; after all, males that are eaten prior to mating don't pass on their genes and are consequently selected against.

→ Every country in which a species of *Latrodectus* resides seems to have a common name for the local species, presumably because it is venomous to humans. These names usually describe the spider's color or pattern for easy identification—for example, brown widow, black widow, white widow, redback.

CUPIENNIUS SALEI

Tiger bromeliad spider

Wind-catcher

SCIENTIFIC NAME	*Cupiennius salei*
FAMILY	Trechaleidae
BODY LENGTH	Females 1 ⅓ in (35 mm), males 1 in (25 mm)
NOTABLE ANATOMY	Large wandering spider with very long legs (reaching 4 in/10 cm)
MEMORABLE FEATURE	Jumping from leaves to catch flying prey at night

A sit-and-wait nocturnal hunter, the tiger bromeliad spider uses hairs to discern the slightest movement of wind that gives away an insect on the wing. Then, solely on the basis of the detected air disturbance caused by the unsuspecting flying prey, with pinpoint precision *Cupiennius salei* leaps up and snatches its meal on the fly in utter darkness.

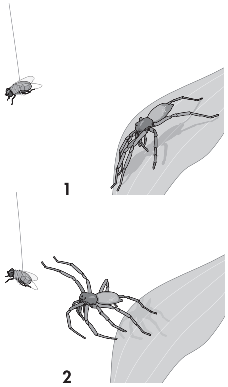
A HAIRY BODY

Hiding during the day, *C. salei* typically lives on broad, unbranched leaves, such as bromeliads or banana plants. The leaves make for a springy platform from which to leap into the air to catch flying prey. Both substrate-borne vibrations and disturbances in the surrounding air are detected by inordinately sensitive mechanoreceptory hairs, which trigger the correct behavioral response to the detected situation, such as confronting a rival or escaping a predator.

Cupiennius have about 1,000 stiff hairs on their legs that are used to detect airflow. Called trichobothria, these hairs are arranged in groups of differing lengths. Each hair's length determines its best response to a different pressure load, deflecting in turn with stronger forces, or responding with mechanical sensitivity to miniscule levels. These hairs are thought to be the most acute sensory system known—it has been calculated that they respond to one hundredth of the energy contained in a single photon of green light! By having trichobothria of different lengths sensitive to and deflecting at different flows or air pressure, these spiders can calculate the distance, direction, and speed of an insect flying nearby, and use this information to calculate where and when to jump into the night air to catch their prey.

A MECHANOSENSORY MINEFIELD

In addition to the trichobothria, *C. salei* uses hundreds of thousands of tactile hairs, stimulated by direct contact, for mechanoreception. Tactile hairs are not designed to deflect. Instead, they bend, making them both strong and sensitive to the tiniest flection. As if this mechanosensory world were not enough, about 3,500 "slit sensilla," or slits in the exoskeleton located at the joints, form sensory organs informing the spider of external vibrations of the leaf, such as the approach of a potential prey or predator, but also the pressure the spider itself is exerting on its cuticle.



Mid-air ambush

Frames of a video showing how *Cupiennius salei* reacts to the airflow produced by a tethered fly, from undetected at a distance of over 12 in (30 cm), to initiating a jump and leaping to catch the prey in mid-air once the insect is closer.

→ The tiger bromeliad spider's sensory systems have been described as "masterpieces of engineering" resulting from 400 million years of evolution.

HABRONATTUS DOSSENUS

Paradise spiders

Serenading sweetheart

SCIENTIFIC NAME	*Habronattus dossenus*
FAMILY	Salticidae
BODY LENGTH	⅕–⅓ in (5–8 mm)
NOTABLE ANATOMY	Striking coloration of face and legs of males
MEMORABLE FEATURE	"Singing" courtship behavior of males

Iridescent greens and oranges ornamenting male *Habronattus dossenus* are put to great effect during courtship displays. One would be forgiven for thinking that the dynamic color vision-based components of courtship would be sufficient for males to convey their prowess to the rather drab females. However, sensory channels, such as pheromones and near-field sound, are likely extra modes of communication, and the use of seismic signaling comprises another staggeringly complex sensory modality.

SEISMIC SIGNALING

Living on exposed ground, the diverse jumping spider genus *Habronattus* is known for its colorful visual courtship displays and the complexity of its seismic "songs." Although we cannot detect it, mechanoreception through substrate-borne vibrations is a key sensory channel for communicating sex and species, and potentially more detailed information such as body condition. In *H. dossenus,* the seismic component of the male display is crucial for his mating success. Studying seismic songs and their relation to the concurrent visual displays of courting males requires coupling information gleaned from high-speed video and laser vibrometry. A laser is beamed at the surface on which the male is displaying, and the reflected (doppler-shifted) "echo" of the displacement of the surface caused by the signals is measured. Based on these studies, we now have a mechanism to understand *Habronattus* signaling patterns—one based on musical annotation.

ANNOTATING VIBRATIONS

Songs can consist of dozens of distinct vibrational signals, or elements, which can be repeated, even as new elements are added to the song as it progresses. A novel way to understand these songs is to annotate the vibratory oscillations as a musical score, allowing for distinct repeated motifs, each consisting of a variable number of elements to be discerned within each movement. An unresolved question is why this complexity in male signaling is necessary, since visual signals alone can provide species identification and other important information. Furthermore, there are major physiological limitations on information processing and memory experienced by females simultaneously assessing so much complexity in multiple sensory modalities. We have immense brains compared with the poppy-seed-sized brains of jumping spiders, and we have a name for this occurence: sensory overload. Theory suggests that signals that are reliable and simple should be favored, yet many female *Habronattus* seem to favor complexity, which may in turn be leading to further speciation.

→ Male paradise spiders often add a visual component to their displays to females by showing off their colorful knees, or a section of their third pair of legs (here in orange), during courtship dances.

PORTIA FIMBRIATA

Fringed jumping spider

Jack of all trades

SCIENTIFIC NAME	*Portia fimbriata*
FAMILY	Salticidae
BODY LENGTH	⅓–⅖ in (7–10 mm)
NOTABLE ANATOMY	Very large forward-facing eyes and tufty appearance of legs
MEMORABLE FEATURE	Hunting other jumping spiders

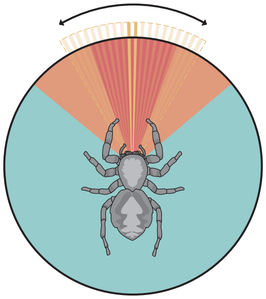
***Portia fimbriata* is fairly large by jumping spider standards. It uses extraordinary visual prowess to locate and hunt its dangerous, yet preferred prey: other jumping spider species. Having visually identified its prey, *Portia* stalks its target using a slow, robotic, "dead leaf drifting" pattern of approach, known as cryptic stalking. This may hinder the target spider's ability to detect *Portia* and either escape or attack.**

MODULAR VISION

With supreme miniature telescopes for eyes, *Portia* also has superior visual skills to other jumping spiders, giving it a slight advantage over its prey. Jumping spiders have one large forward-facing pair of principal eyes and three smaller pairs of secondary eyes that surround the head. Combined, the eyes can see almost 360 degrees around the spider. This wide field of view enables the secondary eyes to detect and track a source of motion, such as a predator or prey, with great precision. They can also see detail and so play a role in quickly categorizing moving objects and initiating responses, such as escape or prey capture. A target detected by the secondary eyes evokes a rapid turning response to bring the object of interest into the field of view of the principal eyes, which then process further detail.

A VISUAL MASTERCLASS

Jumping spider principal eyes have a unique anatomy. They consist of a lens, a long eye tube (see page 50), and a boomerang-shaped retina with a diverging pit located deep inside the head at the end of the eye tube. This increases the focal length of the system and forms a Galilean telescope, which magnifies the image but restricts the visual field to about 5 degrees. To compensate, the spiders can move the eye tube side to side and up and down by 30 degrees, allowing them to perform detailed visual scanning of objects over a much larger field of view and to discern intricate detail. Capable of discriminating individual items placed 1/250 in (0.1 mm) apart at a distance of 4 in (20 cm), *P. fimbriata* has visual spatial acuity unrivaled by any other studied animal of remotely similar size.



Fields of view

Fields of view of the eyes of most jumping spiders. Yellow: The large forward-facing principal eyes. Each yellow band represents the tiny field of view of each eye. Being movable about 30 degrees to either side, this small field of view is extended. Red: The overlapping fields of view of one pair of secondary eyes. Green: Another pair of secondary eyes completes the picture for a 360-degree world view.

→ With amazing cognitive abilities, this spider is often regarded as the Einstein of spiders, but its problem-solving is somewhat slow.

DEINOPIS SPINOSA

Net-casting or ogre-faced spider

Night watcher

SCIENTIFIC NAME	*Deinopsis spinosa*
FAMILY	Deinopidae
BODY LENGTH	Females ½–⅔ in (12–17 mm), males ⅖–½ in (10–14 mm)
NOTABLE ANATOMY	Largest eyes of any spider (posterior median eyes 1⁄400 in/0.07 mm)
MEMORABLE FEATURE	Use of expanding silk net to catch prey at night

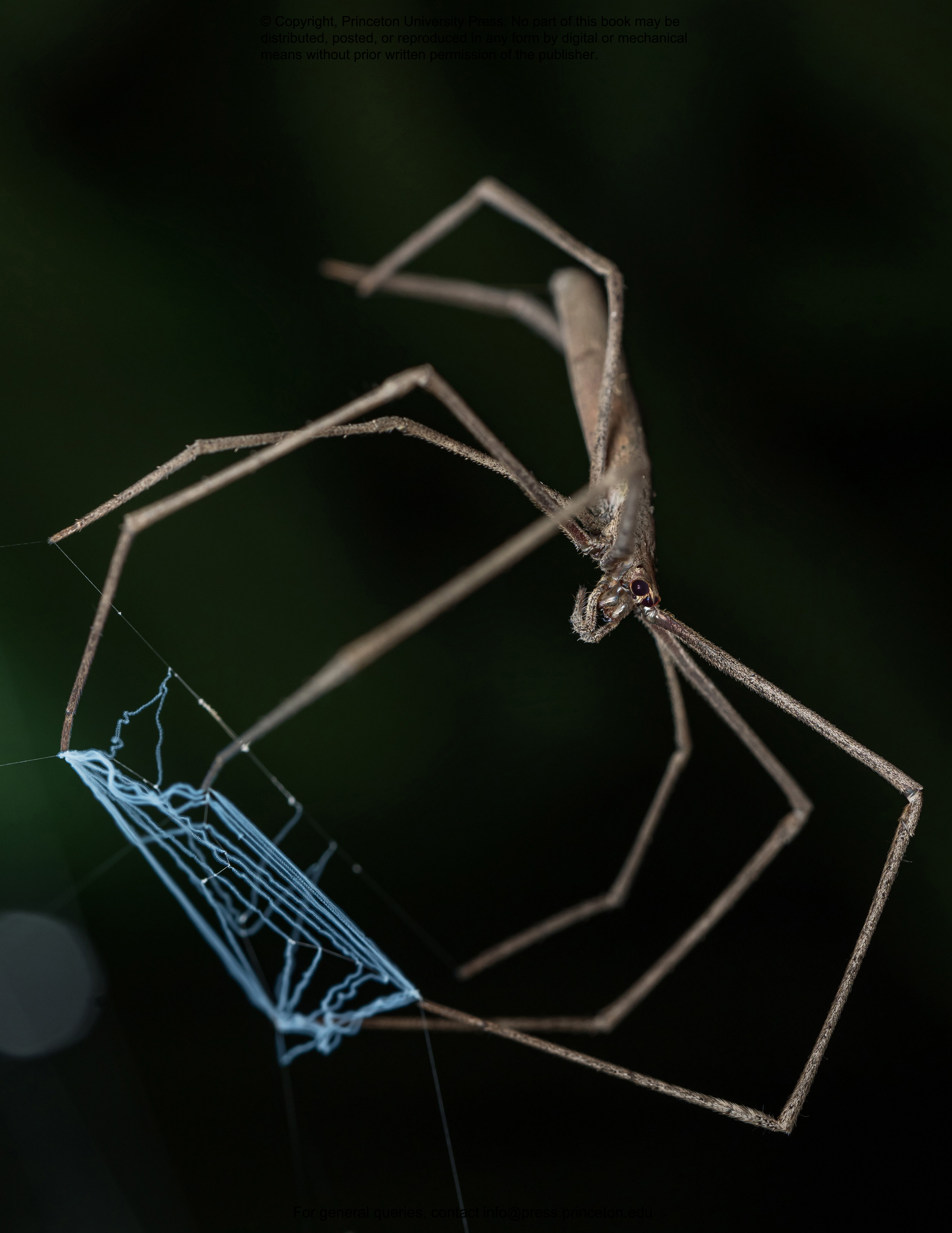
As it hangs upside down with an expandable silk web spun between its front legs in the dead of night, the net-casting spider uses vision to ensnare prey walking beneath it by stretching the silken trap as it lunges, as if cast in a sci-fi movie. Web-building spiders generally have poor eyesight, but *Deinopis* is an exception.

Good eyesight can be as much a matter of spatial acuity as of sensitivity. Sensitivity is the amount of light an eye is able to capture and process, enabling vision in low light. Net-casting spiders are to nocturnal vision what *Portia fimbriata* is to diurnal vision, but unlike the enlarged principal eyes of the diurnal jumping spider, a massively enlarged pair of secondary eyes is responsible for *Deinopis*' visual accomplishments. While the nocturnal *Deinopis* uses sound to capture flying prey, vision is required to capture ground-based prey. Their huge (about 1⁄20 in/1.4 mm) posterior median pair of secondary eyes, earning them the name ogre-faced spiders, are thought to be 2,000 times more sensitive to dim light than our eyes. But how, when their eyes are so much smaller than ours?

THE DETAIL VS. NIGHT VISION TRADE-OFF

Each photoreceptor samples a specific part of a given image, so, if photoreceptors are small and densely packed, the image is sampled in detail, providing high spatial acuity. This is the case in the foveal region of our eyes (cone-based vision) and enables us to differentiate between strands of hair, but it comes at the cost of sensitivity. In low light, the limited number of photons reaching individual small photoreceptors makes them perform poorly, whereas large photoreceptors can capture enough photons to form a crude image or detect motion. However, this has negative impacts on visual acuity, as is the case with the poor resolving detail of our rod-based night vision. This leads to a classic trade-off: Spatial acuity improves as the ratio of photoreceptor diameter to focal length decreases, and sensitivity improves as the same ratio increases. The only potential solution is to have a very large eye, like our own, to accommodate both of those roles, but that is impossible in spiders, which are constrained by their exoskeleton to have small eyes. By having a short focal distance and large photoreceptors in their enlarged, yet relatively tiny eyes, *Deinopis*' posterior median eyes are well adapted to detect motion at night.

→ Being strictly nocturnal, during the day *Deinopsis spinosa* hides in plain sight by resembling a twig.



CYRBA ALGERINA

Algerian jumping spider

Stone dweller

SCIENTIFIC NAME	*Cyrba algerina*
FAMILY	Salticidae
BODY LENGTH	Females ⅛–⅓ in (4–7 mm), males ⅛–⅕ in (3–5 mm)
NOTABLE ANATOMY	Bright-orange head of males
MEMORABLE FEATURE	Hunting spiders in poorly lit areas

Unusually, the jumping spider *Cyrba algerina* visually distinguishes conspecifics and assesses its prey in both very dim and very bright light, despite not having atypically large eyes. Living under dim light conditions beneath stones in arid habitats, the Algerian jumping spider hunts web spiders in preference to insects as prey, and visually discriminates between prey under light conditions equivalent to early or late dusk. Using intricate predatory behaviors, *C. algerina* often hunts under stones, but using a visual system able to achieve sufficient spatial acuity for object identification under a range of lighting conditions, it can also hunt in more open and brightly lit areas above stones.

A COMPLEX PREDATOR

Possibly due to the dangerous nature of its preferred prey, *Cyrba*'s venom is specialized to rapidly subdue spiders compared with insects (12 times faster, in fact), and its predatory behavior is complex. Spider-specific predatory behavior includes using trial and error to derive vibratory signals which are plucked on the prey's web to gently coax the resident spider toward the awaiting hunter without evoking a predatory response from the web spider.

When it invades a prey spider's web, *C. algerina* also capitalizes on wind disturbances on the web, masking its own vibrations by using the wind as a smokescreen and rapidly advancing toward the resident web spider prey, while ignoring any insects caught in the web. These intricate behaviors are visually mediated, irrespective of whether they are performed in bright sunlight or under ambient light levels associated with nocturnal species.

A BLENDED LIFESTYLE

Since the amount of light captured is usually related to eye size, species with small eyes face major difficulties. Compared to most jumping spiders, which live in bright light, the principal eyes of *Cyrba* have a short focal length, and its small photoreceptors have evolved strategies to merge photon capture, essentially making the photoreceptors larger and favoring sensitivity without fully compromising acuity. These adaptations may be beneficial for a jumping spider with a "blended" lifestyle: generally living and hunting under stones in the dark, but sometimes venturing above them in dramatically different light conditions. *C. algerina* illustrates how sensitivity seems to have been favored over spatial acuity, allowing this species to minimize the constraints imposed by its particular microhabitat.

→ Populations in different regions specialize at eating different types of spiders, and each population learns the specific odors of the locally abundant prey to facilitate prey detection.

SILK & WEB-BUILDING

An unusually versatile material

Sensing an oncoming storm due to the electrical fields in the atmosphere, a baby spider (spiderling) climbs to the tallest area of foliage it can reach and deploys—perhaps for the first time in its life—silk. The silk filaments waft into the air, caught by the breeze and the electrical fields in the atmosphere, and the spider is lifted away to new areas, sometimes hundreds of miles away, to make a new home.

This tiny spider, barely visible to the human eye, has detected the electrically supercharged atmosphere due to the storm through its trichobothria, now acting as electromechanical receptors. This has triggered a behavior known as ballooning, whereby the spider seeks an exposed area and, standing on tiptoe, lifts its abdomen in the air and releases silk to prepare for its first flight.

All spiders produce silk, which, being both tough and flexible, is very versatile. With a few adjustments, silk can be made to have slightly different properties for different tasks. Consequently, a given spider may have multiple types of silk glands in their abdomen, each producing a different type of silk. Within the gland, the silk is a protein-rich liquid that flows through a duct that removes water from the liquid. The spider uses its hind legs to pull silk out from its highly mobile spinnerets, creating tensile stress. This tensile stress further solidifies the viscous fluid by causing the protein molecules in the silk to align and form strong bonds with each other, transforming it into a solid.

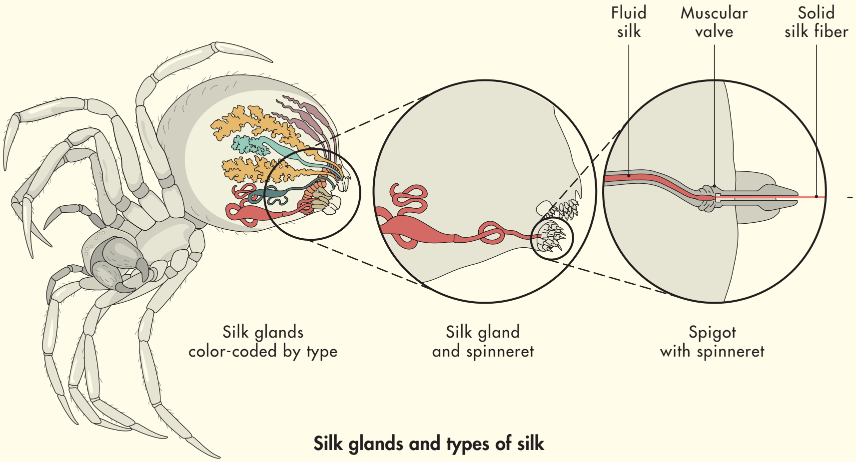
MULTIFARIOUS SILK

Spiders have capitalized on the versatility of silk, using it to disperse or build webs, protect their eggs, or line their burrows. They use silk to communicate and to subdue prey. They use silk as a sensory system. Males produce sperm in a different organ to the one used to transfer sperm, so they build "sperm webs" in which they deposit the semen to fill the palps with sperm for future use. In short, silk plays a fundamental role in all aspects of a spider's life, and this requires them to produce silks with distinct physical properties to perform different functions.

↑ Spiders can have two, four, six, or eight spinnerets, each ending in tiny spigots to provide the tension required to turn the internal liquid silk into the extruded solid threads.

← Ballooning is a key dispersal mechanism for spiders, allowing them to colonize new lands. It is believed much of New Zealand's spider fauna arrived this way from Australia, thousands of miles away.

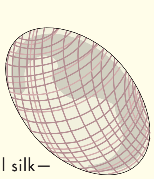
Even when deployed in the "traditional sense" of building a web, spiders produce an array of silks corresponding to the different roles they play within the web, such as elastic silk that is stronger than steel to anchor the web to the surroundings, or sticky silk to ensnare prey. An orb web contains up to five types of silk. Tough dragline silk, produced by the major ampullate gland, creates the frame in which the hub will be built, as well as the radial threads that crisscross through the final structure and provide structural support, like spokes on a bicycle wheel. The spirals within the web are produced by silk from the flagelliform gland; this is coated in silk with glue droplets produced in the aggregate gland to make the "capture zone" of the web sticky.



Silk glands and types of silk

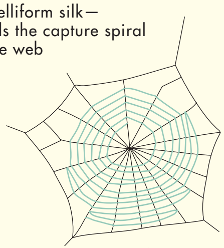
Flagelliform, aggregate, cylindrical, aciniform, piriform, and minor and major ampullate glands within the spider's abdomen produce silks with different characteristics when extruded through the spinnerets, turning the viscous silk fluid into a solid.

Minor ampullate silk from its corresponding gland can be used as reinforcement silk for the spirals, or as scaffolding during construction, which is removed on completion. Finally, the silk cementing the web to its anchor points is made using pyriform silk spun as an attachment disk. Say that the spider then catches prey: She wraps it using aciniform silk. She also uses aciniform silk to make a soft lining for the protective case in which she houses her fertilized eggs until they hatch, coating the case with tough cylindriform or tubiliform silk for protection.

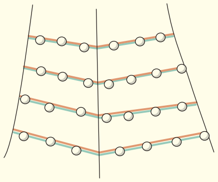


Cylindrical silk—
covers eggsac

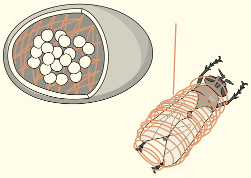
Flagelliform silk—
builds the capture spiral
of the web



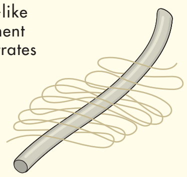
Aggregate silk—
sticky droplets on web
capture zone



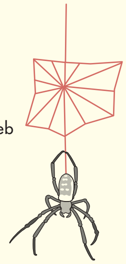
Aciniform silk—
inner lining of eggsac and
prey wrapping



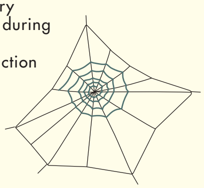
Pyriform silk—
cement-like
attachment
to substrates



Major
ampullate
silk—
draglines,
frame and
radii of web



Minor
ampullate
silk—
auxiliary
spirals during
web
construction



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