Annu. Rev. Entomol. 1994. 39:81–99

BIOLOGY OF BOLAS SPIDERS

Kenneth V. Yeargan
Department of Entomology, University of Kentucky, Lexington, Kentucky 40546

KEY WORDS: Araneae, *Mastophora*, moths, chemical mimicry, pheromones

---

INTRODUCTION

Bolas spiders are so named because late-stadia immature and adult females swing a droplet of adhesive on a silk thread at their flying prey (moths). Although this weapon superficially resembles the bolas used in South America to entangle the legs of cattle, the spider's bolas is swung rather than literally thrown at prey, and its effectiveness depends on adhesion to the droplet rather than entanglement in the line to which this globule is attached (18).

Early observers of bolas spiders suspected that prey were attracted to the spiders by an odor imperceptible to humans (e.g. 28, 36), and circumstantial evidence convincingly confirmed this suspicion in 1977 (17). While their method of capturing prey is unique to bolas spiders, the ability to attract prey is known in other spiders. For example, insects appear to be attracted to ultraviolet-reflecting silk produced by certain diurnal web-building spiders (14). Members of several araneid spider genera, in addition to bolas spiders, apparently use chemical lures to attract male moths. These include *Celaenia, Taczanowskia,* and *Kaira,* all of which hang upside down from a leaf or silk support and capture approaching moths with their outstretched legs (19, 36, 48). Chemically mediated attraction also may be used by some spiders to capture nematocerous Diptera (20).

In a paper on the taxonomy of bolas spiders in North America, Gertsch (25) presented an excellent summary of their biology as it was known up to 1955. More recent reviews of prey specialization in araneid spiders (48) and chemical mimicry in plants and animals (49) summarized information about bolas spiders relevant to those topics.

Although this review is not organized chronologically, a brief historical

0066-4170/94/0101-0081$05.00

perspective is worthwhile. Work before 1900 consisted of taxonomic descriptions of several genera and species now known as bolas spiders. In 1903 Hutchinson (28) was the first to report the unusual hunting behavior of this group, based on his observations of a species that occurs in southern California; that description was followed in the early 1920s by reports of similar behavior observed for other species in Australia (31) and South Africa (1). With the exception of Gertsch's taxonomic study mentioned above, a popular article that he published in 1947 (24), and fragmentary observations by individuals in Australia (13, 36), little was reported regarding bolas spiders until 1977 (17). Research on bolas spiders during the past two decades has been done primarily at a few locations in North and South America. While this review attempts to summarize current knowledge of bolas spiders worldwide, the most detailed studies of these spiders to date all have been done with one genus, *Mastophora*.

MORPHOLOGY, TAXONOMY, AND GEOGRAPHIC DISTRIBUTION

Bolas spiders belong to the large family Araneidae, whose members are commonly called orb weavers. Most orb weavers produce a two-dimensional web consisting of dry threads (frame, radii) and sticky spiral threads. The large garden spiders of the genus *Argiope* are examples of commonly encountered orb weavers. Bolas spiders, and a few other members of Araneidae, do not construct typical orb webs.

The presence of conspicuous outgrowths on the dorsal surface of the cephalothorax morphologically distinguishes bolas spiders from typical Araneidae. Males of many orb weavers are smaller than conspecific females, but this dimorphism is particularly extreme in bolas spiders. Body lengths of the diminutive adult males are typically less than 2 mm, while those of females usually range from 10 to 15 mm (25, 36) and occasionally reach 20 mm (37). The abdomen of adult females is quite large with respect to the cephalothorax, which it partially covers; various authors have described the abdomen as obese or voluminous. In some species, the female's abdomen is relatively smooth, while in others it possesses humps, lobes, or tubercles (25).

Late-stadia and adult female bolas spiders in the genus *Mastophora* resemble various objects. For instance, females of several *Mastophora* species can be easily mistaken for bird droppings (7, 18, 25). Atkinson (4) stated that females of *M. bisaccata* in North Carolina mimicked the shell of a snail that was abundant in the spider's habitat. Interestingly, while *Mastophora* species that resemble bird droppings often are found on the upper surface of leaves (18), *M. bisaccata* females frequently rest on the undersides of leaves during the day (2, 4).

Apparently, large females of all *Mastophora* species rest exposed, rather than in a retreat, during the day with their legs held tightly to their bodies, and the spider clings to a silk circlet it deposits on the substrate. If forcibly removed from the substrate, *Mastophora* females emit a distinctive, pungent odor by producing a droplet of regurgitant (18, 28). This presumably defensive response is very unusual for spiders and is known only for bolas spiders and a species of *Cyrtarachne* (18). Unlike most spiders, *Mastophora* females do not attempt to flee when handled. Instead, as Gertsch (24) noted, the spiders maintain their resting posture with legs close to the body and can be rolled around in one's cupped hand "like a nut or marble."

At least some African bolas spiders (*Cladomelea*) also rest exposed on plant surfaces during the day (1). The Australian bolas spider *Ordgarius magnificus,* however, ties leaves together with silk to form a diurnal retreat (31).

Bolas spiders are known from most parts of the world except temperate Eurasia. Gertsch (25) recognized six genera of bolas spiders, which comprise the tribe Mastophoreae: *Cladomelea* (three species) and *Acantharanea* (six species) in Africa; *Ordgarius* (seven species) and *Dicrostichus* (three species) in Oriental Asia, the East Indies, New Guinea, and Australia; and *Agatostichus* (two species) and *Mastophora* (20 species) in North, Central, and South America and the West Indies. More recently, *Dicrostichus* was declared a junior synonym of *Ordgarius,* and the number of species formerly in *Dicrostichus* dropped from three to two by synonymy (15). Also since Gertsch's revision, Eberhard (18) described *Mastophora dizzydeani,* which he named "in honor of one of the greatest baseball pitchers of all time, Jerome 'Dizzy' Dean" (p. 144). Several other generic names were used for *Mastophora* species in the older literature, including *Cyrtarachne, Epeira, Glyptocranium,* and *Ordgarius* (see synonymies in 25, 38). About half of the known species of *Mastophora* occur in South America (25, 38).

The distribution of African bolas spiders is poorly known. *Ordgarius* ranges from India to Australia (25, 38). Within Australia, this genus is found throughout much of the eastern part of the continent from Queensland to Victoria (36). Specimens of the American genus *Agatostichus* are extremely rare in collections; the South American species was described from a single specimen from Baia, Brazil, and the North American species from two specimens collected in southern Texas and adjacent Tamaulipas, Mexico (25). The other American genus, *Mastophora,* has a particularly broad distribution range that extends from southern Chile through the American tropics to the extreme northern US (to 45° north latitude in Minnesota).

The distribution of *Mastophora* species within the US is better known than that of most other bolas spiders. Four species, *archeri, bisaccata, hutchinsoni,* and *phrynosoma,* occur widely in the US east of the Great Plains. The fifth species, *cornigera,* occurs from Alabama to California across the extreme southern US, as well as in northern Mexico (25).

Although only five *Mastophora* species have been described from the US, Gertsch (25) pointed out that what is now called *M. bisaccata* may actually be more than one species. His suspicion was based primarily on what appeared to be three distinct types of egg cases made by this species. Until 1955, only two species of bolas spiders were recognized in the US, namely *M. bisaccata* and *M. cornigera*. The three new species described at that time all had previously been confused with *M. cornigera* (25). Several references to, and figures of, *M. cornigera* and its egg cases in the older literature (e.g. 29, 35) actually pertained to what is now known as *M. hutchinsoni*. Currently, *M. bisaccata* may represent a similar, but unresolved, situation.

Several authors have addressed phylogenetic relationships of bolas spiders to other orb weavers (18, 45, 48), focusing particularly on those that specialize on moths as prey. Conventional orb webs, although sticky, are not very effective for capturing moths (22, 43, 45). The loose scales covering the moths' bodies and wings detach onto the viscid threads of typical orb webs, thus frequently allowing moths to escape. Although some orb weavers are diurnally active (e.g. *Argiope* spp.), many use their webs to catch prey primarily or only at night. Given that moths constitute a significant portion of the flying nocturnal insect fauna, one might expect selection to favor adaptations that improve nocturnal orb weavers' ability to use this resource.

The ladder webs of *Scoloderus* species in North and South America (16, 47) and of an unidentified genus in New Guinea (44) appear to be adaptations in web design that increase moth capture. These fine-meshed webs extend vertically some seven times their width. When a small moth strikes the web, the fine mesh seems to make immediate escape difficult, and the moth slides down the web, leaving a trail of scales until its body adheres (16, 42). Moths constitute a majority of the prey caught (47), but there is no evidence that attractants are involved. The webs capture both male and female moths, as well as other prey. Ladder web spiders are not considered closely related to bolas spiders (48).

Araneids in the tribe Cyrtarachneae of the Old World tropics, however, may share common ancestry with bolas spiders (12, 18, 45, 48). Several lines of evidence, in addition to specialization on moths, suggest this relationship. The webs of Cyrtarachneae contain a few slack spanning threads that are beaded with viscid droplets; these threads are strongly attached to the web at one end but break at the other end (low-shear joint) when struck by a flying moth. This leaves the tethered moth dangling below the more-or-less horizontal web, as illustrated for *Pasilobus* by Robinson & Robinson (45). Other attributes similar to those of bolas spiders include the method of actively pulling sticky silk from the spinnerets and the moth-holding properties of the adhesive (18). It is not known whether any of the Cyrtarachneae chemically attract moths, but the possibility has been suggested, particularly for those with reduced webs (42).

The Celaenieae (*Celaenia* spp. in Australia and *Taczanowskia* spp. in South America), which apparently use chemical lures to attract moths (19, 36), also may be closely related to bolas spiders. Eberhard (18, 21) argued that these spiders, along with Cyrtarachneae and Mastophoreae, should be placed together in the same section of the subfamily Araneinae. Stowe (48), however, questioned whether the Celaenieae were closely related to the other two groups.

Females of *Kaira alba* also attract male moths and, like the Celaenieae, capture their prey without using sticky silk, instead using their outstretched legs. Stowe (48) concluded that *K. alba* probably evolved the ability to attract moths independently from the Mastophoreae species, and in a recent study of araneid phylogeny, cladistic analyses indicate that *K. alba* is not closely related to members of Mastophoreae (N Scharff & JA Coddington, personal communication).

Thus, the general consensus is that bolas spiders are closely related to the Cyrtarachneae, a group that exhibits various degrees of web reduction, but the phylogenetic relationships of bolas spiders with other members of the Araneidae are less certain. Adaptations that enhance the capture of moths, including modified webs and the ability to attract moths, probably evolved independently several times in the Araneidae.

LIFE HISTORY

Many aspects of bolas spider life history are difficult to study. Despite their widespread geographic occurrence, these spiders are not common and appear to be patchy in distribution (48; KV Yeargan, personal observations). Young spiderlings and adult males are quite small, making them difficult to spot in the field. The larger females are sedentary and highly cryptic during the day, although they are somewhat easier to find at night while they hunt.

Complete seasonal phenology has been determined for only one species of bolas spider, *M. hutchinsoni* (55). As is probably the case for other *Mastophora* species in temperate regions, *M. hutchinsoni* is univoltine. It overwinters in the egg stage, and spiderlings emerge from egg cases in late May (in Kentucky). Although many spiders are protandrous (52), with males frequently requiring fewer molts than females, this sexual disparity is especially pronounced in bolas spiders. *M. hutchinsoni* males mature by the end of June or early July, while females do not mature until early September (55). Males survive until at least late September, the month in which mating presumably occurs for this species in Kentucky. Females produce egg cases during September, October, and occasionally early November; adults of this species do not survive the winter.

Collection dates for various life stages of the other four species of *Mastophora* in the US (25; KV Yeargan, unpublished data) indicate that the seasonal phenology described above probably applies (with adjustments for latitude) for three of those species, but not for *M. cornigera*. Adult males and females of this more southerly distributed species have been collected both in the fall and in February, March, and April (25). In southern California, adult females of *M. cornigera* captured prey and produced egg cases during every month of the year (MK Stowe & WR Icenogle, unpublished data). This species and others in warm climates apparently depart from the simple univoltine life cycle of *M. hutchinsoni*. Adult females of *M. dizzydeani* captured prey in Colombia at a location less than 5° north latitude during the months of February, March, and August through December; newly emerged spiderlings were observed in November (18).

Seasonal phenology of bolas spiders in the Southern Hemisphere is known only from fragmentary observations. Longman (31) observed emergence of *O. magnificus* spiderlings in Queensland, Australia, during autumn and winter from egg cases made a few months earlier. A female *Ordgarius monstrosus* matured in June and produced 10 egg cases between late June and early September in Edmonton, Australia (about 17° south latitude) (13). Adult females of *Cladomelea akermani* were observed with egg cases during July in Pietermaritzburg, South Africa (about 30° south latitude) (1).

The distinctive egg cases of bolas spiders attracted the attention of early observers, even before the hunting behavior of the spiders was known (e.g. 23, 35). The cases have a very tough outer layer and, depending on the species, range in shape from fusiform (*O. magnificus*) to spherical or pear shaped (*O. monstrosus, C. akermani,* and many species of *Mastophora*). Egg cases of some species are smooth, while others are ornamented with points, scallops, or other characteristic projections; those of many species resemble plant buds, galls, or hard, dry berries (4, 13, 25). Gertsch (25) and Davies (15) have provided excellent illustrations of *Mastophora* and *Ordgarius* egg cases, respectively.

Usually tough silken lines attach a stem or stalk extending from the egg case to the substrate. Additional silken lines may be used to guy the case. Egg cases of *M. hutchinsoni* differ from those known for other bolas spiders in that the spherical base is firmly attached to twigs with the stem projecting away from the twig. Akerman (1) found egg cases of *C. akermani* on grasses in Africa, but those of other bolas spiders usually occur on woody plants (25, 36). No evidence indicates that bolas spiders prefer to hunt or construct egg cases on any particular plant species. *Mastophora* egg cases usually are found between 1.5 and 3 m above the ground (25), but sometimes lower or higher.

Females produce only one egg case per bout of oviposition, typically at one- to three-week intervals, and two or more cases may be clustered in the same support threads. The typical number of egg cases produced by individual females varies widely among species, but species in warmer climates generally produce more than those in temperate regions. Three species of *Mastophora* (*bisaccata, hutchinsoni,* and *phrynosoma*) usually produce one to three egg cases in temperate regions of the US (23, 25, 29, 35, 55; KV Yeargan, unpublished data). On the other hand, *M. cornigera* is known to produce as many as seven cases per female in southern California (25), with the typical number ranging from three to five (28). At a similar latitude (about 35°S) in Argentina, a female of *Mastophora extraordinaria* was found in late autumn with five egg cases (7). At latitudes of less than 30°, individual females of *C. akermani* produce up to six egg cases, *O. magnificus* and *O. monstrosus* as many as nine and ten, respectively, and (near the equator) *M. dizzydeani* up to eleven egg cases (1, 13, 18, 36).

In the US, *Mastophora* egg cases typically give rise to about 150–300 spiderlings (24, 55). An egg case of *M. extraordinaria* from Buenos Aires contained approximately 530 eggs (7); Eberhard (18) reported that a "representative" egg case of *M. dizzydeani* in Colombia contained 826 eggs. Combining the number of eggs per case and the number of cases produced per female, total progeny per female in *Mastophora* ranges from several hundred for some species in the temperate US to several thousand for *M. dizzydeani* in Colombia. In Australia an *O. monstrosus* egg case contained 487 eggs (13), while *O. magnificus* typically produces about 600 eggs per case (36).

Eberhard (18) suggested that the disparity between the number of eggs per case he found for *M. dizzydeani* and Gertsch's (24) report of 147 spiderlings emerging from an egg case of *M. cornigera* may have resulted from cannibalism by spiderlings inside the egg case. However, whether significant cannibalism occurs in the egg case is questionable. *M. hutchinsoni* egg cases contain about 150–300 eggs (29; KV Yeargan, unpublished data), and similar numbers of spiderlings emerge (55). Furthermore, unlike many spiders, *Mastophora* spiderlings show virtually no propensity toward cannibalism after emergence from the egg case, even when crowded in cages (48).

All bolas spiders studied to date appear to have a sex ratio of approximately 1:1 at the time of spiderling emergence (18, 24, 36, 55). The sex of most spiders cannot be determined until they are older, but the sex of bolas spiders can be discerned at emergence by the enlarged palpi of the tiny precocious males. Upon emergence from the egg case, males of *M. dizzydeani, M. hutchinsoni,* and *M. phrynosoma* seem to require one or two molts before maturity (18, 55; KV Yeargan, unpublished observations), and males of *M. cornigera* and *O. magnificus* seen emerging from their egg cases appeared to be mature (25, 36). In contrast, *Mastophora* females undergo numerous molts, perhaps as many as eight (55). Information on male and female bolas spider survival, dispersal, operational sex ratios, and mating behavior is lacking, so we cannot evaluate this group with regard to hypotheses that have been put forth to explain cases of extreme sexual dimorphism in spiders (40, 53).

Records of natural enemies of bolas spiders all pertain to predators or parasitoids of the egg stage. A gryllacridid was observed feeding on the eggs of *O. magnificus* (31), and a sarcophagid parasitoid has been reared from egg cases of this spider (32). Five species of hymenopteran parasitoids are known to attack *Mastophora* eggs. *Tromatobia notator* parasitized *M. cornigera* (10), as well as *M. bisaccata* and *M. phrynosoma* (MK Stowe, unpublished data); *Gelis* sp. parasitized *M. cornigera* (EI Schlinger, personal communication). The eupelmids *Arachnophaga abstrusa, Arachnophaga ferruginea,* and *Arachnophaga picea* parasitized *Mastophora* sp. (8), *M. hutchinsoni* (KV Yeargan, unpublished data), and *M. cornigera* (8), respectively.

HUNTING BEHAVIOR AND ECOLOGY

Most studies of predation by bolas spiders have dealt with the behavior of large immature and adult females, which use a bolas to capture prey. Stowe (48) reported that newly emerged *M. cornigera* spiderlings occasionally produce a bolas in captivity, but others have observed that young spiderlings hunt without a bolas in the field (18, 55). Researchers have surmised, based on scanty evidence and the limitations suspected to result from small size, that the hunting tactics and prey of young spiderlings of both sexes, and perhaps the tiny adult males, differ from those of the adult females.

Spiderlings and Adult Males

Eberhard (18) observed that newly emerged *M. dizzydeani* hunted without a bolas and suggested this might be because the small sticky globule these spiders could produce would dry out easily owing to its high surface-to-volume ratio. He reported the capture of two nematocerous flies (further identification not given) by newly emerged spiderlings. I (55) found that newly emerged *M. hutchinsoni* spiderlings stationed themselves along the undersides of leaf margins with the front two pairs of legs periodically extended and held motionless in a position that would allow capture of prey walking along the leaf margin. I observed prey capture (thrips) by this technique only twice in the field, but numerous times with spiders that were held with various prey in captivity. Young *M. phrynosoma* spiderlings also hunt without a bolas in a manner similar to *M. hutchinsoni* and have been observed in the field feeding on ceratopogonid and psychodid flies (KV Yeargan, unpublished data).

Preliminary evidence gathered recently in Florida (MK Stowe, unpublished data) and Kentucky (KV Yeargan, unpublished data) indicates that newly emerged *Mastophora* spiderlings attract nematocerous flies and then capture them by using the technique described above for *M. hutchinsoni*. In those studies, psychodid flies were attracted to traps baited with live spiderlings, but not to identical traps without spiderlings. In Australia, spiderlings of another moth-attracting spider (not a bolas spider), *Celaenia* sp., were observed feeding strictly on male psychodid flies (CS Lauder, personal communication cited in 18).

Predatory habits of adult male bolas spiders are not known, but their tiny size and certain morphological evidence suggest that they continue to hunt in a manner similar to that of young spiderlings. During the first few stadia, juvenile females possess a single row of strong bristles on the prolateral surface of the tibiae and metatarsi of each of their first two pairs of legs. These bristles occur on both juvenile and adult males. Eberhard (18) illustrated these bristles on a juvenile female and suggested that they may aid in the interception of prey. If they indeed function for this purpose, their presence suggests that adult males continue to hunt in a manner similar to spiderlings. After the first few stadia, female *Mastophora* no longer have these bristles.

In the field, female *M. hutchinsoni* lose the bristles around the first of July, several weeks after emergence (55); loss of the bristles may coincide with a change in hunting tactics (i.e. initiation of bolas use). Female size increased sharply during the weeks following the loss of bristles, compared with the growth rate during the preceding weeks (55). This species begins to hunt with a bolas by early July in Kentucky (KV Yeargan, unpublished observations).

Late-Stadia Immature and Adult Females

Although there are scattered records of predation by mid-sized immature female bolas spiders, most data have been gathered on adults or immature females that were near maturity. Thus, unless noted otherwise, the following descriptions pertain to mature or nearly mature females.

PRODUCTION AND USE OF THE BOLAS Bolas spiders in all genera studied (*Cladomelea, Ordgarius,* and *Mastophora*) behave similarly during preparation for hunting and differ primarily in the way they manipulate the completed bolas. Vivid descriptions are available for each of these three genera (1, 24, 28, 31), a brief summary of which is presented here.

Spiders hunt with a bolas only at night. The spider begins hunting by crawling from a daytime resting site to a nearby leaf or twig, then prepares a more-or-less horizontal line between two attachment points (twigs or leaves) several centimeters apart. The spider, hanging upside down, then moves along the horizontal line and attaches a second thread to the horizontal line (position of attachment is variable). Crawling along the horizontal thread, the spider draws the second thread out to a few centimeters, keeping it below and clear of the other. With the second thread still attached to the spinnerets, the spider uses its hind legs in alternating strokes to comb viscid material from the spinnerets onto the second thread. As described below, during this phase the spider is combing out both silk and liquid material (18). After approximately 30–60 s of such combing, either the supply of viscous material and silk is terminated (18) or a hind tarsus is used to sever the thread between the spinnerets and the viscid globule that has accumulated (28). In either case, the weight of the globule causes the second thread to swing away from the spinnerets and hang perpendicular to the horizontal line. The structure resembles the letter T with a small droplet at its base.

Upon completion of the bolas (i.e. the vertical thread containing the viscid globule), the spider turns around on the horizontal thread and grasps the vertical thread with a single leg and, at least for *Mastophora* species, the mouthparts (28). *Mastophora* species use a front leg to manipulate the bolas thread (28 and others), while *Ordgarius* species use one of the second legs (31, 34, 36). Akerman (1) reported that *Cladomelea akermani* grasps the bolas thread with one of the third legs, which are the shortest legs on all bolas spiders. While this surprising observation may be correct, the photograph of a hunting spider in Akerman's paper does not show a live specimen, but instead shows a "dried specimen placed in natural attitude with sling" (p. 88). Photographs of live specimens of *Mastophora* and *Ordgarius* clearly document their hunting posture (e.g. 17, 36, 55).

The manner in which the bolas is swung differs among groups from the three major regions of distribution. In the Americas, *Mastophora* species hold the bolas essentially stationary with a front leg until a moth approaches, at which time the spider cocks the leg and swings the bolas toward the prey with a very rapid, pendulum-like stroke (28 and others). In contrast, *Ordgarius* species in Australia begin to rapidly whirl the bolas when they detect an approaching moth (13, 34, 36). The African *C. akermani* apparently does not wait for a moth to approach, but instead whirls the bolas immediately after it is prepared and does so continuously for about 15 minutes (1).

Hutchinson (28) noted that *M. cornigera* would strike a hand-held moth if the moth's wings were fluttering, but not if the wings were immobilized. Bolas spiders probably detect prey by the sound of their approaching flight (17).

The adhesive globules of various bolas spiders have been reported to be about 2.4 mm in diameter (28) or a little larger than the head of a pin (1, 31). *Mastophora* and *Cladomelea* species usually produce only a single droplet per bolas (1, 28), but the bolas of *Ordgarius* species sometimes have a few smaller globules above the terminal droplet (13, 31, 42).

Eberhard (18) studied the morphological structure of the globule produced by *M. dizzydeani* and found that the internal structure was complex, consisting of a mass of curled or folded fiber(s) embedded in a viscid matrix that was, in turn, surrounded by a less viscous layer. Combining these morphological observations with photographic documentation that the globule reversibly extends (up to 4 cm) into a line when swung, he concluded that the globule may function as follows: "The low viscosity liquid is sufficiently wet and abundant to flow past the moth's scales and reach a relatively large area of the cuticle below. The more viscous liquid forms the actual bond to the thread which sustains the moth's weight, and the thread folded inside the ball functions to permit quick, reversible elongations which extend the spider's striking range and perhaps also serves to hold prey once it is hit" (p. 157).

The viscid globule of a bolas shrinks with passage of time, presumably reducing its effectiveness as an adhesive (18, 28). After unsuccessful bouts of hunting (typically 15–30 min), bolas spiders consume the unused bolas. The spider may prepare a new bolas and resume hunting within a few minutes, or it may cease hunting for an hour or more before constructing another one (1, 18, 28, 55).

Mastophora frequently miss their targets, and the same bolas can be swung at prey repeatedly. When a moth is struck, it rarely escapes, despite its struggles (18). It adheres to the sticky globule and hangs twirling on the vertical line. The spider descends to the moth, or sometimes draws the prey up by the line, and bites it. After waiting several seconds the spider wraps the prey, mummy-like, in silk. The wrapped prey may be fed upon immediately, but often the spider will attach it to the horizontal line and prepare a new bolas. Several moths may be caught and stored before the spider ceases hunting and begins to feed (18, 31, 48, 55). Two studies indicate that adult female *Mastophora* catch an average of about two moths per hunting night, but occasionally an individual catches as many as six or seven moths during a single night (18, 55).

An interesting departure from the typical hunting behavior has been observed in at least four *Mastophora* species (18, 48; KF Haynes, unpublished observations; KV Yeargan, personal observations). In those instances, the spider made a longer than normal horizontal line and, rather than preparing a single bolas, hung several on the line (as many as nine have been observed). The spider then positioned itself at one end of the horizontal line but did not hold a bolas. This technique has not been observed to result in capture of prey, although moths have been seen approaching spiders hunting in this manner. The same spiders were seen at other times, in some cases on the same night, hunting in the usual way with a single bolas. Eberhard (18) noted the remarkable resemblance of *Mastophora*'s unusual multiple-bolas line to the midline of a *Pasilobus* sp. web in which the low-shear joints of spanning threads have been broken [e.g. by vibration (see illustration in 42)]. *Pasilobus* spp. belong to the Cyrtarachneae, which as discussed earlier, are thought to be closely related to the Mastophoreae.

EVIDENCE FOR AGGRESSIVE CHEMICAL MIMICRY In the first report of bolas spider hunting behavior, Hutchinson (28) concluded that moths probably were attracted to the spider by an odor. Nearly 75 years passed, however, before evidence was presented that convincingly demonstrated this to be the case (17). The evidence included the following: only male moths were captured; they always approached the spider from downwind; a cardboard baffle placed downwind from the spider at a slight angle from perpendicular to wind direction deflected airflow and visually hid the spider, but moths continued to approach, arriving by way of the trailing edge of the baffle; and only a few moth species were captured, although dozens of species were active in the immediate area. More recently, similar evidence has been obtained for other *Mastophora* species (48, 49, 55), and volatile chemicals that occur in the sex pheromones of its moth prey have been identified for one *Mastophora* species (50).

PREY SPECIES CAPTURED More than 40 species of male moths in seven families have been documented as prey of bolas spiders (virtually all of the records are for *Mastophora* species). Longman (31) reported that he observed a female *O. magnificus* repeatedly feeding on the catocaline noctuid species *Mocis* (= *Remigia*) *frugalis* in Brisbane, but he did not specify the sex of the moths. Norris (41) stated that bolas spiders capture males of additional (unspecified) moth species in other areas of Australia. Among the prey species presently known for five species of *Mastophora,* 28 belong to the family Noctuidae; one to four species also have been recorded for the families Gelechiidae, Geometridae, Pyralidae, Plutellidae, Tineidae, and Tortricidae (Table 1). Three of the prey species were caught by more than ble 1 Moths captured by female bolas spiders of the genus *Mastophora*

ider	Prey species (reference)	Family: subfamily[a]	(Semiochemicals)[b]
astophora bisaccata	*Autographa precationis* (KVY)[c]	Noctuidae: Plusiinae	(AAA)
	Feltia subgothica (KVY)	Noctuidae: Noctuinae	(AAA)
	Metalectra quadrisignata (48)	Noctuidae: Catocalinae	(HCE)
	Mocis texana (48)	Noctuidae: Catocalinae	(HCE)
	Palthis asopialis (KVY)	Noctuidae: Herminiinae	(HCE)
	Pseudaletia unipuncta (KVY)	Noctuidae: Hadeninae	(AAA)
	Scolecocampa liburna (48)	Noctuidae: Catocalinae	(HCE)
	Acrolophus piger (48)	Tineidae	(AAA)
	Acrolophus plumifrontinellus (48)	Tineidae	(AAA)
	Choristoneura parallela (KVY)	Tortricidae: Tortricinae	(AAA)
	Ptycholoma peritana (KVY)	Tortricidae: Tortricinae	(AAA)
astophora cornigera	*Euxoa messoria* (50)	Noctuidae: Noctuinae	(AAA)
	Euxoa olivia (50)	Noctuidae: Noctuinae	(AAA)
	Euxoa selenis (S & I)[d]	Noctuidae: Noctuinae	(AAA)
	Euxoa septentrionalis (S & I)	Noctuidae: Noctuinae	(AAA)
	Euxoa serricornis (S & I)	Noctuidae: Noctuinae	(AAA)
	Heliothis phloxiphagus (50)	Noctuidae: Heliothinae	(AAA)
	Heliothis virescens (S & I)	Noctuidae: Heliothinae	(AAA)
	Lacinipolia quadrilineata (S & I)	Noctuidae: Hadeninae	(AAA)
	Leucania phragmatidicola (50)	Noctuidae: Hadeninae	(AAA)
	Peridroma saucia (50)	Noctuidae: Noctuinae	(AAA)
	Protorthodes alfkeni (S & I)	Noctuidae: Hadeninae	(AAA)
	Protorthodes melanopis (S & I)	Noctuidae: Hadeninae	(AAA)
	Pseudaletia unipuncta (50)	Noctuidae: Hadeninae	(AAA)
	Pseudorthosia variabilis (S & I)	Noctuidae: Noctuinae	(AAA)
	Discestra trifolii (50)	Noctuidae: Hadeninae	(AAA)
	Parapediasia teterrella (S & I)	Pyralidae: Crambinae	(AAA)
	Plutella xylostella (50)	Plutellidae	(AAA)
	Acrolophus kearfotti (S & I)	Tineidae	(AAA)
	Acrolophus variabilis (S & I)	Tineidae	(AAA)
	Phthorimaea operculella (S & I)	Gelechiidae: Gelechiinae	(AAA)
astophora dizzydeani	*Spodoptera frugiperda* (18)	Noctuidae: Amphipyrinae	(AAA)
	Leucania sp. (18)	Noctuidae: Hadeninae	(AAA)
	Unidentified species (18)	Tortricidae: Olethreutinae	(AAA)
astophora hutchinsoni	*Lacinipolia renigera* (55)	Noctuidae: Hadeninae	(AAA)
	Nephelodes minians (55)	Noctuidae: Hadeninae	(AAA)
	Tetanolita mynesalis (55)	Noctuidae: Herminiinae	(HCE)
	Parapediasia teterrella (55)	Pyralidae: Crambinae	(AAA)
astophora phrynosoma	*Disclisioprocta stellata* (KVY)	Geometridae: Larentiinae	(HCE)
	Eulithis diversilineata (48)	Geometridae: Larentiinae	(HCE)
	Nephelodes minians (KVY)	Noctuidae: Hadeninae	(AAA)

[a] Taxonomy follows that of Hodges et al (27).

[b] Chemical groups (see text for explanation of AAA and HCE) to which sex pheromones for each prey species are known or spected to belong; for every species listed, all or virtually all species in its family or subfamily for which information is ailable produce or respond to compounds belonging to either the AAA group or the HCE group, but not both (3).

[c] KV Yeargan, unpublished data.

[d] MK Stowe & WR Icenogle, unpublished data.

one species of bolas spider: *Pseudaletia unipuncta* by *M. cornigera* in California and by *M. bisaccata* in Kentucky; *Parapediasia teterrella* by *M. cornigera* in California and by *M. hutchinsoni* in Kentucky; and *Nephelodes minians* by *M. hutchinsoni* and *M. phrynosoma* at the same site in Kentucky (48, 55; MK Stowe & WR Icenogle, unpublished data; KV Yeargan, unpublished data).

Extensive prey records have been obtained for four species of bolas spiders: *M. dizzydeani* (18), *M. bisaccata* (48), *M. cornigera* (48, 50; MK Stowe & WR Icenogle, unpublished data), and *M. hutchinsoni* (55). Each of these species captured moths from two or more families, but in each case noctuids were most frequently caught. Individual females of *M. cornigera* have been reported to catch as many as nine different moth species (50).

Many of the prey species of bolas spiders have wide geographic ranges (e.g. *Spodoptera frugiperda*). Remarkably, *P. unipuncta* has been documented as prey for two bolas spider species in North America (as noted above) and for another moth-attracting spider in Australia (*Celaenia kinbergi*) (36). Several of the prey species of bolas spiders are economically important pests, and many are polyphagous as caterpillars. Collectively, these characteristics indicate that many of the moth species preyed upon by bolas spiders are abundant and ubiquitous (at both a geographic and local scale).

SEMIOCHEMICALS Collection and identification of chemicals emitted by bolas spiders have proven difficult. These uncommon spiders apparently only produce the chemicals while hunting. Furthermore, the precise source of the chemical attractants is unknown, although it appears that the substances emanate from the spider rather than the bolas (18). Lopez (33) suggested that glands on the front legs of *Mastophora* may be the source, but this has not been confirmed. Despite these difficulties, Stowe et al (50) collected and pooled enough volatiles from several hunting *M. cornigera* to identify three compounds produced by this species: (Z)-9-tetradecenyl acetate, (Z)-9-tetradecenal, and (Z)-11-hexadecenal. These compounds are components of the sex pheromone blends of several of *M. cornigera*'s prey species. In the female moths, these compounds could be produced by similar biosynthetic pathways (6). No other identification of chemicals emitted by bolas spiders has been reported.

Information based on either pheromone identification or effectiveness of compounds as attractants in replicated field tests is available for more than a dozen species of moths captured by *Mastophora* species. Similar information is known for congeners of several additional prey species (3 and references therein). Examination of current knowledge of prey sex pheromones and attractants may provide additional clues regarding the types of semiochemicals used by bolas spiders to attract male moths.

Moth pheromones and effective synthetic attractants typically consist of blends of two or more compounds. Blends used by many noctuids, as well as members of several other moth families, consist of unsaturated straight-chain aliphatic aldehydes, alcohols, or acetates that have chain lengths of 10–18 carbons and possess from one to three double bonds in either *Z* or *E* configuration (5 and references therein). This review refers to compounds in this set as the AAA group.

Wong et al (54), however, noted the failure of extensive field tests with more than 300 compounds in the AAA group to attract moths in Geometridae and several subfamilies of Noctuidae, and they tested in the field a set of compounds whose structures are quite different. Their work and other studies (references in 3) have shown that the moth taxa not attracted by compounds in the AAA group are attracted to a set of pheromones or attractants consisting of branched or unbranched straight-chain hydrocarbons or epoxides. These compounds usually are multiply unsaturated at the 1, 3, 6, 9, 12, or 15 positions in the *Z* configuration and may possess an epoxide instead of a double bond at one of these positions (5 and references therein). Many of these compounds have chain lengths of 19–21 carbons. The limited evidence available about moths' biosynthesis of these compounds (called the HCE group herein) suggests that they are produced by biosynthetic pathways that differ from those that have been well documented for the AAA group (6, 11, 46). Most moths appear to utilize compounds from either the AAA group or the HCE group, but not blends of both. Among the rare exceptions found utilizing pheromones consisting of aldehydes and epoxides are the arctiids *Estigmene acrea* and *Hyphantria cunea* (3).

All three compounds identified in volatiles emitted by *M. cornigera* (50), as well as those present in the pheromones or attractant blends known for its moth prey, belong to the AAA group. The predominant prey species reported for *M. dizzydeani* were *S. frugiperda* and an unidentified *Leucania* sp. (18). The pheromone of *S. frugiperda* and the pheromones or attractants known for eight species of *Leucania* all belong to the AAA group (3, 51).

Apparently some bolas spiders produce attractants from the HCE group. Prey caught by *M. bisaccata* include two species for which pheromones have been identified [*P. unipuncta* and *Choristoneura parallela* (KV Yeargan, unpublished data)] as belonging to the AAA group (3). However, other prey records for this bolas spider include three species of *Catocalinae* (48) and *Palthis asopialis* (KV Yeargan, unpublished data). All catocalines studied to date produce or respond to compounds in the HCE group, rather than those in the AAA group (3). Similarly, all studied noctuid species in the Herminiinae, including a congener of *P. asopialis,* respond to compounds in the HCE group (3). As noted earlier, spiders currently called *M. bisaccata* may actually belong to more than one species. This raises the possibility that one cryptic species might be using attractants from the AAA group while another uses compounds from the HCE group.

Even if that is the case for *M. bisaccata,* data on prey captured by two other bolas spider species suggest that those spiders produce attractants from both categories. Limited data show that *M. phrynosoma* captures two species of geometrids in the Larentiinae (48; KV Yeargan, unpublished data); virtually all members of this subfamily studied to date use or respond to compounds in the HCE group (3). The other prey species documented for *M. phrynosoma* is *N. minians* (KV Yeargan, unpublished data), a moth that was attracted to compounds in the AAA group in field tests (3).

The two predominant prey species of *M. hutchinsoni* are *Lacinipolia renigera* and *Tetanolita mynesalis,* which accounted for 40 and 53% of 460 prey items, respectively (55). The pheromone of *L. renigera* recently was found to consist of (*Z*)-9-tetradecenyl acetate and (*Z,E*)-9,12-tetradecadienyl acetate (26); the known attractants of two minor prey species of this spider also consist of compounds in the AAA group (3). No pheromones or proven attractants are known for any *Tetanolita* species, but evidence suggests that *T. mynesalis* probably uses compounds from the HCE group: First, this species belongs to the Herminiinae (see above). Second, a triunsaturated 21-carbon hydrocarbon has been tentatively identified from the pheromone gland of *T. mynesalis* (KF Haynes, unpublished data). Furthermore, the sex pheromone blend of compounds from the AAA group identified for *L. renigera* did not appear to be attractive to *T. mynesalis* in field tests, even though *M. hutchinsoni* females were concurrently catching both moth species at a nearby site (26). Individual *M. hutchinsoni* females frequently capture both *L. renigera* and *T. mynesalis* on the same night (55), suggesting that individual spiders can produce attractants belonging to both the AAA and HCE groups (Table 1). If that is the case, then some bolas spiders apparently have the biosynthetic capability to produce diverse chemical attractants, including compounds that are seldom produced in combination by moths.

One might expect that young female bolas spiders (soon after beginning to use a bolas) would catch smaller prey than older spiders, but data on the prey of young females are scarce. Adult female *Mastophora* capture both small and large moths (18, 55); for example, adult *M. hutchinsoni* females capture moth species that range in fresh weight from about 10 mg to about 200 mg (55). One of its small prey species, *T. mynesalis,* is available throughout the summer and fall, while the larger prey species are available primarily after the spiders reach the adult stage. Young female *M. hutchinsoni* may catch additional, unknown prey species in midsummer.

Alternatively, young females may capture a subset (i.e. small moths) of the prey species caught by subadult and adult females.

Moths have distinct diel periods of sex pheromone emission and male responsiveness, typically lasting for a few hours. Although subject to temperature modulation (9), the periodicity of these circadian mating rhythms is generally characteristic for each moth species. *Mastophora* females capture particular prey species at characteristic times of the night (48, 55). For example, *M. hutchinsoni* captured *L. renigera* early in the evening (always before 10:30 PM), while its other three prey species were caught later, usually after 11:00 PM (55). Whether individual bolas spiders can capture different prey species with a single compromise blend of compounds or if different blends are produced at different times during the night is not known.

CONCLUDING REMARKS

Over the past 90 years, bolas spiders have fascinated those fortunate enough to observe their remarkable method of capturing prey. Scientific study of the group has progressed slowly, but in recent years has revealed some aspects of their biology.

Unanswered questions about the group abound. For example, nothing is known about the chemical properties of the viscid adhesive used to catch moths, nor about the enzymes that permit its digestion by the spider. The regurgitant produced by the spiders when disturbed is presumed to be defensive, but this has not been demonstrated. Do individual spiders change semiochemicals over diel or seasonal periods, and do these compounds vary significantly among individuals or species? The distinctive geographic distribution of the group raises interesting questions for the biogeographer. Very little is known about predation by spiderlings of either sex, by adult males, or by young females soon after they begin to use a bolas. Nothing has been reported regarding the mating systems of bolas spiders. How might sexual selection account for the extreme sexual dimorphism found in this group? Answers to these and many other questions about bolas spiders await those who are persistent enough to find them.

ACKNOWLEDGMENTS

I thank WE Barney, KF Haynes, and DA Potter for helpful comments on an earlier version of the manuscript, CV Covell Jr for identifying moths captured by bolas spiders, and KF Haynes for providing unpublished data and sharing his insights regarding semiochemicals. I have benefited from many discussions with MK Stowe, who freely shared unpublished information. This contribution (no. 93-7-35) is in connection with a project of the Kentucky Agricultural Experiment Station and is published with the approval of the Director.

Literature Cited

1. Akerman C. 1923. A comparison of the habits of a South African spider, *Cladomelea,* with those of an Australian *Dicrostichus. Ann. Natal Mus.* 5:83–88
2. Archer AF. 1940. The Argiopidae or orb-weaving spiders of Alabama. *Ala. Mus. Nat. Hist. Mus. Paper* 14:1–77
3. Arn H, Toth M, Priesner E. 1992. *List of Sex Pheromones of Lepidoptera and Related Attractants.* Montfavet: International Organization for Biological Control. 2nd ed.
4. Atkinson GF. 1888. New instances of protective resemblance in spiders. *J. Elisha Mitchell Sci. Soc.* 5:28–30
5. Baker TC. 1989. Sex pheromone communication in the Lepidoptera: new research progress. *Experientia* 45:248–62
6. Bjostad LB, Wolf WA, Roelofs WL. 1987. Pheromone biosynthesis in lepidopterans: desaturation and chain shortening. In *Pheromone Biochemistry,* ed. GD Prestwich, GJ Blomquist, pp. 77–120. New York: Academic
7. Brèthes J. 1909. Sobre la *Mastophora extraordinaria* Holmberg y su nidification. *An. Mus. Nac. Buenos Aires* (Series 3) 10:163–68
8. Burks BD. 1979. Family Eupelmidae. See Ref. 30, pp. 878–89
9. Cardé RT, Comeau A, Baker TC, Roelofs WL. 1975. Moth mating periodicity: temperature regulates the circadian gate. *Experientia* 31:46–48
10. Carlson, RW. 1979. Family Ichneumonidae. See Ref. 30, pp. 315–740
11. Charlton RE, Roelofs WL. 1991. Biosynthesis of a volatile, methyl-branched hydrocarbon sex pheromone from leucine by arctiid moths (*Holomelina* spp.). *Arch. Insect Biochem. Physiol.* 18:81–97
12. Clyne D. 1973. Notes on the web of *Poecilopachys australasia* (Griffith and Pidgeon) (Araneida: Argiopidae). *Aust. Entomol. Mag.* 1(3):23–29
13. Coleman C. 1976. Notes on a local fishing or bolas spider *Ordgarius monstrosus. North Queensland Naturalist* 44:2–4
14. Craig CL, Bernard GD. 1990. Insect attraction to ultraviolet-reflecting spider webs and web decorations. *Ecology* 71:616–23
15. Davies VT. 1988. An illustrated guide to the genera of orb-weaving spiders in Australia. *Mem. Queensl. Mus.* 25: 273–332
16. Eberhard WG. 1975. The "inverted ladder" web of *Scoloderus* sp. and the intermediate orb of *Eustalia*(?) sp. (Araneae: Araneidae). *J. Nat. Hist.* 9:93–106
17. Eberhard WG. 1977. Aggressive chemical mimicry by a bolas spider. *Science* 198:1173–75
18. Eberhard WG. 1980. The natural history and behavior of the bolas spider *Mastophora dizzydeani* sp. n. (Araneidae). *Psyche* 87:143–69
19. Eberhard WG. 1981. Notes on the natural history of *Taczanowskia* sp. (Araneae: Araneidae). *Bull. Brit. Arachnol. Soc.* 5:175–76
20. Eberhard WG. 1981. The single line web of *Phoroncidia studo* Levi (Araneae: Theridiidae): a prey attractant? *J. Arachnol.* 9:229–32
21. Eberhard WG. 1982. Behavioral characteristics for the higher classification of orb-weaving spiders. *Evolution* 36: 1067–95
22. Eisner T, Alsop R, Ettershank G. 1964. Adhesiveness of spider silk. *Science* 146:1058–61
23. Emerton JH. 1884. New England spiders of the family Epeiridae. *Trans. Conn. Acad. Arts Sci.* 6:295–341
24. Gertsch WJ. 1947. Spiders that lasso their prey. *Nat. Hist.* 56:152–58, 189
25. Gertsch WJ. 1955. The North American bolas spiders of the genera *Mastophora* and *Agatostichus. Bull. Am. Mus. Nat. Hist.* 106:221–54
26. Haynes KF. 1990. Identification of sex pheromone of bristly cutworm, *Lacinipolia renigera* (Stephens). *J. Chem. Ecol.* 16:2615–21
27. Hodges RW, Dominick T, Davis DR, Ferguson DC, Franclemont JG, et al. 1983. *Check List of the Lepidoptera of America North of Mexico.* London: EW Classey
28. Hutchinson CE. 1903. A bolas throwing spider. *Sci. Am.* 89(10):172
29. Kaston BJ. 1948. Spiders of Connect-

icut. *Conn. State Geol. Nat. Hist. Surv. Bull.* 70:231–32, 638–39

30. Krombein KV, Hurd PD, Smith DR, Burks BD, eds. 1979. *Catalog of Hymenoptera in America North of Mexico*. Washington, DC: Smithsonian Inst. Press
31. Longman HA. 1922. The magnificent spider: *Dicrostichus magnificus* Rainbow. Notes on cocoon spinning and method of catching prey. *Proc. Roy. Soc. Queensland* 33:91–98
32. Lopes HS. 1985. A new genus of Sarcophagidae (Diptera) based on an Australian species living on spider egg cases. *Aust. Entomol. Mag.* 12(3,4): 51–53
33. Lopez A. 1987. Glandular aspects of sexual biology. See Ref. 39, pp. 121–32
34. Mascord R. 1970. *Australian Spiders in Colour.* Sydney: Reed Books
35. McCook HC. 1890. *American Spiders and Their Spinningwork,* Vol. 2. pp. 95–99. Philadelphia: HC McCook, Acad. Nat. Sci. Philadelphia
36. McKeown KC. 1952. *Australian Spiders*. Sydney: Sirius Books, Angus and Robertson (1963 revision by NL Roberts)
37. Mello-Leitão CF. 1925. Pequenas notas arachnologicas. *Bol. Mus. Nac. Rio de Janeiro* 1:455–63
38. Mello-Leitão CF. 1931. Contribuicao ao estudo da tribu Mastophoreas. *Ann. Acad. Brasileira Sci.* 3:65–74
39. Nentwig W, ed. 1987. *Ecophysiology of Spiders*. Berlin: Springer-Verlag
40. Newman JA, Elgar MA. 1991. Sexual cannibalism in orb-weaving spiders: an economic model. *Am. Nat.* 138:1372–95
41. Norris KR. 1991. General biology. In *The Insects of Australia,* ed. ID Naumann, PB Carne, JF Lawrence, ES Nielsen, JP Spradbery, et al, pp. 68–108. Melbourne: Melbourne Univ. Press. 2nd ed.
42. Robinson MH. 1982. The ecology and biogeography of spiders in Papua New Guinea. *Monogr. Biol.* 42:557–81
43. Robinson MH, Robinson B. 1970. Prey caught by a sample population of the spider *Argiope argentata* (Araneae: Araneidae) in Panama: a year's census data. *Zool. J. Linn. Soc.* 49:345–57
44. Robinson MH, Robinson B. 1972. The structure, possible function and origin of the remarkable ladder-web built by a New Guinea orb-web spider (Araneae: Araneidae). *J. Nat. Hist.* 6:687–94
45. Robinson MH, Robinson B. 1975. Evolution beyond the orb web: the web of the araneid spider *Pasilobus* sp., its structure, operation and construction. *Zool. J. Linn. Soc.* 56:301–14
46. Rule GS, Roelofs WL. 1989. Biosynthesis of sex pheromone components from linolenic acid in arctiid moths. *Arch. Insect Biochem. Physiol.* 12:89–97
47. Stowe MK. 1978. Observations of two nocturnal orbweavers that build specialized webs: *Scoloderus cordatus* and *Wixia ectypa* (Araneae: Araneidae). *J. Arachnol.* 6:141–46
48. Stowe MK. 1986. Prey specialization in the Araneidae. In *Spiders: Webs, Behavior, and Evolution,* ed. WA Shear, pp. 101–31. Stanford: Stanford Univ. Press
49. Stowe MK. 1988. Chemical mimicry. In *Chemical mediation of coevolution,* ed. KC Spencer, pp. 513–80. San Diego: Academic
50. Stowe MK, Tumlinson JH, Heath RR. 1987. Chemical mimicry: bolas spiders emit components of moth prey species sex pheromones. *Science* 236:964–67
51. Tumlinson JH, Mitchell ER, Teal PEA, Heath RR, Mengelkoch LJ. 1986. Sex pheromone of fall armyworm, *Spodoptera frugiperda* (J.E. Smith): identification of components critical to attraction in the field. *J. Chem. Ecol.* 12:1909–26
52. Vollrath F. 1987. Growth, foraging and reproductive success. See Ref. 39, pp. 357–70
53. Vollrath F, Parker GA. 1992. Sexual dimorphism and distorted sex ratios in spiders. *Nature* 360:156–59
54. Wong JW, Underhill EW, MacKenzie SL, Chisholm MD. 1985. Sex attractants for geometrid and noctuid moths: field trapping and electroantennographic responses to triene hydrocarbons and monoepoxydiene derivatives. *J. Chem. Ecol.* 11:727–56
55. Yeargan KV. 1988. Ecology of a bolas spider, *Mastophora hutchinsoni*: phenology, hunting tactics, and evidence for aggressive chemical mimicry. *Oecologia* 74:524–30