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A review of the anti-predator devices of spiders*

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Summary

The predators of spiders are mostly either about the same size as their prey (arthropods) or much larger (vertebrates), against each of which different types of defence have evolved. Primary defences include anachoresis, phenology, crypsis, protective resemblance and disguise, spines and warning coloration, mimicry (especially of ants), cocoons and retreats, barrier webs, web stabilimenta and detritus, and communal webs. Secondary defences are flight, dropping to the ground, colour change and thanatosis, web vibration, whirling and bouncing, autotomy, venoms and defensive fluids, urticating setae, warning sounds and deimatic displays. The anti-predator adaptations of spiders are extremely complex, and combinations of the devices listed frequently occur.

Introduction

The enemies of spiders are frequently mentioned in arachnological literature. In contrast, surprisingly few authors, with the notable exceptions of Bristowe (1941), Edmunds, J. & M. (1986), Main (1976) and Preston-Mafham, R. & K. (1984), have discussed at any length the various defences that have evolved specifically among spiders in response to predation. The intention of the present article has therefore been to review the literature on this somewhat neglected aspect of arachnology. No attempt, however, has been made to cite every minor reference to the various aspects of the topic. Nevertheless, it is to be hoped that most if not all of the more important publications on the subject have been quoted. Attack by dipteran parasitoids has not been discussed since, apart from fleeing, there is little that a spider can do to protect itself, and the literature on this topic is extensive. Neither kleptoparasitism (reviewed by Nentwig, 1985b; Vollrath, 1987) nor aggressive mimicry have received much attention either, except in so far as they are associated with escape from enemies rather than with the capture of prey.

Predatory enemies

Spiders and their eggs are eaten by a variety of animals. Bristowe (1941) devotes a long chapter to the enemies of spiders. In this, he includes mantids, earwigs, other spiders, fishes, frogs and toads, lizards, and birds. This list includes neither taxa of minor predatory significance nor parasitoids — ichneumons, chalcids, pompilid and sphecid wasps. (No attempt has been made in the present review to repeat the extensive observations cited by Bristowe (1939, 1941) on the defences of spiders). Foelix (1982) agreed that the principal enemies of spiders are spiders themselves. Many wandering spiders attack each other, and web-spinners often drive invaders away or kill and eat them. The pirate spiders (Mimetidae) that have been studied feed almost exclusively on other spiders, whilst certain Salticidae (*Portia* spp.) feed not only upon insects, but sometimes also on other jumping spiders, and even tackle large orb-weavers in their webs (see below). Several other families and genera, including Archaeidae, *Palpimanus* (Palpimanidae), *Argyrodes* and *Theridion* (Theridiidae), and *Chorizopes* (Araneidae) contain species that include other spiders in their diet. Sexual cannibalism has been reviewed by Elgar (1992). Other books in which the enemies of spiders are discussed include: Berland (1932), Bristowe (1958), Cloudsley-Thompson (1958, 1980), Edmunds (1974), Gertsch (1949), Main (1976), Millot (1949), Preston-Mafham, R. & K. (1984), Savory (1928), Thomas (1953) and Wise (1993). (For earlier references, see Warburton, 1909).

The major predators of spiders fall into two categories: (a) those about the same size as their prey (mainly arthropods) and (b) those much larger than their prey (mainly vertebrates): against each of which different types of defence have evolved. Spider eggs, for instance, may be protected from predation by earwigs by means of the barrier imposed by their thick cocoons, while the crypsis of the cocoons is largely effective against lizards and birds, which do not see them. Some enemies prey only on spiders (Mimetidae and wasps), many others take spiders occasionally, along with insects. One type of defence may operate against several different kinds of predator, and more than one defence may be effective against the attacks of a single kind of predator. Losses due to natural enemies may well contribute significantly to the apparent lack of exploitative competition among spiders according to Wise (1993), but it has not yet been demonstrated experimentally that enemies limit the population densities of spiders, or that competition would occur among spiders if these were to be removed. Wise (1993) has recently summarised the extensive research carried out by himself, T. W. Schoener and D. A. Spiller on the natural enemies of spiders.

Primary defences

Primary defences are defined as those which operate regardless of whether a predator is in the vicinity or not: they reduce the chance of an encounter between predator and prey, and include living in a burrow or hole, some forms of protective coloration, and the avoidance of detection by sight or sound (Cloudsley-Thompson, 1980; Cott, 1940; Edmunds, 1974).

Anachoresis

Many otherwise defenceless animals spend almost their entire lives hidden from predators in crevices, beneath bark or in holes in the ground. Such recluses are known as "anachoretes" (from the Greek word meaning "one who has withdrawn himself from the world") (Edmunds, 1974). It must be remembered, however, that even those spiders that are anachoretes need to emerge in order to feed and mate. For example, most of them

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*The survey of literature pertaining to this review was concluded on 31 December 1993.

are sit-and-wait predators and, like many Theraphosidae and Lycosidae, dart from their lairs to capture prey. In summer, male *Aphonopelma* sp. (probably *A. chalcodes* Chamberlin) (Theraphosidae: Grammostolinae) leave their burrows and are to be found at night, wandering across the Sonoran desert in search of sedentary mates. They are also not infrequently seen in daylight, especially after storms. At most times, crypsis is valuable since the intensity of moonlight in the clear desert air is surprisingly high. Even when there is no moon, starlight alone can be very bright in the desert. In tropical America, theraphosids hide in hollow trees and make a web over the surface of an opening in the bark. At night, as they sit behind the web, they can be seen with the aid of a flashlight but, during the day, the white patch looks just like any other light patch on the bark of the tree (H. W. Levi, in litt.). Salticids in the moist tropics hang on a thread at night, protected thereby from some nocturnal predators, while most Zodariidae hide in the ground during the day.

Various species of Lycosidae have burrowing habits, the burrows being dug with the chelicerae. Small packets of soil are bound with silk and transported by the chelicerae to a disposal dump outside the burrow. Bristowe (1958) has illustrated how the cryptic *Arctosa perita* (Latreille) draws a curtain of silk across the entrance to its burrow, making this invisible to human eyes — but not safe from pompilid wasps. The Australian *Lycosa snelli* McKay stops the entrance to its burrow with a pebble seated on a cushion of silk. "It is disconcerting when watching a spider peering out of its open hole amongst a scatter of angular pebbles to suddenly realise it has vanished, spider *and hole*!" (Main, 1976: 141). According to Miller (1984), the tendency for *Geolycosa turricola* (Treat) and *G. micopany* Wallace to build new burrows in crevices and surface irregularities may be advantageous in providing protection from predators, as well as in thermoregulation and foraging.

Preston-Mafham, R. & K. (1984) give several illustrations of the silken doors of trapdoor spiders, including the North American *Cyclocosmia truncata* (Hentz). This is protected, not only by a normal hinged trapdoor but, when molested, the spider retreats head first down its gradually narrowing burrow until its armoured abdominal shield fits exactly, and covers the hole above the spider, which cannot then be pulled out without damage. Main (1976) describes numerous similar adaptations among Australian Mygalomorphae. Several species of trapdoor spiders and some theraphosids have independently evolved dummy arms and emergency exits to their burrows so that, if the burrow is discovered by an enemy, the spider may yet escape. In addition to a trapdoor, the burrows of *Idiops pylorus* Schwendinger (Idiopidae) have a movable soil pellet attached to a silken collar and resting in a chamber in the side of the burrow. If disturbed, the spider pulls the collar downwards and plugs the passage (Schwendinger, 1991). A similar defence mechanism is employed by *Stanwellia nebulosa* (Rainbow & Pulleine) (Nemesiidae) (Main, 1976).

Phenology

The temporal distribution of spiders may reduce predation and thereby be defensive. Diurnal rhythms of activity enable nocturnal species, such as many Dysderidae, Gnaphosidae, Clubionidae, Corinnidae and Amaurobiidae to avoid day-active predators, while numerous orb-weavers (Araneidae) remove their webs during the day (Carico, 1986; Eberhard, 1972; Edmunds, J. & M., 1986). Some araneids (e.g. *Metazygia* and *Hypognatha* spp.) build very rapidly, just as the sun goes down, thereby avoiding visual predators and capturing insects that emerge at dusk (W. G. Eberhard, in litt.). Little attention has been paid to the adaptive significance of diurnal rhythms of locomotory activity in spiders, but it has been argued that biotic factors, especially predation, predominate in determining the time of spider activity (Cloudsley-Thompson, 1978). In a comparison of rhythmic locomotory activity in tropical forest Arthropoda with that in desert species, it was found that the former tend to be much less active than desert forms and that their rhythms of activity are far less marked. They are also less nocturnal: this may well be interpreted in relation to the greater degree of exposure to predation in the desert where it is dangerous and perhaps too hot to sit and wait for prey in the open during the day (Cloudsley-Thompson, 1981). Thermal considerations must undoubtedly also be relevant.

Crypsis

Probably most day-active spiders escape the notice of predators, and suffer less predation, thanks to their cryptic or concealing coloration and behaviour. Many Salticidae, for instance, such as *Menemerus semilimbatus* (Hahn) are quite inconspicuous unless they move, which they must do to capture prey. A cryptic spider, therefore, has two possible solutions to the problem: either it can remain motionless during the hours of daylight and be active at night, or it can move very slowly and stealthily during the day (like *Portia* spp.: see below) (Preston-Mafham, 1991). There are, however, some notable exceptions to this generalisation, especially among fast-moving hunting spiders. The wolf spider *Arctosa perita* (Lycosidae) for instance, an inhabitant of dunes throughout Europe and the Mediterranean region, has a mottled coloration much like that of the sand on which it lives. When disturbed, it moves very rapidly and then stops abruptly, blending so well with its background that it becomes almost completely invisible to the human eye, just as insects with flash coloration (Cott, 1940) seem to vanish when they become still. This may be typical of wolf spiders in general (M. Edmunds, in litt.). The North American *A. littoralis* (Hentz) is similar in appearance and mode of life. Despite their marked crypsis, spiders of the genus *Arctosa* are temporary anachoretes (Edmunds, 1974) and spend much of the time in silk-lined burrows from which they pounce on passing prey (Preston-Mafham, R. & K., 1984). The great diversity of colour patterns found in *Arkys roosdorpi* (Chrysanthus) (Mimetidae) enables these spiders to resemble multi-coloured fragments of plant debris on the forest floor according to Robinson (1980); but in fact, they are nearly always to be found on shrubs and tall grass. This, nevertheless, may not invalidate Robinson's (1980) claim (W. G. Eberhard, in litt.), although it is very difficult to acquire a search image for, and to find these spiders (H. W. Levi, in litt.). Some species of *Arkys* may well mimic birds' droppings (see below) since they rest on the surface of leaves with all their legs folded in, creating a uniform outline without projections (Y. D. Lubin, in litt.). R. R. Jackson (in litt.) points out that even if *Arkys* spp. are indeed mimetids and not Araneidae, in which family they were formerly placed, they are probably non-araneophagic.

The bark of trees is a favoured habitat for cryptic spiders. Many species, belonging to several different families, spend the entire day in full view on the bark of trees. The greatest number, and some of the best camouflaged examples, live in tropical rainforest. Many species of Hersiliidae, such as *Hersilia caudata* Audouin, exhibit this habit and, in common with almost all bark-dwelling spiders, their bodies tend to be flattened and cast little shadow that might otherwise betray them. Selenopidae, which are also flattened, hide underneath the bark during the day, and emerge at night. *Stephanopis altifrons* O. P.-Cambridge (Thomisidae), *Herennia ornatissima* (Doleschall) (Tetragnathidae) and *Pandercetes gracilis* L. Koch (Heteropodidae) are well illustrated by Preston-Mafham, R. & K. (1984), the last named species showing a remarkable resemblance to lichen (see below). *Araneus bicentenarius* (McCook) looks like a lichen and is difficult to locate among lichens on the bark of trees (H. W. Levi, in litt.). *Drapetisca socialis* (Sundevall) and *D. alteranda* Chamberlin (Linyphiidae) of temperate regions are also cryptic on bark, but very much smaller in size than the tropical species mentioned earlier.

The unusual appearance and cryptic posture when at rest of *Portia fimbriata* (Doleschall) (Salticidae) are adaptations that conceal the spider from many predators. It is extremely cryptic and difficult to distinguish from its background when standing on silk or debris in a web or on a tree trunk or rock. Even when seen, it is often not recognisable as a spider on account of its protective resemblance to debris. Additional antipredator adaptations are associated with locomotion since the spider moves very slowly and jerkily, some movements taking much longer than others. When walking, *P. fimbriata* does not at all resemble an animal (Jackson, 1986a). Some Homalonychidae actually camouflage their bodies with debris (Roth, 1984). Robinson (1969) has reviewed the subject of defences against predators that hunt visually.

Protective resemblance and disguise

Although the selective process resulting in protective resemblance is probably the same as that which produces mimicry, it is often convenient to restrict the latter term to instances in which one animal looks like another, and to use the words disguise or special protective resemblance in cases where an animal looks like a stick, bark, lichen, a stone, or some other inanimate object that is of no significance or interest to potential predators (Cott, 1940). Even so, it must be realised that crypsis, disguise, special protective resemblance and mimicry tend to blend into one another, and thus render precise definition difficult. For instance, should the resemblance of the bolas spider *Mastophora bisaccata* (Emerton) (Araneidae) to a snail shell (Atkinson, 1888) be regarded as mimicry or protective resemblance? According to Gertsch (1955: 230), "The resemblance of the mastophorids to common objects has been mentioned in many reports on the group and the inference has been drawn that they derive some protection from it. Their lumpy bodies, prolonged inactivity, and close correspondence to the forms and colors in their microhabitats contribute to make plausible such characterizations". *Mastophora carpogaster* Mello-Leitão is said to look like a raspberry (Mello-Leitão, 1925). Again, some spiders that are cryptic from a distance display protective resemblance when seen close up. Starrett (1993) uses the term "adaptive resemblance" to unify the concepts of mimicry and crypsis.

Araneus spp. often have brown abdomens patterned with the outline of a leaf which helps to improve their camouflage. They hide in the debris of fallen leaves and are difficult to recognise as they spend their days curled up in dead leaves. Many green spiders are very hard to see on the undersides of leaves when looking up (e.g. *Modisimus* spp. (Pholcidae) and *Synotaxus* spp. (Synotaxidae)) according to W. G. Eberhard (in litt.). Deeleman-Reinhold (1986a,b) pointed out that the females of many leaf-dwelling species of tropical rainforest Pholcidae carry elongated egg-parcels. When sitting adjoining a leaf-rib, the legs are spread out and resemble lateral veins and the spiders are well camouflaged: but individuals often sit away from the rib and then can easily be spotted. They remain motionless during the day and move mainly at night. *Agalenatea redii* (Scopoli) (Araneidae) habitually sits on the brown seed-heads of thistles and knapweeds where it resembles a dry fruit, *Portia schultzi* Karsch like all *Portia* spp. (Salticidae) is a detritus mimic, *Tetragnatha extensa* (L.) (Tetragnathidae) and *Tibellus* spp. (Thomisidae) are inconspicuous on stalks of grass, while *Deinopis longipes* F. O. P.-Cambridge (Deinopidae) closely resembles a twig. *Caerostris* spp. (Araneidae) resemble buds or knots on a branch (Ward, 1979), while *Dolophanes* spp. (Araneidae) look like the bases of broken twigs (Main, 1976).

An often quoted example of protective resemblance is afforded by *Phrynarachne decipiens* (Forbes) (Thomisidae). This South-east Asian crab-spider constructs an irregularly-shaped film of web on some prominent dark green leaf. On this the whitish, wrinkled spider looks like the central dark portions of the excrement of a bird, while the thin web resembles the marginal watery portion becoming dry and trickling off the leaf (Cott, 1940). In addition, the spider actually smells of dung. Although this disguise may be an example of alluring coloration or aggressive mimicry — many butterflies regularly feed on birds' droppings — it is probably even more important as an anti-predator device. The sharp eyes of a bird are better able to distinguish between excrement and a spider than are the compound eyes of a butterfly. Therefore predation by birds would be a more important factor in natural selection than the attraction of food items. Brèthes (1909) drew attention to the case of *Mastophora extraordinaria* Holmberg which, like other *Mastophora* spp., closely resembles bird droppings. Other examples of resemblance to birds' droppings are illustrated by Preston-Mafham, R. & K. (1984).

Mastophora spp. are sometimes known as "bird-lime" spiders because they resemble bird droppings so closely. *M. dizzydeani* Eberhard does not attempt to flee when disturbed — as might be expected from a cryptic species or one which displays protective resemblance. It crouches, immobile, even when picked up, and discharges a fluid having a disagreeable odour reminiscent of that of lampyrid beetles. The fluid is regurgitated from the mouth: later it is sucked back and the mouth parts cleaned. *Cyrtarachne* sp. (Araneidae) also produces a fluid with an unpleasant odour, according to Eberhard (1980), as does the bolas spider *M. cornigera* Mello-Leitão (Hutchinson, 1903). Over a century ago, Peckham (1889: 76) wrote: "As a general rule the forms and colors of spiders are adapted to render them inconspicuous in their natural homes. Bright coloured spiders, except where sexual selection has been at work, either keep hidden away or are found upon flowers whose tints harmonize with their own". Although *Thiania* spp. are brightly coloured iridescent salticids which live on leaves, not flowers, they are nevertheless cryptic (Jackson, 1986c). *Epicadus heterogaster* (Guérin) (Thomisidae) is a leaf-dwelling species disguised as a flower rather than simply camouflaged (Robinson, 1980). Some crab spiders double themselves up at the bases of leaf stalks so that they look like flower buds, and hunting spiders are also sometimes disguised in a similar manner. They station themselves in the axils of leaves and other parts of plants, drawing in their legs so that they resemble buds. The function of all this could be aggressive but, as in the case of *Phrynarachne decipiens*, the anti-predator role is probably more important. Several Thomisidae and some of the Araneidae are able to change colour so that they match their backgrounds, a useful attribute to sit-and-wait predators resting in flowers. *Gea heptagon* (Hentz) and a few other araneids also change colour rapidly after dropping from the web (Sabath, 1969 — see below). This is possibly also an example of flash coloration (Cott, 1940). Coloration in spiders has been reviewed by Holl (1987).

Spines and warning coloration

Some spiders, especially *Gasteracantha* and *Micrathena* spp. (Araneidae), are covered by a leathery integument and an armature of strong, sharp spines. In some cases, where the spiders are cryptically coloured, these spines may help to break up the outline of the abdomen; but in others, where their owners have brilliant colours and hang, always exposed, in the centre of the web, it is probable that their function is defensive (Peckham, 1889; Robinson, 1980) perhaps by rendering them relatively inedible to birds or too large to fit into a wasp's nest. Of course, no defence is perfect and some do get eaten. It is also possible that spines may be a cooling device much needed by a spider that hangs on its web in the sun. No doubt the spines have more than one function.

Muma & Jeffers (1945) found only 8 small spiny *Micrathena* sp. out of 1,000 araneids in the nests of mud-dauber wasps (*Sceliphron caementarium*). *Micrathena* spp. hang in the centres of their webs. Their long fourth legs enable them to hold the abdomen horizontal. The dark colours of the underside, which is above in this position, and the bright colour of the dorsum, which is below, makes it very difficult to find them (Levi, 1985, 1986). Edmunds, J. & M. (1986) produced evidence that conspicuous morphs of *G. curvispina* (Guérin) survived longer than cryptic morphs. According to Robinson (1980), *G. brevispina* (Doleschall) is the only species of *Gasteracantha* in New Guinea that does not have aposematic coloration and its spines are poorly developed.

Conspicuous red markings on the jet black abdomens of "widow" spiders (*Latrodectus* spp.: Theridiidae) may well represent warning coloration associated with potent neurotoxic venom, but this has been disputed (see below). Hinton (1976) suggested that the red patches of the female *Misumena vatia* (Clerck) might also function as some kind of "warning colour for birds and other vertebrates, which are not red-blind"; but I find this conclusion somewhat unconvincing because the red patches are quite small. Nor is there any evidence that *M. vatia* is distasteful or in any way unpalatable.

Mimicry

As long ago as 1889, Elizabeth Peckham had reviewed protective resemblance and mimicry in spiders, and Pocock (1909) described a number of additional instances. The models he listed included snails, beetles, ants and mutillid wasps. The male *Eresus cinnaberinus* (Olivier) (Eresidae) is thought to mimic a ladybird beetle (Coccinellidae) and *Argiope* spp. (Araneidae) are sometimes referred to as "wasp spiders". It is significant that the male *E. cinnaberinus* is the only instar which runs on the surface of the ground; the female and all other developmental stages are black and hidden in burrows (P. Merrett, in litt.). Batesian mimicry of ants (Formicidae) and, to a lesser extent, of Mutillidae is widespread throughout the world, especially in the tropics. The families of spiders involved include Thomisidae, Aphantochilidae, Araneidae (males of some *Micrathena* spp.), Theridiidae, Gnaphosidae, and Zodariidae, but the phenomenon is most marked among Corinnidae and Salticidae. Ants are presumably unpalatable to many reptiles and birds which do not eat them but feed readily on other insects: ants are aggressive, bite, sting or spray formic acid. Ant mimicry of course would be no defence against those lizards and birds that specialise on eating ants: but an ant mimic with good eyesight (e.g. a salticid) might well see a predator approaching and take evasive action, whereas ants have poorly developed sight and would not do so.

Ant-mimicking spiders have long, slender legs and, in some species, the pedicel is constricted so that it resembles the waist of an ant. Alternatively, pale bands across the body may contribute to the deception. In several genera (e.g. *Myrmarachne, Zuniga*: Salticidae), the chelicerae or enlarged pedipalps are extended forwards so that they resemble the mandibles or entire head of an ant, and this is accompanied by corresponding coloration.

Most ant-mimicking spiders use the first or second pair of legs as "antennae": the terminal portion of the raised legs may be covered with dense hairs which give the impression of a club, as in *Zuniga magna* Peckham. Some spiders mimic the compound eyes of ants with pigment spots on the prosoma (e.g. *Myrmarachne plataleoides* (O. P.-Cambridge)), chelicerae or pedipalps (Oliviera, 1988; Reiskind, 1977). Others (e.g. *Mazax, Myrmecium*: Corinnidae) and *Zuniga* spp. possess transverse bands of pigmented hairs on the abdomen which resemble the segmentation of an ant's gaster (see review by McIver & Stonedahl, 1993). The rugose and usually shiny appearance of an ant's cuticle is achieved by microstructural modifications of the spider's integument, including glistening, scale-like setae and dense mats of reflective hairs. Scattered plumose hairs on the prosoma and opisthosoma of *Mazax pax* Reiskind accurately mimic the shining troughs on the head, alitrunk and petiole of its model, *Ectatomma ruidum* (Reiskind, 1977), while *Aphantochilus rogersi* O. P.-Cambridge (Aphantochilidae) has an integument similar in appearance to that of its models *Zacryptocerus* spp. and *Cephalotes atratus*. The lateral spines on the cephalothorax also correspond to the thoracic spines of these ants (Oliveira & Sazima, 1984).

In the castianeirine spider *Pranburia mahonnopi* Deeleman-Reinhold (Corinnidae) of Thailand, the first pair of legs bears a thick brush around the distal part of the femur. When disturbed, the spider joins the femora together in front of and slightly above the prosoma. In this way, the illusion of an ant's head is created, while the tibiae and metatarsi are waved in the air so that they look like antennae (Deeleman-Reinhold, 1993).

A particularly interesting deception is practised by thomisid spiders that carry a dead ant on their backs, thus resembling ants carrying dead ants (Bristowe, 1941). Furthermore, the spiders exhibit ant-like movements, vibrating their front legs, moving their abdomens and walking in the manner of ants. *Myrmarachne lupata* (L. Koch) has an unusual method of preying on insects by lunging instead of leaping, after pre-attack tapping. This is consistent with the maintenance of ant mimicry (Jackson, 1986b). The unusual features of the predatory and nesting behaviour of *Myrmarachne* spp. are important in enabling these spiders to preserve their ant-like appearance (Jackson & Willey, 1994).

Although a few elongate forms of *Myrmarachne* (e.g. *M. foreli* Lessert) might be mistaken for reeds or stems, the majority are ant-like in appearance and are considered to be mimics although the majority of these species have no known models. The range of ant mimicry varies from species-specific to generalised, in which no single species of model can be designated. Only certain distinctive species can properly be described as ant mimics according to Wanless (1978, cf. Edmunds, 1978). *M. plataleoides* mimics the Indian weaver ant *Oecophylla smaragdina* (Mathew, 1954), and *M. foenisex* Simon the African *O. longinoda* (Collart, 1929a,b, 1941).

At Legon in Ghana, each species of *Myrmarachne* is positively associated with different, mutually exclusive, species of ants. Thus, *O. longinoda* is the model for *M. foenisex*; *Camponotus acvapimensis* for *M. legon* Wanless; and *Tetraponera anthracina* for *M. elongata* Szombathy. The early instars of these spiders mimic smaller species of ants than do the adults — *Crematogaster castanea, Acantholepis* sp. and *Cataulacus* sp., and *Pheidole megacephala*, respectively, in the case of *M. foenisex, M. legon* and *M. elongata*. In *M. foenisex*, the model for the young spiders is positively associated with that for the adults, so that it is easy for the young spiders to remain associated with an appropriate species of ant as they grow older. No such association is seen in the models for young *M. legon* and *M. elongata*, but these are so numerous that it is likely that the spiders associating with them will find the correct models when they become adult (Edmunds, 1978).

In their review of the ethology of jumping spiders, Richman & Jackson (1992) agreed that the ant-like salticids must be Batesian mimics (Edmunds, 1974) although evidence to support this presumption is scarce. However, Engelhardt (1970) has shown that blue tits (*Parus caeruleus*) fail to distinguish between ants (*Lasius niger*) and their mimic *Synageles venator* (Lucas) (Salticidae) while Edwards (1984) demonstrated that lizards which feed on other invertebrates will not prey on mutillid wasps and ignore the salticid *Phidippus apacheanus* Chamberlin & Gertsch which, he claimed, mimics them.

The subject of myrmecophilous spiders has also been discussed by Parker & Cloudsley-Thompson (1986), who listed numerous references to the mimicry of ants and other arthropods by spiders. For instance, the males of *Cosmophasis nigrocyanea* (Simon) (Salticidae) resemble ants while the females look like mutillid wasps (Cloudsley-Thompson, 1991). Yet another instance of ant mimicry is provided by *Seothyra henscheli* Dippenaar-Schoeman (Eresidae): adult males mimic the ant *Camponotus detritus* in the western and central Namib. They are active during the day in early winter, when the temperature is lower than in summer, moving on the sand surface in search of females' burrows. In the eastern Namib, where *C. detritus* is absent, males of *S. henscheli* mimic another species of *Camponotus* (Y. D. Lubin, in litt.). According to Curtis (1988), this is *C. fulvopilosus*, a more widespread but not sympatric species of ant. *Cosmophasis* spp. feed on their models, but whether they actively catch and kill the ants, which are larger than themselves, or merely take workers that are weakened, injured or recently dead, remains to be determined. When an ant and a spider were confined together, "the spider came off worse, suggesting that if they do actively prey on ants, they would have to rely on stealth, surprise and speed to catch their prey. Thus this behaviour cannot really be regarded as aggressive mimicry" (p. 69). Numerous salticids, including species of at least four genera (*Agassa, Sassacus, Cylistella* and *Coccorchestes*) resemble chrysomelid beetles. *Orsima formica* Peckham & Peckham is apparently a generalised insect mimic in reverse (Reiskind, 1976). Several other species of spiders likewise mimic ants in reverse, with the opisthosoma and spinnerets resembling an ant's head and antennae. This could be aggressive mimicry (see below).

A common predator of spiders at Legon, Ghana, is the sphecid wasp *Pison xanthopus*. Its prey, according to Edmunds (1993) consists mainly of salticid spiders (96%). Comparison of species in the wasps' cells with those found in nearby vegetation indicated that fewer ant mimics (*Myrmarachne* spp.) were taken than would be expected if the wasps were capturing salticids in proportion to their occurrence. (This, of course, assumes that all species were equally available to the wasps). Moreover, some individual wasps specialised in capturing *Myrmarachne* spp., others *Rhene* or *Pseudicius* spp. (Salticidae). This implies that sphecids hunt visually, and may be using a "search image" like birds. (Chalcids probably use scent and touch rather than sight — M. Edmunds, in litt.). Again, Jocqué (1988) did not find any *Myrmarachne* spp. in the prey of mud-dauber wasps, *Sceliphron spirifex*, although many other species were captured. By means of choice experiments using *Phidippus clarus* Keyserling (Salticidae) and *Tibellus* spp. (Philodromidae) as predators, Cutler (1991) showed conclusively that *Synageles occidentalis* Cutler (Salticidae) benefits from its resemblance to ants.

Berland (1932), Bristowe (1941), Donisthorpe (1927), Edmunds (1978), Hingston (1927b), McIver & Stonedahl (1993), Oliviera (1988) and others, list numerous examples of mimicry by spiders of ants and Mutillidae. Preston-Mafham, R. & K. (1984) illustrate a *Myrmecium* spp. (Corinnidae) which is almost indistinguishable from *Megalomyrmex* spp., an *Aphantochilus* sp. (Aphantochilidae) which mimics *Cephalotes* spp. and the male of *Cosmophasis* sp. which, as mentioned above, mimics ants. Ant mimics are probably only rarely aggressive mimics as well as Batesian mimics: the exceptions, according to Bristowe (1941), are in the families Thomisidae, Aphantochilidae, Theridiidae and Zodariidae. However, as Reiskind & Levi (1967: 20) wrote of *Anatea formicaria* Berland (Theridiidae): "while it is unlikely that the mimicry would deceive an ant, the occurrence of the spider near the ants (a prey-predator relationship) could account for strong selection pressure applied by predators of the spider". A similar view has been expressed by Edmunds (1993) with respect to *Myrmarachne* spp. Harkness (1976) noted that the myrmecophagous spider *Zodarion frenatum* Simon (Zodariidae), when carrying its prey (*Cataglyphis bicolor*) is not attacked by other members of the colony, and Couvreur (1990) observed the same when *Z. rubidum* Simon is carrying an ant of the species *Formica cunicularia*. While holding an ant not belonging to the same colony, however, it is attacked violently and forced to release its prey.

A convincing example of aggressive mimicry is afforded by the adult *Amyciaea forticeps* (O. P.-Cambridge) (Thomisidae) which attacks *Oecophylla smaragdina*. Although it does not closely resemble its model in appearance, it adopts a form of behaviour while hunting which makes it look like a dying or struggling ant. When worker ants draw near to investigate, the spider pounces on them (Mathew, 1954). Again, *Aphantochilus rogersi* (mentioned above) not only mimics ants of the genus *Zacryptocerus*, but is a specialised predator of them (Oliviera & Sazima, 1984). Trimen (1885) pointed out that hunting spiders are, in size, colouring, and movement sometimes very like the flies on which they prey: but this is probably an example of speed mimicry rather than of aggressive mimicry. Speed mimicry is the name given to cases in which the model is a fast-moving species, not worth chasing. (Mimicry of jumping spiders by tephretid flies is discussed below).

A mimicry complex between Mutillidae and spiders has been described by Nentwig (1985a) in which a group of Müllerian models is imitated by various Clubionidae and Salticidae. Only one termite-mimicking spider has so far been recorded. This is *Thaumastochilus termitomimus* Jocqué (Zodariidae) which lives on trees where it constructs a silken retreat (Jocqué, 1994). It joins the ranks of those strange cases such as that of the salticid spider *Cheliferoides segmentatus* F. O. P.-Cambridge which mimics pseudoscorpions (Platnick, 1984), as well as mimics of flies (see above), and other insects.

In tests on the gut contents of field-collected predators, a strong correlation was found between attack rates for each predator-prey pair, as measured in the laboratory, and per cent positive reactions, as measured among field-collected predators. In particular, the antiserum of the aposematic bug *Lopidea nigridea* has been shown by enzyme-linked immunosorbant assay to be significantly less reactive against the crab-spider *Xysticus montanensis* Keyserling when compared with that of the related ant-mimicking bug *Coquillettia insignis*, thus paralleling the results of laboratory no-choice experiments (McIver & Tempelis, 1993). When specimens of *L. nigridea* were offered to the spiders under controlled conditions, 83% rejected them after attack, compared with a rejection rate of 0% for *C. insignis* (McIver, 1989). This provides further evidence of the value of ant mimicry.

Cocoons and retreats

Not only do cocoons and retreats help to control the ambient climatic conditions to which the eggs of spiders are exposed, but they afford protection from enemies (Nielsen, 1932). Austin (1985) has reviewed the literature on the insect predators and parasitoids of spiders and found a close relationship between cocoon architecture and the mode of attack by enemies. He suggested that this might have been evolved through a process of co-evolution. As spiders gradually reduced the total number of predators and parasites capable of reaching their eggs, insects evolved that specialised on different types of cocoon.

In testing this hypothesis, Hieber (1984) demonstrated that the dense cover and flocculent silk layers of the cocoons of both *Mecynogea lemniscata* (Walckenaer) and *Argiope aurantia* Lucas (both Araneidae) act as specific barriers to oviposition by parasitic Diptera, Mantispidae and Hymenoptera. They are also effective barriers against small generalist predators such as ants, but fail to stop large generalists such as birds. Cocoon covers are effective not only against generalist predators, but also against attack by specific guilds of predators, such as burrowing larvae; while flocculent silk is a deterrent to specialist parasitoids with long ovipositors (Hieber, 1992). Although Austin (1985) suggested that cocoon covers might be effective against generalist predators, Hieber (1992) found that they contributed little to prevent access by ants or birds.

Males and females of the theridiid species *Achaearanea globispira* Henschel & Jocqué inhabit spherical retreats composed of silk, sand and pebbles dangling from a rock or branch. Their structure has a tiny opening at the bottom which leads into a spirally-coiled tunnel. Males and females build spirals in opposite directions which enables the male to construct his retreat against that of the female in such a way as to form a brood chamber. The configuration of the narrow, suspended retreat may decrease the spiders' vulnerability to enemies while foraging for ants in a typical theridiid fashion. Packing a relatively long tunnel into a globule minimises the amount of material required as fortification, and the tunnel is not a cul-de-sac because a threatened spider could break out through the sealed central chamber. This would permit escape from parasitoid wasps and araneophagous spiders that invade the tunnel (Henschel & Jocqué, 1994).

Spiders of many kinds lay their eggs inside their retreats, and different types of cocoons and retreats may occur within the same family. Foelix (1982) quotes examples from the Salticidae, Clubionidae and Gnaphosidae, citing Holm (1940) who claimed that, when the walls are camouflaged, the females' guarding of the eggs becomes superfluous. With this I disagree: camouflage is effective only in relation to large predators against which it would not be possible to defend the eggs, while small enemies, apart from Salticidae, tend not to be visual hunters. A silk-lined retreat also provides both a defensive mechanism and mechanical protection for orb-weaving spiders, many of which are unwilling to leave their retreats during the day. Indeed, many tropical araneids have a web present only during the night. According to Edmunds, J. & M. (1986), this would not be feasible in temperate regions when the nights are short. Nevertheless, H. W. Levi informs me (in litt.) that *Acacesia* sp., a night-web araneid, common in the south-eastern United States, and *Eustala* spp., which are found as far north as New England, also take their webs down during the day.

Grasshoff & Edmunds (1979) suggested that the free sector in the web of many Araneidae may have evolved to allow the spider to respond rapidly to prey while, at other times, remaining hidden in the retreat. This was first proposed by Wiehle (1927). The igloo-shaped retreat of *Zodarion, Diores* and some other zodariid genera is an interesting means of survival in the vicinity of ants' nests (R. Jocqué, in litt.). *Thiania demissa* (Thorell) (Salticidae) makes a nest by binding together a pair of green leaves by means of a crudely circular or elliptical array of silken rivets — usually 6–10. The nest is spun between these leaves, and here the juvenile spiders moult and adult females lay their eggs (Jackson, 1986c).

Barrier webs

Barrier webs form an integral part of the support system of the orb webs of many tropical Araneidae and the suggestion has been made that they may have the function of preventing certain predators from reaching the spider that spins them, and also of giving warning of an enemy's approach. This may sometimes be even more important than their supportive function according to Edmunds, J. & M. (1986), Lubin (1975) and Tolbert (1975). W. G. Eberhard (in litt.) finds this argument unconvincing because in many cases (e.g. *Nephila, Leucauge, Metepeira, Philoponella* spp.) the barrier web can be cut completely away without damaging the orb web. The spider remains in the centre of a three-dimensional orb web in the case of the Uloboridae and, when disturbed, assumes a stick-like, cryptic posture oriented along its resting thread with the first and second pairs of legs held straight forwards and the fourth pair straight behind. The small, third pair holds the resting thread or the substrate but pressed close to the body and does not break the stick-like outline (Lubin, Eberhard & Montgomery, 1978). Defence lies in crypsis rather than in the barrier web.

Web stabilimenta and detritus

In certain cases of protective resemblance, an animal resembles some object that is normally avoided or ignored by its predators. Sometimes, however, the animal alters its surroundings so that it blends into them. Orb-web spiders occasionally make a number of dummies of themselves, thereby decreasing the chances of attack (Hinton, 1973). Many spiders which remain on their webs during the day rest near objects they have fastened to the web. These objects are usually called "stabilimenta" when found in orb webs made by diurnal spiders in the families Uloboridae and Araneidae. Stabilimenta consist of bands or tufts of silk, egg sacs and detritus (Eberhard, 1973, 1990). Although egg sac and detritus stabilimenta are generally thought to serve as camouflage (e.g. Bristowe, 1941; Cloudsley-Thompson, 1980; Gertsch, 1949; Hingston, 1927a), the function of silk stabilimenta has been controversial. If the term "stabilimentum" were to be restricted to bands of silk (possibly to tufts, although these may incorporate cocoons or eggs), then much confusion would be avoided (J. Edmunds, in litt.). W. G. Eberhard (in litt.) comments, however, that information might also be lost as a result of this. For instance, *Cyclosa* spp. make detritus stabilimenta when detritus is present, but silk stabilimenta when no detritus is available!

Tilquin (1942) summarised early hypotheses regarding the function of silk stabilimenta as follows: (a) consolidation and strengthening the web, (b) as a site for mating, (c) as a platform for moulting, (d) for storing the carcasses of prey, and (e) for providing camouflage from predators: only the last of these seems tenable today. Another hypothesis, recently proposed by Craig & Bernard (1990), is that the stabilimentum reflects ultraviolet light and thus attracts insect prey to the web. These authors found that primitive spiders produce silks that reflect UV light and that primitive aerial weavers spin UV-reflecting catching silk which attracts *Drosophila* spp. *Argiope* spp. (Araneidae) produce catching silk that reflects little UV (or visible light), but decorate their webs with UV-reflecting bars and crosses that were shown, experimentally, to attract prey which are intercepted: this is not a defensive function. (For further discussion of the function of spider webs, see Eberhard, 1990). Hingston (1927a) listed what he claimed to be no less than 22 different devices among orb-web spinners worldwide. There are many variations on the common theme.

Silken stabilimenta were first thought to stabilise webs, as their name implies, by strengthening the connections between hub threads. Eberhard (1973) listed many other suggestions that have been made regarding their function and used evidence from construction behaviour to suggest that stabilimenta are anti-predatory devices. Horton (1980) provided experimental evidence that predatory birds dislike coming into contact with spider silk and hence learn to avoid webs with stabilimenta; while Eisner & Nowicki (1983) claimed, on the basis of somewhat limited data, that webs endowed with artificial equivalents of stabilimenta tended to survive intact during the early hours of the morning when birds are on the wing, while unmarked webs showed a high incidence of destruction. This does not, however, militate against the function of concealment from predators, although Robinson, M. H. & B. (1970, 1973) argued that the stabilimentum is an improbable defence against predators — pointing out, among many other things, that stabilimenta are frequently incomplete. This fact could, however, equally well be used in support of the anti-predator hypothesis (Edmunds, J., 1986). Ewer (1972) pointed out that a variable device lessens the chances of a predator associating any particular shape with its prey — i.e. there are more search images to be learned.

Other contributors to the discussion include Lubin (1975) who found that stabilimenta are infrequent where there are few predators that hunt visually, and Rovner (1978) who noted that *Cyclosa turbinata* (Walckenaer) (Araneidae) carries detritus from one web to another, while the spider's own size and coloration resembles a cluster of such detritus. Consequently, the spider is difficult to distinguish among the line of debris and egg cases that form the stabilimentum of the web. Neet (1990) confirmed the camouflage function of the linear stabilimentum of *Cyclosa insulana* (Costa) and claimed that the circular stabilimentum probably aids in strengthening the web. (The term "stabilimentum" is appropriate for the circular device, but "camouflage silk" would seem to be more correct for the linear one). The subject has been reviewed by Edmunds, J. (1986), Hansell (1984), Lubin (1986), and Nentwig & Heimer (1987) among many others. Nentwig & Rogg (1988) concluded from field experiments in Panama and laboratory experiments, supplemented by a review of the literature, that there is no convincing evidence that thermoregulative, mechanical or protective functions, aposematism, or crypsis apply to the stabilimentum of *Argiope argentata* (Fabricius) (Araneidae).

Konigswald *et al.* (1990) have proved experimentally that debris in the nest of *Latrodectus revivensis* Shulov (Theridiidae) provides both defence and concealment against a visually oriented diurnal predator, the great grey shrike (*Lanius excubitor*). They also pointed out that the upper part of the nest of *L. revivensis* is hotter in summer than in winter, but an increase in summer in the area covered with detritus permits behavioural thermoregulation to take place without increased risk of predation. No doubt stabilimenta and web debris have several different functions in addition to defence (see discussion in Eberhard, 1990).

Communal webs

Subsocial behaviour, in which the mother spider cares for her cocoon or young, is found among numerous families of Araneae; but true social behaviour, depending on its definition, is only developed fully in Eresidae, Dictynidae, Thomisidae, Pholcidae, Amaurobiidae, Uloboridae, Agelenidae, Theridiidae and Araneidae (D'Andrea, 1987). Communal webs not only enhance predatory efficiency, but provide a defence against enemies. According to Seibt & Wickler (1988a,b) social spiders of the genus *Stegodyphus* (Eresidae) benefit in a number of ways from their colonial habits. Not least in importance is the fact that by combining their spinning activities, they are able to construct very dense and compact nests which act as a protective shield against predators, although they are of very minor importance against adverse physical conditions (Seibt & Wickler, 1990). Individuals emerging from the colony would be in great danger of predation, as shown to be the case with the comparable social species *Anelosimus eximius* (Keyserling) (Theridiidae) by Vollrath (1982) and with *Agelena consociata* Denis (Agelenidae) by Riechert *et al.* (1986). Vollrath (1982) found that the survival of webs begun by a single female was very low, and few foundations survived for more than 10 days. Mortality was mainly due to invertebrate predators such as *Trypoxylon* wasps, damsel flies (Zygoptera), and predatory spiders including kleptoparasitic *Argyrodes* spp. (Theridiidae). Prey is less likely to be stolen by *Argyrodes ululans* O. P.-Cambridge when more host spiders are present to defend it (Cangialosi, 1990).

An abundance of prey, and a consequent reduction in cannibalism may be the first step towards sociality in spiders (Rypstra, 1986; Shear, 1970), but protection from predation must also be a very important factor. No doubt communal species, such as *Oecobius civitas* Shear (Oecobiidae), *Mallos gregalis* (Simon) (Dictynidae), *Amaurobius socialis* Rainbow (Amaurobiidae), *Philoponella republicana* (Simon) (Uloboridae) and *Metepeira spinipes* F. O. P.-Cambridge (Araneidae) have evolved through an increase in tolerance of conspecifics, as recorded in *Achaearanea tepidariorum* (C. L. Koch) (Theridiidae) when plenty of food is available (Rypstra, 1986). The benefits of social behaviour include the ability to capture large prey but, according to Kullmann (1968, 1972), construction of a safe retreat is the first basic step towards sociality.

Tietjen (1986) has reviewed the advantages that accrue from group living, one of which is shelter (including protection from both predators and climate) although, according to Siebt & Wickler (1990), *Stegodyphus* webs only protect from wind and radiation, but not at all from high temperatures and desiccation. Rypstra (1979) indicated that birds are attracted to the conspicuous webs of *Cyrtophora citricola* (Forskål) (Araneidae) where they attempt to steal prey from the outer sections of the colony. The silk of the web, however, irritates the eyes and clings to the feathers of the kleptoparasites which probably learn to avoid such webs. The edges of the colony generally require the most repair but, in general, communal spiders remain in an inaccessible part of the web during the hours of daylight, foraging for snared prey and repairing their webs at dusk.

Communal webs thus provide two kinds of defence: (a) physical defence due to the presence of an increased amount of silk and, (b) combined defence of the members of the colony. The latter occurs in both colonial and social species. For example, individuals of *Cyrtophora moluccensis* (Doleschall) (Araneidae) shake their webs in response to airborne vibrations set up by tachinid flies, and may also do the same when other members of the colony do so, even when they themselves are so far away that they presumably do not hear the flies (Y. D. Lubin, in litt.). Again, colony members of *Stegodyphus dumicola* Pocock spin cribellar silk around the nest openings in response to invasion by ants (*Crematogaster* sp.) (J. Henschel, in prep.).

Actual evidence for anti-predator benefits in colonial spiders is limited. Spiller & Schoener (1989) found no substantial evidence that coloniality functions to reduce predation by lizards on *Metepeira datona* Chamberlin & Ivie (Araneidae), but Hodge & Uetz (1992) found that both intraspecifically grouped and colony associated *Nephila clavipes* (L.) (Tetragnathidae) had significantly greater response distances than did solitary individuals, indicating that they could respond better to the threat of predation as previously postulated (Lubin, 1974; Rypstra, 1979; Uetz, 1985). Opell & Eberhard (1984) concluded that it may be advantageous for species that are facultatively colonial, e.g. *Philoponella* and *Uloborus* spp. (Uloboridae), to be cryptic rather than to exhibit protective resemblance.

Secondary defences

Secondary defences of a prey animal come into play when a predator has found it, and decrease the chances of successful capture of the latter (Edmunds, 1974). Flight, moving away from an attack or dropping to the ground are the most widespread responses of spiders to disturbance or attack, but many other types of defence are also invoked and will be described below.

Flight

Spiders are almost defenceless against large vertebrate predators, parasitic wasps, dragonflies and asilid flies. Burrowers driven from their holes, for example, have recourse to little more than flight. *Thiania* spp. use a specialised leaping behaviour when approached by a predator, and then immediately adopt a cryptic posture (Jackson, 1986c). A habit common to many web-building spiders, especially among the Araneidae, is that of dropping to the ground, sometimes on a life-line, and remaining motionless in the humus and vegetation which they resemble in colour (see below).

Some Lycosidae (e.g. *Pirata* spp.) and Pisauridae (e.g. *Dolomedes* and *Thalassius* spp.) disappear under water when threatened, as do certain araneids. *Actinosoma pentacanthum* (Walckenaer), which spins its web on water plants in the centres of ponds, will drop and dive under water when disturbed (H. W. Levi, in litt.). Similarly, *Alpaida quadrilorata* (Simon) builds its webs on the thistle-like umbellifer *Eryngium horridum*. This plant usually has trapped water among the bases of the leaves. When disturbed, the spider submerges — it goes in head first and wedges itself so tightly into the base of the leaf that the plant must be destroyed to get the spider out (Levi, 1988). Crab spiders, too, submerge themselves in the fluid of pitcher plants. Bristowe (1939) confirmed the earlier observations of R. I. Pocock on *Misumenops nepenthicola* (Pocock), which restricts itself to, and is adapted for, life within the pitchers of *Nepenthes gracilis*. When threatened, it slides down on a thread below the surface of the plant's digestive liquid, and remains there for a period of a few minutes before regaining its former position. Nentwig (1993) found that spiders of many species and families flee into the water of large tank bromeliads and may stay motionless on the bottom for a long time.

Cart-wheeling, with legs curled up, is an unusual mode of escape among desert sand dunes, recorded only in spiders. *Carparachne aureoflava* Lawrence (Heteropodidae) uses little energy while rolling down the slope of a dune to reach speeds of 0.5–1.5 ms^{-1} when escaping from pompilid wasps etc. and, at 10–14 rotations per second, the spider's outline becomes blurred to a vertebrate eye, and no longer presents the normal stimulus to its adversary (Henschel, 1990). Some Salticidae of the Namib desert also cart-wheel when disturbed.

Dropping, colour change and thanatosis

Dropping to the ground from a web or retreat is an extremely effective means of escaping from a predator.

In *Argiope flavipalpis* (Lucas), the abdomen darkens as the spider falls so that it becomes cryptic on the earth and leaf litter, according to Edmunds, J. & M. (1986). These authors also quote other examples. Brignoli (1975) recorded a species of *Gasteracantha* which turns upside down after dropping so that its dark and spotted underside is exposed — this is presumably a defence against birds. Dropping followed by crypsis is even more effective as a defence when the spider afterwards remains motionless, feigning death (thanatosis) (Edmunds, J. & M., 1986). Thanatosis not only decreases the likelihood of a predator finding a cryptic animal but is also of value because predators are less likely to attack a still than a moving object (Edmunds, 1974). Salticidae are among the few spiders able visually to detect quiescent prey — mainly other spiders (Jackson & Tarsitano, 1993). Apart from *Gea heptagon* (Araneidae), Sabath (1969) found reports of rapid colour change in only four other species (see above).

Araneus cornutus Clerck (Araneidae) appears to have two effective close-range defences against the attacks of pompilid and sphecid wasps according to Eberhard (1970). These are a quick, unobserved exit from its retreat, and crypsis when it lands below. Both these tactics may help to explain why some orb weavers build retreats with two open ends while others, such as *A. cornutus*, are cryptically coloured even though they are normally hidden during the day. While there may be selective pressure on orb weavers to hide themselves, there is probably little or no pressure to hide their webs from predatory wasps.

It has often been noted that orb-web spiders may cut dangerous prey, such as wasps, out of their webs. *Chorizopes* sp. (Araneidae) preys on other spiders, using the aggressive response of its prey toward smaller-sized intruders in their webs, to lure them to their death. One prey species, *Leucauge* sp. (Araneidae), however, avoids attacks by cutting free the sectors of the web that hold its predator (Eberhard, 1983).

Web vibration, whirling and bouncing

Web vibration has been observed in numerous araneid spiders (for references, see Edmunds, J. & M., 1986). It blurs the outline of the spider, making it appear less spider-like, and is particularly effective on webs with a stabilimentum. Tolbert (1975) has described how web-dwelling *Argiope* spp. avoid predators by (a) "web-flexing", in which the spider sets the web in motion along its short axis by rapid extension and retraction of the legs so that both spider and web swing parallel to the ground; (b) "stilting", in which all four pairs of legs are straightened simultaneously, thereby changing the sign-stimulus of the spider to its predators; (c) "rebuff", in which the spider pushes the enemy away with its legs and exposes its chelicerae, although it seldom bites; and (d) flattening the body against the hub of the web. Moreover, the sudden appearance of a concealed stabilimentum may function as a threat stimulus.

In *Argiope appensa* (Walckenaer) (Araneidae), defence includes "pumping", shuttling around the hub, dropping from the web, and "tugging" (Jackson, Rowe & Wilcox, 1993). Pumping — vibration of the body upwards and downwards — has been shown experimentally to be an effective defence against predators (Jackson, 1992b). Shuttling around the hub of the web occurs less frequently. Dropping from the web is more common among juvenile than adult spiders, while tugging on the web is primarily a component of prey-catching sequences (Jackson, Rowe & Wilcox, 1993). Similar and probably homologous behaviour patterns are performed by other members of the genus *Argiope* (Robinson & Olazarri, 1971; Robinson, M. H. & B., 1973) although what Jackson and his colleagues call "tugging" has been referred to as "plucking" by most other authors. Jackson's term is probably better, because "plucking" implies releasing contact with the thread, and spiders seldom do this except occasionally some courting araneids (W. G. Eberhard, in litt.). Other papers of importance by Jackson and his colleagues in which various responses of spiders to their predators are discussed include Jackson & Hallas (1990), Jackson & Wilcox (1990) and Richman & Jackson (1992).

Certain species of spiders regularly invade the webs of other spiders on which they feed (Jackson, 1992d). Such web-invaders may be major predators of many web-building species (Bristowe, 1941). The subject has been investigated in great detail by Jackson and his co-workers. Three of the web-invaders tested have poorly developed vision: *Mimetus maculosus* Rainbow (Mimetidae), *Taieria erebus* (L. Koch) (Gnaphosidae) and *Pholcus phalangioides* (Fuesslin). Besides being a web-invader, *P. phalangioides* builds a prey-catching web of its own, and *T. erebus* hunts prey away from webs, but *M. maculosus* is exclusively a web-invader especially of ecribellate sticky orb-webs. Various Salticidae, including *Portia fimbriata*, are also web-invaders, but have acute vision and are more efficient than are spiders with poorly developed vision (Jackson, 1986a). *P. fimbriata* is better at catching Pholcidae than are web-invading salticids that do not use aggressive mimicry (Jackson, 1990, 1992a). The latter attack by leaping from outside the web but *Portia* spp., and especially *P. fimbriata*, make special vibratory signals that deceive the prey so that it approaches instead of fleeing (Jackson, 1990).

Pholcus phalangioides, Psilochorus sphaeroides (L. Koch) and *Smeringopus pallidus* (Blackwall) (Pholcidae) defend themselves by "whirling" and "bouncing" (Jackson, 1990; Jackson, Brassington & Rowe, 1990; Jackson, Jakob *et al.*, 1993; Jackson, Rowe & Campbell, 1992). These actions have been shown experimentally to protect the pholcids against web-invading salticids (Jackson, 1990, 1992a,c). Small juveniles differ from adults in that they more often drop from their webs. The reactions of web-building spiders to kleptobionts are summarised by Vollrath (1987). If disturbed, *Uloborus conus* Opell (Uloboridae) drops from the hub on to the dragline thread of its web and bounces up and down on it (Lubin *et al.*, 1982).

Autotomy

When attacked, spiders may autotomise the limb that has been grasped by a predator and thereby make their escape (Foelix, 1982; Savory, 1928). The missing leg is then regenerated at the next moult, but it may take several ecdyses to attain normal size. A cryptic desert heteropodid lacking two legs is illustrated by Cloudsley-Thompson (1991). From experiments on *Kukulcania hibernalis* (Hentz) (Filistatidae) with scorpions and centipedes, Formanowicz (1990) showed that leg autotomy can be an effective defence against certain kinds of predator. It increased survival in encounters with scorpions, but not with centipedes; the differences result from the behaviour and morphology of the two types of predators. Eisner & Camazine (1983) observed in the field that *Argiope* spp. undergo leg autotomy when bitten in the leg by venomous insect prey (*Phymata fasciata* (Hemiptera: Phymatidae)). The response occurs within seconds, before the venom can take lethal effect by spreading to the body of the spider. *Portia* spp. too, may lose legs when the spider that they are stalking turns upon them. They undergo autotomy more readily than do most other salticids (Jackson & Hallas, 1986). Roth, V. D. & B. M. (1984) have reviewed appendotomy in spiders and other arachnids.

Venoms and defensive fluids

Few spiders have chelicerae sufficiently powerful to penetrate mammalian skin and, in even fewer, is the poison painful or dangerous to Man. Spider venoms are not primarily defensive. They have been discussed by numerous authors, including Bücherl (1971), Cloudsley-Thompson (1993) and Sheals (1973), and will not therefore be considered here.

When disturbed, some of the larger Neotropical Mygalomorphae turn their rear ends towards the enemy and squirt from the anus a clear liquid that may have irritating properties (Preston-Mafham, R. & K., 1984). *Phoneutria rufibarbis* Perty (Ctenidae) ejects from its anus drops of milky fluid smelling slightly of ammonia to a distance of more than 50 cm when it is alarmed; and *Scytodes* spp. (Scytodidae) squirt poisonous gum from their chelicerae, both in offence and possibly in defence (Bristowe, 1941; McAlister, 1960).

Defensive retaliation is found in a number of araneid spiders (Edmunds, J. & M., 1986). It may be effective against some other spiders and wasps, but Bristowe (1958) considered it unlikely to succeed against spider-hunting wasps and asilid flies. Cooke (1965) commented that *Dysdera* spp. (Dysderidae) are among the few spiders that will attack rather than retreat from molestation. The same may apply to male *Atrax* spp. (Hexathelidae) (Mascord, 1970) and some Old World mygalomorphs (P. Merrett, in litt.), *Loxosceles* spp. (Loxoscelidae) (H. W. Levi, in litt.), and to *Phoneutria nigriventer* (Keyserling) (Ctenidae) (Cloudsley-Thompson, 1993).

Urticating setae

The spines of *Gasteracantha* spp. and other tropical Araneidae have already been mentioned as a possible explanation for apparently aposematic coloration. The urticating setae of Mygalomorphae (Cooke *et al.*, 1972), however, are almost certainly a greater deterrent to would-be mammalian aggressors. In contrast to those of Lepidoptera, the urticating hairs of mygalomorph tarantulas rely upon mechanical irritation alone. They are characterised by a penetrating end, which may be either proximal or distal, with fine barbs located along it and longer barbs on the shaft. The base of the hair has a constriction at which it breaks off (Cooke *et al.*, 1972). Most tarantulas possess a suite of behavioural responses which accompany defensive hair-shedding by rapid downward strokes of the fourth legs. These include stridulation (see below), rearing, striking with the first two pairs of legs, and attempting to bite. In *Megaphobema* and *Theraphosa* spp., urticating hairs are incorporated into the egg sacs and the silk mats upon which the spiders moult (Marshall & Uetz, 1990).

Warning sounds

Despite numerous descriptions of stridulatory organs and other mechanisms of sound production in spiders (Barth, 1982), comparatively few references to their possible functions have been made. Warburton (1912: 106) appears to be one of the first people to have suggested that some sounds might be defensive, stating: "There are two quite distinct purposes for which sounds may be produced; they may either serve as a call from one sex to the other, or as a warning to intruders. Obviously the first purpose requires a sense of hearing in the sex appealed to, and it is interesting to note that in the Theridiidae, which are among the spiders which show some appreciation of sound, the (stridulatory) organ is well developed in the male only, being rudimentary or altogether absent in the female, while in the Aviculariidae [=Theraphosidae], which appear to be quite deaf, both sexes possess it equally. In them its function is probably to warn off its enemies — a purpose for which it is not at all necessary that the spider itself should hear it."

More recently, Uetz & Stratton (1982) divided the functions of the sounds made by spiders into three broad categories, defensive, aggressive, and courtship sounds. They defined aggressive sounds as those used in agonistic encounters between rival males or to threaten conspecific intruders. Among defensive sounds, were included the snake-like "hissing" produced by some theraphosid tarantulas when cornered.

Berland (1932) and Legendre (1963) rejected the hypothesis that mimicry might be involved, and assumed that sound production must be a by-product of other activities: but Weygoldt (1977) did not consider this argument to be convincing. However, as Uetz & Stratton (1982) pointed out, whether or not hissing sounds constitute snake mimicry is irrelevant. As with visual colours and displays, auditory signals may sometimes represent real warning; sometimes they are mimetic, and sometimes deimatic or startling behaviour (Cloudsley-Thompson, 1980; Edmunds, 1974).

In their description of the stridulatory organ of the spiny orb-weaver *Micrathena gracilis* (Walckenaer), Hinton & Wilson (1970) concluded that the low-pitched buzz emitted by this (and a few other genera of Gasteracanthinae) is probably defensive in function because it is produced when the spiders are touched or otherwise disturbed. They also commented that in *M. schreibersi* (Perty) but not in *M. gracilis*, the spacing of the ridges on the stridulatory file is sufficiently close for it to function optically as a diffraction grating at incidences near grazing, and it is just possible that the spectra so produced may function as warning colours. Uetz & Stratton (1982) agreed with the hypothesis that stridulation may have a defensive function. They pointed out that defensive stridulation by insects has been demonstrated to deter attackers, or may alert them to potential harmfulness (acoustic aposematism) (Masters, 1979). Again, Rovner (1980) speculated that the vibrations produced by *Heteropoda venatoria* (L.) and other Heteropodidae during bouts of leg oscillations may mimic the wing-beat frequencies of certain Hymenoptera, as may the web vibrations of araneid spiders when disturbed. These could thus not only result in the spider becoming blurred (Tolbert, 1975) but also serve to scare potential predators.

Deimatic display

When discovered by a predator, many animals respond by adopting a characteristic threatening posture which appears to intimidate and startle the enemy, thus providing an opportunity for escape (Cott, 1940; Edmunds, 1974). Such deimatic (frightening) behaviour has been recorded in numerous insects, scorpions, and Mygalomorphae and Ctenidae (*Phoneutria* spp.) as well as Araneidae. Eye patches are found on the underside of the abdomen in *Molinaranea* species. H. W. Levi (in litt.) was startled in Chile when, after touching the web, "a female zoomed to the middle showing white patches on the abdomen (is it a defence against lizards?)". *Araneus illaudatus* Gertsch & Mulaik also has a pair of black patches framed in white on its underside (Levi, 1971). Warning sounds, too, may well have a deimatic function, as discussed above.

Discussion

Any animal that possesses an effective means of defence is likely to provide a model for defenceless mimics. But visual mimicry is probably directed more toward vertebrate predators than toward invertebrate enemies. Mimicry directed against invertebrates has been discussed by Edmunds (1978, 1993), McIver & Stonedahl (1993), Mathew (1954) and Oliviera & Sazima (1984): cited above. Spiders are seldom offensive or formidable as far as vertebrates are concerned. Consequently, there are few known examples of spiders being mimicked by other animals and the validity of these is somewhat dubious. According to Poulton (1890) the larva of the lobster moth *Stauropus fagi* mimics a large spider, but no specific model was suggested.

More recently, Levi (1965) described an unusual instance — the malmignatte *Latrodectus tredecimguttatus* (Rossi) (Theridiidae) of southern Europe being mimicked by the woodlouse *Armadillidium klugii* and the pill millipede *Glomeris pulchra*. Hinton (1976) argued that, if mimicry is indeed involved, which he considered to be unlikely, it is either an instance of Müllerian mimicry or the less common spider is mimicking the isopod and millipede, both of which have defensive glands. Glomerids are not found in North America, however, and, since the European *L. tredecimguttatus* is coloured like other species of the genus while the millipede has a unique coloration, it may well be assumed that the spider is the model and the millipede the mimic (H. W. Levi, in litt.). Cases in which prey mimic their own predators and thereby avoid predation are rarely reported; but strawberry flies (*Zhagoletis zephyria*) resemble the jumping spider *Salticus scenicus* (Clerck) and the success of the mimicry is decreased by obliterating its wing-stripes (Mather & Roitberg, 1987). Again, Greene *et al.* (1987) found that another tephretid fly (*Zonosemata vittigera*) also has a leg-like pattern on its wings, and a wing-waving display. Together, these mimic the agonistic territorial displays of Salticidae, as has been demonstrated experimentally. The display is initiated when the fly is stalked by *Phidippus insolens* (Hentz). It causes the jumping spider to display back and retreat, but affords no protection against non-salticid predators (Greene *et al.*, 1987). In general, however, the mimicry of spiders appears to be relatively uncommon.

The anti-predator adaptations of spiders, especially tropical species, are extremely complex, and combinations of the various devices, described above, are frequent. Furthermore, selective pressure has not infrequently produced parallelism with insects and other arthropods. For instance, the dorso-ventrally flattened *Pandercetes gracilis* (Heteropodidae) has morphological adaptations that resemble those of bark-dwelling mantids, phasmids, katydids, and even of geckoes (Cott, 1940). (A thomisid found on the same trees has lichen particles on most of its dorsal surface.) Stick-insects, mantids, and many other insects, like deinopid spiders, show protective resemblance to twigs; while mantids, butterflies and other insects, as well as spiders, may resemble flowers. Other examples are cited by Robinson (1980).

In his satirical poem *Hudibras* (1664), Samuel Butler wrote: "the fool can only see the skin, the wise man tries to peep within". Only a fool would attempt to review a topic as wide as anti-predator defences in spiders, because, to provide a balanced account, it is necessary to discuss many important aspects of the subject in a rather superficial manner. On the other hand, to be wise might result in imbalance, and in the reader not being able "to see the wood for the trees". These pages represent an attempt at a compromise between the two extremes.

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