4

Sexual dimorphism in the Hymenoptera

J. WILLIAM STUBBLEFIELD and JON SEGER

Spectacular sex differences of many kinds occur abundantly among the wasps, bees and ants that make up the insect order Hymenoptera. In some cases these differences are so extreme that males and females of the same species have been classified in different genera for decades, until a chance observation of mating, or emergence from a single nest, establishes their identity. Even where the sexes are similar in morphology they lead very different lives. The hard-working females hunt for prey or other larval provisions, and in many taxa they carry these provisions back to a nest that they have constructed to protect their offspring. The males, by contrast, lead short lives (sometimes nasty and brutish), devoted to the single purpose of inseminating females. Countless variations on this theme have evolved during the long and successful history of the order, and other features of hymenopteran biology have allowed these sex differences of ecology to be translated into equally striking sex differences of behavior, morphology and physiology.

Hymenoptera provide excellent illustrations of the classical principles of sexual selection, and we believe that they also present opportunities to extend the study of sex differences in several directions. These opportunities are created by four basic characteristics of the group. First, the sexes tend to be more different from each other in Hymenoptera than they are in most other animals (see Figures 4.1, 4.4, 4.7, 4.9 and 4.10). Some possible reasons for this tendency will be mentioned below, but whatever the cause, it means that the 'signal' to be studied is relatively strong. Second, alternative phenotypes also occur *within* one sex or the other in many species (see Figures 4.2, 4.3 and 4.9). The most familiar example of intrasexual dimorphism is the difference between the female reproductive and worker castes in many social taxa, and in some ants there are further distinctions among two or more castes of workers. But there are also
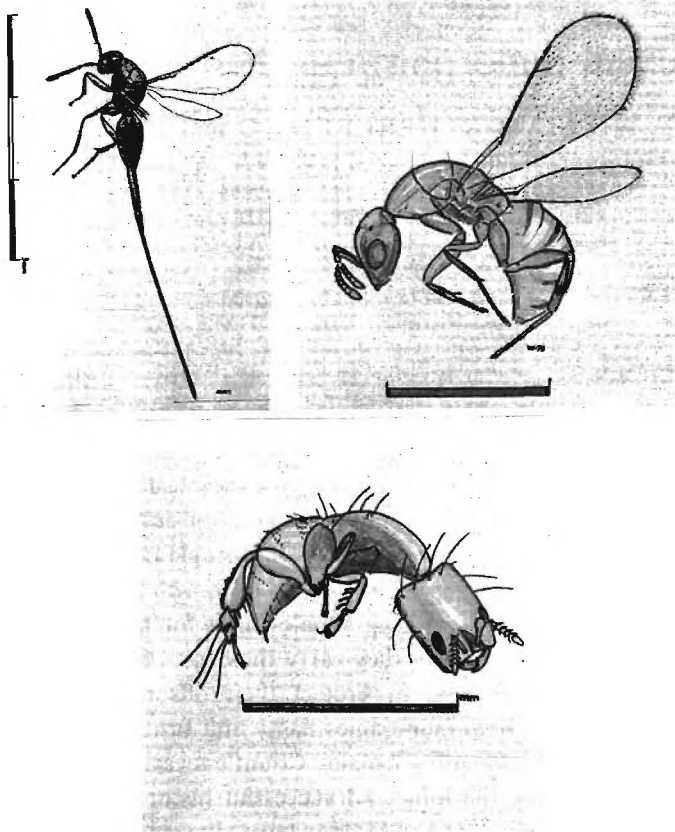
71

Figure 4.1. *Philotrypesis parca*, a parasitic fig wasp in the family Torymidae. The female (top left) uses her long ovipositor to place a few eggs into each of many different figs. Two kinds of male occur in this species. The winged form (top right) leaves its natal fig to search for mating opportunities elsewhere, while the wingless form (bottom) remains within the fig and fights with other wingless males for access to females that have not yet left the natal fig (scale in mm). (From Bouček, A., Watsham, A. and Wiebes, J. T. (1981) The fig wasp fauna of the receptacles of *Ficus thonningii* (Hymenoptera, Chalcidoidea). *Tijdschrift voor Entomologie*, **124**, 149–233.)

dramatic dimorphisms among males, both in solitary and social taxa, and distinct quantitative or qualitative differences between female morphs in various solitary taxa. Thus, within the order, and in some cases within a single species, it is possible to study alternative developmental pathways both within and between the sexes.

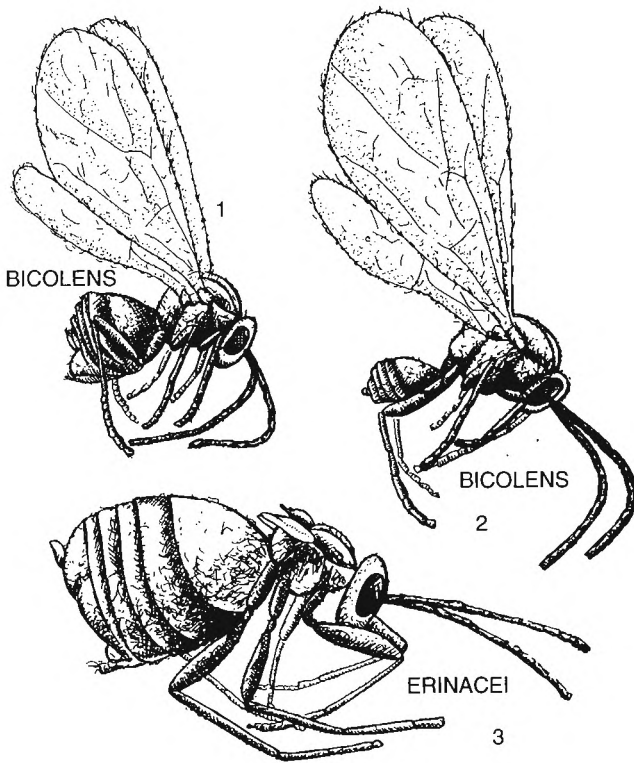Third, the order is huge (perhaps as large as the beetle order

Figure 4.2. The gall wasp *Cynips erinacei*. Like many other members of the Cynipidae, this species alternates between sexual and asexual generations. Females (1) and males (2) of the sexual form mate, producing females of the asexual or 'agamic' generation (3), which do not mate but produce sexual males and females parthenogenically. (Redrawn from Kinsey, A. C. (1929) *The Gall Wasp Genus Cynips*. Indiana University Studies, vol. 16.)

Coleoptera), with many large families that are major groups in their own right. Because many kinds of sex differences (and alternative morphologies within one sex) have evolved repeatedly within the order, its abundance of related taxa can be used to generate detailed statistical descriptions of the relationships among morphological and other variables, and, as detailed phylogenies become available, comparative methods can be applied with unusual power. Fourth, many species can be reared in the laboratory or induced to accept artificial nesting substrates in the field. Thus, manipulations of many kinds are possible, and these can often be replicated more extensively than is feasible with vertebrates.
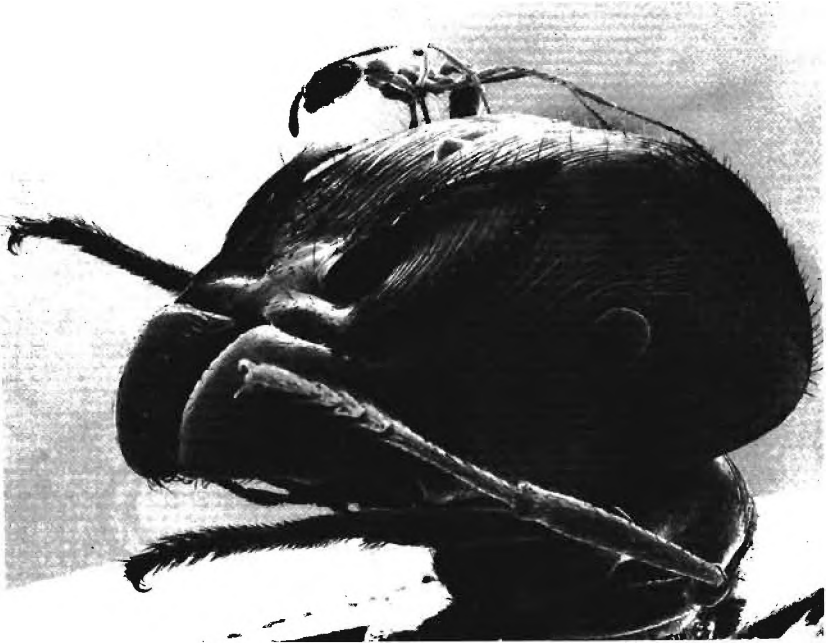
Figure 4.3. Major and minor workers of the Asian marauder ant *Pheidologeton diversus.* These nestmates (presumably sisters) differ in weight by a factor of 500, the largest known difference in adult size within any species of Hymenoptera (and probably any insect). Scanning electron micrograph by Mark W. Moffett/Mindon Pictures.

Although Hymenoptera are unequalled as a natural laboratory for the study of sex differences, we still have an incomplete and somewhat fragmented understanding of the distributions and correlates of such differences within the order, and of the proximate and ultimate mechanisms that give rise to them. For example, there is a rich tradition of behavioral study, but it has tended to focus on descriptions of mate finding and courtship (on the male side) and prey location and nesting (on the female side) in particular species, with relatively little attention to ecological and phylogenetic analysis. Morphological sex differences are described frequently in systematic works, but quantitative comparative studies are rare. And the developmental and physiological aspects of sexual dimorphism have hardly been touched.

As far as is known, all Hymenoptera have haplodiploid genetic systems, in which haploid males develop parthenogenically from unfertilized eggs, while diploid females develop from fertilized eggs. (Female

parthenogenesis also occurs in a few groups, where it is derived from haplodiploidy.) Among the interesting consequences of this system is that mothers can determine precisely the sex of each offspring, by releasing (or not releasing) a stored sperm cell from the spermatheca, just prior to oviposition. Precise sex-ratio control has allowed the Hymenoptera to explore a universe of sex-allocation strategies that is not accessible to most other animals. Much effort has gone into unravelling the intricacies of hymenopteran sex allocation, but there has been little work on the implications of sex-ratio control for the evolution of adult sexual dimorphisms.

In the next section, we review briefly the evolution and diversity of Hymenoptera. Then we focus on some characteristic differences between the selective environments of the sexes and the ways in which these ecological differences have shaped male and female biologies. Next, we review the evolution of winglessness, which has occurred many times in both males and females, often in connection with unusual ecologies and mating systems. Males and females are often very different in size. In the final section we attempt to show why the Hymenoptera offer superb opportunities to study the evolution of size differences, both within and among species.

Who's who: a brief overview

The order Hymenoptera comprises a very large and diverse group of insects that play profoundly important roles in terrestrial ecosystems. More than 100 000 species have been described, but this is a small fraction of the species believed to exist; current estimates range from 250 000 to over a million species worldwide. We will never know with confidence how many species exist today (much less how many existed 100, or 1000, years ago), owing to the accelerating rate of habitat destruction around the globe.

Most Hymenoptera are carnivorous, preying on a great diversity of terrestrial arthropods including phytophagous insects, and, undoubtedly, their appetites keep the world greener than it would otherwise be. The order also includes phytophagous species; some attack leaves or stems, but a much larger number are invaluable pollinators of flowering plants. The evolution of flowers has been shaped in large part by the sensory physiology of bees, with their well-developed color vision and their fondness for pleasing fragrances and sugary fluids. These fortunate attributes have made the world a far prettier and sweeter place than it might otherwise have been.
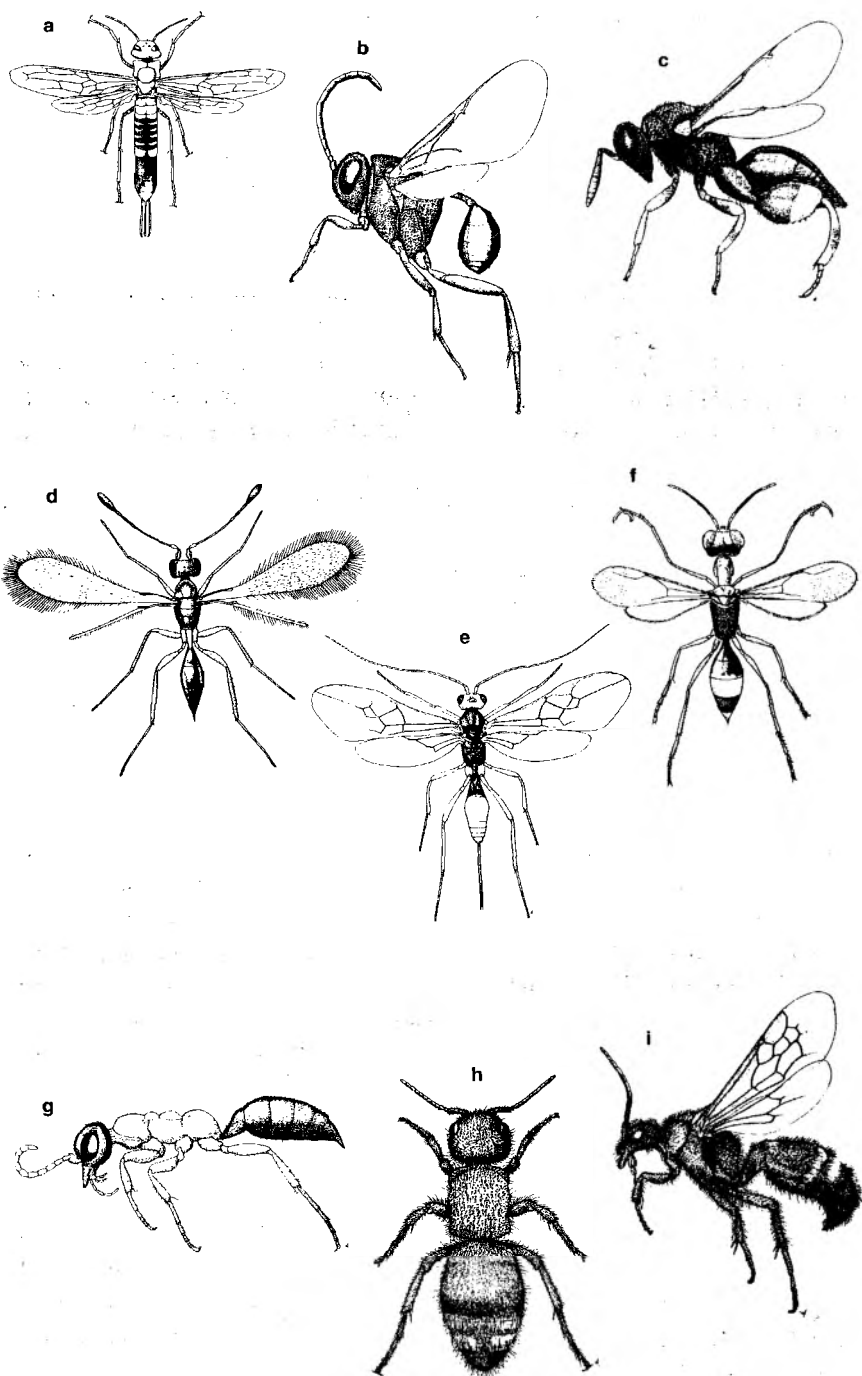
We are not aware that anyone has attempted to estimate the direct economic value of the regulation of insect numbers by carnivorous Hymenoptera and the pollination of wild and domesticated flowers by thousands of species of wild bees, but we are confident that the total would run to hundreds of billions, perhaps even trillions, of dollars in benefits received annually. Moreover, it is impossible to place a merely monetary value on the more general contributions that Hymenoptera make to the functioning of natural ecosystems (for example, the scavenging and soil-turning services of ants), but these activities are vital to our survival. Imagine a plague that eliminated only the order Hymenoptera. Uncontrolled outbreaks of destructive insects and the rapid demise of bee-dependent plants would totally transform terrestrial ecosystems all over the world. Life would survive, but it is doubtful that civilization would do so.

The order Hymenoptera includes the familiar wasps, ants and bees as well as many less familiar insects (Figure 4.4). Traditionally, the order is divided into two suborders, the Symphyta and the Apocrita. The suborder Symphyta, which includes the woodwasps, sawflies, and stem flies, is structurally the most primitive of extant groups (Figure 4.4a). The earliest known fossils are symphytans from the Triassic, around 200 million years ago. Almost all symphytans are phytophagous, but the family Orussidae parasitizes wood-boring symphytans. The larvae of many symphytans are external feeders on leaves or other plant parts and, thus, behave much like caterpillars, while others are internal plant feeders, living a concealed existence boring in leaves, stems or wood. Sexual and intra-sexual dimorphisms tend to be relatively modest in this group.

The suborder Apocrita is a monophyletic group derived from symphytan ancestry and characterized by a remarkable morphological innovation that is unique among insects, a new articulation between the first and second abdominal segments. Like most insects, symphytans have the abdomen broadly joined to the thorax (Figure 4.4a). In Apocrita, however, the apparent thorax is actually the true thorax

---

Figure 4.4. Representatives of several major branches of the Hymenoptera. All except (i) are females. (a) a symphytan, the pigeon horntail. (b–e) Various 'Parasitica'; (b) an evaniid or 'ensign wasp'; (c) a chalcid; (d) a mymarid, one of the smallest insects in the world; (e) a braconid. (f–i) Various aculeates; (f) a dryinid; (g) a wingless tiphiid; (h) the female and (i) the male of a mutillid wasp or 'velvet ant'. (a and f are from Evans and West Eberhard, © The University of Michigan (1970); the others are from Gauld and Bolton (1988) © The Natural History Museum, London.)

together with the first segment of the abdomen, which is separated from the true second abdominal segment by a narrow petiole, forming the 'wasp waist' (Figure 4.4b–i). This invention greatly increased the maneuverability of the ovipositor and accompanied a shift from phytophagy to parasitism of other arthropods. Apocrita include most members of Hymenoptera, and is therefore one of the most successful of all insect groups. The earliest known fossils date from the Jurassic with an extensive radiation during the Cretaceous.

Traditionally, Apocrita are divided into two major groups: 'Parasitica' and Aculeata. The former is an informal grouping including many thousands of species, most of which are parasitoids attacking other arthropods, but with some notable reversions to plant foods. Included here are the great superfamilies Chalcidoidea (see Figures 4.1 and 4.4c–d) and Ichneumonoidea (Figure 4.4e) with tens of thousands of species each, as well as a number of smaller groups such as Cynipoidea which produce the familiar galls on oaks (see Figure 4.2). A typical life history of a parasitican can be described as follows. Newly emerged adults mate, after which males soon die while inseminated females, each carrying a lifetime supply of sperm in a spermatheca, search for suitable host insects or spiders which will provide the sole food for their offspring. Single or multiple eggs are then laid on or in each host and these hatch into larvae which undergo several molts as they grow on a rich diet of host tissue. Eventually, they spin cocoons from which they emerge as adults to repeat the cycle. Since the host dies in the process, 'parasitic' Hymenoptera are usually referred to as parasitoids rather than parasites. If they feed at all, the adults generally have a very different diet from their larvae. Although the adults of some species are known to feed on the haemolymph of their hosts, most subsist entirely on sugary solutions such as the nectar of flowers or the 'honeydew' secretions of plant-sucking Homoptera such as aphids, scale insects and leaf hoppers.

Aculeata are an apparently monophyletic group derived from the 'Parasitica' and characterized by another dramatic morphological innovation, the sting. The females of all other Hymenoptera possess an ovipositor employed to place the egg on, near or within the larval food source. Glands associated with the ovipositor produce secretions that lubricate the passage of the egg and that also affect the host in various ways. Thus, the ovipositor serves both to place the egg and to introduce substances that modify host behavior, physiology or development. In Aculeata, however, the egg is released at the base of the ovipositor, which has become highly specialized for its one

remaining role, that of injecting paralyzing or irritating venoms into prey or enemies.

The venoms of different aculeate taxa vary greatly in their composition and effects. In some species, the effects wear off quickly and the prey resumes its normal activities while the larva develops as a parasitoid. In species that construct nests, the venom induces permanent paralysis, but the prey remain physiologically alive for extended periods, until they are consumed by the developing larva. Although the sting evolved originally as an organ used to immobilize prey, in many social species it functions as a fearsome defensive weapon against vertebrates, as billions of people know from personal experience. The pharmacology of wasp and bee venoms is a vigorous field of research with important applications in medicine and neurobiology.

Since the aculeate sting is a modified ovipositor, only females have it. In some groups, however, males have evolved pseudo-stings. These are modifications of the male genitalia or associated sclerites into sharply pointed structures that can prick the skin of a vertebrate attacker. Pseudo-stings lack venom glands, but pseudo-stinging behavior often wins a male's release from predators which have prior experience of female aculeates. Freud would surely have been amused to learn of this evidence for 'sting envy' in aculeate males.

Many aculeates are parasitoids, with ways of life quite similar to those of their parasitican ancestors. Eggs are laid on the host wherever it is found, and there is no transport of prey or construction of a nest. This pattern is undoubtedly primitive for the aculeates, and it is found in a wide diversity of familes including Dryinidae (Figure 4.4f), Bethylidae (see Figure 4.10), Embolemiidae, Scoliidae, Tiphiidae (see Figures 4.4g and 4.10) and Mutillidae (Figure 4.4h–i), as well as some Chrysididae and Pompilidae. However, the aculeate radiation is dominated by taxa in which females transport larval food back to a central location: the nest. This breakthrough in domesticity has had major consequences for the evolution of sex differences, and it also set the stage for the evolution of sociality. The nest may be simply an existing cavity in which the egg and its food supply are sealed, or it may be constructed by the nesting female. Many species dig burrows in the ground; some make tunnels in wood; and still others build free-standing nests out of paper, mud, or tiny stones and mortar. Various glandular secretions may be used to glue together nesting materials and to waterproof the cells in which offspring will be reared.

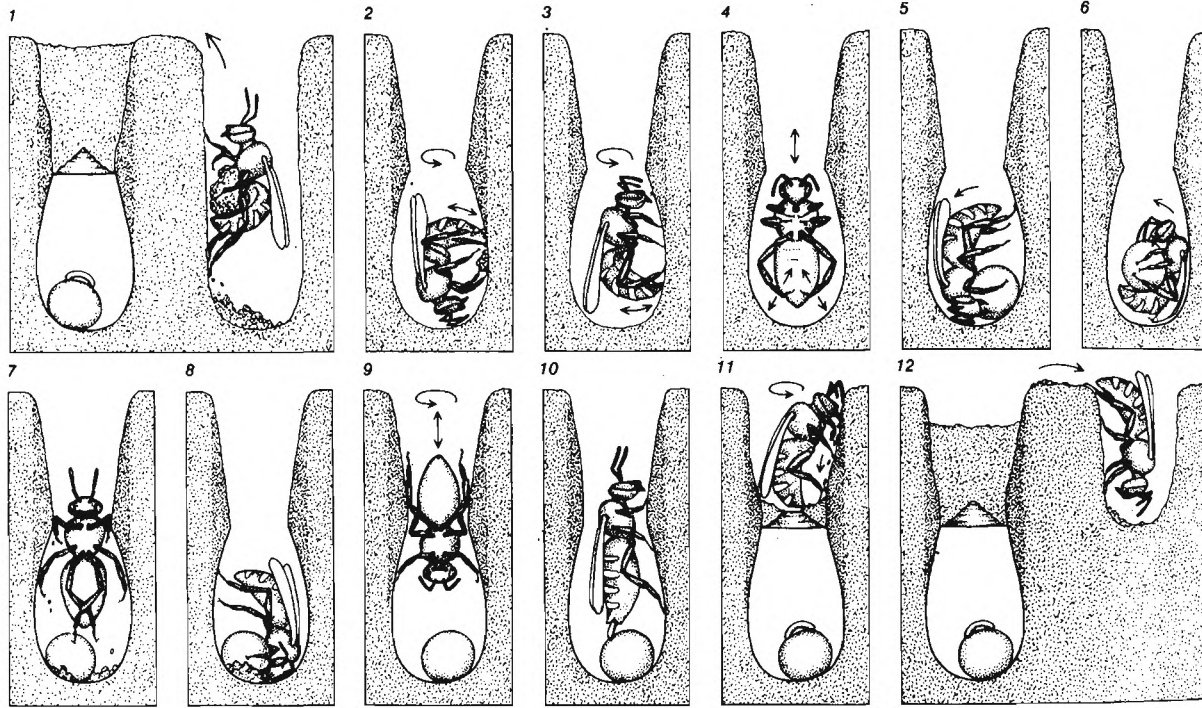The nest is the focal point of a female's life: the place to which she

Figure 4.5. A female sweat bee (*Nomia melanderi*) constructs and provisions a nest cell. (1) Having completed a previous cell (left) the female excavates a new one, using the underside of her abdomen and her middle legs to carry loads of soil out of the cell; (2–4) sculpting, smoothing, and waterproofing the cell with Dufour's gland secretions; (5, 6) forming the provision mass, a ball of pollen moistened with nectar; (7, 8) grooming the ball and removing debris from the cell; (9) polishing the cell walls; (10) laying the egg; (11) closing the cell with a plug of soil; (12) beginning the next cell. This sequence of events takes roughly 24 hours. (From Batra, S. W. T. (1984) Solitary bees. *Scientific American*, **250**, 120–7. Copyright © (1984) by *Scientific American, Inc.* All rights reserved.)

returns repeatedly with larval food and with building materials. Remarkable powers of orientation and memory are required to find a nest entrance that may be no more than a tiny hole in the ground. In a few species, females maintain several nests simultaneously, at distances of tens of meters from each other. Most species rear several offspring per nest, each sealed in a separate cell. Some provide only a single prey item per offspring, but most provide several items. In most groups, larval food consists of paralyzed insects or spiders, but bees and some vespid wasps have switched to pollen and nectar; the bees are literally 'vegetarian wasps'. Larval provisions have proved to be an irresistible target for some aculeates who behave as cuckoos, laying their eggs in the nests of other species. The egg of the cuckoo species hatches into a larva that destroys the host larva and then consumes its food. The cuckoo way of life has evolved repeatedly and is found in most Chrysididae and in some spider wasps (Pompilidae), digger wasps (Sphecidae) and bees.

The nest-building aculeates differ from most other insects, and indeed from most other animals, in the very high levels of maternal care they provide for each offspring. Constructing and provisioning a rearing cell is typically a hard day's work, and may take even longer (Figure 4.5). As a consequence, species that pursue this way of life have mean and maximum lifetime fecundities that would be low even by avian or mammalian standards. In most solitary species, a female that produces 10 or 15 offspring is well above average, and in social species the productivity per worker is the same or even lower.

Most aculeates are solitary, with each female providing for her offspring entirely on her own. Even among nest-building species, the primitive and still typical condition is for each female to locate, to harvest and to transport larval provisions to a nest occupied by her alone. However, sociality has evolved repeatedly within several groups of wasps and bees and at least once among the ancestors of ants. The reasons for its relative commonness in aculeate Hymenoptera and its extreme rareness in all other animals are still not entirely clear, but the nest, the sting and haplodiploidy are all high on the list of probable contributing factors.

This brief sketch of hymenopteran evolution has identified some key features of the biology of the order that have strongly influenced the evolution of sex differences, often by placing males and females in what amount to different worlds. But it has certainly not done justice to the rich diversity of the group, or to its importance. The articles and books cited as further reading will give immediate help to anyone whose curiosity has been aroused.

The selective environments of females and males, and some of their effects

Natural selection can be viewed metaphorically as a contest among genes or individuals, in which the object is to contribute as many genes as possible to future generations. Even in species with haplodiploid genetics, half of all genes in future generations will come from females and half from males; females compete among themselves for their half, while males compete for their half. Parental investment is an almost exclusively female activity in many groups of animals, including Hymenoptera, and this has important consequences for the nature of the evolutionary competition within each sex. The reproductive success of females is limited mainly by their ability to invest in offspring, while the reproductive success of males is limited mainly by their ability to father the offspring produced by females. In short, females compete for resources that can be converted into offspring, while males compete for females.

Many female morphological adaptations are tools of the parental-investment trade. For example, in many ground-nesting species, only the females have a foretarsal rake which is employed to move soil during construction of the burrow system. Similarly, many females have a pygidial plate, a trowel-like modification of the apical segment of the abdomen, which is used in nest construction. The females of some ground-nesting wasps have greatly modified mouthparts that serve as baskets for carrying sand out of the nest during construction. And female leaf-cutter bees have massive, sharp-edged mandibles that are used to cut precisely shaped pieces of leaves that are used to line the rearing cells in their nests.

Some female wasps have remarkable adaptations used for prey capture and transport. For example, the end of the female foreleg is modified in most dryinids to form a grasping organ used to hold the prey while it is being stung (Figure 4.4f). Nesting species use different techniques to carry prey home. Some species simply grasp the prey in their mandibles and drag them back to the nest, and others use their legs to cradle the prey beneath the body while flying home (often from distances of hundreds of meters). But many other species employ more exotic methods. Digger wasps of the genus *Clypeadon* prey exclusively on worker ants which they carry with the aid of an 'ant clamp', a modification of the apical segment of the abdomen (Figure 4.6). In the digger-wasp genus *Cerceris*, females often have prominent, species-specific projections on the front of the head. These projections are thought to facilitate prey transport by fitting precisely with the morphologies of the beetle prey and thereby helping
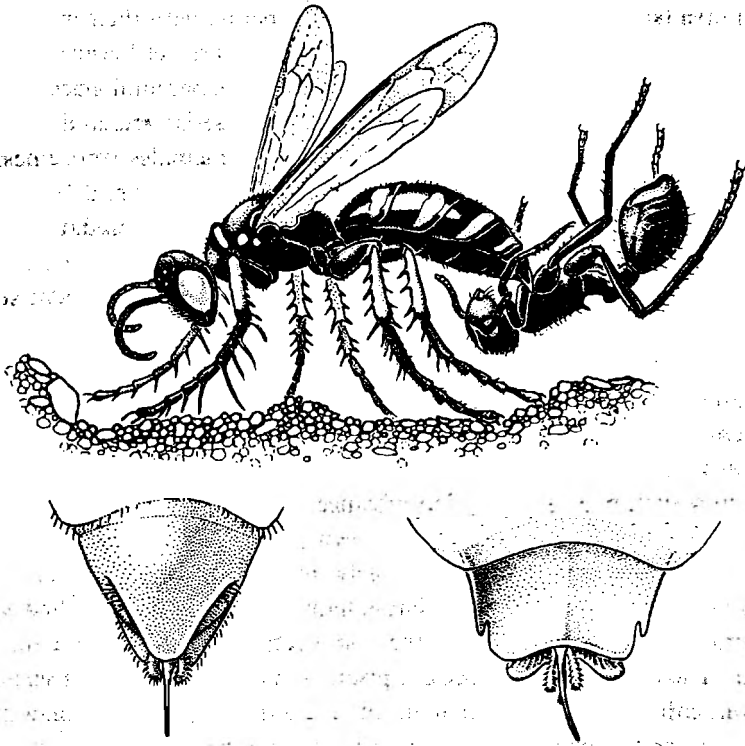
Figure 4.6. A solitary sphecid wasp, *Clypeadon laticinctus*, returning to her nest with a worker harvester ant (*Pogonomyrmex*) attached to the end of her abdomen. This feat is made possible by unusual modifications of the apical abdominal segment (lower right) that fit precisely into a space between the legs of the prey. For comparison, the apical abdominal segment of a related species that does not practice abdominal prey carriage (*Aphilanthops frigidus*) is shown on the left. (From Evans and West Eberhard, © The University of Michigan (1970).)

the female to maintain a firm grasp on it during flight. None of these specialized structures are present in males.

Bees provide pollen for their larvae and have evolved a variety of structures to facilitate pollen transport. Most female bees carry pollen on their hind legs, which are modified in various ways depending on the nature of the pollen. Megachilid bees carry pollen on the under surface of the abdomen, with the aid of long, highly specialized hairs. The machinery of pollen transport is always absent in males and in cuckoo bees of both sexes.

The reason why males do not develop these tools is presumably that they are costly and of little or no potential use to males. There are other

animal taxa (such as birds) in which males cooperate with their mates in the defense and feeding of offspring. No such cases are yet known in the Hymenoptera, where the only significant form of male parental investment appears to be nest guarding. But even nest guarding is rare, and in the majority of cases where the guards are mates of the females whose nests they are protecting (as opposed to brothers or sons) the defense is probably as much against conspecific males as against predators or parasites.

One consequence of the fact that females are the high-investment sex is that they are expected to be much more selective in their choice of mates than are males, who have little to lose and who, therefore, can afford to be less discriminating. The relative lack of male discrimination has been exploited by certain orchids that induce males to copulate with structures that mimic females, both in appearance and in odor. Males duped into such pseudocopulation advance the orchid's reproduction at a (presumably) minor expense to their own.

As in other animals, many uniquely male characteristics can be understood as being adaptations that enhance a male's ability to find, to court or to defend females, even at the cost of a possible reduction in male survival. The males of many species appear to be subject to strong sexual selection, either through direct male–male competition (which tends to favor large size, conspicuous weaponry and pugnacious behavior) or through female choice (which tends to favor bright colors, ornaments and ritualized displays).

Current theories for the evolution of mating systems predict that the type and intensity of sexual selection will tend to be related in a logical way to the ecology of females, especially their spatial distribution. Many of these ideas can be tested in the Hymenoptera. To mate, a male must either go where the females are, or wait where they can be expected to appear. The males of most hymenopteran species search individually for receptive females, and engage in little or no male–male competition. Usually, males emerge before females and immediately begin searching at nesting areas, nectar sources, or other places where females are likely to be; in some species, they simply perch in promising areas and wait for the approach of females. As expected, searching and perching strategies are most common where females and their resources are dispersed widely.

Territorial defense is expected only where females or their resources are spatially clumped in a way that makes them defensible. In some bees, for example, males defend clumps of flowers against other males and attempt to mate with any females that come to harvest nectar or pollen. Another

form of 'resource-defense polygyny' occurs in species where females emerge from nests that are clustered in small patches of suitable nesting substrate.

In the solitary wasp genera *Oxybelus* and *Trypoxylon*, a male often defends the nest of a provisioning female (both from other males and from parasitic flies) and mates with the female on most of her visits to the nest. This arrangement is highly unusual in at least two respects. First, it is unusual for hymenopteran females to mate more than once in their lives. And second, as was mentioned above, this is almost the only context in which male Hymenoptera provide any form of parental investment. However, there is a strong conflict of interest between the guarding male and his mate. Owing to haplodiploidy, the male may father daughters but not sons. In theory, this leads to a disagreement over the sex ratio of the female's offspring, and, as expected, in at least one species where this prediction has been tested, males tended to cease guarding nests at times when the female was likely to produce sons.

Male–male competition is expected to reach its extremes where females are so clumped that a single male might successfully defend many of them at once. This situation occurs in several groups of Hymenoptera, with spectacular consequences. Large size, special mechanisms for seizing females, and powerful mandibles have evolved repeatedly in groups where females are highly concentrated. For example, in bees of the genus *Nomia* the hindlegs of males are modified for holding on to the abdomens of females. These bees nest in dense aggregations and there are typically many suitors for each virgin female, so the ability to hold on to a mate is highly advantageous. The ultimate in male- male competition occurs in several unrelated taxa where males fight to the death for access to the females available within a restricted (often enclosed) mating arena or 'lek'. Such fighting males often have bizarre modifications including wingless-ness (as discussed in the next section) and enlarged, heavily sclerotized heads with powerful mandibles that can literally crush an opponent (Figure 4.1).

Just as male–male competition often leads to grotesque modifications and violence, female choice often leads to male structures and behaviors of unusual beauty. Well-known examples include the spectacular displays of some male birds such as peacocks and birds of paradise, but some male bees and wasps are also highly ornamented, with colorful markings, luxurious pubescence, or striking enlargements of various exoskeletal elements, especially segments of the legs (Figure 4.7) or antennae. In theory even arbitrary female preferences can drive the evolution of
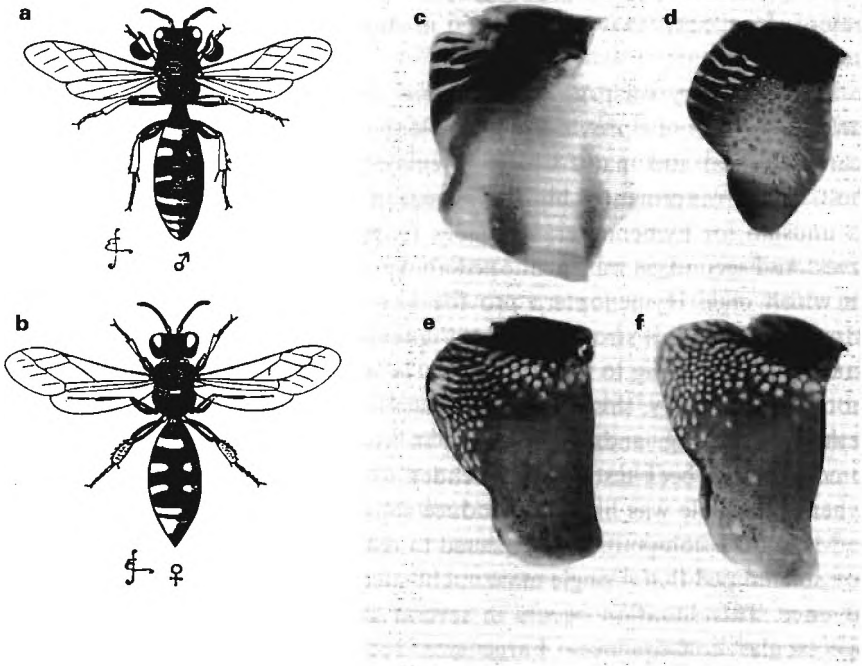
Figure 4.7. Tibial shields in males of the solitary sphecid wasp genus *Crabro*. In his book on sexual selection (*The Descent of Man, and Selection in Relation to Sex*, 1871), Darwin illustrated these plate-like enlargements of the foretibia in the British species *Crabro cribarius*, and discussed the idea that they might help the male to hold on to the female during copulation (a, b). Recent work has shown that instead they seem to be designed and used so as to provide the female with an informative 'light show'. The shields are thin, transluscent, and highly patterned (c–f). During courtship and copulation, the male places them over the female's compound eyes. The photographs on the right are interior views, showing the patterns of transmitted light that a female would see. The two upper panels are for *C. latipes* (left) and *C. tenuis* (right); the lower panels show two different individuals of *C. cribellifer*. (From Low and Wcislo, 1992.)

male characters, but it is also thought that female choice may involve characteristics that reveal something about the ecological 'quality' of a male's genotype. This seems especially likely to be true in Hymenoptera, where a male's genes pass immediately only into daughters. Unfortunately, very little is known about the mating systems of species with highly ornamented males, and we are not aware of any attempts to analyze the possible ecological relevance of such ornaments. The most thorough studies of Hymenopteran courtship concern small parasitoids that are not

highly ornamented; in these species, males perform elaborate, ritualized behavioral displays that involve head bobbing, wing vibrations and other forms of 'dance'.

Several kinds of mass displays and leks occur in species where the only resource provided to females is sperm. Some male wasps establish territories on the tops of hills or ridges where females apparently come to choose among a number of potential mates. Some social Hymenoptera form immense mating swarms that consist of male and female reproductives from many colonies. Such swarms are especially dramatic in ants that have synchronized 'nuptial flights'; tens of thousands of reproductives (mostly males) may gather in a small area, with many males scrambling intensely in attempts to mate with each female that enters the swarm.

These systems seem to have elements of *both* male–male competition (physical combat) *and* female choice (purposeful travel to a concentration of males where comparisons can be made and acted on). And, more generally, it is not always obvious that a given structure or behavior is likely to have evolved more through female choice or through male–male competition. In the digger-wasp genus *Crabro*, for example, the male foretibiae of most species are greatly expanded into thin, flexible 'tibial shields' (Figure 4.7). Conspicuously patterned in contrasting yellow and black, tibial shields show major differences between species and minor differences among individuals. Darwin was familiar with tibial shields in a British species, and he argued that they serve as claspers to prevent separation during mating. However, more recent work has shown that they could not plausibly work as claspers, and that males hold them over the eyes of females during mating. This suggests that they indicate the male's species identity, or signal some attribute of his phenotype that females use in assessing male quality. Female choice is implicated as being the evolutionary mechanism, but the basis for the presumed preference remains obscure.

Mixtures of different male strategies may occur within populations of the same species, and are sometimes associated with striking (even discontinuous) variation in male morphology. Cases where small males employ a different mating strategy than do large ones are known in a number of wasps and bees. In the digger wasp *Bembecinus quinquespinosus*, for example, large males compete intensely to grab emerging females, and then fly off with them to mate without interference, while small males search for opportunities to mate with females that may have been missed by large males (Figure 4.8). More dramatic cases are known in which there are two distinctive male morphs that pursue different mating
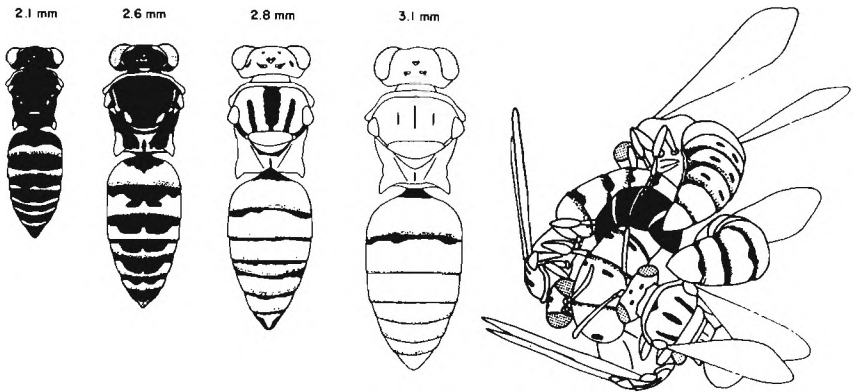
Figure 4.8. Male polymorphism in size, coloration, and mating strategy in the solitary sphecid wasp *Bembecinus quinquespinosus.* Males of this species vary enormously in size (left). Large males have predominantly light coloration and they search for newly emerging females by flying and walking over the open, sandy areas where nests occur. There is little shade in these areas, and temperatures near the ground can be very warm. Emerging females are often discovered by several large males who struggle with each other and with the female in an attempt to mate with her (right). Small males patrol nearby vegetation, presumably searching for females that escaped the notice of large males or that may be willing to re-mate. (From O'Neill and Evans, 1983.)

strategies. In some bees, ants and torymid wasps there is a flightless, fighting morph that engages in fierce combat over females at the site of emergence, and a fully winged morph that flies away to seek matings elsewhere (see Figures 4.1, 4.9 and 4.11).

Like dogs, most insects perceive a vividly fragrant world of chemical signals that go mostly unnoticed by visually and aurally specialized creatures such as ourselves. Chemical communication is particularly important in the sex lives of many insects (see Chapter 16 by Jean-François Ferveur and colleagues), including many Hymenoptera. In some wasps and bees, for example, males mark their territories with secretions that they spread on plants or other surfaces using clumps of hairs that have been modified to serve as brushes for this purpose. The resulting odor plumes advertise the territory (and its holder) both to females and to other males, and may indicate the male's specific identity and aspects of his phenotypic quality.

Chemical communication is often more important and more elaborate than this among female Hymenoptera, who have evolved an unparalleled diversity of exocrine glands. (Dozens are known, and, undoubtedly, more remain to be discovered.) As with other female adaptations, these glandular systems tend to be used in various aspects of parental
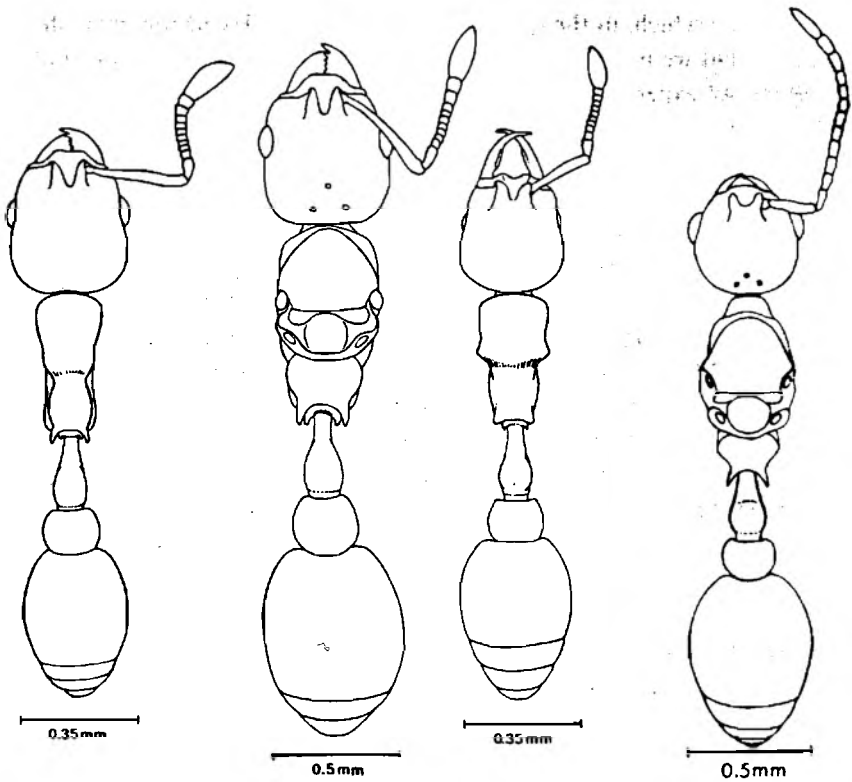
Figure 4.9. Winged and wingless males and females in the ant *Cardiocondyla wroughtonii*. From left to right: wingless worker, (initially) winged queen, wingless (ergatoid) fighting male, and winged dispersing male. Wingless males engage in lethal fights using their enlarged mandibles (see Stuart, R. J., Francouer, A. and Loiselle, R. (1987). Lethal fighting among dimorphic males of the ant, *Cardiocondyla wroughtonii*. *Naturwissenschaften*, **74**, 548–9; and Hölldobler and Wilson (1991), p. 186. Adapted from Kugler (1983). The males of *Cardiocondyla* with a description of the winged male of *Cardiocondyla wroughtonii*. *Israel Journal of Entomology*, **17**, 1–21).

investment. In social species, particular chemical signals arc used to recruit nestmates to food sources, and others are used to arouse group defensive responses when the colony is threatened by attack. Many exocrine secretions serve purposes other than communication, such as nest construction, the suppression of bacterial and fungal infections within the nest, and others, but the line between 'communication' and these other functions is not always clear cut (as when the volatile components of a venom recruit workers to the site of an attack), and this line has probably been crossed repeatedly during the evolution of such systems. Understanding an organism is often a matter of learning to 'see' and to 'think' the

way it does, which, in the case of insects (including Hymenoptera), often requires that we imagine ourselves in a world of tastes and smells unlike anything we experience directly.

To fly or not to fly

Winglessness (aptery) or near-winglessness (brachyptery) in one sex or the other has arisen many times in Apocrita, but it is very rare in Symphyta where only three species with apterous females are known. Two of these are tropical sawflies in which females guard eggs in confined locations. Many cases of aptery are known among the 'Parasitica' (including some species in several families of Cynipoidea, Chalcidoidea and Ichneumonoidea) and the Aculeata (including at least some species of Dryinidae, Embolemidae, Bethylidae, Sclerogibbidae, Formicidae, Tiphiidae, Mutillidae, Bradynobaenidae and Sphecidae).

Although either sex (rarely both) may be wingless, by far the most frequent pattern is female aptery (see Figures 4.2, 4.3, 4.4g, h, 4.9, 4.10). The typical syndrome is one in which females spend most of their lives in confined situations, such as burrows in the ground, where wings are worse than useless, while males spend much of their time flying in search of sugary food and females. For example, mutillid females parasitize the immature stages of ground-nesting wasps and bees, and spend much of
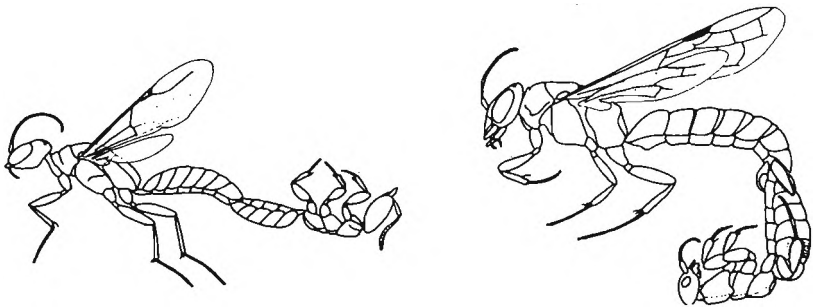

Figure 4.10. Phoretic copulation evolved independently in two different families of wasps. The pair on the left are bethylids (*Apenesia nitida*), and the pair on the right are tiphiids (*Dimorphothynnus haemorrhoidalis*). The female's position is venter-up in the bethylid pair, but venter-down (relative to the male) in the tiphiid pair, which requires an unusual rotation of the male's genitalia. Wingless females typical hunt for prey underground or in other confined spaces, and often (as here) have greatly reduced compound eyes; this bethylid female is completely blind. (From Evans, H. E. (1969) Phoretic copulation in Hymenoptera. *Entomological News*, **80**, 113–24.)

their time burrowing through the ground in search of hosts. Similarly, wingless female tiphiids parasitize underground beetle larvae. In these groups the females are obviously specialized for burrowing; for example, they tend to have short, stout, and powerful legs. In other cases, apterous females may be more gracile, but they also tend to live or to hunt in confined spaces.

Aptery improves a female's maneuverability in restricted places, and saves her the energetic cost of building wings and flight muscles. However, it also creates some problems. In particular, it restricts the area that she can search for adult food or larval provisions, and it may also restrict her ability to locate a mate. These potential disadvantages have been overcome in various ways. In ants, for example, only the reproductives have wings while the workers do not, and queens shed their wings after mating, thereby combining the advantages of having wings to locate mates and to disperse to new areas, with the advantages of unencumbered movement within the nest (Figure 4.9). Wingless females in the Australian tiphiid *Diamma* are sleek, metallic blue creatures with long legs that enable them to run at surprisingly high speeds.

In some tiphiids, mutillids and bethylids, males are larger than females and carry their mates about while joined *in copulo* (Figure 4.10). Such phoretic copulation has been studied in the thynnine tiphiids of Australia. Virgin females climb vegetation, assume a characteristic posture, and presumably release an advertising pheromone. An arriving male literally picks up the calling female, gives her a meal of nectar, and then drops her off at a site where she is likely to find the scarab larvae on which she will lay eggs. In some species, females are carried to flowers where they feed on nectar. In others, the male head is modified to form a 'nectar basket' used to carry an offering of food, and the female can sample the food before agreeing to indulge in aerial sex.

Wingless males seem to occur only in species that mate in a restricted area near the place of adult emergence (see Figures 4.1, 4.9 and 4.11). The most striking examples involve chalcidoid wasps associated with figs. A fig is an inflorescence 'turned inside out' to form a hollow structure in which hundreds of flowers line the inside surface. Figs are pollinated by tiny wasps in the family Agaonidae. The typical life history is one in which a mated female emerges from her natal fig and flies to another fruiting tree where she selects a fig and enters it through a tiny opening at the distal end. This involves negotiating a very narrow passageway, and, typically, females lose their wings in the process. Once inside, the one or more females entering a given fig oviposit in the tiny flowers lining the
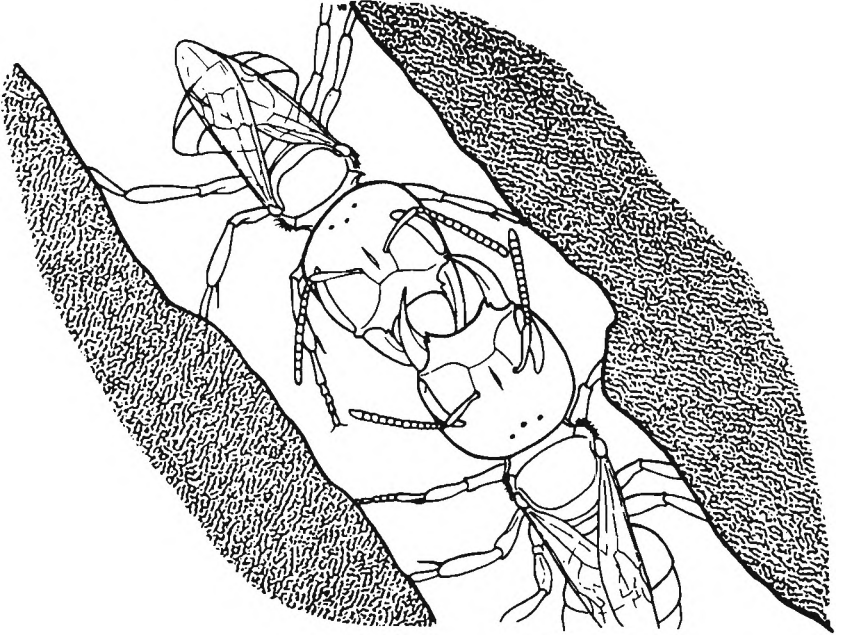
Figure 4.11. Flightless fighting males in a communally nesting sweat bee, *Lasio-glossum erythrurum*. In this species, as in other bees known to have fighting males, there is also a fully winged form that disperses from the natal nest, and the fighting males have disproportionately large heads and small, non-functional wings. (From Kukuk, P. F. and Schwarz, M. P. (1988) Macrocephalic male bees as functional reproductives and probable guards. *Pan-Pacific Entomologist*, **64**, 161–7. Reprinted by permission of Pacific Coast Entomological Society.)

interior cavity. Then they die having completed their lifetime reproduction within a single fig. The offspring develop into adults after feeding as larvae on tissues of the fig. The wingless males emerge prior to females and seek out virgin females before they emerge. A male gnaws a hole in the female's natal chamber, inserts his abdomen inside, and mates with the still imprisoned female, providing her with a lifetime supply of sperm. The female then leaves the fig, coated with pollen from the male flowers, and flies off to another tree to repeat the process. The wingless males spend their entire lives in their natal figs and all dispersal is by the winged females.

This life history favors a strongly female-biased sex-ratio. If only one foundress female entered the fig, then she should produce just enough sons to ensure that all her daughters are mated, because she maximizes her genetic contribution to future generations by maximizing the number of fertilized daughters that disperse to other figs. This contrasts strongly

with the situation in large, randomly mating populations, where the evolutionary equilibrium is one in which equal totals of investment should go into each sex, as shown by R. A. Fisher in 1930. But, as first pointed out by W. D. Hamilton, where mating is local and only mated females disperse to establish new mating groups, males compete only for a limited subset of all females, and a given female can make a larger contribution to future generations by devoting more of her resources to female production than to male production. As expected, female-biased sex ratios are observed in fig wasps as well as in numerous other parasitoids with local mating and dispersal of mated females.

Several other parasitoids depend on figs for their reproduction without providing any pollination services for the fig. In particular, several genera in the family Torymidae parasitize the fig or the agaonid wasps that pollinate them. These parasitic forms have long ovipositors which they employ to introduce eggs into the fig from the outside. Typically, females oviposit in a number of figs, laying only a few eggs in each one. The females of parasitic species are always winged, but the males may be winged, wingless or a mixture of both. The level of male winglessness tends to be correlated with wasp abundance. Complete male aptery is favored where wings are rarely of any value. This occurs if populations are dense, so that males always find mates in their natal figs. Where populations are diffuse, males may find themselves without mates unless they can fly to other figs. As expected, common parasites tend to have wingless males, while rare ones tend to have winged males. In cases of intermediate abundance, both kinds of males have reliable expectations of finding mates and selection may favor a mixture of winged and wingless males.

Winglessness in parasitic fig wasps is associated with intense, often lethal male–male combat. Some males are modified bizarrely with large heads and powerful mandibles that can literally chop an opponent in two (Figure 4.1). Describing his observations in Brazil (see Blum and Blum), W. D. Hamilton remarked that the situation in the fig 'can only be likened in human terms to a darkened room full of jostling people among whom, or else lurking in cupboards and recesses which open on all sides, are a dozen or so maniacal homicides armed with knives'.

Not all fig wasps are so pugnacious, however, and the situation is quite different in the pollinating agaonids. The heads of male agaonids are not unusually large, and fighting is rare if it occurs at all. Instead, male–male competition takes the form of a scramble for access to virgin females in the galls where they develop. W. D. Hamilton pointed out that the intensity of fighting should be related to the average relatedness among

males sharing a fig. In the agaonid case, only a very few females enter a given fig, and they each produce their entire brood within that fig. Consequently, males are often brothers and share many genes in common. In the torymid case, on the other hand, females visit numerous figs and lay only a few eggs in each one so that males are often unrelated, and male–male competition is correspondingly more intense.

Figs, and the community of wasps that depend on them, constitute a unique situation that is duplicated nowhere else in the living world. None-the-less, the ecological factors that influence the evolution of male winglessness and fighting in fig wasps have their parallels elsewhere with similar, if less extreme, consequences. For example, male aptery and lethal fighting occur in the ant genus *Cardiocondyla*. In most species of *Cardiocondyla* there is no nuptial flight, and mating takes place within the nests which are shared by several queens. Males in these species spend their entire lives within their natal nests where they fight intensely for access to virgin queens. A few species have both wingless (fighting) and winged (dispersing) males, which differ greatly in morphology (Figure 4.9). A similar situation occurs in a few bees in the genera *Lasioglossum* (Figure 4.11) and *Perdita*. These are communal nesters in which several females share a common nest but care only for their own offspring. As in some torymid fig wasps and some species of *Cardiocondyla*, the males are dimorphic. One morph is fully winged and substantially smaller than females, as is usual for bees. The other morph is much larger with reduced wings, enlarged head and powerful mandibles. The small morph leaves the nest and seeks females at flowers or other encounter sites, while the large morph remains within the nest and mates repeatedly with returning females. In keeping with what is now a familar pattern, the large males are highly pugnacious and fight to the death for possession of the nest and its female residents.

Male flightlessness in fig wasps, ants and bees is currently a subject of con-siderable interest among hymenopterists, because it illuminates a number of general issues in evolution. Dimorphic males are especially important owing to the unique opportunities they provide for examining fitness tradeoffs between alternative male strategies within a single population.

The economics of size dimorphism

Many fundamental aspects of an organism's ecology depend on how big it is. These include such things as metabolic rate, life span, fecundity and

prey size, all of which tend to increase with size. Size can have very different consequences in the two sexes, leading to selection for size differences. Many studies involving a wide variety of different kinds of animals have shown that the degree of size dimorphism between the sexes tends to be correlated with the type of mating systems occurring in different species. In particular, males tend to be relatively large in taxa where they fight for control of females, or for control of limited resources needed by females. This makes sense, since the larger of two combatants is likely to have an advantage that may offset any disadvantages of large size, such as longer development time or greater nutritional needs. Males tend to be smaller than females in the Hymenoptera, but relatively large, combative males occur in some taxa, and there is much quantitative variation in size dimorphism even within groups where males are smaller than females. These overall patterns have long been appreciated, but there have been no large-scale comparative surveys of sexual size dimorphism and few attempts to explain why size differences tend to fall within certain characteristic ranges.

The nest-building aculeates differ from most other animals in two ways that make them uniquely valuable for testing general theoretical ideas about the evolution of size. First, the primary determinant of an individual's adult size is the amount of larval food provided by its mother. In other animals (including those with extended parental investment), most of the final difference in size between males and females is generated by growth *after* the offspring are released to fend for themselves. Thus, adult size differences are likely to reflect both early investment by the parents and later decisions by the offspring themselves. In most aculeates, however, adult size is determined almost entirely by the amount of food provided to each offspring by its mother, and the relationship between the size and number of offspring is expected to reflect the interests of the mother alone. Moreover, because larval provisions are such a major component of parental investment in aculeates, offspring size is probably a better index of investment in these insects than it is in most other animals.

Second, the ability to predetermine the sex of each offspring opens up a world of opportunities that are denied to most other animals. Some parasitoids, for example, produce female offspring on relatively large hosts and male offspring on relatively small hosts. This makes good sense if female offspring gain more from being large than do male offspring. Nest-building aculeates take this strategy a step farther, freely adjusting both the *number* of offspring of each sex they produce, and the amount of effort or *parental investment* they put into each male or female offspring,
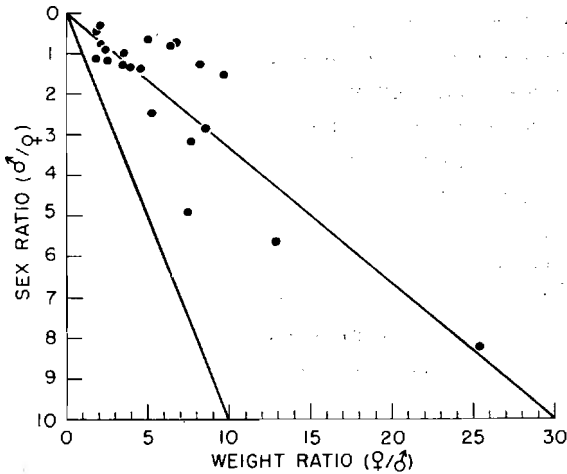
Figure 4.12. The sex ratio (males/females) as a function of the weight ratio (female/male) for 21 species of ants with one queen per colony. This famous figure illustrates the first test of the prediction that workers in some species of social Hymenoptera should tend to bias their colony's investment ratios toward female reproductives. The upper line shows the 3:1 ratio expected if the queen typically mates with just one male and the workers control the investment ratio; the lower line shows the 1:1 ratio expected if the queen mates many times or if she controls the ratio of investment. Note that in this sample of species, females are always at least twice as large as males, often five to 10 times as large, and in one case 25 times as large. (From Trivers, R. L. and Hare, H. (1976) Haplodiploidy and the evolution of the social insects. *Science*, **191**, 249–63. Copyright 1976 by the AAAS.)

so as to produce an appropriate overall sex ratio of investment. This intimate relationship between cost and number of offspring forms the basis of many tests of sex-ratio theory that have been performed in a variety of hymenopteran taxa. Owing to the great range of relative male and female sizes that can be found within many groups of aculeates (especially ants), these tests provide the strongest evidence yet obtained in support of R. A. Fisher's basic theoretical insight (as refined by W. D. Hamilton, Robert Trivers and others), that the target of selection should be the population-wide *ratio of investment*, not the numerical sex ratio *per se* (Figure 4.12).

Typically, sex-ratio studies treat male and female sizes as given, and regard the sex ratio as the only variable of interest. Although appropriate for the purposes of such studies, this may have tended to deflect attention from the equally interesting problem of size itself, as a dependent variable that is expected to reflect ecological and other factors. In contrast to animals lacking precise sex-ratio control, hymenopteran females can

compensate efficiently for large differences between the costs of males and females by producing relatively *fewer* of the *more expensive* sex. Therefore, large cost differences can evolve without causing either the inefficiencies entailed in culling partially reared broods, or unbalanced (hence unstable) population-wide ratios of investment. Thus, for much the same reasons that they are the organisms of choice for the study of sex-ratio evolution, aculeate Hymenoptera are ideal organisms in which to ask fundamental questions about the economics of size in general and of sexual size dimorphism in particular.

Substantial size dimorphisms are the rule throughout the nest-building aculeates, but while females are usually larger than males, the magnitude of the difference varies considerably within and among taxa. What determines how much a mother should invest in each son or daughter? A general theoretical framework for thinking about offspring size was proposed by Christoper Smith and Stephen Fretwell, who pointed out that parents should attempt to adjust offspring size and number so as to maximize the fitness produced *per unit invested*. It is reasonable to assume that fitness increases with each additional unit invested, at least up to some point, but that the gain per unit invested declines for sufficiently high levels of investment. Under this very general assumption, the optimal investment from the parent's point of view is less, and often much less, than that needed to yield an offspring of maximal fitness (Figure 4.13). This amounts to the familiar economic distinction between getting 'the best' and getting 'the best value for the money'.

An important corollary is that the optimal investment per male or female offspring depends on the shape of the fitness gain curve within each sex. Since male and female Hymenoptera live very different lives, it is likely that their fitness gain curves also differ such that mothers are selected to make male and female offspring of different sizes. If the male gain curve begins to saturate (show declining fitness gains per unit invested) more quickly than the female curve, then each male should receive relatively less investment. Conversely, if the male curve saturates more slowly than the female curve, then males should receive relatively more investment. Thus, the question of why male aculeates are usually smaller than females amounts to asking why the male gain curve usually, but not always, saturates more quickly than the female curve. It seems likely that larger females tend to produce more eggs, live longer, and forage more efficiently than smaller females. For males, however, the advantages of large size may be more modest, since even a small male can produce many more sperm than a female will use in her lifetime. Only
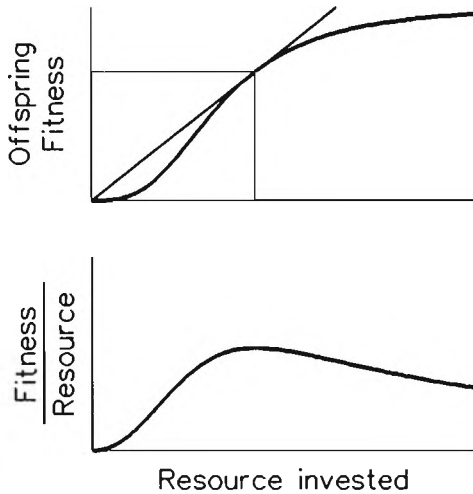
Resource invested

Figure 4.13. The Smith–Fretwell model of optimal offspring size. The optimal investment in an offspring depends on the shape of the fitness gain curve, which specifies offspring fitness as a function of the level of parental investment (upper panel). If the slope of the gain curve has an interior maximum (i.e. is steepest at intermediate levels of investment), then offspring fitness *per unit invested* will be greatest at some intermediate offspring size (lower panel). This size or level of investment in individual offspring is optimal from the parent's point of view because it gives the parent the greatest total offspring fitness under the constraint that total investment is limited. The optimal offspring size can be found graphically by drawing the line of greatest possible slope from the origin to a point on the gain curve; this slope is the 'rate of return' on investment at optimum. An important assumption of the model is that parents control both offspring number and offspring size with sufficient precision to make the size–number tradeoff meaningful. This model was first derived in 1974 by C. C. Smith and S. D. Fretwell (The optimal balance between size and number of offspring. *American Naturalist*, **108**, 499–506).

in species with intense male–male competition will large males tend to have substantially higher fitness than small males. To date, only a few studies have attempted the difficult task of directly assessing the relationship between size and reproductive success in nest-building aculeates, but the findings are generally consistent with these assumptions.

As part of an ongoing study of size structure in bee communities, we have made head-width and other morphological measurements on hundreds of species of bees and wasps. (Head width is a standard measure of size that is correlated strongly with dry weight, and one that can be determined easily from pinned museum specimens.) Although our primary focus is on female size, we have also measured males where available.
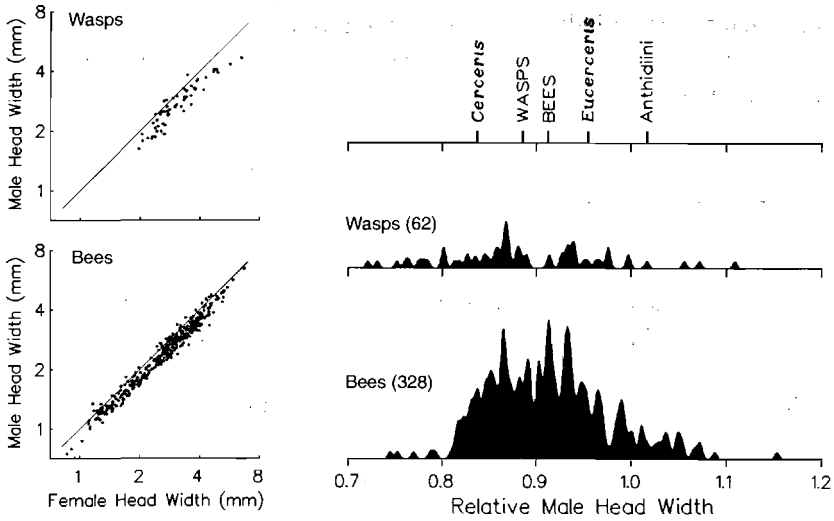
Figure 4.14. Size dimorphism in bees and sphecid wasps. Each point in the scattergrams (left) represents the mean male and female head widths for one species. The sample of wasps consists almost entirely of North American Philanthinae (mainly *Cerceris*, *Eucerceris* and *Philanthus*); the much larger sample of bees represents the faunas of New England and two localities in Wyoming and Utah. Note that the axes are scaled logarithmically, and that the 45-degree lines indicate equal male and female head widths. The distributions on the right show the same data as ratios of male to female head width (relative male size); means for several taxonomic groups of interest are shown at the top. Bees and wasps as a whole do not differ significantly from each other, but *Cerceris* (in which males tend to search individually for females) and *Eucerceris* (in which males are often territorial) differ significantly from each other and from the mean for all wasps, while Anthidiini (which tend to be highly territorial) differ significantly from the mean for bees.

Figure 4.14 shows scatterplots of mean male head width by mean female head width, for 328 species of bees and 62 species of sphecid wasps. On average, there is a remarkably constant proportionality of male and female sizes, independent of a species' absolute size, with male head widths typically about 0.9 times those of females. (If males and females were geometrically similar, this would imply an average relative male weight of 0.9^3 (0.73); in fact, males are usually more slender than females, and thus weigh even less than implied by their relative head widths.) However, there is much variation about this average relationship. Some of the variation is associated at generic and tribal levels with known tendencies of certain taxa to have particular kinds of mating systems (Figure 4.14). As expected, males tend to be larger than average (relative to females) in

taxa, such as the anthidiine bees, where, typically, they defend territories; in some of these cases males are absolutely larger than females. Conversely, males tend to be relatively small in taxa where they are known to search for widely dispersed females. This suggests that extreme mating systems (or ones atypical of a given taxon) might be found easily by looking for extreme levels of size dimorphism (where males are relatively large or relatively small) within the taxon of interest.

Also, there is often much variation of size *within* the sexes, and our survey reveals a tendency for males to be more variable than females. There are several possible explanations for this pattern. One is that males, being haploid, express greater genetic variance than do diploid females; if the population contains genetic variation for traits that affect final size (given a fixed provision mass), then male size will be more variable, other things being equal. Another possibility is that male development is less well canalized than female development. Both hypotheses predict that the correlation between provision mass and adult size will be lower for males than for females, but we are not aware that this prediction has ever been tested. Yet another possibility is that the male optimum is usually defined less sharply than the female optimum, so that females allow themselves more latitude in determining the size of the provision mass when making a son than they do when making a daughter, but we know of no general reasons for thinking that this would often be true.

Finally, it is likely that in at least some species, females are selected to produce males of different sizes. There is good evidence from several wasp and bee species that males of different sizes tend to pursue different strategies (see Figure 4.8). What is not clear is whether any of the observed variation in male size is adaptive, and produced deliberately by mothers, or whether it is merely accidental, with the unfortunate smaller males adopting alternative strategies that 'make the best of a bad lot'. The dimorphic males considered above (wingless fighters and winged dispersers) provide a reasonably convincing case for the adaptive production of different kinds of males. The value of producing additional fighters that stay home to compete for a restricted set of females is likely to decline very rapidly after only a few are produced. If so, it would still pay to produce winged males if they have opportunities to find receptive females elsewhere, perhaps at sites that happen to lack sedentary fighters. Females might even prefer mating with dispersing males to avoid producing inbred offspring, where they are closely related to the fighting males at home.

Females can also be highly variable, and they too may sometimes

exhibit multiple strategies associated with size. The most dramatic cases of intrasexual size variation occur among the workers of ant species with complex caste systems, where the largest and smallest workers may differ by one to two orders of magnitude in weight (see Figure 4.3). Such cases demonstrate that the hymenopteran developmental program is able to produce viable adults spanning a huge range of sizes, from a single genome, and that such variation may in fact evolve where ecological conditions call for it. The difference in size between reproductive male and female ants can also be enormous (see Figure 4.12) proving that aculeates of very different sizes can mate successfully.

These facts about ants raise an interesting question: Why is there not sometimes even more size dimorphism in bees and wasps? Why do males seldom weigh less than half as much as females? Why not a quarter, or an eighth? One possibility, which seems never to have been explored, is that females are selected to favor relatively large males because their size indicates both their mother's superior provisioning ability and their own metabolic efficiency in converting larval provisions into adult tissues. This bias might indeed prevent a slide toward really tiny males, but it would simultaneously create another dilemma: If females prefer large males produced by large, vigorous mothers, then why are males not sometimes two or three times the size of females? The formal answer is simply that various factors conspire to keep the male and female gain curves from diverging very far; in the end this merely restates the question in a different way. We need to measure the gain curves themselves in a variety of taxa and to learn what shapes them.

Conclusion

Generations of biologists have been drawn to the Hymenoptera by their great diversity and ecological importance, and by their endlessly fascinating behavior. The order is rich in sexual dimorphisms that are of interest in their own right, and that raise problems of fundamental significance for the biology of sex differences. Much of the relevant literature is scattered and known only to specialists, but increasing amounts of effort are being devoted to organizing existing knowledge according to principles of evolutionary ecology, and increasing numbers of field studies now focus on general theoretical issues. These developments have contributed to a growing awareness of the order's potential importance for research on sex differences.

Much remains to be done in quantifying sex differences, in describing

general patterns of sexual dimorphisms, in finding the ecological correlates of such patterns, and in assessing how variation in sexually dimorphic character states affects male and female fitnesses. For example, size differences between the sexes depend in theory on the fitness gain curves within each sex, but there have been very few attempts to estimate these curves in nature. The gain curves are expected to depend (in part) on mating systems, but the mating systems of most species still await description. Likewise, some groups exhibit strikingly dimorphic male structures that undoubtedly play roles in courtship, display or male–male competition, but we know very little about how these structures are actually used in most species, and even less about their fitness consequences.

The developmental and physiological bases of sexual dimorphism in the Hymenoptera remain largely unknown, although there is increasing interest in the mechanisms of caste differentiation in social species. Both quantitative and qualitative differences in larval nutrition play important roles in caste differentiation, and larval nutrition might well play a similar role in solitary species that have multiple morphs within one sex. Such morphs always differ both in shape and size. Allometric changes in shape as a function of size can be studied using natural variation, but more could be learned by altering larval nutrition experimentally. Such studies would allow us to explore the set of nutritionally accessible morphologies, and would surely deepen our understanding of the ecological consequences of varying the level of investment in each offspring.

Major advances in our understanding of hymenopteran phylogeny are occurring at a rapid pace, owing largely to the application of powerful new techniques for inferring phylogenetic relationships, and to the availability of new sources of phylogenetically informative characteristics such as DNA sequences. As evolutionary relationships within the group become known with more certainty and in greater detail, it will become increasingly feasible to test historical and adaptive hypotheses using the sophisticated comparative methods now being developed. Hymenoptera provide unequalled opportunities to apply these methods to a broad range of questions about the evolutionary forces that shape differences between the sexes.

Further reading

Blum, M. S. and Blum, N. A. (eds.) (1979) *Sexual Selection and Reproductive Competition in Insects.* Academic Press, New York.

Danforth, B. N. (1991) The morphology and behavior of dimorphic males in *Perdita portalis* (Hymenoptera: Andrenidae). *Behavioral Ecology and Sociobiology,* **29**, 235–47.

Evans, H. E. and O'Neill, K. M. (1990) *The Natural History and Behavior of North American Beewolves.* Cornell University Press, Ithaca.

Evans, H. E. and West Eberhard, M. J. (1970) *The Wasps.* University of Michigan Press, Ann Arbor.

Gauld, I. and Bolton, B. (eds.) (1988) *The Hymenoptera.* First published by Oxford University Press in association with the Natural History Museum, London.

Hölldobler, B. and Wilson, E. O. (1990) *The Ants.* Springer-Verlag.

Krebs, J. R. and Davies, N. B. (1993) *An Introduction to Behavioural Ecology* (third edition). Blackwell Scientific Publications, Oxford.

Kukuk, P. F. and Schwarz, M. P. (1988) Macrocephalic male bees as functional reproductives and probable guards. *Pan-Pacific Entomologist,* **64**, 131–7.

Low, B. S. and Wcislo, W. T. (1992) Male foretibial plates and mating in *Crabro cribellifer* (Packard) (Hymenoptera: Sphecidae), with a survey of expanded male forelegs in Apoidea. *Annals of the Entomological Society of America,* **85**, 219–23.

O'Neill, K. M. and Evans, H. E. (1983) Alternative male mating tactics in *Bembecinus quinquespinosus* (Hymenoptera: Sphecidae): correlations with size and color variation. *Behavioral Ecology and Sociobiology,* **14**, 39–46.

O'Toole, C. and Raw, A. (1991) *Bees of the World.* Facts on File, New York.

Ross, K. G. and Matthews, R. W. (eds.) (1991) *The Social Biology of Wasps.* Cornell University Press, Ithaca.

Seger, J. (1991) Cooperation and conflict in social insects. In *Behavioural Ecology, An Evolutionary Approach* (third edition). Eds. Krebs, J. R. and Davies, N. B. Blackwell Scientific Publications, Oxford.

Thornhill, R. and Alcock, J. (1983) *The Evolution of Insect Mating Systems.* Harvard University Press, Cambridge.

Trivers, R. (1985) *Social Evolution.* Benjamin/Cummings, Menlo Park.

Waage, J. and Greathead, D. (eds.) (1986) *Insect Parasitoids.* Academic Press, London.

Wilson, E. O. (1971) *The Insect Societies.* Harvard University Press, Cambridge.