Crypsis
Brakefield, P.M.

MATING SYSTEM

The long-range female-attracting songs and long tactual cerci of crickets are components of a unique mating system, some aspects of which evidently trace to the earliest instances of copulation in the insect line and help explain changes leading to the current major groups of insects. Thus, none of the primitively wingless modern insects copulate, while all winged and secondarily wingless insects do, the majority with the male mounting the female and in some way holding or forcing her. In primitively wingless insects, however, a sac or bulb containing the sperm (a spermatophore) is transferred indirectly to the female without direct copulation. Like crickets, some of these particular primitively wingless insects possess prominent tactual cerci (e.g., Thysanura), used to guide the female during spermatophore transfer, as also in cockroaches and mayflies. In all insect groups of ancient origin that have prominent tactual cerci, transfer of the spermatophore is a luring act in which the female either mounts (winged and secondarily wingless forms) or stands beside the male (primitively wingless forms). In some crickets, such as the field cricket genus *Gryllus*, the copulatory act appears unique among all animals in being entirely luring, with no evidence of controlling force by the male at any stage. The female is attracted initially by the long-range calling song and then by the male's close-range courtship song and probably the fluttering touches of his antennae (Fig. 7). As in nearly all crickets, most close relatives of crickets, and most cockroaches and mayflies (the last aerially), the female mounts (or flies above) the male in the copulatory act. Apparently in correlation with the male field cricket having minimal ability to clasp the female's genital parts, the spermatophore is transferred quickly, in 15 to 90 s. The spermatophore is osmotically self-emptying, so that sperm injection occurs largely after the female dismounts from the male. In forms related to crickets, such as Tettigoniidae and Caelifera, in which males have evolved terminal claspers on the abdomen, the tactual cerci have disappeared and copulation is much lengthier. In Caelifera the mating act has evolved such that the male mounts the female, though still reaching beneath her to attach the genitalia; here, unlike Tettigoniidae, the antennae have also become much shorter. Apparently luring copulatory acts in insects have repeatedly evolved into acts involving significant force, but the reverse does not seem to have happened. Groups of features related to the history of insect mating acts have significance for interpreting changes in diagnostic features of major groups of insects, including cerci, antennae, genitalia, wing structure, long-range communication, and modes of pair formation.

FIGURE 7 Adult female (left) and male (right) *Phyllopalpus pulchellus*, the latter with forewings in singing position. (Photograph courtesy of David H. Funk.)

Distinctive morphological and behavioral features of crickets, especially those related to their methods of pair formation and mating behavior, make them a pivotal group in understanding insect evolution and phylogeny.

See Also the Following Articles

Cultural Entomology • Folk Beliefs and Superstitions • Hearing • Orthoptera

Further Reading

Alexander, R. D. (1961). Aggressiveness, territoriality, and sexual behaviour in field crickets (Orthoptera: Gryllidae). *Behaviour* **17,** 130–223.

Alexander, R. D. (1966) The evolution of cricket chirps. *Nat. History Mag.* **75,** 26–31.

Alexander, R. D. (1968). Life cycle origins, speciation, and related phenomena in crickets. *Q. Rev. Biol.* **43,** 1–42.

Alexander, R. D. (1969). Arthropods. *In* "Animal Communication" (R. Sebeok, ed.), 1st ed., pp. 167–215. Indiana University Press, Bloomington.

Alexander, R. D., and Otte, D. (1967). The evolution of genitalia and mating behavior in crickets (Gryllidae) and other Orthoptera. University of Michigan Museum of Zoology Miscellaneous Publication No. **133,** pp. 1–62.

Huber, F., Moore, T. E., and Loher, W. (eds.) (1989). "Cricket Behaviour and Neurobiology." Cornell University Press, Ithaca, NY.

Otte, D. (1992). Evolution of cricket songs. *J. Orthoptera Res.* **1,** 25–49.

Otte, D. (1994). The crickets of Hawaii: Origins, systematics, and evolution. *In* "Publications on Orthopteran Diversity." The Orthopterists' Society, Academy of Natural Sciences, Philadelphia.

Otte, D. (1994). Orthoptera species file 1: Crickets (Grylloidea). *In* "Publications on Orthopteran Diversity." The Orthopterists' Society, Academy of Natural Sciences, Philadelphia.

Otte, D., and Alexander, R. D. (1983). The Australian crickets (Orthoptera: Gryllidae). Academy of Natural Sciences of Philadelphia Monograph No. **22,** pp. 1–447.

Otte, D. and Naskrecki, P. (1997). Orthoptera species file online at http://viceroy.eeb.uconn.edu./Orthoptera.

Crypsis

Paul M. Brakefield
Leiden University

Organisms with bright and conspicuous color patterns tend to attract the most attention both scientifically and aesthetically. However, the majority of insects and other animals rely on camouflage or crypsis for survival from predators that hunt them by sight. Furthermore, crypsis may extend to include the other senses, namely, smell, touch, and sound. Indeed, any stimulus or signal that can alert a potential predator could be expected to become part of a

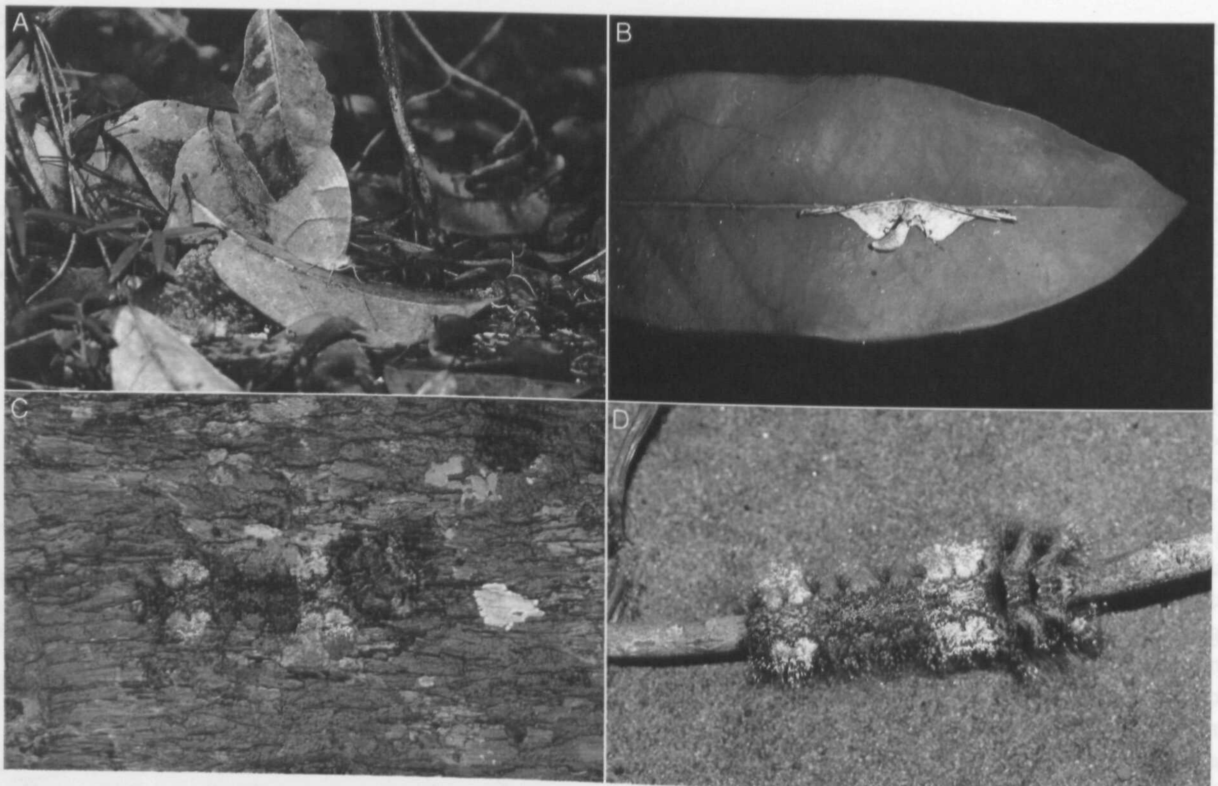

FIGURE 1 Crypsis illustrated for different insects. (A) An individual of the dry season form of the evening brown, *Melanitis leda,* resting among dead leaves on the forest floor in the Shimba Hills, Kenya. The insect is at the center with head pointing to the right; forewing length is ca. 4.5 cm. (B) A small moth that resembles a dead patch on a large leaf in a forest in Costa Rica (wing span is ca. 3 cm). (C) The caterpillar of a moth of the family Lasiocampidae resting on a tree trunk in the Shimba Hills, Kenya; it is ca. 6 cm in length and is positioned horizontally, head to the right, in the center of the photo (image has been rotated 90 degrees). (D) The same larva when actively moving in the same direction along a twig. See text for further details. (Photographs by the author.)

coordinated suite of cryptic traits. A form of crypsis is also shown by some predators that disguise themselves by assuming the same color and patterns as the background on which they hunt. H. B. Cott in 1940 wrote perhaps the best known book on animal color patterns, but many of the great entomologists of the 19th century had already considered insect camouflage. It is not usual to consider insect crypsis as a subject of applied biology but there are certainly many parallels with military expertise in either the hiding of or the searching for personnel and armaments in a landscape.

COLOR MATCHING AND CRYPSIS

An insect that is perfectly camouflaged is perhaps one of the most striking exhibitions of the power of evolution by natural selection to mold and adapt organisms to fit their environment and to maximize survival and reproductive success. Wonderful examples of camouflage are presented by many species of insects, including some butterflies in tropical forests (Fig. 1A), which rest on carpets of dead brown leaves. The apparent perfection of crypsis is emphasized in many such insects by a similarity of, and matching of, the color pattern of the wings, body, and appendages to the background on which they normally rest. The color pattern of these different body parts and structures must involve different genetic and developmental pathways, and yet evolution has led to a corresponding perfection of matching, albeit using entirely different mechanisms of pattern formation. Such an example of an underlying complexity of patterning is given by some caterpillars of the family Lasiocampidae that rest on the bark of trees and survive by resemblance to the background color pattern of the bark, including epiphytic lichens and algae (Fig. 1C). Such larvae are encircled by long hairs that are flattened around their margin when at rest. This breaks up their shape, smoothing their outline. These hairs are also patterned in a very specific way and one that is fully coordinated with the body cuticle, including the short bristles of the dorsal areas of the body segments. These elements are exposed, and the whole insect becomes highly conspicuous as soon as a larva is forced to move along a twig of fine diameter (Fig. 1D).

Furthermore, color matching in cryspis is almost always only one component of the strategy for survival; both habitat choice and, frequently, the adoption of very specific patterns of behavior and activity are required for effective crypsis. One such example is shown by some species of moths that attain crypsis by appearing to be a dead patch of tissue within a large leaf on which they rest (Fig. 1B). They achieve this not only through the generally brown color of their wings and some details of patterning, which may resemble small patches of fungal-attacked leaf tissue, but also through a precise positioning on the leaf. For example, the moth in the photograph of Fig. 1B has rolled up the leading edge of its forewing, wrapped its abdomen along the trailing edge of one hind wing, hidden its appendages, and positioned itself alongside the midrib of the leaf.

Despite the potential fascination of understanding crypsis, it is only relatively recently that scientists have begun to analyze what is meant precisely when it is stated that an organism is well camouflaged. John Endler in 1978 stated that "a color pattern is cryptic if it resembles a random sample of the background perceived by predators at the time and age, and in the microhabitat where prey is most vulnerable to visually hunting predators." There are several crucial components in this definition. First, a color pattern is cryptic only with respect to the specific environment in which the organism is potentially encountered by the predator or the guild of predators to whom the pattern is an adaptive response. What is a cryptic pattern on the resting background of that environment may be conspicuous and ineffective on any other background. Second, the effectiveness of a particular pattern is considered with respect to the normal time and lighting conditions under which crypsis is functional. Third, to be cryptic the color pattern of a prey organism must essentially reflect a random sample of the background on which it rests.

INDUSTRIAL MELANISM AND CRYPSIS

Perhaps the first analysis of crypsis and the evolution of a color pattern from the perspective of changes in camouflage involved industrial melanism in the salt-and-pepper moth, *Biston betularia*. Industrial melanism refers to an association of high frequencies of dark, melanic forms or phenotypes of a species with high levels of air pollution. The fundamental components of this classic example of the evolution of an adaptive trait also apply to numerous other species of moth and other insects that have evolved melanism as a response to environments influenced by air pollution. These components are: (1) the environment was changed by air pollution in such a way that the camouflage of the "typical" or wild type of color pattern was impaired, (2) a mutant phenotype occurred in this new environment that had a functional design or color pattern that improved survival from birds hunting the moths at rest, and (3) the dominant allele at the gene that specified this favored mutant phenotype then increased in frequency under the influence of natural selection, leading to the species exhibiting industrial melanism.

In the salt-and-pepper moth, we know from museum collections that prior to the middle of the 19th century in northern England the moths had pale-colored wings with a speckling of dark dots (the typical form). Also, up until that time in the early industrial revolution the bark of trees was predominantly pale and covered in epiphytic lichens and algae. The salt-and-pepper moth rests on bark, and females lay their eggs under foliose lichens or in cracks in the bark. The moths are active at night and rely on background matching and crypsis for survival from birds during daylight hours. Survival enables males to mate at night and females to lay their eggs over a number of nights. The gaseous (e.g., sulfur dioxide) and particulate (soot) air pollution produced by industry both killed the epiphytic communities on the trees and blackened the resting surfaces of the moths. The typical, pale-colored moths became more conspicuous. The fully black, melanic form known as *carbonaria* was not collected until 1848, near Manchester. It may have occurred shortly before through a mutation (producing a new allele of the gene), or perhaps it had already existed for some time in that region as a rare allele. Whatever its precise origin, the *carbonaria* form rose rapidly in frequency and spread extensively through the industrial regions of Great Britain over the following decades; the adult moth as well as newly emerged larvae can move long distances. Clear geographical associations were established between the amount of air pollution and the frequency of the fully melanic *carbonaria* and also of several intermediate melanic forms known as *insularia*.

Up until the mid-20th century this remained a verbal, albeit persuasive, reasoning for the evolution of melanism as an adaptive response to a changed environment. It was only then that some classic early experiments in evolutionary biology began to add scientific rigor to this explanation. Several researchers performed a series of experiments that showed beyond doubt that, whereas the survival of the pale typical form was higher in rural, unpolluted regions of Great Britain than that of the *carbonaria* form, this relationship is reversed in the polluted industrial environments. Although there have been discussions about the precise details of some of these types of experiments, the fundamental finding of a switch in survival and relative fitnesses (reproductive success) of the pale and dark phenotypes across the extreme environments, principally the result of corresponding changes in crypsis, has been corroborated. Other differences in fitness among the phenotypes that are not directly related to the visual differences in color pattern may also be involved in determining the precise dynamics of the evolution.

There has, however, more recently been an additional finding that proves beyond any doubt the role of evolution by natural selection. Great Britain and other countries in northern Europe have over the past few decades reduced levels of air pollution from soot and gases such as sulfur dioxide. This has in turn led to declines in the frequencies of the melanic forms and the coining of the phrase "evolution in reverse." As the resting environment returns, at least in a qualitative sense, back toward the original, unpolluted state, the relative fitnesses are also reversed, leading to present-day declines in melanism. Although it has not been precisely quantified, the conclusion must be that in previously polluted regions, while the fully black melanic *(carbonaria)* has again become conspicuous and vulnerable to birds, the paler typicals have become well camouflaged on the changed background.

ANALYSIS OF CRYPSIS

This example of the salt-and-pepper moth illustrates that crypsis still needed to be scientifically measured and fully quantified. In 1984 Endler began to use early techniques of image analysis to mathematically describe how well matched in terms of color patterning were moths in a North American woodland community with respect to different potential resting environments. If crypsis is "optimal" the patterning of the insect will represent a random assemblage of the pattern elements of the background. Endler also pointed out that there will be matching with respect to different components of the color patterns of both insect and resting background, namely, size, color, shape, and brightness. In some backgrounds, such as pine needles or bark with striations, the component of orientation should also be added. Failure to match with respect to any one of these components will lead to mismatching and ineffective crypsis. Because the color vision of many predators, including birds and insects, extends into the ultraviolet part of the spectrum, when color matching in crypsis is considered it often has to include the UV. Researchers have recently begun to use computer-generated patterns, image analysis, and "visual predators" to explore more fully the potential effects of interactions among predators and their prey that lead to the evolution of cryptic color patterns.

Cryptic color patterns may also include an element of banding, which is disruptive and can serve to break up the outline of the prey. Usually, such an element also has to blend into the resting background in terms of the prey representing a random assemblage of its pattern. However, this restriction is perhaps relaxed when crypsis is used only to protect a prey from a distance, such as in the brightly colored, banded moth caterpillers, including the cinnabar, *Tyria jacobaeae,* and the strikingly striped forewings of some arctiid moths, for example, *Callimorpha quadripunctaria.*

CRYPSIS AND NATURAL SELECTION

Although testing of these ideas, at least in the context of animal color patterns and their camouflage, has not been completed, Endler has also performed experiments with guppies that dramatically illustrate the power of natural selection to lead to the evolution of effective crypsis. Male guppies can be very colorful with a patterning of bright spots and patches on their lateral flanks and fins. Laboratory experiments in which females can choose whether to mate with males of different patterns show that there is female preference for the more brightly colored males. In the wild in Trinidad, there is a correlation between the degree of color patterning on males in a population and the presence of predatory fish and invertebrates ranging from weak to strong mortality factors on guppies. Male fish are colorful and brightly patterned when either no predators or only weak predators are present, whereas they are drab and unpatterned brown fish when strong predators such as certain cichlids are present. A series of experimental pools with natural backgrounds in a greenhouse was established to examine the efficacy of natural selection on crypsis in this system. Endler showed that guppy populations with the weak predators showed no divergence over subsequent generations in their average color pattern; in contrast, in those pools to which strong predators were added the guppies showed a marked and progressive decline in the brightness and spottiness of the males. This result was highly consistent with selection favoring a more effective crypsis through a lower conspicuousness and improved background matching of the prey populations. In the absence of such strong predators, the balance of sexual selection through female choice and of natural selection by visually hunting predators favors colorful males because they survive to maturity and then achieve a higher mating success than their less colorful competitors.

Such a balance of selection on animal color patterns is probably the norm in natural populations. Thus, in animal communication, a color pattern is usually a compromise between being conspicuous to conspecifics and being poorly visible to predators (or prey). Indeed, one of the potential disadvantages of adopting crypsis as the primary means of survival is that it almost inevitably ties the organism down to a sedentary style of life at least during the hours of daylight. In contrast, when organisms are distasteful and adopt a conspicuous, aposematic lifestyle or when they evolve Batesian mimicry to resemble such warningly colored species, there is no such disadvantage associated with daytime activity.

INTERACTION OF CRYPSIS AND OTHER DEFENSES

In many insects, an organism may not rely only on crypsis for survival. There may be some secondary means of defense once crypsis has failed and the prey has been detected by a potential predator. Insects that are cryptic at a distance but conspicuous when seen close up (including the banded larvae and arctiid moths mentioned above) are often chemically protected. This type of multiple defense is also illustrated by the moth caterpillar in Fig. 1C. If the caterpillar is disturbed and begins to move it can expose a series of glands in the dorsal cuticle of several segments toward the front of the body. These are visible as a pair of partial bands in Fig. 1D, the largest immediately to the right of the largest white-colored region. These produce a pungent odor and probably provide a potential chemical defense against birds and other predators.

The effectiveness of crypsis will also show complex interactions with the visual processing abilities of the specialist predator or the guild of predators. Some insects that rely on camouflage for survival often exhibit extreme individual variation. One example is the tropical evening brown, *Melanitis leda.* This large brown butterfly is common throughout the Old World tropics. In wet–dry seasonal environments, the species shows classical seasonal polyphenism (i.e., distinct color patterns that result from phenotypic plasticity), with a wet season form having conspicuous marginal eyespots and a cryptic dry season form without such eyespots. The latter form relies on survival through crypsis on a resting background of dead brown leaves (Fig. 1A). In large numbers of the dry season form it is difficult to find two individuals with exactly the same color pattern. Dramatic variation across individuals is produced by high genetic variation in several different pattern elements across the wing (such as the contrast and brightness of particular patches and bands and the background wing color in different regions). This variation can be interpreted as an evolutionary response involving "apostatic selection" to make it more difficult for browsing predators in the leaf litter to form a specific "search image" for a particular form of dead leaf pattern corresponding to the color pattern of the prey. Although like many of the detailed ideas about the significance of crypsis and particular animal color patterns, this hypothesis remains to be tested rigorously, it does once again illustrate the fascination of crypsis.

See Also the Following Articles

Aposematic Coloration • Defensive Behavior • Eyes and Vision • Industrial Melanism • Mimicry

Further Reading

Bond, A. B., and Kamil, A. C. (2002). Visual predators select for crypticity and polymorphism in virtual prey. *Nature* **415,** 609–613.

Bradbury, J. W., and Vehrencamp, S. L. (1998). "Principles of Animal Communication." Sinauer, Sunderland, MA.

Cott, H. B. (1940). "Adaptive Coloration in Animals." Methuen, London.

Endler, J. A. (1978). A predator's view of animal colour patterns. *Evol. Biol.* **11,** 319–364.

Endler, J. A. (1984). Progressive background matching in moths, and a quantitative measure of crypsis. *Biol. J. Linn. Soc.* **22,** 187–231.

Kettlewell, H. B. D. (1973). "The Evolution of Melanism." Clarendon Press, Oxford.

Majerus, M. E. N. (1998). "Melanism: Evolution in Action." Oxford University Press, Oxford.

Sargent, T. D. (1976). "Legion of Night: The Underwing Moths." University of Massachusetts Press, Amherst.

Thery, M., and Casas, J. (2002). Predator and prey views of spider camouflage. *Nature* **415,** 133.

Cultural Entomology

James N. Hogue

California State University, Northridge

Since the dawn of humanity, the organisms that share our world have captured our imagination and influenced our thoughts, dreams, and fears. This influence is particularly true of insects, which impact nearly every facet of human activity. In addition to serving as objects of scientific inquiry, competitors for resources, carriers of disease, and food, insects have made a marked impact on the cultural aspects of human societies. Cultural entomology is the study of the role of insects in those human affairs that are practiced for the nourishment of the mind and soul, such as language and literature, music, folklore, religion, art, and recreation. These activities that pervade primitive and modern human societies are concerned primarily with life's meaning rather than its function.

Despite their extra appendages and different strategies for making a living, insects look and behave enough like humans to serve as models for friends, enemies, teachers, and entertainers. This status permits insects to act as objects on which to impart human qualities and as the source of qualities that can be incorporated into the framework of human ideology and social structure. It is not surprising then to find insects playing a host of roles in the oral and written traditions throughout human history, ranging from folk tales to the holy writings of the world's most prominent religions.

FOLKLORE, MYTHOLOGY, AND RELIGION

The derivation of stories and myths is a universal tendency of all human societies. Both myths and folk tales differ enormously in their morphology and their social function. They are used to mediate perceived contradictions in phenomena observed in the natural world, they serve as vehicles of wish fulfillment, they may embody a lesson, or they may serve to preserve a piece of a culture's history. Myth and folklore also differ from one another in their origin and purpose, but application of these distinctions is difficult to discuss here. Originally, mythology meant no more than telling stories, such as traditional tales passed from generation to generation. Later, some of these tales acquired new meaning and status and evolved more symbolic or religious functions. All tales, whether classified as folklore or myth, are not generated in isolation, but derive their inspiration, elements, and messages from the environment, including the host of other species that surround us. These tales are often used to derive commonsense explanations of natural phenomena observed in the environment. Conversely, such observations may also serve as the basis for the superstitious beliefs and tales surrounding aspects of human existence such as healing practices and other utilitarian activities such as agriculture.

Entomological mythology commonly employs transformations of beings between the insect and the human form (and combinations thereof), the acquisition of souls by insects, and ultimately the deification of insect forms. Insects are also used symbolically throughout the world's religions in a variety of roles.

Insects figure prominently in the creation myths of many cultures. The widespread recognition of insects in this role probably stems from an innate recognition of insects as ancient members of the living world that must have been