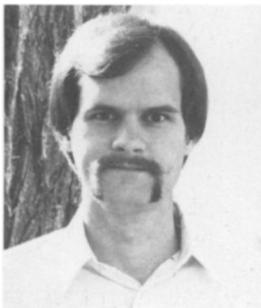


Sexual Selection and Insect Mating Behavior

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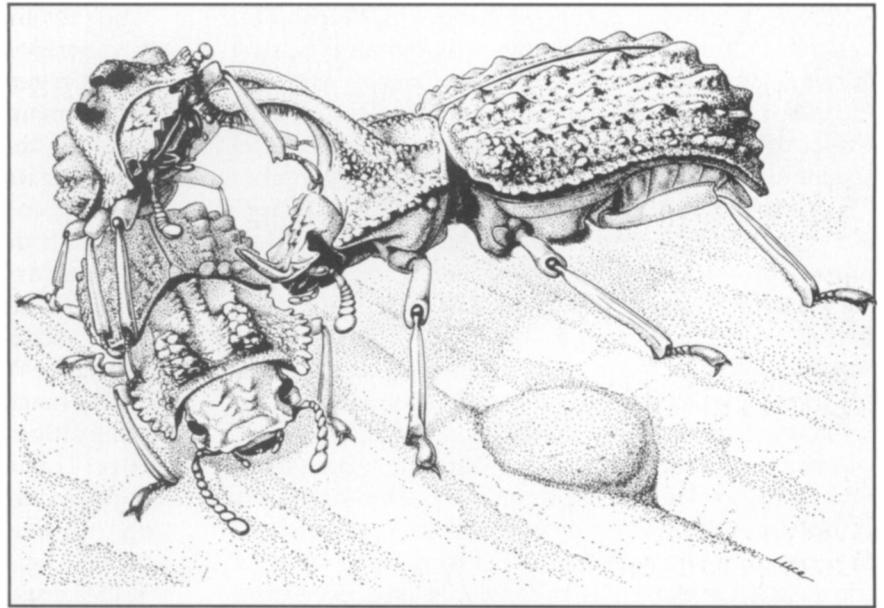
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The evolutionary process consists of the following components: selection, mutation, inheritance, drift (random genetic change), and isolation of populations. These components can be called facts of evolution, because their action in every organism can be demonstrated at will. These five factors acting together have led to the diversity of life on Earth. It has also been demonstrated that the chief factor in guiding evolutionary change is selection, which is differential reproduction of individuals. Charles Darwin did not invent the idea of selection; he discovered it, as did Alfred R. Wallace independently at about the same time. Selection has acted continuously on all living things throughout the history of life and continues to do so today. This omnipotence of selection provides the foundation for scientific study of all life. It says that the features of life are what they are largely because of selection in the past, and thus all features of all living things are expected to ultimately promote reproduction or genetic propagation of individuals. This theoretical framework tells the biologist how to ask questions and proceed in order to gain further understanding of life through experiment and observation. Since life itself is a product of selection, an understanding of this process and how it can be applied to elucidate living things provides the practicing biologist with the best direction and insight, regardless of whether he or she is interested in molecules, behavior, physiology, morphology, etc. See R.D. Alexander's paper (1978) for a detailed treatment of the nature of the evolutionary process.

Selection is of two types: natural and sexual. Both types stem from differential reproduction of individuals, but the differential reproduction is affected in different ways. Natural selection is differential reproduction of individuals due to differences in survival. Since reproduction is necessary for selection to act, natural selection includes differential reproduction of individuals in the contexts of obtaining a mate of the right species, proper fertilization, etc. Sexual selection is differential reproduction of individuals in the context of competition not just for mates, but for the *best* mates. Although both forms of selection involve competition between individuals for genetic representation, competition for mates is a key factor for distinguishing natural vs. sexual selection.

Consider the "horns" of the male stag beetle, which are absent in females. In this species the horns of a male are actually mandibles that are elaborated into antler-like structures. If horns increase survival prospects for a male, perhaps by use in stabbing predators, then they are the product of natural selection. Natural selection is also the cause of horns if they function in increasing the probability that a male can inseminate a female, perhaps by giving him better balance during copulation. But these two hypothesized selective

FIGURE 1. The horns of male forked-fungus beetles are used in male-male contests for females which lack horns. (Drawing courtesy of Don Luce.)



contexts are incorrect. Instead, horns serve males in sexual competition for mates. Male stag beetles use their horns in contests with other males for females. It has recently been shown in a diversity of horned beetle species that horn morphology for each species is suited to the nature of fighting conducted by males (Eberhard 1980) (fig. 1). Horns require energy that could be used in body maintenance and hence survival, and beetle horns are sometimes so massive that the male cannot feed. Thus the horns are contrary to survival—maladaptive under natural selection—but evolved because they contribute to greater mating success in male-male competition for females. Features such as the horns of male beetles, the gaudy plumage of some male birds, and the energetically demanding courtship of many male animals led Darwin to his discovery of sexual selection. He reasoned that as long as the benefit of a trait to reproduction via sexual competition exceeds its cost to survival, the trait will evolve.

Darwin outlined two forms of sexual selection: intrasexual selection, competition among members of one sex (usually males) for individuals of the opposite sex; and intersexual selection, preferential choice by members of one sex (usually females) for certain members of the opposite sex. Both forms of sexual selection ultimately involve competition for females. Intersexual selection or female choice occurs because some males are better than others in providing appropriate courtship stimuli and thereby coaxing discriminating females to mate.

For reasons that are still not completely clear, sexual selection was controversial upon its discovery by Darwin (Thornhill 1980a). Biologists A.R. Wallace and Julian Huxley and Anthropologist E. Westermarck, staunch natural selectionists, argued in the late 1800s and early 1900s that sexual selection is of minor or no

importance in bringing about evolutionary change. Their criticisms were largely directed at Darwin's view of the important role of female choice in evolution. Between Darwin's time and recent years, the study of sexual selection was neglected. The present enthusiasm among behaviorists about sexual selection stems from the contributions of George Williams, Geoffrey Parker, and Robert Trivers, which revived interest and provided research direction, and the numerous studies in the last ten years showing that sexual selection is real and important.

Williams' book *Adaptation and Natural Selection* (1966) initiated a revolution in the study of behavior, because it identified the flaw in much of the thinking about how behavior has evolved; that is, the notion that behavior functions for the good of the population or species. Because selection acts on individuals, it can only favor traits that promote individual genetic propagation. If the group survives better as the result of some adaptation of individuality it is merely an incidental effect of individual selection.

Trivers (1972) identified why the male is typically the charming (courting) sex and the female the choosy sex. The answer lies in the sexual asymmetry in parental contribution to offspring, what Trivers calls parental investment. The sexual disparity in investment begins with gametes; males produce many small, streamlined gametes containing only genes, the females produce a few large, nutritive gametes. Eggs contain the nutrient necessary for offspring survival (and ultimately reproduction). Male reproduction is not limited by gamete production but by male ability to fertilize female gametes. Female reproduction is limited by gamete number and not by difficulties in getting gametes fertilized. It is typically also the female that provides postzygotic care of young when this occurs, and this too is an important factor contributing to the

sexual asymmetry in parental investment. Parental investment ultimately determines whether an offspring survives and reproduces and thus females, who are the major parental investors, become the object of male competition. The more parental investment a male can secure via copulation with multiple females the higher his reproductive success. Because females are the object of competition among males, and because they lose more reproductive potential from an improper mate choice, they choose mates. Females are expected to prefer males that can provide them with the best material benefits (protection, food, egg-laying sites, etc.) and genetic benefits (genetically sound offspring).

Parker (1970) clarified the often subtle nature of intrasexual selection. He pointed out that sexual selection among males may continue after insemination via competition among ejaculates from different males for the eggs of a single female. This form of intrasexual competition is especially prevalent in insects because females store sperm and often mate several times.

It is now realized that female choice can also be very subtle (Thornhill and Alcock 1983). Darwinian female choice involves premating choice by females; females do not respond to certain conspecific males or refuse to mate with them, preferring others. We now know that female choice may also occur during and even after mating. Female choice during mating involves situations in which females terminate mating with certain males, but not others, before insemination or complete insemination occurs. When the number of sperm transferred is related to mating duration, females can bias fertilization toward preferred mates by control of mating duration. Postmating female choice occurs when females primarily or only use sperm of preferred mates for fertilizing eggs. It is the general rule in insects that the last male to mate with a female fertilizes most of the eggs she lays until she mates again. Despite the temporal overlap of ejaculates inside a female insect caused by multiple mating, the last male has an advantage in fertilizing eggs. Thus a female, by her remating behavior or patterns of egg laying, can influence which males fertilize her eggs and thereby exercise postmating female choice.

Research on scorpionflies can be used to illustrate the distinction between the two forms of sexual selection and to clarify the three forms of female choice. Scorpionflies are insects of the order Mecoptera (Byers and Thornhill 1983). Mecopterans of the families Bitacidae and Panorpidae have proved to be ideal organisms for study of the causes and effects of sexual selection in part because males provide females with a nuptial gift at mating and females choose mates on the basis of the gift. Specifically of interest here are the bittacids, *Hylobittacus apicalis* (fig. 2) a common species in the eastern U.S., and *Harpobittacus nigriceps* (fig. 3), which is endemic to southeastern Australia.

The sequence of sexual behavior in *H. apicalis* begins when a male catches for himself or steals from another male a prey insect and begins to feed on it. After a brief feeding males usually discard the prey and obtain another if the prey is small (<16mm² in surface area). Only about 10% of males do not discard small prey prior to premating flights and use these prey as nuptial gifts. If the prey is 16 mm² or larger, after the brief feeding and while still holding the prey in his hind tarsi, the male initiates short premating flights among the herbs. After each flight the male exposes his abdominal pheromone-dispersing vesicles (fig. 3). Females respond to males from a distance by olfaction. When the female arrives at the male, he presents the nuptial prey to her. The female, after receipt of the prey, feeds as the male attempts to couple with her. If the prey is large, the female will couple with the male and copulation will be male-terminated after a duration of 20 minutes or more. Complete insemination of the female requires about 20 minutes of mating time; when males have passed their complete ejaculate, they terminate copulation and retrieve the prey which they may finish consuming or, if it still contains enough nourishment, will use it to coax another female to copulate. But if the prey is small, the female may terminate the interaction with the male after sampling the prey and prior to mating, or if the female allows mating to take place it will be terminated earlier than 20 minutes by the female. About five minutes of mating are required for any sperm to be transferred. This is roughly the average mating duration when females terminate mating with a male possessing a small prey if such males are allowed to mate by a female in the first place. Between five and 20 minutes of copulation there is a direct positive relationship between the number of sperm transferred and mating duration. Only the female feeds on the prey during copulation and she feeds throughout copulation. After mating with a male with a sufficiently large prey, females become sexually nonreceptive (i.e., females do not respond to male pheromone and therefore do not mate) and begin laying eggs. The period of oviposition and nonreceptivity is 3-4 hours, after which females become receptive and mate again, preferring again a mate with a large prey (Thornhill 1980b).

Although *H. apicalis* males are usually selective of prey that they use as nuptial offerings, preferring large prey and discarding small prey, females that catch prey on their own do not discard small prey. When males become abundant seasonally females are rarely observed catching prey on their own and they depend on prey provided by males during mating.

Female *H. apicalis* discriminate before mating, preferring males with large prey. They discriminate during mating by adjusting copulation duration according to prey size and thereby control the number of sperm

received from a mate. Female *H. apicalis* who receive small nuptial gifts do not lay eggs, remate immediately, and continue to remate until they mate with a male with a large prey. Remating represents postmating female choice, because it leads to a bias in fertilization of eggs toward males with large prey.

Female choice is adaptive in *H. apicalis*. Choosy female *H. apicalis* clearly receive material benefits from preferred mates. Females show higher lifetime fecundity when they select males with large as opposed to small prey. Also, females who prefer males with large prey probably have enhanced survival via reduction in their exposure to web-building spiders, the most important form of predation on *H. apicalis*. Spider webs are encountered during flights among the herbs and movement associated with hunting by males leads to greater exposure to spiders and higher male mortality. The act of discrimination against a male may result in some exposure to web-building spiders because the female has to fly to another male possessing prey. However, males with large prey are usually readily available, and females can locate a second male with little risk.

Choosy female *H. apicalis* also may receive genetic benefits from preferred mates. This hypothesis derives from the observation that females who mate with a male possessing small prey often terminate copulation and feeding at the time when sperm begin to be transferred. If hunting prowess and ability to obtain large prey are inherited in bittacid scorpionflies, discriminating females may produce successful offspring of both sexes. The sons of discriminating females would be very attractive to females and perhaps also reproduce more because of increased survival associated with greater prey-securing ability; their daughters might have better survival (and hence reproduction) when required to catch prey on their own.

The subtle nature in which female choice can be exhibited is seen in research on *Harpobittacus nigriceps*, another species in which males provide females with a nuptial arthropod gift during mating. The general choice behaviors before, during, and after mating in *H. nigriceps* and *H. apicalis* are similar, but after mating, females of the former species also regulate egg laying in relation to both body size and nuptial prey size of their mate, which probably results in greater use of sperm from large males and males with large prey during fertilization. It is likely that postmating female choice in the form of egg laying in *Harpobittacus* represents an important form of sexual selection on males. That is, it represents a strong force of differential success of males in competition for fertilizing eggs of females. Furthermore, it is likely that postmating female choice enhances female fitness in *Harpobittacus* because a female's progeny would be sired by males who are better at obtaining large prey and good at



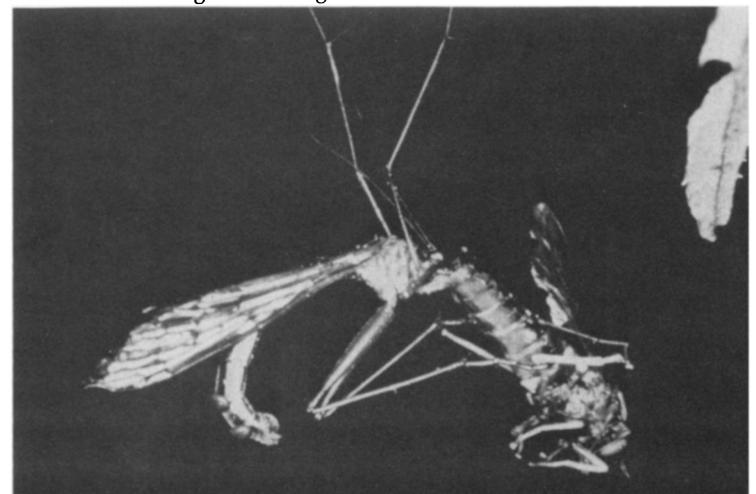
FIGURE 2. A copulating pair of *Hylobittacus apicalis*. The female is feeding on a nuptial gift (blow fly) provided to her by the male.

securing resources for growth during immature stages—abilities of reproductive value to a female's offspring when inherited.

Intrasexual and intersexual selection are often so intimately intertwined that they cannot be separated, preventing an understanding of the role of each in success and failure of different males. Bittacid scorpionflies have been useful in this regard, because even after male-male competition for prey has ended—that is, some males have obtained prey and others have not—choosy females operate to influence which males secure matings, pass complete ejaculates, and fertilize eggs.

In systems in which males are under intense sexual competition, sexual selection has led to almost incredible means of increasing probability of an individual's success. For example, male *Hylobittacus* exhibit a repertoire of tactics associated with attempts to steal the prey of other males, and including male mimicry of female behavior (Thornhill 1979). A female-mimicking male flies up to a male holding prey and releasing pheromone and assumes the same wing and abdominal as females in the same context. The prey-holding male delivers the prey to the mimic two-thirds

FIGURE 3. Male *Harpobittacus nigriceps* releasing pheromone from a pair of abdominal glands and holding prey that he will offer to a female in exchange for mating.



of the time and about one-quarter of the time female mimics can steal the prey which they use to coax a female to mate. Compared to hunting prey, successful prey theft reduces time necessary to obtain prey and probably exposes males to less spider predation.

The female mimicry example is clear cut deception. The male with prey behaves as if the individual in front of him is a female, and this is to his reproductive disadvantage. The natural history literature is full of examples of between-species deception in the form of mimicry. Within species mimetic deception has only recently begun to be examined by behaviorists and many examples from a diversity of organisms are coming to light.

When a behaviorist says that deception or female choice occurs in some animal, he does not mean that conscious motivation is involved. Instead these terms refer to the fitness consequences of behaviors for the actors. A scorpionfly is probably no more aware that its behavior (and nonbehavioral features) serves reproduction than a flower is aware that its pollen, ovules, and leaves promote this end. All that is necessary for selection to favor a trait is that the trait contribute to greater reproduction than alternative traits.

Female mimicry in *Hylobittacus* introduced a very exciting area of behavioral investigation: the role of sexual selection in the evolution of alternative tactics within populations (Cade 1980; Thornhill and Alcock 1983). Within populations, males (and occasionally females) may employ different behavioral tactics. It was once felt that such variation was uninteresting, and that researchers should strive to characterize the typical behavior of species or populations and not concern themselves with other "nontypical" patterns. When competition for mates is intense, some males unsuccessful in the mainstream of competition may drop out and employ behaviors which, although not as successful as the major alternative, allow them to achieve some reproductive success. Again scorpionflies can be used to illustrate this area of investigation, but here we focus on *Panorpa* scorpionflies (Thornhill 1981).

Unlike bittacids which are predators, adult *Panorpa* are scavengers, feeding on dead arthropods that they locate among the low-growing herbs by olfaction. Male *Panorpa* exhibit three alternative forms of mating behavior which are present within the behavioral repertoire of each individual male. Males attempt to obtain a dead arthropod to offer the female during courtship. If unable (because of intense male-male competition for dead arthropods) to secure a dead arthropod, they manufacture a nuptial offering using specialized salivary glands. If a male has been excluded from food by other males for a couple of days he cannot secrete salivary masses. Males unable to employ the two alternative behavioral patterns involving resource provision to females become force-copulators.

Forced copulation results in actual insemination of females in 11% of the attempts and females who experience forced copulation lay few eggs relative to females receiving resources during mating. Despite lower male reproductive success associated with forced copulation compared to the resource-providing alternatives, force-copulators opt for a chance for successful reproduction when the other two behavioral patterns cannot be used.

Studies of *Panorpa* scorpionflies have also contributed to our understanding of sexual conflict, another active area of research (Parker 1979; Thornhill and Alcock 1983). The evolutionary or fitness interests of the sexes are different. Males strive to maximize number of copulations, but females gain by evaluation of males and preference of males who are superior resource-providers and genetically superior. Female *Panorpa* prefer resource-providing males as mates and try to keep away from force-copulators. This is expected from the differences in female fertility following matings with males employing the different alternatives. Also, force-copulators may be inferior genetically as revealed by their inability to compete for resources. Clearly in *Panorpa* forced copulation circumvents female choice and lowers female fitness relative to unforced copulation.

As mentioned previously, the relative investment made by the sexes determines which sex is choosy and to what degree. As males increase their investment relative to females there will be a concurrent increase in male selectivity in their pursuit of mates. Such a scale of increasing selectivity can be divided into two categories. The first of these deals with circumstances when males invest sufficiently to result in their reproductive success being somewhat limited by their ability to obtain those resources but still not enough so that male investment exceeds that of females. We will use examples from the Lepidoptera (butterflies and moths) to exemplify such systems. The second category of male selectivity involves circumstances when male investment exceeds female investment. The best documentation of such a system is that of a katydid, *Anabrus simplex*, and it will be used to illustrate such a mating system.

During copulation, male Lepidoptera secrete into their mate a spermatophore. The spermatophore contains not only sperm, but chemicals absorbed by females which are then used in egg production. Chemical composition of spermatophores may vary across the species but for *Colias eurytheme* and *C. philodice*, both pierid butterflies, spermatophores contain proteins, water, and lipids (hydrocarbons, cholesterol, and di- and triglycerides). The value of chemical investments should vary depending on availability and/or cost of acquisition as well as the importance of such chemicals to egg production, either directly or indirectly by maintenance of the female dur-

ing the oviposition period (Marshall 1982a). In *Colias eurytheme* and *C. philodice* this investment represents approximately 6% of the male's body weight and the ability to produce spermatophores appears to limit how often males can successfully mate (Rutowski 1979).

Colias philodice and *C. eurytheme* hybridize readily and yet maintain species integrity by means of female preference for conspecific males. In spite of such a preference a hybrid frequency of approximately 20% is maintained from year to year. If males vary their courtship in response to variables affecting their reproductive success, we should expect in this case that males would respond to two such variables. The first is the probability that any female will accept them. Since females preferentially mate with conspecifics, we expect males to court conspecifics for longer periods of time. While this is the case (Marshall 1982b), this preference is based on female willingness to mate and is not dependent upon the degree of male investment, so such preferences will not be discussed here. The second variable affecting male courtship persistence should be female quality (i.e., how many eggs will be fertilized by a male inseminating a particular class of female). The number of eggs produced by a female pierid butterfly is positively related to size and inversely related to age. Males should benefit by preferentially courting young and/or large females. *Colias eurytheme* females are larger than *Colias philodice* females and thus produce more viable eggs regardless of their male partner (Grula 1980). We would expect from this that male courtship persistence toward the female types will reflect such a difference. Comparison of Grula's data on average number of surviving adults produced by conspecific and interspecific matings to the courtship persistence of males toward female phenotypes indicates that males indeed are more interested in larger females even when such preferences cross species boundaries. Further evidence of male selection of large females comes by comparing the size of females found in mating pairs to sizes of females randomly collected from the population. Females found mating are significantly larger (Marshall 1982b). While no attempt has been made to see if male *C. eurytheme* and *C. philodice* mate preferentially with young females, Rutowski (1982) has recently shown that males of another species of pierid, *Pieris protodice*, do preferentially court large, young females.

As male investment increases relative to female investment, not only should males become more selective but females should become less coy, because access to male investments will begin to limit female reproductive success. Rutowski *et al.* (1981) have shown that female *C. eurytheme* and *C. philodice*, having depleted the spermatophores from a first mating, will actively solicit courtship from males in an attempt to remate and thus gain a new supply of nutrients.

As predicted by parental investment theory, behavior of both males and females of *C. philodice* and *C. eurytheme* are affected by the increased investment made by males relative to the more typical case where males invest little or nothing in offspring. It should be made clear that increased selectivity in this case is limited, that is, males prefer some females over others but it can be demonstrated that they will mate with any female regardless of type (Silberglied and Taylor 1978). As we will see, this is not the case when male investment exceeds female investment.

Though investment theory predicts the sex investing most will be choosy, no assumptions are made as to which sex invests the most. Typically, however, females invest more heavily in offspring than males and so "normal" sex roles can be described as choosy females and charming males. Cases have been documented however, where males invest more heavily than females. In such cases we expect and find that males become the choosy sex and females compete for access to them.

Gwynne's study (1981) of mate choice in the Mormon cricket (actually a katydid), *Anabrus simplex*, provides a striking example of such a case. Mormon crickets often form roving bands somewhat similar to those of migratory locusts. In this context, food is limited and the large nutritious spermatophore of the male (up to 27% of male body weight) becomes valuable to females. This results in a sex role reversal in competitive and choice behavior. A male who is ready to mate ascends a plant and begins to sing. Females in the vicinity quickly respond and approach the calling male. Females often interact aggressively by grappling as they converge on a singing male. The winner of direct female-female competition is not guaranteed that male's large spermatophore because of the male's discrimination against about two-thirds of the females that fight their way to his singing perch (fig. 4). Such discrimination is adaptive in that it results in males mating with the heaviest females. Gwynne has shown that these females carry the most eggs.

Gwynne has also studied *A. simplex* populations at lower densities in areas where protein is readily available relative to need. Although protein is still needed for egg production and males under low density invest as much as those at high density, males are evenly spaced due to aggression and fights between neighboring males are also seen. There is no evidence of mate rejection by males and males eagerly descend from their calling perches to meet responding females.

We see then that increased male investment in offspring can affect the nature of the mating system. Further, it has been established via these examples and many others that sexual selection theory can predict the nature of the mating system if information is available about the relative investments in offspring

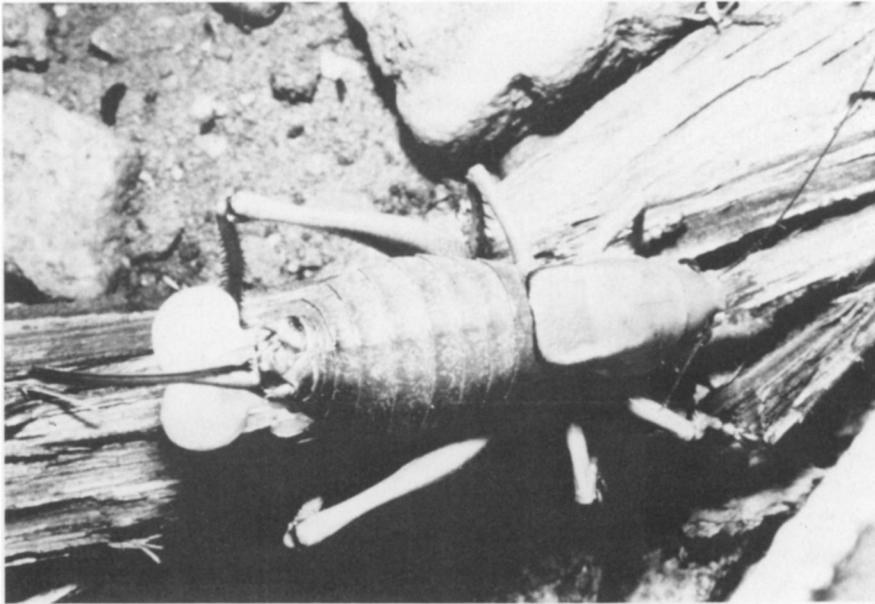


FIGURE 4. Female Mormon cricket with spermatophore attached to her genitalia. (Photo courtesy of D.T. Gwynne.)

made by the sexes.

The examples we have focused on thus far have illustrated the question of sexual selection upon species with materially investing males. Scorpionflies and Mormon crickets provide resources upon which females feed, while lepidopteran males transfer important compounds directly into the female reproductive tract. In the majority of insects, however, males appear to make only a genetic contribution (sperm) to the mating process. Sexual selection theory predicts that in species where males do not invest materially or through parental care of offspring, females should select mates based on some phenotypic indicator of overall "fitness." In other words, if genes are the only male contribution toward successful offspring, females should hold out for the best genes they can get. The assumption underlying this prediction is that the character(s) or behavior used by females to select a mate must have a heritable basis. Put more simply, the phenotypic indicator must represent genetic superiority which *can be passed along* to offspring. This could directly involve both male and female offspring (e.g., an inherited capacity to compete for resources) or it could be expressed through a like-father-like-son process. In the latter case, females who prefer males that have demonstrated superior ability in obtaining mates will produce sons that are equally successful and daughters that make the same adaptive choices (Dawkins 1976).

The corollary of the "good genes" theory is that selection should favor males who are the best at advertising and "selling" themselves as potential mates. At the same time we expect the coevolution of female ability to recognize truly superior males and discriminate against less-than-honest suitors. These evolutionary processes have apparently led to the myriad elaborate and complex morphologies and

courtship rituals exemplified by the tail plumage of peacocks and dewlaps of male lizards.

We will illustrate these aspects of sexual selection by looking at an insect family with an extraordinarily wide range of mating systems. The Tephritidae, or true fruit flies, are considered the most economically important family of insects in the world, and include among their ranks the infamous Mediterranean fruit fly. The 400 or so species in this family share the habit of laying their eggs into plant tissue upon which the larval stages feed. They are also similar in that most have beautifully patterned wings which they characteristically wave like semaphores as they dash around their plant substrates. Beyond this, however, tephritid mating systems are practically as numerous as tephritid species.

In order to make the record complete, it should be noted that there are tephritid flies which transfer materials during mating. There are several species which secrete salivary masses (like the *Panorpa* scorpionflies already discussed). Other species exhibit a peculiar "kissing," which involves males and females engaging their mouthparts for extended periods of time. There is some evidence of material transfer during the "kiss" (Friedberg 1982). We would expect selection to operate on these species in the same manner as we discussed for the previous "investing" species. But what about all the noninvesting tephritids which represent the *status quo* in insect mating systems? How do we expect selection to mold their mating behavior? Obviously, the rendezvous of the sexes is the first step for any successful sexual reproductive strategy. Males providing nothing but gametes cannot typically "expect" females to expend the energy or incur possible risks in searching for mates. Mate-finding then should be a male problem and its resolution will be greatly dependent on the ecology of the species (Emlen and Oring 1977).

If resources valuable to females are distributed such that individual males can afford to defend them, then we would expect males to meet potential mates at such sites (as with the *Panorpa* scorpionfly males defending dead arthropods). A resource that is important to tephritid females is suitable oviposition substrate. In some environments these sites can be patchily distributed and relatively limited. In these situations theory predicts that individual males should monopolize oviposition sites as much as possible, "knowing" that females must visit them (fig. 5). This phenomenon is well documented in several species of the tephritid genus *Rhagoletis* (Prokopy 1980). A good example is *R. completa* whose males defend cracks in the husks of walnuts (the only place where eggs are deposited). They immediately chase off intruding males and mate with females after they have oviposited (Boyce 1934).

It is true, however, that for many (perhaps most) tephritids neither oviposition sites nor any other resources are economically defendable. This is true for the polyphagous fruit infesting species common to the warmer climates and for many of the monophagous species which parasitize composite plants as gall formers or seed infestors. In these cases oviposition sites can be superabundant. Waiting for a mate at any one spot could be a long, lonely ordeal. Two basic strategies have evolved under this constraint, one male-controlled and the other female-controlled. The former involves males actively searching for females to court or to attempt a forced copulation. Male searching behavior is apparently most profitable in those species that are tightly associated with one species of plant. When mating and oviposition occur in the same location with large numbers of individuals present, encounters with potential mates are relatively frequent. Gary Dodson has been studying two species in the genera *Aciurina* and *Valentibulla* which fit these criteria well. The larvae of these species are gall-formers on rabbitbrush, a desert grassland shrub. This shrub is often found in dense stands and individual plants can support many flies. Male flies move frequently around the plants and orient toward any movement. When females are located, males display their wings vigorously to wary females or cautiously approach unsuspecting ones. In either case, males almost invariably make a sudden leap at a female, grasping her hindlegs and pulling them off the substrate with their own forelegs. Females that do not escape this grip typically begin running along plant stems dragging the amplexed male behind. Eventually they slow or stop long enough for the male to scramble onto the female's back and attempt to couple with her. Usually copulation is achieved.

Given the obvious importance of the ability to "capture" females in these species, there is an interesting sexual dimorphism in morphology. Tephritid females

are larger than males as a rule, and obviously so in these flies. But in both species male forelegs are significantly larger than those of females, apparently in response to selection for good grasping ability. This leads to the prediction that males with bigger legs (up to some optimum) should experience greater success at mating. This was found to be true in both species. Males collected while copulating have significantly larger forelegs than a random sample of the male population.

This does not preclude the possibility or importance of female choice in this system. It is possible for females to resist coupling after a male has mounted, but this is not commonly seen. Theoretically females could be choosing mates based on their ability to mount, that being an assessment of their size and strength.

The final tephritid examples we will discuss represent a mating system which has been classically interpreted as driven by female choice. It has been shown that the outcome of aggressive interactions can determine the relative reproductive success of males because some are able to monopolize access to receptive females (see Thornhill and Alcock 1983, for review of these studies). Even when males cannot literally prevent others from mating, the establishment of dominance hierarchies can become an integral part of the mating system due to female choice. When faced with the absence of any material investments to compare, mating with a male of proven dominance would seem to be a likely indicator of genetic quality. Females could refuse to mate with males that have not demonstrated their superior aggressive capabilities. This does not mean that constant fighting should be seen in all male-dominance mating systems. Through evolutionary time selection is expected to favor behavioral and morphological modifications which ac-

FIGURE 5. Female tephritid fly ovipositing in a flower head. Males of some species defend territories at egg-laying sites and attempt to mate with arriving females. (Photo courtesy of F.L. Blanc and California Department of Food and Agriculture.)



curately correlate with agonistic ability. Assessment of an opponent's display, size, or weaponry will still allow a fair settlement of an encounter at a diminished cost to all participants. Females making the same assessment would mate with dominant individuals.

Outside the possible receipt of "good genes" in such matings, there can be more immediate benefits to choosy females as well. Guarding of females by males during and after copulation can result in an increase of time for ovipositing and sometimes a decreased risk of damage by other suitors. A genus of tephritid endemic to Australia is characterized by curious projections from their heads found only on males. Moulds (1977) found that these fruit flies use their head modifications just like deer and elk use their antlers. Interacting males run at each other, first making contact with their "horns" and engaging in extended pushing matches until one gives up. As predicted, small males retreat immediately from much larger ones and only males similar in size actually come to blows. After mounting a female, males continue to ward off competitors trying to displace them. Females gain from male dominance after copulation because her mate remains with her as she oviposits, warding off competitors intent on engaging her in copulation again. This increases a female's opportunity for successful, uninterrupted egg laying. Although Moulds did not determine whether females preferentially approach more dominant males, he did note that smaller males, but not larger, were sometimes separated from females by intruders.

Probably the most striking examples of the female-controlled, male-dominance mating systems are those referred to as lekking systems. The term lek means an arena or site of assembly. In mating system parlance it refers to assemblages of males which exist solely for the purpose of establishing dominance status and mating with females that visit the lek. Of course, some degree of aggregation is necessary for the establishment of any dominance hierarchy. Lekking is unique in that by definition, the aggregations form separately from areas already frequented for other reasons, e.g., foraging or oviposition sites. According to data existing on lek mating systems in birds, they are marked by high levels of variance in male reproductive success, with very few individuals getting most of the matings. It appears that this results from females refusing to mate with any but the most dominant males, and only at the lek.

There is evidence for lekking behavior in at least three species of tephritids (see review in Burk 1981). Best studied is the Caribbean fruit fly, *Anastrepha suspensa*. *A. suspensa* males defend individual territories comprising the undersides of single leaves of their host trees (Dodson 1982). From their territories, which are commonly clumped together, males emit a chemical

attractant, wave their wings, dance around, and make loud, buzzing sounds. In his work on the Caribbean fruit fly, Burk (in press) found that larger males win aggressive encounters with smaller males. This probably leads to larger males having greater success in maintaining control of a territory. Since most matings take place at the territories, males able to hold them will mate more often. Additionally, acoustic behavior is different between large and small males (Burk and Webb, 1983). When given a choice, 70% of the females mated with large over small males. Their choice might be based on cues in the calling songs.

We have only touched on the great diversity of mating systems found within the insects. In the process we hope to have provided an insight into the extraordinary explanatory power of Darwinian selection theory. The strong confidence that modern biologists have in selection theory stems from an understanding of the scientific method. If we only looked around for corroborating circumstances certain to be consistent with theory, we would have a weak case at best. Evolutionary biologists regularly explore the theory by posing new hypotheses, making predictions, and then testing these predictions. Through this process has accumulated the overwhelming substantiation which we have outlined here. For a more detailed account of this approach, we especially recommend the books by Thornhill and Alcock, and Gwynne and Morris, listed in the references section.

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