Mating behaviors of insects

Luc Tran
tranluc@lamar.colostate.edu

Abstract

Mating behavior is typically viewed as comprising all events from pair formation through courtship to the final breakup of the mating pair. There are many kinds of insect mating; each insect species has its own characteristics. However, this paper only concentrated on some main points that generalize this behavior. Mating behavior starts by locating mates. Male and female have different strategies toward copulation and reproduction. After locating mates is courtship; one male and female have encountered each other, they may proceed directly to copulation or may first engage in various rituals, collectively known as courtship. The final ritual is copulation. Copulation and/or insemination are the end result of a successful mating. In addition to mating sequences there are some aspects that generalize insect mating behavior: (1) Sexual conflict during mating: This occurs when reproductive interests of males and females of some insects are so often at odds or male and female interests are similar. (2) Sexual differences in mating behavior: In most insect species, males are intense competition with each other to fertilize a limited number of extremely choosy receptive females. (3) Signal to mates during mating includes material benefits and mate choice, genetic quality and mate choice, mating preferences for the correct species. (4) Signals to rivals during mating: These signal patterns appear to have evolved as honest indicators of fighting ability. And (5) Homosexual behavior and mating mistakes: Homosexual mating mistakes occur when certain males adaptively
resemble females and homosexual mounting can also occur among insects of which the males have not evolved to mimic females.

**Introduction**

Mating behavior is typically viewed as comprising all events from pair formation through courtship to the final breakup of the mating pair. In most pterygote insects, sperm transfer is achieved through copulation. In contrast, in the few studied apterygotes, sperm transfer is indirect; the spermatophore is placed on the substrate, and is picked up by the female either following a period of courtship or with the pair making no contact at all. This paper focuses on events occurring after the male and female have made physical contact, pair formation in insects is covered elsewhere. The main theme here is the function and adaptive significance of mating behaviors.

**Locating mates**

For males of many species, the number of offspring sired can depend on the number of females mated. While pre-and postcopulatory choice by females can affect the outcome of potential mate encounters, mate location is a necessary prerequisite to any possible courtship and subsequent mating (Nahrung et al. 2004). There was considerable variation in the mating frequency of both sexes; however the skew in mating success was comparable for males and females (Jones 2006). Males and females have different strategies toward copulation and reproduction. Generally, males invest energy in locating mates and producing sperm; therefore they often search out and copulate with what appears to be any available and receptive female. Persistence increases the likelihood of
successful mating. Females, on the other hand, produce fewer gametes, provide most of nutrients for progeny development, and are far more selective in mate selection because their investment in energy is considerable. Locating a mate that results in copulation and embryo formation evolves a complex series of exacting conditions and behavior for both sexes. First, both sexes must be active at the same time and the same locality. Second, at least one sex must be capable of locating the other, recognition must occur, and each must possess the correct genitalia and be physiologically ready to carry out the process. This section will deal primarily with the second set of conditions (Elzinga 2003).

**Courtship**

Most courtship studies have measured male courtship while considering the role of the female as limited only to accepting or rejecting the male (Lasbleiz et al. 2005). Other authors have mentioned female precopulatory behavior without distinguishing between its separate components (Cobb et al. 1989). Once males and females have encountered each other, they may proceed directly to copulation or may first engage in various rituals, collectively known as courtship. Although both sexes may play active roles, involving two-way communication, usually the male conducts most of the overt performances and appears to be seeking acceptance (Triplehorn et al. 2004). However, sometimes females respond to adapt male behavior. For example, the spermatophylax synthesized by male *Gryllodes sigillatus* contains substances designed to inhibit the sexual receptivity of their mates but the female have evolved reduced responsiveness to these substances (Sakaluk et al. 2006).

**Copulation**
Copulation and/or insemination are the end result of a successful mating. In some apterygote insects, including many Collembola, not only is sperm transfer indirect, but the male may place spermatophores on the substrate and never encounter the female that picks them up. Yet various forms of non-contact and contact courtship also occur in Collembola. Even copulation, which involves direct transfer of sperm from male to female, may not occur between genitalia but rather between genitalia and some other structures on the opposite partner (Triplehorn et al. 2004).

**Sexual conflict during mating**

Conflict between males and females over reproduction influences the evolution of numerous aspects of reproductive behavior, including how frequently individuals mate. Typically, females optimize the benefits of mating with a limited number of copulations, whereas males may benefit from increasing the number of copulations, leading to sexual conflict over female mating rate (Shuker et al. 2005).

Nowhere was the effect of discriminating between group selectionists and individual selectionist hypotheses more dramatic than in area of sexual behavior. Whereas group selectionists took it for granted that males and females reproduced cooperatively for the greater good of the species, the renewed interest in individual selection led biologist to anticipate conflict and competition at all levels of the reproductive enterprise (Alcock et al. 1991). It is surely not coincidental that by the early 1970s there was the rebirth of enthusiasm for sexual selection theory, which emphasizes precisely these things. Gwynne (2003) showed that these episodes of insect mating reveal how Darwinian selection theory can be used to understand variation in behavior. The basic underlying assumption of this theory is that individuals behave in such a way as to yield the greatest
number of surviving progeny. This theoretical insight suggests that courtship and
copulation should rarely be a cooperative venture. Cooperation in courtship was the
prevailing view among biologists at one time, in part because courtship was thought to
synchronize mating events. In contrast to this view, much research indicates that the
sexes are often in conflict. Sexual conflict is expected to be common because the
reproductive interests of male and female are so often at odds. Conversely, cooperation is
expected in the few cases in which male and female interests are similar.
For example, interactions between pair of burying beetles are mainly cooperative after
they have interred a mouse-sized carcass. In contrast, when, when a larger carcass is
buried, conflict is evident because, unlike the situation with small carcasses, the male has
an opportunity to increase his reproductive success by attracting additional mates,
whereas any added larvae from such matings probably decrease the initial female’s
success. The latter situation exemplifies a type of sexual conflict expected in the
reproductive activities of animals because of a sexual difference in reproductive strategy:
males typically maximize the number of females mated so as to maximize fertilization
success, whereas females maximize fecundity and offspring quality.
This sexual difference also causes conflict when already-mated females are harassed by
promiscuously mating males. Examples come from the precopulatory struggles often
observed in insects. A well studied case involved water striders (Heteroptera: Gerridae).
When a male uses forelegs and genitalia to secure a female for copulation, the vigorous
struggle ensues during which the female attempts to dislodge him. Superfluous matings
can be costly to females in terms of increased of predation risk and energetic cost. To
reduce such costs, female *Gerris incognitus* have evolved upcurved abdominal spines that appear to function in thwarting male mating attempts.

Precopulatory struggles appear to be a result of sexual conflict in species in which males feed their mates. For example, katydid males feed their mates during the mating process (Thornhill 1976). The food item presented by male katydids is a large spermatophore that the female eats after mating (Lynam et al. 1991). This is because females pay a cost if the size of their meal is reduced in any way. Thus, a newly paired male and female scorpionflies (Mecoptera: Bittacidae) can both be seen to pull on the prey offering. Conflict comes from males holding back the prey in order to conserve food for copulations with other mates and the female attempting to begin her meal as soon as possible. Conflict in some mate-feeding insects is particularly evident in the struggle between sexes when a male attempts to force a copulation without providing the beneficial meal to his mate. To overcome female resistance, males of both panorpid scorpionflies and haglid orthopterans have specialized abdominal organs that function in holding onto females during forced matings.

**Sexual differences in mating behavior**

Advantages that females might obtain from choosing to mate with more than one male include acquiring goods and services such as nuptial meals or enhancing offspring quality by remating when high quality male is encountered. This point highlights the basic sexual difference in mating behavior: typical females are choosy when it comes to the males that father their offspring, whereas males compete and display as a way to obtain multiple matings.
The factors controlling these typical sexual differences in behavior stem from the basic
difference in the way males and females maximize reproductive success. Females usually
invest more in individual offspring than males by providing materials for egg production
and, in some species, caring for progeny. These maternal activities mean that fewer
females than males are available for mating, thus causing males to compete for the
limiting sex. Therefore sexual selection is greater on males than on females. This theory
predicts that in species in which males invest more in offspring than females, sexual
selection on the sexes will be reserved, causing the reversal in the mating roles. This
prediction has been upheld in experiments with several katydid species (Orthoptera:
Tettigoniidae). These species are useful experimental organisms because mating roles are
flexible, when food in the environment becomes scarce females compete for mates and
males are choosy. Hungry females fight to obtain matings because each copulation comes
with nuptial meal. In support of theory, food scarcity causes an increase a relative
investment in individual offspring (egg) because there is an increase in the material eggs
derived from males. Members of sex are expected to be choosy if variation in the quality
of potential mating partners is high (Gwynne. 2003).

**Signals to mate during mating**

(1) *Material benefits and mating choice*: Rejection of a mate (usually of males by
females) is only one of the explanations for the failure of a pair to mate successfully.
Other causes of breakup of pairs are certain changes in the physical environment and a
threat of harm from predators or rival males. Sometimes the failure is due to sex-biased
timing. This is explained by the earlier arrival of males to breeding areas than females
(Morbey et al. 2001).
As predicted by theory, female choice of mates is more widespread than male choice. Only a male that transfers a large prey will complete copulation by supplying both a full complement of sperm and chastity-inducing substances (Gwynne 2003).

(2) Genetic quality and mate choice: In theory, females are expected to show choice to obtain indirect benefits, i.e., benefits that enhance the genetic quality of offspring (Gwynne 2003). Female *Dryomyza* flies appear to do this by biasing fertilization after evaluating male copulatory courtship. But what sorts of indirect benefits do choosing females obtain? In yellow dung flies, *Scathophaga stercoraria* (Scathophagidae), females can favor the stored sperm from males with genotypes likely to enhance offspring growth.

(3) Mating preferences for the correct species: One result of the expected rapid evolutionary change from run away sexual selection may be speciation through behavioral isolation. Speciation results when there is sufficient between population divergence in the female preference and the linked male display that the site effect of intraspecific mating preferences is discrimination against males from other population. This effect hypothesis for species discrimination differs from hypothesis that certain female mating preferences have evolved to function in avoiding costly interactions with other species (Gwynne 2003).

Signals to rivals during mating

In another North American calopterygid, *Hetaerina Americana*, variation in wing-spot displays reflects an evolutionary history of competition between males; males with lager wing spots are more successful in defending mating territories than males with smaller spots. As males with experimentally enhanced spots suffer a cost (increased mortality),
these signal patterns appear to have evolved as honest indicators of fighting ability. These
signal indicators may convey information about male ability to rivals during wing-way
displays directed at females (Gwynne. 2003).

**Homosexual behavior and mating mistakes**

Chemical communication requires the release of specific chemicals from a producer
(emitter), the transmission of these chemicals to a receiver, and the processing of these
signals leading to appropriate behavior responses in the receiver. In some groups of
insects, chemical attraction is a major means of sexual recruitment. Females
predominantly are the emitters and males the receivers of the signal offered to as a sex
pheromone. When a member of one sex produces a signal that attracts others of the same
sex, the cue is termed an aggregation signal, such as the aggregation pheromone of bark
beetles (Leal et al. 1998).

A male *L. versicolor* beetle can be duped into courting a small female-mimicking rival
and there are a few other examples, such as in some butterflies and dragonflies, of
homosexual mating mistakes when certain males adaptively resemble females.

Homosexual mounting can also occur among insects of which the males have not evolved
to mimic females. This male behavior is widespread in animals and appears to be simply
an effect of poor sex recognition; strong selection on male to mate frequently cause them
to mount any object that resembles a female. Examples of mating mistakes can even
include inanimate objects, such as in the case of *Julidomorpha bakewelli*, an Australian
buprestid beetle, the males of which attempt to copulate with beer bottles with a
coloration and reflection pattern resembling the female’s elytra (Gwynne 2003).
Poor sex recognition appears to be the explanation of why males of another beetle, *Diaprepes abbreviatus*, mount conspecific males. A big difference between this species and others, however, is that females also perform homosexual mountings. In this case, however, mounting appears to be an adaptive reproductive strategy rather than a mating mistake. Laboratory experiments with this species reveal that a mounted pair of females attracts males. In fact, large males attempt to mate more often with paired females than with single large or small females. As both the mounting and the mounted females had similar probabilities of copulating with the attracted male, it appears that the mounted pair mimics a heterosexual pair in order to incite the attraction of large, competitive males (Gwynne. 2003).

**Conclusion**

Observations of insect mating behaviors reveal a great diversity, some of which is a result of plasticity within species. The understanding of the function of both inter and intraspecific variation in mating behaviors can be gained by examining the consequences of behavior for the reproductive success of the mating male and female. Any observation of synchronized courtship in a species inevitably lead to the question of how such synchrony enhances the reproductive success of the male and female. There is a wealth of behavioral diversity for future research, including apterygote insects, a virtually unstudied group and one of great interest because they lack copulation.
References


