

# 1 • Evolutionary perspectives on insect mating

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We need a new theory of mating systems . . . [one] that incorporates the conflicting interests of males and females, and the factors determining which sex is in control, in order to predict patterns of male-female pairing.

Gross, 1994

Given that females, to one extent or another, subvert male interests by the internal manipulation of ejaculate, it is not inconceivable that males will have evolved little openers, snippers, levers and syringes that put sperm in the places females have evolved ("intended") for sperm with priority usage – collectively a veritable Swiss Army Knife of gadgetry!

Lloyd, 1979

## ABSTRACT

The male-female interaction is an asymmetrical, usually obligate mutualism in which there are conflicts of interest whenever multiple potential partners that vary in quality are available for either sex. Understanding male-female conflouences and conflicts of interest is required to explain the sexual sequence and how it evolves. Mating interactions involve multiple steps or stages, distinguishable because of differences arising out of changes in selection that occur during the sequence. Sexual selection and competition take several different forms, which must be understood before accurate interpretations can be made of mating events in any particular case.

Sexual selection guided primarily by male-female conflicts of interest can result in resolvable evolutionary chases that lead to evolutionarily stable strategies but perhaps more frequently lead to chases that tend to be unending (Parker 1979). In the latter, successful changes in one sex lead to countering evolutionary changes in the other sex, so that conflict is repeatedly exacerbated by evolutionary changes in the participants that enhance their ability to overcome countering traits evolving in the other sex. In contrast, sexual selection controlled primarily by female choice should yield directional changes which, if long-term, have some likelihood of becoming Fisherian runaway selection because females favor males with extreme traits. When conflict is a trivial component of such interactions, runaway selection will tend to accelerate, then reach

an equilibrium, because the external environment imposes penalties on the individuals with extreme traits, and these penalties counteract the benefits of the traits in mating success (Fisher 1958). It is evidence of a conflict-of-interest chase when males evolve to make extreme traits less expensive (thereby less valuable to females in choosing males) and also evolve modifiable handicaps that can be adjusted according to condition or available resources (Hill 1994).

With runaway evolution of traits wholly involved in mating success, such as some courtship or copulatory structures and behaviors, costs from the external environment may be minimal or absent from the start because costs are mainly from caloric or genetic consequences of step-by-step evolutionary changes *per se* (i.e. not from the external environment). The resulting long-term directional change can take the form of a runaway process if females gain from favoring males best able to achieve fertilization (Eberhard 1985); but such changes may also represent chases based on continuing conflict.

Males and females each evolve to control fertilization at some expense to one another. The uncoupling of insemination and fertilization that characterizes most or all copulatory acts (Eberhard 1985) is evidence of male-female conflict. Males are expected to value zygotic success less than do females because of their concern for the success of their own sperm; hence they are less concerned than the female with timing of fertilization and placement of zygotes. Uncoupling is thus in the female's interests because she is concerned with timing of fertilization in

relation to appropriate placement of zygotes, and because she may gain from additional matings. It is difficult to imagine that male and female interests in this regard ever have been identical.

For various reasons insects appear less likely than birds and mammals to generate directional changes in female choice that can result in runaway processes. Female insects often choose passively or indirectly (for example by mating with the fastest male in a lek) and they may mate with males that meet minimal criteria as a result of thresholds generated independently of the variation in quality of males available to any particular female. Females can also choose 'best-of-*n*' males directly, by elevating internally generated thresholds with successive matings. To the extent that adult females can compare males directly, they can also select extreme males in groups.

It is evidently important to distinguish between evolutionary changes in courtship, copulation, genitalia, and titillatory devices that are owing to continuing conflict, and those owing to females evolving structures and behaviors that match or accept – and therefore favor – traits of males showing superiority in mating effort (Eberhard 1985). In the latter case, both sexes change so as to yield better matches between the shapes of structures or the nature of actions used in the sexual sequence, rather than one sex changing to increase the match and the other sex evolving to decrease it or not evolving at all in that context.

Courtship during copulation is a consequence of the uncoupling of insemination and fertilization; thus it could not have evolved, and could not be maintained, except as a consequence of a male–female conflict of interest. If copulatory courtship involves females evolving to favor certain males, rather than males overcoming female resistance (Eberhard 1985), then the apparent universality of uncoupling of insemination and fertilization means there must be no instances in which male and female interests are both served by recoupling insemination and fertilization.

## INTRODUCTION

The male–female reproductive interaction is unique among social interactions, and is characterized by seven features: (1) it is an asymmetrical, intraspecific mutualism that is typically obligate; (2) it involves multiple potential mates for each sex; (3) it most often takes place between non-relatives or distant relatives (therefore it tends not to be directly nepotistic); (4) the two sexes play predictably

different roles; (5) the interests of the interactants overlap, but they are not identical; (6) neither interactant overwhelmingly controls all aspects of the mating process; and (7) prospective mates are able to exploit the interaction at one another's expense. These features generate a complex mix of cooperation and conflict. The male–female interaction resembles the investments of partners in a temporary social reciprocal interaction, or in a nepotistic interaction in which the reproductive benefits of investment in another individual are realized indirectly, via the descendants of the investor. Unlike in either of these interactions, however, the male and female share reproductive interests in their jointly produced offspring. Because there are partial and obligate overlaps and conflicts of interest, the male–female interaction also resembles the parent–offspring interaction (Dawkins 1976; Parker 1979; Queller 1994), except that parents tend to be considerably more dominant over individual offspring than members of one sex are over members of the other (Trivers 1972; Alexander 1979). If female and male interests were wholly coincident, the study of mating systems would be of little theoretical interest.

With respect to natural selection the hostile forces of nature are predators, parasites, pathogens, food shortages, climate and weather (Darwin 1859). With respect to sexual selection (Darwin 1871), the hostile forces are (1) members of the other sex that reduce (or deny) the reproductive success of an individual by (a) rejecting it as a mate or (b) coercing it against its interests (for the latter, see Smuts and Smuts 1993; Clutton-Brock and Parker 1995); and (2) members of the same sex that compete for mates. Conflict and competition occur because some potential mates are likely to be better than others, and individuals gain from mating with the highest-quality partner available (Andersson 1994). Overlaps of reproductive interest between partners can be eliminated as a result of the appearance of a better potential mate for either.

The importance of intersexual conflicts and competition in shaping the mating sequence is compounded by males and females having evolved different life strategies. Evidently, an original disruptive selection on smaller and larger gametes was caused by differences in success before and after zygote formation, respectively (Parker *et al.* 1972), and was followed by a long history of multiple mates being available for both sexes. As a consequence, the two sexes produce different-sized gametes, invest differently at different stages of offspring production, and have correspondingly divergent life strategies (Bateman 1948; Trivers 1972;

Alexander and Borgia 1979). Females can be defined as the sex that invests more prezygotically in the individual gametes (ova), evidently owing to a long history of tending to invest more postzygotically in the individual offspring (although females do not invariably do so now). Males, in contrast, have evolved to invest more extensively in collections of gametes (i.e. ejaculates rather than individual gametes), hence they typically exert more effort in securing multiple mates and thereby potentially fertilizing more ova. This divergence of life patterns has caused males (generally) to seek control of fertilization in the interest of fertilizing more ova. In contrast, females (generally) seek control of fertilization in the interests of (1) restricting advantageously the paternity of offspring, and (2) controlling the timing and context of production of zygotes so as to increase the likelihood of survival of offspring in ways that typically go beyond, or oppose, the interests of the male. Exceptions are species in which males (secondarily) invest more in offspring (zygotes) than do females.

The male-female difference is evidence that dramatic effects can arise from even slight conflicts of interest if such conflicts are long continued (Parker *et al.* 1972; Haig 1993). The ultimate consequences of the male-female divergence, discussed by Bateman (1948), Trivers (1972), and Alexander and Borgia (1979) are that competition and conflict between males and females are inevitable (Borgia 1979; Clutton-Brock and Parker 1995), and that in most species females are limiting for males rather than vice versa (see, for example, Emlen and Oring 1977; Andersson 1994).

In this chapter we explore sexual conflicts and confluences of interest, and develop a theoretical framework for understanding stages of the mating sequence. Using this framework, we develop general predictions about the role of sexual conflict in trait evolution and speciation, and attempt to test alternative theories.

## COMPONENTS OF THE MATING SEQUENCE

For sexual animals with internal fertilization the mating (reproductive) sequence can be divided into eight components, not all of which are represented in all animal groups. As with all biological phenomena, it is useful to consider the events of this sequence as (1) the product of past evolution and (2) what selection has to work on presently. Distinctness of events in such a sequence suggests the extent to which selection has operated on them differently.

Our discussion is biased towards insects, especially towards the pterygote clade (winged and secondarily wingless insects), and, with respect to examples, towards certain groups of Orthoptera and Homoptera with long-range acoustical signals (see also Gwynne and Morris 1983; Otte 1977; Bailey and Ridsdill-Smith 1991; Alexander in prep.). Because we are most concerned with male-female interactions, we do not discuss direct male-male competition, oviposition, or parental care by the female alone.

### (1) Rapprochement or pair formation

This phase involves (a) members of one or both sexes actively seeking one another in the appropriate habitat, (b) members of both sexes gathering at some locale as a result of extrinsic stimuli such as the odor of oviposition plants or visual patterns in the environment, or (c) members of one sex signaling ('calling') to members of the other sex. During the different events of rapprochement, one sex may perceive the other through a single sense, either or both sexes may be guided by localized extrinsic stimuli, or neither sex may perceive either the other or any particular aspect of the environment, even though one or both may be searching for the other.

### (2) Courtship

The courtship phase may be defined structurally as that part of the mating sequence, typically but not exclusively prior to copulation, when *both* male and female are in range of the other through at least one sense and are responding to one another, at least one of them (the courter) sexually and positively. In functional definitions we generally assume that one individual is exerting effort toward reducing the other individual's resistance to copulation either (1) by signaling the presence of a courter (usually the male), causing a change in motivational state or 'willingness', as by accelerating a general physiological change to mating readiness, independent of the particular male; or (2) by advertising positive qualities that may bias the other individual's choice toward the particular courting individual. Watson and Lighton (1994) include in the functions of courtship: (1) closing the distance between male and female (attractant courtship: including our rapprochement); and (2) influencing the female's choice of courting male (persuasive courtship: largely, our second

function of courtship). In general, and for reasons well reviewed, males tend to court and females to choose (Bateman 1948; Trivers 1972; Alexander and Borgia 1979).

Our functional definition would include in courtship not only the usual close-range interactions, but also exchanges of acoustical or visual (and possibly olfactory) signals that occur during later stages of rapprochement in insects such as katydids (while the pair is still outside tactical range) (Spooner 1968) and fireflies (Lloyd 1983). In these insects females go only part way towards the signaling males during rapprochement and then begin answering the males' signals while waiting for the males to approach them. Courtship would also include behaviors, primarily by the male, that facilitate insemination and fertilization through altering the female's behavior after engagement of the genitalia. Courtship evolves to end when actions of the courting individual can no longer affect the likelihood of his paternity, either because paternity is decided or because the female controls remaining events leading to fertilization and he cannot influence her. As Eberhard (1985) points out, to the extent that female choice can occur after onset of copulation, or that coupling does not automatically ensure insemination or fertilization, there might be 'copulatory courtship' or even postcopulatory courtship.

### (3) Copulation

During this phase the genitalia are engaged, and intromission may be involved. One sex or the other may be resisting, but the pair is mechanically or physically coupled. In many sexual invertebrates and vertebrates (e.g. all primitively wingless insects) coupling does not occur because spermatophores (sperm clumps or drops, usually encased) are transferred indirectly. All winged and secondarily wingless insects, however, actually copulate (Alexander 1964), although odonate males must first load sperm into an intromittent organ evolved on the second and third abdominal sternites, separate from the opening of the genital tract (Corbet 1962). Spermatophores occur generally, not only among both vertebrates and invertebrates that transfer sperm indirectly, but also in copulating forms, including nearly all anciently derived pterygote groups (Kristensen 1981). In many forms, (e.g. the Orthoptera Ensifera), only devices that thread the spermatophore tube enter the female's body; the bulb of the spermatophore remains external.

### (4) Insemination

In this phase sperm enter the body (usually the spermatheca) of the female, either during or following copulation. In arthropods that do not copulate directly (gonopore-to-gonopore), insemination can be under the female's control and occur even in the absence of the male, for example in Collembola in which spermatophores are placed in 'fields' and picked up by females independently of the presence of males (Alexander 1964, in prep.; Kristensen 1981).

### (5) Postcopulatory and intercopulatory events

Alcock (1994) reviews what he terms 'postinsemination associations' and various hypotheses offered for them, focussing on the mate-guarding hypothesis (Parker 1970). Included are such behaviors as holding and guarding of the female by the male, formation of mating plugs, manufacture and installation of spermatophylaxes (Sakaluk 1984) and prolonged copulation. These behaviors may take place either following insemination or while insemination is proceeding, the latter for example after copulation in insects such as *Gryllus* that copulate via spermatophores with long tubes through which the sperm pass during a period following the actual coupling (Alexander and Otte 1967a; Lohr and Rence 1978). Postcopulatory holding includes the evolution of extended periods of coupling maintained by males that are able to prevent disengagement of the genitalia (review by Thornhill and Alcock 1983, p. 345). In some insects, postcopulatory or intercopulatory behavioral interactions, which are appropriately seen as a part of the mating sequence, continue until fertilization has occurred (Sivinsky 1984). During the same periods, females may engage in various activities that influence paternity (reviewed by Eberhard 1985).

### (6) Fertilization

In this phase sperm penetrate eggs and zygotes are produced. In pterygotes, fertilization tends to occur at the time of oviposition, the sperm stored in an internal spermatheca. Special mechanisms bring the sperm and the egg together as the egg passes the opening of the spermathecal tube.

### (7) Cooperative parental care

In this phase, both sexes invest in rearing their jointly produced offspring. Examples are some monogamous carrion

beetles (Milne and Milne 1976), cockroaches, and dung beetles (Thornhill and Alcock 1983; Matthews and Matthews 1978). Presumably confidence of paternity is high in all such cases, with postcopulatory guarding or holding virtually certain unless the pair is isolated from possibilities of philandering. In some cases, as in *Anurogryllus* (and probably other genera of the typically deep-burrowing, parental Brachytrupinae, such as *Gymnogryllus*: R. D. Alexander, unpublished), males provide extensive burrows stocked with food which are sometimes commandeered by the female through maneuvers associated with the copulatory act (Alexander and Otte 1967a). These burrows are subsequently used to rear the brood (West and Alexander 1963; Walker 1983).

### (8) Bonding

Bonding ceremonies are a component of long-term cooperative parenting. Such ceremonies, well-known in birds and mammals, may be erroneously interpreted as courtship because they include courtship-like behavior (cf. Daly and Wilson 1983). They may, however, occur outside oestrus or circumovulatory periods, and they may involve little or no evidence of sexual interest by either partner. On the other hand, they can also involve actual copulation, or behaviors otherwise restricted to events surrounding fertilization, which, in bonding, have nothing directly to do with zygote formation (as, for example, in humans). Evidently, no-one has reported bonding ceremonies in insects; this may not be surprising, since individual recognition seems not to have been demonstrated in insects, unlike in many birds and mammals. If bonding has evolved in insects, likely candidates are cockroaches, beetles, and termites that remain monogamous for long terms; one might examine the details of tandem behavior of male and female termites after rapprochement (cf. Thornhill and Alcock 1983, p. 241).

## HOW SELECTION WORKS ON THE MATING SEQUENCE

### Conflicts and confluences of interest between male and female

Despite the fact that for both sexes any sexual interaction is better than none (= no reproduction, excepting nepotism to collateral relatives), divergences in the ways the two

sexes deal with (1) competitors of the same sex and (2) zygotes mean that, at every point in the sexual sequence, there are potential conflicts as well as confluences of interest between male and female. These conflicts and confluences, which are always mediated by ecological factors, determine the manner of evolution of the mating sequence (a) by determining the nature and intensity of sexual competition within the sexes and (b) by causing evolutionary chases in trait changes (see below).

Conflicts between the sexes should be absent only in cases of lifetime monogamy with little or no opportunity for reproductively profitable philandering, and consistently equal investment in the offspring by the sexes. Once copulation has begun, conflicts will be much reduced in species in which females typically mate but once (e.g. screwworms: Leopold 1976) or mate multiply with but a single male (e.g. probably in some termites), even if males are polygynous and do not participate in care of the offspring. Single copulations by females, however, do not eliminate conflicts of interest if copulations that are terminated 'prematurely' cause females to remate (Thornhill and Alcock 1983). Moreover, because remating by females can reduce the parentage of the first male (e.g. in Tettigoniidae: Gwynne 1988), repeated mating is a form of female choice, hence it might be expected to be employed in some cases in which females normally mate but once (Walker 1980; Thornhill and Alcock 1983; Eberhard 1985; Westneat *et al.* 1990). Males with opportunities to be polygynous may still gain from controlling events of mating in ways that conflict with the interest of even a wholly monogamous female (e.g. minimizing time or investment on any one female).

Fertilization (phase 6) represents the culmination and *raison d'être* of the sexual part of the reproductive sequence (i.e. phases 1-6). To some degree the evolution of the entire sequence can be interpreted as competition between the sexes for control of fertilization. Control of the final aspects of fertilization by the female increases her control of which male sires her offspring, therefore control over all aspects of sexual selection. Similarly, any degree of male control of fertilization thwarts female choice and serves the male's interests against those of the female. As Parker (1979, p. 149) notes, '...the asymmetry of aims [of the sexes] may ultimately be a much more important determinant of the evolutionary outcome than selection intensity, though the result must depend on the interactions between the two'.

### Conflicts of interest and evolutionary chases

In whatever respects male and female interests differ there will be evolutionary chases (or races) between the two, which may be unending. Parker (1979, pp. 124–5) describes the asymmetry of this conflict as follows.

... consider a case in which a characteristic yielding a mating advantage to males causes some disadvantage (cost) to the females with which they mate. The female will always benefit from a mating with a male possessing the characteristic, provided that the cost is infinitesimal, if this means that some of her sons will inherit the advantage (see Fisher 1930; O'Donald 1962; Maynard-Smith 1956). Similarly for the male, if the costs are felt by his own progeny via the damage to his mate, then his mating advantage must be correspondingly greater than for zero costs. Hence as the cost increases there will be two thresholds of cost, one for the male and one for the female, beyond which the male characteristic (or a mating with a male possessing the characteristic) becomes disadvantageous. If these thresholds differ, then sexual conflict exists when conditions lie between the two, for example, when the characteristic is favorable to males but not to females.

Parker (1979) divided complex evolutionary chases between males and females into resolvable chases, which lead to an eventual evolutionarily stable strategy, and unresolvable chases which do not.

... if there is nothing one sex can do to avoid disadvantages inflicted by the other, then evolution simply favors making the best of things. Alternatively, there appear to be some instances where each sex can 'retaliate' against the other and where benefits become conditional on the strategy of one's opponent. This can lead to complex and sometimes apparently unresolvable 'evolutionary chases'.

He notes that unresolvable chases can occur when the game involves costs that are independent of the opponent. Thus:

... a male might have an anatomical feature ... which causes enhanced success against female rejection, and vice versa. The cost of the morphological specialization is thus constant and independent of conflicts, though *gains* from conflicts do depend on the level of cost 'chosen'. This sort of game could be fundamentally a rather important one, especially for prey-predator systems as well as sexual conflicts.

Thus, if females evolve to resist males (or to be selective in ways that exclude certain males or cost all males in time and effort), males will evolve to overcome resistance of females (see, for example, Arnqvist and Rowe 1995; Jormalainen and Merilaita 1995). Each change in one sex that helps its members with the change secure their own

interests to a greater degree is likely to be countered by changes in the other sex. Directions of change will not be entirely predictable because changes in strategy by each sex will be responses to alterations of behavior or morphology in the other sex that may occur by chance or for reasons independent of the interactions between the sexes (hence Parker's word 'chase'). Any change in one sex may incidentally thwart members of the other sex in serving their interests, and initiate responses that will also be unpredictable, except that they will be favored if they counter the changes in the first sex.

Complexity of structure and function, seemingly an inevitable development when male and female interests conflict, will tend to accelerate evolutionary change in mating traits, and increase unpredictability, by providing ever more different avenues of effective change. Thus, when sexual conflict drives the evolution of traits, great complexity and diversity are expected both between and within species, in the latter case depending on degrees of isolation among conspecific populations.

Evolutionary chases between the sexes will result not only in complexity but in 'matches' between the complex genitalia of the female and the male, in ways that may sometimes deceive observers into thinking that some kind of cooperative or convergent evolution has taken place, when in reality each sex may have been evolving to thwart the other, one changing first and the other following so as to counteract the change. The clue to this interpretation will often be evidence of forcing or manipulation by one sex, usually the male.

Because females are generally more limiting for males than vice versa, forcing or coercive mating behavior (cf. Smuts and Smuts 1993; Clutton-Brock and Parker 1995) tends to evolve more in males than in females. Even though females are sometimes able to counter male coercive tactics, the general evolutionary trend has been toward greater male control of events prior to fertilization (for a reversal in insects, see Simmons and Bailey 1990). This is because males tend to gain more from evolving risky coercive mating strategies than females gain from evolving to counter them. Parker (1979) notes that males are likely to persist more in an attempted mating than females can afford to resist: 'An important condition in the "war of attrition" game is that the costs to each opponent are set by the opponent willing to persist least' (see also Parker 1983). We do not argue that the female is designed to thwart every action of the male, but that she is designed to prevent the male from controlling fertilization completely.

Evidence supporting the concept of persistent conflicts of interest between males and females can be found in the nearly universal 'uncoupling' (Eberhard 1985) of insemination and fertilization in organisms that copulate, as compared with many kinds of non-copulating organisms (e.g. some fish and amphibians) in which sperm are deposited directly on eggs, causing immediate fertilization. When insemination and fertilization are 'uncoupled', insemination of a female by a male does not guarantee that his sperm fertilize the eggs at that time, or even at all. Females gain from maintaining the distinctness of these processes because (1) they retain the ability to determine the appropriate (for the zygotes) time and context for future reproductive events such as oviposition, and (2) they may retain the ability to use the sperm of different males. Both of these female advantages thwart male interests. Delay of fertilization means increased potential for a male's gametes to be supplanted by those of other males. It is thus unlikely that males and females will ever share exactly the same interests regarding fertilization, especially when males are polygamous or nonparental. Males, then, should evolve to place their gametes directly on eggs, except in the absence of male-male competition (e.g. extreme isolation of monogamous pairs, in which timing and placement of zygotes is equally critical for both sexes). Given the above characterization of male-female interests, the apparent absence of such 'direct fertilization' in copulating species is likely explainable by females evolving counteradaptations that reduce the effectiveness of male traits for controlling fertilization. If females always gained from favoring males that tended to serve their own interests by placing the sperm closer to the eggs, then the uncoupling of insemination and fertilization could not persist. Copulatory courtship (Eberhard 1985) is a consequence of the uncoupling of insemination and fertilization; it could not have evolved, and could not be maintained, except as a consequence of a male-female conflict of interest. Further, if copulatory courtship involves females evolving to favor certain males, rather than males overcoming female resistance, there must not be any instance in which both male and female interests are served by recoupling insemination and fertilization.

## EVOLUTION OF COMPONENTS OF THE MATING SEQUENCE

### Evolution of *rapprochement*

The evolution of the initial coming together of the sexes, and its developmental background in insects, has been

shaped by confusing signals or noise from other sources, predators and parasites attracted by signals, sexual selection, and changes in patterns of parental investment. With respect to signal evolution we consider only the first three of these four factors.

### Long-range signals and resources

Sexual selection can occur during *rapprochement* as soon as traits of either sex become involved in the search. Long-range signals, for example, may vary in range, precision, and amounts and kinds of interruption. Even ability to be in a certain habitat at a certain time is a trait on which sexual selection can act.

There are three possible situations with respect to whether or not males signaling at long range have resources to offer responding females: (1) the male has no resources except genes; (2) the male has mobile gifts such as nutritious gland secretions, large spermatophylaxes, or other kinds of food offerings; and (3) the male has stationary resources (such as burrows or crevices) that can be used by the female as: (a) shelter, (b) oviposition sites, (c) sources of stored food (including the male's own body), or (d) locations suitable for rearing young, usually including all of the above. All of these variations occur in the acoustical Orthoptera and Homoptera, and appear to have influenced the forms of acoustical signaling and the female's approach to the male.

When males with long-range signals (as opposed to males that search for females) have no resources but genes, males tend to develop dense aggregations called leks (more specifically non-resource-based leks: Alexander 1975) to which females are attracted. This situation has evidently been promoted by females (by their refusal to mate except when multiple males are present) because it provides them with the possibility of securing a high-quality mate with the least expense (Wrangham 1980; Bradbury 1981; Reynolds and Gross 1990). Once a female has approached such an aggregation, she may signal no further, requiring the male to locate her and then court her, sometimes extensively, or she may signal nearby calling males (e.g. in *Magiccada*: Alexander *et al.* ms.). Presumably, there is a better chance that a more vigorous male will locate a female sooner.

When the male's resource is movable, as with glands and spermatophylaxes, females may approach males producing long-range signals but stop and engage in an exchange of signals, eventually requiring the male to approach the female rather than vice versa. This system

fosters competition among males in the vicinity, several or many of whom may attempt to disrupt the communication between male and female, replace the signaling male, and establish themselves as the successful copulating individual (Spooner 1968; Otte 1970). This system may sometimes protect the female from parasites or predators attracted to the male's calling song (see, for example, Walker 1964; Cade 1975; Bell 1979; Burk 1982; Heller and von Helversen 1993). If the spermatophylax becomes valuable enough, males become limiting and coy, and females compete for them (Gwynne 1981; Gwynne and Simmons 1990; Will and Sakaluk (1994), however, failed to obtain evidence that the large spermatophylax of the cricket *Gryllodes sigillatus* has reproductive value for the female).

When the male's resource is a burrow or other stationary resource the female approaches him directly and may copulate quickly. In the Ensifera, in which the female mounts the male in copulation, she may walk directly into the mating position. In certain Brachytrupinae (Gryllidae) the female sometimes copulates only after entering the burrow and establishing herself in a position from which she can retain ownership of the burrow; after mating, the female usurps the male's burrow and its stored food and uses them to rear offspring (West and Alexander 1963; Alexander and Otte 1967a; Walker 1983).

The nature of a male's resources may thus affect the evolution of the mating sequence; presumably, long-range signaling is always associated with some kind of stationary resource, whether it be a safe haven (for the female), an oviposition site, a group of males from which to select a mate, or food, including glandular secretions, spermatophores, wings, or the male's blood (Alexander 1964; Alexander and Otte 1967b). Luring sequences can continue only so long as the appropriate resource remains part of the male's portfolio.

#### Long-range signals and risks

When long-range signals are involved in rapprochement, there are two general situations: (a) signaling is more dangerous or expensive than moving to the signaler; or (b) moving to the signaler is more dangerous or expensive than signaling. In each case it appears that the female has assumed the less risky task, so that the male is required to perform the more expensive task (Alexander and Borgia 1979; Sakaluk 1990; Bailey 1991). This outcome is possible because females invest more in individual offspring; hence they are able to be choosier (Trivers 1972). When investment patterns are reversed, so, correspondingly, are the

patterns of communication and coyness (Williams 1966; Trivers 1972; Alexander 1974; Morris 1979). When long-range signals are acoustical or visual they tend to be made by males rather than females. Such signals are calorically expensive and also easily followed by predators and parasites, which only need to hear them and not to decode them. Males are more likely to accept these costs. Apparently, when long-range signals are made by females rather than males, they are likely to be chemical signals because chemical signals are more difficult for predators to notice; thus, males are taking the larger risk. With chemical signals predators are more likely to have to evolve to respond to the actual signals, in contrast to an acoustical frequency channel that can carry a wide range of different sound patterns.

Williams (1992) doubts that most chemicals produced by females have evolved as chemical signals, referring to 'the female pheromone fallacy'. He expresses skepticism about females signaling to males at long range, and argues that female-produced pheromones are not designed as signals; male pheromones, he argues further, function in courtship but not in long-range signaling. He suggests that females do not typically have organs designed to disseminate pheromones, that female pheromones are not typically species-specific, and that only minute amounts of chemical are released compared with male pheromones and alarm pheromones (Greenfield (1981) reviews these questions). Numerous female insects, however, have prominent scent-producing glands, some of them protrusible, and many females signal using special positions of the abdomen (Jacobson 1972; Roelofs 1975; Hölldobler and Wilson 1990; see also Phelan, this volume). Moreover, many scents produced by females are indeed species-specific; that these may be '...precise blends of a number of components' (Roelofs 1975) rather than separate individual chemicals does not alter this point. Neither Williams (1992) nor Hammerstein and Parker (1987) cites the argument of Alexander and Borgia (1979) that females signal with pheromones because pheromones are less available to predators, so that travel to the signaler is more dangerous in such species than is the signaling. Production of small amounts of pheromone is consistent with minimizing risk of predation, and possibly with mate choice by females (Greenfield 1981). Nevertheless, predators do sometimes locate pheromonal signals of prey. Thus, Thornhill and Alcock (1983, p.127) relate a case in which a predacious clerid beetle responds to the sex pheromone of tunneling female *Dendroctonus* bark beetles (Vité and Williamson 1970). It appears that male bark beetles alighting on a tree infested with burrowing females

are at greater risk than the signaling females in their burrows, which can account for females continuing to produce pheromones despite the predator having evolved to detect them.

#### Long-range signals and confluences of interest

The effectiveness of a calling signal is determined by the number of sexual partners that respond positively to it. This means, first, that such signals will be most effective if produced when the greatest numbers of potential sexual partners are active and willing to respond, so there will be restriction of calling to daily periods when, for example, predators are least dangerous. Second, it means that signals that carry farther will be more effective. So there will be directional selection on the intensity of male rapprochement signals: in the case of acoustical signals, loudness, or carrying potential for the female. Insofar as pitch (frequency or kilohertz) is concerned, the auditory organs that evolve in conjunction with calls lacking in melody but temporally patterned (all acoustical insects) tend to hear some frequencies as 'louder' than others. As might be expected, the auditory organs of a species tend to be most sensitive to the particular frequencies present in the calls of conspecifics (Ewing 1984; Huber and Thorson 1985). The calls and the auditory organs are tuned together so that conspecific calls can be perceived at the lowest possible level, or such that the range of the call is maximized (Walker 1957; Gerhardt 1994; Forrest 1994). In this feature conflict of interest between males and females is only expected if variation in frequency or frequency spectrum in the male's call involves a cost that prevents the male from achieving an extreme that allows the female to use the frequency trait in mate choice (for possible examples, see Bailey 1985; Bailey *et al.* 1990).

There are two aspects of temporal patterning in a signal: the particular species-specific pattern, and the overall continuity or 'uninterruptedness' of signaling ('uninterruptedness' does not refer to call differences such as those between chirping and trilling, but to signals not broken as by disturbances). We hypothesize that an uninterrupted flow of signaling attracts more sexual partners than a frequently interrupted or broken pattern, for two possible reasons. First, if females move only toward the loudest call, then any break in the call will presumably cause a female to turn temporarily toward the next loudest call (see, for example, Minckley 1995). The longer the break lasts, the more likely it will be that the female will have moved to a point where the second male's call is louder than that of

the first male, so that the female will continue to respond to it even when the first male resumes calling.

Second, amounts and kinds of interruption in a male's calling may give a female information enabling her to discriminate against a frequently broken pattern. Unbroken calling patterns could indicate that (1) the male's vicinity is safe, lacking predators and parasites that could interrupt the male and endanger the female; (2) the male has access to a safe retreat or burrow and takes greater risks; (3) the male is unusually healthy or capable (not only expending more calories but also less susceptible to predation); (4) there is an abundant food supply; or (5) the male is old and can afford greater risks. Singing is extremely costly, because of high caloric costs (Prestwich and Walker 1981), because parasites (Cade 1975) and predators (Burk 1982) are attracted, and because a male cannot easily forage while calling. These kinds of information may be so important that females have evolved positive responses to uninterrupted or rhythmically interrupted calling, and negative ones to irregularly broken calling, over and above the purely mechanical effects described earlier (see, for example, Hedrick 1986).

The effective range of an acoustical call depends not merely on its intensity, and its frequency in relation to the response curve of the hearing organs of conspecifics, but also on its structure: on the rates and patterning of pulses and chirps within it (Bailey 1985). Fainter signals are harder to recognize because, with greater distance from the signaler, the signal's distinctiveness becomes less apparent (Simmons 1988; Forrest 1994). Thus, a signal's range may be increased by selection causing a signal's pattern to be relatively invariant. This effect can occur whether or not there are other similar signals in the acoustical environment. In human communication, a call for help is less likely to be identified as such as distance from it increases, whether or not there are other calls (similar or not) in the environment at the time. With greater distance from the caller, there is also likely to be an increasing number and variety of potentially confusing or obscuring signals. These signals may be those of related or similar species, or they may come from any acoustical source at all. When a call has a complex within-chirp pattern that is demonstrably not necessary to attract the female from long distance, as Walker (1957) showed with the snowy tree cricket (*Oecanthus fultoni*), it is reasonable to wonder if the within-chirp pattern becomes important to the female at close range. In the bladder cicada, *Cystosoma saundersii*, song frequency works at long distance, and pattern up close (Doolan and MacNally 1981).

When songs of species are confusingly similar – as is often true when two species are newly sympatric and synchronous – females presumably gain when their auditory tympana and central nervous systems are tuned to match the frequencies and pulse patterns, respectively, of the males most different from confusing species (Otte, 1992). Males, in turn, will change to match the most common frequency tuning of female auditory tympana and the most common pulse rate or pattern receptivity (see Fig. 1-1). Both sexes will then stabilize on the same ranges in these features. On the other hand, males will continue to evolve to produce more intense (longer-range) songs and steadier wings, including any profitable deceptive elements if possible. The parts of the song in which there is the least conflict of interest between male and female are those expected to be under stabilizing selection. Alexander (1962a) identifies the particular elements in different kinds of cricket songs that are expected to be under stabilizing and directional selection, respectively, by contrasting the kinds of changes that occur within species repertoires, and between species in the same signaling context.

We believe that the effects just described will cause the temporal patterns of calling signals in insects and anuran amphibians to evolve in roughly the same way that the auditory organs and sounds are frequency-tuned to one another. Loudness in calling increases signal range as a result of directional selection on the male, while both frequency (kHz) and consistency in temporal patterning maximize signal range as a result of stabilizing selection on both sexes.

### Evolution of courtship

When males change from calling (*rapprochement*) signals to courtship, they tend to shift to less intense or different signals (Alexander 1962a, 1975; Thornhill and Alcock 1983), either because such changes render males less available to competitors and predators, or because the female is being asked to do something different from *rapprochement*, or both. The combination of these shifts and tendencies is surely responsible for the ability and tendency of biologists to make confident distinctions between *rapprochement* and courtship. Nevertheless, there is a long history of confusion on these topics, partly because it has commonly been assumed that female selection of males terminates when copulation is initiated (but see Thornhill and Alcock 1983; Eberhard 1985; LaMunyon and Eisner 1993), and partly because courtship in humans (almost unavoidably used as

a frame of reference) has often been regarded as beginning with the initial actions of pair formation. Moreover, confusion has existed about which aspects of human sexually significant interactions parallel sexual interactions of organisms such as insects, and which of them parallel bonding ceremonies in organisms such as birds and mammals in which both sexes participate in parental care.

Courtship behaviors usually serve one of two functions (mentioned above): to signal the arrival of a ready mate (and cue subsequent reproductive behaviors on the part of the courted individual), or to advertise qualities that may bias the choice of the courted individual toward the courter. The former function need not involve conflicting interests between male and female, while the latter function invariably does.

### Evolution of genitalia and copulation

The above assumptions about sexual conflict lead us to predict that, whenever such conflicts of interest are driving genitalic evolution, genitalic diversity and complexity will tend to be exaggerated when (1) females mate multiply, (2) sperm precedence is not complete, (3) fertilization is separated from insemination, (4) males cannot entirely sequester females following insemination, and (5) males do not participate in parental care. Moreover, particular species may embark upon sequences of evolutionary change that lead to increasing conflict between individual males and females (see, for example, melanopline grasshoppers below) and accelerate changes relating to copulation in entire species groups. Changing the above circumstances may reduce the extent of complexity and diversity in genitalia, copulatory and postcopulatory holding devices, and behaviors associated with postcopulatory guarding. Complexity and diversity in such attributes are expected to be minimal when male and female participate about equally in parental care and remain monogamous either for the rearing of an entire brood or for life.

The above predictions probably fit most insect species, herd-living mammals, polygynous birds that lack male parental care, and other forms with the appropriate conditions of life. In contrast, genitalia are virtually absent in some birds, and in termites in which the reproductive pair is isolated for their adult lives; in some of the latter sperm are not motile (Sivinski 1984). These situations remain to be clarified, but may stem either from reduced conflict (as in termites) or from special kinds of conflicts (as in birds: Isabel Constable, unpublished manuscript).

## FEMALE CHOICE AND THE MATING SEQUENCE

If males have heritable variations in quality with fitness consequences for females, and if females have heritable differences in tendencies to mate with the particular males that tend to maximize the females' reproduction (Maynard Smith 1987), then selection on females will lead them to make pre-mating 'choices' among males in several ways (Otte 1974; Janetos 1980; Maynard Smith 1987). With respect to choice we use the terms 'direct' and 'indirect' to describe the manner in which the 'best' male is identified to the female: choice is indirect if processes such as male-male competition allow the female to mate with the best male without need for relative comparisons.

1. A female may choose directly among males, judging traits such as size, color, fighting or courting activities, the size or quality of a copulatory gift proffered, or a signal quality such as continuity of song that suggests a safe retreat.
2. A female may favor a particular male indirectly, rather than directly, in one of four ways:
  - a. By being attracted to the loudest or most easily located signals, without comparing males (i.e. with regard to nearness).
  - b. By mating with a male who removed other males from contention by dominating in a contest.
  - c. By favoring a male on the basis of some trait or resource: for example, the female may feed on a glandular secretion or other male gift as she copulates, breaking off the mating when the gift is gone and thereby incidentally disfavoring a male with an inadequate gift.
  - d. By favoring a male on the basis of his performance with respect to some environmental cue: for example, females may mate with whatever male happens to be in the right place at the right time, and he may be there because of particular sensory, thermoregulatory, or neuromuscular capabilities.

### Female choice and runaway selection

We suggest that insects tend not to show extremes of directional sexual selection comparable to the widely studied sexual ornaments of (especially) birds, and that this restriction arises from a difference in the kinds of female choice employed by birds and insects (we do not intend here to refer to visual ornaments *per se*, but to the concept of

ornaments having evolved in fashions parallel to the sexually selected ornaments of birds; excluded are traits evolved directionally as a consequence of male-male competition, such as beetle horns). Often, it may not be necessary to invoke direct comparison (direct choice of 'best-of-*n*'), especially involving learning and memory, to explain mate choice in insects. For example, if females mated with particular kinds of males are more likely to remate than females mated with some other kind of male (e.g. heterospecific versus conspecific matings), the variation may be owing to the female's ability to identify incomplete or 'imperfect' matings, rather than a 'best-of-*n*' choice. Other mechanisms, such as male-male interference, could also give the impression of 'best-of-*n*' choice: Wilkinson and Reillo (1994) found that males of stalk-eyed flies that had wider eyes also had more females in their aggregations. However, it does not necessarily follow that females actively choose, as, for example, by moving from group to group and stopping more often or for longer periods where they perceive more widely spaced eyes on the male. One must first eliminate the possibility that the contests between males, described by the authors, result in males with wider eyes being located where resources perceived by females are more plentiful or where more females are present for incidental reasons. Goulson *et al.* (1993) found that female death watch beetles are more likely to accept larger (heavier) males; it is not necessary, however, to argue that they are comparing males and choosing after the comparison: they may be using a threshold (see below).

Instead of using 'best-of-*n*' comparisons, insects appear more often to use tests involving sets of minimal criteria ('threshold choice') that can be applied even to lone individuals, minimal here meaning only that the criteria are the minimum needed to cause female acceptance. This is what Janetos (1980) called 'fixed threshold' or 'fixed threshold with last chance option' (the latter referring to cases in which a threshold of acceptance drops as time passes without opportunity to mate; threshold can also rise after mating without eliminating further mating). For example, female periodical cicadas fly into huge leks of singing males, attracted by the males' songs, and become motionless there, apparently mating with the first male to locate them and engage in at least a minimal set of courtship behaviors (Marshall and Cooley *ms.*; Alexander *et al.*, *ms.*). Even in insects that mate in huge aggregations the 'minimal criterion' may involve chiefly being in the right place at the right time (Otte's (1974) 'female accepts the most available male', p. 413).

Animals are restricted to the use of thresholds when mate criteria are developed in the individual without involvement of social (extrinsic) stimuli (what some authors intend by the term 'hard-wired'); such mate criteria work only if the internal developmental program yields a uniform response across the breeding population (Alexander 1969, 1990). Unlike birds and mammals, individual insects frequently do not encounter members of the other sex before beginning to signal or respond sexually. Most insect juveniles, for example, do not have learning experiences with their parents, as do virtually all mammals and birds, that can influence how they select mates as adults. Thus, in temperate climates, at least, all adults of one generation are usually dead before juveniles of the next generation hatch. Even when adults remain after the next generation hatches, unless there are parent-offspring interactions, possibilities of juveniles learning from adults are practically non-existent. In a high proportion of insect species a significant proportion of individuals may never encounter another individual, even of their own generation, before mating; insects in which this is the case must be prepared to perform without social experience. Adult life is often extremely short, and mating may occur soon after eclosion, which may be evidence that for various reasons, including some of the above, learning has been unlikely to yield net benefits. Insect juveniles often live so differently, and are so different from adults, that learning experiences useful in adult sexual behavior as a result of juvenile socialization seem unlikely. Finally, there seems to be no evidence from actual studies that insects show learned modifications of sexual behavior as a result of social interactions with other individuals; individuals reared in isolation seem to perform in sexual contexts in ways indistinguishable from those reared with social experience (see, for example, Alexander 1969). Although insects with migratory and non-migratory phases change some aspects of reproductive behavior as a result of crowding or isolation during rearing (see, for example, Kennedy 1961), it is not obvious that even adult insects learn socially in ways that influence sexual behavior. For example, Goulson *et al.* (1993) recorded no sequential changes (i.e. changes consistent with learning) in the behavior of females exposed successively to different males.

All of the consequences of an absence of social learning about mate choice are by no means clear. Differences in the modes of development of variable traits of males, and of female responses to such variable traits, can affect the possible kinds of runaway sexual selection (see, for example,

Moore and Moore 1988). Females of many birds and mammals appear able to learn about male traits during successive encounters of potential mates and other conspecifics so as to compare the range of variation in any group of males and choose the extreme regardless of precisely where it may fall (Lande's (1981) 'relative' and 'open-ended' preferences, the latter yielding a so-called super-optimal stimulus: see, for example, Williams 1992). This mode was that described in Trivers' (1972) version of runaway sexual selection. When females generate their preferences without learning from external or social stimuli, they necessarily enter into mating with either a threshold or a preference for some particular state of the male trait (Lande's (1981) 'absolute' preference). In such a case females can still select the 'best-of-*n*' mate in the following ways: (1) indirectly, for example by favoring the fastest male in a mating flight (as in honey bees: Page 1980; Thornhill and Alcock 1983); (2) by sensing multiple males simultaneously (rather than successively) and responding only to the extreme individual (Otte 1974); (3) by copulating multiply using minimal criterion choice and raising mating thresholds in a way that modifies the minimal criteria upward with each successive mating; or (4) by favoring the extreme males incidentally. The last case assumes that the female threshold may be set beyond the range of available males, and that females in such situations can lower their criteria and accept males less extreme than the female's (otherwise) 'absolute' minimum preference. This is the 'fixed threshold with last chance option' of Janetos (1980). In this last case, the female's original criterion may or may not exceed the range of male variation in the trait; if it does, the male trait will evolve to match the females' preference and then stop, unless somehow the females are again moved to even higher extremes of preference: for example, according to Lande (1981) by genetic drift. We do not regard this as nearly so likely as the kind of runaway selection described by Trivers (1972), in which females can evolve an ability to choose the extreme of male traits in long-lasting directional selection. The kind of choice excluded from this list is successive comparisons of possible mates causing learned changes in the female's willingness to mate with certain kinds of males, or in her mate criteria, with the result that she mates with only one male or a specific subset of males.

Following is a list of differences between female choice using minimal criteria or 'threshold' choice (TC) and the 'best-of-*n*' mate (BN); all assume females as the limiting sex. These criteria seem to suggest that insects are more likely to possess TC systems. They predict generally that,

because internal development of mate criteria without social experience is more likely in insects, (1) extreme polygyny is less likely, (2) single matings by females are more likely, and (3) degrees and diversities of ornamentation should be less extreme.

1. In TC systems, females are expected more often to mate only once because there will be fewer easy possibilities of identifying better males following mating (but see threshold changes, above).
2. A female using BN is not expected to mate only with the first male she encounters.
3. In TC systems females are not expected to reject a male at first and then return to choose him after examining other males; this should happen frequently in at least some BN systems.
4. Directional selection on male traits will be less intense in TC systems because usually a higher proportion of males will possess the minimal criteria.
5. Assuming that females tend to agree on 'best' male features, the degree of polygyny will tend to be higher in BN systems because more females will exert effort to mate with the extreme male(s); extreme polygyny tends to increase sexual dimorphism and extreme traits in the more variable sex (for a likely exception, see Robertson 1986).
6. The degree of polygyny in BN systems will increase as the number of males available for comparison increases; this will not always happen in TC systems.
7. If it is typical for each male to be encountered only once, and one at a time, the system is likely to be TC, because females will be unable to make comparisons.
8. If development of choice is entirely internal (there are no social possibilities), the system is likely to be TC or indirect BN choice; minimal criteria can be generated internally, but ability to choose extreme males, which may differ from situation to situation, is unlikely to be generated internally.
9. When individuals mate across multiple years (or bouts), there are more likely to be learning opportunities that promote appearance of BN systems.
10. With successive years (or bouts) of mating experience, females should become measurably better at picking the extreme male only in BN systems; and long-lived iteroparous males can continue to develop extremeness in behavioral traits, including learning about fighting and competition.
11. Memory and individual recognition are likely in BN systems, unlikely in TC systems.
12. If all of the acceptable males in a TC system are removed, females are expected to reject the remaining males (unless the female employs a 'last-chance option'); if the extreme male is removed in a BN system, females should mate readily with the next (second) ranked (extreme) male.

### Changes in females' ability to choose during the mating sequence

A female choosing a male, in whatever fashion, is in a curious bind. Early in the sexual sequence she has less information about a male on which to base a decision to accept or reject. As the sequence advances it becomes more costly and sometimes less possible for her to reject him. As she acquires information that would make exercise of choice significant, she may lose the ability to make the choice, even though as the interaction proceeds into closer proximity and greater physical intimacy she is also likely to be presented with a more rapid flow of information about the male. Rejection is obviously easiest (and involves the least investment) during rapprochement, particularly in species in which the male produces long-range signals so that the female is aware of him before he is aware of her. At the other extreme, rejection is probably most difficult (and costly) after insemination (Eberhard (1985) and Birkhead and Møller (1993) review possible ways to reject a mate late in the mating sequence). Thus a female gains from securing as much information as she can about a male from the nature of his long-range signals, while retaining, if possible, control in late stages, such as the ability to keep sperm from fertilizing her eggs even if they have already been deposited in her body. When possible, males may be expected to evolve to exploit this situation, as by manipulating information in long-range signals (e.g. uninterruptedness) and evolving to reduce the female's ability to reject sperm following insemination.

With respect to the actions of the female, one could divide copulations into three kinds: (1) those in which the female never rejects the male upon initiation of copulation; (2) those in which the female rejects the male only in particular situations, such as when only a single male is present and she gains from stimulating lek formation; and (3) those in which the female tries, at least briefly, to reject every male that initiates copulation. In the end, the female must accept the sperm of some male, so whenever males tend to

interact with females one at a time, and not as simultaneous competitors, it also behooves females either to (a) create situations in which males compete simultaneously (e.g. by advertising ovulation, forcing ostentatious courtship chases, or only mating when or where multiple males are present) or (b) store a male's sperm in such a fashion as to be able to use either it or the sperm of a subsequent male should the subsequent male somehow be judged a better father for her offspring. LaMunyon and Eisner (1993) believe they have found such a case, stating that 'In our judgment postcopulatory sperm sorting in *Utetheisa* is exercised by the female herself'. At the least, females that store sperm can reduce one male's success in favor of that of another by mating again.

Under these circumstances males are expected to evolve to (1) defeat or avoid simultaneous competitors and (2) strive to bring about fertilization of the female's eggs by (a) placing the sperm as close to the eggs as possible or on them (hence, in part, the evolution of insemination and copulation: Alexander 1964, and see below), (b) positioning the sperm so as to reduce or preclude superseding by other males (Smith 1984), (c) removing the sperm of previous males (as in Odonata: Waage 1979), (d) preventing the female from copulating after insemination by guarding or holding her (Alcock 1994), or (e) copulating multiple times or putting more sperm in each ejaculate. It seems unlikely that either sex can secure complete control over fertilization indefinitely, although females in species in which indirect sperm transfer has reached the point where the female alone is responsible for insemination may represent such a case.

### The contrast between luring acts and coercive copulatory acts

With respect to differences in conflicts of interest, we will consider two divergent examples within the Orthoptera, illustrating two major kinds of insect mating acts: luring or persuasive acts, and coercing or forcing and manipulative acts. These two examples illustrate opposite extremes on the scale of sexual conflict. Evidently, luring copulatory acts involving transfers of spermatophores are primitive in the Pterygota, having evolved from the persuasive indirect acts of thysanuran-like ancestors. Seizing and forcing acts in Pterygota, involving either spermatophores or free sperm, are apparently all derived, often independently (Alexander 1964, in prep.), implying a general trend toward use of force by male insects.

### A luring act

All field crickets studied in the widespread and speciose genus *Gryllus* copulate with the female mounting the male and the male reaching up from underneath to connect the genitalia and insert the tube of the spermatophore into the spermathecal tube of the female (Alexander 1960; Alexander and Otte 1967a). This luring act can be terminated at any moment by the female simply walking off the male's back. *Gryllus* males are also unusual among Gryllidae in lacking dorsal chemical or other gifts that could keep the female in the copulatory position for long periods. Not surprisingly, *Gryllus* mating is a brief act, usually lasting 20–30 seconds, and the male genitalia of all *Gryllus* are not only simple but essentially identical in the 69 known species found over almost all the world (Alexander 1964, 1990). On a spectrum between the two theoretical extremes of an entirely luring or enticing act and one involving force, manipulation, or coercion at every stage, these field crickets would be near the first end. Evidence of conflicts of interest between males and females of *Gryllus* is relatively slight, and exists mostly with respect to behaviors immediately prior to mating and during postmating behavioral guarding of the female by the male. Nevertheless, the long spermathecal tube of some grylline females, and the correspondingly long spermatophore tube of the male, in one species at least twice the length of the female's body (D. Otte, personal communication), suggest an unending evolutionary chase (cf. Nilsson 1988).

Numerous field crickets in other genera have both long-range calling signals and grasping genitalia (Alexander 1962b; Alexander and Otte 1967a; D. Otte, unpublished). In such cases, however, the female mounts the male and the copulatory act continues to be a luring act until the genitalia are engaged; the long cerci and antennae are thus retained (they appear inevitably to be reduced significantly when male-mounting acts evolve). The grasping and holding aspects are apparently all (still) assignable to the postinseminatory guarding situation, even though they appear to have facilitated copulation that (later) begins end-to-end in some cases (Alexander 1964), and were probably the forerunner of male-above copulation of the caeliferan (grasshopper) type in which the male reaches below the female's abdomen to attach the genitalia.

### A coercive act

In contrast to field cricket males, all grasshoppers, apparently, have evolved an act (evidently anciently derived from a cricket-like luring act: Alexander 1964, in prep.) in

which the male seizes the female from above and then passes the abdominal terminalia under the end of her abdomen to engage the genitalia. In species in which the male seeks the female visually and pounces on her (e.g., species of Melanoplinae: Acrididae (Cantrall and Cohn 1972; Cohn and Cantrall 1974; Otte 1970)), the female presumably has little or no information about the male at the moment he pounces upon her. A female thus pounced upon by a male is also more likely to be non-receptive because she is not mature or has already mated. In striking contrast to females in the field cricket genus *Gryllus*, then, the female melanopline's interests are apt to be strongly divergent from those of the male, at least at first contact. 'In all species [of Cyrtacanthacridinae and Catantopinae observed: 13] males appear to approach females stealthily and to jump onto the females without warning... Struggling between male and female occurs frequently, sometimes resulting in the separation of the pair, other times in copulation.' (Otte 1970, p. 113).

The male grasshopper not only mounts the female but employs genitalia that seize and hold the female's genitalia during a protracted copulatory act that in its length is almost surely contrary to the female's interests. Conflict of interest can be estimated by the extent of female efforts to pull free, which, for example, we have observed repeatedly in cicadas (Alexander *et al.* ms.); we expect such efforts to be universal in species in which the male genitalia are employed to prolong copulation significantly. As expected, grasshopper genitalia tend to be complex and species-specific, and also vary unpredictably – and sometimes dramatically – among small populations that have been allopatric for differing lengths of time (see, for example, Cantrall and Cohn 1972; Cohn and Cantrall 1974). As also expected, genitalia of grasshoppers that pounce on females without prior acoustical or visual signals have been highly useful to taxonomists but *Gryllus* genitalia have not (Alexander 1962b, 1964, 1990); the same is true for the genitalia of other Ensifera in which the male grasps and holds the female. Indeed, the general usefulness of insect (pterygota) male genitalia in distinguishing sister species, and in all aspects of taxonomy, is probably attributable in large part to conflicts of interest between males and females, and resultant unending evolutionary chases. If long continued, such conflicts need not be large to cause quite large differences (Parker 1979; Haig 1993). Obviously, from the nature of this argument, there is no reason to expect universal genitalic differences between sister species or uniformity within species. Indeed, genitalia should vary within

species, although their complexity may still yield species-specific differences.

#### How luring and forcing acts have evolved

Aside from earlier speculations about stationary and movable resources, the particular historical reason why the kind of difference between cyrtacanthacridine grasshoppers and field crickets exists between specific groups is moot; in this case, the ancestral caeliferan (grasshopper) line may have lost long-range signaling, or else possessed only short- or intermediate-range signals that operated when another sensory cue was also available (e.g. an acoustical signal between individuals within view of one another, or vibrations produced after the male has mounted the female). The long-range acoustical rapprochement signals of some grasshoppers evidently evolved later from short-range visual signals involving leg and wing movements that became acoustical (Otte 1970). The interpretation that the ancestor of grasshoppers probably had a short- or intermediate-range male signal derives from: (1) the indication that ancestors of grasshoppers copulated female-above and were in the luring or attracting mode (these are universal correlates); and (2) the independent evolution of both stridulatory and auditory structures in Caelifera and Ensifera (Alexander 1964, in prep.). After an early stage when females approached and mounted males, male caeliferans evidently came to gain by seeking out females and then by leaping on them and holding them. Cricket males, however, continued a luring or attracting mode in achieving the copulatory position, and most retained long-range signals.

In some respects a luring mode is incompatible with modifying the onset of copulation to include a male seizing or grasping mode. From an initial luring or enticing act, one can envision the addition of more benefits or gifts (e.g. secretions or spermatophylaxes) or the incorporation of force, but, even considering what is known of alternative mating strategies, it is not easy to visualize increases in both gifts and force used simultaneously or for the same function. This incompatibility may indicate a significant divergence point in evolutionary history, sometimes, at least, caused by the addition of manipulatory or holding acts by the male near the end of copulation, which then tend to involve events earlier and earlier in the mating act until the entire act is changed. This evolutionary sequence has been repeated independently many times in the Pterygota. It is represented within the Gryllinae in modern crickets (Alexander 1964; Alexander and Otte 1967a). Thus,

some crickets have evolved holding devices on the genitalia that function after copulation has begun, and that replace postcopulatory guarding. Such a change could have been a repeated transitional route to copulations initiated by the male seizing and holding the female. Loss of long-range signals in the early caeliferan line could have occurred during a stage in which the two sexes aggregated using extrinsic stimuli, as is evidently happening in some Gryllidae (Alexander and Otte 1967b). Subsequently, aggregations may have become the main attractant for females in some species, and in others the males may have begun seeking females outside aggregations and leaping upon them; both methods of rapprochement are represented among Caelifera today (Otte 1970).

Not all polygynous males lacking parental care and transformed from signalers into seekers and seizers have genitalia of comparable complexity and diversity. Sometimes it may be difficult to compare quite different kinds of genitalia with respect to complexity, and that fact may account for some of the variation in interpretations, as may differences in phylogenetic precursors when the above selective forces began to operate. Sometimes the relevant variations may not be in genitalia *per se*, but in some other structure or activity associated with copulation, such as claspers, the spermatophore and its attachment devices, or mate-guarding actions. Spermatophore attachment devices should be predictable from knowledge of the structure of the devices (molds) that produce them, but such molds may not be hardened and pigmented, and as a result they may be difficult to understand morphologically. To some extent, the same problem exists with respect to the internal genitalia of females, as compared to the intromittent and clasping devices of males.

Some variations in complexity and diversity among groups may occur because of differences in the intensity of competition among males: as in the extent to which there is simultaneous competition over copulation. In some cases males may compete by fighting at the copulatory site, or they may compete using structures (genitalia and otherwise) that differentially enable them to initiate copulation. Finally, there may be variation in how much of the control of fertilization is effected by males sequestering or holding females after copulation. Females may vary in how quickly after copulation they oviposit (or give birth), and they may also vary in the number of times they copulate, or in how well they can control fertilization following insemination (which is related to environmental factors that influence how important it is for them to

delay oviposition or to exert effort in hiding or placing the eggs). All of these factors can influence the extent to which selection favors elaboration of the genitalia in male-female races to control fertilization, and all must be taken into account as the relevant comparisons are developed.

Presumably, rapid directional changes are more likely in genitalic evolution when there are no long-range signals. The genitalia of grasshoppers in which males pounce on females without prior signals, for example, may be expected to change rapidly even in the absence of interspecies interference, causing divergence even during allopatry. In effect, such genitalia are *always* under the kind of selection that works on long-range calling signals only following establishment of new sympatry between species with confusingly similar songs. If species are largely defined by genitalic differences in such groups, then many more species, many more allopatric species, and many more species with small ranges are likely to be encountered. Such a difference seems to exist between the Ensifera with long-range acoustical signals and the Caelifera that lack them. Caelifera with long-range acoustical signals, however, tend to compare in these regards with Ensifera rather than with the other Caelifera (Cantrall and Cohn 1972; Cohn and Cantrall 1974; Otte 1970).

### The role of the spermatheca in genitalic evolution

Particular directions in the evolution of genitalia and sperm storage devices influence future directions of change. Thus, as female insects evolved sperm storage structures and the ability to restrict egg fertilization to the moment when the micropyle is held against the spermathecal tube opening, males evidently could gain only via those sperm that happened to end up in the evolving spermatheca. This situation greatly influenced the subsequent evolution of the male genitalia, and female responses to them.

The evolution of spermathecae resulted, generally, in sperm precedence tending to favor the last male to inseminate the female – the last male to place sperm in the spermatheca – rather than the first inseminator, as is more likely in mammals that do not store sperm. This situation may sometimes place the female in the position of being able to ensure that the last male with which she mates fertilizes most or all of her eggs. At least potentially, it gives her an opportunity to choose among males, even after multiple copulations. Evidence of sperm mixing in the spermatheca, however, tends to argue against total female

control of paternity since mixing nullifies the outcome of sperm competition. Competition among males is expected to result in such mixing, whereas females may be expected to evolve means of giving precedence to the last sperm to enter the spermatheca. This is so because a fully inseminated female is only likely to mate with additional males when they possess attributes superior to those that have already inseminated her (Sherman *et al.* 1988).

Evolution of spermathecae and delayed fertilization places males in a position of being able to control fertilization only by somehow causing the female not to mate again, or to oviposit soon after copulation, and it must have led to a variety of postinsemination techniques (Alcock 1994) as well as the kinds of male structures such as are used by damselfly males to clean out the sperm of previous males from the female's spermatheca (Waage 1979). In some cases it may have led to a nullification of genitalic evolutionary races, placing emphasis instead on males' ability to control females after insemination, as in *Gryllus* (Alexander 1960; Alexander and Otte 1967a).

### Genitalic complexity and copulatory courtship

We have argued above that genitalic evolution may often be explained as the result of sexual conflict over control of fertilization. Eberhard (1985) argues that genitalia have evolved under the influence of female choice, with the principal advantage from genitalic changes being that males with the changes sired more offspring because they caused females to do things that increased the likelihood that those particular males' sperm would fertilize eggs. This postinsemination, internal sexual selection scenario is one way that conflicts of interest between male and female could be characterized, and one way they could be resolved. But Eberhard essentially restricts his hypothesis to female choice that can lead to Fisherian runaway sexual selection, in the sense that females choose males solely on the basis that their sons will also be capable of titillating females more effectively and thereby fertilizing more eggs. The conflict-of-interest race emphasized in this essay does not preclude any kind of 'female choice', but it ties male-female conflicts of interest about the use and structure of genitalia (and other holding devices and guarding behavior) to the question of who controls fertilization, and it seems unlikely to lead to runaway sexual selection. In this hypothesis, information that the female is securing about a male with whom she is mating, or who has just inseminated her, is not restricted to the degree or ways in which

his genitalia stimulate her internal (or external) parts, but to any and all attributes that might indicate the kind of offspring he will produce. Moreover, copulatory courtship can also evolve as a facilitator of insemination as precopulatory courtship presumably does. As with the act of capturing the female, the act of coupling the genitalia does not necessarily insure insemination, and the possibility must be considered that variations in success of insemination result from force or coercion rather than titillation.

### The problem of 'matches' between male and female structures

Eberhard (1985) notes that females sometimes have special structures that appear to have evolved to fit the males' clasping devices. He believes these cannot be explained as outcomes of sexual conflict, but that the match evolved through the female changing to fit the male or both sexes changing so as to fit each other. Several possible explanations, however, are consistent with the conflict of interest hypothesis, and require only that the male evolves to fit the female and for some reason she does not or cannot prevent this outcome.

First, there is no incompatibility between some male and female devices evolving to fit one another, and others evolving so as to look as though they fit but actually resulting from conflicts. Not all events in the mating sequence involve conflicts of interest, but long-term tracking of one structure by another, even when conflicts of interest are involved, can give the impression of a mutually beneficial fit. An excellent example may be found in the bewildering complexity of the mammalian placental-uterine interface, long interpreted as serving cooperative homeostatic functions; this complexity may instead have resulted from protracted conflict between mother and fetus over resource allocation (Haig 1993).

Second, devices that male claspers fit may have existed in more or less their present form since before the male began to use them, so that we have only to ask why the female did not alter them to prevent use by the male; some other conflicting function may be one answer. An example of a structure difficult to change may be the constriction behind the pronotum in many carabid beetles, used for example by the male of *Pasimachus punctulatus* to hold the female during courtship and copulation by grasping her there with his long mandibles (Alexander 1959).

Third, the male's and female's interests may be convergent by the time (in the sexual sequence) that the claspers are used. Thus, females may sometimes be injured or killed

if a male whose genitalia are coupled with hers is torn off her body by another male; if the male has grasped her with, for instance, his mandibles as well, this result may be prevented.

This list of possibilities is surely not exhaustive, but it demonstrates that even seemingly perfect correspondences between male and female parts need not jeopardize the conflict of interest hypothesis. We think it also places the burden of proof on investigators who hypothesize mutually beneficial fits of male and female genitalia.

#### Genital complexity and courtship complexity

Eberhard (1985) shows what he calls a 'weak correlation' between complex courtship and simple genitalia (and vice versa). He developed these data to test the question whether interspecific interactions or intraspecific sexual selection is responsible for species differences in courtship and genitalia. In his version of the latter hypothesis (pp. 82, 86-7), females get so much information prior to copulation that they do not gain as much by seeking additional information during or after copulation (Thus, Eberhard says, p. 82: 'Females of species that discriminate among males on the basis of premating signals have already discriminated strongly using nongenital cues before copulation begins; they may sometimes use additional genitalia criteria and sometimes not' and, p. 147: 'In effect, they [the genitalia] could be sheltered from sexual selection by prior strong screening according to other criteria').

These statements would suggest that, for example, because *Gryllus* females do not terminate copulations once they are initiated (i.e. because they have already 'discriminated strongly'), males do not gain from evolving genitalia that prevent termination of copulation. But males in many genera of crickets with complex, species-distinctive genitalia signal during courtship as extensively and complexly as do *Gryllus* males (Alexander 1962a,b, 1964; Alexander and Otte 1967a; Otte and Alexander 1983); they, however, remain coupled after attachment of the spermatophore, and the complex genitalia are used to hold them during postcopulation (and in some other genera have, presumably from this beginning, evolved to be attached at the onset of copulation). But *Gryllus* males may have simple genitalia because they have a luring copulatory act, not because they have complex songs or courtship. Cicadas have long- and short-range acoustical signals, but the males mount the females and have complex genitalia that apparently enable them to hold the female for hours (Alexander and Moore 1962; Alexander 1968).

Although a female responding to a long-range male signal and then to a bout of complex courtship doubtless obtains more information about the male prior to copulation than does a female abruptly seized from above by a male of which she was previously unaware, it seems unlikely that any female secures sufficient information to forego additional selection of males at any time prior to fertilization. One might as well say that when females locate males by responding to long-range calling signals, extensive or complex courtship is unlikely; however, numerous examples exist of species with both calling signals and complex courtship.

Conflicts should, by definition, become reduced when a female has received sufficient information to choose a given male, but one cannot thereby assume that females in species with relatively complex courtship receive sufficient information about potential mates. The generalization may be that conflicts over copulation should be reduced in species in which females have the most control over continuation of the mating sequence from the start of rapprochement until the point of genitalic contact (that is, when males must lure females until the beginning of copulation). Eberhard's female choice hypothesis requires that females not suffer significant direct costs as a result of male adaptations that increase control of fertilization. However, we propose that these costs can instead result in selection favoring females who regain control from males. This leads to a prediction opposite to the one described by Eberhard regarding genitalic complexity and courtship complexity: species with luring acts (and generally more complex courtship), such as *Gryllus* species, perhaps should be predicted to have been more likely to undergo the kind of selection on male genitalia that Eberhard (1985) describes, because the luring nature of the act reduces conflicts that might otherwise constrain the evolution of female choice on genitalia. In other words, females who control the initiation of copulation are less likely to benefit from evolving to thwart males who are better able to ensure their own paternity.

If a female has this control, one can assume that she will less often attempt to terminate a given copulation before insemination, and manipulating or grasping genitalia in males will be less likely to evolve in response to such a threat. However, this does not imply that males of any such species might not begin to evolve grasping devices to prolong copulation, or thwart female interests involving any later event in which male and female interests diverge. Once a mating sequence begins to take the form of a lure, it

is likely to continue to evolve in that direction unless changing to a coercive act does not interfere with the success of the lure. Major change in the genitalia can be effected through postcopulatory holding, and change in the species' way of life. If, for example, the sexes begin to assemble for reasons other than male signals, males might then gain by moving to nearby females and taking the initiative in copulation. This could lead to evolution of seizing and grasping actions and devices, as evidently happened in the Caelifera (Otte 1970; Alexander in prep.). Once grasping devices have been evolved to function late in copulation or in postcopulatory mate guarding, they can be employed earlier and earlier in the mating sequence.

#### Attended and unattended spermatophores

The most extreme cases of female control of insemination appear to be those in which females independently take up spermatophores after males have produced them and left the area (references in Alexander 1964; Kristensen 1981). Because there is so little opportunity for manipulation of females by males, and because females pick up the spermatophores (presumably after inspection), little conflict of interest is expected at the point of insemination, and spermatophore complexity designed to thwart female interests is not expected. Similarly, greater spermatophore complexity is expected in species in which males are present and have the opportunity to coerce females into accepting spermatophores. Indeed, spermatophores do seem to be less complex in those species in which males and females are not in contact with one another during insemination, and more complex in those species in which the sexes are in contact (Eberhard 1985, fig. 3.5, p. 48).

Eberhard attempts to explain the pattern of spermatophore complexity as support for a female choice hypothesis, stating that complex spermatophore devices for copulatory courtship '...would be superfluous in species without male-female contact since only receptive females ever bring their genitalia into contact with spermatophores' (Eberhard 1985). Eberhard's overall theory, however, is based on the idea that male genitalic devices are initially selected to stimulate females in ways that will promote postinseminatory events in the sexual sequence, such as effective transfer of sperm to storage sites, non-receptivity to future mates, maturation of eggs, and oviposition. His hypothesis does not give a reason for the decision to take up a spermatophore being different from the decision to copulate with a male (although he notes that a female 'does not touch her genitalia to the [unattended] spermatophore

unless she is receptive', implying that males attending spermatophores must overcome some female reluctance); thus, the hypothesis does not predict a difference in complexity between the two classes of spermatophores discussed above, and might predict that spermatophores picked up by the female when she is alone should possess complicated stimulatory devices. Although Eberhard eventually uses the term 'persuasive' for structures such as 'any characteristic of a spermatophore, such as a guiding spine or an injecting mechanism, that makes it more likely that the female's genitalia will actually take up the spermatophore', earlier he says that 'Males that do not contact females cannot *oblige them to be inseminated*...' and 'males will sometimes *maneuver less receptive females* into positions in which spermatophores are in the near vicinity of the female's genitalia...' and 'Both attended and unattended spermatophores can be sensed by *marginally receptive females*, but only attended spermatophores are likely to stimulate and/or fit into such a female's genital area' (emphasis added). Spermatophores left unattended by males for later pickup by females do not seem different from male genitalia with respect to variations capable of initiating female choice and runaway selection. All of the statements quoted from Eberhard (1985, p. 153) appear to fit a conflict-of-interest hypothesis and to argue in a general way against Eberhard's explanation.

The copulatory courtship hypothesis and the conflict-of-interest/control of fertilization hypothesis both predict erratic, unpredictable directions and rates of evolution. The courtship model involves males racing to keep up with ever-changing female preferences. The conflict-of-interest hypothesis involves males evolving to coerce females, and females evolving to evade coercion. Eberhard's model almost exclusively requires the operation of 'best-of-*n*' choice, because threshold decision processes do not readily yield the open-ended preference that most easily leads to runaway selection. Eberhard is explicit (p. 71) that his model includes runaway selection: 'A key aspect of this model of genitalic evolution (and of runaway evolution by female choice in general) is the arbitrary nature of the cues used by females to discriminate among males'.

In insects 'best-of-*n*' choice mechanisms can only operate in female choice of genitalia if females copulate with a set of males and differentially favor the sperm on the basis of genitalic differences. The hypothesis of conflict over control of fertilization does not require large numbers of species in which females mate but once, but if females in large

numbers of species do mate only once, the generality of Eberhard's (1985) hypothesis of copulatory courtship is reduced.

The question of the evolution of genitalia must ultimately be settled by understanding the extent to which male and female interests differ over use of male genitalia. Eberhard's hypothesis requires that females suffer only minimal costs when males evolve more effective ways of ensuring paternity; otherwise these costs will constrain the evolution of female preference for those males, and females will be selected instead to counter males and enhance their own control. For all the above reasons, and because we regard runaway evolution as less likely in insects than in vertebrates, we doubt the generality of Eberhard's hypothesis that insect genitalia evolve as a result of female choice.

#### Forced copulation and female control of fertilization

Controlling the final aspects of fertilization does not appear an unlikely evolutionary possibility for female insects; indeed, in some Hymenoptera females can control whether or not eggs being laid are fertilized, evidently by contracting or relaxing a sphincter that is responsible for whether or not sperm are released from the spermathecal tube (Gerber and Klostermeyer 1970; Werren 1980). It is possible that females could use such a device to control whether or not the sperm of any particular copulating male enters or leaves the spermatheca. A female may be inseminated by a male that (1) has traits indicating high quality prior to mating (see earlier), (2) is extremely adept at securing matings, or (3) is extremely good at forced mating. If there is no evidence of females of a given species having evolved to prevent certain males' sperm from entering the spermathecal tube, then it is likely that (1) the males have some exceedingly unusual kind of intromittent organ that is effective at thwarting female efforts to exert control or (2) it is in the interest of a female to accept the sperm of any male that has actually been able to couple with her. This rather startling hypothesis implies that, for whatever reasons, female choice is largely finished prior to intromission or insemination. It also implies that the evolution of male genitalia is a matter of male-male competition (e.g. getting the sperm closer and closer to eggs, removing sperm, and plugging the female's reproductive tract) and that females have evolved to accept the sperm of the male most able to get his sperm into their genital tracts

and nearest to their eggs, once the competition has become internal to the female.

If these arguments are correct, then one wishes to predict the kinds of animals in which females would be most likely to resist male attempts to control fertilization. One may at first imagine that such control should occur in species in which (1) males give no parental care, (2) males are plentiful and vary greatly in worth as mates, and (3) males are very effective at forced copulation. But this combination of conditions is paradoxical. When there is no paternal care, then one of the best signs of a male's quality as a mate is his ability to get sperm into females, and, if forced copulation is highly successful, then males who inherit the ability to be good at forcing copulation will tend to be reproductively successful. Females might be expected to resist forced copulation, even as strenuously as possible (without sacrificing actual reproduction in the effort), because presumably a copulation that must be forced is in some way contrary to their interests (see, for example, Cooley 1995). When force becomes a principal indicator to the female of male quality, females are not expected to exert as much effort to prevent a forced copulator's sperm from fertilizing their eggs once they have been placed in the reproductive tract. In other words, in the particular species in which a female's ability to control fertilization by rejecting certain males' sperm would appear at first to have its greatest potential benefit, the benefit is largely canceled by the fact that the quality of males is determined primarily by their ability to get sperm into females when they are resisting (the situation that in general would be expected to cause intense selection for postinsemination female choice). However, if only because non-parental males serving their own interests almost inevitably reduce the reproductive success of their individual mates, females may be expected to resist yielding complete control of fertilization to males.

What about species in which there is much paternal care, and paternal care is dependent on exclusive mating rights (or, in insects, birds, and reptiles, last mating rights) with the female, and high confidence of paternity? If males cannot identify or respond to variations in females' ability to control the fate of sperm once they have entered the female's body, mate-guarding (and, in some animals, infanticide when guarding fails) will be the only successful strategy for the male in controlling fertilization. If a female can obtain parental care by a superior father not good at causing or forcing mating, she may be in a position to gain by using his paternal care and the

sperm of a superior male or the sperm of a male good at forcing matings. Eberhard (1985) reviews the evidence that a large amount of differential paternity occurs as a result of events during copulation, and sometimes following insemination.

#### Origin of copulation

The above arguments about sexual conflict help us to reconstruct the evolution of internal fertilization. Males' efforts to control fertilization in ancestral external fertilizers (to outcompete other males in the vicinity) presumably caused them to gain from placing the sperm or spermatophore closer and closer to the female's genital opening, nearer and nearer to the time of oviposition, finally inserting the sperm into the female's body before oviposition (Eberhard 1985). Thus began the process whereby females withheld the eggs at the time of copulation, males evolved longer intromittent organs, and both sexes added to the complexity of the devices they used in copulation and insemination; both sexes thereby were exerting effort to control fertilization of the eggs. Evolution toward internal fertilization surely was also abetted, at least in some cases, by a female tendency to protect eggs, especially as mating began to occur in terrestrial environments. Did side pockets in the female genital tract (as in salamanders: Salthé 1967; Boisseau and Joly 1975), and eventually spermathecae, evolve because sperm survived longer in such sites, and because females possessing such structures could time fertilization and oviposition to the best reproductive advantage? Or did such structures evolve because females were initially sequestering sperm so as to control which males fertilized their eggs?

Uncoupling could have been furthered (and maintained) by females evolving to favor males that placed sperm where the female gained from having them (e.g. in spermathecae). In such case, females would continue to disfavor males that tended to place their sperm in more direct contact with the eggs. This disagreement would tend to cause an unending evolutionary race.

#### THE MATING SEQUENCE AND SPECIATION

Calling (rapprochement) signals have been discussed extensively in connection with speciation because they tend to be species-specific among sympatric synchronic species, for reasons that are not entirely clear. Here we discuss evolutionary changes in signals, their consequences for

speciation, and why character displacement is infrequently documented.

Despite growing acceptance of arguments that species signaling differences may often be due more to sexual selection within species than to interactions between members of different species, and therefore reproductive isolation (see, for example, West-Eberhard 1983, 1984), it is tempting to assume that interspecies interactions are the reason for widespread signal uniformity within species, and similarly for the consistency of differences between species. For insects, however, another explanation must be dismissed first. When social learning is absent, the only way that members of a breeding population can identify one another reliably (and, incidentally, populations can be potentially panmictic) is through an evolutionary tracking of signal structure and signal response capabilities. There may be brief periods of directional selection when evolutionarily divergent populations with confusingly similar signals initially become sympatric and synchronic. However, unusual signals and unusual responses will be disfavored even when there are not confusingly similar signals from other species. Internally regulated development of signals and responses, and the resultant stabilizing selection, can lead to convergences between male and female; sometimes, the same or linked genes may influence both signal structure and signal response (Alexander 1962a; Hoy 1974; Pires and Hoy 1992). Nevertheless, only arguments including species interactions, such as character displacement, can explain *both* species distinctiveness among signals of sympatric and synchronic species *and* lack of species distinctiveness among signals of similar allopatric or allochronic species.

Male visual and acoustical calling signals, more than other signals, emphasize the puzzle of apparent shifts between rapid directional selection around the time of speciation coupled with intense stabilizing selection at other times. Only male calls tend to be structurally complex, or patterned temporally, spatially, or both. Long-range visual and acoustical answering signals of females tend to be simple and nondescript in structure, with their precision often a matter of timing in relation to the male's signals. When females are the limiting sex they evidently gain little by advertising more than their sexual receptiveness. The apparent uniformity of long-range chemical signals seems less puzzling because fairly simple changes may yield great differences between species and there are probably few chemical attributes that can change on more or less continuous scales as can rates in the patterning of

acoustical and visual signals. Probably, quick changes upon sympatry following speciation depend on multiple chemicals being present in a signal (Roelofs 1975), especially when their proportions and importance already vary within the species (as in different signals used in different parts of the mating sequence). Much of the apparent difference between chemical signals and acoustical and visual signals in this respect may also be illusory, or result from greater difficulty in humans comparing chemical signals. Whatever the case, principles that apply to visual and acoustical signals probably also apply to chemical signals, so we can use one kind of signal to make some arguments applying to all three kinds. In the rest of this discussion we will emphasize acoustical signals, as they occur in crickets, katydids, grasshoppers, and cicadas.

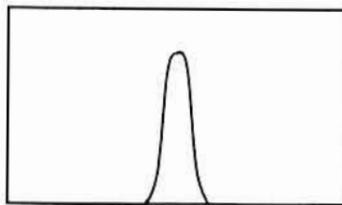
Various authors have made claims, not necessarily compatible with one another, about the importance of sexual selection (1) in initiating speciation, or (2) in cementing species differences immediately following speciation, and (3) on character displacement. Thus, West-Eberhard (1983, 1984) argues that sexual (or social) selection is a principal initiator of population divergences that later lead to speciation. Paterson (1993) argues that sexual signals are under stabilizing selection, diverge during the allopatry that leads to or allows speciation, and prior to sympatry between the newly divergent populations, and that this divergence occurs without interaction between the two evolving species. Otte (1994) in general agrees with Paterson, expecting that the acoustical environment in general causes song differences to begin in allopatry, and that this initial divergence facilitates subsequent divergence under sympatry and therefore accelerates speciation (D. Otte, personal communication). Otte attributes somewhat more significance to the general acoustical environment during allopatry than we do. Our position stems from a consideration of allopatric or allochronic species that lack any song differences, or apparently significant song differences (e.g. *Gryllus veletis*, *G. pennsylvanicus* and *G. campestris* (Alexander 1957, 1969); *G. firmus* and *G. bermudensis* (Alexander ms.); *G. rubens* and *G. undescr.* [integer of authors] (Walker 1974); *Oecanthus quadripunctatus*, *O.* [dwarf *quadripunctatus*] (Walker and Rentz 1967); *O. pini* and *O. laricis*; *O. nigricornis* and *O.* [undescribed on willow] (Walker 1963); *Magicalcanda septendecim* and *M. tredecim*; *M. cassini* and *M. tredecassini*; *M. septendecim* and *M. tredecim* (Alexander and Moore 1962)).

Species-specific patterns in calling songs may be the best example of traits that evolve towards commonality of

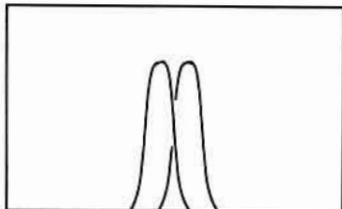
interests between males and females. Traits that evolve under similar selection should not vary within populations and should not diverge quickly in allopatry. In contrast, traits that enable the male to act in his own interests and contrary to those of the female, or vice versa, involve continuing conflicts of interest between male and female, and thus result in unending evolutionary chases. Examples are changes in a male's genitalia or other features that enable him to capture the female for mating, hold her more securely during copulation, or hold her longer after copulation against her interests. Such traits should evolve rapidly within populations and differ extensively and in many and unpredictable ways among newly allopatric populations. They can be responsible for speciation because once they diverge far enough to prevent copulation between species they cannot be bypassed. Thus, there are likely several times as many grasshopper (caeliferan) species in North America as crickets and katydid (ensiferan) species. Most of those grasshopper species are concentrated in the Melanoplina (D. Otte, personal communication), where the greatest evidence exists of conflict of interest between males and females over use of the male genitalia (Otte 1970). Allopatry of forms with genitalic differences is also likely greater in the Melanoplina than in other Saltatoria. Thus, when genitalic evolution appears to result in large extent from male-female conflicts, correlating with use of force by males, genitalia are more complex and diverse, and speciation appears to have been more rapid. If Fig. 1-1 portrayed genitalic evolution in melanopline grasshoppers, rates of change between stages 1 and 6 would be more alike, individual populations would show greater variation, and the genitalic changes themselves might often have been causal in speciation.

Eberhard (1985, 1993a,b) has argued that the genitalia of male animals evolve in ways that benefit females as well as males, and as a result they are extensively involved in female choice even following insemination and evolve rapidly on that account. We have argued (above) that animal genitalia typically evolve rapidly because they involve conflicts of interest between male and female with respect to the details of copulation. We also suspect that character displacement is a frequent or virtually universal aspect of the evolutionary divergence of similar species newly returned to sympatry (as well as a continuing aspect of competition among species within communities, often when they are not related or highly similar overall). We also suspect that this divergence in sympatry, rather than in allopatry, accounts for most of the divergence between

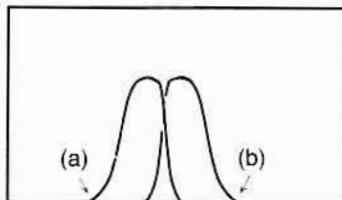
Stage 1. A single species with the female-attracting parts of its song under stabilizing selection



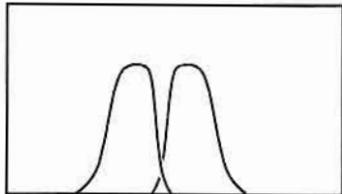
Stage 2. Two allopatric populations with songs diverged slightly through drift, pleiotropy, or slight differences in the acoustical environment



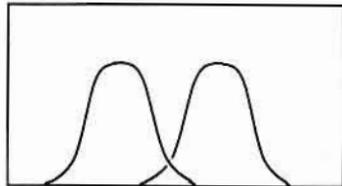
Stage 3. Sympatry occurs after postmating difficulties have appeared; song extremes at points (a) and (b), respectively, are favored in the two populations



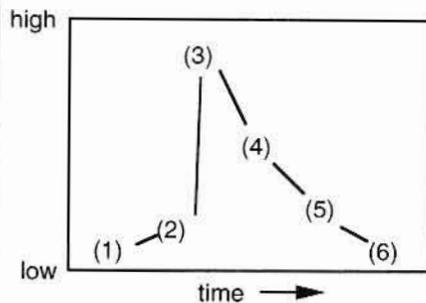
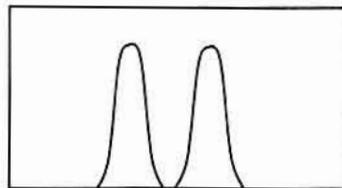
Stage 4. Strong selection for divergence in song; strong selection favoring divergence as a result of interference and wasted effort because of overlap in songs between incompatible populations.



Stage 5. Two sympatric species with songs still overlapping; selection for divergence (directional selection) still strong



Stage 6. Songs of sympatric species have become non-overlapping; selection for divergence is essentially absent; stabilizing selection is strong within each species.



Presumed rates of evolution at each of the six stages of song divergence. Stages 1 and 6 will evolve slowly because, on average environments will have been effectively stable for longer. Stage 2 will evolve more rapidly because populations in allopatry are likely to have different environments. Stage 3 will evolve fast, and faster than 4 and 5, because selection favoring divergence, and minority extremes, will be strongest then.

If stages 2 and 3 are heavily represented among allopatric populations, and very little of stage 6, the hypothesis that most divergence occurs during allopatry is denied. Moreover, if songs are so sensitive to acoustical overlap that selection is effective in allopatry, in the absence of extensive overlap with the songs of other species, then it should be that much stronger when species with closely similar songs become sympatric and synchronic.

In this hypothesis, stages 1, 2, and 6 occupy the vast majority of time; 3, 4, and 5 occur so swiftly as to be observed only rarely. If stages 3, 4, and 5 are passed through very rapidly, this model may be able to account for all observations to date.

Fig. 1-1. A character-displacement model to explain song relationships among similar species that are either allopatric or sympatric. The crucial question is when sympatry appears after allopatric divergence.

similar species in sexual characters, therefore that it tends to be an effect of speciation rather than a cause, and occurs late in speciation rather than early.

If sexual selection in allopatry were a frequent initiator of speciation, as opposed to being primarily incidental to speciation or occurring near the end of the process, we should find such divergence on a large scale among recently allopatric populations. If divergence under sexual selection is sufficient to cause speciation, we should find numerous sympatric cognate species differing only in pre-mating sexually selected traits: that is, lacking postmating differences that could maintain the interbreeding failure. If reproductive character displacement is prevalent, sympatric related species should always differ in sexually selected traits but allopatric forms similarly diverged in other respects should not (similarly diverged is a crucial phrase here, for in the alternative hypothesis divergence would be unaffected by sympatry). We should also find that recently formed species which overlap geographically only partially should be more different in the regions of overlap than in the regions of allopatry, although this requirement has to be restricted. Our argument depends on such character displacement happening so quickly that it is rarely observed in the form of great divergence in regions of overlap of newly formed species than in their regions of allopatry. Fig. 1-1 shows the process.

With respect to their roles in these kinds of events, there are several different kinds of traits under sexual selection. Traits that attract the other sex and are apparently under directional selection (such as bright coloration or tail length) are probably the sort West-Eberhard would regard as central to her argument. They are also the ones most likely to become involved in runaway selection. These are also traits (1) for which confusion among different species is likely minimal, because the signals are not broadcast great distances, (2) which tend to be attention-getters, with additional traits immediately in view, and (3) for which there are not large numbers of species signaling in the same modality (as is possible with acoustical signals). Such traits should diverge rapidly in allopatry, but because they can be bypassed during the mating sequence they are not likely to cause speciation in the absence of significant postmating differences that cause hybrids to be at a disadvantage. If these traits are involved in causing speciation one should frequently find newly formed species differing in these traits but able to produce hybrids in induced matings which survive and reproduce as well as the parental forms in the field.

Traits that attract the other sex and are evidently under stabilizing selection, including aspects of the pattern of acoustical signals or the molecular structure of chemical signals, are the kind that Paterson might include in his arguments. They are signals for which the channels are likely to be noisy because (1) they are broadcast great distances, (2) they tend to operate alone without additional confirming traits that are brought immediately into sensory range (for example, when an animal sees a bright spot, its attention is at the same time drawn to the rest of the individual's attributes), and (3) they can easily be patterned almost endlessly in the same modality. Such traits should diverge slowly in allopatry but may diverge quickly in sympatry because they will be temporarily placed under intense directional selection. If these traits diverge primarily in sympatry, one should expect to find evidence of character displacement between partially overlapping species unless there is good reason to invoke quick changes that also spread quickly to the species limits outside sympatry. Specifically, among singing insects one finds that species that breed in the same places at the same times never have the same songs; instead one finds dramatically different signals no matter how similar the species are in other regards. Species that do not breed in the same places, or in other cases at the same times, sometimes do have the same songs, or songs that overlap almost completely in their attributes, sometimes when the species involved are not even similar. The paradox is that, despite dramatic differences between the songs of sympatric, synchronic sister species, and the frequent absence of such differences between allopatric or allochronic sister species, species that partly overlap in breeding places and times do not show greater song differences in the regions of such overlap that are obvious and on the same axes of variation as the species differences (Alexander 1979, pp. 119-120). This fact has impressed workers in this arena such as Alexander (1968), Walker (1974), Otte and Alexander (1983), and Thomas and Alexander (1962) who have documented them in tapes of, overall, perhaps a thousand species of Gryllidae, Tettigoniidae, and Cicadidae with overlapping ranges. These cases are from published and unpublished reviews of, usually, the vast majority of acoustical Orthoptera and Cicadidae traced geographically throughout numerous regions including virtually all of North America and Australia.

Howard (1993) thoroughly and carefully reviewed the topic of character displacement. He concluded, certainly without disagreement from any of the above authors, that

character displacement has not been studied well enough to show that it is rare or absent. However, the discovery, from meticulous studies, of even large numbers of subtle or cryptic cases (Benedix and Howard 1991) will not resolve the question of why obvious cases of the sort expected from the particular and dramatic differences among the songs of sympatric and synchronic species remain undiscovered. The reason may be that suggested in Fig. 1-1: that they are extremely short-lived.

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The Evolution of

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