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Sexual Selection, Competitive Communication and Species-specific Signals in Insects¹

M. J. WEST-EBERHARD

¹Dedicated to Professor O. W. Richards, FRS, FRES.

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INSECT COMMUNICATION

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I. INTRODUCTION

Charles Darwin (1871) noted that some of the most strongly selected and rapidly evolving traits of animals had nothing to do with ecological adaptation or the "struggle for existence" but instead served to enhance success in intra-specific social competition, especially for mates. He regarded these traits as evolving under "sexual selection" as distinct from "natural selection", or selection for success in survival. He also documented its occurrence using many examples from insects: the elaborate horns of beetles and flies, the songs of crickets and cicadas, the colours of dragonflies and butterflies and the courtship of springtails and gnats (see also Richards, 1927).

Recently, entomologists have played a leading role in reviving the idea that sexual selection can influence the evolution of courtship (e.g. Alexander, 1975; Lloyd, 1979; Otte, 1972; Spieth, 1974; Thornhill, 1981; Thornhill and Alcock, 1983; Baker and Cardé, 1979; Silberglied, 1984). The special characteristics of evolution under sexual selection extend to the evolution of traits used in social competition for resources other than mates (West-Eberhard, 1979, 1983). This review summarizes the special characteristics of evolution under social competition, describes the kinds of competitive communication found in insects and shows how the species specificity of competitive signals can evolve as a result of social selection.

II. THEORY: THE EVOLUTION OF COMPETITIVE COMMUNICATION

Intraspecific communication may be either co-operative or competitive in function. "Co-operative" signals, like the food-source communication of honeybees and the scent trails of ants, co-ordinate the activities of different individuals in the performance of tasks having survival or reproductive value for the interactants. "Competitive" signals, on the other hand, lead to differential success in obtaining some resource (food, space, mates). While competitive signals may eventually promote "co-operation" (e.g. defeated *Polistes* females "co-operate" by serving as workers, and successfully courted females "co-operate" by copulating), competitive communication implies some conflict of interests and some effect on the outcome of socially mediated intraspecific contests.

The distinction between "competitive" and "co-operative" communication, like Darwin's distinction between "sexual" and "natural" selection, is justified by the special nature of selection on socially competitive traits (West-Eberhard, 1983). These special theoretical considerations are summarized with reference to insects below.

A. Strength of Selection

Traits important in social competition are frequently subject to unusually strong selection.

The strength of social selection (variance in reproductive success associated with degree of success in social interactions) varies with the structure of the social (or mating) system. In gregarious species social competition can be a prime determinant of differential access to critical resources. Extreme examples occur in some gregarious or "lek" mating systems (see below) and in the social insects, where winners in social competition ("queens") make a genetic contribution to future generations many times that of losers ("workers") (for examples, see West-Eberhard, 1981). There is likely to be unusually strong selection on signals contributing to this enormous reproductive dominance of socially dominant individuals, with small differences in signals associated with large differences in reproductive success.

B. Potential for Runaway Change

Fisher (1930) suggested that the special premium on the courtship signalling ability of males can produce unusually rapid ("runaway") evolutionary change: If superior signalling ability is at a premium (and not countered by selection for other kinds of mate superiority), then there is selection on females to favour superior signallers as mates, due to the advantage of producing sons who are superior signallers. This would lead to increasingly strong selection on the signalling ability of males and the establishment of a genetic correlation of preference and signalling ability (Fisher, 1930; Lande, 1981) greatly accelerating the evolution of both.

"Runaway" selection should theoretically be curtailed in the evolution of agonistic signals by selection on opponents to detect true ability to fight (to call the bluff of superior signallers who are in fact weak fighters) (discussed in West-Eberhard, 1979). In the case of courtship, a runaway process could be checked by natural selection against extreme (costly, unwieldy, or predator attracting) characters (Fisher, 1930), as well as selection for true mate quality (genetic; or phenotypic, e.g. in species showing feeding or defence of mate or offspring). Runaway selection is thus most likely in species in which males contribute nothing (other than genes) to mates or offspring and in which male-male threat or combat plays no role in female choice of mates.

C. Continuing Evolution of Socially Competitive Signals

Social communication is theoretically subject to unending evolutionary change, with continued exaggeration of particular elements eventually limited

only by selection in other contexts (Darwin, 1871; Fisher, 1930). As in the unending coevolutionary races of specialized parasites and their hosts, there is no "optimal" solution limiting the evolution of competitive signals, only unending selection to more effectively outcompete the existing (and evolutionarily changing) tactics or signals of competitors. This means not only that there is no ceiling to change (except by selection in other contexts), but also that divergence can occur even without environmental differences, with competitive innovations themselves initiating new directions of evolutionary change. Thus the evolution of social communication differs in a fundamental way from that of adaptations to non-evolving (e.g. physical) aspects of the environment, or biotic aspects which change only slowly in response to the adapting organism (see Darwin, 1871; West-Eberhard, 1983).

D. Manipulation of Established Sensory Response Repertoires

Vast, already established species-distinctive, sensory and response repertoires serve as a basis for signal evolution and diversity. Competitive (courtship and threat) displays build on the multitude of sensory capacities and responses already present in the organism. Ethologists and sensory physiologists have amply investigated both the sources of displays and the neural and behavioural phenomena that influence the modification and elaboration (or enhancement) of signals (for reviews, see Hinde, 1970; Manning, 1966; Smith, 1977). Displays frequently incorporate signals eliciting responses already profoundly (sometimes virtually inescapably) established through strong selection in other contexts. Threats often mimic the movements or postures of true fights; and courtship displays may incorporate movements performed by food-offering parents or soliciting young. Although much of the research revealing these patterns concerns vertebrates, there is no doubt that the same principles apply to insects. For example, the auditory courtship signal, or "love song", of *Drosophila* is produced by wing oscillations similar to those used in flight, and the sound receptors (antennal arista) used to perceive it were originally used to monitor and control flying [they resonate at flight wingbeat frequency (Ewing and Bennet-Clark (1968))]. The sex attractant pheromones of bees (see Bergström *et al.*, 1981; Velthuis and Camargo, 1975) at least sometimes mimic floral odours (M. J. West-Eberhard, personal observation of hovering males of *Xylocopa* species in Meta, Colombia), evidently capitalizing on the foraging responses of females. By using responses strongly selected in other contexts, the signal in effect creates a sensory trap to manipulate behaviour in the signaller's own favour.

There may be many such established responses in the behavioural repertoires of insects. Their effect as potential sources of diverse signals is multiplied by the fact that each one can potentially become associated with a great variety of

signals. For example, courtship tapping and rubbing of the female's body occurs in at least nine families of beetles and appears to induce immobility (Alcock, 1976), suggesting that in the Coleoptera there is a widespread reflex (immobility) response to being touched which is capitalized upon by courting males. This one kind of response by females has given rise to a great variety of male signals: In some groups males rub with their feet (Alcock, 1976), whereas in others they tap or rub with antennae (Pinto, 1980), genitalia (Alexander, 1959) and/or mouthparts (Pinto, 1980). Signal diversity is even further increased by the evolution of signal enhancement devices within signal modes: In species groups with antennal tapping, the form and use of the antennae varies from species to species, as do the palps in species groups employing the mouthparts, etc. (Selander and Mathieu, 1969; Pinto, 1980).

This development of diversity due to the "embellishment" or amplification of established signals is illustrated by the behavioural devices employed by male crickets to amplify their calling songs (see Chapter 10, this volume). Some observations of Carson (1978, p. 105) on the courtship of *Drosophila* show how embellishment can lead to the evolution of structural oddities whose function is hard to imagine without actual observation of their use in behavioural interactions. In 14 species of the *D. adiantola* species group the male stands before the female, curves the abdomen upwards and forwards like that of a stinging scorpion and vibrates it while nearly touching the female's head. In 13 of the 14 species there is no obvious morphological modification of the male abdomen. But in 1 (*D. clavisetae*) the end of the male's abdomen has acquired a brush of long clavate hairs, which sweep over the female's head during display. Thus an established behavioural signal has in 1 species become embellished—more complex and distinctive. Whether or not embellishment occurs could depend on such a "chance" circumstance as whether or not the unembellished character has persisted long enough in a reproductively isolated population to have allowed time for some mutation to occur. [*Drosophila clavisetae* occurs only on one Hawaiian island and is, according to chromosomal data, "phylogenetically very advanced" (Carson, 1978, p. 105); it has diverged further, and perhaps for longer, from the likely ancestral form than have the species with unmodified abdomens.]

Signal enhancement or embellishment can occur due to well-studied sensory-response phenomena. The common occurrence of enhanced, or *supernormal responses* to exaggerated versions of normal stimuli demonstrate that an (artificially) mutated signal can elicit an improved response in a normal (unmutated) receptor. This occurs in insects—in butterflies, in response to increased frequency of signal (Magnus, 1958), and in the auditory signalling of crickets (*Teleogryllus oceanicus*), in which females are more attracted by a song consisting of 100% chirps than they are by the normal song (16% chirps). *Summation*, the additive effect of piling on different stimuli in eliciting a reaction (see Manning,

1979), means that there can be a premium on increased display complexity per se. *Habituation*, or a tendency to stop responding to continued or repeated stimuli, could favour the introduction of novel signals or behaviour sequences in which the sensory modality changes or alternates. Thus in the evolution of competitive displays novelty per se can be an advantage (West-Eberhard, 1983).

The multiplicity of signal forms possible would be further augmented by the fact that each species must differ somewhat from other species in its particular sensory-response characteristics—differences that would tend to increase as the evolution of communication proceeds, leading to even further signal divergence.

These findings of ethologists and sensory physiologists mean that a signal may be selected (effective in eliciting a certain response) simply because it is a superior stimulator (or inhibitor) of some sensory, hormonal, behavioural or developmental process giving one signaller (or his gametes) an advantage over others. Although a positive response might also be selected because the stimulus (signal) is associated with male superiority under natural selection as suggested by Fisher (1930), this need not be the case.

It is also important to realize that *increased signal complexity need not involve parallel, step-by-step coevolutionary change in the capacity of the receptor to respond*. Some signal innovations may originate with a change in the *receptor* causing it to respond to some existing behaviour [e.g. an intention movement of a sign of superiority such as large size (see Hinde, 1970)], but the evolution of signal diversity can proceed using already existing sensory and response capabilities.

E. Perpetuity of Social Selection

Competitive signal evolution is a virtually self-perpetuating process. Since it can proceed under selection for advantageous social manipulation (see above; see also Dawkins and Krebs, 1978), it does not *depend* for its continuance on a response's being "worthwhile" to the signal receptor, though this impression might be obtained from many discussions of female choice, beginning with Fisher (1930, p. 151). Social (and sexual) selection occurs as long as (1) there is signalling competition among individuals (theoretically, in the case of sexual selection, this is virtually forever—as long as there is asymmetry in the parental investment of the two sexes) and (2) there is any phenotypic variation in the ability of individuals to signal effectively. The obvious fact that the signal variation need not be genetic in order for selection (differential effects on social or reproductive success) to continue is discussed by West-Eberhard (1979) and Wade and Arnold (1980). Given the very large number of signal elements that can occur and, apparently, be screened by insects and the large pre-existing sensory and response field against which they can act (see above), signal evolu-

tion under sexual selection must be virtually universal and perpetual in most insect species (see also Section VI,B).

III. KINDS OF COMPETITIVE COMMUNICATION IN INSECTS

Given the special nature of competitive communication, what kinds of signals in insects should be regarded as "competitive"? Some kinds of signals—threat, territorial and dominance displays—are obviously competitive. They fit the ethological definition of "agonistic" behaviour, i.e. behaviour directed towards another individual which when escalated could lead to physical injury to the latter and/or results in settling status, precedence or access to some object or space between the two (Hinde, 1970). Courtship is also competitive communication, insofar as it affects the success of courting males in obtaining mates. Following the tradition initiated by Darwin's (1871) treatment of sexual selection, I shall refer to male courtship and male—male threat in competition for females as "sexual" competitive communication and to signals used in competition for resources other than mates as "non-sexual" competitive communication.

A. Non-sexual Competitive Communication in Social Insects

Ritualized dominance behaviours (e.g. of *Polistes* and stingless bees) and queen control pheromones (e.g. of honeybees and some ants) are instruments of reproductive competition within colonies of social insects (see Velthuis, 1977b, 1982; Röseler and Röseler, 1977; Sakagami, 1982; West-Eberhard, 1977, 1981). Escalated behavioural interactions clearly occur in *Polistes* (Pardi, 1948; West-Eberhard, 1969). Recent work on queen control pheromones indicates that dominance pheromones are also expressed in graded fashion, so that escalated pheromonal battles are possible. The proportions of fatty acids in the pheromone bouquet produced by *Apis mellifera* females vary from "worker-like" [containing relatively more (*E*)-10-hydroxy-2-decenoic acid] to "queen-like" [containing relatively more (*E*)-9-hydroxy-2-decenoic acid] (Crewe, 1982). Likewise, fire ant (*Solenopsis invicta*) workers are able to distinguish the degree of physogastry (ovarian development) of queens, presumably on the basis of the kinds or amounts of pheromones found in the abdomen (Fletcher and Blum, 1981, 1983). Graded amounts of queen pheromones may also accompany the behavioural dominance signals of *Polistes* and *Metapolybia* (Polistinae, Polybiini) (West-Eberhard, 1977, 1981; Downing and Jeanne, 1982). In the halictid bee *Lassioglossum zephyrum* recognition of worker sub-caste occurs even among bees from different colonies (Breed *et al.*, 1978).

B. Sexually Monomorphic Threat Signals

With the exception of the social Hymenoptera and Isoptera, adult insects only rarely and briefly compete socially with conspecifics in non-sexual contexts. In some species both sexes perform simple threats that seem to keep individuals apart. As in other animals (see West-Eberhard, 1983), these simple competitive signals are performed with distinctively marked sexually monomorphic appendages. Examples include the hindleg-shaking and leg-raising threats of many genera of melanoptine grasshoppers (Otte, 1970), which in at least some species have brightly coloured hind tibiae (Otte, 1970; Cohn and Cantrall, 1974); the aggressive "slashing" of "picture-winged" Hawaiian *Drosophila* (Spieth, 1974) and wing waving of tephritid flies (Prokopy and Bush, 1973; Burk, 1981), in which the wings are distinctively marked in both sexes (Freidberg, 1974); and the wing-waving threat display of coenagrionid damselflies [*Argia* and *Enallagma* species (Bick and Bick, 1963) and *Hetaerina macropus* (Eberhard, 1985a)].

C. Competitive Signals of Immature Insects

Although most competitive communication in insects occurs among adults, there are a few examples of aggressive signalling by immatures. Aoki and Makino (1982) describe ritualized duelling between first instar aphids (*Epipemphigus niisimae*, Pemphigidae) competing for the possession of galls in which to feed and reproduce. These first instar "fundatrices" have specialized strongly sclerotized tergites and enlarged forelegs that are lost in the subsequent (non-duelling) instars (Aoki and Makino, 1982). Caddis fly larvae (Hydroptychidae) stridulate during fights over retreats used for shelter and feeding. The sounds produced and the cephalic files used to produce them have a measurable effect on the ability to win fights (Jansson and Vuoristo, 1979). The scraping "hunger signals" of some larval social wasps (Vespinae) (Ishay and Brown, 1975) and the stridulations of larval passalid beetles (Schuster and Schuster, 1971; Reyes-Castillo and Jarman, 1980) may affect the attention given them by attending adults (adult passalids feed early instar larvae and aid in construction of the pupal cocoon) (Schuster and Schuster, 1971). If so, larval sounds would represent a kind of competitive communication affecting or directing the care bestowed on larvae by adults.

D. Male-Male Threat and Territorial Signals

Elaborate courtship displays are familiar to most entomologists, but the extent to which *fighting* can be ritualized—an exchange of aggressive signals rather than a physical contest based on force—is less familiar.

Crickets and other acoustical Orthoptera often have aggressive songs differing

from those used in close-range courtship and distance calling (Alexander, 1961; Boake, 1983). Dragonflies, primarily visually signalling insects, have specialized male-male threat interactions using different movements and markings than those displayed during courtship. The conspicuous white dorsal surface of the abdomen of the dragonfly *Plathemis lydia* is raised and lowered in "duels" between males, and males with the abdomen painted black are less successful in aggressive displays (Jacobs, 1955). The male abdomen is also used in aggressive displays in *Pachydiplax longipennis* and in *Libellula* species (Libellulidae) (Robey, 1975; Campanella, 1975) (Fig. 1). As noted by Wynne-Edwards (1962), the threat-display colouration of dragonflies is bird-like in that some species have adult colour phases, with young males resembling the drab females in colour, e.g. in *Plathemis lydia* (Jacobs, 1955), *Orthetrum albistylum speciosum* (Itô, 1980) and *Argia moesta* (Borrer, 1934). The immature colouration may be an antipredator (camouflage) device, but could also perhaps be a means of avoiding the potentially dangerous attacks of hyperaggressive older males, a major source of mortality in mature males (Corbet, 1962).

A dragonfly-like hovering "stripes display" is described by Pagden (1958) and Turillazzi (1983) in males of some Indonesian social wasps (Stenogastrinae). If one of the opponents does not leave following a brief threat, the display escalates into an ascending tandem flight with sudden reversals of position (alternating display by first one male, then the other), culminating in physical clashes in the air (Turillazzi, 1983).

Territorial male speckled wood butterflies (*Parage aegeria*) repeatedly engage in elaborate upward spiralling flights until one of the contestants withdraws (Davies, 1978). Males of many other butterflies engage in fighting at mating sites (reviewed by Thornhill and Alcock, 1983). The brightly coloured wings of male butterflies probably function in male-male aggressive interactions rather than in courtship as believed by Darwin (1871) (see Silberglied, 1984).

Like courtship (see below), the ritualized aggressive communication of males can be bizarre and complex, as well as beautiful. Some tephritid flies (*Phytalmia* species) have outlandish lateral head projections, long noticed by naturalists

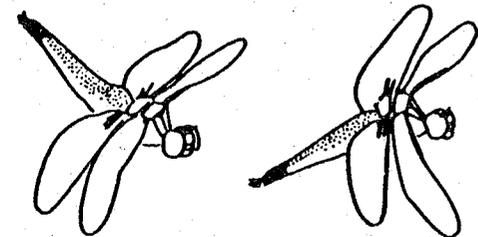


Fig. 1. Territorial display of male dragonflies (*Pachydiplax longipennis*). (From Robey, 1975.)

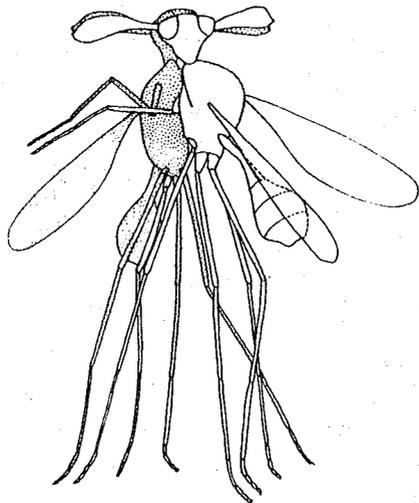


Fig. 2. Male-male aggressive display of a tephritid fly (*Phytalmia mouldsi* McAlpine). (After Moulds, 1977.)

(e.g. Wallace, 1869) because of their spectacular appearance (Fig. 2). It was difficult to imagine a function for these structures until Moulds (1977) observed their use in ritualized battles between territorial males. Similar eyestalks in seven other families of Diptera (McAlpine, 1979) probably also function in ritualized male combat, as indicated by observations of threat displays (sparring with forelegs with heads together) in *Achias australis* (Platystomatidae) (McAlpine, 1979). Males of some Hawaiian *Drosophila* also display head-to-head in the climax of "upright fighting" at mating sites (Spieth, 1974).

The large and often ornately curved and toothed forceps of earwigs—another long-unexplained exaggerated specialization of males—also function in some species in ritualized male-male interactions. The males of a Costa Rican species of *Doru* perform intricate tactile duels in which the forceps of opponents are rapidly and deliberately vibrated and tapped against each other. Only in very intense escalated interactions do males of this species engage in physical fighting, a brisk pushing at each other with a relatively small and simple sharp protuberance at the tip of the abdomen between the forceps (D. Briceño, unpublished) (Fig. 3).

E. Courtship

Courtship has not always been considered a "competitive" interaction. Many prominent authors (e.g. Huxley, 1938; Tinbergen, 1953; Wynne-Edwards, 1962; Mayr, 1972) have emphasized the "epigamic", or mate-locating and syn-

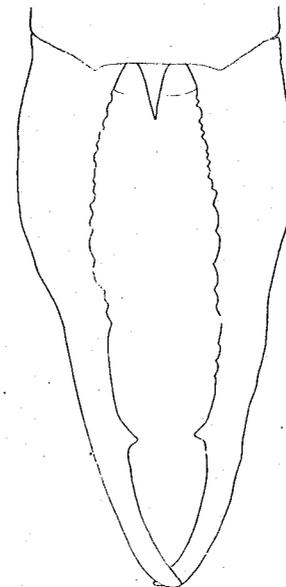


Fig. 3. Forceps of male earwig (*Doru* sp.) used in ritualized aggressive tapping displays among males. (Courtesy of D. Briceño.)

chronizing (co-operative), functions of courtship, its importance for efficiency in propagating the species and its role in species recognition. Two kinds of research, however, have yielded compelling reasons for considering courtship as a kind of competitive communication.

1. Studies of insect mating systems. Many aspects of insect mating systems fit the predictions of sexual selection theory, which views male (and, in exceptional cases, female) courtship as a form of intraspecific competition for mates (see Section III,G; Alexander, 1975; Lloyd, 1979, 1980, 1981; Blum and Blum, 1979; Gwynne and Morris, 1983; and a recent extensive review in Thornhill and Alcock, 1983).
2. Behavioural observations. It is often clear from experiments or from watching the behaviour of mating pairs that particular aspects of courtship signals produced by the male alter the behaviour of the female in ways likely or known to increase the male's success in mating relative to that of competitors. Female response is known to be influenced by the nature of courtship sounds in *Drosophila* (Ewing and Bennet-Clark, 1968), by pulse rate in crickets (Pollock and Hoy, 1979), by the size of the nuptial gift in scorpionflies (Thornhill, 1977), by the width of the antennal scape in soldier beetles (Mason, 1980), by song loudness in mole crickets (Forrest, 1983) and by dominance-associated odour in cockroaches (Breed *et al.*, 1980). Ewing (1961) experimentally demonstrated the competitive nature

of a courtship display by observing the behaviour of small *D. melanogaster* males in different social situations. In the company of large (competitively superior) individuals, males facultatively increased the amount of receptivity-increasing wing vibration in their courtship display compared to that performed in the absence of competitors. [Later research has shown that the sounds produced during wing vibration are critical determinants of female choice, females preferring larger males on the basis of their "songs" (Ewing and Bennett-Clark, 1968)].

Perhaps the principal barrier to considering insect courtship as an aspect of male competition for mates is the implied acceptance of the idea of "female choice". The concept of female choice met with vigorous objections (see especially Wallace, 1878) as soon as it was proposed by Darwin as an aspect of sexual selection. Darwin's discussion was perhaps unfortunate in its anthropomorphic tone. He referred to an "aesthetic sense" of females, and the ability of males to "charm" females. And he emphasized examples in birds and mammals in the belief that it would prove more common in animals having "higher faculties". The concept of female choice might have gained wider and more prompt acceptance had it been called from the outset "differential female responsiveness to different male-produced stimuli". Defined in this way and given the observations just described, it is clear that "female choice" occurs in insects. Indeed, any behaviour, morphology or secretion of males having a stimulatory or "synchronizing" effect on females is subject to "female choice" and is potentially competitive in function.

A prerequisite for sexual selection and female choice is the presence of sufficient detectable variation in male signals to make discrimination possible. In spite of the presumed stereotypy of sexual signals in insects (Templeton, 1979), numerous studies show considerable variation in courtship and calling signals, including the species-specific elements known or supposed to function in species recognition (for examples, see Alexander, 1960 on Orthoptera and cicadas; Claridge and Reynolds 1973, on *Oncopsis* species (Homoptera: Cicadellidae); Greenfield and Shaw, 1983 on the effects of individual signal differences on mating success in chorusing species). Courtship stereotypy may be largely a myth arising from the assumption of a species recognition function (see Section V) and a consequent tendency to emphasize the invariable, rather than the variable, aspects of courtship.

Female choice in nature may often involve simply mating with the winners of contests among males (for documented examples, see Boake, 1983; Burk, 1983; Thornhill and Alcock, 1983). The great importance of male—male combat as a means of mate screening prior to courtship cannot be overemphasized, especially in interpreting the results of laboratory studies in which there is usually no opportunity for this to occur. In some pilot experiments with *D. silvestris*

(Spiess, 1982), two males were put into mating chambers and allowed to interact prior to introduction of a female. However, only winners were used in mate preference tests when it was found that losers hardly achieved any matings. Then females failed to show any preference among winners. This is as one would expect in "passive" female choice (Lloyd, 1979) via male combat. Similarly, in the chalcid wasp *Nasonia vitripennis*, females invariably mate with winners of fierce battles among males; and both male courtship and female response are unusually stereotyped, with courting males always successful unless experimentally interrupted (van den Assem, 1980; van den Assem and Jachmann, 1982).

The ultimate function of competitive courtship is to increase mating success, i.e. the success of the gametes of the courting male in uniting with those of the courted female to form zygotes. It is necessary to define mating success in terms of zygote formation because research on insect reproduction has shown that copulation does not necessarily mean that insemination (sperm transfer) has occurred (Manning, 1962; Matthews, 1975), and even insemination may be followed by differential success in fertilizing zygotes (reviewed by W. Walker, 1980; see also Wade and Arnold, 1980). Competitive courtship communication should thus be thought of as including all signals or stimuli enhancing male mating (zygote fertilization) success in relation to that of competing signallers. It should therefore include sexual calling in species (such as crickets) in which calling is known to be competitive in the sense of affecting the mate-attraction success of different individuals (Forrest, 1983), courtship in the narrow sense (short-range precopulatory signals and displays) and, as argued below (after Eberhard, 1985b), genitalic stimuli affecting female receptivity, insemination and fertilization.

F. Male External Genitalia as Competitive Signalling Devices

Courtship displays often continue during copulation (Alcock, 1976; Burk, 1981; Bennet-Clark *et al.*, 1980; McAlpine, 1973; Batra, 1978; Ewing, 1983). This raises the question of the possible use of male genitalia to stimulate females internally. If genitalic stimulation occurs and if it affects the success of males in fertilizing zygotes, then the genitalia would have to be regarded as competitive signalling devices subject to sexual selection. Numerous observations suggest that mate stimulation is indeed one important function of male genitalia (after Eberhard, 1985b).

1. Use of Genitalia Suggesting a Stimulation Function

In a few cases it has been possible to observe courtship-like use of genitalia on the outside surface of the female. Alexander (1959) observed rapid and rhythmic

tapping of the tip of the female's abdomen by the parameres of the male's genitalia just prior to copulation in the carabid beetle *Pasimachus punctulatus*. In other beetles (*Meloe* species) the genitalia are tapped or rubbed on the female abdomen (Pinto and Selander, 1970). Spines and teeth on the valves of the male genitalia in the lepidopteran genus *Erebia* are used not to hold the female, but to rub the female's abdomen during copulation (Lorkovic, 1952). Similar use of the valves occurs in other lepidopterans (see Scott, 1978, on the nymphalid *Limenitis*). Tapping or rubbing with the male genitalia near the female genital orifice prior to intromission is known in several species, including beetles [e.g. *Tenebrio obscurus* (Wojcik, 1969)], wasps [*Ancistrocerus antilope* and *Parancistrocerus pennsylvanicus* (D. Cowan, unpublished)], ants (Hölldobler, 1976) and a fly [*Hylemya* species (Swales, 1961)].

Of course one of the difficulties of demonstrating the signalling or stimulatory function of male genitalia is that one cannot usually watch them in action. It is therefore of interest to describe the genitalic movements performed by a lightly anaesthetized male wasp, *Parachartergus apicalis*, observed in the laboratory with a stereomicroscope. The living genitalia performed movements of startling complexity. The aedeagus, which looks rigid and stalk-like in dead specimens, proved flexible and capable of both side-to-side waving and 180° rotation on its long axis, making the slightly bulbous tip face either the right or the left. Each of two highly manipulable, finger-like lateral digiti can move independently of each other and of the aedeagus; when one digitus is touched with a pin both move reflexly ventrad, while the aedeagus moves dorsad, sometimes rotating while in the raised (dorsal) position. These are the most fluid and subtly modulated movements I have ever observed in wasps; all other structures, including mouthparts and antennae, are capable of only relatively restricted movements by virtue of their segmentation and hinge-like articulations. Thus the finger-like movements of the genitalia were unusual and unexpected. The vision of wasp genitalia as rigid insertion devices is clearly inadequate. This maneuverability is consistent with (though not proving) a stimulation-function hypothesis, and raises the possibility that even when genitalia appear to be morphologically uniform in a population there may be important variation in how they are moved.

2. Effects of Male Activities during Copulation on Success of Zygote Fertilization

In species with internal fertilization (all organisms with external genitalia, and all insects) fertilization itself usually (perhaps always) occurs some time after copulation is over, and frequently following copulation with more than one male. There is evidence that female insects can exercise "choice" during multiple copulations, and that it is influenced by events during courtship and copulation. For example, in Scorpionflies (*Panorpa* spp.) whether or not copulation results in insemination depends on the length of copulation, which in turn depends on

the size of a nuptial gift offered by the male during courtship (Thornhill, 1976). Copulation without insemination occurs in various other insects, as already mentioned. Females can inhibit the transfer of sperm to the spermatheca (see W. Walker, 1980) and can affect the pattern of sperm precedence (reviewed in Thornhill and Alcock, 1983). Furthermore, stimuli received during copulation are known to modify the speed and number of oocytes matured and the likelihood and rate of oviposition (Englemann, 1970). [For a valuable review of the physiological effects of mating in insects see Manning (1967).] These facts mean that genitalic stimulation is not too late in the mating process to affect the mating success of males.

3. Simplicity of Male Genitalia in Species with Reduced Competition for Mates

Species in which sexual selection (competition for mates) is absent or relaxed (e.g. whose females copulate with only one male, such as termites, or which are highly inbred and therefore not highly competitive, such as some parasitic wasps) have unusually simple genitalia (Eberhard, 1985b).

In conclusion, it would be surprising *not* to find that internal (genitalic) courtship stimulation is a factor affecting the evolution of insect genitalia, given the complexity of male genitalia in so many groups, the observed ability of males to move the genitalia, the importance of courtship stimulation in mating success and the continuance of effective courtship signalling during copulation.

G. Female Sexual Calling: Is It Competitive?

Basic to the evolution of insect mating behaviour is the inherent asymmetry of reproductive roles between the two sexes. Individual females invest more in gametes and produce relatively few of them; males produce large numbers of less costly gametes and engage in correspondingly stronger competition with each other to fertilize as many eggs as possible. As a result, it is usually the male sex that is more pugnacious during the breeding season, more active in courtship signalling and the possessor of more specialized behaviour and morphology (signalling and grasping devices and elaborate external genitalia) used in mating (Darwin, 1871; Alexander and Borgia, 1979; Eberhard, 1985b). Many features of insect courtship communication are consistent with this pattern of sexual asymmetry. Males usually take the more active, costly and competitive signal or response role. They not only are more active producers of signals, but also show the greater development of mate-sensing and searching devices (e.g. antennae, eyes, in accord with the type of stimuli provided by females) (reviewed by Thornhill and Alcock, 1983). When sexual calling is relatively inexpensive in terms of energy expenditure and risk of predation (e.g. pheromonal) compared to the energetic cost and risk of searching, it is the female that calls and the male

that searches (see reviews in Shorey, 1973; Jacobson, 1972). On the other hand, in crickets, whose calling is known to be energetically expensive (Prestwich and Walker, 1981) and to subject males to increased predation (Cade, 1975), the males call and the females respond. Sex-role reversals, with increased potential investment by males, are often accompanied by signalling role reversals, with males adopting a less costly (and females a more competitive) role. Examples include the pine-dwelling bark beetles (*Ips* species) and the sugarcane scarab *Podischnus agenor*, in which the male excavates a nuptial chamber (Barr, 1969; Eberhard, 1979); Orthoptera producing large nutrient spermatophores (Gwynne, 1981, 1983); termites in which males take the lead in excavating a burrow prior to mating (Leuthold, 1977); and scorpionflies with male nuptial gifts (Bornemissza, 1966a; Thornhill, 1979).

It is not clear to what degree the sexual calling of females, so common in insects (Thornhill and Alcock, 1983), should be considered competitive in nature. Often "calling" is a by-product of female activities (e.g. a secretion associated with reproductive maturity, or attacked host) that has probably become a "signal" primarily by virtue of selection on males to detect it. While females might be unable to mate without calling, variations in the calling ability of females are not known to differentially affect the mating success of females in the same way they do in males. That is, it is not certain to what degree females engage in calling contests with other females. Possible causes of evolutionary change in female calling signals include (1) species recognition (see Waage, 1979, and below), (2) the protective advantage of facilitating sex recognition in species (like dragonflies) in which males are hyperaggressive and capable of harming or killing conspecifics (Corbet, 1962), (3) the advantage of attracting more than one male, allowing comparison of potential mates (female choice) and (4) mutual sexual selection, in which due to some kind of parental investment by males, females as well as males compete via competitive signalling for mates. Only the last two are "competitive" causes.

H. Behavioural Observations and Evolutionary Interpretations

The importance of actually observing a structure in use in order to determine its function cannot be overemphasized. Darwin was handicapped in his discussion of the competitive functions of sexually dimorphic characters by the paucity of behavioural studies available to complement detailed knowledge of insect morphology. For example, he mistakenly concluded on the basis of their appearance that the enormous and elaborate horns of male beetles must be used in displays and are products of female choice, whereas recent research has shown them in every well-studied case to be used only in male combat in ways illuminating the details of their structure (Eberhard, 1977, 1979, 1981). Darwin

(1871, p. 626) included a figure showing the male of a *Crabro* wasp (Hymenoptera, Sphecidae) whose front tarsus is "dilated into a broad horny plate, with minute membraneous dots, giving to it a singular appearance like that of a riddle", or sieve (see Fig. 4). This was listed among examples of devices used to hold females during mating, an interpretation based on morphological appearance and followed by subsequent authors (e.g. Richards, 1927). A recent observation of *C. argusinus* revealed that during mating the male places these shields over the eyes of the female in such a way that the distinctively patterned transparencies of the shield could transmit a specialized light signal to the female

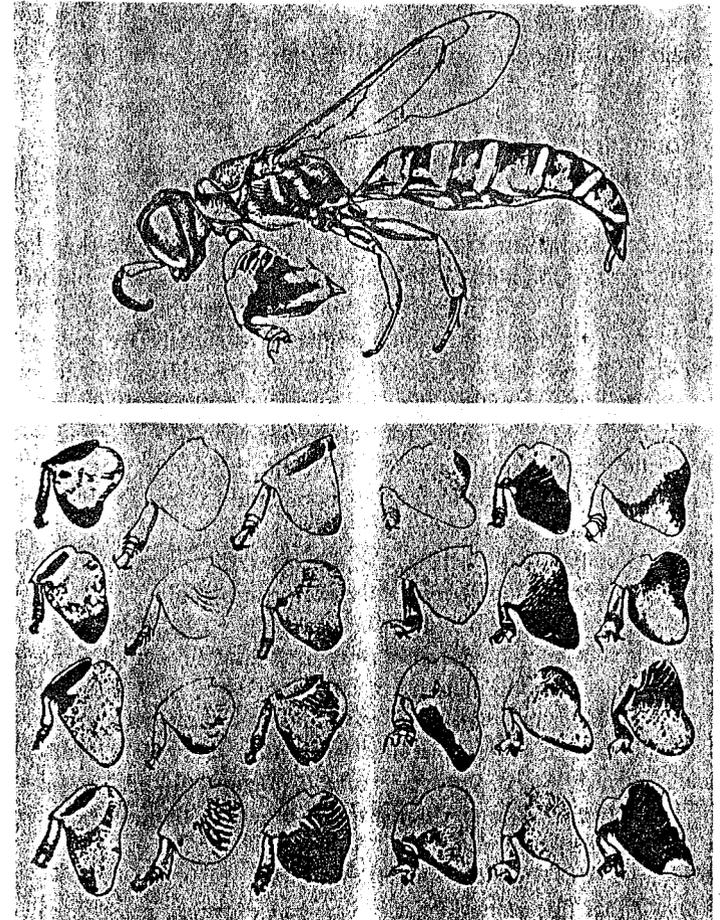


Fig. 4. (Above) Male *Crabro latipes*, showing tibial shields. (After Bohart and Menke, 1976.) (Below) Species specificity of variation in male tibial shields in 24 *Crabro* species. (After Bohart, 1976.)

(Matthews *et al.*, 1979). Although males also display these structures by holding them conspicuously out to the side when perched on vegetation (L. Kimsey, personal communication), it seems likely from their transparencies and the precision of their correspondence to the shape of the eye (H. E. Evans, personal communication) that the courtship function has been fundamental in determining the details of their form (Fig. 4). Many other devices long assumed to be levers, clamps or graspers used in mating or fighting prove on closer observation to have a signalling function. The superior anal "clasping" appendages of male damselflies (*Enallagma* species) are such an example (Robertson and Paterson, 1982). The well-developed parameres of certain carabid beetles, thought on the basis of structure and location to be "pries", are used to tap the tip of the female's abdomen until she opens the genital aperture (Alexander, 1959).

IV. SPECIES SPECIFICITY IN THE COMPETITIVE DISPLAYS OF INSECTS

The theoretical considerations summarized in Section II suggest that intra-specific signalling competition is likely to cause rapid and divergent evolution of competitive signals. One way to investigate whether or not this expectation is fulfilled is to examine the degree to which competitive signals are species or subspecies specific. Since closely related species (e.g. members of the same genus) and geographic isolates within species have been reproductively isolated relatively recently, the species-specific (or subspecies-specific) characters distinguishing them must be of relatively recent origin, evidence that they are subject to relatively rapid evolutionary change compared to the more "conservative" traits characterizing genera or higher taxa.

The competitive signals just described, and the specialized morphology used to produce them, are in fact often species specific in form (Tables I-III; Figs 4 and 5). This has long been recognized in the case of courtship. Mayr (1963) discusses some of the best known examples of species-specific sexual signalling in insects, including the courtship displays of *Drosophila* and the calling signals of fireflies, crickets, cicadas and moths. Some additional examples are listed in Table I. This is only a meagre sample illustrating this very widespread phenomenon; indeed, Mayr (1963, p. 95) went so far as to suppose that "the males of every species have specific courtships or displays to which, on the whole, only females of the same species are receptive."

Observation of insects (Tables II and III) and other organisms (West-Eberhard, 1983) indicate that this statement could be made even more general, to read: "The members of every species having strong social competition (for any resource) involving competitive communication are likely to have species-specific

TABLE I. Species Specificity in Insect Courtship Signals*

Taxon	Species-specific character	Function
Odonata		
Coenagrionidae		
<i>Enallagma</i>	Male superior anal appendages (Robertson and Paterson, 1982)	Stimulates head, thorax of mounted female (Robertson and Paterson, 1982)
Orthoptera		
Blattidae		
<i>Blattella</i>	Male tergal glands (Roth, 1969)	Exposed to, contacted by mounted female (Roth, 1969)
Coleoptera		
Meloidae		
<i>Meloe</i>	Male antennae (Pinto and Selander, 1970)	Touch female antennae during mounting (Pinto and Selander, 1970)
<i>Pyrota</i>	Male antennae, maxillary palps, legs I (Denier, 1934)	Touch female antennae, elytra, legs III during mounting (Selander, 1964)
<i>Epicauta</i> spp.:	Courtship behaviour:	Moved against courted female
group a	antennae	Moved against courted female
group b	maxillary palps	(Selander and Mathieu, 1969; Pinto, 1980)
Carabidae	Number, arrangement of bristles on male genitalic parameres (Banninger, 1950)	Tap female during courtship (Alexander, 1959)
Hemiptera		
Gerridae		
<i>Rheumatobates</i>	Antennae, legs II (Matsuda, 1960; Hungerford, 1954)	Contact female antennae, body during courtship (Silvey, 1931)
Cicadellidae		
<i>Oncopsis</i>	Form of song (Claridge and Reynolds, 1973)	Close-range courtship

(continued)

TABLE 1. (Continued)

Taxon	Species-specific character	Function
Neuroptera		
Chrysopidae		
<i>Meloe</i>	Frontal horns and associated cavity (Tauber, 1969)	Female "licks" glandular products (Tauber, 1969)
Lepidoptera		
Nymphalidae		
<i>Danaus</i> spp.	Hairpencil pheromones (Myers, 1972)	Aphrodisiac (Roelofs and Cardé, 1974)
Diptera		
Drosophilidae		
<i>Zaprionus</i>	Pulse period, male song (Bennet-Clark <i>et al.</i> , 1980)	Courtship (Bennet-Clark <i>et al.</i> , 1980)
<i>Drosophila</i>	Sounds produced by wing vibrations (Ewing and Bennet-Clark, 1968)	Courtship display (Ewing and Bennet-Clark, 1968)
<i>Drosophila</i> (Hawaiian)	Male antennae, mouthparts, head shape and setal pattern; forelegs, wing markings, body colors (Spieth, 1974)	Courtship displays (Spieth, 1974)
Platystomatidae		
<i>Euprospia</i>	Structure of hind trochanter; color of male fore tarsi (McAlpine, 1973)	Rubbed on female abdomen; waved before female eyes (McAlpine, 1973)
Chloropidae		
<i>Lipara</i>	Substrate-vibrating pattern of male (Chvala <i>et al.</i> , 1974)	Stimulates female to answer (Chvala <i>et al.</i> , 1974)
Muscidae		
<i>Musca</i>	Rapid movements (Tobin and Stoffolano, 1973)	Courtship (Tobin and Stoffolano, 1973)
Hymenoptera		
Megachilidae		
<i>Megachila</i>	Modified male forelegs (G. C. Fickwort, personal communication)	Rubbed over female eyes by mounted male (Batra, 1978)
Sphécididae		
<i>Crabro</i>	Shape, adornment, male fore tibia (Bohart, 1976)	Rubbed over female eyes by mounted male (Matthews <i>et al.</i> , 1979)
Vespidae		
<i>Belonogaster</i>	Male antennae (Richards, 1982)	Used to vibrate, lift female antennae by mounted male (Marino and Pardi, 1970)
Chalcidae		
<i>Melittobia</i>	Male antennae (Evans and Matthews, 1976)	Manipulate female antennae during mounting (Evans and Matthews, 1976)
Apidae		
<i>Bombus</i>	Composition, labial gland pheromones of males (Bergström <i>et al.</i> , 1981)	Female attractant, aphrodisiac (Bergström <i>et al.</i> , 1981)
Formicidae		
<i>Camponotus</i>	Proportion of substance in male mandibular pheromones (Blum, 1981)	Stimulates female to join mating flight (Hölldobler and Maschwitz, 1965)

*For additional examples see Mayr (1963).

ic competitive displays." That is, the species specificity shown in courtship extends to other kinds of competitive displays.

Tables II and III list examples illustrating species specificity in non-sexual competitive signals and in sexual displays other than courtship. In some cases the species distinctiveness of displays was revealed by comparative behaviour studies. In other cases morphological characters known on the basis of behavioural observations to function in competitive communication are used as diagnostic or "key" characters in species-level taxonomy or show geographic variation within species. In all cases the data cited in the tables were collected "blind". That is, the authors cited were unaware of an expected association between competitive function and species specificity when they published their conclusions.

Eberhard (1985b) documents the widespread species specificity of male genitalia, a phenomenon well known to entomologists. Examples include representatives of virtually all insect orders, except the Isoptera (perhaps due to a relative lack of mating competition in these monogamous insects). Even more to the point as far as the stimulation hypothesis of genitalic function is concerned is the fact that the particular parts of genitalia described above as being moved, or used in courtship stimulation of the female, are those distinctively modified (species specific) in closely related species (see Banninger, 1950, on the carabids observed by Alexander; Lorkovic, 1952, on *Erebia*; Burns, 1970, on the hesperiids observed by Scott; Platt *et al.*, 1970, on *Limenitis*; Pinto and Selander, 1970, on *Meloe*; and Richards, 1978, on *Chartergellus*, formerly synonymous with *Parachartergus*) (Fig. 5).

Rates of evolutionary change in signals are expected to reflect the strength of selection on (reproductive variance associated with) particular signals or signal elements. Thus the most rapidly evolving species- or subspecies-specific signals and signal morphology should be those expressed in the most strongly competitive situations, or those most importantly affecting differential access to contested resources.

It is therefore not surprising that the most complex and species-specific sexual signals usually occur in males, rather than in the usually less sexually competitive females. Silberglied (1977), in reviewing chemical communication in the Lepidoptera, concluded (p. 376) that "the most interesting feature of these pheromones is the contrast between the low chemical diversity of female-produced sex pheromones and the high chemical diversity of the pheromones produced by males." In chloropid flies of the genus *Lipara*, male calls (vibrations of grass stems where females oviposit) are species specific, whereas female answering vibrations are not (Chvala *et al.*, 1974). And in delphacid planthoppers (*Muellerianella* spp.), male calling songs are clearly species specific, whereas female signals are less so (Booij, 1982). This pattern is explicable and predicted by the sexual selection hypothesis: the stronger sexual competition among males compared to females should lead to more rapid divergence of their signals.

TABLE II. Species-specific and/or Geographic Variation in Male-Male Aggressive Signals or Display Morphology in Insects

Taxon	Species-specific or geographically variable character	Function
Odonata Libellulidae <i>Libellula</i> spp.	Wing, abdomen markings (Silberglied, 1979)	Aggressive male wing and abdomen flicking (Campanella, 1975)
Agridae <i>Heteretina</i>	Geographically variable wing markings (Johnson, 1961)	Wing display flights (Johnson, 1961)
Calopterigidae <i>Calopteryx</i> spp.	Wing movements, markings (Bick and Bick, 1971; Johnson, 1961)	Wing clapping (Bick and Bick, 1971)
Orthoptera Oedipodinae	Brightly colored male underwings and flight behavior (Alexander, 1960)	Crepitating aggressive flights of males (Alexander, 1960)
Gryllidae Dermaptera Forficulidae <i>Doru</i> spp.	Form of song (Alexander, 1960)	Aggressive threat (Alexander, 1961)
Diptera Tephritidae <i>Phytalmia</i>	Form of male abdominal forceps (Brindle, 1971)	Tapping threat displays towards other males (D. Briceño, personal communication) (see text)
Hymenoptera Stenogastridae	Male lateral head projections (McAlpine and Schneider, 1978)	Male heads pressed together during ritualized combat (Moulds, 1977)
	Colour patterns on male gaster tergites 4-6 (van der Vecht, 1977)	Hovering "stripes display" (van der Vecht, 1977; Turillazzi, 1983)

TABLE III. Species Specificity and Geographic Variation in Non-sexual Competitive Signals

Taxon	Species-specific character	Function
Orthoptera Melanoplinae	Colours of hind tibiae, both sexes (Cohn and Cantrali, 1974, on <i>Baryvertix</i>)	Hindleg shaking and raising in aggressive displays, both sexes (Otte, 1970; many genera)
Trichoptera Hydropsychidae	Cephalic files of larvae: sounds of larvae (Jansson and Vuoristo, 1979)	Aggressive stridulation (Jansson and Vuoristo, 1979)
Diptera Tephritidae	Wing markings, both sexes (Freidberg, 1974, many genera)	Both sexes perform aggressive wing waving (Prokopy and Bush, 1973, on <i>Ragoletis</i> ; Burk, 1981, on <i>Anastrepha suspensa</i>)
Hymenoptera Vespidae <i>Polistes</i>	Displays of females within colonies (West-Eberhard, 1982)	Establishment of trophic and reproductive dominance (West-Eberhard, 1981, 1982)
Apidae <i>Apis</i>	Composition of queen mandibular gland secretions (Crewe, 1982)	Establishment of reproductive dominance within colonies (Velthuis, 1977a,b)
Meliponini	Oviposition rituals of queens and workers (Sakagami, 1982)	Maintenance of dominance within colonies (Sakagami, 1982)

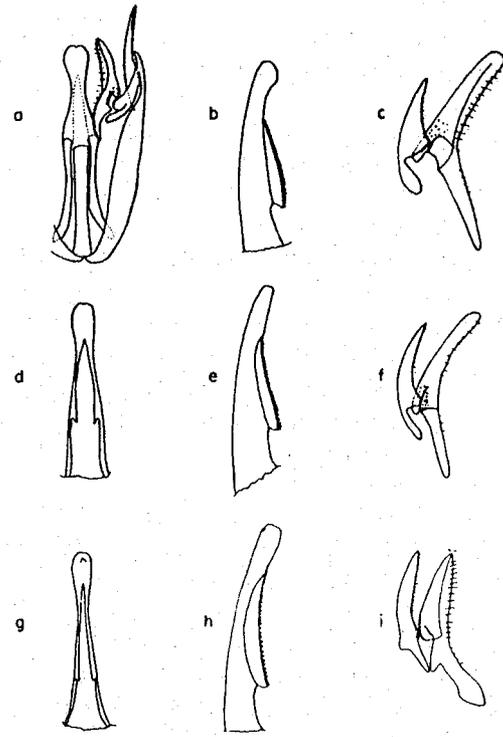


Fig. 5. Species-specific variation in movable parts of male genitalia in *Chartergellus* (Hymenoptera, Vespidae). (a-c) *C. communis*. (a) Dorsal view; (b) aedeagus from left; (c) volsella enlarged. (d-f) *C. atectus*. (d) aedeagus, ventral view; (e) aedeagus from left; (f) volsella. (g-i) *C. punctator*. (g) aedeagus, ventral view; (h) aedeagus from left; (i) volsella. Granulate areas (stippled) of cuspis are moved against those of digitus (volsella). (After Richards, 1978.)

As a consequence of this asymmetry in sexual competition, reproductive character displacement may prove more common in female than in male sexual signals. Because they are more weakly sexually selected, female sexual signals should diverge more slowly and are therefore more likely than are male signals to be similar in recently overlapped diverging populations. This would leave room for the occurrence of character displacement in females under selection for species recognition; and it may explain why one of the few carefully documented examples of reproductive character displacement in insects, that in the damselflies of the genus *Calopteryx* (Waage, 1975, 1979), involves a signal produced by *females*. As pointed out by Walker (1974), one possible cause of the paucity of examples of reproductive character displacement may be that rapid divergence of (male) sexual signals usually precedes contact of diverging populations.

Different degrees of social selection may also help to explain different rates of evolution (degrees of species specificity) of different elements of a species signal repertoire. For example, closely related species of bark beetles (*Ips*) show marked cross-attraction to the male calling pheromones which seem to correspond to close chemical resemblances of the signal (weak species specificity) (Lanier and Burkholder, 1974). This would seem to contradict the expectation of rapid divergence in male sexual signals. However, the strongest competition during sexual interaction in many of these beetles (especially the pine-inhabiting species) may be not among calling males (whose signals attract both males and females to the host tree and may be more synergistic than competitive when several males are in the same region), but among females, who push to gain entrance to the male burrow and are accepted in only a limited number per male (Barr, 1969). In keeping with this interpretation, the female sounds and stridulatory apparatus are clearly species specific even when closely related species are compared (Barr, 1969; Lanier, 1970).

It is important to clarify that by "species specificity" I mean distinctiveness of the signal repertoire. Closely related species often share signal elements, and consequently react to some degree to each other's signals. For example, it could be said that honeybee queen substance is not "species specific" in that a principal active component, 9-oxo-2-decenoic acid (9-ODA), has been found in several *Apis* species, and drones of a given species react to the queen pheromones of the others. However, in *A. mellifera*, queen dominance involves at least five other mandibular gland substances (Crewe and Velthuis, 1980) whose proportions show subspecies differences, as well as other chemical, tactile and acoustical signals (see Velthuis, 1977a; Korst and Velthuis, 1982). It is this set of characters (the signal repertoire in a particular competitive context) which should show species specificity and unusual complexity indicating rapid and continued evolution under strong social selection. The presumption that signal variants are evolved implies that they are differentially responded to. Although experimental studies confirm this for some examples (see Section III,E), in many cases detailed response data are not available. One could therefore argue that the signal differences noted could be functionless noise or pleiotropic effects of genes selected in other contexts. To be considered of general importance this interpretation would require explaining how traits known to be subject to unusually strong selection could at the same time be unusually subject to pleiotropic effects. It seems more reasonable, given present information, to hypothesize that most though probably not all species signals have been elaborated in the social contexts in which they are known to be used.

Species specificity, e.g. of nest structure or camouflage colouration, may obviously evolve in contexts other than social competition, especially when strong or persistent selection (e.g. by a coevolving predator) is evolved. The examples given in the tables are an illustrative sample intended simply to show

that in a wide variety of insects species-specific signals have evolved in all of the several kinds of sexual and non-sexual competitive contexts discussed above. This suggests that social competition per se is an important context in which insect communication evolves rapidly and divergently.

V. THE SPECIES RECOGNITION HYPOTHESIS

Biologists often assume that species-specific courtship functions primarily in species recognition—that signal divergence evolves to prevent wasteful interaction and promote reproductive isolation of related species in zones of overlap.

Species recognition is one context in which courtship signals can conceivably evolve. However, many entomologists have expressed doubt that species recognition is the primary basis for divergence in the sexual signals of insects. Their evidence is of several kinds (see also West-Eberhard, 1983).

A. Signal Divergence without Geographic Overlap

Sexual signal divergence can occur without geographic overlap with other closely related or similarly signalling species. For example, divergent courtship characters occur in allopatric sibling populations of *Drosophila hemifera*, *D. paenehamifera* and *D. varipennis*, isolated on different mountaintops on Maui Island (Spieth, 1974). Two species of Australian scorpionflies (*Harpobittacus*) known to have been allopatric since the Middle Cretaceous have divergent (species-specific) sex pheromones which serve as an effective barrier to cross-mating in the laboratory (Bornemissza, 1966b). The cricket *Anurogryllus arboreus*, a species not sympatric with any congeneric or potentially confusing species in any part of its range, nonetheless has a distinctive courtship song (Alexander, 1967).

B. Species Recognition Prior to Courtship

Species recognition frequently occurs prior to courtship or very early on, and therefore is not likely to explain distinctive or complex courtship signals. Examples of pre-courtship recognition include species having species-specific and/or complex courtship even though reproductively isolated from related species by (1) courting in different habitats, e.g. trypetid flies (Zwölfer, 1974), (2) mating at different non-overlapping times of day, e.g. *Leptothorax* ants (Plateaux, 1977), (3) mating at different times of year, e.g. *Leptothorax* and related ants (Buschinger, 1975), (4) a distinctive calling signal, e.g. fireflies (Lloyd, 1966) and moths (Roelofs and Comeau, 1969) or (5) very early elements in complex courtships, e.g. *Drosophila* (Manning, 1966) and grasshoppers [*Syrbula* (Otte, 1972) and *Myrmeleotettix* (Bull, 1979)]. Some closely related species (e.g. those

of the *Epicauta aldiba* group of meloid beetles) fail to court even when they meet, with males evidently not recognizing non-conspecific females as sexual objects (Pinto, 1980). Yet these species have distinctive, species-specific courtship displays (Pinto, 1980).

In some species having extraordinarily complex courtship displays, copulation frequently occurs without performance of the entire sequence. For example, Bull (1979) found that in the grasshopper *M. maculatus*, males often copulated with females after simply calling—the first step in a complex courtship whose complete performance involves femur vibration, accelerating body swaying, violent body shakes, tibial and antennal flicking, jerking, escalated (in rate and loudness) calling, ritualized abdomen exposure, stereotyped head turning accompanied by a co-ordinated call rhythm, ticking and femoral humming. Copulation after only a brief portion of a comparably complex display also occurs in the otitid fly *Physiphora demandata* (Alcock and Pyle, 1979) and grasshoppers of the genus *Syrbula* (Otte, 1972), leading those authors to question the adequacy of the species recognition hypothesis to explain the evolution of courtship in their groups.

C. Paucity of Examples of Reproductive Character Displacement

Reproductive character displacement appears to be rarer in insects than would be predicted by the species recognition hypothesis. If courtship divergence is primarily due to selection for species recognition, sexual signals should show "character displacement" and be more distinctive in areas of overlap and possible interaction with related species than in populations in non-overlapping (or allopatric) portions of a species' range. However, few such cases have been found, in spite of a determined search. In a review of evidence from acoustic insects, a group considered "ideal" for testing this hypothesis, "no convincing example of character displacement" was found (Walker, 1974, p. 1137; see also Booi, 1982).

Greater courtship differences in sympatric species pairs compared to those in allopatric species pairs is fairly common in insects and has often been taken to represent character displacement (Ehrman, 1965; Koref-Santibanez, 1972; Bailey, 1976; Claridge and Reynolds, 1973; Blum, 1981; Buschinger, 1975). However, as pointed out by Pinto (1980), the association of geographic overlap and courtship dissimilarity may simply mean that by the time isolated populations have spread and diverged ecologically enough to achieve sympatry their signals show marked divergence. In bark beetles (*Ips*) there are many sympatric species, but they usually represent different species groups within the genus. Species from the same species group are usually allopatric or parapatric (Lanier and Burkholder, 1974). Indeed, parapatric distributions (contiguous boundaries

with little geographic overlap) are common in animal groups showing rapid divergence under social selection (see West-Eberhard, 1983). Furthermore, it is quite common (though not universal) for the degree of divergence in social signals to be related to the taxonomic distance of the species concerned (Buschinger, 1975; Payne, 1974; Lanier and Burkholder, 1974; cf. Ewing and Bennett-Clark, 1968). This is consistent with Pinto's (above) interpretation of the significance of interspecific courtship differences, because it suggests that signal divergence is often roughly proportional to time since isolation rather than depending on some other variable, such as overlap with related species. As pointed out by Walker (1974), a proper test of the species recognition hypothesis using reproductive character displacement requires study of related species overlapping in a portion of their ranges while allopatric (non-overlapping) in another.

It is still not clear to what degree species recognition affects the evolution of courtship. However, it is at least possible to conclude that (1) selection for species recognition is not a satisfactory explanation for all of the observed complexity and diversity of sexual signals and (2) species recognition is a much less important factor in the evolution of insect communication than formerly believed.

VI. CONCLUSIONS

A. Significance of Species Specificity

It seems likely that sexual selection is a principal determinant of the species distinctiveness of competitive sexual signals, whether in allopatric or sympatric reproductively isolated populations. The use of competitive signals as species recognition cues, when it occurs, may often be a secondary function of characters diverged under sexual selection prior to contact.

Rapid signal evolution under social selection might play a key role in insect speciation, especially if it affects courtship (West-Eberhard, 1983). Extraordinarily rapid divergence in courtship signals has been documented by van den Assem and Povel (1973) in some pteromalid wasps (*Muscudifurax* spp.) parasitic on houseflies. Several distinct species, sympatric ones reproductively isolated by their courtship behaviour, have evolved in the Americas since their introduction by man, probably less than 500 years ago (van den Assem and Povel, 1973). These authors cite "founder principles" as a possible basis for this rapid evolution, but sexual selection has probably been important (alone or in addition), since courtship differences are more obvious than any morphological differences in these very closely related sibling species.

Rapid divergence in *non-sexual* signals could accelerate speciation by producing severe disruption in the social interactions of hybrids (West-Eberhard, 1983).

Plateaux (1977) may have discovered an example of this. Laboratory crosses of two closely related ant species (*Leptothorax parvulus* and *L. lichtensteini*) gave viable offspring and well-developed hybrid colonies. However, hybrid workers spent one-quarter to one-third of their time in fighting, and the sexuals they produced also fought with each other. Thus, the social behaviour of workers has perhaps diverged sufficiently in the two species for hybrids to show severely disrupted interactions. Such disrupted social communication might contribute to the origin or maintenance of barriers to interbreeding (speciation) if hybridization of such socially divergent populations were to occur in nature.

B. Maintenance of Sexual Selection

The ideas and observations presented in this review suggest that a current theoretical controversy regarding the maintenance of sexual selection is unnecessary. Many authors (Williams, 1975; Borgia, 1979; Maynard Smith, 1978; Hamilton and Zuk, 1982; Dominey, 1983) have discussed the "paradox" of sexual selection (female choice) in polygynous or "lek" breeding systems where males evidently contribute only genes to mate and offspring. Their concern is that strong sexual selection in such species should quickly drive favoured male traits to fixation, leaving little or no heritable variation to serve as a basis for genetically profitable female choice. Yet courtship evolution clearly proceeds in such species, producing some of the most striking and complex morphological and behavioural traits known in animals.

These discussions emphasize one special quality of sexual selection, namely its strength (high variance in the reproductive success of competing males), while disregarding others: perpetuity even in the absence of heritable variation and the potential for simultaneous evolution on several fronts, due in part to the complexity of female sensory-response repertoires potentially subject to manipulation by males. Furthermore, they mistakenly imply that there must be some advantage to females for sexual selection (female choice) to persist—that once heritable variance in a male signal is absent, females will no longer be selected to discriminate that trait, and the signal should eventually disappear along with the preference for it. However, as discussed above, competitive courtship by males would continue even in the complete or temporary absence of heritable variation in courtship signals, because it ultimately depends not on the existence of heritable differences, nor on the advantage to females of detecting them, but only on the opportunity for differential mating success of males. That opportunity persists as long as there is (1) a sex difference in parental investment and (2) some phenotypic variation in the mate-obtaining abilities of males.

Observations of insect behaviour support this solution to the "lek paradox", for they indicate that male courtship is best regarded not only as male propaganda (advertisement of quality), but also, and perhaps more fundamentally, as an

array of devices or gimmicks (tactile, visual, auditory, pheromonal) for manipulating the responses of females. The devices employed may involve material offerings or indicators of genetic superiority, but they need not do so. They may simply happen to induce certain established reactions in females—responses that may have originated and be maintained in other contexts, like the attraction of female bees to floral scents, capitalized on by the floral mimicry of male bee pheromones (see above). In anisogamous sexually reproducing species, particular complex and competitive courtship signals of this kind can be maintained indefinitely (and females will continue to respond to them), even without heritable variations, simply because (mutant) males failing to perform some element of courtship are at a disadvantage in stimulating females. And female responses that have originated in other contexts can continue to be maintained independent of sexual selection and female choice.

Thus selection can continue through episodes of low or even zero additive fitness variance, maintaining a ready framework for discrimination of harmful or favourable signal mutations as they arise. Relevant mutations (sources of heritable signal differences in the form of transient polymorphisms) may occur with higher frequency than heretofore appreciated, given the complexity of the female sensory-response repertoire and the numerous devices capable of manipulating it (discussed in Section II). These conditions mean that a large number of mutant forms have a chance of being favourably selected. Therefore, the maintenance of evolution via selection on transient polymorphisms (Maynard Smith, 1978) may be a realistic resolution of the heritability problem when combined with the realization (see above) that competition and selection can persist even when not affecting gene frequencies. The very rapidity of courtship evolution, amply documented here (see also West-Eberhard, 1983; Eberhard, 1985b) is evidence that transient genetic polymorphisms are common. Therefore the various theoretical reasons for expecting such rapid evolution (see above) likewise constitute a list of reasons for expecting a high level of heritability (transient polymorphism) in competitive communication.

The idea that evolutionary stagnation could occur as a result of gene fixation under strong selection may be an artefact of thinking in terms of oversimplified (e.g. single-locus) genetic models. Experimental studies of *Drosophila melanogaster* reveal that females use multiple criteria in screening mates (reviewed by Ewing, 1977), and the courtship of *D. melanogaster* is simple compared to that of many other insects (for examples, see Bull, 1979; Otte, 1972). Furthermore, females vary greatly in their degree of sexual receptiveness, with age, with time since last mating and for other, as yet unknown, reasons (Manning, 1967; Connolly and Cook, 1972; and Bull, 1979). In many species the courtship behavior of males may be most strongly selected in the context of bringing somewhat refractory females to a receptive state (Las, 1980), with different facultatively performed courtship elements (or combinations and repe-

tions of them) effective in different situations. This interpretation is supported by the observation that *Drosophila* males alter courtship in accord with female response (Willmund and Ewing, 1982) and "tend to increase their courtship when continuously rejected by recalcitrant females" (Spiess, 1982) and by the fact that in many insects copulation may occur at any point in courtship, without the necessity of male performance of an entire or repetitive sequence (Bull, 1979; Alcock and Pyle, 1979; Connolly and Cook, 1972; Las, 1980). So courtship occupies a complex adaptive landscape conducive to the generation of allelic polymorphisms on many fronts.

The overall picture of the evolution of competitive communication in insects is one of perpetual and sometimes rapid evolution, with frequent changes in the focus of selection. Even within genera, some species pairs or groups show species specificity in one element of a display, while others show interspecific diversity in another (see Claridge and Reynolds, 1973; Pinto, 1980), suggesting a recent change, or fluidity, in the degree of importance of different parts of the signal repertoire. This accords with the above interpretation of the evolution of competitive communication as a multifaceted, opportunistic and continuing process of changing focus in which the principal constant is competition, and hence change.

Emphasis here on the lack of *necessity* of screening for quality (of mates, or queens in social insects) in maintenance of social selection is not intended to deny that such screening is important (e.g. as suggested by Fisher, 1930; Hamilton and Zuk, 1982; Dominey, 1983; and others). Thornhill and Alcock (1983) review a multitude of ways in which female insects apparently test mate quality, including by size (as indicated by various signal parameters), quality of nuptial gifts and dominance in male-male interactions. It has also long been clear that the dominance interactions of wasps are a way in which next mates could screen for queen quality in the form of relative ovary development of potential queens (West, 1967), and since the dominance and "queen recognition" pheromones of various ants and bees also correlate with differences in ovary development (Section III,A), advantageous "worker choice" of queens may be common in social Hymenoptera (see West-Eberhard, 1983).

C. Runaway Selection and Genitalic Evolution

As soon as a competitive signal is established, whether as successful propaganda (initially linked to true quality) or simply a sensory trap (manipulation of female responses maintained in other contexts), there is an opportunity for runaway evolution based on signal value per se. Runaway selection of purely manipulative signals is particularly likely, because the signal is from the outset unlinked to any aspect of quality other than signalling ability itself. Selection for signal value per se will always tend to reduce the efficiency of selection for true quality.

Where is the best place to look for examples of runaway change in the competitive signals of insects? The answer may be in the evolution of male genitalia. Genitalia are not involved in male-male competition and are therefore not subject to the checks on exaggeration inherent in the evolution of agonistic signals. Nor are they likely indicators of any aspect of mate superiority other than the ability to insert or attach, signal (stimulate favourable mating responses) and transfer sperm. Though some aspect of male superiority could conceivably happen to be (pleiotropically) linked to some genitalic character, such fortuitous associations seem less often likely to provide cues as to mate superiority than morphology and abilities better displayed during ordinary (external) courtship. Furthermore, even extreme complexity of genitalia does not expose the male to unusually severe risks of predation or unwieldiness; and the production of complexity on such a small scale probably entails little energetic cost. At the same time selection on genitalic characters must be strong due to their likely important influence on female receptivity and handling of sperm (see above). Thus all of the special conditions favouring runaway selection may be met by male genitalia more consistently than by any other category of competitive signalling device in insects.

D. Postscript

The haunting memory of an era when species recognition seemed so neat and comprehensive an explanation for all courtship diversity serves to remind today's sexual selection enthusiast that unseen complications undoubtedly still lurk in the behaviour of organisms, even in those that seem best adapted to current theory. Words like "coyness", even when precisely defined as a high threshold of receptivity to mating, presume a cause (selectivity on the part of females) of an observed phenomenon (e.g. prolongation of courtship). Such built-in assumptions could suffocate efforts to discover alternative explanations and perpetuate a new dogma. So far, much of the new excitement about sexual selection and insect mating systems has come from what is really only part of an evolutionary explanation, i.e. the discovery of consistent and general patterns in the structure of insect mating systems as predicted by selection theory. A comprehensive evolutionary approach would go on to record the details of behaviour in groups of related species, in an attempt to reconstruct the series of changes that might have produced the "useless" and extravagant details of observed rituals and the circumstances giving rise to each step. Very few recent studies go beyond single-species analyses to contemplate this level of explanation, and many modern analyses even neglect the details of behaviour whose description is required to begin [for a notable exception, see Baker and Cardé (1979) on sexual selection and the evolution of hairpencil displays in the Lepidoptera]. The older ethological literature, on the other hand, documented the sensory basis of particular displays and attempted phylogenetic reconstruction via comparative study, but

was not aware of special implications of sexual selection theory and thus failed to comprehend certain broad evolutionary patterns. Entomology is perhaps now equipped for the synthesis of these approaches that could produce a comprehensive evolutionary account of insect communication.

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