MATING SYSTEMS, PATERNAL INVESTMENT AND AGGRESSIVE BEHAVIOR OF ACOUSTIC ORTHOPTERA

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The term mating system has been defined as a “behavioral strategy employed in obtaining mates” (Emlen and Oring 1977). Such a definition makes differences in the mechanisms of pair formation the logical basis of distinguishing and classifying system types. For crickets, katydids, and many grasshoppers, sound signals have a special importance to mating. Among these acoustic Orthoptera 2 broadly distinct mating systems recur frequently: male call and male search.

The males in a call system remain geographically localized for long periods and by repetition of an acoustic display, the calling song, elicit the approach of non-singing females. The calling song functions as a navigational aid, the basis of phonoacoustic response. By contrast, the males of a search system are not sedentary. They actively explore their environment for females. Instead of functioning as a fixed beacon, sounds call attention to the momentary location of an exploring male or they occur in conjunction with visual and chemical signals exchanged at close range with encountered conspecifics.

A meadow katydid, Orchelimum gladiator Bruner (Tettigoniidae), and a band-winged oedipodine grasshopper, Dissosteira carolina (L.) (Acrididae), provide a contrasting illustration of male call and male search types, respectively.

Orchelimum gladiator live in visually occluded swale habitats where they form aggregations of relatively sedentary, stridulating males. Within these aggregations, likened by Alexander (1975) to the leks of certain vertebrate species, males repeat through daylight hours, a calling song consisting of a series of ticks alternating with a buzz. Each song is only a few seconds in duration, but 1 follows another in rapid succession and the result is an acoustic display remarkable for its continuity. At peak densities, singers within the aggregation are separated from their nearest stridulating neighbor by an average distance of 1.7 m (Morris 1967). Experiments with speaker broadcasts of recorded calling song have shown that the song evokes and guides the approach of both sexually receptive females (Morris et al. 1975a) and of nearby male competitors (Morris 1972).

Dissosteira carolina occurs in areas with little or no vegetation. During the heat of the day males walk and make short flights (1 to 3 m) with no apparent goal (Kerr 1974). Over the last part of these flights their yellow-bordered black wings move in a visual display accompanied by a crackling sound known as crepitation. As they detect other D. carolina, the males approach by flying and/or walking. After arriving next to a conspecific male or female, a male invokes a diverse repertoire of signals involving movement of his jumping legs. Certain of these signals, e.g. femur-tipping with wing striking (Kerr 1974) generate sound. Dissosteira carolina also produces a
hovering crepitation display in which a male flies up 0.5 to 2 m, crepitates without lateral displacement, and then returns to approximately its original ground location. Only other males have been observed to approach these crepitating flight displays (Otte 1970).

The strategy of generating a beacon by which the female will navigate requires that the male provide her, for at least many minutes, with a relatively fixed goal. *Oreothinum gladiator* males therefore show strong site fidelity. This in turn means that a higher proportion of their competitive interactions will involve a rather small group of nearby males. The system tends to be static with reduced social contact. Conversely, for *D. carolina* crepitating flight draws conspecifics to a site only momentarily occupied by the calling male. Crepitating displays are ephemeral in both time and space. Such a system is more dynamic and the incidence of contact with strangers very high. Individuals do not show fidelity to display sites.

The site fidelity of call systems is most marked where the singer occupies a burrow. Field crickets (*Gryllus* spp.) have a burrow-based call system. They defend geographically fixed territories for which the burrow is the focal point (Alexander 1961). *Oreothinum gladiator* males do not construct or occupy burrows. They apparently shelter in the lower reaches of the grass and sedge. Consequently, within limits of habitat suitability, they are indifferent to their exact geographical location; the area of their activity (one might better say the "volume" of their activity since they move vertically as well as horizontally within the vegetation) drifts many meters over the course of several days (Morris 1967).

The signalling in *D. carolina*’s search system is intermittent and opportunistic. It is given in response to an encountered conspecific. What follows initial contact is a rapid alternation of the roles of sender and recipient as the 2 (or more) insects exchange leg signals. By contrast the signalling in a call system is sustained and endogenous. No evoking stimulus, such as another conspecific, is required. Information is broadcast rhetorically, without anticipation of imminent female response. For hours on end the sender remains the sender and the recipient, if even present, remains the recipient.

The mating systems of most Tettigoniidae including *O. gladiator*, in contrast to those of most crickets and grasshoppers, seem to involve substantial nutritional investment by the male in his future offspring. This investment takes the form of a remarkably large gelatinous mass, the spermatophylax, which accompanies the sperm ampullae and is consumed by the female after copulation.

The food value of tettigoniid spermatophores (sperm ampullae and spermatophylax) is practically unknown. But in the meadow katydid *Conocephalus brevipes* (Scudder) about 20% by weight of the spermatophore is protein, the remainder being largely water (personal communication, Gordon E. Kerr). The spermatophore with its spermatophylax is such a substantial fraction of a male’s body weight, as much as 25% in *Ephippiger biterensis* Fl, that taken together with its probable high protein content, it is best viewed (Thornhill 1976) as paternal investment.

In addition to the spermatophore and various glandular products (Fulton 1915), nutritional investment by males of acoustic Orthoptera can extend to female consumption of male body parts. For example, males of the tettigoniid *Cyphoderris buckelli* Hebard possess fisheye, cream-colored wings
beneath their tegmina upon which the female feeds during copulation, consuming both wing substance and accompanying haemolymph.

*Cyphoderris buckelli* is also an instructive example of the potential for female exploitation of the male, which is inevitably linked to the evolution of a sizable paternal investment. This species, occurring in northwestern North America, is one of only 4 survivors of an ancient and large insect group, the Haglidae (Prophalangopsidae) considered ancestral to modern-day katydids and crickets (Zetter 1939). Males produce their calling songs at night from low understory shrubs and the lower trunks of trees. On reaching a male, the female mounts over his back, the primitive mating posture of ensiferan Orthoptera (Alexander and Otte 1967) and begins to chew on his wings (Fig. 1A). A substantial spermatophore, suggesting tettigonoid rather than Gryllloid affinity, is passed to the female.

Typically, female katydids can only obtain the spermatophore food package by submitting to insemination. But in *C. buckelli* it would be possible for a female to begin copulation, obtain nourishment via a male's wings and then withdraw before the male succeeds in attaching his spermatophore. Mated females might pursue *coitus interruptus* with a succession of partners as a foraging technique. The presence of what Hinton (1946) terms a *gin trap* (pinching organ) on the male's abdominal tergites testifies to past selection that limits this sort of exploitation. *Cyphoderris buckelli* 's gin trap (Fig. 2) consists of recurved hooks, 1 pair directed forward and another directed backward, on the 10th and 8th tergites, respectively. As the terminal abdominal segments are telescoped inward, the hooks converge on a portion of the female's venter and prevent her from pulling away (Fig. 1B).

Katydid males, via their spermatophores, make a large parental invest-
ment with each copulation. In oedipodines and other Acrididae, the spermatophore has been reduced in the course of evolution to a temporary sac like extension of the penis, penetrating to the spermatheca (Davey 1960). Oedipodines thus invest little in mating beyond their sperm. Low parental investment by a sex is linked to the practice of multiple mating by that sex and to increased variance in reproductive success (Trivers 1972, Wilson 1975a). Oedipodine males will tend to be polygynous and compete with other males of their species to inseminate as many females as possible. Katydid on the other hand will tend toward monogyny; having apparently evolved with a lower expectation of contacting mates, they invest heavily in the 1 or 2 matings that they do secure.

There is abundant experimental evidence that the calling song in male call mating systems governs pair formation and that it evokes and guides the approach of receptive females (Regen 1913, Duijm and van Oyen 1948, Busnel et al. 1955, Walker 1957, Morris et al. 1975b). Use of this same calling song to simultaneously mediate male competitive interactions, though probably next to universal in Tettigoniiidae, has been neglected as a subject for experimentation and understated in the literature.

Most tettigonids never or only rarely fight. But among males of *Orthelimium vulgare* Harris and *O. gladiator*, overt intraspecific aggression is common (Morris 1971). Such fighting is ultimately a manifestation of
male competition. Somehow the dominant male must be improving his access to females.

An *Orchelimum* singer will periodically 'track' a neighbor's song sequence by interposing his own songs in a fixed time relationship (personal communication, Marianne Feaver). Then suddenly he may move from the relative permanence of his singing post to walk and leap a meter or more in the direction of the other male. A grappling fight often ensues, involving vigorous biting and kicking. So far 6 species of *Orchelimum* are known to engage in grappling aggression.

The role of *Orchelimum* calling song in aggression also has been demonstrated experimentally. *Orchelimum gladiator* males will track song broadcast from a distant speaker, then make a phonotactic approach. If the speaker is repositioned one can evoke further approaches (Morris 1972). There can be no doubt that *Orchelimum* calling song releases attack by nearby males. The tracking leads us further to assign a role for the song in the threat of attack.

Among Tetigoniidae a high incidence of overt aggression is known only in *Orchelimum*, but tracking and other forms of phonoresponsese are almost universal in the family. Some type of male-male mutual calling song influence (alternation, synchrony) seems to have been uncovered wherever it has been sought (Jones 1966, Shaw 1968). Given that in *Orchelimum* phonoresponsese via calling song is aggressive, then we may suppose that in other katydid species, even though overt aggression is absent, the occurrence of phonoresponsese reflects the function of calling song in mediating male competitive interactions.

In support of this one can cite also the universal tendency for regular spacing of singing katydid males (Alexander 1956). Such regularity implies ongoing knowledge of the location of singing neighbors; at night or in visually occluded habitats only the calling song seems likely to provide this information. Almost all katydids, therefore, can be expected to use the calling song in aggression and *Orchelimum* differs only in the readiness of competitors to escalate to an extreme expression of competition for mates.

In a search system male-male contesting signals occur independently of female solicitation. Femur tips are a display separate from crepitation. In systems employing a calling song, male-male aggressive information is intimately combined with information directed at females. This goes some way to explain the amplitude modulation complexity of many katydid calling songs (Morris and Walker 1976). The remarkable diversity of odeipodine signal repertoires is less a reflection of greater need for information transfer than a result of the feasibility of employing different information units in different contexts. In search systems the context, intra or inter-sexual, is usually known to the signaler. Senders in a call system are, by contrast, true broadcasters; since information about recipients is often lacking, senders must allow simultaneously for these 2 contexts.

Game theory has recently been applied to animal contests (Maynard Smith 1976, Maynard Smith and Parker 1976). It provides some insight into the readiness of *Orchelimum* spp. to escalate male aggressive encounters. We should expect escalation to be associated with the following conditions: (A) the protagonists are evenly matched, (B) the species has very limited potential for inflicting severe damage, and (C) the pay-off for success in a particular encounter is substantial.
Only evenly matched animals need escalate. If an obvious asymmetry in fighting ability exists (i.e. substantial size or weight difference) it could be used by the participants early in the interaction to predict the outcome. *Orechelimum* males meet on vegetation that moves readily beneath their weight and being diurnal with well-developed eyes, they have good visual information about their opponent's size. Selection will favor individuals that can anticipate the loss of a fight and thereby avoid both risk and wasted energy.

Because of the large spermatophylax, *Orechelimum* males undergo a substantial weight loss with the passage of a spermatophore. Thus we might suspect that recently mated males are at a disadvantage in aggressive encounters and yield more readily. Escalation to overt fighting should be occurring most often between males of comparable size and with well-formed spermatophores.

There are some emphatically predatory katydids (*Cophobotes, Rehnia, Ptilus*) but most acoustic Orthoptera, and certainly *Orechelimum*, are not adapted strongly for predation. They lack formidable weapons and it seems unlikely that fighting *Orechelimum* males could inflict serious damage on each other. However, one should bear in mind the immense importance of stridulation in securing a mate. A torn tegmental cell will reduce a singer's intensity (Morris and Pipher 1967) and compromise his chances of attracting females.

The reward for success in aggression is improved access to females. Ready escalation by *Orechelimum* males suggests that their pay-off per encounter is unusually high. In *D. carolina* domination in an aggressive encounter gains for a male only a short-lived opportunity to search without the presence of a rival (Kerr 1977). The incessant exploration by males in search systems ensures a high challenge rate. Thus an oedipodine male's improvement in mate access per encounter is comparatively trivial; the pay-off does not warrant escalation.

In *Orechelimum's* mating system, with males calling rather than searching, challenges may occur at a much lower rate, contributing to greater per encounter gain in exclusive calling time. Calling systems may thus have an inherently greater pay-off per encounter than search systems, but this improved pay-off cannot account for the extent of *Orechelimum* escalation. Most other tettigonids have call systems yet they do not show a comparable incidence of fighting.

Perhaps *Orechelimum* fighting is linked somehow to a scarcity of sexually receptive females and to the adaptiveness of paternal investment. There is evidence that *O. gladiator* females become unresponsive to the calling of males after mating once (Morris et al. 1975a). Suppose that most females mate with only 1 male in their lifetime. Together with tendencies toward synchronized female maturation, this would cause receptive females to be a relatively scarce commodity in an *Orechelimum* population. The operational sex ratio (Emlen and Oring 1977) would become rapidly skewed in favor of males in the course of the breeding period. The increasing rarity of potential mates would give increased importance to success in aggressive encounters and perhaps justify more frequent escalation.

The existence of the spermatophylax tells us that females have benefited historically from a large nutritional input on the part of the male. There must have been strong selection for females to mate with sedentary sustainedingers because this mechanism of male aggression mediated by song ensured
that a female would obtain an adequate food gift. Females respond preferentially to singers. Steady singing from a fixed location (necessary if the female is to successfully navigate to the male) can only be achieved by repeatedly defeating competing males in aggressive interactions. The presence of an adequate spermatophore confers a weight advantage which enables a male to win fights. Recently mated males, males only just become adult, or males for whatever reason inefficient in foraging, will have a smaller spermatophylax, weigh less, and tend to lose encounters. Escalation, its cost of less significance in species lacking formidable weapons, may be seen as the most effective way to avoid deceit. In a grappling fight it is hard to lie about one’s weight.

The mating systems of acoustic Orthoptera range from active searching to sedentary calling. Call-answer systems and burrow-centered territoriality are among several variations in the kinds of mating systems. Many structural and behavioral peculiarities of males e.g. a large spermatophylax, overt fighting, a gin trap, can only be properly understood as evolutionary products of a system maximizing individual reproductive success. The different interests of males and females have shaped these systems. Each sex has evolved to exploit features of the other’s behavior and to defend against such exploitation. Thus, males vulnerable to ‘eat and run’ females evolved a structure that restrains feeding females and ensures paternity. Females may benefit by preferring males whose ability to sing undisturbed derives from success in overt fighting; this success is in turn derived from the presence of a large spermatophylax that confers upon the male a competitive weight in his aggressive encounters.

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LITERATURE CITED


MATING BEHAVIOR AND NATURAL SELECTION

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Laymen get the impression that biologists have an inordinate preoccupation with sex. We are immoderate, and it is excusable: sexual behavior is the key to understanding biological species. Only when he turns his attention to mating behavior does the biologist begin to use more than inferential evidence for species "boundaries." Most basic and applied investigations ultimately depend upon a knowledge of species, whether for acquiring species-pure samples, or for identifying and manipulating vulnerable points in the ecology of some competing organism. Questions that are addressed to the way species found their origin, got to be the way they are, and exist today, begin and end with a discussion of biological species.

Gene flow is the phenomenon at the center of understanding and definition of biological species. In the final analysis, when reduced to its smallest moment of flux, to its irreducible whiff of displacement, genes flow down an aedeagus and into another individual, and the genes of 2 parents flow together. (Sometimes the actual mechanics are not exactly like this—genes are handed over in sacks, left on posts, or squirted into the surrounding medium.) Mating behavior arranges for and accomplishes gene flow. It comprises the activities and events that take place as the animals seek, identify, win over and appraise, and finally accept partners in reproduction. Thus sexual behavior, in all its intimate and diverse detail in the animal kingdom, becomes a necessary obsession with biologists. Further, because the biologies of most organisms are constructed around sexual success, there is more at stake in understanding mating behavior than "merely" straightening out species. This knowledge is fundamental to understanding biology at all, and its most important principles.

Natural selection is the choreographer, composer, and lyricist of the entire sexual performance. It brings about change in gene (=allele) frequencies, and this, in a reasonable working definition, is evolution. Natural selection occurs when certain genetic sorts of individuals in a population leave a greater number of progeny than do others. As simple and old-hat as it sounds, this elementary fact can be used with considerable reward and success when one addresses mating behavior studies. Surprisingly, many

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2In Shakespeare's The Merchant Of Venice copulation is "the deed of kind" (Shipley 1977).