

NATURAL SELECTION  
AND SPECIALIZED CHORUSING BEHAVIOR  
IN ACOUSTICAL INSECTS

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INTRODUCTION

*Specialized chorusing behavior* refers to rhythmical interactions, such as alternation or synchrony of successive song phrases, by neighboring calling males. Included are the massive synchronies sometimes achieved by large populations of cicadas, crickets, and katydids (Alexander and Moore 1958; Alexander 1960, 1967; Walker 1969). Some male fireflies also flash in synchrony (Buck and Buck 1968; Lloyd 1971, 1973a, b; Otte and Smiley, unpublished), and some anuran amphibians alternate (Rosen and Lemon 1974); their behavior may be considered part of the general problem analyzed here.

The choruses of acoustical insects and anurans, and the mass synchronies of fireflies, involve adult males. These males are producing signals which attract sexually responsive females. This conclusion can be drawn for all chorusing species, both from the circumstances of their performances and from comparing them with more thoroughly studied related species that do not chorus (for references see Alexander 1967; Spooner 1968; Morris, Kerr, and Gwynne, in press; Otte and Loftus-Hills, unpublished). That signals produced in chorus do attract females has been demonstrated for such species as the synchronizing snowy tree cricket, *Oecanthus fultoni* (Walker 1969), and two of the three chorusing species of seventeen-year cicadas (*Magicicada* spp.) (Alexander and Moore 1958, 1962).

The cicada signals have been shown also to attract males, as have those of the synchronizing katydid, *Orchelimum vulgare* (Morris 1971, 1972). In other chorusing species, such as the true katydid, *Pterophylla camellifolia*, there is evidence that a male's calling may cause unusually close male neighbors to move away (Shaw 1968). Whether or not more distant males in such cases tend to approach a calling male is not

yet known. Attraction of both males and females to synchronous swarms has been demonstrated in fireflies (Lloyd 1973b).

Adult males in polygynous species are among the most competitive of all possible classes of individuals, and what they are competing for most intensively are females. That they carry out acoustical interactions, such as synchrony in chorus, giving the superficial appearance, at least, of cooperative behavior, and especially that they aggregate and chorus at breeding time, has to arouse our greatest curiosity and puzzlement.

It has not always been so. Only a few years ago most biologists referred to insect choruses as mating assemblies and supposed that a sufficient explanation had thereby been provided. There were two reasons for this attitude. First, we had not yet considered the probable outcomes of conflicts between the effects of selection at different levels in the hierarchies of organization of living matter: genes, chromosomes, genotypes, families, social groups, populations, and so on. Second, we casually and constantly regarded function at the population or species level, as we tend to see it in our own social, economic, and political affairs.

These attitudes are changing, thanks to a series of revolutionary events in biology beginning with R.A. Fisher's announcement in the 1958 revision of his 1929 book, *The Genetical Theory of Natural Selection*, that selection as he had been referring to it explains attributes only insofar as they benefit their individual possessors, and not insofar as they benefit the population or species. That should have been an explosive revelation to ecology, behavior, population genetics, and evolutionary biology in general, but for some reason it was not. Wynne-Edwards (1962) exposed the significance of Fisher's remark by generating the controversy which has since surrounded the concept of group selection, and Williams (1966a) developed the first serious argument against group selection as a general explanation of the traits of organisms. Two other major components in social theory were added when Hamilton (1964) and Trivers (1971) developed theories accounting for the evolution of much of what looks like cooperative or altruistic behavior—namely, kin selection and reciprocation—by natural selection acting principally at or below the individual level.

It is no longer possible casually to regard social groups of animals as functioning somehow to assist the reproduction of the population or species, and those cases like chorusing behavior in which functions at individual or genic levels have not been clearly established require our close scrutiny.

The revolution in biology which is reflected in this change of attitude has literally pushed the study of social behavior back into an almost entirely theoretical state, because most of the previous work was done with inadequate models. This means that much of this early work will have to be done over again, even if one defines social behavior so broadly as to include most of the field of behavior (see Alexander 1974; West-Eberhard, in press). In regard to the study of insect acoustical behavior, for example, the entire topic of sexual selection has failed to become a prominent aspect of our theorizing because we have not concentrated on the effectiveness of selection at the individual level.

This paper is largely a reinterpretation of my own earlier writings on chorusing behavior (Alexander 1960, 1967), in light of the changing attitude toward selection, and a review of the recent literature on chorusing.

In 1967 (p. 512) I suggested the following four possible explanations for chorusing:

- (a) Elaboration of the role of auditory feedback in rhythmical, long-continued calling of individual males may have incidentally rendered them "captive" phonoresponders to close neighbors in many species; (b) two or more males singing in alternation or synchrony may produce sound more regularly for longer periods of time (make up a more stable sound-producing unit) than lone-singing males because of stimulative and inhibitory effects upon one another . . . ; (c) phonoresponses may assist in the formation and maintenance of aggregations of males in situations in which individual males increase their chances of securing mates by joining such groups; and (d) rhythmic interaction (chorusing) by numerous males within a restricted area may prevent obscurement of the species-specific and female-attracting portions of the song or even enhance their distinctiveness.

The major shortcomings of these hypotheses are three: (1) There is no clear distinction between evolved functions and incidental effects (Williams 1966a); (2) there is a tendency to invoke physiological limitations to explain traits; and (3) there is no emphasis on competition between individual males, which seems to be at the heart of all male-male acoustical interactions.

The first hypothesis implies that phonoresponses, whether advantageous or disadvantageous, cannot be avoided. The second hypothesis implies that individual males cannot evolve

to be stable sound-producing units, and it suggests that they assist one another, without explaining what benefits each might receive from such cooperation. The third hypothesis does not distinguish between advantages to joining males and the advantages to the already grouped males whose signals they may be using to join the group; such joining may be advantageous to one but disadvantageous to the other (see Otte's 1974 definition of *communication*). The fourth hypothesis does not face the question of why males should remain in close proximity, or even aggregate, such that special behavior to reduce acoustical interference should evolve.

In other words, these hypotheses were largely developed without the modern view that selection is principally effective at or below the individual level and that explanations invoking physiological limitations are open to question unless selective conflicts which force compromises are identified. The shortcomings of these hypotheses illustrate the magnitude of the revolution in evolutionary thinking that has occurred within the past decade and the value of this revolution in enabling us to develop appropriate models of the evolutionary background of phenomena like specialized chorusing in acoustical insects.

Walker (1969), Otte (1972, in press), Lloyd (1971, 1973a, b, in press), Otte and Loftus-Hills (unpublished), and Otte and Smiley (unpublished) have written more recently on aspects of chorusing behavior (or synchronous flashing), and all have endorsed versions of the fourth of the above hypotheses. The problem of why males aggregate or remain in close proximity is still unsolved, with only Otte (in press) considering it in some detail. Walker, discussing the snowy tree cricket, suggested that males in groups may be less vulnerable to acoustically orienting predators. Otte (1972) and Lloyd (1973a) were the first to emphasize in print that male-male phonoresponses are likely forms of competition for females, and Lloyd (1973a) and Otte and Smiley (unpublished) specifically suggested that mass synchronies are most likely incidental effects of such competition.

#### THE NATURE OF CHORUSES

Choruses of singing insects and flashing synchronies of fireflies sometimes reach astonishing proportions, impossible to describe adequately to someone who has not observed them directly. They are easily the most awesome performances in animal behavior that I have witnessed in the field. I will

discuss a few examples briefly before trying to dissect or model their functions and reconstruct their evolutionary histories.

In early June 1957 after several consecutive days of unsynchronized chorusing during rainy weather, the males of one of the two seventeen-year cicada species I was studying (Alexander and Moore 1958) suddenly (within a few seconds) entered into a massive synchrony extending several hundred meters, from one end of the forest to the other. The only record that could be made of this observation was a tape recording of the sound (Alexander 1960) and a line graph showing the regularity of highs and lows in the intensity of sound as recorded by a sound-level meter (Alexander and Moore 1958, fig. 8).

In subsequent years I made two similar observations on other signaling insects, one of synchrony in a 400-meter-long population of fireflies (probably *Photinus pyralis*) in a river-bottom pasture in Kentucky, and the other of synchronized alternation in dense populations of true katydids in the Appalachian Mountains (Alexander 1960).

For a long time biologists have claimed on occasion to have observed phenomena like these. But most field biologists fail to notice events of such magnitude, and the rare reports may often be attributed to exaggeration or overenthusiasm. Thus mass synchrony in *P. pyralis* has been reported only rarely (see Buck 1935), and it has never been witnessed by Dr. James E. Lloyd of the University of Florida, who has surely spent more time than any other person studying firefly behavior in the field in eastern North America. Recently Otte and Smiley (unpublished) have analyzed mass synchrony of a related species, *P. concisus*, in Texas.

Similarly, in 1960 (p. 78) I described the synchrony of a dense population of the meadow katydid, *Orchelimum vulgare*, in a bed of tiger lilies on the campus of the Ohio State University. This species is one of the most widespread, abundant, and noticeable roadside singing insects in North America, but my description of its chorusing synchrony was novel. That description was also one of the items doubted by the reviewers of the publication, who had worked extensively with the same species in the laboratory. That particular population of long-winged immigrant males synchronized every day almost within hearing of my laboratory, and I have repeated the observation in the same location on two different years since 1960; but I have rarely observed synchronize choruses of this species elsewhere.

Even if such difficult-to-corroborate observations are

accepted, these extremes of chorusing behavior are achieved but rarely. As a result, we can legitimately doubt that truly *massive* synchronies, in these cases, have an evolved function. Instead, we are likely to speculate that they are incidental effects of a function that yields a somewhat less spectacular result and is realized more consistently.

On the other hand, Melanesian fireflies in the genus *Pteroptyx* regularly achieve massive synchrony (Lloyd 1973a, b), leaving us with the question whether or not they may be more than incidentally different from those which achieve synchrony only infrequently. Likewise, the synchronizing species of seventeen-year cicada (and its thirteen-year counterpart or cognate species) (Alexander and Moore 1962) regularly achieves and maintains synchrony within fairly large subpopulations even if it only rarely does so throughout an entire forest. Neither of the other two seventeen-year (nor the other two thirteen-year) cicadas seems to synchronize at all. Again, we must ask whether the frequently achieved smaller-scale synchrony of such species has an evolved function, or is an incidental effect of, say, a structural difference between the species' calls, or of a function not so dramatic in its results and shared with those species that never achieve synchrony.

Considering still smaller groups, we can note that, when two male insects that signal acoustically are placed near one another, they do not signal independently, each as if the other were not there. Instead, they interact, perhaps inevitably—see hypothesis (a) above (Alexander 1960)—and these interactions, termed *phonoresponding* (Busnel and Loher 1961), take certain forms that can be related to the chorusing behavior of larger groups. Thus some males synchronize calls with neighbors, some alternate calls, and some sing overlappingly or sequentially in ways that are not easily categorized as either synchrony or alternation (Alexander 1960, 1967; Dumortier 1963; Jones 1966; Shaw 1968; Otte, in press).

Even in interactions between two males, we can derive evidence that phonoresponses may occur as incidental effects. The coneheaded grasshopper, *Neoconocephalus ensiger*, is a common nocturnal singer along roadsides in northeastern North America. It produces a lispy pulse in series of indefinite length at rates varying from 4-5 per second at the lowest singing temperature of about 9°C to about 15 pulses per second at 30°C (Borror 1954). At high temperatures neighboring males do not synchronize; one can hear their songs go in and out of phase, even though the pulses come too rapidly to be counted.

This lack of synchrony is not surprising, since specialized chorusing behavior (synchrony and alternation) seems to be restricted to those species "in which the normal calling song contains a precise or highly uniform chirp or phrase rate within the range of two to five per second . . ." and to include all such species (Alexander 1960, p. 82). The pulses of *N. ensiger* are uniform in rate, but only at the lowest singing temperature are they delivered slowly enough to allow synchrony. At temperatures within a degree or two of the minimum at which this species will sing (approximately 8.6°C), I have on three occasions listened to males less than one meter apart synchronizing uninterruptedly for several minutes. It scarcely seems likely that these males have been selected to synchronize when the conditions under which they can do so effectively are rarely encountered. Rather, their songs appear to become synchronizable at very low temperatures as an incidental effect of their structure at more usual singing temperatures.

Additional support for synchrony or alternation as an incidental effect may be derived from its occurrence between individuals of different species (Alexander 1960; Littlejohn and Martin 1969). Alternation between sympatric species that sing together may be adaptive, but one can also obtain alternation regularly in the laboratory between species that are unlikely to interact in the field. In my laboratory a male of the katydid *N. exiliscanorus* (120 phrases/min) sang only between the phrases of a nearby male of *N. nebrascensis* (30 phrases/min), the two males thus effectively alternating with one another (see Alexander 1956 for song descriptions and audiospectrographs). Yet the males of these broadly sympatric species synchronize with conspecific males in the field.

Males may be selected to alternate with any sounds with frequencies near enough to their own to interfere significantly, or this particular case might have been an incidental result of the song difference between the species. If phonoresponses between near neighbors should prove inevitable, even if sometimes maladaptive, the conflict in selection that is responsible could lie in the value of auditory feedback to the maintenance of steady, rhythmic singing by lone individuals.

At the outset, then, it would appear that we can draw five tentative conclusions about the particular form of chorusing behavior called synchrony:

1. Synchrony is not always an evolved phenomenon, evidently appearing sometimes as an incidental effect of

close proximity of singing males having certain kinds of calls.

2. Synchrony occurs so regularly in some species, between neighboring males or throughout populations, as to suggest that its likelihood and scale have been enhanced, directly or indirectly, by natural selection.
3. The likelihood of synchrony is increased by close proximity; hence its expression throughout a population depends upon relatively high densities or tendencies to aggregate.
4. In at least some species (e.g., *Magicalcada cassini*, *M. tredecassini*, *Orchelimum vulgare*) males are attracted into close proximity by the same signals that they synchronize once they have aggregated.
5. A noticeable effect of synchrony, to the human observer, is an emphasizing of the synchronized pattern in the song, which would otherwise be obscured increasingly as more males called while near one another.

Since males evidently must be close to one another to synchronize or alternate effectively, chorusing behavior raises two basic questions: (1) what advantages to individuals derive from synchrony or alternation? and (2) what advantages derive from closeness or aggregation of competing males?

For any case of specialized chorusing that is not simply an accident of close proximity, there are three possibilities.

1. Dense populations or aggregations have recurred so consistently and for such a long time that males have evolved to compete with their neighbors through phonoresponses that lead incidentally to chorusing (Lloyd 1973a; Otte and Smiley, unpublished).
2. Aggregating has been favored, with an adaptive significance to individuals that is enhanced by chorusing.
3. Chorusing has been favored by selection, leading to tendencies in males to enhance chorusing by aggregating.

These questions are part of the larger problem in biology of discovering how sexual selection and mate competition have led to various kinds of male signaling and breeding aggregations. What have been the roles of differential parental investment, environmental patchiness, and predation in determining the forms of these activities?

#### HOW CAN MALES COMPETE BY PHONORESPONDING?

Consider the dilemma of a male cricket or katydid calling near another male. He can respond to his competition by leaving the vicinity to try his luck elsewhere, but this may entail moving to a location that is more exposed to predators, farther from food, or farther from the females when they are newly sexually responsive. Moreover, he may have to travel a great distance to escape similar competition from other males.

He can attack the other male and try to drive him from the area, but this may be an expensive act involving time, energy, and the risk of damage in the fight or exposure to predators. It also requires temporary cessation of signaling, and it may be unsuccessful. There may be more than one such competitor, and displaced males may be quickly replaced, necessitating repetition of the whole expensive act, with every outcome doubtful. Evidently, there are limits to the benefits realized from aggression toward nearby competitors, or retreat from them, which restrict the circumstances in which these responses are expressed.

A third strategy, which may be employed whenever the expense, risk, or uncertainty of outcome of retreat or attack is too great, is to remain in the same location and outsignal the competitor. Among species with long-range signals, some expression of this strategy is likely to be universal, for males will rarely be able to signal in complete isolation.

To outsignal a nearby competitor, a male may, first, call more loudly or more frequently than his neighbor. We may assume that the resulting selective "races" would lead to the loud, persistent calling of modern crickets and katydids, and also to tendencies by males to direct or concentrate the broadcasting of their signals in the most favorable directions, to whatever extent and in whatever fashions those might be determinable (see Lloyd 1973b for evidence of directional signaling in fireflies).

Additionally, a male should gain from maximizing the fit between the pattern of his song and that favored by the females of his species. This he can do by (1) producing the appropriate pattern and (2) minimizing its loss of distinctiveness or its obscurement as a result of the singing of nearby competitors.

Suppose that the song of the species is a long trill composed of very rapidly delivered pulses, and the pulse rate (not the length or spacing of some group of pulses) is the chief pattern element of significance to the females (e.g.,

various *Oecanthus* species: Walker 1957). Aside from singing whenever his neighbors sing, a male in such a species has three possible strategies of phonoresponding: start first, stop last, or continue singing during periods when neighboring males are forced to stop. This behavior would lead to mutual stimulation into song by neighboring males, and to bouts of singing by groups of males; and it would lead to the evolution of long-continued songs that overlap one another. Such interactions in fact characterize species with songs of this type (Alexander 1960, p. 77; Otte 1972).

Now suppose instead that the song consists of series of short, multipulse chirps, with the pulse rate, pattern, or number within the chirp a key signal to the female (e.g., B<sub>1</sub> pattern: Alexander 1962). Zaretsky (1972) demonstrates the significance of pulse pattern in a song of this general type in the cricket *Scapsipedus marginatus*. To keep his own song maximally effective, a male in such a species should place his chirps between those of nearby competitors so that the critical within-chirp elements are in the least danger of being blurred. This tendency would lead to alternation of chirps, or a minimizing of signal overlap. Such behavior, again, is characteristic of species with songs known, or likely, to fall into this category—that is, songs with widely spaced chirps and slow or intermediate pulse rates (Alexander 1960, p. 79). It also occurs in hylid frogs with long, single-pulse, frequency-slurred chirps (Rosen and Lemon 1974).

Two kinds of alternation may be distinguished: (1) that in which the chirps or phrases of two males tend to be equidistant in series (e.g., the true katydid, *Pterophylla camellifolia*: Alexander 1960; Shaw 1968) and (2) that in which one male's chirps or phrases follow those of the other by a closer interval (e.g., *Hyla versicolor*: Rosen and Lemon 1974). Only in the former case, evidently rare, does mass alternation occur, giving the effect of a synchrony, in which male A alternates with male B, male B alternates with male C, and male C is thereby synchronized with A.

Finally, consider species in which the communicative unit or morpheme (at least at long range) is a pattern element repeated slowly, such as the entire chirp and its interval, irrespective of the fact that each chirp may be made up of several rapidly delivered pulses or wingstrokes (e.g., the snowy tree cricket: Walker 1957). In this case, neighboring males singing in alternation would deliver an abnormally fast song to a female far enough away to hear both of them. Only if two such males synchronized their chirps would the female

be attracted to them, and then she might be attracted to them rather than to an equally distant single male because of the greater intensity of their combined songs. Again, males in species with such songs seem inevitably to synchronize with their neighbors (Alexander 1960, p. 77-78; Walker 1969). Otte (in press) reports an observation of a South American treetop species with a snowy-tree-cricket type of song alternating, but he could not determine the pulse rate,<sup>1</sup> and it seems likely that this was instead one of the chirping eneopterines with the B<sub>1</sub> pattern in which chirps are alternated.

Otte and Loftus-Hills (unpublished) note that an additional strategy may be to interfere with the song pattern or rhythm of a neighbor to prevent females from being attracted to it. Such "spiteful" behavior (Hamilton 1970) would obfuscate the rhythms of both singers, and would have to be more beneficial to the individual practicing it than alternatives yielding more direct benefits, such as keeping his own rhythm separate and clear. Hence it seems relatively unlikely to evolve.

The above analysis includes the three major classes of phonoresponses (Alexander 1960, 1967) and the major categories of simple song patterns (Alexander 1962), and it seems to predict accurately the phonoresponses of acoustical insects on the basis of the rates and patterns of delivery of the morphemes, or communicative units, in their songs. It also leads to the tentative conclusion that the phonoresponses that form the bases of chorusing behavior are in fact means of signaling competition between neighboring males. The question that remains, and which we will defer temporarily, is: Do males ever gain by aggregating because group synchrony is thereby promoted, or do they aggregate for other reasons, with the group synchrony either an incidental effect or an enhancer of the function of aggregation?

#### MALE COMPETITION AND SIGNALING/SEARCHING TIME

An additional competitive strategy is possible in aggregations of singing males. At low or moderate densities, males unable to secure suitable (e.g., predator safe) signaling locations may obtain matings by lurking in the vicinity of calling males and intercepting responsive females on their way to the callers.

<sup>1</sup>Personal communication.

This strategy should be least profitable (1) when callers are so far apart that only one male can be cuckolded at a time and (2) when there are no decidedly superior males or singing locations. It should be profitable (1) at moderate densities when a nonsinger can effectively patrol the peripheries of the territories of several signalers, (2) when calling males are very unequal in signaling prowess, and (3) when resources are clumped and one or a few males are able to retain decidedly superior signaling sites. The last two conditions are likely to be maximized for some anurans in which adult males continue to grow and develop better voices and fighting ability for several years, and in which breeding sites such as ponds or streams frequently contain but one or a few superior singing sites. Restricted directions of approach by females will further increase the likelihood of cuckoldry by silent males searching near a signaling male.

It seems apparent that as densities increase males will profit from increasing the proportion of their time spent (a) patrolling for interloping males or (b) searching for approaching females to reduce the likelihood of cuckoldry (fig. 1). At high densities males may sometimes profit from searching without signaling, even if males and signaling sites are not decidedly uneven in value. Only one such case has been suggested among vegetation-inhabiting acoustical insects (Otte and Joern, in press)—the grasshopper, *Goniatrum planum*—and it is apparently associated with the presence of relatively few singing sites (bushes). Lloyd (1973b) also notes that many nonsignaling individuals occur in swarm trees of *Pteroptyx*.

On the other hand, parasitism of callers by small, silent (usually younger) males may be common among anurans (Axtell 1958; Emlen 1968)<sup>1</sup> and probably occurs among surface-dwelling crickets<sup>2</sup> and grasshoppers.<sup>3</sup> Surreptitious matings on the periphery of harems, and other alternative routes to mating success by males, are described by Le Boeuf (1974) in the highly polygynous elephant seal. Probably, the peculiar satellite males of the ruff (Hogan-Warburg 1966) can be interpreted as an extreme case in which the evolution of dimorphism in male behavior has led to a divergence in plumage as well. Gadgil (1972) develops a theoretical argument for this situation.

<sup>1</sup>Richard Howard: personal communication.

<sup>2</sup>William Cade: personal communication.

<sup>3</sup>Daniel Otte: personal communication.

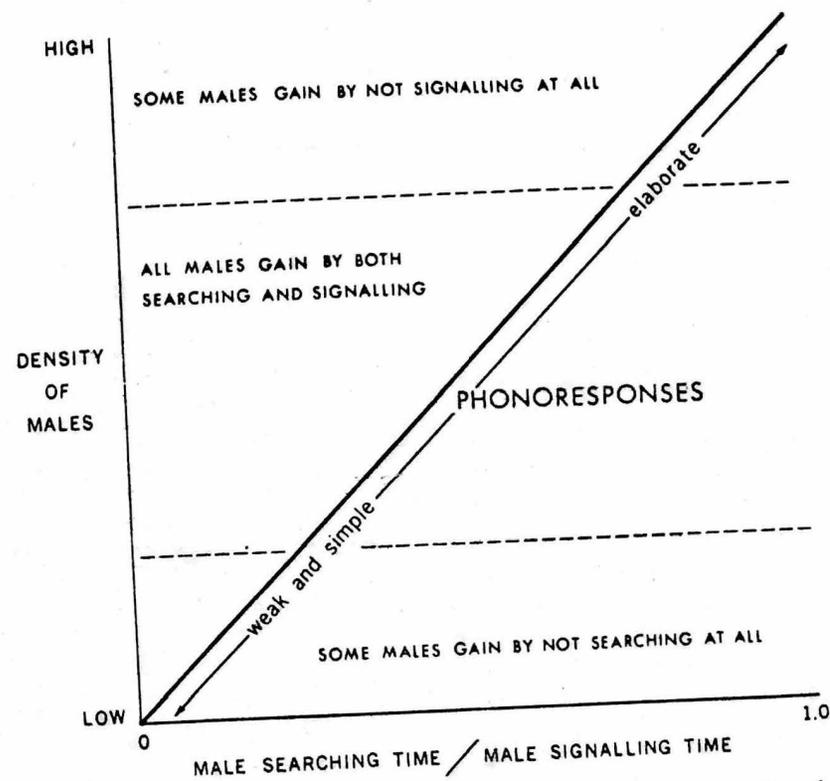


Fig. 1. Postulated relationships between density of males of acoustical insects and proportions of time spent signaling and searching. Densities may be increased by active aggregation. Signaling/searching time will also be affected by signaling ability of males, quality of signaling sites, and distribution of females.

Among male-dimorphic insect species, the possibility must also be considered that the two kinds of mating situations resulting in two male morphs may not be coincident in time or space, and there may be no direct sexual competition between the two kinds of males. Thus, in species living in temporary habitats, some males may gain by being relatively aggressive and territorial because they mature in established but still desirable habitat, while others gain from being better fliers and searchers because they mature in deteriorating habitat.

Failure to find evidence of nonsinging males searching through cicada choruses implies that the male's song remains

an essential part of his ability to acquire females. This hypothesis is strengthened by the similarity of the initial courtship song to the calling song (Alexander 1968) and by observations (Alexander and Howard, unpublished data) that the time from landing by a chorusing male to the start of his next song is shorter and more uniform in length than the time from termination of a song until the subsequent flight. These data indicate that incoming females at some point orient on the songs of individual males.

The periodical cicadas may provide a test of the effects of varying densities on proportions of time spent by males in searching and signaling, if the flights of male cicadas between songs can accurately be interpreted as reflecting time spent searching for females (fig. 2). The three *Magicicada* species with each of the two life-cycle lengths (Alexander and Moore 1962) differ rather consistently in population density, and their calls and behavior are somewhat different. The two *-decula* cognate species are usually sparse and have an obligatorily long call, which may be interpreted as a relatively low searching-to-signaling ratio if flights between calls do not differ greatly in length from those of other species. The other two pairs of species are commonly abundant and have short calls which they produce in series of two to three between flights. However, when most dense, males in both of these pairs of species appear to reduce the number of calls between flights, implying an increase in the searching-to-signaling ratio. When densities are very high and weather conditions are optimal, the *-cassini* cognates reduce calls between flights consistently to one and synchronize their calls. As might be predicted from these species differences, males of the *-cassini* cognates are sexually more aggressive and more successful at interspecific matings (Alexander and Moore 1962). The observations leading to these correlations (Alexander and Moore 1958, 1962; Alexander 1969) were carried out in the absence of the hypothesis they seem here to support.

#### OTHER COMPETITIVE STRATEGIES

Competitive strategies of males signaling in groups, in addition to the general categories discussed above, include the following:

1. Seek out other males that appear to be courting or to have located a female (perhaps even neighboring males that have simply stopped singing) and attack the male

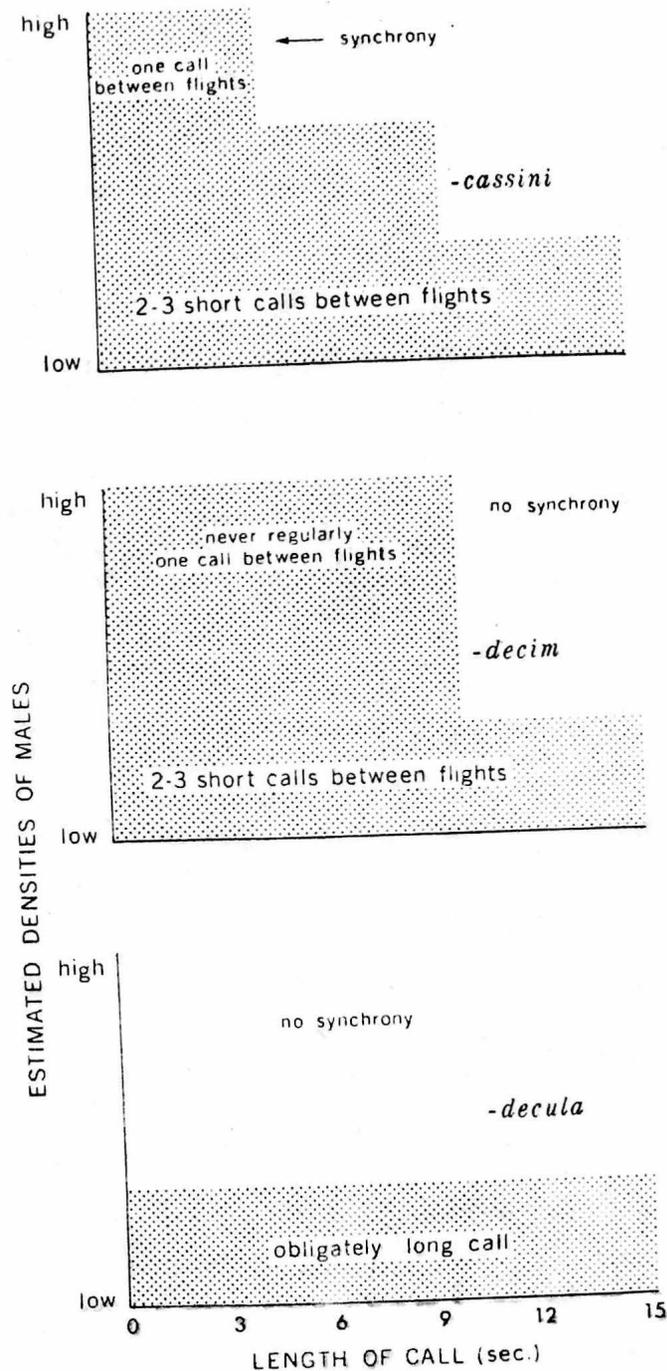


Fig. 2. See legend on next page.

or try to break up the interaction or steal the female. Alexander (1961) reported that a male of a *Gryllus* species, for example, repeatedly searched out and attacked another male out of sight in the same container whenever the latter began to court. Otte (in press) describes similar behavior in a grasshopper. Grove (1959), Spooner (1968), and Lloyd (1973b) describe behavior with the apparent function of usurping the place of another male exchanging signals with a responsive female.

2. Reduce signal intensity when females are near and the likelihood of cuckoldry is high, or change to a less risky channel (e.g., from sound to vision or substrate vibration) (see below and Lloyd 1973b).
3. Rather than ceasing song when it is particularly dangerous (e.g., daytime) or calorically expensive, reduce the intensity of the song or the rate of calling (see below).
4. Change to a pattern, rate, or channel with more directional information or more precision when females are nearby or likely to be nearby (see below).

The last of these strategies should be followed when females are consistently being attracted at such long range that they are using some simpler unit to determine that the male is a proper one to approach (see also Lloyd 1973b). At long range, for example, females of the snowy tree cricket are unlikely to detect the pulse rate or pattern within chirps if several males are synchronized, since synchrony is not exact. Females at long range probably respond chiefly to the chirp pattern and the frequency of the sound. Snowy tree crickets deliver the pulses within their chirps in two or three groups, raising the question whether the pulse pattern within chirps represents a hierarchy of patterns maximally effective at different distances in a synchronized chorus. Whether or not this interpretation is correct, I suggest that shifts in the critical signal parameters with distance from the signaler will prove to be common among acoustical insects.

Fig. 2. Evident relationships between density of males and alternation of calls and short flights in males of the three pairs of cognate species of periodical cicadas (*Magicicada* spp.). Densities of males in choruses are enhanced by active aggregation in the -cassini and -decim cognates (Alexander and Moore 1958), and probably also in the -decula cognates.

#### INTRASPECIFIC COMPETITION AND COMPLEX SIGNALS

Spooner (1968), Lloyd (1973b), and Otte (1972, in press) describe the functions of complex repertoires in katydids, fireflies, and grasshoppers, respectively, in signal systems involving alternating responses between males and females during rapprochement. Evidently, all four of the strategies described above are involved in these interactions, with males changing the intensity, pattern, or communicative channels of their signals as females approach, and with other males carrying out competitive or usurping behavior. In these cases, males can respond directly to approaching females because the females signal, and other males can interlope for the same reason. These cases may provide clues toward the difficult problem of explaining complex signals in species in which the females do not signal back to calling males.

Pace (1974) noted that the song of the male northern leopard frog, *Rana pipiens*, to which females do not respond acoustically, is composed of three main kinds of phrases most often produced in a particular sequence, A-B-C. If A sounds are played at a group of silent males, they respond with increased proportions of B and C sounds. A similar observation has been made on the cicada *M. cassini* (Alexander and Moore 1958) and on certain meadow grasshoppers with two-part songs (Alexander 1960).

Pace and I noted in the field that from a great distance humans, at least, are likely to hear only the A sound of *R. pipiens*, which is a long guttural trill (Pace 1974). The other sounds are easily heard only at fairly short range, and they are sometimes missing from the repertoire of males of the related species, *R. palustris*.<sup>1</sup> Accordingly, Pace speculated that the B and C sounds of *R. pipiens* are, respectively, close-range, direction-giving and male-male, aggressive signals. Whether or not this is precisely correct, the important point is that such changes in intensity or pattern may represent specializations for long-range attraction and short-range direction giving, or alterations, such as in intensity, that specifically reduce the likelihood of cuckoldry.

In frogs, approaching females may be detected by swimming sounds; splashing causes approach and clasping in some species (Eibl-Eibesfeldt 1954) and production of the "mating

<sup>1</sup>A.E. Pace: personal communication

call" in *R. utricularia*.<sup>1</sup> Some katydid males respond to agitation of the plant on which they are calling (as by an approaching female) by vigorously shaking or vibrating the plant (Busnel, Pasquinely, and Dumortier 1955), which may be an aggressive signal commonly directed against other males, but is also a signal potentially transmissible to the female but not to nearby males on other plants. Such a signal would result in less cuckoldry than an acoustical signal that other males could use to discern that a female was approaching the signaling male. It seems a logical extension that call changes may evolve not only to occur when acoustical responses or other evidences of approaching females are detected by calling males, but also in some cases to be regularly interspersed or alternated with long-range calls, even when the male has received no direct evidence of approaching females.

The kinds of selection discussed above could have several different effects on a male's singing; these effects may relate to the variety of complex calling known in acoustical insects in six ways.

First, long trills may change progressively, as in *Amblycorypha rotundifolia* (Alexander 1960). In this species trills tend to increase in length during a singing bout, and each trill series ends with one very long trill followed by a few short trills.

Second, long trills may alternate between two speeds or intensities, as in *Conocephalus strictus*, *Tibicen* species (Alexander 1956), and *Metrioptera sphagnorum* (Morris 1970; Morris, Kerr, and Gwynne, in press). Alternation of slow and fast pulse rates in the trill of *C. strictus* suggests that at long distances females may respond chiefly to the frequency spectrum of the sound, while at short range a distinctive pulse rate becomes more important, favoring a slower pulse rate with each pulse made distinct. In several cricket species, such as *Allonemobius allardi*, *A. tinnulus* (Alexander and Thomas 1959), and *A. griseus* (Alexander, unpublished data) the pulse rate in the courtship sound is slower than that of the calling song.

In *Tibicen* species loud and soft buzzes alternate, with the loud portions in many species containing a slower vibrato superimposed on the basic trill (Alexander 1956). The presence of the louder, slower vibrato implies that at longer ranges the rapid pulse rate in the buzz is not easily discerned. The soft buzzes may represent an advantage over

silence during the same periods because they attract nearby females. Similarly, the so-called daytime songs of *Scudderia* species (Spooner 1968) could be low-effort signals which profit a male only if females are nearby, but are also less likely to attract birds than normal nocturnal calling.

Morris, Kerr, and Gwynne (in press) have shown that the two parts of the song of *Metrioptera sphagnorum*, alternated twice each second, and termed by them the *ultrasonic* and *audio* modes, are both functional in pair formation, but "the ultrasonic plays the primary role in pair formation. . . . A courtship song, apparently derived from the audio mode, is given by the male after pair formation is achieved." This finding strongly supports the hypothesis presented here that long- and short-range signals may be alternated regularly in the singing of a male not yet in contact with a female.

Third, some species seem to have two distinct calling songs, as do *Microcentrum rhombifolium* (Alexander 1960) and a Fijian species of Nemobiinae (Alexander and Otte, unpublished). In some *Scudderia* species females respond acoustically to one of the male's calls, causing the male to change to another calling sound (Spooner 1968). Males of *M. rhombifolium* alternate two calls (lisps and ticks) without acoustical responses from females. Results obtained by Grove (1959) and Spooner (1968) indicate that females move toward low-intensity male lisps but not toward high-intensity lisps. Females tick in reply to male ticks, and males then go to the female. Evidently, the lisp (a very rapid series of toothstrikes) is a long-range signal, and the tick series (approximately the same series of toothstrikes produced very slowly) is a short-range signal used by the male to locate the female.

As with *Scudderia* species, a *M. rhombifolium* male apparently mimics the female's response to his ticks, which probably confuses potential cuckolders (Spooner 1968; Grove 1959; Alexander 1960, recording); Grove (1959) has observed otherwise silent interloping males producing this sound while approaching a phonoresponding pair.

The Fijian nemobiine may be similar. Males have been seen to change from one call to the other without touching other individuals. Females, however, are not known to call. The two calls of this species differ most dramatically in wing-stroke rate; both are composed of short, multipulse chirps.

Fourth, each phrase or chirp may change progressively, as in *Orchelimum volantum* (Alexander 1960) and *Magictada* species (Alexander 1968). In these species the pulse rate slows at the end of the phrase, and the frequency of the

<sup>1</sup>A.E. Pace: personal communication.

sound drops. In all *Magicicada* species the initial courtship sounds consist of phrases resembling the calling phrases. In the *-cassini* and particularly the *-decim* cognate species pairs, the initial courtship sounds are shorter than calling phrases, and separated by shorter intervals, so that in effect the terminal part of the phrase is repeated rapidly. This part of the phrase may thus be principally a short-range signal with a function near that of the courtship signals. In at least one cricket, *Allonemobius fasciatus* (Alexander and Thomas 1959), a progressive change at the end of the chirp, involving a slowing pulse rate and a lowering frequency, appears only in the courtship song.

Fifth, phrases or chirps may have a distinct two-part pattern, as in most *Orchelimum* and *Conocephalus* species, *Magicicada -cassini* cognates and *Teleogryllus* species (Alexander 1956, 1962, 1968; Zaretsky 1972; Hill 1974). These songs can be compared with the two-part trills described above. Some *Teleogryllus* species are somewhat intermediate in that their phrases are repeated rapidly without noticeable intervals, so as to sound like continuous two-part trills. Males of this group tend to answer one part of their two-part phrase with the other part (Alexander 1960). The *M. -cassini* cognates seem to reverse the order of the two parts of their calling phrase in the initial stage of courtship, and to reduce the length of the silent intervals, as do the *M. -decim* cognates.

Sixth, there may be a complex multipart song, as in *Amblycorypha uhleri* and its (undescribed) siblings (Alexander 1960; Walker and Dew 1972; Walker, unpublished) and *Scudderia septentrionalis* (Alexander 1956). The song of *A. uhleri* is an astonishing output for a signaling insect. While *Amblycorypha* females do respond acoustically to males, lone males of *uhleri* nevertheless repeat a programlike sound lasting 45-60 seconds each time they sing, its chief variables being the number of repetitions of certain parts (Walker, unpublished).

In light of the above analysis, the parts of this complex song may be more understandable. In its early phase the song consists of a two-part trill, the first part longer and with a faster pulse rate. This is followed by ticks and a series of phrases, each phrase slowing in pulse rate and dropping in frequency and intensity, as in the calling phrases of *Magicicada* species and *Orchelimum volantum* and the courtship sounds of *Allonemobius fasciatus*. *Amblycorypha* females, like those of several Tettigoniidae (Spooner 1968), seem to fly while initially approaching males, and males move frequently between songs. Perhaps the males in some such species have

evolved to deliver a series of sounds normally sufficing to attract step by step through much or all of her approach any responsive female near enough when the male begins song to reach him (or signal to him) before he flies to another singing location. Supporting this hypothesis are observations by Thomas J. Walker<sup>1</sup> that females are most likely to phonorespond acoustically to the second (slow) trill in the song, especially if the slow trill is preceded by the fast trill (evidently the long-range signal). The third and fourth parts of the song of *uhleri*, its ticks and gradually changing phrases, are produced during the male-female rapprochement (which is not yet completely understood), and variations in the numbers of their repetitions are chiefly responsible for variations in the length of a male's song.

Some recently published results with frogs are perhaps relevant to the above hypotheses and observations. Oldham (1974) found that two females of *Rana utricularia* (Oldham used the name *sphenocephala*, but see Pace 1974) approached only to within 60-65 cm of a recording of the "mating song." Perhaps, as suggested by Pace (1974) for *pipiens*, additional signals, which also characterize *utricularia* calls, are needed for closer approach. Littlejohn and Watson (1974), in a study of the responses of *Crinia* species to acoustical signals, suggested that "the introductory note in the mating call of *C. victoriana* . . . may be used for directionality . . . the more distinctive repeated notes [providing] . . . the temporal coding for specificity of response." The possibility that gross elements of rhythm, and perhaps frequency, may be more significant at longer ranges, with finer or at least different aspects of pattern more important at closer range, is a problem that must be taken into account in designing and assessing the results of experiments with phonotaxis. An additional problem in such experiments is that females of some species are probably sexually responsive only in the presence of several or even a large number of signaling males (see below).

Complex or multipart songs, then, may be expected to evolve (1) when males have reliable ways of discerning that responsive females are nearby (as when females signal acoustically or approach noisily) or are likely to be nearby (as in chorusing aggregations); (2) when likelihood of cuckoldry is high (as when the male-female rapprochement is mediated by alternating responses); and (3) when the signal structures optimal for long- and short-distance attraction of females are different. Interspecific interference leading to character displacement remains a possibility (Alexander 1969;

<sup>1</sup>Personal communication.

Walker 1974), as does the alternation of signals significant to the female and to the male (Alexander 1960; Spooner 1968; Morris 1970).

#### CHORUSING AGGREGATIONS AND COURTSHIP SIGNALS

Alexander (1962) noted that the long-range, pair-forming signals of crickets and their relatives must have evolved from short-range, simpler sounds, most likely functioning in a courtship context. This plausible argument nevertheless leaves several questions unanswered. First, what exactly is a "courtship context," and is it the same in all species? Second, why do so many crickets and grasshoppers have complex and distinctive acoustical courtship signals, while most katydids and cicadas lack them? Third, under what circumstances might courtship (short range) sounds evolve secondarily from calling (long range) songs (suggested for some nemobiine crickets by Alexander 1962)?

Alexander and Otte (1967b) discussed a cricket species, *Hapithus agitator*, in which the long-range calling sound has evidently been lost in part of the species' domain, leaving only a soft sound produced at short range and described as a courtship sound. We have since (Alexander and Otte, unpublished) located several species lacking calling songs which, like *H. agitator*, tend to live in sedentary colonies or clusters, often on certain plant species (unlike most crickets with long-range acoustical signals).

These observations imply that, when crickets begin to live in dense clusters, often associated with a narrowing range of host plants, they tend to lose their long-range signals. Presumably, this happens when searching without signaling becomes profitable for most males. This point may be reached when the species starts to live on one or a few patchily distributed plant species, when odors or sights rather than sounds become most effective at long range, or when the adult females become easier to locate by searching out oviposition, hibernating, or other sites.

Species that live on the ground communicate in a two-dimensional environment, tend to have more distinctive courtship and aggressive sounds, are more likely to be diurnal than those living in vegetation (except for species that fly readily, as with cicadas), and do not synchronize or alternate in large choruses. The prevalence of aggressive sounds can be explained partly as a correlate of burrow or territory ownership; and the diurnal behavior, as a correlate of

greater protection from predators, including burrows and retreats beneath surface litter, leaves, stones, logs, and so on.

The prevalence of courtship sounds is more difficult to explain. As contrasted with equally complex courtship involving chemical, visual, or tactual signals, acoustical courtship may also correlate with presence of retreats from predators, both because a courting surface-dweller usually has an escape location and because the importance of the retreat may make him more sedentary at closer range. (Such retreats may also be resources important to the females.) Males on vegetation are not so bound to special locations, hence perhaps can afford to pursue females during courtship.

Among species carrying out sexual behavior on vegetation, elaborate acoustical courtship signals have been known only in certain cicadas, namely the seventeen-year and thirteen-year species, in which the males compete in huge, dense choruses (Alexander 1968); their apparent absence in other cicadas, the above arguments on the evolution of complex signals, and the resemblance of the initial courtship sounds to calling all suggest that they have evolved secondarily.

The evolutionary order of appearance and loss of different kinds of signals provided by these observations and speculations is: (1) short-range signals (probably courtship) (numerous beetles and other insects may still be in this evolutionary stage: Alexander 1967), (2) long-range signals (pair forming) (most modern acoustical Orthoptera are in this stage), (3) loss of courtship in many species (e.g., most cicadas), (4) aggregation of signalers in a few species (for reasons not yet clear), (5) secondary evolution of courtship signals in some cases, (6) loss of pair-forming signals in a few of the aggregated species, and (7) loss of all acoustical signals in still fewer of the aggregated species.

These suggestions lead to the further implication that the long-range signals of insects did not arise as systems whereby groups of males could improve their ability to attract females from outside the group. Instead, they imply that the long-range signals of acoustical insects, today produced by both widely spaced and aggregated males, evolved in nonaggregating species, and that the leklike behavior of chorusing males in some species today is a secondary phenomenon. This hypothesis is supported by the rarity of acoustical species that aggregate clearly to sing.

It is worth noting here that mass chorusing is known only among vegetation-inhabiting species, and grasshoppers that crepitate in flight, although surface-dwelling species

exhibit phonoresponses (Alexander 1960, 1967). This still unexplained correlation may relate partly to the importance of densities and distribution of signalers in chorusing behavior. A chorus on vegetation is three-dimensional, while a group on the surface is two-dimensional, with peripheral members close to few other individuals. An approaching female or male on vegetation or in flight can receive simultaneously the signals of numerous males in a three-dimensional (or two dimensional) chorus, while a walking individual approaching a signaling group on the surface will be much more limited in the number of signalers it can hear at once.

#### WHY DO SINGING MALES AGGREGATE?

When Fisher (1958) analyzed sex-ratio selection as an aspect of parental investment, he pointed up the necessity of weighing in the obligate cost of every act or trait, in caloric expenditure as well as risk of death or disablement, in calculating its net benefit (see also Williams 1966b; Trivers 1972, 1974). For two reasons, this view of the selection process has an immense value for the study of social behavior. First, it focuses attention on the altruism of acts that raise the fitness of others more than that of the actor, and on the difficulty of the concept of acts neutral to reproduction. Second, it reminds us that group living or aggregation entails certain universal-expenses to the individual which must in every group-living species be overcompensated by advantages, none of which is universal (Alexander 1974).

Two disadvantages of grouping seem universal: increased competition for resources and increased likelihood of disease and parasite transmission. Perhaps no others are universal, although some may be frequent. For example, groups sometimes draw the attention of predators.

Most of the benefits assumed in the past for group living are wrongly based upon group effects detrimental to individuals. Elsewhere (Alexander 1974), I have argued that there may be only three categories of benefits from forming groups: (1) predator protection, either because of group defense or because the opportunity is afforded to place some other individual's body nearer the predator; (2) nutritional gains when utilizing food, such as large game, difficult to capture individually or clumped food difficult to locate; and (3) use of clumped resources (see fig. 3). Students have noted that

two cases of grouping are difficult to fit into these categories: (a) communal winter clusters of flying squirrels, which may chiefly gain from reducing temperature loss (Muul 1968); and (b) the V-formation of migrating waterfowl, which may gain from combining their information about the migratory route (Hamilton 1968). Biologists studying mating aggregations, and social biologists in general, have not considered the severity of the problem of identifying the advantages of grouping behavior to individuals.

This brings us to the second major question relevant to this essay. Males of acoustical insects intensified their competition for females as their signals evolved to be effective at increasing distances. We can easily understand that there might be distances beyond which it was unprofitable for males to disperse to avoid singing near competitors. But how have males come to aggregate during signaling, as they do in some species of katydids, cicadas, and fireflies? Such aggregation, I believe, necessarily increases the intensity of competition for females once they have been attracted to the aggregation.

#### KINDS OF MATING ASSEMBLIES

There are two major classes of mating assemblies. First are the clusters of males competing to mate with females where the females are already aggregated, or are likely to aggregate: emergence sites, oviposition sites, feeding sites, hibernacula, and so on. Excellent examples are (1) the scavenging flies (*Scatophaga* spp.), studied extensively by Parker (1970) in England, whose males compete violently for females at the dungpats where oviposition occurs; (2) the brown paper wasp (*Polistes fuscatus*), which mates on the nest or near hibernacula (West 1969); and (3) cicada-killer wasps (*Sphecius speciosus*), whose males emerge first and set up territories where emergence holes are most dense (Lin 1963). These are not necessarily signaling groups of males, nor are they easily perceived as direct precursors of signaling male aggregations (the situation most difficult to explain), since they seem more closely linked to female signaling. They are clearly examples of males competing for already aggregated females or controlling areas containing resources valuable to the females.

The second kind of mating assembly, which remains puzzling, is that (such as the periodical cicadas and Melanesian fireflies) in which the signaling males definitely

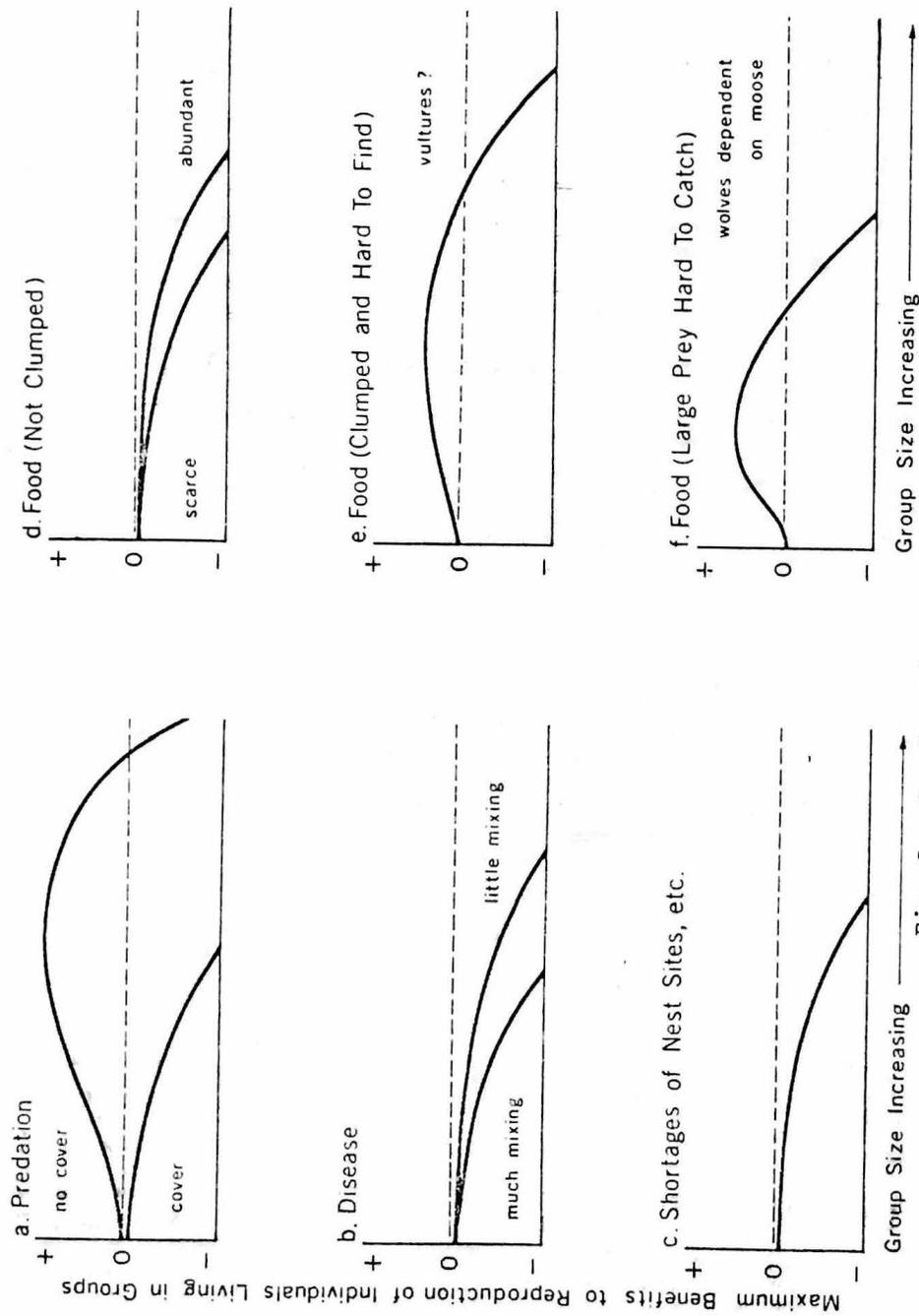


Fig. 3. See legend on next page.

aggregate (whether or not they synchronize or alternate in chorus), but not necessarily where the largest number of females is expected to occur, and which appears to attract large numbers of females from outside the group. In some cases, such as the snowy tree cricket in which males regularly synchronize or alternate in chorus, it is not clear whether or not males actually aggregate or whether or not they regularly attract females from outside the chorus.

What are the males in these cases doing? In some species males may in fact be aggregating where the females are likely to be, but that is not obvious to us. For example, Spooner (1968) found that males of the katydid, *Inscudderia strigata*, aggregate on their food plant, *Hypericum strigata*. Marianne N. Feaver<sup>1</sup> has evidence that males of the synchronizing katydid, *Orchelimum vulgare*, aggregate and sing in the vicinity of clumps of those plant species in the stems of which the females are most likely to oviposit. Morris (1972) has shown that males of *O. vulgare* are attracted to the songs of other males. The last two observations together suggest that both females and males of *O. vulgare* probably use male songs (as well as other cues) to locate appropriate breeding sites. Even if the females are attracted principally by the songs of the males, rather than by the presence of the appropriate plants, the situation is easy to understand.

The mating assemblies of periodical cicadas and Melanesian fireflies, as well as those of some dipterans and other insects (Downes 1958, 1969), take on the appearance of "lek," or "arena," behavior in various vertebrates. Lek-breeding vertebrates include species such as the Uganda kob (Leuthold 1966; Buechner and Roth 1974), the sage grouse (Patterson 1952; Wiley 1973), the European ruff (Hogan-Warburg 1966), and many others in which the males form groups and signal visually, acoustically, or both ways in special arenas, or courts, which are apart from the nesting or feeding grounds and do not seem to represent locales where the females are expected to aggregate for reasons other than mating itself (Lack 1968). In other words, the females come to these groups of males as they do to the choruses of the males in at

<sup>1</sup>Personal communication.

Fig. 3. Benefits to the reproduction of individuals from living in groups. Each curve is intended to approximate the maximum benefits likely from each context of group living, the actual benefits in any case representing a summation of the effects of predation, disease, and shortages of nest sites, food, and other resources. See also Alexander (1974).

least periodical cicadas.

Explaining insect choruses and explaining lek-breeding behavior seem to be part of the same general problem. Much has been written about vertebrate leks, but there seems to be no general theory of their origins. Nevertheless, valuable comparisons can be made between the reflections of vertebrate biologists and those of entomologists on this subject, and I shall use them both in this discussion.

#### THEORIES OF LEK-BREEDING BEHAVIOR

Lack (1968) stated that "communal leks" have evolved nine times in birds. In all cases, the males signal elaborately, most with exaggerated postures, some with bright plumage, and some principally with calls. Bird leks occur at traditional places used generation after generation by long-lived birds that presumably remember them. The only known case of similar behavior in insects is the recurrence of swarms of honeybee drones year after year in the same locations (Zmarlicki and Morse 1963; Strang 1970). This case is a puzzle, for no drones survive winter, and the queens that come to the swarms are also young virgins on their first extended flights. It is unlikely that chemical markers could be effective year after year. The most plausible explanation, based on data in the above publications, is that certain kinds of places, such as "clearings among trees," "slight summits" in open areas, or "areas marked by some form of vertical relief, whether it be forest, single trees, or buildings" (Strang 1970) are selected by both drones and queens, with drones and queens both also attracted by the presence of drones. But an explanation of the kinds of places selected for such aggregations does not explain the aggregations themselves.

Lack (1968, p. 155-56) supposes that arenas of bird leks are reused because they previously proved safe from predators. He notes that the behavior of the performing males of a lek appear "in all the species concerned" to be "adapted to reduce the risk of predation so far as possible." He even suggests that early detection of approaching predators, "may, indeed, be the main advantage of communal display," adding that "it perhaps helps the females to find males in breeding condition. . . ." He also suggests that "the final stage, from solitary to communal display, would follow if the males tend to display within earshot of each other, and if a clear grouping increases the chance, either of their detecting

predators or of each male acquiring a mate."

Lack's predator explanation is important to us because it was taken up by Spieth (1974) to explain apparent lek behavior in Hawaiian *Drosophila*, and because Walker (1969) implied a similar explanation for the synchronized choruses of snowy tree crickets. If predation is invoked as the principal or primary cause of aggregations of males at mating time, then it will be difficult to suppose an historical relationship between lekking behavior and the widespread phenomenon of aggregations of males competing for females at emergence, oviposition, nesting, feeding, or overwintering sites. Yet it seems difficult to deny such a relationship.

Perhaps predation is invoked as an explanation for "true" leks because no other explanation has been apparent. But the presence of obvious adaptations to reduce predation may only be evidence that leks are particularly vulnerable to predation. One might as well argue that, because flocks of birds and herds of ungulates are almost always seen feeding, they must have originally formed their groups in order to feed more effectively. Unfortunately, this is the argument most prevalent in the literature, probably because feeding is obvious while predation in most cases is not (Alexander 1974).

Furthermore, for a long time it was not acknowledged that special advantages to individuals compensating the automatic disadvantages must always be present to account for grouping. So long as this requirement was waived, it was possible to interpret as a "feeding advantage" nothing more than a greater efficiency by the group in utilizing the food available in a particular area even if some individuals suffered; no one felt compelled to explain why these individuals didn't leave the group. In a similar fashion, Leuthold (1966) suggested that the leks of Uganda kob "offer certain advantages, such as providing a social organization and a spacing mechanism to the population and ensuring maximum efficiency of reproduction." Wynne-Edwards (1962) saw leks as "a method of controlling density of breeding birds." These explanations describe advantages to the population without explaining how the individuals of the population came to behave as they do (see also Lloyd's 1973a and b evaluations of similar arguments for firefly aggregations).

Brown (1964) used the sage grouse as a principal example in an effort to give a general explanation of leks; his explanation is similar to that advanced by Crook (1965). Brown stressed that for the sage grouse (from the work of Patterson 1952; see also Wiley 1973) food does not appear to

be a critical factor in breeding behavior. There is no parental feeding of offspring or evidence of nutritional deficiencies in either adults or young during the breeding period, and nearly all of the mortality of the young seems to result from predation. Thus not only is the male evidently unimportant as a parent, his absence from the nesting area "is advantageous by decreasing conspicuousness of the family, and by reducing the potential prey population there (even if he were protectively colored)." Brown goes on to say:

Thus freed from the responsibilities of protection and care of the nest and young the males have full freedom of competition for the fertilization of females. To this end have evolved the elaborate and conspicuous plumage and display in the males and the lek system of mate selection. Once evolved, the lek system tends to perpetuate itself through the demonstrated preferential success of the dominant males within the lek.

Brown's explanation does not face the question of how the individual males gain by initiating lek behavior. It does not explain, therefore, how tendencies to aggregate actually evolved. One wonders again why the males do not search out females individually rather than join a group of competitors who presumably will strive against one another to obtain whatever females may be attracted to the group.

Both Brown and Crook stress the value to the females of lekking birds of having the ruckus of intermale competition in the polygynous breeding system take place, with a minimum of risk, time, and effort, away from her nesting ground. There seem to be two ways by which this might have come about. Males may have originally held territories on the nesting grounds of the females. As long as the males were providing some benefits other than genes to the females, or at least were not affecting the females' breeding in a deleterious fashion by their presence and their competition, this system might have persisted. If, however, as Lack and Brown imply, the males were not only providing the females with no direct or indirect parental benefits, but were causing deleterious effects such as predator attraction, then females would be favored which tended to move away from the breeding ground to nest. In this hypothesis the traditional nature of the breeding grounds and considerable differential mating success among males could both precede the lek system as such. In a similar hypothesis females may have evolved early to remove themselves from their nesting ground so

effectively with the onset of the breeding season that it became unprofitable for males to seek sexually responsive females there.

While these explanations may account for the separation of mating and nesting areas, they fail to account for aggregations that seem to serve no function for either sex other than mating. To solve this problem it may be profitable to consider certain general questions related to sexual selection (see also Otte, in press; Borgia, unpublished).

#### PARENTAL INVESTMENT, RESOURCE CONTROL, AND SEXUAL SELECTION

Among acoustical insects the only species in which the males are likely to be correctly viewed as investing parentally are the following:

1. some burrowing crickets in which the male gives up his burrow to a female after mating with her (West and Alexander 1963), and a South African species, whose males may even sometimes allow females with which they have mated to consume their bodies (Alexander and Otte 1967a);
2. some katydids in which the male's spermatophore is huge, as much as one-fourth his body weight (Busnel, Dumortier, and Busnel 1956), consisting chiefly of a gelatinous mass consumed by the female and perhaps properly viewed as a protein meal contributing to successful egg production and oviposition (see also Thornhill 1974).

When males do not invest parentally, one parameter of mate selection by females is removed from significance, and because polygyny is a correlate the reproductive variance of the males is likely to be greater than that of the females (Bateman 1948; Trivers 1972). This increased reproductive variance is important to the females, since it may be reflected in the reproductive success of their sons. Females in polygynous species in which the males do not invest parentally, including nearly all acoustical insects and fireflies, will thus evolve to judge males by their prowess in activities related to high mating success; this kind of selection will in turn reinforce trends toward intense mating competition among males.

Males of polygynous species may gain matings by controlling resources valuable to females (Sherman, unpublished) or by controlling areas where females are dense (Le Boeuf 1974). If males are unable to gain matings in either of these

fashions, then another set of parameters by which females might usefully judge males has been eliminated. Males in such species may evolve to become either better searchers or better signalers. Searching seems the more likely strategy when females are relatively sedentary, as in web-building spiders. Evolution of signaling by males also seems unlikely in polygynous species if the males cannot control resources valuable to females or areas where females are dense. The female who mates with a male that has told her only that he is a sexually responsive male of her species has not been very selective.

Females in species whose males do not invest parentally and cannot profitably control resources valuable to the female or areas in which females are dense must judge males on their ability to locate or attract females and to mate successfully with such females. Female criteria for mate selection might include a male's vigor and searching ability, the intensity, persistence, or excellence of his signal, or the presence of other females in his vicinity.

Females in such species are also likely to gain by encountering the largest number of sexually active males in the shortest time with the least risk, thereby having the greatest opportunity to compare males and mate with a highly successful individual. The importance of the opportunity for the female to select among males may lead to tendencies by females to become more responsive in the presence of numerous males, to refuse to mate with lone males, or to seek out regions in which males are most dense. As a result of such behavior by females, males in aggregations or groups may do all or most of the mating. Larger aggregations or aggregations attracting females from greater distances may secure more females per male than others (see also Otte, in press), providing a reasonable selective background for Lack's (1968) second hypothesized function of leks (above).

The importance of the male signals in this model suggests that chorusing synchrony, which in *M. cassini* increases a group's attractiveness to females (Alexander and Moore 1958), is advantageous to each male because it increases the number of females attracted to his group. It implies that in some cases aggregation and synchrony may have evolved together in resource-based as well as non-resource-based male aggregations. Furthermore, it is at least possible that, in both acoustical insects and lek-breeding birds and mammals, female sexual selection may be powerful enough to cause breeding aggregations even though in such groups each male's and each female's susceptibility to predation is increased.

The breeding aggregations of periodical cicadas, honeybees, and the lek-breeding vertebrates mentioned above are likely to have been forced by female sexual selection. In birds and mammals the same locations may be remembered from year to year by both sexes; in honeybees certain kinds of terrain may be used by successive generations; in *Drosophila* certain locations on plants may be used. In acoustical insects the locations of choruses within habitats are less predictable, with areas of greatest emergence and relative predator invulnerability perhaps more important than other factors.

The term *lek* is often applied to the places where the animals in question aggregate, rather than to the aggregations themselves or their activity (e.g., Wiley 1973; Spieth 1974; Buechner and Roth 1974). But the significant generality appears to be the kind of aggregation rather than the specific location. If leks were localities, the term could not be applied easily to most insect mating assemblies. *Lek*, however, is derived from Swedish and implies play (*leka*), activity (*-lek*), or copulation (*leker*).<sup>1</sup> Thomson (1964) and others confirm this usage (i.e., as a kind of activity) and Otte (in press) uses the term in this apparently appropriate fashion. The words *arena* and *court* may be retained to describe the locations of leks.

*Lek*, then, appropriately refers to mating aggregations or assemblies, regardless of their locations or permanence of location. Some leks may have no function other than mating for either sex; they may be designated as non-resource-based or purely mating leks. Although such aggregations have been suggested previously, for lek-breeding birds and mammals and by the term *mating assemblies* (for example, Downes 1958 concluded that dipteran swarms "serve to concentrate the population, otherwise widely dispersed . . ."), it appears that such designations were casual results of our ignorance of the difficulties in explaining the adaptive significance of aggregations of males through benefits to individuals, rather than evidence of perception of the unusual selective background of strictly mating aggregations.

Leks with no function other than mating will be difficult to identify. Their failure to be associated with traditional locations in insects has probably concealed them in that group, where they should be prevalent owing to lack of parental investment by males. The possibility always exists that gain can be realized from tendencies to concentrate leks on food or oviposition sites, or in locales that are

<sup>1</sup>Ann E. Pace: personal communication.

relatively predator safe, even for individuals not chorusing or mating. Thus mating clusters of the cicada, *Diceroprocta lympusa*, in Florida resemble those of *Magicicada* species but characteristically occur on an aromatic shrub, Hercules' Club (*Xanthoxylum clava-herculis*) (Alexander and Moore, unpublished data). Dipteran swarms occur near oviposition sites, but "markers" resembling such sites may suffice (Downes 1969). Hence mating assemblies tend to shift in and out of the category of being purely products of the pressure by females for opportunities to compare males in the absence of male control of resources, and often it will be difficult to characterize mating aggregations in regard to these questions.

I suggest that resource-based mating aggregations, in which males cluster around resources valuable to females or in regions where females are dense for reasons other than mating alone, be included in the concept of *lek* whenever there is reasonable evidence that the males actively aggregate—that is, whenever males and groups of males can be shown to attract other males as well as females. As with purely mating leks, such aggregations are likely to involve much sexual selection by females, and to reflect a history of females favoring groups of males over single males and larger groups over smaller groups. Males in resource-based leks as well as those in non-resource-based leks are likely to gain from cooperating to increase female attendance at the lek.

#### EVIDENCE OF SEXUAL SELECTION IN CHORUSES

To human observers, male insects in choruses appear quite similar to one another, and, although they are more difficult to observe individually than birds and mammals, there seems to be no evidence of the incredible mating differentials that occur in vertebrate leks (e.g., Wiley 1973). Vertebrate males differ obviously from insect males in several ways that could account for their greater differentials in mating success.

First, lekking vertebrates are iteroparous across two or more breeding seasons, while for chorusing insects the breeding season is short and continuous, extending across a few weeks or months, and often essentially coincident with the period of adult life. This means that individual recognition is less likely to be important in insects and that male insects are more restricted in ability to progress gradually toward the best location in a lek as they grow, learn, and

increase in dominance status.

The long adult life and iteroparity of vertebrates also provide multiple opportunities for the favoring of alleles improving the ability of their possessors to utilize innumerable environmental variables to adjust their phenotypes advantageously in the race of sexual selection.

Finally, young vertebrates receive considerable parental care from at least the female, as compared with chorusing insects. This parental care is an additional source of phenotypic differences between males (hence their differential reproduction as a result of selection by females) even after genetic uniformity among males is approached as a result of extreme polygyny. Some differences in male success may depend chiefly upon differences in the maternal behavior of their mothers, including differential investment by the mother in offspring of the two sexes (Trivers and Willard 1973).

In dipteran swarms, mating typically requires but a few seconds, and a male scarcely needs to drop out of the swarm to mate (Downes 1969). Cicada matings, on the other hand, sometimes occupy two or three hours, and the process of pair formation may take equally long (Alexander 1968). This particular feature of cicada choruses suggests that more selection of mates by females may be going on in the chorus than is evident. If so, we can only speculate about what attributes vary among males, for variations are not obvious to the human observer, as they are in bird leks.

If the unusually long period of copulation is due to the advantage to the male in removing the female from the chorus as long as possible, then perhaps the female's coyness is related to the relatively great investment she makes with whatever male she mates, considering the likelihood that she will be forced to remain in copula with him for a long period and the fact that females mate more than once (Alexander 1968). Again, how she might identify a suitable or superior male is totally unknown. Alternatively, the long period of "courtship" may reflect the value to a male of remaining near any female, because of the probability that she will become sexually responsive before they are accidentally separated. Unfortunately, because we were not aware of these problems when most of the periodical cicada work was done, there are no data from which to test these or other alternatives. The question of sexual selection within mating aggregations of insects thus remains open.

## IS KIN SELECTION INVOLVED IN CHORUSING AGGREGATIONS?

Wild turkeys are reported to travel in sibling groups during the breeding season, with most males defending a dominant brother while he mates (Watts 1969; Watts and Stokes 1971). Chorusing insects are unlikely to recognize their brothers and profit by kin selection in the fashion suggested by the turkey example. There is a sense, however, in which average relatedness of males could be involved in their chorusing tendencies. Both sexes may gain from outbreeding, but the lower intensity of sexual competition among females in polygynous species means that they are more likely to evolve special behavior promoting outbreeding, whereas males profit from mating with any available responsive female. If cicada populations are somewhat viscous, we may envision groups of males evolving to sing where they emerge, and cooperating as signaling groups to outcompete other groups of males emerging elsewhere. Even if females disperse to mate, a tendency to oviposit near where they mate could lead to males being more closely related to members of their natal group than to males elsewhere. If females gain more from outbreeding than do males, their dispersal to this end may promote the tendency of males to compete as groups to attract females moving between choruses.

## CONCLUSIONS

With the exception of the recent work of a few authors, studies on insect acoustical behavior, as with studies on mating assemblies in general, have tended to ascribe function at the population level rather than the individual level, and thus have failed to discern evidence of male-male competition and to elucidate functions in sexual selection.

Synchrony, alternation, and other phonoresponses which sometimes occur in insect choruses appear to be mostly explainable as competitive interactions between neighboring males. Insect choruses are probably most often incidental effects deriving from the aggregate of such responses when large numbers of males are for one reason or another closely spaced. Most mating "assemblies," including insect acoustical choruses, may ultimately be explained as males competing for females at oviposition, hibernating, feeding, or other locations where females are likely to occur.

Among choruses of acoustical insects, those most difficult to explain in this fashion are produced by the periodical

cicadas. Males are known to be attracted to choruses in large numbers, and many if not most females appear to be attracted from outside the choruses; there is no obvious control by males of resources valuable to females, and no obvious tendency to form choruses where females are most dense. A model is proposed which suggests that males in these species have evolved to compete by cooperating in groups, including chorusing in synchrony, because of the importance to the females of comparing males at mating time, and resulting tendencies in females to mate only where males are dense. Such female selection is expected to force male aggregation even in the absence of ability by males to control resources valuable to females or areas where females are likely to be dense, and even, sometimes, when individual males and females both are thereby rendered more susceptible to predation. Once mating is largely or entirely restricted to male aggregations, either resource-based or non-resource-based (i.e., those in which mating is the sole function for both sexes), every male profits from cooperation, such as synchrony in chorus, which increases the number of females attracted to his particular group.

In insects, mating aggregations cannot be restricted to traditional (remembered) sites, as they appear to be in some vertebrates, and there is as yet no evidence of the enormous differences in male reproductive success reported in bird and mammal leks. In both vertebrates and invertebrates, however, the *lek* concept is appropriately applied to actively aggregating male groups within which all or nearly all mating occurs.

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