

Evolution of Cricket Songs

DANIEL OTTE

Academy of Natural Sciences, Philadelphia, Pennsylvania, 19103

"It would seem like a very foolish whim of nature to provide many insects with elaborate sound-producing mechanisms if they could not hear their own music."

B. B. Fulton 1928

About 250 million years ago a silent world, or at best a world with a few grunts and groans, was replaced by a world full of diverse musical sounds. True crickets were among the first musicians on the planet and were part of the nocturnal circumambience for some 150 million years before there were human ears to hear them. Long before birds, but perhaps contemporary with amphibians, crickets were producing their chorus out in forests, grasslands and swamps. Long before the glaciers pushed across the American continent, long before there even was a human species, crickets were singing in deep verdent ravines in the Hawaiian islands. Their songs evolved in multifarious directions—becoming faster and slower, less complicated and more complicated, lower pitched and higher pitched.

That songs evolve is not disputed, but that they evolved in certain directions or that song structure is due to the action of certain forces, or that differences are due to random evolutionary events, or that they are the result of selection, or that they arise mainly in association with speciation—these are matters for speculation, debate, and analysis. These are matters whose solution can have a bearing on general theories of how diversity arises and how behavior changes.

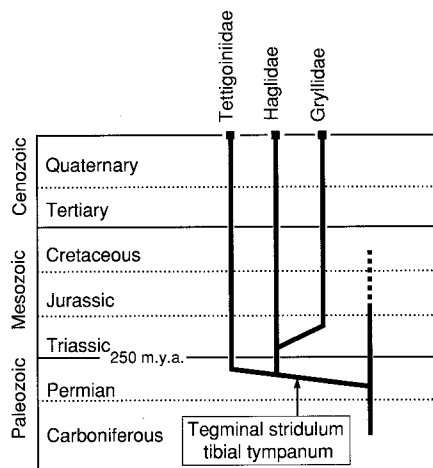


Fig. 1. Origin of the forewing stridulum and foreleg tympanum in relation to the origins of major ensiferan groups (after Sharov 19xx).

Biologists have studied cricket songs intensively for over fifty years. Because they are audible to almost everyone and because crickets are amenable to sophisticated neurophysiological techniques and behavioral experimentation, and because crossing of species makes genetic analyses feasible, the cricket communication system must be ranked as the most thoroughly understood communication system in the animal kingdom.

In this paper I discuss certain aspects of evolution of acoustic behavior. Some may argue that such a discussion must rely more on clairvoyance than on hard evidence. But the accepted theories, principles, and generalizations about evolution of behavior are based largely on systematic comparisons of anatomy and behavior of recent organisms and not only on historical (paleontological) data or on experiments (mainly genetical) on living organisms. It has been claimed, for example, that for behavior "direct evidence about the ancestral species, which morphologists can obtain from paleontology, is not available; comparison between living taxonomic units is thus the only method available, and this is naturally indirect." This is incorrect in many cases, for there are many instances in which, although action does not fossilize, the tools of action and the products of action do. And in the case of orthopteran sound production, the tools are so specialized that there can be little doubt about how they were used or what they were used for. As I will show in a section below, the fossil record has been misleading even to experts in orthopteran palaeontology and can be misinterpreted without comparative information from the extant fauna.

The sound system, more or less as we see it today was already present in the ancestral lineage which gave rise to Gryllidae and Tettigoniidae by the end of the Permian some 250 mya (Fig. 1). The tympana and stridula are too much alike and too complex in structure to have appeared more than once in their present form. Major differences existing among recent species are due to secondary reduction and modification.

Acoustical communication subsequently was lost many times (Otte and Alexander 1983, Otte 1990). Numerous modes of making sounds evolved in Orthoptera, most of them in the grasshoppers, but none has proved as durable or universal or as unvarying as the forewing-file foreleg-ear system. This is virtually the only system used by ensiferans, which gives the impression that it involves a mechanism that is difficult to improve upon (Zeuner 1939, Alexander 1962, Sharov 1971, Walker 1989: 2).

Evidence that the evolution of cricket communication has taken particular courses comes from a comparison of more than 700 species tape recorded over the past 20 years mainly by Walker, Alexander, and Otte in North America, Australia, Africa, and various Pacific islands and the Caribbean.

Crickets have exploited most available signalling channels open to insects (Huber et al. 1989 and refs therein). In lineages leading up to true crickets, olfaction, touch and substrate vibration probably preceded vision and hearing as important communication channels. Gryllidae, Haglidae, and Tettigoniidae represent the branches of a lineage that exploited long distance acoustic broadcast of signals perhaps earlier than any other animal group. Subsequently many ensiferan lineages lost or partially lost acoustic signaling, by returning to olfactory, visual, or substrate vibrating modes of signaling.

Together this body of work allows us to make some general remarks on the function and significance of songs:

1. Acoustic behavior is connected with reproduction and appears to be the principal mode of non-contact information transfer between males and other individuals (Alexander and Walker refs here, Huber et al. 1989 and references, Loher and Dambach 1989, Doherty 1991).

2. The song of each species is quite different from those of others singing in the same place and at the same time (Fulton 1930, 1931, 1932, 1934, Alexander 1960, 1962a, 1962b, Walker 1957, 1964, Otte and Alexander 1981, Otte, Alexander and Cade 1987, Otte 1992).

3. Song divergence among species usually precedes visible morphological divergence. Previously unrecognized sister species have been recognized in almost all groups in which acoustic signals have been studied (Alexander 1956, 1957, 1960, Alexander and Thomas 1959, Alexander and Bigelow 1960, Otte and Alexander 1983, Walker 1957, 1962, 1964, 1974, Love and Walker 1979, Nickle and Walker 1974, Fulton 1928, 1933, 1934, 1952, Otte 1992).

4. Song differences in the majority of species tested prevent (or reduce) interactions between males and females of different species as shown by the fact that individuals respond almost

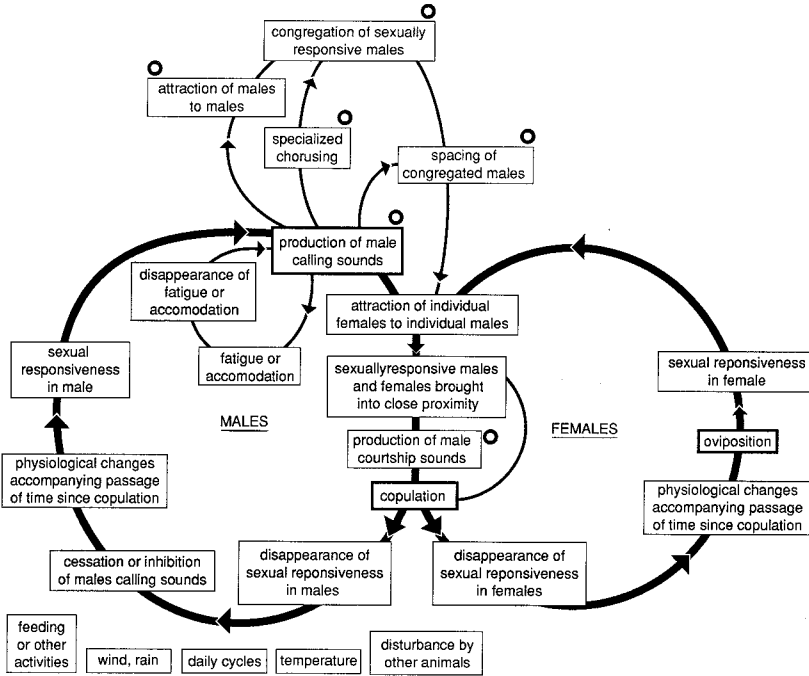


Fig. 2. The breeding cycles in *Gryllus* (modified from Alexander 1962). The components of the cycles that involve acoustic signals are indicated by an open circle. They indicate the contexts in which signal evolution must be considered.

exclusively to the songs of their own species. Evidence on this point is of three kinds: (a) under appropriate temperature conditions both sexes respond only to the call of their own males (Busnel and Busnel 1954, Walker 1957, Cade 1975, Hill, Loftus-Hills and Gartside 1972, Ulagaraj and Walker 1973, 1975, Forrest 1983, Doherty and Callos 1991, Doherty and Storz manuscript); (b) males of species which synchronize their songs do so only with conspecific males (Fulton 1934, Walker 1957, Otte, Alexander, and Cade 1987); and (c) males of species which alternate do so only with conspecific males (Otte and Cade 1983, Otte in prep.; Otte, Alexander, and Cade 1987).

5. Although crickets communicate (in the strict sense) only with their own species, their signals are exploited by predators and parasitoids (Cade 1975, 1981, 1984, Cade and Rice 1980, Sakaluk and Belwood 1984, Walker 1964, 1992, Lakes-Harlan and Heller 1992).

6. The song features used by crickets to recognize their own kind vary from species to species: the crucial parameters used for discrimination may lie in the structure of individual pulses (see below for definition), in the pulse rhythm, the structure of the chirp, the chirp rhythm, or in a combination of several, usually temporal features (Walker 1957, 1962, Doherty 1991, Hubert and Thorson 1985, Hill 1974, Doolan and Pollack 1985, Doherty and Hoy 1985, Stout, DeHaan and McGhee 1983, Weber 1984).

7. The song parameters which are used by females to find their own males are remarkably consistent within species. Geographical variation is minor compared to degrees of difference which exist between species (Walker 1963). (But some exceptions are noted below).

8. Taxonomic discrimination of species based on song is usually easy and reliable, but may be

confusing when (a) species have two distinct calling songs, e.g., *Teleogryllus*, *Thebella*, *Neogryllopsis* (Otte and Alexander 1983, Otte and Cade 1983, Otte, Toms, and Cade, 1988); or (b) different species do not sing at the same place and/or time, e.g., *Gryllus pennsylvanicus* and *G. veletis* (Alexander and Bigelow 1960); *Aritella curtiperennis*, *A. murwillumbra*, *A. ulmarra*, and *A. fabria* (Otte and Alexander 1983); Hawaiian *Laupala* and *Anaxipha*—numerous cases (Otte 1992).

9. Cricket songs are not learned. The song rhythm, once produced, can be changed substantially only by changing the temperature or by mutilation (Fulton 1928, Alexander 1960). (But see section — below).

10. Acoustical signals operate mainly between adults, but aggregations of nymphs with adult males suggest they also respond to male calls.

11. Hearing is achieved mainly by the tympanal organs on the forelegs (Atkins et al. 1989), but the cerci and subgenital organs of the middle tibiae can respond to low intensity, low-frequency vibrations, especially when these are transmitted through the substrate (Wever and Vernon 1959). The subgenital organs may be used in communication in a few species that have lost their acoustical signals.

Breeding System

The usual cricket breeding system is one in which one male fertilizes the eggs of one female or of several females in successive sexual acts. There is no association of the sexes for the purposes other than mating. Fertilization is internal. Adaptations ensuring efficiency of mating include characters for discovery of the other sex, for advertisement of a sexual situation, for

stimulating or predisposing the female to coition for prehension of the females by the males, and for combat and threat. In crickets the sperm are transferred by a vesicle, the spermatophore, produced and filled by the male and attached to the female. This empties upon exposure after a pair has separated. The device allows males to transfer large amounts of sperm in one short act, but it opens the possibility for females to manipulate the sperm and the delivery vesicle in ways that benefit her but which may not benefit the males (see Funk 1989, Gwynne and Morris 1983, Eberhart 1984, Sakaluk 1987; Sakaluk, Morris and Snedden 1987). The participants in the cricket breeding system and the cyclic nature of physiological states are depicted in Fig. 2.

Song Structure and Pattern

The basic unit of sound discernible to the human ear is the pulse; it is the burst of sound which results from a rapid train of tooth strikes, produced during one closure of the wings. Rarely, the wings are closed slowly enough for individual tooth strikes to be heard (*Amphiacusta* sp.).

A simple, continuous sequence of pulses is believed to be the most elementary (primitive) of cricket songs and repeatedly gave rise to songs with more complex structure. It is probable that the calling song

Table 1. Incidence of different song types in Australia, Africa, Hawaii and New Caledonia (N, and percent of total). (ch = chirp; ch l = long chirp; tr s = short trill; tr i = intermediate length trill; tr l = long trill; tr = trill; mix ch = mixed chirp; mix tr = mixed trill; mix tr/ch = mixed trill and chirp (Data from Appendix 1).

	AUS N(%)	AFR N(%)	HAW N(%)	NC N(%)
ch	104(49)	51(48)	30(17)	17(41)
ch l	3(1)	6(6)	34(19)	9(22)
tr s	10(5)	2(1)	21(12)	2(5)
tr i	1(.5)	0	29(16)	5(12)
tr l	0	0	4(.5)	0
tr	62(29)	16(15)	58(33)	8(20)
mix ch	28(13)	13(12)	0	0
mix tr	5(2)	9(8)	0	0
mix tr/ch	0	9(8)	0	0
Total	214	106	176	41

Table 2. Summary of data given in Appendix 1. Mix = mixed trills and chirps.

	Austr N(%)	Afr N(%)	Haw N(%)	N Cal N(%)
all ch	107(50.0)	57(53.8)	64(36.4)	26(63.4)
all tr	73(34.3)	18(17.0)	112(63.6)	15(36.6)
mix	33(15.5)	28(29.2)		

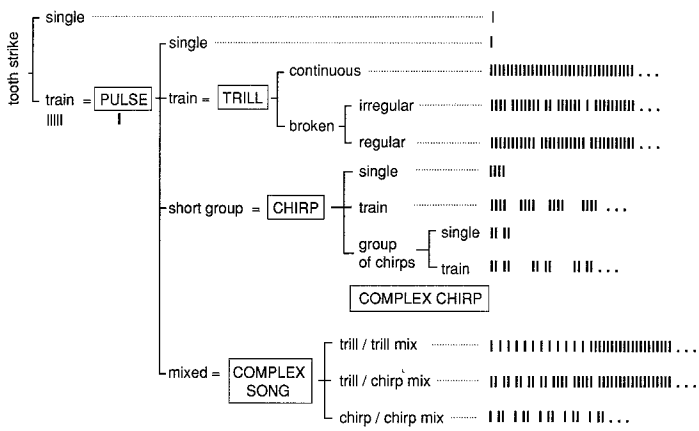


Fig. 3. The smallest audible unit of sound is here called a pulse. Long trains of pulses are termed trills. Short trains of pulses (small groups of pulses) are termed chirps. Complexity in songs is generated by varying the pulse rate and or the intensity within trills or chirps (Alexander 1962a).

primitive acoustical signal was probably some kind of trill; these are the simplest kinds of signals from the physiological, morphological, and information-carrying point of view and they are produced by activities most similar to flight movements of crickets; they are also the most abundant kinds of signals found in crickets today.

Evolution of Pattern

Figs. 3-5 depict the major elements of cricket songs as discussed in this paper. Starting from the presumed primitive condition—a simple pulse train — comparative data from numerous species indicates how the components which define song patterns in crickets probably evolved.

Changing the Pulse Period (Pulse Rate)

There are two ways in which pulse period can change; the first is probably common and the second rare. (a) Successive pulses are loosened or tightened (this is the predominant mode of pulse rate modification in crickets) or (b) alternate pulses are dropped, leaving a train of more widely spaced pulses (this mode of change may be rare; it is known from two Hawaiian Trigonariinae—*Anaxipha olomea* and *Prolaupala kukui*).

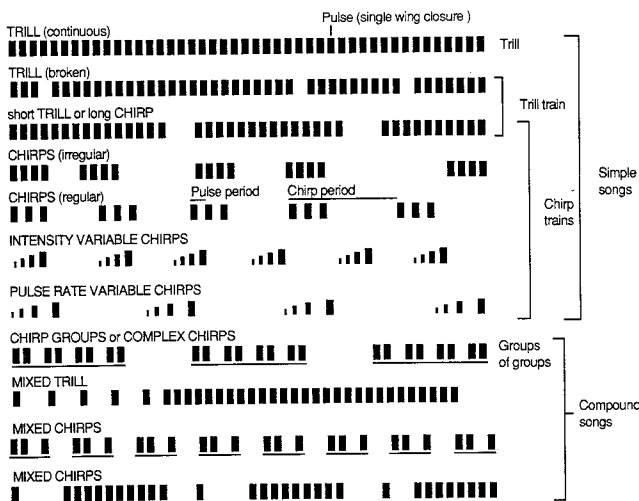
Loosening of pulses results in a reduction of the pulse rate.

Tightening of pulses is of three general kinds: (a) tightening of all pulses, thereby producing a general increase in pulse rate or (b) tightening of pairs of pulses to produce 2-pulse chirps, (c) a graded tightening or loosening of pulses to produce accelerating or decelerating songs. I know of no cases where, starting from a simple pulse train, spacing of pulses involves groups larger than 2 but smaller than entire pulse train (entire trill or entire chirp). For example, I know of no cases where three or four consecutive pulses in a longer pulse train are tightened to form triplets or quadruplets, respectively. Two-pulse chirps are produced when alternate intervals, e.g., intervals 1, 3, 5 etc. are tightened. The earliest stages in pulse pairing can be seen in some *Ornebius* species where differences between intervals 1 and 2 are just barely discernible (*O. wanella*). Related species (*O. immarna* and *O. gumbalera*) show increasing tightening within doublets.

Pulse tightening or loosening may be uneven: some species have accelerating pulse intervals (•••••) others decelerating intervals (•••••). Decelerating intervals seem to be especially common in Gryllinae and is associated with increasing sound intensity.

Reducing the pulse period by dropping alternative pulse rates is known in *Prolaupala kukui* and *Anaxipha olomea*.

Fig. 4. Further depiction of the major elements and types of songs as discussed in this paper.



PULSE AND CHIRP CHANGES

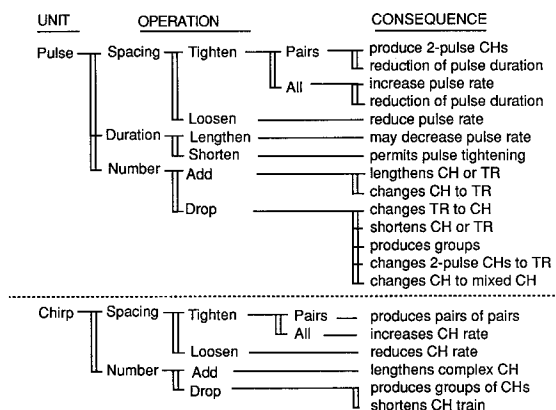


Fig. 5. Evolution of song patterns which result from altering the number and spacing of two basic units: pulses and chirps.

evolved from low intensity wing fluttering movements which operated among individuals in close proximity (Alexander 1962). Lifting and fluttering of the forewings as visual and auditory stimuli and in association with exposing dorsal glands, occurs not only in many cricket subfamilies, but also among tettigoniids and roaches.

Either soundless or acoustical vibration of the forewings occurs during courtship in the males of orthopterans in which the female mounts the male during copulation, except in wingless species and in a few winged species in which males have tibial glands. Thus, the first signal was probably a courtship signal (Alexander 1962). The

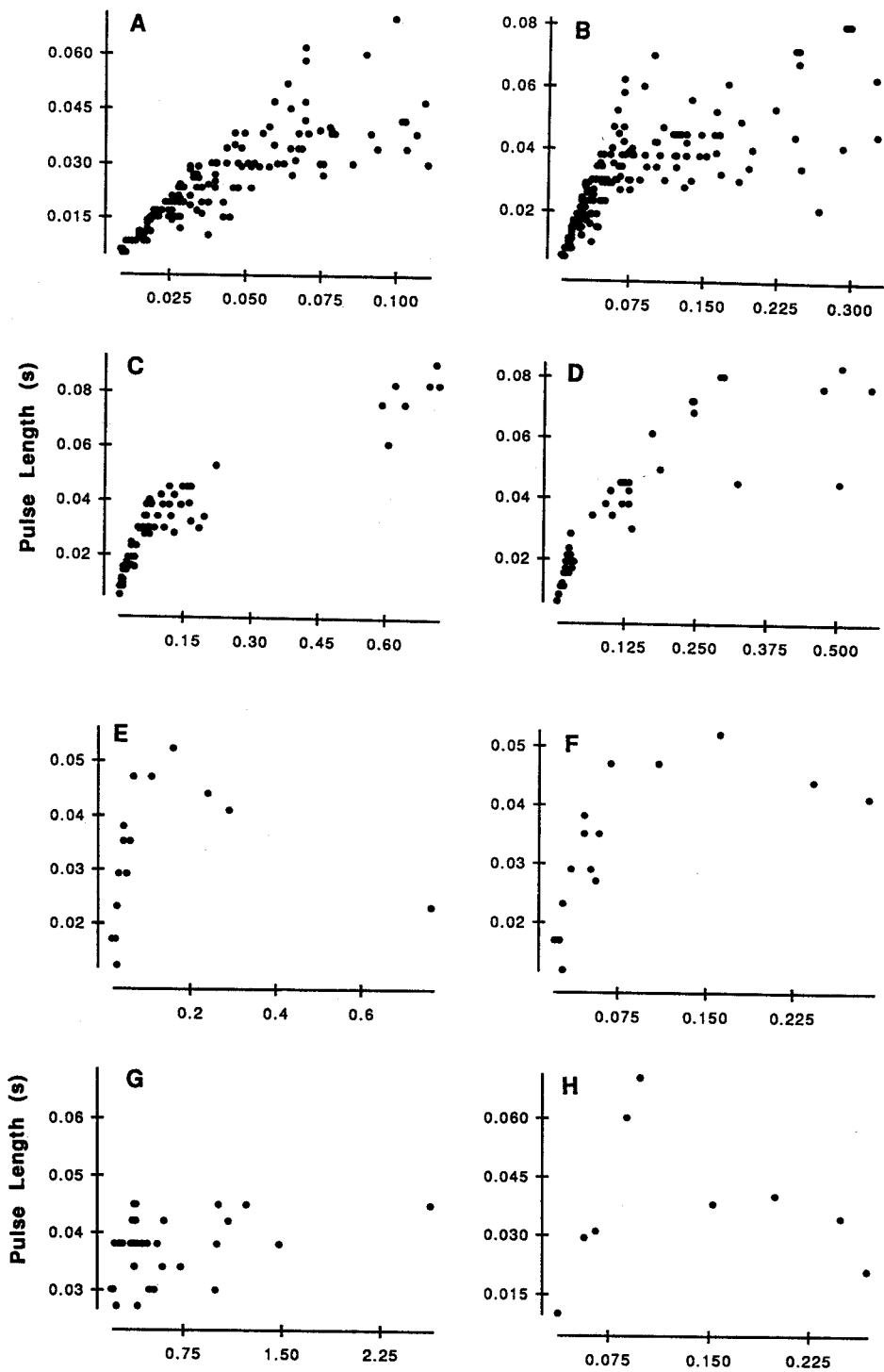


Fig. 6. Relationship between pulse duration and pulse period in Hawaiian *Anaxipha* and *Prognathogryllus*. A, all *Anaxipha* (pulse period under 150 msec). B, all *Anaxipha* (pulse period under 350 msec). C, Kauai Island *Anaxipha* (one species may be represented by several points). D, Oahu *Anaxipha* (one species may be represented by several points). E, African *Teleogryllus* type I songs only. F, African *Teleogryllus*, includes types I and II songs. G, all Hawaiian *Laupala* species. H, Australian Mogoplistinae.

Pulse Duration

Because sound is produced only on the closing stroke crickets cannot produce a continuous tone of sound. The nearest crickets can come to a continuous sound is to produce long closing strokes and to cock the wings rapidly. Females, however, may translate a set of pulsed sounds into a continuous tone (e.g. *Oecanthus fultoni* Walker 1957)

Pulse duration is usually, but not always functionally associated with pulse interval (Figs. 6, 7). In short interval species there is a close linear relation between pulse length and pulse interval. The only way to decrease the pulse period is to decrease the pulse duration and/or opening stroke. Below pulse periods of 70 msec, pulses occupy most of the time available to them, the wings are constantly in motion and males have only enough time reopen their wings. With increasing pulse intervals there is a corresponding increase of pulse duration. But a point is reached when pulse period no longer increases as pulse period continues to increase, in part, perhaps, because the mechanism is incapable of producing pulses long enough to fill the gaps. In such species males pause between opening and closing strokes; the wing closes, then opens, then is held motionless in the cocked position before the next closure (Hawaiian *Laupala* etc.). Above pulse periods of 75 ms pulse duration stabilizes at 30-60 msec. In African *Teleogryllus*, for example, pulse duration increases in length until a pulse interval of approximately 75 milliseconds is attained. However, in Australian *Eurygryllodes* pulse length tends to increase continuously with increasing pulse interval—even to pulse intervals in exceeding 1.5 seconds. Figs. 6 and 7 suggest that a pulse duration of 30 to 60 milliseconds represents an optimal pulse duration in crickets. In Hawaiian *Laupala* species, where all species have pulse periods greater than 75 msec, there is no correlation between pulse length and pulse duration, and all species have a pulse duration between 30 and 45 msec. Even if long bursts of sound constituted better signals, the forewing file/scraper mechanism is not well suited to producing them. Pulse duration could be limited by the space available for adding new teeth and by the cost of building them.

Doherty and Callos (1991) note that pulse duration and dominant frequency were less affected by temperature than pulse period in *Gryllus rubens*.

From Trills to Chirps

Chirping songs can evolve from trilling songs in two ways: commonly by the dropping of pulses, and, less commonly, by

pulse coupling (pulse pairing).

Pulse dropping: The transitional stages involving pulse dropping are probably as follows: (a) sporadic (or occasional) dropping of single or multiple pulses to produce broken trills (or chirps of irregular length) (e.g., *Oecanthus filiger*, *Gryllus rubens*); (b) production of trills or chirps of regular length and irregular chirp intervals (numerous species) and (c) production of chirps (or short trills) of regular duration and period.

Pulse pairing: The transition from trills to chirps via pulse pairing may be uncommon for crickets as a whole, but it is common in some groups, especially in Mogoplistinae where it appears to be the only mode of chirp production (see # below).

From Chirps to Trills

Chirps can revert to trills by the addition of pulses or by the dropping of pulses. In the first mode, pulses are added to short trains to produce longer trains. This is almost certainly what has happened in some Mogoplistinae, though in that group the transition is from a mixed chirp to a mixed trill (see # below).

Chirping songs can revert to trilling songs when all but one pulse is dropped from each chirp. The transitional stage is seen in several species in which chirp length varies between one and two pulses. In some species some of the males produce chirps and others simple pulse trains (e.g., *Prognathogryllus waikemoi*).

Several species appear to have acquired simple ungrouped pulse trains in this fashion. The transitional stages through which a signal evolves from chirps to simple pulse trains can be observed in species belonging to various groups (*Prolaupala*, *Anaxipha*, *Teleogryllus wernerianus*, *Gryllus* sp. (Brazil)).

Evolution of Complex or Mixed Chirps (Groups of Groups)

In many species chirps consist of groups of paired pulses. Pairs of paired pulses are seen in Gryllinae, Oecanthinae and Mogoplistinae. Groups of groups probably originated through different routes in different lineages. In one direction the process begins with pulse dropping; in the other direction no pulses are lost:

(1) Pulse dropping to form chirps of variable length, followed by pulse coupling within the chirps (pairs of pulses within a chirp begin to tighten) (e.g., *Oecanthus fultoni*, *Gryllus* sp *Scapsipedus* sp). The resulting chirp structure then depends on the number of pulses in the original chirp. The following transitions involving pulse pairing may have occurred in various lineages:

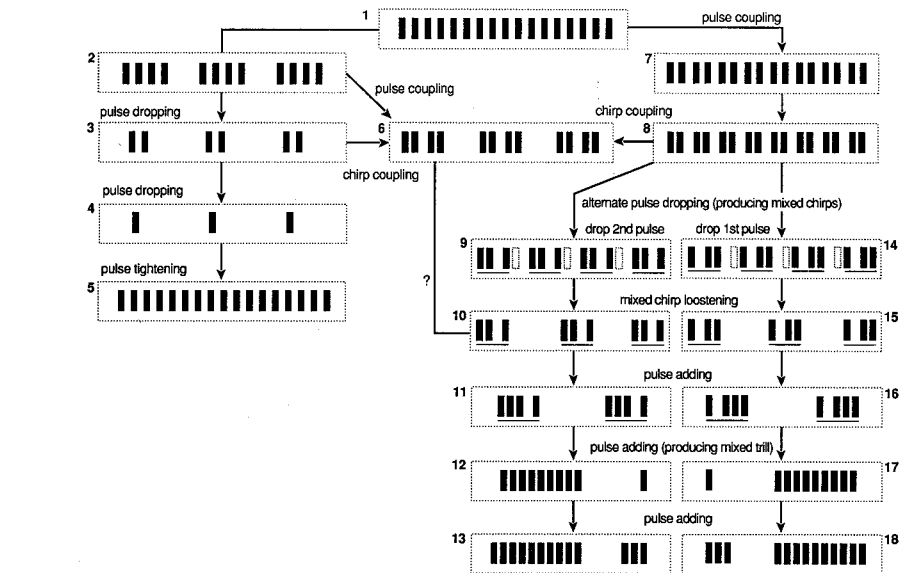


Fig. 7. Transformations in song thought to be important in crickets. On the left, a transformation from a simple trill to a chirp—1 to 2 and 3—and back to a simple trill—3 to 4 and 5. In the center, the evolution of groups of groups by three different routes—2 to 6, 3 to 6 and 8 to 6. On the right are various transformations from two pulse chirps to more complicated songs which involve first a dropping of pulses and subsequently addition of pulses.

4 p: •••• •••• >> •• •• ••••
 3 p: •• •• >> •• ••
 5 p: •••• •••• >> •••• ••••

Fig. 7 shows some songs that probably originated in this fashion.

(2) Pulse dropping to produce 2-pulse chirps followed by chirp coupling. Two pairs of chirps begin to tighten thereby producing pairs of pairs. This mode requires first a reduction in the number of pulses in a chirp to two, then a coupling of alternate pairs.

(3) Pulse pairing then chirp pairing. In Mogoplistinae groups of groups evolved directly from trills. This occurred when pulses within trills begin to pair to produce a series of doublets. This is followed by a tightening between pairs of doublets which in turn can produce pairs of pairs. Groups of four doublets seen in American *Cycloptilum* (Love and Walker 1979) could result either from an initial grouping of four pairs or from the tightening of pair of pairs. The same pattern can be produced by dropping chirps, e.g., every third doublet to produce two pairs, or every fourth doublet to produce three pairs etc. Although it is certain that doublets often evolve by pulse pairing (as opposed to pulse dropping) we are uncertain as to whether four pairs of pulses evolved by chirp dropping or chirp tightening.

Thus it seems to be a rule that pulse tightening involves either just pairs of pulses or all pulses in a train of pulses. It should be

noted that no cricket songs are known which are the result of pulse tightening consisting of groups of pulses larger than 2 pulses. For example we know of no song in which 3 consecutive pulses have been tightened to form a group.

Origin of Variable Pulse Rate Songs

Many species (especially Gryllinae) have variable within chirp pulse rates—starting with a faster rate and slowing down. The difference between beginning and ending pulse periods is slight and may be coupled with an increase in sound intensity, which in turn may be the result of increasing stroke amplitude (increase in number of teeth struck). A few species show a nearly regular deceleration of pulses and a few others a regular acceleration.

From Trills to Mixed Chirps to Mixed Trills

By a mixed chirp I mean one which mixes groups of different size—for example a doublet and a singlet or a triplet and a singlet or a triplet and a doublet etc. The best indication of an evolutionary progression is seen in the subfamily Mogoplistinae. Here we can trace with some confidence the transition from trills, through chirps, or complex chirps, to mixed chirps and finally to mixed trills.

The process begins with pulse pairing within a trill. In the first stage successive pairs of pulses are slightly closer together. In *Ornebius wandella* males seemed to wander back and forth between barely paired pulses and unpaired pulses. Other species in the

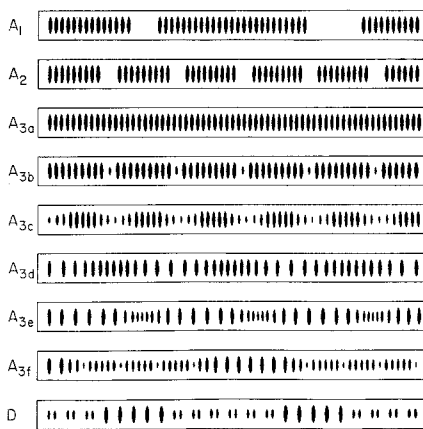


Fig. 8. Trilling song types as depicted by Alexander (1962).

genus show increasingly stronger pairing and still others very strong pairing (See subfamily Mogoplistinae in Otte and Alexander 1983).

Two kinds of changes then occurred in different lineages—both involved dropping one pulse from every other doublet. Dropping the first pulse of every other pair produces a • • • • • pattern. Dropping the second pulse produces a • • • • • pattern. In a number of species the spacing of these triplets strongly suggests that the pattern originated from a pulse drop (the appropriate gap is there). In other species the triplets are widely spaced, indicating either that the triplets evolved from the dropping of one pulse from a pairs of pairs song or that the triplets began to loosen after the dropping of the pulse. I favor the latter mode because pairs of pairs are rare in the Australian fauna. It appears that once the • • • or • • • triplets are established they acquire a kind of unity and can begin to drift apart.

As triplets (• • •) move apart, space becomes available between them for adding pulses to the doublet of each chirp. Thus

• • > • • • • • • • • etc.
• • • > • • • • • • • • etc.

Eventually mixed chirps can produce mixed trills:

• • • >> • • • • • • • • • •
• • • >> • • • • • • • • • •

Finally, pulses could be added to the singlet also:

• • • • • • • • >> • • • • • • • • • •
• • • • • • • • >> • • • • • • • • • •

Mixed Songs from Calling and Courting

Courting males of some *Teleogryllus* males produce long trains of pulses. These are sometimes preceded by a shorter group of pulses of different chirp interval and intensity. The two kinds of songs are combined in calling males of *Teleogryllus*

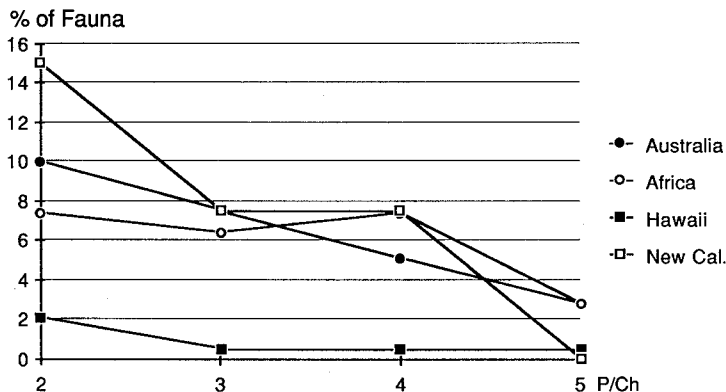
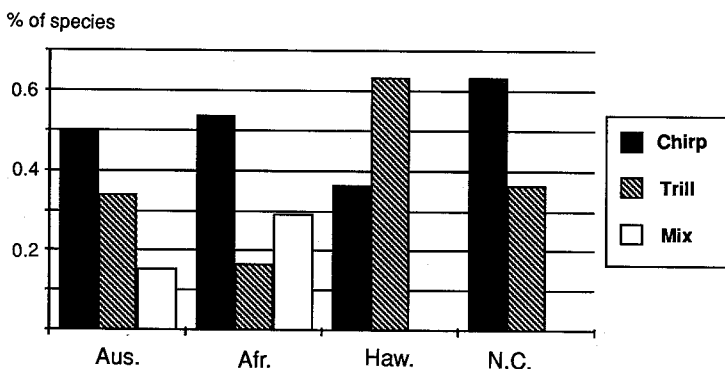
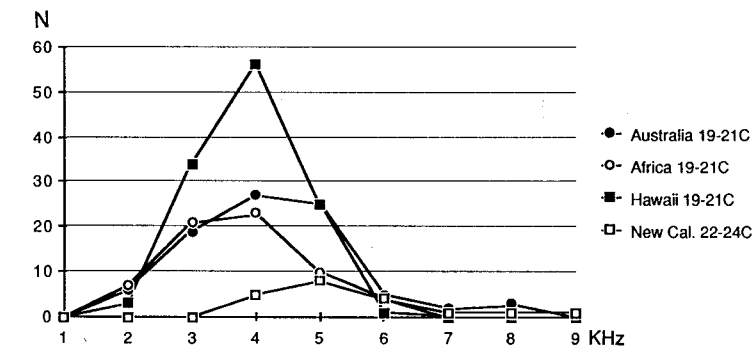


Fig. 9. **A.** Comparison of carrying frequency in Australian, African, Hawaiian and New Caledonian crickets (the slightly higher frequency in New Caledonia is partially due to the higher recording temperature). **B.** Comparison of frequency of trilling, chirping and mixed song species in Australia, Africa, Hawaii and New Caledonia. **C.** Comparison of 2- 3- and 4-pulse species in Australia, Africa, Hawaii and New Caledonia.

and a few other species (In *Neogryllopsis* and *Thebella*).

Pollack and Hoy (1981) showed that female *T. oceanicus* oriented more often to the type I song than to the complete song when signals were broadcast in the laboratory. In African *Teleogryllus* the incidence of type I and type II songs depends on the time of day. In *T. africanus* males usually sing a combination of type I and II songs. However, in the early evening males often sing a succession of type I songs, omitting the type II altogether. Several males we recorded (Otte and Cade 1983) (Fig. 13) began with type I songs and produced longer and longer trills of type II songs as the evening progressed. By 9 PM the full song with the normal ratio of parts I and II phrase

was restored. The full song was also produced during daylight hours. *T. leo* males usually sing only type I songs, but late at night and in the morning they sing a combined type I and II song. *T. natalensis* produced only type I song early in the evening. Late night songs consisted of both parts. *T. natalensis* produced only type I song early in the evening. Late night songs consisted of both parts. Similar early evening emphasis on Part I and songs has been tape recorded in *T. oceanicus* and *T. marini* in Hawaii and New Caledonia.

We speculate that *T. africanus* and other *Teleogryllus* species may produce type I songs mainly when females are likely to be flying early in the evening.

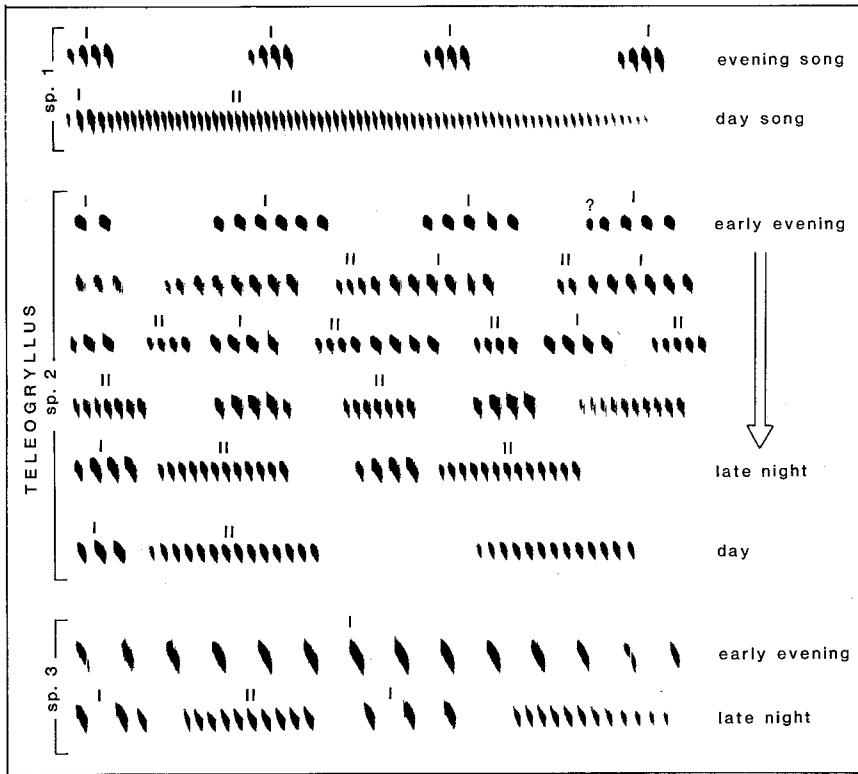


Fig. 10. Changes in song structure in three African *Teleogryllus* in relation to the time of day.

Interregional Comparisons

The carrying frequency of the great majority of songs lies between 3 and 5 kHz (Fig. 8) and the most common frequency globally is around 4kHz. New Caledonia has a significantly larger number of species with a frequency of 5 kHz. These numbers indicate that a frequency of between 3 and 5 works best for crickets around the world and that regional differences are largely attributable to historical factors, namely to what groups originally colonized an area. There is only a weak association between frequency and body size.

The proportion of chirping species varies between region. The continental faunas of Africa and Australia have similar numbers of simple chirping species (Fig. 9). Australia has more trilling species than Africa while Africa has a correspondingly larger number mixed song species. The latter difference has historical causes because the fauna is composed of numerous species belonging to two groups that commonly have mixed songs (*Teleogryllus* and *Turanogryllini*).

In the island comparison, Hawaii has a much higher than usual proportion of trilling species and New Caledonia a higher than usual number of chirping species (Fig. 10). The original composition of the fauna has probably had an important role. For Hawaii speciation involved mainly a trilling group while in New Caledonia it involved mainly a chirping group. New Caledonia has large

number of species with two-pulse chirps while Hawaii has very few. Africa and Australia are quite similar.

Fig. 13 shows that temperature at which crickets were tape recorded is lower and more constant in Hawaii.

Adaptive Significance of Song Type

Why do not all crickets have trilling songs? or chirping songs? In the context of mate recognition both trills and chirps give much leeway for evolving differences. In Hawaiian Trigonidiinae large numbers of closely related species coexist in various combinations and most produce trills. Similarly, numerous Hawaiian *Prognathogryllus* coexist on one island but most are chirpers. Possibly chirping evolves from trilling at the time of speciation, or perhaps it arises as a consequence of selection for a distinctive song in a particular acoustic environment. But there are some other possibilities. Two possible selective contexts might involve energy and/or predators.

1. A triller could economize on energy by dropping portions of the trill sequence, but keep enough pulses for receivers to recognize the pattern. In this fashion trills could evolve into chirps. Australia, Africa and Malaysia have a number of species which vary their songs from continuous trilling to chirping (*Oecanthus*, *Aritella*, *Podoscirtinae*). A species which produces both kinds of songs could easily be transformed into one which makes

only chirps.

2. A steady chirper could likewise drop short or long sequences of chirps, leaving behind a group of chirps. In some Australian species all degrees of variation from continuous trains of chirps to short groups of chirps are represented; but the conditions influencing this variation are not known. In Africa long silent periods often separate one or two pulses in *Scapsipedus meridianus*, making it very difficult for cricket collectors (and probably other predators) to locate a singing male.

3. When two temporal patterns are combined in one song as in *Teleogryllus*, it may be that several functions (male-male separation, female attraction) normally assumed by one kind of song, are transmitted separately by two song types. In African *Teleogryllus* there is a change in the proportion of Part I and Part II songs at different times of the day, suggesting that the song is designed to accomplish different functions during the course of the day (Fig. 10).

The Sound Space

The sound environment of crickets may be perceived as the multidimensional space which defines the limits of all acoustical parameters (pitch, temporal modulation and frequency modulation etc.). The boundaries of the sound space within which a set of species adjust their songs is determined by a combination of capabilities in the emitter and the receiver. If the pulse repetition rate is important, the lower bounds of the pulse rate axis (not much less than one pulse every two seconds) may be set either by how slowly the emitter's timing system can be made to operate accurately, or by the receiver's capacity to respond to iteration when pulses are delivered at very low rates. The upper limit (about 200 pulses/s—recorded in one Malaysian mole cricket) may be set by the limitation of the emitter's sound producing apparatus, or alternately by the ability of the receiver system to discriminate among very high pulse rates. Number of file teeth and width of the wing are anatomical features that set limits on pulse length.

Ecological theory predicts an upper limit to the permissible degree of niche overlap. To date no attempts have been made in any group of animals to examine quantitatively the distribution of song types in the sound space. We predict that there will exist some minimum difference in songs. What is that minimum which must obtain if species are to exist in stable associations.

The sound space can be likened to a room (but one with more than three dimensions). If the species occupying the room remain together for long periods (evolutionary time)

there will be precise adjustment of song one to another or one to all other room occupants. If species move from room to room or if the inhabitants of the room constantly change (i.e., the mix of species varies within ecological time), then adjustment of a given species will be in relation to all occupants of the house; selection will be for good mixers. In an old community a larger proportion of the species will be distantly related, so species would adjust their songs mainly to the songs of already different resident species. In a young expanding biota a greater proportion of the fauna will consist of close relatives and so most co-adjustment of song would tend to be among them and divergence of songs would be expected to be especially pronounced and greater than would be predicted by random divergence. When the sound space is relatively empty, an expanding and diversifying taxon has greater freedom, so to speak to evolve in any direction. In the case of a closely related set of species one might find that expansion or diversification is along one axis and when all positions along that axis are filled, exploitation of another axis may begin (Fig.). In the Hawaiian genus *Laupala* divergence has involved only one axis (the pulse rate axis). In *Anaxipha*, a much larger genus most divergence has been along the pulse rate axis, but there has been divergence along the chirp rate and chirp length axes as well. The axis along which divergence occurs will be the one whose parameters are used to differentiate the species, or that individuals use for discrimination.

Evolution in Viscous and Fluid Communities

The constancy with which a certain set of species interacts with one another must have important consequences on signal differentiation. The two ends of the scale are: at one end communities of species which are extremely stable over long periods; the stability is owing to habitat stability, and secondarily to the sedentariness which evolves in stable situations; the result of sedentariness is a reduction of mixing which promotes recombination and retards specialization. The opposite end of the scale is one in which the composition (mix) of species interacting in any given place changes constantly. I will contrast two real situations with which I am familiar.

Perhaps the most stable situations are to be found in forests. Communities appear to be especially stable in Hawaiian forests, where it is possible to find small isolated populations consisting of not more than a few dozen singing males year after year for nearly two decades, and in which the contact zone between any two species can be

mapped precisely almost to the square meter, or in which an isolated population is confined to a known tree for over a ten-year period. We can do this repeatedly in various species on all islands.

At the other extreme are situations of extreme mixing as occur in semideserts, or in desert grasslands or along the fringes of deserts and savanna grasslands. In such situations crickets, along with other insects are usually winged and during some parts of the year fly great distances. Such a situation occurs along the southern border of the Sahara. Extreme mixing even daily changes in the composition of the fauna can be observed in the Sahel when insects move northwards and southwards with the wind in different seasons. A given species comes into contact with different mixes of species both temporally and spatially and the loose, constantly changing associations would seem to make it impossible to establish a fixed position relative to any species. In Hawaii and other more stable situations the set of species which cohabit for long periods must adjust their songs to a given set of songs, and a highly uniform spacing of songs is observed, not necessarily uniform over the entire sound space but for axes in which differentiation is occurring. Two examples illustrate the situation even better. *Gryllus bimaculatus* is associated with thousands of different combinations of species over its range (from the tip of Africa to the Malaya Peninsula). It must mix with a bewildering variety of species over its range. *Laupala kohalensis* is a Hawaiian sword tail cricket

which is restricted to a small range where it interacts with a small set of species, where its song can become optimally adjusted to a standard and unchanging set of species.

Becoming a good mixer may have the important consequence of retarding local specialization and the chance that a local population will become so different that communication is disrupted and speciation occurs.

Origin of Song Differences

In much of the foregoing discussion there has been the implication that species differentiate in relation to other species. I shall now consider and evaluate the various forces which may operate to bring about song differences. There is a need to

explain the large differences which arise between closely related species. Two related and almost indistinguishable cricket species may have pulse rates which differ by 800%. Species which cannot be distinguished by morphology, chromosomes or proteins commonly display large differences in songs. In Hawaii it is common for related species to differ by a factor of two or more.

What causes the songs of related species to diverge so greatly?

Alexander (1962) listed six factors which influence evolutionary change in cricket songs. The four most important ones in the present context are: (i) The habitat a species occupies. The physical characteristics of the habitat should select for particular frequency spectra in the songs, such that the spectra of arboreal species should be predictably different from terrestrial species due to frequency-dependent attenuation of sound over distance (Konishi 1970, Morton 1975). (ii) The number and kinds of signals in its repertoire; the greater the number of signals in its repertoire, the more difficult it will be to modify calling signal in a given direction, since all of the songs are functionally, if not structurally linked, and a change in one will necessitate a change in the others. (iii) The nature of the minimal information carrying units its signals. (iv) The particular number and sort of acoustical neighbors.

We can expand his discussion to include a more exhaustive set of possibilities. At the most general level we must consider three possibilities: (a) that the evolutionary changes are accidental, or (b) that the

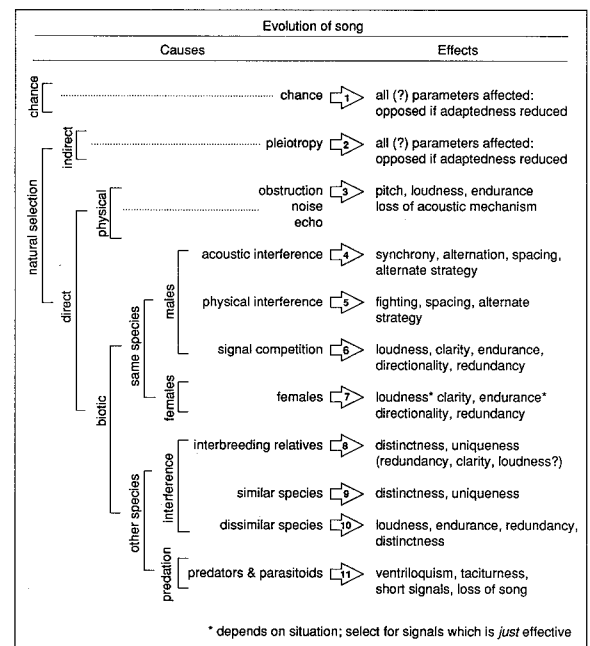


Fig. 11. The probable influences of chance and various kinds of selection on the nature of songs.

Table 3. Acoustically signalling crickets may interact in many ways.

A. RANDOM ACOUSTIC ACTIVITY

Signals seemingly acoustically independent of one another. Males interact indirectly by influencing same females. Most acoustically communicating crickets probably fall into this category.

B. SPATIAL CLUSTERING

1. *Loose aggregations*

Hapithus agitator—Alexander and Otte 1967
Gryllus integer—Cade 1980, *Scapteriscus* spp.
Ulagaraj and Walker 1973, 1975, Forrest 1983

2. *Tight aggregations*

African Itarine—this paper

C. TEMPORAL CLUSTERING (SPREES) Singing for

a short time and at the same time of the day
Scapteriscus (Gryllotalpinae)—Forrest 1983;
Anurogryllus arboreus (Brachytrupini)—Walker
1983; *Stenocephalinus yungellus* (Brachytrupini)—
Otte and Alexander 1983; African itarine—this
paper

D. ALTERNATION

Acanthogryllus fortipes—Cade and Otte 1982
Cryncus alternatus and *C. duplicatus*—Otte 1985
Prognathogryllus alternatus—(Fig. 12).
Notosciobia spp.—Otte, Alexander and Cade
1987

E. SYNCHRONIZED SINGING

1. Synchronized chirping

Oecanthus fultoni—Walker 1969

African *Oecanthus* sp.

Cyrtoxipha columbiana and *C. gundlachi*—
Alexander 1960

2. Synchronized pulsing

Hawaiian *Laupala* species—(Fig. 13).

F. FIGHTING

Various *Gryllus* species—Alexander 1961

G. INTERLOPING

Gryllus integer—Cade 1979

changes arise because they are developmentally or physiologically (pleiotropically) linked to other characters under selection, or (c) that the changes are due to direct but different selective pressures acting on the two populations. A more exhaustive list of the possible influences is shown in the accompanying figure (Fig. 14).

Chance

Because it is unlikely that random genetic events occurring in two separated populations will be the same, some portion of the differences between populations must be due to chance. The random genetic changes are important, for they provide the raw material—the variation—upon which selection acts. But can chance alone be responsible for large signal divergences which occur among closely related animals, while at the same time other phenotypic characters remain unchanged? It seems unlikely. Similarly, it is also unlikely that chance alone could repeatedly produce changes of a particular kind in one character and leave all other characters unaffected. For example, the parameter that is known to

be used by females in discrimination is the pulse rate. It is just this character that diverges most, while other factors such as pitch and pulse character remain relatively unchanged.

Selection: Indirect (Pleiotropy)

Signals may change because they are developmentally linked to characters under selection. Mayr and Patterson argue that linkage of signals to other characters under selection is an important mode by which differences between species are acquired and that the divergence takes place principally while the speciating organisms are extrinsically separated. Because development of the signalling system, like any other complex character, is the result of innumerable integrated reactions, selection on many other characters must affect it. Disagreements center on the relative importance of indirect selection.

If two species differ from one another in many respects, then any signal differences between them could well be due to the extensive remodelling of the gene-action system. In the absence of a strong association between signal and environmental differences in any particular instance one could, more or less by default, accept pleiotropy as the only known agency of change. But one should invoke pleiotropy as the principal mode of change only if one can show that there are no conceivable functions served by a particular trait or if differences observed between animals make no difference to their welfare. A large role for pleiotropy in signal differentiation is especially unlikely if the signals are very different while other features remain relatively unchanged. Indeed, such a situation tends to discount an important role. For example, pleiotropy is one of the least likely explanations if anatomic, ecological, physiological, developmental, chromosomal and protein differences which could modify songs are not apparent? Furthermore, it is unlikely that indirect selection could produce the consistent patterns observed among related, sympatric species. Why for example, of all the measurable song parameters should only pulse rate (or pulse rate and pulse length in high pulse rate songs) change? Similarly, of all measurable morphological differences, why should only the tools of sound production change? Allopatric sister species do show some song differences. However, the changes are not nearly so great as those among coexisting sister species (Otte 1989 in Hawaiian crickets).

The above considerations lead me to favor direct selection as the principal agent of change in many cases of signal divergence.

Selection: Direct

For convenience, selection forces acting directly on signals can be grouped into two kinds: physical features of the environment (which favor or retard signal transmission) and other organisms. Components of both may act on the system in any case, though not with equal force.

Physical Environment

The best evidence that the habitat, and specifically, that the physical surroundings have an important influence on cricket signalling systems comes from an examination of species that have moved into caves. As a rule these species no longer signal acoustically. Sound is lost in other circumstances as well, but not so consistently as in caves. It seems likely that signaling systems in such situations are affected by the transmission characters of the habitats, but the presence of acoustical species in the latter situations indicates that the causation is more complex. The attenuation of sound with distance and directionality seems to be very different in deserts and tropical forests. Because of echoing and muffling of sounds in forests it is more difficult to pinpoint the location of a singing male. But is sound communication affected by such environmental differences?

The extent to which signals are molded by the physical circumstances has been little explored in crickets.

Collections of sound from forests and grasslands suggests that loud low frequency sounds are more often encountered in forests. But this may be a result not of selection acting on the sound production itself, but on other characteristics (body size, wing configuration) which have secondary effects on the types of signals produced. There may be historical explanations for some differences between regions. The frequencies observed may be explained mainly by what groups are present. Mole crickets and *Oecanthinae* usually have lower pitched sounds than *Gryllinae* and *Nemobiinae*. Remaining to be explored is whether loudness, frequency and other characters are effected by obstacles.

Biotic Environment

The biotic environment which influences the direction and course of evolution of songs can be separated into two components: members of the same species, and members of other species.

Same Species Influences: Males.—Members of the same and opposite sex, rivals, and mates may have various effects—both similar and opposing.

Effective mating signals must permit potential mates to discover one another (i.e., they must inform that a mate is present and indicate its location), and ensure that the

mate belongs to a class of genetically compatible partners. What components of cricket songs are likely to convey such information? Loudness, clarity, directionality, and redundancy might all affect efficiency of pairing and could also be used to evaluate the quality of a mate, at least at a gross level (is he effective or defective?). It is improbable that females will be indifferent to the quality of the signal. The observation that females discriminate between at least some males led Darwin to the notion that females, and in the absence of extraneous selective influences (i.e., in a selectively neutral environment) can cause evolution in male characters to proceed in directions which are opposed by other selection forces. There is now a huge literature on this subject, but no convincing evidence that within the bounds of the normal females are very selective. It remains quite likely that selectivity will be proportional to the departure of male characters from the mean. This means that if male characteristics are close to the mean selectivity will be very hard to demonstrate and could require huge sample sizes. Although it can be shown in crickets that females are selective, no directional effect has been demonstrated, i.e., that females prefer deviants on either side of the mean.

For songs to become either faster or slower over evolutionary time, females must prefer songs faster or slower than the mean. What causes them to prefer such songs? We believe that they will tend to mate with males that stand out against the acoustical background or that indicate a compatible genotype.

A constant and important part of the environment in which signals operate is other males.

Singing males interact in various ways. They (a) sing at the same time of day without synchronizing any of the elements within the song (b) synchronize their chirps or (c) alternate their chirps (Table 3).

Direct influences include attacking the singer, or intercepting his females (interloping). Indirect influences include acoustic interference among two or more males.

Chirp alternation is especially likely when the internal structure of the chirp (e.g., the pulse period) is important. Through alternation males place their signals into silent windows where interference is minimized. Alexander (1960: 77) mentions alternation of chirps in *Orocharis saltator*. Cade and Otte (1983) recorded and studied alternation in the South African *Acanthogryllus fortipes*. In this species alternation occurs regularly among males within two meters of one another. When males are not alternating, their chirp rate

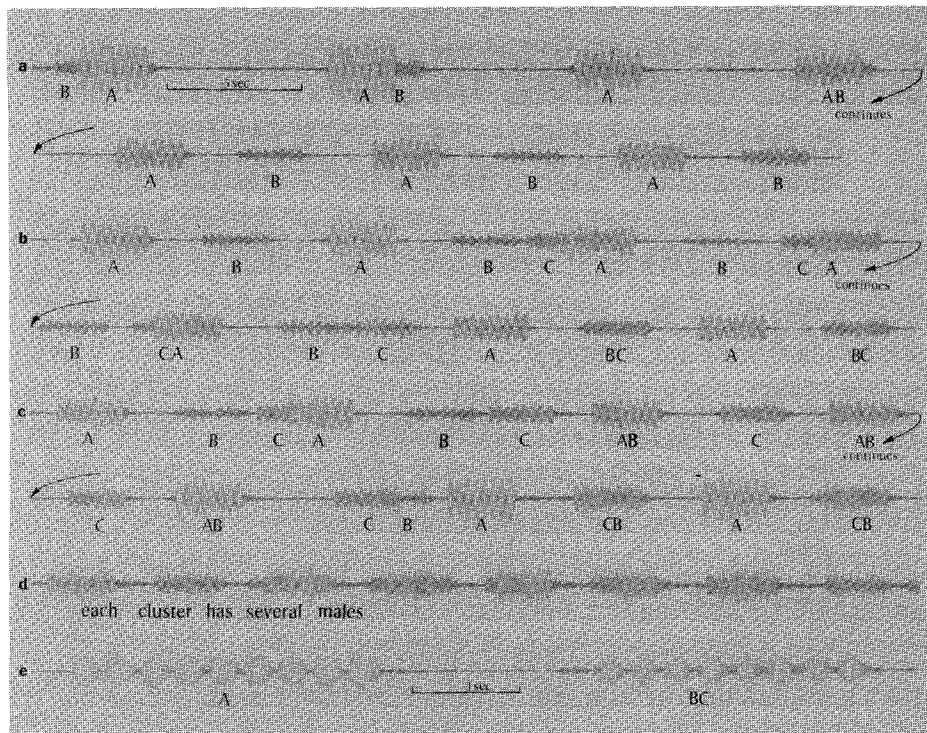


Fig. 12. Chirp alternation in Hawaiian *Prognathogryllus alternatus*. Alternation is sometimes not precise when more than two males are interacting. Occasionally two males by alternating with a third male synchronize with one another.

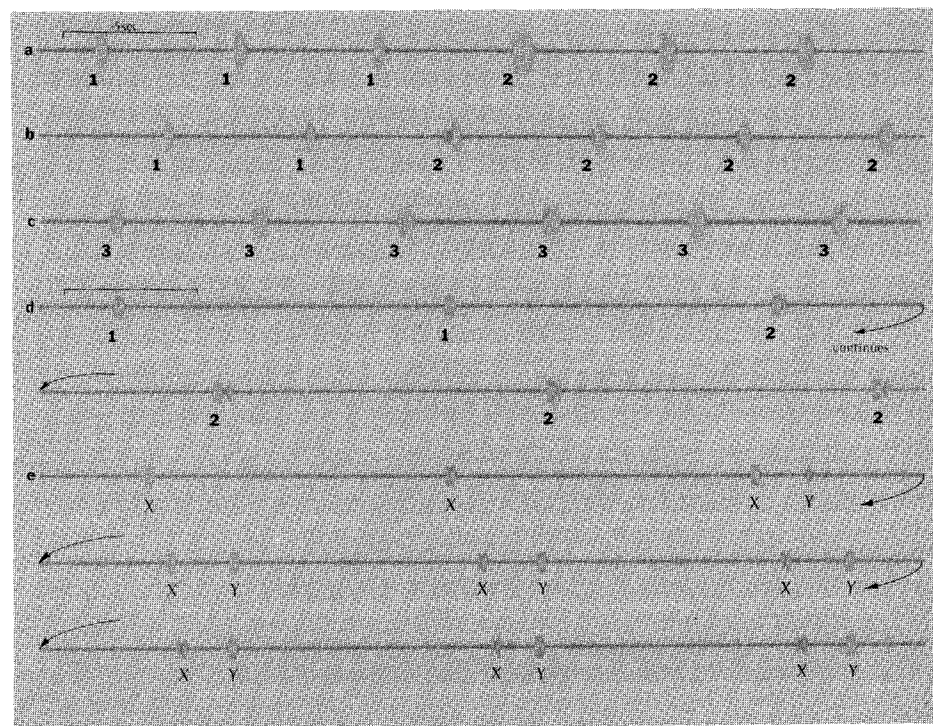


Fig. 13. Pulse synchronizing in Hawaiian *Laupala* species. In these species synchronizing is sudden—there is no gradual increase in synchrony.

increases somewhat. Such a rate change also occurs in Caribbean *Orocharis* species and an ability to slow down their chirp rate to facilitate alternation indicates that the species specific information is contained not in the chirp repetition rate but within the chirp itself (possibly pulse rate and chirp length). Alternation has also been recorded in *Cryncus alternatus* from Kenya and in *Notosciobia* species in New Caledonia.

The problem of pulse interference can also be avoided if individual pulses are synchronized, but, judging from its rarity, is normally difficult to achieve when pulse rates are delivered at more than a few pulses a second. A synchronizing of pulses has only been observed in species with rates of 2 pulses per second or less. It occurs frequently in Hawaiian *Laupala* both in the lab and the field. The behavior proves that males, at least, are attentive to pulse repetition rate (Fig. 16).

In Hawaii *Prognathogryllus alternatus* males alternate their chirps rather precisely (Fig. 15). But in this species we could detect no change in the rate of chirping in soloing males. Occasionally several males in this species synchronize, but only because they are both alternating with a third male. This species demonstrates that acoustic interference can occur over considerable distances in some cases. I heard males separated by 50 m alternating with one another.

Synchronizing of chirps is expected to be used only in species in which the chirp rhythm is an important species recognition criterion. Snowy tree crickets (*Oecanthus fultoni*) synchronize their chirps in such a way that a tree full of males can be perceived as a single rhythmically pulsating unit (Walker 1969). Synchronous chirping results in an intensification of the total sound produced and emphasizes those particular elements of rhythm which would otherwise be obscured. The adaptive value of synchronizing appears to be that a male by synchronizing reduces the interference of a neighbor which has his chirp rhythm, which is the component of the song most significant to females searching for males. Whether or not synchronizing also facilitates attraction of males from outside the chorus is problematical. If several males singing in unison increase their quota of females as against solitary or non-synchronizing males, they can be viewed as cooperating with one another.

Synchronization of chirps is known to occur in *Cyrtoxipha columbiana* and *C. gundlachi* (Trigonidiinae) from the United States (Alexander 1960). In the Australian fauna we tape recorded no synchronizing species. In Africa we have tape recorded

one species and in Hawaii another.

The mechanism of establishing synchronizing in *Oecanthus* involves either a temporary lengthening or shortening of both chirp intervals and chirp lengths by the individual attempting to synchronize with another male or with a chorus (Walker 1969). In Hawaiian *Oecanthinae* the mechanism is not known. In several Hawaiian *Laupala* (Trigonidiinae) males synchronize their individual pulses. Pulse rates in these species are slow and males only synchronize when they are within six inches of one another. Males can readily be made to synchronize in the lab and have also been heard synchronizing in the field. The synchrony, which may involve two or three males, is quite precise. Although a leader can always be detected (Fig. 16). Synchrony is achieved instantaneously. In these species we presume that the pulse delivery rate is important in species recognition.

Besides adopting modes of singing which ensure that signals are not interfered with, males may adopt other modes of behavior which circumvent the interference problem: they may space themselves to reduce interference or one male may exploit another by becoming silent, remaining close to a singing male intercepting females attracted to the song. Loudness, clarity, endurance, directionality, and redundancy must all be important features in males attempting to attract females.

Spatial clustering of males: Aggregations are common in some grasshoppers and in cicadas, but they are rare or not obvious in crickets. Loose aggregations are formed in some species (*Gryllus integer*, two *Scapteriscus* species) when flying males and females are attracted to the songs of males on the ground (Ulagaraj and Walker 1973, 1975, Forrest 1983); but in *G. integer*, within loose aggregations of singing males, are tighter aggregations consisting of a singing male and or more silent ones. Tight aggregations of singing males occur in a Kenyan species (Itarinae). This species was recorded twice in different parts of Kenya and encountered again in Mali, West Africa. Males begin to sing at sundown and sing only for about 20 minutes. They are strongly clustered spatially. Near Namanga, Kenya, a group of about 10 males was heard within a five square meter area in a large uniform grassland. Within this area one group consisted of about 5 males, several singing simultaneously and extremely loudly, within a meter of one another. I approached the group within 10 minutes after singing had commenced. While searching for singing males I accidentally stepped on a copulating pair a few inches from a singing male. I do

not know if this male had been singing prior to copulation. All males and the females had very long hind wings; all were walking on the surface. Probably all had congregated by flying to the song of a singing male. Several questions arise: Are males more likely to settle and sing near other males because several males, acting in unison, are more likely to draw females than a single male is (Alexander 1975, Otte 1977), or does one male settle near another singing male because it is more probable that a female will be near him than at some random point in the field that has no males?

Temporal clustering of songs: Mole crickets in all continents often sing intensively or for a short period at dusk (see Forrest 1983, Walker 1983 for data on *Scapteriscus* species). *Anurogryllus arborius* (Brachytrupini) (Walker 1983) several east African Brachytrupini and the Kenyan Itarine discussed above behave similarly. The itarine species discussed in the previous paragraph displays both temporal and spatial clustering. Walker (1983) presents various schemes which would tend to cause males to concentrate their efforts early in the evening. If females become receptive at any time of day but pairing occurs only at night, then there would tend to be an accumulation of receptive females at the beginning of darkness and it would benefit males to do most of their calling then. Or if females move about and search for males most actively in the early evening, for reasons unknown, it would also benefit males to be most active then. In the Australian rainforest we noted a burst of singing in *Stenocephalinus yungellus* right after a rain shower. Possibly females of this species move about most actively at such times.

Other Species Influences: Interference.

I will divide into four groups the major possible influences involving other species:

(a) *Related (Cognate), potentially interbreeding species:* Since closely related species are on average more similar to one another they are more likely to experience communication interference; and since such species are also more likely to interbreed there are additional cost associated with interactions between them. Combined, these two influences lead to stronger selective force than that exerted by an interference by a non-interbreeding relative. If this is so we expect the greatest divergence to occur among cohabiting cognates.

Reinforcement in behavior which prevents interbreeding is most likely where some pre-mating isolation has developed before secondary contact. Although the intensity of selection favoring reinforcement might diminish as the degree of

hybridization decreases conditions favoring reinforcement do not quickly disappear (see next paragraph).

(b) *Similar species*: Sound space considerations lead one to the possibility or likelihood that all potentially interfering sounds can influence the evolution of song. Since similar species are more likely to have similar songs they are more likely to cause distinctiveness or uniqueness in call. Because the chances of interbreeding between these species is low the consequences of interaction may be somewhat less severe than between potentially interbreeding species.

(c) *Dissimilar species*: Because unrelated, dissimilar species are likely to have different calls, selection would be expected mainly to produce signals which evade the circumambient noise that such species contribute to. A number of dissimilar species acting in concert may push a species into an unoccupied region of the sound space.

(d) *Predation and parasites*. Various studies have shown that predators and parasites use male calls to find crickets (Cade 1975, 1981, 1984, Cade and Rice 1980, Sakaluk and Belwood 1984, Walker 1964, 1992, Lakes-Harlan and Heller 1992) It is highly probable that species exposed to such selection pressures have modified their songs to reduce such risks. Perhaps the usual way is to sing less and from more secluded sites (see 11 on Fig. 14).

(e) *Summary*: Our experience with cricket communities, but especially with *Anaxipha* and *Laupala* sibling complexes in Hawaii, leads us to believe that the sound environment consisting almost exclusively of other cricket species and vegetation noises, and this is the selective context in which most evolution and divergence of songs occurs. In Hawaii we do not see other factors which could have such profound effects and discount the potency of pleiotropy because almost no other kind of evolution is detectable.

Calls, Mate Choice and Speciation

"A population consists of organisms of common ancestry, more or less contiguous in space, similar or coordinated in ecological role, somatic characteristics, and behavior, and reproductively continuous over several or many generations." GG Simpson

In the past few years there has been much interest in sexual components of selection (mate choice, sexual rivalry etc.). Virtually all of the discussion is focussed on selective forces coming from within the species. But mating is molded by a much wider field of factors (already outlined in Fig. 11 above).

Here I will briefly consider the relationship between mate choice and speciation. The following quotes define the selective context in which one can view the evolution of mate choice and associated signals.

"If mating and procreation are observed, it will soon be found that organisms form usually quite discrete reproductive communities. These communities consist of individuals united by the bonds of sexual unions, as well as of common descent and common parenthood."

Dobzhansky 1951

"Often numerous individuals of diverse species are seen in close proximity yet seeming wholly indifferent to each other."

Spieth

"Regardless of the ontogeny of the avoidance and ignoring reactions, the behavior seems not only to serve as an isolating mechanism but also to guard the organism against the numerous dangers that constantly beset it while allowing the individuals to carry on their normal activities *without incessantly responding to each other and every other organism in the immediate vicinity.*" [ital.added] Spieth

"Individuals of phylogenetically widely divergent species that are simultaneously sympatric and sexually mature respond to each other with an avoidance reaction such as is elicited by strange or strong stimuli. This automatically prevents even the beginning of courtship." Spieth

"Individuals of phylogenetically closely related species universally show similar mating behaviors, and these may or may not be effective isolating mechanisms."

Spieth

"There are compelling reasons for believing that animals should not mate indiscriminately, but should choose their mates. Since individuals vary in their quality as mates, we should expect natural selection to have favored mechanisms that ensure that mating occurs with partners of the highest possible quality." Halliday 1983

These statements equate reproductive communities with species, emphasize not only the absence of a sexual bond but the existence of almost a repulsion between cohabiting reproductive communities and illustrate the broader context in which pairing must take place — from members of distantly related species to the members of the same species with whom mating should not or cannot take place. The last quote, made in reference to mate choice occurring within species, is applicable across species and even generic boundaries. Within species there exists a continuum in the quality of mating types. The mate fitness landscape

consists of hills on top of which mates high in fitness reside; on the slopes are less fit members and at the bottom of the slopes and in the valley are immatures, the senile, members of the same sex, and teratologies. And from the standpoint of any given reproductive community all members of other reproductive communities are either at the foot of the mountain or on the plain, and there is only one hill on the plain.

Halliday p. 9 notes, quite rightly that "the pay-off from mating reliably with a member of the correct species may be much greater than that to be gained by discriminating between conspecifics." This is especially true in individuals that mate only once. In conspecific matings there is a good chance that reproduction will be successful; in interspecific matings reproduction usually fails. In incompletely speciated populations the failure rate is variable but virtually always greater than failure rates within species. An efficient signal system allows a clear differentiation between the "possibles" (adult-opposite-sex-conspecifics) and the "impossibles" (heterospecifics and various incompatible conspecifics). Much more information must be transmitted for discrimination among the better and worse "possibles", and deceit will be rampant, with relatively unfit individuals attempting to appear more fit. ". . . [I]n the human species one sees sexual preference for certain characters connoting health (although these are often simulated by make-up." (Huxley 1938). Except in rare cases selection on heterospecifics will result in discrete signals which allow yes-or-no decisions.

There may be long periods of time during which there is little coadjustment among species and most evolution probably involves fine-tuning of signals to intraspecific exigencies. The big adjustments occur when different yet similar and related species begin to cohabit. Following that, there may be long periods of adjustment, mainly among conspecifics—of undirected drifting about on the plain of possibilities (or field of possibilities).

The relationships between members of any two species in the reproductive context is always simple and clear-cut. In the absence of additional species which can complicate divergence between two species it is always dispersive, always in opposite directions. It is mutually beneficial to not mate and selection will reinforce any device which prevents needless interaction. Within a species the relationship is often also clear-cut (as between two males or two females or between adults and juveniles) but among adults of opposite sex it may be ambiguous, it may involve selection races selection

chases. It is symbiotic — alternately mutualistically and competitively symbiotic. It involves selling and buying, salesmanship and sales resistance.

The interactiveness between sympatric species (i.e., the degree to which they are aware of one another or respond to one another's signals) will depend on how closely related they are to one another. Until the signal system is clearly differentiated, animals must make decisions and choose*. In a well differentiated system, decisions and choice may be avoided altogether if the window of awareness can be made to exclude the signals of other species. Crickets may not interact at all with katydids and may be deaf to them; but *Gryllus* species are aware of and do respond to one another in varying degrees. We believe the degree of interactions will be greater the more similar they are to one another and they will be more similar to one another shortly after speciation than long after speciation. In time, as signals differentiate, decision making becomes easier and eventually the windows of awareness close out all but the relevant signals. In the extreme case the closing of awareness windows may involve retrogression of receptors which completely shut out unimportant information.

If there was no pressure on a population to be different from other cohabiting (syntopic and synchronic) species we would expect dispersion of song in the sound hyperspace to be similar to (or to be not significantly different from) the dispersion of songs of a similar set of allopatric species.

The term cohabit has come to be used mainly in connection the living together of a man and a woman. Here I use the term in its archaic form: "to dwell or reside in company or in the same place." I will use this term to cover all those cases where two species that are likely to encounter and to interact with one another (however slightly) and are reproductively active at the same place and time, that is, they are both syntopic and synchronic.

Taxonomists have long noted that the songs of coexisting (synchronic and syntopic) species are usually widely spaced, whereas those of related species separated by spatially

Table 3. Degree of reproductive coevolution should depend on the degree of interaction among adults of different species. Three kind of spatio-temporal relations are possible. Under cohabitation reproductive interaction is likely to be greatest.

	cohabiting	syntopic	synchronic
time	same	same or different	precisely same
place	same	precisely same	usually same could be diff.

Table 4. Predictions of signal spacing among cohabiting species under coevolution or no coevolution. If coevolution occurs then spacing among cohabiting species should be no different than among a set of randomly assembled (non-cohabiting) species.

	cohabiting	non-cohabiting
no coevol. occurs	random	random
coevolution occurs	hyperdispersed	random

or seasonally are more similar and may even be identical (Fulton 1933, Alexander 1962, Walker 1964, 1974). The theory that coexisting species probably adjust their songs in a fashion that reduces signal interference and confusion is given credence by experiments that show that acoustical signals of one insect species may interfere with those of another (Walker 1957, Hill et al. 1972, Loftus-Hills et al. 1971, Otte 1979a). Paterson (1978) argues that such differences are accidental and are not the result of one species adjusting its song to that of another.

To examine the question of whether the differences among sympatric species are accidental or not we have used the predictive model above. Specifically we have the dispersion (or spacing) of songs in the sound space among observed sets of species Hawaiian Trigonidiinae (*Laupala* and *Anaxipha*) and compared them with a random dispersion. If spacing is found to be hyperdispersed (as taxonomists have usually assumed it is), then the dispersion may be due to direct interaction among species. Calculating distances between songs in the hyperspace is complicated when songs differ in a number of parameters (pulse rate, pulse length, chirp rate, chirp length, etc.). We first attempted the procedure using Hawaiian *Laupala*, whose simple songs differ significantly only in pulse rate (i.e., they are very nearly arranged along a single axis of the sound space). We began by plotting the pulse rate of the 46 taxa at 68 localities where two or more species coexist (Fig. 14). This gives a picture of spacing among the taxa making up each community. Song differences among these coexisting taxa were then assembled into a frequency histogram. We then took pulse rates of the same 46 taxa

and reassembled them at random, producing the same number of communities and community sizes as before, but not allowing any taxon to be grouped with itself. Two such random assemblages and frequencies of differences are shown in Fig. 17. The results indicate, first, that observed communities of species have a greater average separation than would be expected by chance alone, and second, and more importantly that observed communities show relatively few instances in which closely similar song types coexist in one community. Such hyperdispersion is probably due directly to an interaction among the species.

A similar procedure was conducted using Hawaiian *Anaxipha* species. Fig. 18 shows a comparison of song spacing (pulse rate) in numerous actual associations of *Anaxipha* involving 341 pairs of species with an equal number of randomly composed associations of equal size and 340 pairs of neighbors. At each locality only the slowest song of each species (at 19-22C) was used. The songs of all species in the association were then arranged from slower to faster. The pulse rate of each species was then divided by that of its faster neighbor to give a measure of song spacing. For example, in an

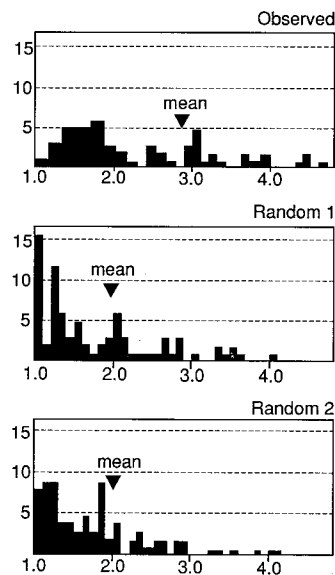


Fig. 14. Pulse spacing in Hawaiian *Laupala* species. Comparison of observed spacing observed at 68 different localities with a spacing in a random set of the same populations. Each dot represents the mean pulse rate of each species at a locality. The histogram to the right plots the frequency of different degrees of spacing between neighboring song types in a community. Spacing on the X axis is calculated by dividing the pulse rate of a species by its next slowest neighbor (e.g., in the set of three species A = 4 p/s, B = 1.5 p/s, C = 1.4 p/s, spacing between A and B is 2.67, and that between B and C is 1.07). Spacing of 5.0 or greater is now shown.

*Halliday defines mate choice operationally as "any pattern of behavior, shown by members of one sex, that leads to their being more likely to make with certain members of the opposite sex than with others." The precise mechanism involved may be simple or complex and variable between groups. Thus, two different mechanisms may have equivalent outcomes. "What is important in terms of the possible evolutionary consequences of mate choice is not whether a true preference is involved, but whether variation in the behavior of members of one sex are correlated with variation in their mating success." Halliday p. 4.

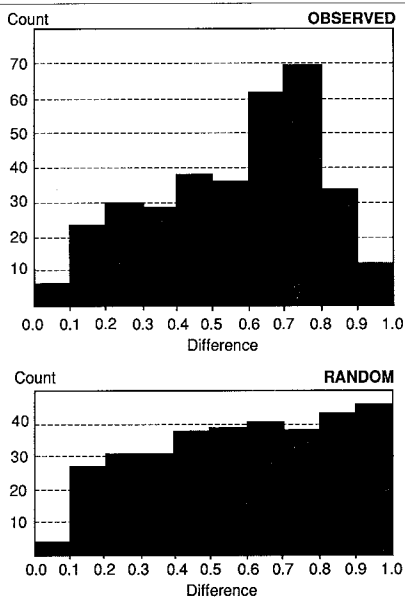


Fig. 15. Pulse spacing in Hawaiian *Anaxipha* species. Comparison of song spacing (pulse rate) in numerous of associations and an equal number of randomly composed associations of equal size. At each locality only the slowest song of each species (at roughly 19-22 C) was used. The songs of all species in the association were then arranged from slower to faster. The pulse rate of each species was then divided by that of its faster neighbor to give a measure of song spacing. For example, in an association of four species (A,B,C,D) with pulse rates 2.0, 10, 40, and 50 p/s spacing between neighbors is 0.2 (A/B), 0.25 (B/C) and 0.8 (C/D). All species at all localities were then reassembled randomly to produce a new set of associations, equal in number and size to the observed associations. Spacing between neighbors was again calculated and the observed and random sets of spacing were compared.

association of four species (A, B, C, D) with pulse rates 2.0, 10, 40, and 50 p/s spacing between neighbors is 0.2 (A/B), 0.25 (B/C) and 0.8 (C/D). All species at all localities were then reassembled randomly to produce a new set of associations, equal in number and size to the observed associations. Spacing between neighbors was again calculated and the observed and random sets of spacing were compared. The *Anaxipha* data again show a significant departure from randomness.

However, these results do not tell how communities came to be spaced in this fashion. The pattern could be due to character displacement (a coevolutionary response) or it could be due to trial and error mixing, with only species sufficiently different in pulse rate in the first place being permitted to coexist in stable communities. In the first hypothesis, incompatible species become compatible through evolutionary changes; in the second similar (incompatible) species fail to mix, whereas dissimilar (compatible) species are permitted to coexist.

Can the results of coevolution and ecological mixing be distinguished? Coevolutionary effects would have to be discounted (1) if there were no greater differences in sympatry than in allopatry in taxa that have partially overlapping ranges, (2) if clines in two or more coexisting species either did not diverge or did not follow parallel tracks, or (3) if taxa living alone showed the same or a lesser amount of phenotypic variation than those living in a multispecies community.

The distribution of *Laupala* species and the

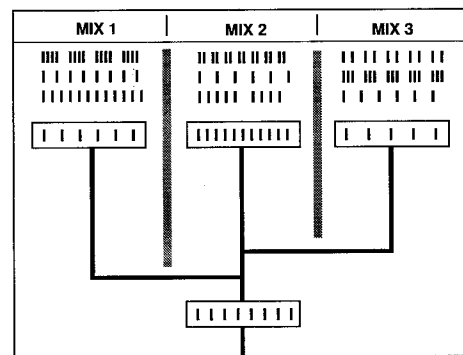


Fig. 16. Preferred model for viewing the evolution of cricket songs. Cricket populations become geographically and temporally isolated and come to be associated with different mixes of species. They then evolve song characteristics which harmonize with the prevailing acoustical environment. This presupposes that much of acoustical signaling is the result of character displacement, but that may often be in relation to species that are not very closely related.

pattern of song within and between species is beginning to suggest that song differences are due to character divergence.

After a species or population has been subdivided by extrinsic factors many outcomes can be envisaged. Here I will focus on just a few—those that are plausible outcomes of the separation and joining of populations and for which there is direct or indirect evidence (Fig. 20).

1. Partial divergence. Populations A and B diverge only slightly and under cohabitation fuse.

2. Populations A and B acquire

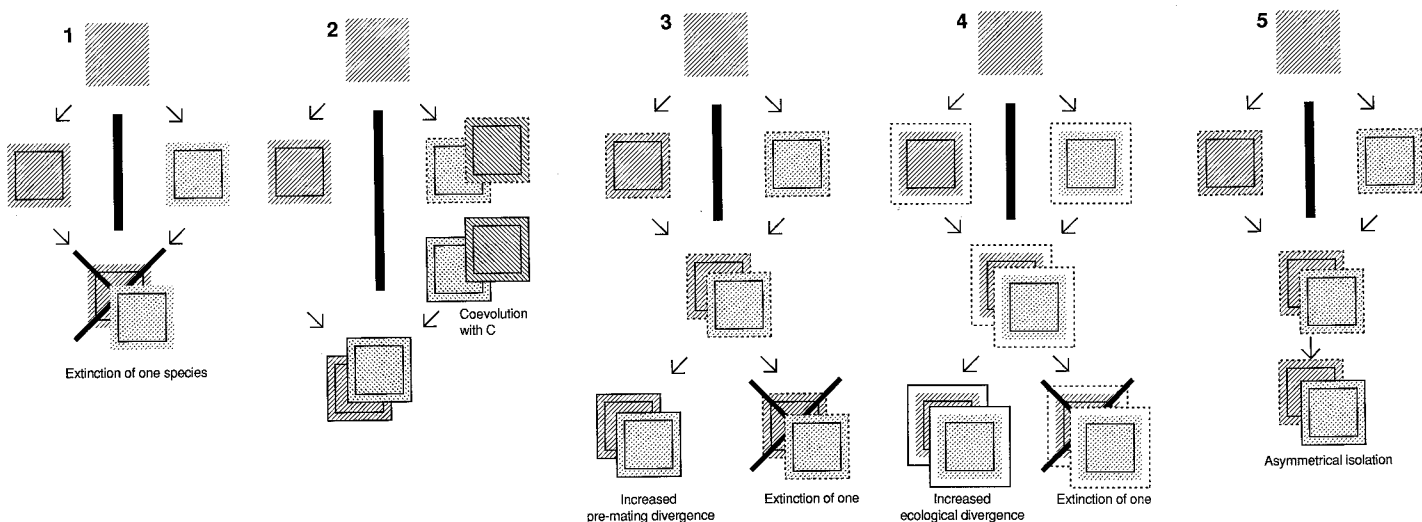


Fig. 17. Some possible outcomes of the separation and joining of populations in relation to speciation. See text for discussion. 1, populations A and B acquire developmental incompatibilities differences (post mating barriers). 2, same as 2, but species B cohabits and coevolves with a third species, C. 3, Species A and B acquire postmating barriers; cohabitation leads to (i) enhancement of signal differences and coexistence or (ii) interbreeding and unilateral extinction. 4, Species A and B develop postmating barriers and partial ecological differences. Cohabitation leads (i) enhancement of ecological differences and coexistence or (ii) interbreeding and unilateral extinction. 5, Species A and B acquire developmental incompatibilities and partial mate recognition differences; cohabitation leads to an asymmetrical development of mating recognition differences.

physiological and developmental incompatibilities (post mating barriers). The absence of mate recognition signals results in interbreeding under cohabitation. One of the two species (the one in the minority?) goes extinct.

3. Same as 2, but species B cohabits with a third related species C and coevolves with it. Such coevolution results in evolution of differences which pre-adapt B for cohabiting and coexisting with A.

4. Species A and B develop developmental incompatibilities and partial mate recognition differences. Cohabitation leads to i) enhancement of signal differences and coexistence or (ii) failure of the signal system, interbreeding and eventual extinction of one.

5. Species A and B develop developmental incompatibilities and partial ecological differences. Cohabitation leads (i) enhancement of ecological differences and coexistence or (ii) failure of the ecological separation to prevent interbreeding and eventual extinction of one.

6. Species A and B develop developmental incompatibilities and partial mate recognition differences. Cohabitation leads to an asymmetrical development of mating recognition differences, such that one species (B) refuses to mate with A, but A continues to mate with B. Such a situation might obtain, for example in the situation where A is common and B is rare.

Loss of Acoustical Signaling

Hearing and flying are closely coupled functions in true crickets (Grylloidea) (Otte 1990). Although the auditory tympana have been lost many times independently in crickets, they are virtually never lost in species that can fly. Since crickets migrate at night it seems likely that tympana are retained to avoid bat predation.

Sound broadcast using a forewing stridulatory mechanism probably evolved but once in a common ensiferan ancestor to crickets, katydids and haglids. Subsequently it has been lost many times independently. For example, the stridulum was probably lost at least 27 times in Australia. In Africa it was lost at least 17 times. It has also been repeatedly lost in crickets on Pacific islands (New Caledonia, Hawaii, Fiji, and Lord Howe—Otte, Alexander and Cade 1988, Otte and Rentz 1985, Otte 1992). It has not been lost in any United States species (exclusive of Hawaii).

How and under what circumstances is the stridulum lost? It is highly probable that the structure was lost after males of a species had stopped using their wing to broadcast long distance sounds. They became behaviorally mute first. Behavioral muteness

Table 5. All possible combinations of three characters: tegminal stridulatory file (stridulum), tibial auditory organ (tympanum) and flying wings in the Australia fauna. S = Stridulum. T = Tympanum. W = Long hindwings

	AUS	AFR	HAW	N C
S T W	No. [%]	No. [%]	No. [%]	No. [%]
A	++ 99 [20]	54 [39]	0	42 [51]
B	+- 285 [57]	55 [40]	198 [87]	34 [41]
C	-+ 0	0	0	1 [<2]
D	-+ 46 [9.3]	3 [2]	0	0
E	-+ 4 [<1]	0	0	0
F	-+ 3 [<1]	0	0	1 [<2]
G	-- 0	0	0	0
H	-- 57 [11.5]	25 [18]	30 [13]	4 [5]

is apparent in United States crickets. Calling behavior has been lost in at least seven species (*Gryllus ovisopis* [Gryllinae], *Oligacanthopus prograptus* [Mogoplistinae], *Tafalisca lurida* and *Hapithus brevipedennis* [Eneopterinae], *Falcicula hebardii* [Trigonidiinae], *Scapteriscus abbreviatus* [Gryllotalpinae] and northern populations of *Hapithus agitator* [Eneopterinae]) (Walker 1974). Walker (1974) notes also that *Gryllus ovisopis* lacks a functional calling song. And in the sibling pair *Hapithus melodius* and *H. brevipedennis*, the former species retains both calling and courtship songs, while the latter has never been heard to produce either song, even though it appears to have a functional stridulum.

Since absence of a calling song must be a precursor to the loss of the stridulum—examination of these species should give one clues as to the selective forces causing muteness and deafness.

The circumstances which cause non-acoustical methods of communication to entirely replace acoustical modes is open to speculation. Do acoustical signals lose their directionality, and therefore effectiveness, in certain situations (caves, burrows), or become ineffective in the presence of noise (seashores), or less effective than other modes of signal transmission (pheromones, substrate vibration, visual signals) under certain circumstances (burrows, caves, or on grasses)?

Walker (1974), noting that all U.S. mute species are flightless, speculates that muteness is associated with their higher degree of sedentariness: "Sedentary populations characteristically occupy relatively permanent habitats and are not subject to the extreme fluctuations in density of breeding adults characteristic of temporary habitats. Consequently, chance encounters or short-range signals become more dependable pair-forming techniques." He suggests two other possible causes: acoustically orienting predators could select

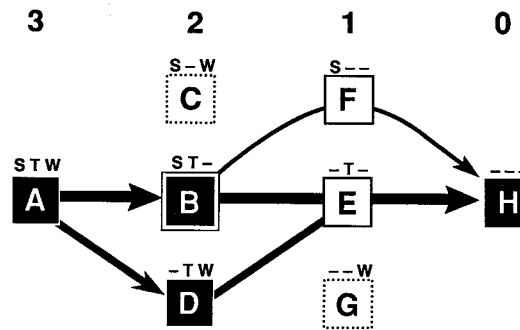


Fig. 18. Evolutionary pathways involving the association of three morphological characters used in detecting sound, producing sound, and flying (in the Australian fauna). S, stridulum present; T, tympanum present; W, flying wings present; — stridulum, tympanum, or flying wings absent. Black boxes indicate the common conditions seen in crickets. Condition B is the most common condition. Arrows indicate the only evolutionary transformations possible. Open boxes (E and F) represent rare conditions and are probably only transitional stages between B and H. C and G do not exist in nature, indicating that the combination —W is unstable and maladaptive.

against singing males; or the loss of song could evolve if it caused reduction in interbreeding with a closely related species possessing a nearly identical song, as may have happened to *Gryllus ovisopis* when it speciated from *G. fulvoni*.

In Australia mute species (those without a functional tegminal stridulatory mechanism) are best represented among the following groups: a) burrowing crickets (from rain-forests and open woodlands) (most belong to the genus *Apterogryllus* [Brachytrupinae] and therefore probably derive from a single mute and wingless ancestor); (b) crickets inhabiting lush grasses along water courses (all are small Trigonidiinae, but the stridulum may have been lost 3 or 4 times in this group); (c) crickets inhabiting canopy foliage in rain forest or seasonally wet woodland (these belong to three groups: Trigonidiinae (*Amusurgus*, *Metiochodes*, *Cyrtoxiphoides*); Podoscirtinae (*Mundeicus*, *Aphonoides*); and Pentacentrinae); (d) crickets inhabiting seasonally moist grasslands (Euscyrinae — probably lost at least twice); (e) crickets inhabiting ant nests (Myrmecophilinae— muteness probably evolved but once in this group); (f) forest floor (leaf litter) species (Nemobiinae and Phalangopsinae — stridulum perhaps lost three times in the Nemobiinae and two or three times in the Phalangopsinae); (g) shore inhabiting species (Nemobiinae, *Apteronomobius*—since this

genus is widespread over the Pacific ocean, the stridulum may have been lost outside Australia; (h) cave-inhabiting species (Nemobiinae, *Nambungia*).

A survey of the Australian crickets shows that auditory tympana are often retained after the tegminal stridulatory mechanism is lost, that is, they continue to hear after becoming mute (*Amusurgus*, *Metiochodes* [Trigonidiinae] *Pentacentrus* [Pentacentrinae] *Mundeicus*, *Umbulgaria*, *Aphonoides*, [Podoscirtinae], *Euscyrtus*, and *Patiscus* [Euscyrtae]). Partial loss of the stridulum is seen in *Hemiphonus*, *Unka* (Podoscirtinae), *Trigonidomorpha* (Trigonidiinae) and *Merrinella* (Euscyrtae). Since a loss of the sound producing mechanism is probably usually accompanied (or followed) by a loss in the listening mechanism, one must presume that some kind of selection pressure opposes the loss of a tympanum in these species.

A survey of the Australian fauna (based on Otte and Alexander 1983) shows that virtually all flying species retain a tympanum, even those species that have lost the stridulum. The only non-hearing crickets are ones that cannot fly.

We can look at the relation between singing, hearing, and flying in the Australian fauna more closely. All the possible combinations of these three characters are shown in Fig. 21 and next to them the number and the percentage of species possessing the condition. Two very common conditions occur in this fauna: A large number of species can sing, hear, and fly (A). But a much larger number of species can sing and hear, and are flightless (B). Of the remainder, 57 species (or 11.5% of the total) cannot fly, cannot hear and cannot sing (H); 46 species (9.3%) cannot sing but can both fly and hear (D). Notice that two of the possible combinations have no representative species: There are no species which can sing and fly but cannot hear (C) and there are no mute and deaf species which can fly (G). Condition C may be absent for two possible reasons: a) A species which cannot hear will not retain its song mechanism; this is probably true in most cases, but rare instances do occur in which males continue to sing even though a stridulum is lost (as in condition F—Evans 1988). b) The condition is rare because flying crickets use acoustical cues to guide them to good habitats or away from poor quality habitats or from predators. I believe the condition is rare because flying is hazardous to species which cannot hear.

Few species have conditions E and F; both conditions are probably transitional between B and H. Outside Australia I know of no species with either of these conditions. Of

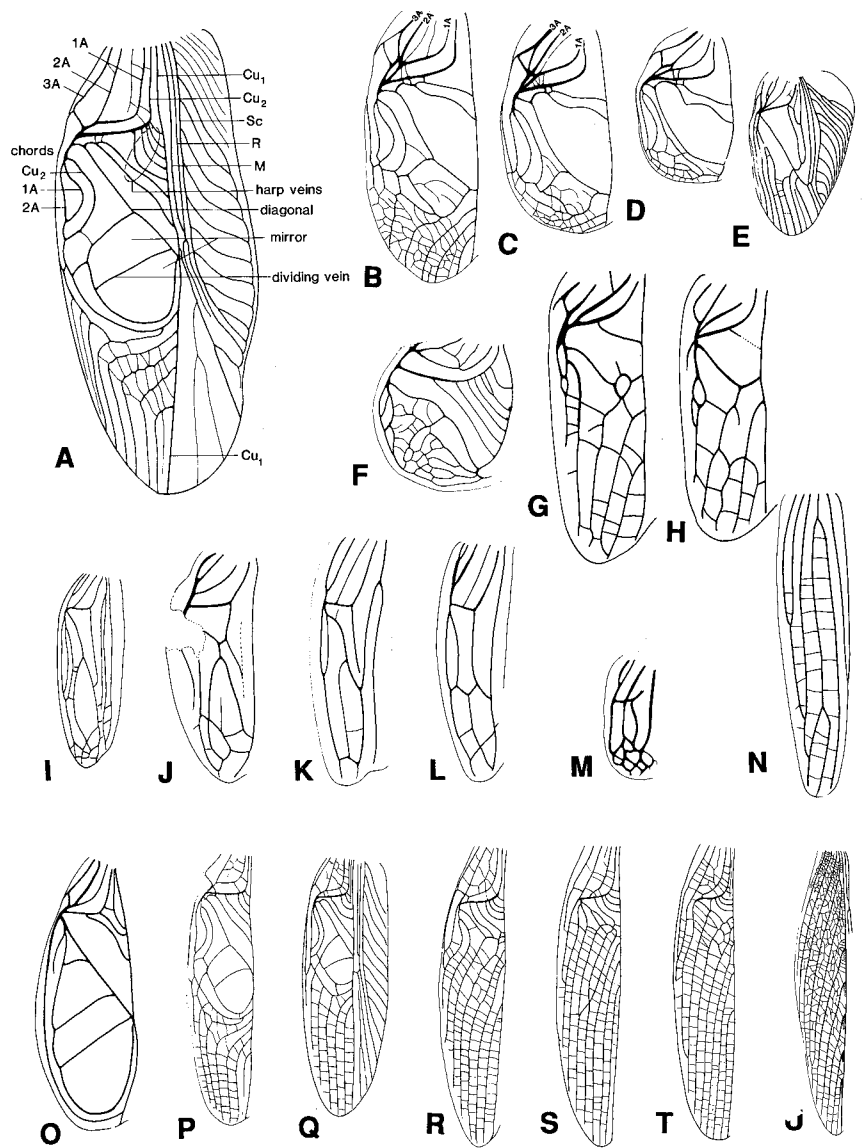


Fig. 19. Cricket male forewings showing various modes of reduction of stridulatory structures. A, Fully developed kind of wing from which all extant crickets probably derive. B, *Aritella ilya* (Gryllinae), C, *Aritella chidnaria*; D, *Tumpalia ruficeps* (Gryllinae); E, *Gryllotalpa africana*; F, *Tathra angulifrons* (Phalangopsinae); G, H, *Cyrtoprosopis stramineus* (Gryllinae); I, *Cyrtoxiphoides planifrons* (Trigonidiinae); J, *Trigonidomorpha ammona* (Trigonidiinae); K, L, *Trigonidomorpha sjostedti* (Trigonidiinae); M, *Specnia grongrongis* (Nemobiinae); N, *Amusurgus nilarius* (Trigonidiinae); O, *Oecanthus angustus*; P-U (Podoscirtinae) P, *Riatina pulkara*; Q, *R. karralla*; R, *R. mundiwindi*; S, T, *R. pilkena*; U, *Hemiphonus yinbilliko*.

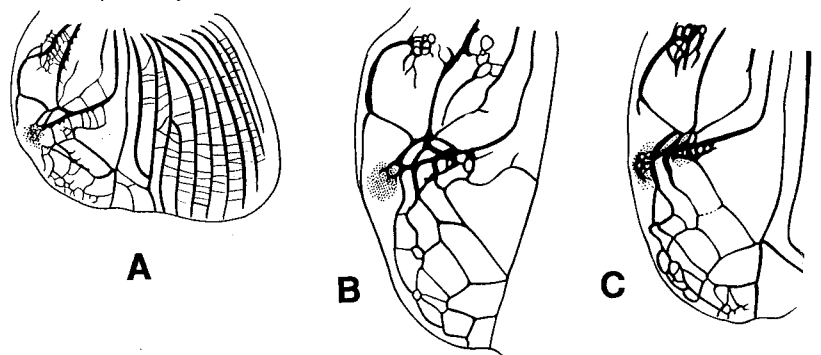


Fig. 20. *Agnotecous* (New Caledonia: Eneopterinae). Male forewing showing great modification of the male forewing. Males retain a few stridulatory teeth but do not sing audible songs. It is believed they communicate through substrate transmission.

the four Australian species which have lost the stridulum but retain the tympanum, one species has a tiny, apparently rudimentary, organ; another species is geographically variable with western Australian specimens retaining a tympanum, and eastern Australian ones having lost it (perhaps in this species occasional individuals are macropterous)(Otte and Alexander 1983).

Condition F, in which the stridulum is retained in a species that has lost its tympana, is also exceptional. Fortunately the acoustical behavior of one of these species is known. Males of *Balamara gidya* have a peculiar mode of signalling (Evans 1988). In the presence of females they tap the grass on which they rest with the abdomen, presumably transmitting information to the females through vibration of the substrate (Fig. 22). Males tap in pairs, and during the first tap of each pair they stridulate. We do not know what *B. gidya*'s nearest relatives do. *B. marroo* possesses both a stridulum and well-developed tympana. *B. albovittata* from eastern Australia has no stridulum and no tympana; in western Australia this species has no stridulum but retains a small tympanum. We speculate that in the lineage leading to *B. gidya* males called females by stridulating; later, males began to vibrate the substratum (grass blades on which both were perched) during stridulation; gradually tapping began to predominate as the information carrier, and tympana were lost when the acoustical component of the signal disappeared; the stridulation now heard faintly during the first tap is perhaps a vestige of the original call. Once it disappears, as it may already have done in *B. albovittata*, the stridulum may also be lost.

Africa and Pacific island crickets hold to this pattern precisely, though we have discovered a single species of *Adenopterus* (Loyalty Islands) which possesses long hind wings and lacks tympana (Otte, Alexander and Cade 1987).

The association between hearing and flying is also evident within some Australian species which show developmental flexibility in both characteristics—further confirming a functional coupling between them. *Euscyrtus hemelytrus* (Euscyrtinae) always possesses tympana, but the outer tympanum is sometimes obsolete in micropterous specimens. *Metioche vittaticollis* and *Trigonidomorpha sjostedti* (Trigonidiinae) are similar to *Euscyrtus* with macropterous individuals possessing large tympana and micropterous individuals having small or no tympana (Table 4).

Evans (1988) has further studied wing length and tympana in *Trigonidomorpha sjostedti*. She crossed the two phenotypes (winged/ +tympana and wingless/ -tympana) and found that the dimorphism does not result from a simple Mendelian 1-locus, 2 allele mechanism, since all crosses produced both phenotypes in both sexes. Field collected wingless/-tympana adults produced winged/ +tympana offspring. She also found that both morphs possessed tympanal organs with well developed scolopidia, attachment cells, and accessory cells, in close proximity to the anterior tympana trachea; but the tympana of the wingless morph were hidden beneath a layer of cuticle.

Several experimental studies have shown that crickets can hear bat sounds and take evasive action in the presence of bat sounds

Table 6. Condition of inner and outer tympana in macropterous and micropterous individuals of *Euscyrtus hemelytrus* (Euscyrtinae). I, larger inner; i, small inner; (i) nearly obsolete inner; O, large outer; o, smaller outer; (o) nearly obsolete outer; -, no tympanum (from Otte and Alexander 1983, Otte 1990).

Locality	MAC	MIC
<i>Euscyrtus hemelytrus</i>		
Manila		i / -
Upper Burma	I / O	(i) / (o)
Assam	I / O	i / -
Australia	I / O	i / o
	i / -	
<i>Metioche vittaticolle</i>		
Australia	I / O	i / o
	i / -	
	- / -	
<i>Trigonidomorpha sjostedti</i>		
Australia	I / O	- / -
	i / -	

(Griffin 1958, Popov and Mirkovich 1982, Moiseff and Hoy 1983, Nolen and Hoy 1984, Doherty and Hoy 1985).

It has also been suggested that the development of receptors sensitive to aerial sounds may have been favored by selection if they enabled individuals to stay within a dispersing group by responding to the flight sounds of conspecifics (Evans 1988, and references therein); this may occur in locusts which fly in unison, but seems highly unlikely in crickets which have not been reported to fly in swarms.

Evolution of Glands

In several groups of crickets glandular structures with openings on the outer surface may have changed the circumstances of signaling so that the calling has been reduced in significance. The metanotal glands present in Eneopterinae, Podoscirtinae, Oecanthinae and Pteroplistinae are probably ancient. They are used by males to feed females during copulation. Both acoustical and mute species possess the glands. But there is no evidence that mute species have larger or more prominent glands. Indeed, the reverse seems to be true in Hawaiian Oecanthinae. In the genus *Leptogryllus* two different lineages have given rise to taxa in which the metanotal glands are reduced to very small openings. The size of the metanotal glands in this genus is related to the size of the forewings. Large metanotal glands are present only in those species with wing pads that meet one another along the midline; those species in which the wing pads have been reduced to small rudiments leaving the dorsum exposed, the glands are represented only by two holes. We do not know the functional difference between the two gland types. It appears obvious, though

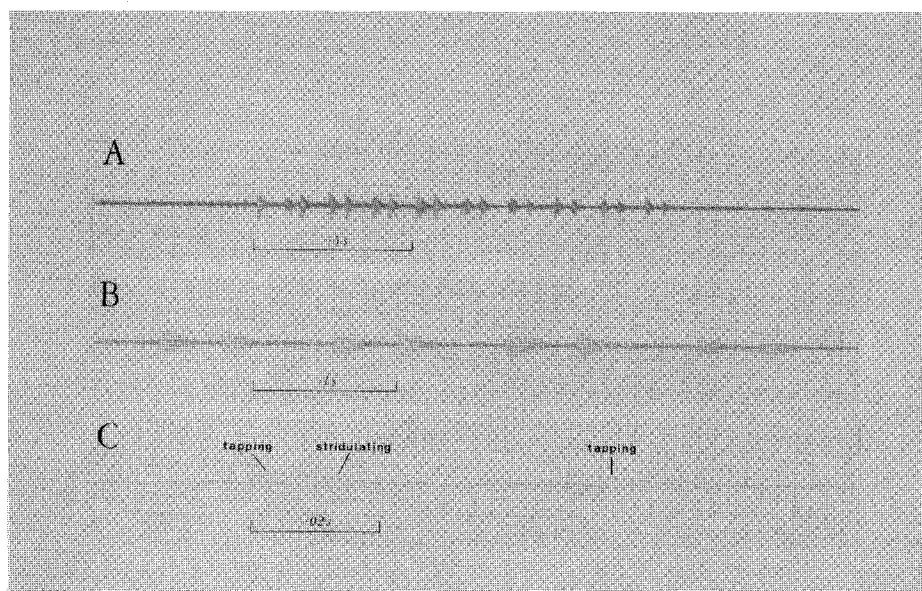


Fig. 21. *Balamara gidya* possesses a stridulum but lack auditory tympana. Signaling in this species involves mainly a tapping of the substrate with the abdomen. However during the first tap of every pair the male also stridulates. Is the stridulation detectable through the surface?

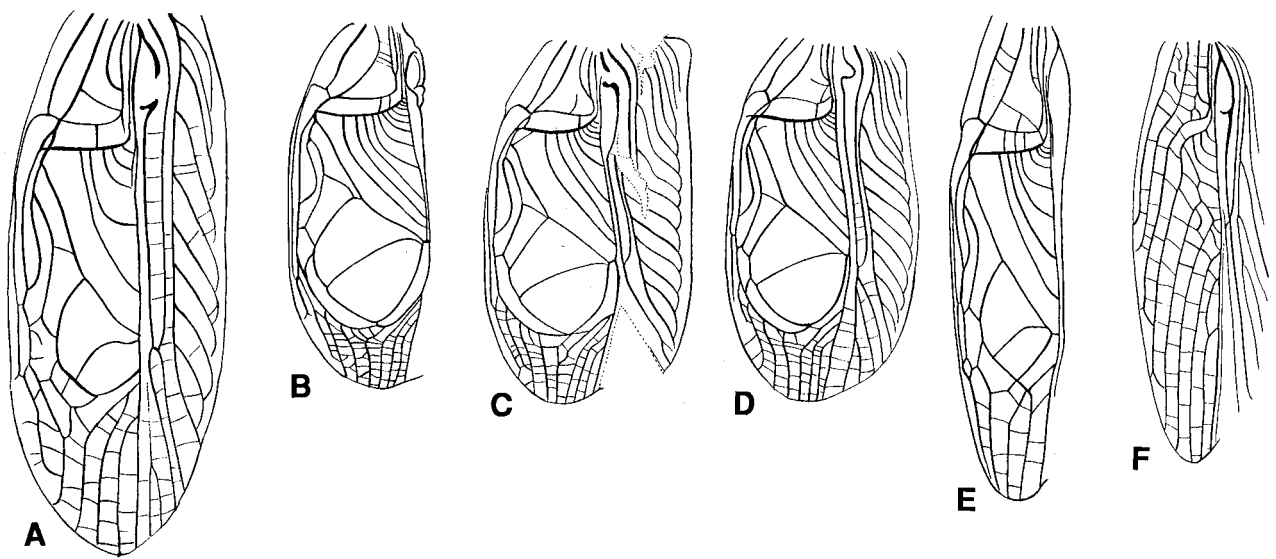


Fig. 22. Wing venation in New Caledonian *Archenopterus* species showing considerable modification of Cu1 and M veins at the anterior end associated with the position of the wing gland believed to be used in feeding the female during courtship. The last figure shows a great reduction of the stridulatory structures present in other species. A, *A. maai*; B, *A. bouensis*; C, *A. hemipteroides*; D, *A. gressitti*; E, *A. amoensis*; F, *A. hemiphonus*.

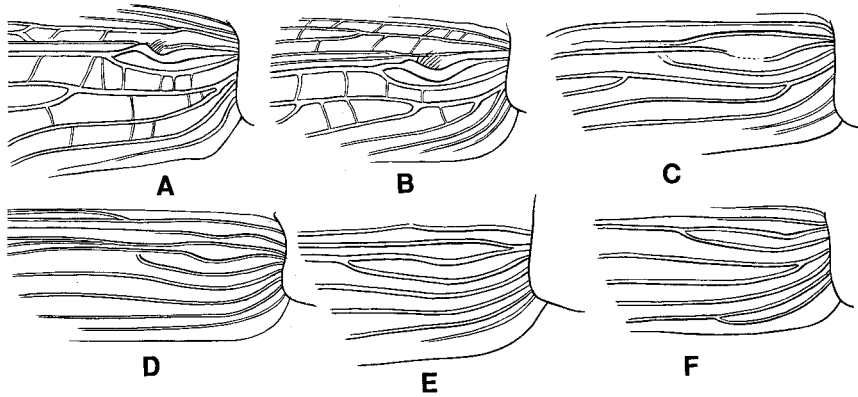


Fig. 23. *Adenopterus* (New Caledonia: Podoscirtinae). Depiction of the glandular region on the male forewing. A, *A. sarrameus*; B, *A. yahouensis*; C, *A. rouxi*; D, *A. bouo*; E, *A. sylvaticus*; F, *A. sarasini*.

that large glandular pits are maintained only in species with covering elytra.

Three other kinds of surface glands are now known in crickets: 1) tibial glands are located on the hind tibiae of some Nemobiinae; 2) tegminal glands are located on the upper exterior surface of the forewings of *Adenopterus* and *Archenopterus* species from New Caledonia (Figs. 19B, 19C); and 3) the entire upper surface of the forewing of a Caribbean phalangopsine is modified into a bowl-like structure. In the last species, rudiments of the file are retained, but the species appears to be mute; the under (hidden) wing is much smaller than the upper. In this instance the forewings may be used only for producing glandular material used in feeding females. In the case of New Caledonian Podoscirtinae, there appears to be no particular relation between size of glands and development of acoustical wings. In *Archenopterus* stridulating wings are fully developed and males produce a

loud song, and the gland varies from species to species from small barely indicated depressions to large pits. In *Adenopterus* all species lack stridulatory devices and they show similar variation from large pits to barely indicated depressions.

The Fossil Record

The loss of acoustical signalling has profound influences on the structure of the male forewings. It is possible to see various taxa the progressive stages by which the sound producing and emitting structures are lost (Figs. 24-27). From a broad comparison of extant crickets and tettigoniids there is no doubt that all crickets which have non-stridulatory wings are derived secondarily from fully acoustical wings. In many groups the wings are lost entirely once acoustical signalling is lost. In other species the wings are retained, sometimes for flying and in them the venation becomes modified in the direction

of the condition possessed by females.

Zeuner (1934, 1939) and Sharov (1971) illustrate an evolutionary progression in the acquisition of sound producing and emitting structures of the male forewing based on fossils (Figs. 28, 29). If songs are in various stages of being lost in many lineages now, there is reason to believe that wings reverted to the non-stridulatory type many times in the past. Comparison of the recent fauna indicates that the evolution may have occurred in the opposite direction in any given lineage. One must therefore be careful in interpreting the fossil record, for structures which might appear to be stages in the acquisition of stridulatory structures are very likely to represent a stage in the loss of such structures.

References

- Alexander RD. 1956. A comparative study of sound production in insects with special referen to the singing of Orthoptera and Cicadidae of the eastern United States. Ph. D. Thesis. Ohio State University.
- Alexander RD. 1957. The song relationships of four species of ground crickets (*Nemobius*). Ohio Journal of Science. 57: 53-63.
- Alexander RD. 1957. The taxonomy of the field crickets of the eastern United States (Orthoptera: Gryllidae: *Acheta*). Annals of the Entomological Society of America. 50: 584-602.
- Alexander RD. 1960. Sound communication in Orthoptera and Cicadidae in W. B. Lanyon & W. N. Tavolga, eds. Animal Sounds and Communication. Am. Inst. Biol. Sci., Washington 1958.

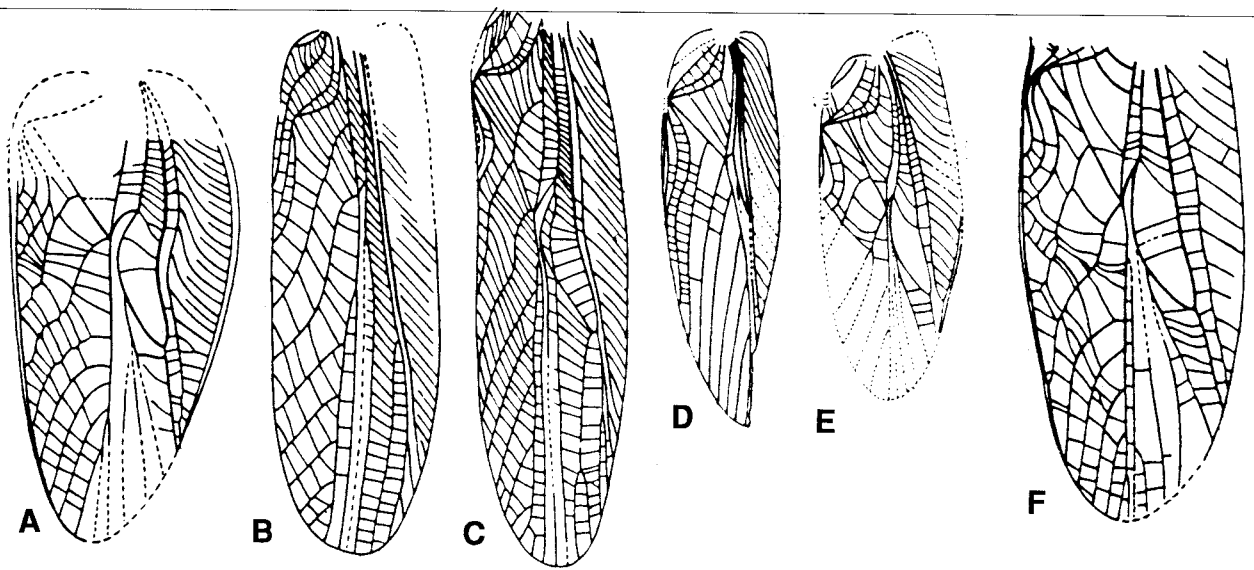


Fig. 24. Male forewings in fossil crickets: A, *Pronogryllus asiaticus* (Lower Jurassic: Issyk-Kul); B, *Gryllavus madygenicus* (Lower Triassic: Madygen); C, *Gryllavus madygenicus* (Lower Triassic: Madygen); D, *Karataogryllus gryllotalpiformis* (Upper Jurassic); E, *Protogryllus karativicus* (Upper Jurassic: Mikhailovka); F, *Protogryllus angaricus* (Middle Jurassic: Ust Balei).

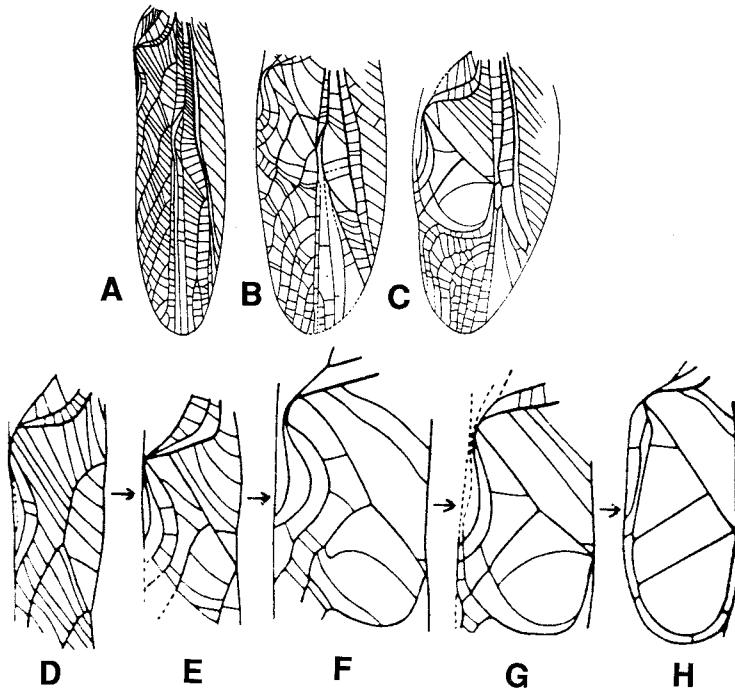


Fig. 25. A-C. Sharov's (1971) depiction of the "evolution of the venation of the fore wing of Gryllidae according to paleontological data." (p. 145). D-H. Sharov's (1971:81) depiction of "evolution of stridulatory apparatus from Gryllidae to Oecanthidae."

Alexander RD. 1961. Aggressiveness, territoriality, and sexual behaviour in the field crickets (Orthoptera: Gryllidae). *Behaviour* 17: 130-223.
 Alexander RD. 1962a. Evolutionary change in cricket acoustical communication. *Evolution* 16: 443-467.
 Alexander RD. 1962b. The role of behavioral study in cricket classification. *Systematic Zoology* 11: 53-72.
 Alexander RD. 1964. The evolution of mating behavior in Arthropods. *Insect Reproduction, Symposium 2*. London, Royal Entomological Society.

Alexander RD. 1966. The evolution of cricket chirps. *Natural History Magazine* 75: 27.
 Alexander RD. 1967. Acoustical communication in Arthropods. *Annual Review of Entomology*. 12: 495-526.
 Alexander RD. 1967. *Singing Insects*. Chicago., Rand McNally.
 Alexander RD. 1968. *Arthropods. Animal Communication*. Bloomington, Indiana, 686 pp., Indiana University Press.
 Alexander RD. 1968. Life cycle origins, speciation, and related phenomena in crickets. *Quarterly Review of Biology*. 43(1): 1-41.
 Alexander RD. 1975. Natural selection and

specialized chorusing behavior in acoustical insects. *Insects, Science, and Society*. New York, Academic Press.

Alexander RD, Bigelow RS. 1960. Allochronic speciation in field crickets and a new species *Acheta veletis*. *Evolution*. 14: 334-346.
 Alexander RD, Meral GH. 1967. Seasonal and daily chirping cycles in the northern spring and fall field crickets, *Gryllus veletis* and *G. pennsylvanicus*. *Ohio Journal of Science*. 67: 200-209.
 Alexander RD, Otte D. 1967. Cannibalism during copulation in the brown bush cricket, *Hapithus agitator* (Gryllidae). *Florida Entomologist*. 50: 79-87.
 Alexander RD, Thomas ES. 1959. Systematic and behavioral studies on the crickets of the *Nemobius fasciatus* group (Orthoptera: Gryllidae: Nemobiinae). 52: 591-605.
 Alexander RD, Walker TJ. 1962. Two introduced field crickets new to eastern United States. *Ann. Entomol. Soc. Am.* 55: 90.
 Atkins G, Chiba A, Atkins S, Stout JF. 1988. Low-pass filtering of sound signals by a high-frequency brain neuron and its input in the cricket *Acheta domestica*. *J. Compl Physiol. A. Sens. Neural Behav. Physiol.* 164: 269.
 Atkins G, Pollack GS. 1986. Sound-activated interneurons descending from the prothoracic ganglion in the cricket, *Teleogryllus oceanicus*: 1. response properties of ultrasound-sensitive neurons. submitted *J. Comp. Physiol.* 9/86. Dept. biology, McGill Univ. :
 Atkins G, Ligman F, Burghardt F, Stout JF . 1984. Changes in phonotaxis by the female cricket *Acheta domestica* after killing identified acoustic interneurons. *J. Compl Physiol. A. Sens. Neural Behav. Physiol.* 154: 795.
 Atkins G, Pollack GS. 1986. Age-dependent occurrence of an ascending axon on the omega neuron of the cricket, *Teleogryllus oceanicus*. *J. Comp. Neurol.* 243(4): 527-34
 Atkins, G., S. Atkins, D. Schoun, and J. F. Stout. 1987. Scototaxis and shape discrimination in the female cricket *Acheta*

- domesticus* in an arean and on a compensatory treadmill. *Physiol. Entomol.* 12: 125.
- Bailey E, Walker PR. 1969. A comparison of the properties of the pyruvate kinases of the fat body and flight muscle of the adult male desert locust. *Biochem. J.* 111(3): 359-64.
- Bentley DR, Hoy RR. 1972. Genetic control of the neuronal network generating cricket (*Teleogryllus*) song patterns. *Anim. Behav.* 20: 478-492.
- Brodfehrer PD, Hoy RR. 1990. Ultrasound sensitive neurons in the cricket brain. *J. Comp. Physiol. [A]* 166(5): 651-62.
- Busnel MC, RG Busnel. 1954. La directivité acoustique des déplacements de la femelle d'*Oecanthus pellucens* Scop. *Ann. Epiphyties, fascicule special consacré au colloque sur l'acoustique des Orthoptères* : 356-364.
- Cade W. 1975. Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science.* 190: 1312-1313.
- Cade W. 1979. The evolution of alternative male reproductive strategies in field crickets. IN: Blum and Blum, eds. *Sexual selection and reproductive competition in insects*. New York, Academic Press.
- Cade W. 1979. Effect of male-deprivation on female phonotaxis in field crickets (Orthoptera: Gryllidae: *Gryllus*). *Can. Ent.* 111: 741-744.
- Cade W. 1980. Alternative male reproductive behaviours. *Florida Entomologist.* 63: 30-45.
- Cade W. 1981. Alternative male strategies: Genetic differences in crickets. *Science.* 212: 563-564.
- Cade W. 1981. Field cricket spacing and the phonotaxis of crickets and parasitoid flies to clumped and isolated cricket songs. *Z. Tierpsychol.* 55: 365-375.
- Cade W. 1984. Effects of fly parasitoids on nightly calling duration in field crickets. *Canad. J. Zool.* 62: 226-228.
- Cade W. 1984. Effects of fly parasitoids on nightly calling duration in field crickets. *Canad. J. Zool.* 62: 226-228.
- Cade W. 1984. Genetic variation underlying sexual behavior and reproduction. *Amer. Zool.* 24: 355-366.
- Cade W, Otte D. 1982. Alternation calling and spacing patterns in the field cricket *Acanthogryllus fortipes* (Orthoptera: Gryllidae). *Canadian Journal of Zoology.* 60: 2916-2920.
- Cade W, Rice R. 1980. Field crickets (Orthoptera:Gryllidae) as prey of the toad *Bufo marinus*. *Canadian Entomologist.* 80: 335-336.
- Cade W, Wyatt D. 1984. Factors affecting calling behaviour in field crickets, *Teleogryllus* and *Gryllus* (Age, weight, density and parasites). *Behaviour.* 88: 61-75.
- Dobzhansky Th. 1951. *Genetics and the origin of species*. Third Edition. Columbia University Press.
- Doherty JA. 1985. Phonotaxis in the cricket, *Gryllus bimaculatus* De Geer: Comparisons of choice and no-choice paradigms. *J. Comp. Physiol.* 157: 279-289.
- Doherty JA. 1985. Temperature coupling and "trade-off" phenomena in the acoustic communication system of the cricket, *Gryllus bimaculatus* De Geer (Gryllidae). *J. Exp. Biol.* 114: 17-35.
- Doherty JA. 1985. Trade-off phenomena in calling song recognition and phonotaxis in the cricket *Gryllus bimaculatus*. *J. Comp. Physiol.* 156: 787-801.
- Doherty JA. 1987. A new microcomputer-based method for measuring walking phonotaxis in field crickets (Gryllidae). *J. Exp. Biol.* 130: 425-432.
- Doherty JA. 1991. Song recognition and localization in the phonotaxis behavior of the field cricket, *Gryllus bimaculatus*. *J. Comp. Physiol. A* 168: 213-222.
- Doherty JA, Callos D. 1991. Acoustic communication in the trilling field cricket, *Gryllus rubens* (Orthoptera: Gryllidae). *J. Ins. Behav.* 4: 67-82
- Doherty JA, Hoy R. 1985. Communication in insects. III. The auditory behaviour of crickets: some views of genetic coupling, song recognition, and predator detection. *Quarterly Review of Biology.* 60: 457-472.
- Doherty JA, Huber F. 1983. Temperature effects on acoustic communication in the cricket *Gryllus bimaculatus* De Geer. *Verh. Dtsch. Zool. Ges.* 1983: 188.
- Doherty JA, Pires A. 1987. A new microcomputer-based method for measuring walking phonotaxis in field crickets (Gryllidae). *J. Exp. Biol.* 130: 425-32.
- Doherty JA, Stortz MM. 1992 in press. Calling song and selective phonotaxis in the field crickets *Gryllus firmus* and *Gryllus pennsylvanicus* (Orthoptera: Gryllidae). In Press.
- Doolan JM, Pollack GS. 1985. Phonotactic specificity of the cricket *Teleogryllus oceanicus*: Intensity-dependent selectivity for temporal parameters of the stimulus. *J. Comp. Physiol.* 157: 223-233.
- Elepfandt A, Popov AJ. 1978. Auditory interneurons in the mesothoracic ganglion of crickets. *J. Insect Physiol.* 25: 429-441.
- Elsner N, Huber F. 1973. [Neural principles of species-specific communication in orthoptera]. *Fortschr. Zool.* 22(1): 1-48 (in German).
- Elsner N, Popov AV. 1978. Neuroethology of acoustic communication. *Adv. Insect Physiol.* 13: 229-335.
- Evans AR. 1983. A study of the behaviour of the Australian field cricket *Teleogryllus commodus* in the field and in habitat simulations. *Z. Tierpsychol.* 62: 269-290.
- Evans A. 1988. Mating systems and reproductive strategies of some Australian crickets (Orthoptera: Gryllidae). Ph.D. Thesis, Univ. of Melbourne.
- Evans AR. 1988. Mating systems and reproductive strategies in three Australian gryllid crickets: *Bobilla victoriae* Otte, *Balamara gidya* Otte and *Teleogryllus commodus* (Walker) (Orthoptera: Gryllidae: Nemobiinae; Trigoniidiinae; Gryllinae). *Ethol.* 78: 21-52.
- Ewing, A. and G. Hoyle. 1965. Neuronal mechanism underlying control of sound production in a cricket, *Acheta domesticus*. *J. Exp. Biol.* 43: 139.
- Forrest TG. 1980. Phonotaxis in mole crickets: its reproductive significance. *Florida Entomologist.* 63: 45-53.
- Forrest TG. 1982. Acoustic communication and baffling behaviors of crickets. *Fla. Entomol.* 65(1): 33-44.
- Forrest TG. 1983. Calling songs and mate choice in mole crickets. *Orthopteran Mating Systems*. Boulder, Westview Press,.
- Forrest TG. 1983. Phonotaxis and calling in Puerto Rican mole crickets. *Ann. Entomol. Soc. Am.* 76: 797.
- French BW, Cade WH. 1987. The timing of calling, movement, and mating in the field crickets *Gryllus veletis*, *G. pennsylvanicus*, and *G. integer*. *Behav. Ecol. Sociobiol.* 21: 157-162.
- Fulton BB. 1915. The tree crickets of New York: life history and bionomics. *Tech. Bull. N.Y. Agric. Exp. Stn.* 42:
- Fulton BB. 1925. Physiological variation in the snowy tree-cricket *Oecanthus niveus* De Geer. *Ann. Ent. Soc. Amer.* 18(3): 363-383.
- Fulton BB. 1926. Geographical variation in the nigricornis group of *Oecanthus*. *Iowa State Coll. J. Sci.* 1(43-61):
- Fulton BB. 1926. The tree crickets of Oregon. *Oregon Agr. Exp. Sta. Bull.* 233: 1-20.
- Fulton BB. 1928. Sound perception by insects. *The Scientific Monthly* 278: 552-556.
- Fulton BB. 1930. A new species of *Nemobius* from North Carolina (Orthoptera Gryllidae). *Ent. News.* 41: 38-42.
- Fulton BB. 1930. Notes on Oregon Orthoptera with Descriptions of new species and races. *Ann. Ent. Soc. Amer. Colu-mbus*, 23 (iv): 611-64 1.
- Fulton BB. 1931. A study of the genus *Nemobius* (Orthoptera: Gryllidae). *Ann. Ent. Soc. Am.* 24: 205-237.
- Fulton BB. 1932. North Carolina's singing Orthoptera. *J. Elisha Mitchell Sci. Soc.* 47: 55-69.
- Fulton BB. 1933. Inheritance of song in hybrids of two subspecies of *Nemobius fasciatus*. *Annals of the Entomological Society of America.* 26: 368-376.
- Fulton BB. 1933. Stridulating organs of female Tettigoniidae (Orthoptera). *Ent. News XLIV*: 270-275.
- Fulton BB. 1934. Rythm, synchronism and alternation in the stridulation of Orthoptera. *J. Elisha Mitches Sci. Soc.* 50: 263-267.
- Fulton BB. 1937. Experimental crossing of subspecies of *Nemobius*. *Annals of the Entomological Society of America.* 30: 201-207.
- Fulton BB. 1951. The seasonal succession of orthopteran stridulation near Raleigh, North Carolina. *J. Elisha Mitchell Sci. Soc.* 67: 87-95.
- Fulton BB. 1952. Speciation in the field cricket. *Evolution* 6: 283-295.
- Fulton BB. 1956. The genus *Anaxipha* in the United States (Orthoptera: Gryllidae). *J. Elisha Mitchell Sci. Soc.* 72: 222-243.
- Funk, D. H. 1989. The mating of tree crickets. *Scientific American.* 260(8): 50-59.
- Griffin DR. 1958. *Listening in the Dark*. New Haven. Yale University Press.
- Gross SW, Mays DL, Walker TJ. 1990. Systematics of *Pictonemobius* ground crickets (Orthoptera: Gryllidae). *Trans. Amer. Ent.*

- Soc. 115: 433-456.
- Gwynne D. 1982. Male nutritional investment and evolution of sexual differences in Tettigoniidae. IN: Gwynne D, Morris GK, eds. Orthopteran Mating System. Westview Press: Boulder, Colorado.
- Gwynne DT. 1984. Male mating effort, confidence of paternity and insect sperm competition. Sperm Competition and the Evolution of Animal Mating Systems. New York, Academic Press.
- Gwynne DT, Morris GK, eds. 1983. Orthopteran mating systems: Sexual competition in a diverse group of insects. Westview Press: Boulder, Colorado.
- Halliday TR. 1983. The study of mate choice. Pp. 3-50. IN: Bateson P, ed. Mate Choice. Cambridge University Press.
- Haskell PT. 1956. Hearing in certain orthoptera. J. exp. Biol. 33: 756-776.
- Hill KG. 1974. Acoustic communication in the Australian field crickets *Teleogryllus commodus* and *T. oceanicus* (Orthoptera Gryllidae). Ph.D. University of Melbourne.
- Hill KG. 1974. Carrier frequency as a factor in phonotactic behaviour of female crickets (*Teleogryllus commodus*). Journal of Comparative Physiology. (1-18):
- Hill KG, Boyan GS. 1976. Directional hearing in crickets. Nature 262. 262: 390-391.
- Hill KG, Boyan GS. 1977. Sensitivity to frequency and direction of sound in the auditory system of crickets. J. Comp. Physiol. 121: 79-97.
- Hill KG, Loftus-Hills JJ, Gartside DF. 1972. Pre-mating isolation between the Australian field crickets *Teleogryllus commodus* and *T. oceanicus*. Australian Journal of Zoology. 20: 153-163.
- Hill KG, Loftus-Hills JJ, Gartside DF. 1972. Premating isolation between the Australian field crickets *Teleogryllus commodus* and *T. oceanicus* (Orthoptera: Gryllidae). Australian Journal of Zoology 20: 153-163.
- Hill KG, Boyan GS. 1976. Directional hearing in crickets. Nature 262(5567): 390-1.
- Hoy RR. 1971. Genetic control of acoustic behavior in crickets. Am. Zool. 14: 1067-80.
- Hoy RR. 1978. Acoustic communication in crickets: a model system for the study of feature detection. Fed. Proc. Am. Soc. Exp. Biol. 37: 2316-2323.
- Hoy RR, Paul RC. 1973. Genetic control of song specificity in crickets. Science. 180: 82-83.
- Hoy RR, G. S. Pollack GS, Moiseff A. 1982. Species-recognition in the field cricket *Teleogryllus oceanicus*: behavioural and neural mechanisms. Am. Zool. 22: 597-607.
- Hoy RR, Hahn J, Paul RC. 1977. Hybrid cricket auditory behavior: evidence for genetic coupling in animal communication. Science. 195: 82-84.
- Hoy RR. 1978. Acoustic communication in crickets: a model system for the study of feature detection. Fed. Proc. 37(10): 2316-23.
- Hoyle G. 1984. Neuromuscular transmission in a primitive insect: modulation by octopamine, and catch-like tension. Comp. Biochem. Physiol. [C] 77(2): 219-32.
- Huber F. 1952. Verhaltensstudien am Männchen der Feldgrille (*Gryllus campestris*) nach Eingriffen am Zentralnervensystem. Verh. deutsch. zoo. Ges. Freiburg. 1952: 138-149.
- Huber F. 1962. Central nervous control of sound production in crickets and some speculations on its evolution. Evolution. 16(4): 429-442.
- Huber F. 1974. Neuronal background of species-specific acoustical communication in orthopteran insects (Gryllidae). The Biology of Brains. J. Wiley and Sons.
- Huber F. 1978. The insect nervous system and insect behaviour. Anim. Behav. 26: 976-981.
- Huber F, Stout JF. 1981. Responses to features of the calling song by ascending auditory interneurons in the cricket *Gryllus campestris*. Physiological Entomology 6:199-112
- Huber F, Thorson, J. 1985. Cricket auditory communication. Scientific American. 253: 60-68.
- Huxley J. 1938. Darwin's theory of sexual selection and the data subsumed by it, in the light of recent research. Am. Nat. 72: 416-433.
- Knyazev AN, Popov AV. 1977. Responses of single cercal mechanoreceptors to sound and sinusoidal mechanical stimulation in the cricket. Dok. Acad. Nauk SSSR. 232: 1211-1214.
- Koudele K, Stout JF, Reichert D. 1987. Factors which influence female cricket's (*Acheta domestica*) phonotactic and sexual responsiveness to males. Physiol. Entomol. 12: 67-80.
- Lakes-Harlan R, Heller K-G. 1992. Ultrasound-sensitive ears in a parasitoid fly. Naturwissenschaften 79: 224-226.
- Loftus-Hills JJ, Littlejohn MJ, Hill KG. 1971. Auditory sensitivity of the crickets *Teleogryllus commodus* and *T. oceanicus*. Nature New Biology. 233: 184-185.
- Love RE, Walker TJ. 1979. Systematics and acoustic behavior of scaly crickets (Mogoplistinae) of the Eastern United States. Trans. Amer. Ent. Soc. 105: 1-66.
- Love RE, Walker TJ. 1979. Systematics and acoustic behavior of scaly crickets (Orthoptera: Gryllidae: Mogoplistinae) of eastern United States. Trans. Am. ent. Soc. 105: 1-66.
- Masaki S, Walker TJ. 1987. Cricket life cycles. Evol. Biol. 21: 349-423.
- Moiseff A, Hoy RR. 1983. Sensitivity to ultrasound in an identified auditory interneuron in the cricket: a possible neural link to phonotactic behaviour. J. Comp. Physiol. 152: 155-167.
- Moiseff GS, Pollack RR, Hoy RR. 1978. Steering responses of flying crickets to sound and ultrasound: Mate attraction and predator avoidance. Proc. Natl. Acad. Sci. USA. 75: 4052.
- Murray JA, Hoy RR. 1988. Courtship success in the cricket *Gryllus bimaculatus*. Differential contribution of carrier frequency and harmonics in courtship song. Soc. Neurosci. Abstr. 14: 310.
- Nohn TC and Hoy RR. 1984. Initiation of behavior by single neurons; the role of behavioral context Science. 226: 992-994.
- Nolan TC, Hoy RR. 1984. Initiation of behaviour by single neurons. The role of behavioural context. Science. 226: 992-994.
- Oldfield BP, Kleindienst H, Huber F. 1986. Physiology and tonotopic organization of auditory receptors in the cricket *Gryllus bimaculatus* DeGeer. J. Comp. Physiol. [A] 159(4): 457-64.
- Otte D. 1970. A comparative study of communicative behavior in grasshoppers. Misc. Publ. Mus. Zool. Univ. Mich. 41: 1-168.
- Otte D. 1972. Simple versus elaborate behavior in grasshoppers. An analysis of communication in the genus *Syrbula*. Behavior. 42: 291-322.
- Otte D. 1974. Effects and functions in the evolution of signaling systems. Annual Review of Ecology and Systematics 5: 385-417.
- Otte D. 1977. Communication in Orthoptera. How animals communicate. Bloomington, Indiana University Press.
- Otte D. 1979. Historical development of sexual selection theory. In Blum and Blum (eds.) Sexual selection and reproductive competition in insects. New York, Academic Press.
- Otte D. 1983. African Crickets (Gryllidae). 2. *Afrogyllopsis* Randell and *Neogryllopsis* n. gen of eastern and southern Africa. Proceedings of the Academy of Natural Sciences of Philadelphia 135: 218-235.
- Otte D. 1984. African Crickets (Gryllidae). 4. The genus *Platygyllus* from eastern and southern Africa. Proceedings of the Academy of Natural Sciences of Philadelphia 136: 45-66.
- Otte D. 1984. African Crickets (Gryllidae). 5. On the East and South African species of *Modicogryllus* and several related genera (Gryllinae: Modicogryllini). Proceedings of the Academy of Natural Sciences of Philadelphia. 136: 67-97.
- Otte D. 1984. African Crickets (Gryllidae). 6. On the genus *Gryllus* and some related genera (Gryllinae, Gryllini). Proceedings of the Academy of Natural Sciences of Philadelphia 136: 98-122.
- Otte D. 1985. African Crickets (Gryllidae). 7. The genus *Cryncus* Gorochov. Proceedings of the Academy of Natural Sciences of Philadelphia. 137: 129-142.
- Otte D. 1985. African Crickets (Gryllidae). 8. Further notes on the genus *Velarifictorus* and other genera. Proceedings of the Academy of Natural Sciences of Philadelphia. 137: 143-152.
- Otte D. 1987. African Crickets (Gryllidae). 9. New genera and species of Brachytrupinae and Gryllinae. Proceedings of the Academy of Natural Sciences of Philadelphia. 139: 315-374.
- Otte D. 1988. Bark crickets of the western Pacific region (Gryllidae: Pteroplistinae). Proc. Acad. Nat. Sci. Philadelphia 140: 281-334.
- Otte D. 1989. Speciation in Hawaiian crickets. In: Otte and Endler (eds.) Speciation and its Consequences. Sunderland, Mass., Sinauer Associates.
- Otte D. in prep. The Hawaiian Crickets: Systematics, Biogeography and Speciation.

- Otte D, Alexander RD. 1983. The Australian Crickets. Academy of Natural Sciences of Philadelphia Monograph 22: 1-477.
- Otte D, Alexander RD, Cade W. 1987. The crickets of New Caledonia (Gryllidae). Proceedings of the Academy of Natural Sciences of Philadelphia. 139: 375-475.
- Otte D, Rentz DC. 1985. The crickets of Lord Howe and Norfolk Islands (Orthoptera: Gryllidae). Proceedings of the Academy of Natural Sciences of Philadelphia. 137: 79-101.
- Otte D, Cade W. 1975. On the role of olfaction in sexual and interspecific recognition in crickets. Animal Behavior. 24: 1-6.
- Otte D, Cade W. 1983. African Crickets (Gryllidae). 3. On the African species of *Velarifictorus* Randell (Gryllinae, Modicogryllini). Proceedings of the Academy of Natural Sciences of Philadelphia. 135: 241 - 253.
- Otte D, Cade W. 1983. African Crickets (Gryllidae). 1. *Teleogryllus* of eastern and southern Africa. Proceedings of the Academy of Natural Sciences of Philadelphia. (102-127):
- Otte D, Rentz DC. 1985. The crickets of Lord Howe and Norfolk Islands (Orthoptera: Gryllidae). Proceedings of the Academy of Natural Sciences of Philadelphia. 137: 79-101.
- Otte D, Toms R, Cade W. 1988. New species and records of east and southern African crickets (Orthoptera: Gryllidae). 34: 405-468.
- Paul RC, Walker TJ. 1979. Arboreal singing in a burrowing cricket, *Anurogryllus arboreus*. J. Comp. Physiol. 132: 217-223.
- Pollack, G. S. 1982. Sexual differences in cricket calling song recognition. J. Comp. Physiol. 146: 217-221.
- Pollack, G. S. 1984. Ultrasound-sensitive neurons descending in the thoracic nervous system of the cricket, *Teleogryllus oceanicus*. Canad. J. Zool. 62: 555-562.
- Pollack, G. S. 1988. Selective attention in an insect auditory neuron. J. Neuroscience. 8: 2635-2639.
- Pollack GS, Hoy RR. 1979. Temporal patterns as a cue for species-specific calling song recognition. Science, N.Y. 204: 429-432.
- Pollack GS, Hoy RR. 1981. Phonotaxis in flying crickets: Neural correlates. J. Insect Physiol. 27: 41-45.
- Pollack GS, Hoy RR. 1981. Phonotaxis to individual rhythmic components of a complex cricket calling song. J. Comp. Physiol. 144: 367-374.
- Pollack GS. 1988. Selective attention in an insect auditory neuron. J. Neurosci. 8(7): 2635-9.
- Pollack GS. 1988. Selective attention in an insect auditory neuron. J. Neurosci 8(7): 2635-9.
- Pollack GS, Huber F, Weber T. 1984. Frequency and temporal pattern-dependent phonotaxis of crickets (*Teleogryllus oceanicus*) during tethered flight and compensated walking. J. Comp. Physiol. 154: 13-26.
- PoPov AV, Shuvalov VF. 1977. Phonotactic behaviour of crickets. J. comp. physiol. A 119 126.
- Popov AV. 1972. Acoustic signals of crickets (Orthoptera. Gryllidae) in southern European parts of the USSR. Entomol. Obozr. 51: 17-36.
- Popov AV. 1973. [Frequency selectivity of the reaction of the auditory neurons in the 1st thoracic ganglion of the cricket *Gryllus bimaculatus*]. Zh Evol Biokhim Fiziol 9(3): 265-77 (in Russian).
- Popov AV and Markovich AM. 1982. Auditory interneurons in the prothoracic ganglion of the cricket *Gryllus bimaculatus*. 11. A high frequency ascending neuron (HF IAN). Journal of Comparative Physiology. 146: 351-359.
- Popov AV, Sergeeva MV. 1988. Ontogenetic changes of positive phonotaxis in the cricket *Gryllus bimaculatus*. Zh. Evol. Biokhim. Fiziol. 24: 210-216.
- Popov AV, Shuvalov VF. 1974. The spectrum, intensity and direction of the calling song of the cricket *Gryllus campestris* under natural conditions. Zhurnal Evolyutsionoi Biokhimii i Fiziologii. 10: 72-80.
- Popov AV, Shuvalov VF. 1977. Phonotactic behaviour of crickets. J. Comp. Physiol. 119: 111-126.
- Popov AV, Shuvalov VF, Knyazev AN, Klar-Spasovskaya NA. 1974. Communication calling songs of crickets (Orthoptera, Gryllidae) from south western Tajikistan. Rev. Entomol. USSR. 53: 258-279.
- Popov AV, Shuvalov VF, Markovich AM. 1976. The spectrum of the calling signals, phonotaxis, and the auditory system in the cricket *Gryllus bimaculatus*. Neurosci. Behav. Physiol. Jan-Mar7(1): 56-62.
- Prestwich KN, Walker TJ. 1981. Energetics of singing in crickets: effect of temperature in three trilling species (Orthoptera: Gryllidae). J. Comp. Physiol. 143: 199-212.
- Rheinlander, Kalmring, Popov. 1976. Brain projections and information processing of biologically significant sounds by two large ventral-cord neurons of *Gryllus bimaculatus* De Geer (Orthoptera, Gryllidae). J. Comp. Physiol. 110: 251-69.
- Sakaluk SK. 1982. Onset of phonotaxis and age at first mating in female house crickets, *Acheta domesticus* (Orthoptera: Gryllidae). New York Entomological Society. XC: 136-141.
- Sakaluk SK. 1987. Reproductive behaviour of the decorated cricket, *Gryllodes supplicans* (Orthoptera: Gryllidae): calling schedules, spatial distribution, and mating. Behav. 100: 202-225.
- Sakaluk SK, Belwood JL. 1984. Gecko phonotaxis to cricket calling song: a case of satellite predation. Anim. Behav. 32: 659-662.
- Sakaluk SK, Morris GK, Snedden WA. 1987. Mating and its effect on acoustic signalling behaviour in a primitive orthopteran, *Cyphoderris strepitans* (Haglidae): the cost of feeding females. Behav. Ecol. Sociobiol. 21: 173-178.
- Sakaluk SK, Cade W. 1980. Female mating frequency and progeny production in singly and doubly mated house and field crickets. Can. J. Zool. 58: 404-411.
- Schmitz B, Kleindienst H, Schildberger K, Huber F. 1988. Acoustic orientation in adult, female crickets (*Gryllus bimaculatus* de Geer) after unilateral foreleg amputation in the larva. J. Comp. Physiol. 162: 715-728.
- Sergeeva MV, Popov AV. 1987. Ontogenetic changes in negative phonotaxis and its neurophysiological correlates in the cricket *Gryllus bimaculatus* (in Russian). Zhurnal Evolyutsionnoi Biokhimii i Fiziologii. 23: 58-67.
- Sergeeva MV, Popov AV. 1988. Ontogenetic changes in positive phonotaxis in the cricket *Gryllus bimaculatus* (In Russian). Zhurnal Evolyutsionnoi Biokhimii i Fiziologii. 24: 210-216.
- Sharov AG. 1968. Phylogeny of the Orthopteroidea. Trans. Paleontol. Inst. Acad. Sci. USSR. 118: 1-216.
- Sharov AG. 1960a. On the System of the Orthopterous Insects. Verhandl. XIth Internat. Congr. Entomol. Wien. 1960 1: 295-296.
- Sharov AG. 1965. Evolution and Taxonomy. Z. zool. Syst. Evolutionsforsch. 3 (3/4): 349-358.
- Sharov AG. 1966. Basic Arthropodan Stock with Special Reference to Insects. Pergamon Press.
- Shuvalov VF, Popov AV. 1973. Significance of some of the parameters of the calling songs of male crickets *Gryllus bimaculatus* for phonotaxis of females (In Russian). J. evol. biochem. physiol. 9: 177-182.
- Shuvalov VF, Popov AV. 1973. The importance of the calling song rhythmic.
- Shuvalov VF, Popov AV. 1971. The reaction of females of the domestic cricket (*Acheta domesticus*) to sound signals and its change in ontogenesis (In Russian). Zhurnal. Evolyutsionnoi Biokhimii i Fiziologii. 6: 612-616.
- Shuvalov VF, Popov AV. 1973. Study of the significance of some parameters of calling signals of male crickets *Gryllus bimaculatus* for phonotaxis of females. Sechenov Inst. Evol. Biochem., USSR. 9: 177-182.
- Shuvalov VF, Popov AV. 1973. Significance of some parameters of calling songs of male crickets. Zh Evol Biokhim Fiziol 9(2): 177-82 (in Russian).
- Shuvalov VF, Popov AV. 1984. Dependence of phonotactic specificity in crickets of the genus *Gryllus* from the character of preliminary sound stimulation. Dokladi Akademii Nauk. 274: 1273-1276 (in Russian).
- Stout JF, DeHaan CH, McGhee RW. 1983. Attractiveness of the male *Acheta domesticus* calling song to females. I. Dependence on each of the calling song features. J. Comp. Physiol., 153: 509-521.
- Stout JF, Atkins G, Weber T, Huber F. 1987. The effect of visual input on calling song attractiveness for female *Acheta domesticus*. Physiol. Entomology. 12: 135-140.
- Stout JF, Huber F. 1972. Responses of central auditory neurons of female crickets (*Gryllus campestris* L.) to the calling song of the male. Z. Vergl. Physiol. 76: 302-313.
- Thorson, J, Weber T, Huber F. 1982. Auditory behavior in the cricket. II. Simplicity of calling-song recognition in *Gryllus*, and anoma-

- lous phonotaxis at abnormal carrier frequencies. *J. Comp. Physiol.* 146: 361-378.
- Toms RB. 1984. Directional calls and effects of turning behaviour in crickets. *J. Entomol. Soc. S. Africa.* 47(2): 309-312.
- Toms RB. 1985. An African tree cricket (Gryllidae: Oecanthinae) with two calls: the two calls and a female phonotaxis experiment. *J. Entomol. Soc. S. Africa.* 48(2): 277-282.
- Toms RB. 1985. Speciation in tree crickets (Gryllidae: Oecanthinae). Species and speciation. E.S. Vrba (ed.) Pretoria, South Africa, Transvaal Museum.
- Toms RB. 1986. Evolution of insect wings: Ensiferan wings used only for communication. *Suid-Afrikaanse Tydskrif vir Wetenskap.* 82: 477-479.
- Toms RB. 1987. Speciation and taxonomic features in tree crickets. *Evolutionary biology of orthopteroid insects.* Chichister, Ellis Horwood.
- Toms RB. 1992. Correlations between hearing, singing, and flight in crickets and other insects.
- Toms RB, Otte D. 1988. New genera, species and records of east and southern African tree crickets (Oecanthinae). *Annals of the Transvaal Museum.* 34: 469-521.
- Ulagaraj SM. 1975. Mole crickets: ecology, behaviour and dispersal flight (*Scapteriscus*). *Environ. Entomol.* 4: 265.
- Ulagaraj SM, Walker TJ. 1973. Phonotaxis of crickets in flight: Attraction of male and female crickets to male calling song. *Science* 182: 1278-1279.
- Ulagaraj SM, Walker TJ. 1975. Responses of flying mole crickets to three parameters of synthetic songs broadcast outdoors. *Nature.* 253: 530-531.
- Walker TJ. 1957. Specificity in the response of female tree crickets (Orthoptera, Gryllidae, Oecanthinae) to calling songs of the males. *Annals of the Entomological Society of America* 50: 626-636.
- Walker TJ. 1962. Factors responsible for intraspecific variation in the callings songs of crickets. *Evolution.* 16: 407-428.
- Walker TJ. 1962. The taxonomy and calling songs of United States tree crickets (Orthoptera: Gryllidae: Oecanthinae). I. The genus *Neoxabia* and the *niveus* and *varicornis* groups of the genus *Oecanthus*. *Ann. Entomol. Soc. Amer.* 55: 303-322.
- Walker TJ. 1963. The taxonomy and calling songs of United States tree crickets (Orthoptera: Gryllidae). II. The *nigricornis* group of the genus *Oecanthus*. *Ann. Entomol. Soc. Amer.* 56: 772-789.
- Walker TJ. 1964. Cryptic species among sound-producing ensiferan Orthoptera (Gryllidae and Tettigoniidae). *Quart. Rev. Biol.* 39: 345-355.
- Walker TJ. 1964. Experimental demonstration of a cat locating Orthopteran prey by the prey's calling song. *Florida Entomologist.* 47: 163-165.
- Walker TJ. 1969. Acoustic synchrony: two mechanisms in the snowy tree cricket. *Science.* 166: 891-894.
- Walker TJ. 1969. Systematics and acoustic behavior of United States crickets of the genus *Cyrtoxipha* (Orthoptera: Gryllidae). *Ann. Entomol. Soc. Am.* 62: 945-952.
- Walker TJ. 1973. Systematics and acoustic behavior of United States and Caribbean short-tailed crickets (*Anurogryllus*). *Ann. Entomol. Soc. Amer.* 66: 1269-1277.
- Walker TJ. 1974. *Gryllus ovisopsis*, n.sp.: a taciturn cricket with a life cycle suggesting allochronic speciation. *Journal of Comparative Physiology.* 57: 13-22.
- Walker TJ. 1974. Character displacement and acoustic insects. *American Zoologist.* 14: 1137-1150.
- Walker TJ. 1977. *Hapithus melodius* and *H. brevipennis*: musical and mute sister species in Florida. *Annals of the Entomological Society of America.* 70: 249-252.
- Walker TJ. 1979. Calling cricket (*Anurogryllus arboreus*) over pitfalls: Females, males, and predators. *Envir. Entomol.* 8: 441-443.
- Walker TJ. 1980. Reproductive behaviour and mating success of male short-tailed crickets: differences within and between demes. *Evol. Biol.* 14: 219-260.
- Walker TJ. 1986. Monitoring the flights of field crickets (*Gryllus* spp.) and a tachinid fly (*Euphasiopteryx ochracea*) in north Florida. *Fla. Entomol.* 69(4): 678-685.
- Weissman DB, Rentz DC, Alexander RD, Loher W. 1980. Field crickets (*Gryllus* and *Acheta*) of California and Baja California, Mexico (Orthoptera: Gryllidae: Gryllinae). *Trans. Am. ent. Soc.* 106: 327-356.
- Wever EG, Vernon JA. 1959. The auditory sensitivity of Orthoptera. *Proc. Natl. Acad. Sci.* 45: 413-419.
- Zeuner FE. 1931. Die Insektenfauna des Bottinger. Marmors. Eine systematische und palaobiologische Studie. *Fortschr. Geolog. Palaeont., Berlin* 9 (28): 247-406.
- Zeuner FE. 1934. Phylogenesis of the stridulating Organ of Locusts. *Nature, London, CXXXIV:* 460.
- Zeuner FE. 1939. Fossil Orthoptera Ensifera. *British Museum (Natural History), London.*

Table 7. List of Grylloidea tape recorded in Australia, Africa, Hawaii and New Caledonia and the type of song they possess. ch=chirps [duration of pulse train 0.00-0.33 sec]; chl=long chirps [0.33-0.66 sec]; trs = short trills [0.66-1.00 sec]; tri=intermediate trills [1.00-3.00 sec]; tr=trills [3.0+ sec].

Genus	Species	Song	Location	Genus	Species	Song	Location			
BRACHYTRUPINAE Brachytrupes	membranaceus	tr	Africa	Phonarellus	fausta	ch	N.Caled.			
	Cephalogryllus	bengali	ch		Australia	goipina	ch	N.Caled.		
		mannena	ch		Australia	hirsuta	ch	N.Caled.		
		mitanina	ch		Australia	[konensis]	ch	N.Caled.		
		tundulla	ch		Australia	nola	ch	N.Caled.		
		tau	trs		Australia	oubatchia	ch	N.Caled.		
		laeviceps	tr		Australia	[parapoya]	ch	N.Caled.		
		liaweena	tr		Australia	poya	ch	N.Caled.		
		pentaringus	tr		Australia	puebensis	ch	N.Caled.		
		brevicauda	tr		Australia	rex	ch	N.Caled.		
		Gymnogryllus	corroboree		tr	Australia	thiensis	ch	N.Caled.	
			capensis		ch	Africa	Stenocephalinus	miurus	ch	Africa
			compactus		ch	Africa		australicus	ch	Australia
			joburgensis		chl	Africa		yungellus	chl	Australia
			amani		tr	Africa		aperensis	tr	Australia
Notosciobia	animata		ch	N.Caled.	australicus	tr		Australia		
	canala		ch	N.Caled.	bookandrini	tr		Australia		
					wirrensis	tr		Australia		
					australicus	trs		Australia		
					mataris	tr		Australia		
					ENEOPTERINAE	Arilpa		wirrilla	ch	Australia
								binderia	mixch	Australia
								gidya	trs	Australia
								wirkutta	mixch	Australia
				eeboolaga				tr	Australia	
				marginipennis			tr	Australia		
				noarana			tr	Australia		
				numrdina			tr	Australia		
				woortooa			tr	Australia		
			yumbena	tr			Australia			
			Eurepa	Eurepella			iando	ch	Australia	
							kulkawirra	ch	Australia	
							lewara	ch	Australia	
							meda	ch	Australia	
					mjobergi	ch	Australia			
					oana	ch	Australia			
					quarriana	ch	Australia			
					tinga	ch	Australia			
					wananga	ch	Australia			
					tjairaia	mixch	Australia			
					wanga	mixch	Australia			
					miripara	ch	Australia			
					muttaburra	ch	Austr.			
					pakaria	ch	Austr.			
			sordida	ch	Austr.					
			unicolor	ch	Australia					
			yurgama	ch	Australia					
			merimbulia	trs	Australia					
			ninbella	ch	Australia					
			taltantris	ch	Australia					
			witlilliko	ch	Australia					
			terba	mixch	Australia					
			allarlis	mixtr	Australia					
			poene	tr	Australia					
			marginatus	mixch	Africa					
			meridianus	mixch	Africa					
			Gryllinae	Acanthogryllus	fortipes	ch	Africa			
					Apedina	ilari	ch	Australia		
			mantunginea	ch		Australia				
			tarcoolina	ch		Australia				
			thurgonalaie	ch		Australia				
				tingha	ch	Australia				

Aritella	winbirris	tr	Australia	capensis	ch	Africa	ingoorala	ch	Australia			
	benganea	ch	Australia	cockbilli	ch	Africa	bumboa	mixch	Australia			
	chidnaria	ch	Australia	arambourgi	mixch	Africa	iranda	mixch	Australia			
	cooma	ch	Australia	ignobiliis	mixch	Africa	jerrima	mixch	Australia			
	curtipennis	ch	Australia	maurus	mixch	Africa	pangaringinda	mixch	Australia			
	derrilinea	ch	Australia	serengeticus	mixch	Africa	ulandi	mixch	Australia			
	duldrana	ch	Australia	primiformis	trs	Africa	Maroa	alawara	ch	Australia		
	dumpalia	ch	Australia	Rufocephalus	chindrinus	ch	Australia	australicus	ch	Australia		
	fabria	ch	Australia	garooris	ch	Australia	Ornebius	dardoana	ch	Australia		
	girralonga	ch	Australia	milyaroois	ch	Australia	bambara	ch	Australia			
	jamberoo	ch	Australia	mirretis	ch	Australia	gumbalera	ch	Australia			
	laticaput	ch	Australia	Teleogryllus	africanus	mixch	Africa	immarna	ch	Australia		
	leengila	ch	Australia	gnu	mixch	Africa	karkalo	ch	Australia			
	murwillumba	ch	Australia	marini	mixch	Australia	wandella	ch	Australia			
	ulmarra	ch	Australia	mosetse	mixch	Africa	yarendilla	ch	Australia			
	wurunga	ch	Australia	oceanicus	mixch	Australia	aperta	mixch	Australia			
	wurrinya	chl	Australia	zululandicus	mixch	Africa	attunga	mixch	Australia			
	fulviceps	mixch	Australia	commodus	mixtr	Australia	balumba	mixch	Australia			
	arina	tr	Australia	grumeti	mixtr/ch	Africa	coomialla	mixch	Australia			
	ilya	tr	Australia	leo	mixtr/ch	Africa	curtipalpis	mixch	Australia			
Astrupia	sodwanensis	ch	Africa	marabu	mixtr/ch	Africa	dirkanala	mixch	Australia			
	gazensis	chl	Africa	meru	mixtr/ch	Africa	kapunda	mixch	Australia			
Birubia	dummala	ch	Australia	natalensis	mixtr/ch	Africa	woomba	mixch	Australia			
	illalanga	ch	Australia	pulchriceps	mixtr/ch	Africa	illaroo	mixtr	Australia			
	mediocris	ch	Australia	xanthoneurus	mixtr/ch	Africa	oradala	mixtr	Australia			
	bogabilla	ch	Australia	wernerianus	tr/ch	Africa	abminga	tr	Australia			
Buangina	diminuens	ch	Australia	Tumpalia	gundialga	ch	Australia	allambi	tr	Australia		
	nullaga	ch	Australia	ilindia	ch	Australia	antakira	tr	Australia			
	scutellata	ch	Australia	marnlia	ch	Australia	baloois	tr	Australia			
	anemba	tr	Australia	ruficeps	ch	Australia	coorumbena	tr	Australia			
Comidogryllus	billabongus	ch	Australia	tau	ch	Australia	elvalina	tr	Australia			
Australia	bilo	ch	Australia	yellena	ch	Australia	jirira	tr	Australia			
	binyaris	ch	Australia	Yurriyappa	ch	Australia	kanya	tr	Australia			
	dallacheus	ch	Australia	kattara	trbr	Australia	indooroopilly	ch	Australia			
	yingally	ch	Australia	amari	ch	Africa	ilara	mixch	Australia			
	adani	tr	Australia	botswanus	ch	Africa	wanboo	tr	Australia			
Cryncus	alternatus	ch	Africa	chobei	ch	Africa	bandumu	mixch	Australia			
	duplicatus	ch	Africa	dedzai	ch	Africa	pitonga	mixch	Australia			
	impiger	ch	Africa	kasungu	ch	Africa	NEMOBIINAE					
	momho	ch	Africa	lengwe	ch	Africa	Amonemobius					
Damarachaeta	kasungu	ch	Africa	matuga	ch	Africa	vexans	ch	N.Caled.			
	mlozi	ch	Africa	mosambicus	ch	Africa	Koghiella	caledonica	ch	N.Caled.		
Eurygrylodes	warrani	ch	Australia	natus	ch	Africa	songsp.	songsp.	chl	N.Caled.		
	warrilla	ch	Australia	nyasa	ch	Africa	songsp.	songsp.	chl	N.Caled.		
	weetapoonis	ch	Australia	obniger	ch	Africa	semibouo	ch	N.Caled.			
	gorimuis	tr	Australia	obniger	ch	Africa	bouo	tri	N.Caled.			
	pina	tr	Australia	shimba	ch	Africa	thio	trs	N.Caled.			
	yerramutta	tr	Australia	viphuis	ch	Africa	Pteronemobius	bakali	ch	Australia		
Gryllodes	sigillatus	ch	Australia	okavangus	ch-odd	Africa	nundra	ch	Australia			
Gryllus	bellicosus	ch	Africa	masambicus	tr	Africa	truncatus	ch	Australia			
	bimaculatus	ch	Africa	Yarrita	caribonga	ch	Australia	ornaticeps	tri	Australia		
	bimaculatus	ch	Africa	fistulator	tr	Australia	bivittata	trs	Australia			
	krugeri	ch	Africa	pikiara	tr	Australia	regulus	trs	Australia			
	krugeri	ch	Africa	GRYLLOTALPINAE			tarrios	trs	Australia			
	maunus	ch	Africa	Gryllotalpa	pluvialis	ch	Australia	gagooris	tr	Australia		
	maunus	ch	Africa	coarctata	tr	Australia	poene	tr	Australia			
	zaisi	ch	Africa	monanka	tr	Australia	tasmani	tr	Australia			
	mzimba	chl	Africa	nitidula	tr	Australia	unicolor	tr	Australia			
	braueri	mixch	Africa	ITARINAE			Thetella	oonoomba	ch	Australia		
	rixator	mixch	Africa	ITARINAE	australis	ch	Australia	OECANTHINAE				
Lepidogryllus	parvulus	ch	Australia	Tremellia	sp.	chl	N.Caled.	Oecanthus	angustus	ch	Australia	
	comparatus	trs	Australia		beta	tri	N.Caled.		capensis	ch	Africa	
Loxoblemmus	pallens	tr	Australia		caledonica	tri	N.Caled.		karschi	ch	Africa	
Modicogryllus	conspersus	ch	Africa		sp.	tri	N.Caled.		socians	ch	Africa	
	conspersus	ch	Africa		tiwaka	trs	N.Caled.		songsp.	ch	Africa	
	garriens	ch	Africa	MOGOPLISTINAE					sycamoros	ch	Africa	
	geonomes	ch	Africa	Biana	arila	ch	Australia		sp.	chl	Africa	
	geonomes	ch	Africa		arupingi	tr	Australia		dissimilis	tr	Africa	
	geonomes	ch	Africa		atalumba	tr	Australia		filiger	tr	Africa	
	geonomes	ch	Africa		iloura	tr	Australia		galpini	tr	Africa	
	mulanje	ch	Africa		larnoo	tr	Australia		neofiliger	tr	Africa	
	ngamius	ch	Africa		ellanora	ch	Australia		neosimilis	tr	Africa	
	parilis	ch	Africa		mamoura	ch	Australia		pseudosimilis	tr	Africa	
	segnis	ch	Africa		ora	ch	Australia		rufescens	tr	Australia	
	zinzilulans	ch	Africa		kira	tr	Australia		rufescens	tr	N.Caled.	
	serengeticus	chl	Africa		pillinda	tr	Australia		rufopictus	tr	Africa	
	perplexus	mixtr	Africa		Kalyra	karrawilya	mixch	Australia	similis	tr	Africa	
Pictorina	bullawarra	ch	Australia		Kiah	palanu	mixtr	Australia	sp.	tr	Africa	
	wombalano	ch	Australia		Lara	cowandilla	mixch	Australia	sp.	tr	Africa	
	kobarina	tr	Australia			kaiimna	mixch	Australia	Prognathogryllus	alternatus	ch	Hawaii
Platygryllus	atritus	ch	Africa		Marinna	natarina	mixch	Australia		epimeces	ch	Hawaii
						barinya	ch	Australia				

	flavidus	ch	Hawaii	haawina	chl	Hawaii	pololu	trs	Hawaii	
	hana	ch	Hawaii	hyperkona	chl	Hawaii	sp.	trs	Hawaii	
	haupu	ch	Hawaii	imitans	chl	Hawaii	sibilans	trs	Hawaii	
	hypomacron	ch	Hawaii	kapipi	chl	Hawaii	awawa	tr	Hawaii	
	makai	ch	Hawaii	kuikawa	chl	Hawaii	crepitans	tr	Hawaii	
	mauka	ch	Hawaii	kukui	chl	Hawaii	exuberans	tr	Hawaii	
	oahuensis	ch	Hawaii	kupinai	chl	Hawaii	hopo	tr	Hawaii	
	parakukui	ch	Hawaii	liuia	chl	Hawaii	ignava	tr	Hawaii	
	puna	ch	Hawaii	mahina	chl	Hawaii	illex	tr	Hawaii	
	spadix	ch	Hawaii	makanina	chl	Hawaii	kaeka?	tr	Hawaii	
	stridulans	ch	Hawaii	mauka	chl	Hawaii	kau	tr	Hawaii	
	waikemoi	ch	Hawaii	nani	chl	Hawaii	sp.	tr	Hawaii	
	awiii	chl	Hawaii	neokukui	chl	Hawaii	languida	tr	Hawaii	
	elongatus	chl	Hawaii	opua	chl	Hawaii	ligna	tr	Hawaii	
	hea	chl	Hawaii	palai	chl	Hawaii	nele	tr	Hawaii	
	kahili	chl	Hawaii	paramana	chl	Hawaii	sp.	tr	Hawaii	
	opua	chl	Hawaii	paraspilos	chl	Hawaii	olomea	tr	Hawaii	
	polani	chl	Hawaii	procrusta	chl	Hawaii	paranoe	tr	Hawaii	
	robustus	chl	Hawaii	rosea	chl	Hawaii	paranoho	tr	Hawaii	
	kahea	tri	Hawaii	septima	chl	Hawaii	paroctonalis	tr	Hawaii	
	alapa	trs	Hawaii	ulaino	chl	Hawaii	pseudonoe	tr	Hawaii	
	weli	trs	Hawaii	venata	chl	Hawaii	ua	tr	Hawaii	
Viphyus	livingstonei	chl	Africa	waialina	chl	Hawaii	sp.	tr	Hawaii	
	victorinox	trs	Africa	waiqua	chl	Hawaii	sp.	tr	Hawaii	
Xabea	tumbarumba	ch	Australia	pahiwa	tr	Hawaii	wiki	tr	Hawaii	
	atalaiaatalaia	tr	Australia	octonalis	trc	Hawaii	Laupala	cerasina	tr	Hawaii
	leai	tr	Australia	acuste	tri	Hawaii		eucerasina	tr	Hawaii
PHALANGOPSINAE				awiwi	tri	Hawaii		eukolea/	tr	Hawaii
Endacusta	pindana	ch	Australia	exigua	tri	Hawaii		eukolea/	tr	Hawaii
	major	tr	Australia	fortuita	tri	Hawaii		eupacifica	tr	Hawaii
Tathra	pyala	ch	Australia	hamumu	tri	Hawaii		fugax	tr	Hawaii
	tatiara	ch	Australia	huapala	tri	Hawaii		kaalensis	tr	Hawaii
	mungarina	tr	Australia	[kokiio]	tri	Hawaii		kanaele	tr	Hawaii
PODOSCIRTINAE				kolekole	tri	Hawaii		kaumana	tr	Hawaii
Archenopterus				kona	tri	Hawaii		kohalina	tr	Hawaii
	bouensis	tri	N.Caled.	makau	tri	Hawaii		kokensis	tr	Hawaii
Caliscirtus	paniensis	chl	N.Caled.	malela	tri	Hawaii		kolea/	tr	Hawaii
Madasomma	affinis	tr	Australia	mauiensis	tri	Hawaii		koloa	tr	Hawaii
	jirranda	tr	Australia	neovarians	tri	Hawaii		kona	tr	Hawaii
	kanina	tr	Australia	novena	tri	Hawaii		molokaiensis	tr	Hawaii
	loorea	tr	Australia	ola	tri	Hawaii		neospisa	tr	Hawaii
Podoscirtinae				ookala?	tri	Hawaii		oahuensis	tr	Hawaii
	sp.	ch	N.Caled.	proalina	tri	Hawaii		olohena	tr	Hawaii
	sp.	ch	N.Caled.	promana	tri	Hawaii		orientalis	tr	Hawaii
	sp.	chl	N.Caled.	pseudokua	tri	Hawaii		pacifica	tr	Hawaii
	sp.	chl	N.Caled.	pseudoli	tri	Hawaii		pacifica-b	tr	Hawaii
	sp.	chl	N.Caled.	puiwa	tri	Hawaii		paranigra	tr	Hawaii
Tamborina	manilla	ch	Australia	robusta	tri	Hawaii		paraprosea	tr	Hawaii
	wypanda	chl	Australia	spilos	tri	Hawaii		ignava	tr	Hawaii
	imurana	tr	Australia	sylvatica	tri	Hawaii		prosea	tr	Hawaii
	ocellata	tr	Australia	triens	tri	Hawaii		pruna	tr	Hawaii
PTEROPLISTINAE				varians	tri	Hawaii		spisa	tr	Hawaii
Mjobergella	warra	trs	Australia	virens	tri	Hawaii		tantalus	tr	Hawaii
				wai	tri	Hawaii		sp.	tr	Hawaii
TRIGONIDIINAE				crusta	tri	Hawaii		vespertina	tr	Hawaii
Anaxipha	anaxiphoides	trs	Australia	pu dica	tri	Hawaii		wailua	tr	Hawaii
	longipennis	ch	Australia	sexta	tri	Hawaii	Prolaupala	kaalensis	tr	Hawaii
	alina	ch	Hawaii	waimea	tri	Hawaii		kukui	tr	Hawaii
	excultata	ch	Hawaii	akaka	trs	Hawaii	TURANOGRYLLINAE			
	hamakua	ch	Hawaii	[betanovena]	trs	Hawaii	Afrogyllopsis			
	kapipi	ch	Hawaii	eumeles	trs	Hawaii		bonga	tr	Africa
	hypermana	ch	Hawaii	flectens	trs	Hawaii		chyulu	tr	Africa
	improba	ch	Hawaii	fritinnia	trs	Hawaii		estesi	tr	Africa
	kahua	ch	Hawaii	hehelo	trs	Hawaii	Neogryllopsis			
	kewai	ch	Hawaii	[hilu]	trs	Hawaii		messinae	mixch	Africa
	kolea	ch	Hawaii	hoahoa	trs	Hawaii		capricornis	mixtr	Africa
	kua	ch	Hawaii	hoku	trs	Hawaii		kuhlgatzi	mixtr	Africa
	laupele	ch	Hawaii	iuka	trs	Hawaii		limpensis	mixtr	Africa
	mana	ch	Hawaii	kohala	trs	Hawaii		mirus	mixtr	Africa
	puukani	ch	Hawaii	lena	trs	Hawaii		orpeni	mixtr	Africa
	rufa	ch	Hawaii	neogrande	trs	Hawaii		satarae	mixtr	Africa
	waipuna	ch	Hawaii	octava	trs	Hawaii		skukuzae	mixtr	Africa
	ahiu	chl	Hawaii	[ohaka]	trs	Hawaii		tshokwane	mixtr	Africa
	attenuatum	chl	Hawaii	pavida	trs	Hawaii		nyandanus	mixtr/ch	Africa
	filicum	chl	Hawaii					pundae	mixtr/ch	Africa