

EVOLUTIONARY CHANGE IN CRICKET ACOUSTICAL COMMUNICATION

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The principal questions asked so far with regard to the acoustical communication of crickets have been analytical: what are the causes and effects of the different kinds and amounts of variation in cricket stridulations; and how is the hierarchy of the nervous system related to the hierarchy of parameters in the song pattern? My problem, in contrast, is chiefly one of synthesis: how has cricket acoustical behavior *evolved*? Obviously there are no fossil cricket songs, and so all evidence must come from comparative study of modern species, supplemented by what we know about cricket relationships from fossil orthopteroids.

Cricket acoustical communication is a good subject for evolutionary analysis. It seems to represent the most complicated invertebrate acoustical system, with some species repertoires including four to six different signals; and we probably know more about it than we do about any other invertebrate acoustical system—from all of the several points of view which include signal structure and function, differences and similarities among species, differences and similarity among signals within species repertoires, and neurophysiological basis.

Most of the information cited in the reconstruction attempted here comes from evidence accumulated by the participants in this symposium, and from a comparative examination of the various stridulatory patterns of about 100 cricket species, representing eight subfamilies, 20 genera, and 30 species groups (tape recordings in the University of Michigan Museum of Zoology). This accumulation of evidence is more impressive than one might at first suspect. For example, we understand fairly well the acoustical behavior of all but two

or three of the North American crickets, and we have acoustical information on crickets from all continents and several islands, from nearly all habitats and modes of life illustrated among crickets, and from a large number and variety of taxonomic groups.

It is difficult to reconstruct evolutionary changes in behavior from comparative study alone, and certain kinds of conclusions must always remain tentative and speculative. But behavioral evolution involves some of the most important problems in modern biology, and many of its questions will undoubtedly be answered much more precisely than most of us believe possible now. Growth of knowledge concerning cricket acoustics has been accelerating rapidly, and it seems to me that we have reached a point where we can begin to reconstruct evolutionary changes on a rather broad scale.

EVIDENCE FOR EVOLUTIONARY CHANGE IN CRICKET ACOUSTICS

That there has been *change* in cricket acoustics since the first cricket, and since the first signal in the cricket acoustical system, goes almost without saying. There are more than 2,000 stridulating crickets in the world today, arranged in some 300 genera and 16 subfamilies; indications are that all of them descended from a single species which lived about 150 million years ago—a species which stridulated in almost the same fashion as some crickets do today. Our tape recordings of crickets presently include about 200 different signals, divided among 90 species; in this entire assemblage there are only three pairs of species, one group of three species, and one group of four species that have identical signals among them.

Changes in cricket acoustics have been

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all or nearly all of an *evolutionary* nature, and this has been demonstrated in part by some of the other papers in this series. Walker (1957, 1962), Alexander (1956, 1957b, 1957c), and Alexander and Thomas (1959) have shown that cricket songs vary surprisingly little among the individuals of a species; and Walker (1957) and Haskell (1958) have presented evidence that neither normal nor abnormal variations in the life histories of individual stridulating insects affect either the sounds they make or the responses they give to the sounds of others. There is no "culture" in cricket signalling. In most species, the young do not even hatch from the egg until long after all individuals of the previous generation have died. Whether or not they are reared in complete isolation; whether or not they have ever encountered another cricket, or courted a female, or had a fight—they still produce the right signal in the right situation and respond to the right signal in the right situation. Differences among species and differences within species have in every case tested been shown to be the result of genetic differences (Fulton, 1933, 1937; Hörmann-Heck, 1957; Bigelow, 1960; Alexander, 1957c).

Given that there has been change, and that this change has been almost entirely evolutionary, our next question is: have there been detectable *differences in rates and directions of evolutionary change* in cricket acoustics, and provided that we can demonstrate their existence, how well can we decipher their significance?

There are several places to look for such differences. On a gross scale, we can note that some crickets today have as many as six different kinds of signals; others have but one; and still others have no stridulatory ability at all. Some crickets have complicated signals; others have simple ones. To find out how this has happened, we must first understand the kinds of signals—both structurally and functionally—that crickets possess. Then we need to have some idea as to what kind of acoustician

the first cricket (or some early cricket) was, and we need to know how the various functional and structural kinds of cricket signals are related, how new functions have evolved, and how structure has changed to accommodate new functions.

ACOUSTICAL BEHAVIOR IN MODERN CRICKETS

The Functional Kinds of Cricket Sounds

Acoustical communication in crickets functions only on an intraspecific basis: there are no "disturbance" or "alarm" squawks as in Tettigoniidae, Cicadidae, and perhaps some Acrididae.¹ Further, it operates only among adults, and only in connection with activities that are directly or indirectly related to the reproductive function: no immature crickets are known to either produce or respond to stridulatory sounds.

Reproductive behavior in crickets is unusually complicated for invertebrate animals, particularly among the surface-dwelling and subterranean species. Its discernible communicative components and their acoustical mediators can be described as follows:

A. Male-Female Interactions

1. Coming-Together (mediated principally by a *calling song* in nearly all species).
2. Courtship (usually mediated principally by a *courtship song* and by *courtship interruption sounds*).
3. Copulation.

¹This is not to say that sound waves play no role in the defensive or flight behavior of crickets. On the contrary, both the cerci and the subgenual organs of the middle tibiae (cf. Pumphrey, 1940; Wever and Vernon, 1959) respond to high intensity, low-frequency vibrations, principally when these are substrate-transmitted, but also when they are air-transmitted if the intensity is sufficiently high. But crickets do not broadcast sounds in these connections, and they are not known to utilize their stridulatory signals or their tibial auditory organs in escaping from predators or in any other kind of interactions with other species. These devices have evolved together in a very specific fashion in connection with the sexual activities of each species.

4. Staying-Together (sometimes mediated partly by a *post-copulatory song*).
 5. Nest Elaboration (including burrowing and food-stocking) (may be mediated partly by "*recognition sounds*").
- B. Male-Male Interactions
1. Residencibility and Territoriality (mediated partly by the *calling song* and by *aggressive sounds*).
 2. Aggression (mediated partly by *aggressive sounds*).
- C. Parent-Offspring Interactions
1. Egg- and Nymph-Guarding.
 2. Nymph-Feeding.

The six functional "kinds" of acoustical signals listed above appear in some cases to be homologous among different species, genera, and subfamilies (that is, to have diverged structurally from a functionally similar signal in a common ancestor); in other cases they seem to be functional analogues that have resulted from parallel or convergent evolution. In most cases we now have experimental evidence as to some of the particular ways that sound operates; but even where we do not, the general function is usually clear because we understand the context in which the signal is produced. Let us review these six functional kinds of signals in more detail.

1. *The calling song*.—This is always a long-continued, intense, rhythmical sound produced by the male on his territory or place of residence, which brings the sexually responsive females to him (Regen, 1913; Walker, 1957; Alexander, 1960b). It also stimulates calling in other males; it may inhibit calling at close range (high intensity); and it is mildly aggressive among males (Alexander, 1961). Its production is regulated by such things as: (1) the presence of a spermatophore in the spermatophore pouch (Huber, 1955); (2) daily cycles of light and dark, (3) a male hearing either another male calling or his own aggressive or courtship interruption signals (Alexander, 1961), and (4) probably cumulative physiological changes as-

sociated with failure to copulate (an old, isolated, unmated male usually becomes so sensitive that he will begin to call if disturbed in almost any fashion, for example, if one blows upon his cerci or jars the substrate).

2. *The courtship song*.—This is also a rhythmical sound; frequently it is soft and noise-like, unlike other cricket sounds which are all strongly dominated by a pure frequency corresponding to the number of stridulatory file teeth struck per second. It is triggered by the females' passive reaction to antennation and aggression, or by a simple touch on the cerci if the male is already calling, has just stopped courting, or is primed for some other reason. Courtship singing (at least in *Gryllus* species) promotes assumption of the copulatory position by the female (Alexander, 1960b, 1961). It is elaborate and distinctive primarily among surface-dwelling and subterranean crickets, but occurs widely in one form or another among different kinds of vegetation inhabitants as well.

3. *The courtship interruption sound*.—This signal is produced when a female breaks contact with a courting male. After a delay of 8–20 seconds (timed for several repetitions in a *Gryllus* male), the male stops courting, turns about, and examines the area immediately behind him (where the female was earlier), simultaneously producing a series of chirps that is very similar to (and in some cases may be identical to) the aggressive sound of the species. Then he may continue stridulating, changing gradually to the calling song, or may stop chirping and turn to other activities. No function has been experimentally determined for this sound, but under certain conditions it could re-attract a responsive, departing female.

4. *The aggressive sound*.—This is always a rather brief, sharp signal; it elicits fighting behavior and reciprocal aggressive stridulation, or else retreat, and it also reinforces dominance and subordinance among males. This is to say, it affects the outcome of future engagements by chang-

ing a male's aggressiveness—reducing it if he loses the encounter and enhancing it if he dominates the encounter (Alexander, 1961). Aggressive chirps are apparently triggered by different parts of the aggressive actions of crickets (depending on the hyper-aggressiveness of the male involved), including single aggressive chirps and the hearing of the calling song. This signal is elaborate and distinctive principally among surface-dwelling and subterranean crickets, where there is long-term attachment to a burrow.

5. *The post-copulatory song.*—This is an irregularly-continued sound which apparently augments tactile and chemical stimuli in the mediation of the peculiar post-copulatory behavior of crickets. The post-copulatory interaction has two functions: it keeps the female from removing the male's spermatophore until it is largely emptied of sperm, and it keeps the compatible male and female together near the male's residence (after the expensive procedure of bringing them together through calling) until the female is maximally inseminated ("maximally" from a behavioral point of view). This kind of signal appears in two genera of surface-dwelling and burrowing crickets where it has not previously been reported (*Miogryllus*, *Anurogryllus*), and in tree crickets (Oecanthinae). Although its specific function has not been tested, the behavioral situation that it mediates is clear, and its general function can be presumed with little danger of error.

6. *The "recognition" sound.*—This is the most poorly known cricket signal. It appears only among extensively burrowing, subsocial genera, and the best guess at this time is that it helps keep the male and female (and in some cases perhaps more than just two individuals) together and in some way "cooperative" around the burrow. There is an interesting possibility that this signal is at least somewhat analogous to what the linguists have termed "phatic communion" (cf. Sebeok, in press) signals that serve principally or solely to keep different parties informed of one an-

other's presence and of the fact that "the channels are open." This suggestion is based on the fact that this signal is produced by males burrowing alone or together with another individual, and by individuals meeting in the burrow. Also, a burrowing *Anurogryllus* male producing this sound will begin courtship and copulatory movements if he is merely touched on the dorsal abdomen or on the cerci. Sometimes a colony of mole crickets (*Gryllotalpinae*) produces this sound almost continually.

Some crickets possess only one of the six functional kinds of signals; some possess two; some three; some four; some five; and at least one species, *Anurogryllus muticus* (De Geer) (Brachytrupinae), the short-tailed cricket of the southeastern United States, includes all six signals in its repertoire (tables 1, 2). With one exception the six signals are produced solely by the males; in some mole crickets the recognition signal is produced by both sexes and has apparently become functionally interchangeable between the male and female (Baumgartner, 1910).² This is interesting, because without knowledge of this signal in subsocial species, it would be easy to assume that the cricket acoustical system could never be utilized in social behavior because it is produced by a strictly male apparatus. Huber (1962) has now shown that a good deal of the nervous and muscular system necessary for stridulation is in fact contained in the female, and this clarifies how the "sparking across" of the entire system to the female could be an evolutionary probability.

From the point of view of predictability, we may relate this kind of evolutionary change to one that has taken place in still another acoustical system—that possessed by the passalid or "betsy" beetles (Passalidae). *A priori*, few of us would argue that

² In contrast, one Australian mole cricket, *Triamescaptor aotea* Tindale, has lost both its wings and all but the vestiges of its auditory organs (Tindale, 1928). Whether or not it too is subsocial is apparently unknown.

TABLE 1. Characteristics, relationships, and acoustical repertoires of 42 tape-recorded, vegetation-inhabiting crickets. Related species are grouped. Acoustical repertoire = patterns of: calling/ courtship/ aggressive/ courtship interruption/ post-copulation/ "recognition"/ signals. For acoustical signals (-) indicates no signal known or suspected; (?) indicates signal suspected, but not known. In other parts of table, (-) indicates none; (?) indicates not known

Crickets	Geographic range	General habitat	Diapause stage	Adult season	Gen/yr	Acoustical repertoire
SUBFAMILY OECANTHINAE						
1. <i>Neoxabea bipunctata</i> (De G.)	ENAmer.	Treetops	Egg	Fall	1	A1/A1/A1?/A1?/A1?/-/
2. <i>Oecanthus niveus</i> (De Geer)	ENAmer.	Tree, bush	Egg	Fall		A1/A1/A1?/A1?/A1?/-/
3. <i>O. exclamatoris</i> Davis	ENAmer.	Tree, bush	Egg	Fall	1	A1/A1/A1?/A1?/A1?/-/
4. <i>Oecanthus leptogrammus</i> (TJW)	Tex. -Guat.	Woody plant	None?	—	-	A1/A1?/A1?/A1?/A1?/-/
5. <i>O. pini</i> Beutenmuller	ENAmer.	Pine trees	Egg	Fall	1	A3a/A1?/A1?/A1?/A1?/-/
6. <i>Oecanthus</i> n.sp. (TJWalker)	ENAmer.	Tamaracks	Egg	Fall	1	A3a/A1?/A1?/A1?/A1?/-/
7. <i>O. nigricornis</i> F. Walker	ENAmer.	Herbs, bush	Egg	Fall	1	A3a/A1/A1/A1/A1/-/
8. <i>O. quadripunctatus</i> Beut.	NENAmer.	Herbs	Egg	Fall	1	A3a/A1/A1/A1/A1/-/
9. <i>Oecanthus</i> n.sp. (TJWalker)	SNAmer.	Herbs	Egg	Sum-Fall	1-2	A3a/A1/A1/A1/A1/-/
10. <i>Oecanthus</i> n.sp. (TJWalker)	SENAmer.	Herbs	Egg	Sum-Fall	1-2	A3a/A1/A1/A1/A1/-/
11. <i>O. varicornis</i> F. Walker	SWNAmer.	Herbs	None?	—	-	A3a/A1?/A1?/A1?/A1?/-/
12. <i>O. californicus</i> Saus.	WNAmer.	Shrubs	Egg	Fall	1P	A3a/A1?/A1?/A1?/A1?/-/
13. <i>O. latipennis</i> Riley	ENAmer.	Herbs, bush	Egg	Fall	1	A3a/A1?/A1?/A1?/A1?/-/
14. <i>Oecanthus jultoni</i> (TJW)	NAmer.	Bushes	Egg	Fall	1	B2/?/?/?/?/-/
15. <i>Oecanthus rileyi</i> Baker	WNAmer.	Bushes	Egg	Fall	1	B2/?/?/?/?/-/
16. <i>O. allardi</i> Walker & Gurney	Dom. Rep.	Bushes				B2/?/?/?/?/-/
17. <i>O. pellucens</i> (Scopoli)	Europe	Bushes	Egg	Fall	1	C/C/C/C/?/?/-/
SUBFAMILY ENEOPTERINAE						
18. <i>Orocharis saltator</i> Uhler	ECNAmer.	Trees	Egg	Fall	1	B2/?/?/?/?/-/
19. <i>Orocharis</i> n.sp. (TJWalker)	Fla.	Mangrove				C/?/?/?/?/?/-/
20. <i>O. gryllodes</i> (Pallas)	SENAmer.	Bushes	Egg	Fall	1	B2/?/?/?/?/-/
21. <i>Hapithus agitator</i> Uhler	ECNAmer.	Bushes, herb	Egg	Fall	1	-?A1-/A1/A1?/-/
22. <i>H. brevipennis</i> Saussure	SENAmer.	Bushes, herb	?	Fall	1P	B1/?/?/?/?/-/
SUBFAMILY TRIGONIDIINAE						
23. <i>Cyrtoxipha columbiana</i> C.	SENAmer.	Trees, bush	Egg	Fall	1	B1/-/-/-/-/-/
24. <i>C. gundlachi</i> Saussure	SENAmer.	Trees, bush	Egg	Fall	1	B1/-/-/-/-/-/
25. <i>Cyrtoxipha</i> n.sp. (R.D.A.)	Fla. Keys	Mangrove	None	—	-	A3a/-/-/-/-/-/
26. <i>Phyllopalpus pulchellus</i>	ENAmer.	Bush, herb	Egg	Fall	1	A3a/-/-/-/-/-/
27. <i>Paratrigonidium</i> sp.	Hawaii	Herbs	None	—	-	A3a/-/-/-/-/-/
28. <i>Paratrigonidium</i> sp.	Hawaii	Herbs	None	—	-	B1/-/-/-/-/-/
29. <i>Anaxipha imitator</i> (Saus.)	Fla., Cuba	Bush, herbs	None?	—	-	A2/-/-/-/-/-/
30. <i>Anaxipha exigua</i> (Say)	ENAmer.	Bush, herb	Egg	Fall	1	A3a/A2/-/-/-/-/
31. <i>A.</i> n.sp. (RDAlexander)	ENAmer.	Trees, bush	Egg	Fall	1	A3a/?/-/-/-/-/
32. <i>A.</i> n.sp. (RDAlexander)	SENAmer.	Bush, herb	Egg	Fall	1	A3a/?/-/-/-/-/
33. <i>Anaxipha scia</i> Hebard	SENAmer.	Herbs	None?	—	-	A3a/-/-/-/-/-/
34. <i>Anaxipha pulicaria</i> (Bur.)	SENAmer.	Herbs	Egg	Fall	1	A2/?/-/-/-/-/-/
35. <i>A. delicatula</i> (Scudder)	ENAmer.	Bush, herb	Egg	Summer	1	A2/-/-/-/-/-/
36. <i>Anaxipha</i> n.sp. (R.D.A.)	ENAmer.	Herbs	Egg	Summer	1	A2/-/-/-/-/-/
37. <i>A. litarena</i> Fulton	ENAmer.	Herbs	Egg	Fall	1	A2/-/-/-/-/-/
SUBFAMILY MOGOPLISTINAE						
38. <i>Cycloptilum bidens</i> Heb.	SENAmer.	Surface	Egg	Fall	1?	C/-/-/-/-/-/
39. <i>Cycloptilum</i> n.sp. (RDA)	SENAmer.	Surface	Egg	Fall	1?	C/-/-/-/-/-/
40. <i>C. trigonipalpus</i> (R. & H.)	SENAmer.	Surface	Egg	Fall	1?	C/-/-/-/-/-/
41. <i>C. antillarum</i> (Redten.)	SENAmer.	Surface	Egg	Fall	1?	C/-/-/-/-/-/
42. <i>Cycloptilum</i> n.sp.? (RDA)	La.	Surface	None?	--	-	C/-/-/-/-/-/

the cricket acoustical system has much chance of becoming operative between adults and juveniles, simply because the sounds are now produced and received strictly by adult structures. But the social Passalidae have an acoustical system which must have begun with the adults stridulat-

ing by rubbing abdominal tergites against the underwings, and in which the larvae have (apparently later) developed a stridulatory device utilizing the second and third larval legs. Although the auditory organs have not been found in either adults or larvae, there is little doubt that the

TABLE 2. Characteristics, relationships, and acoustical repertoires of 48 tape-recorded surface-dwelling and subterranean crickets. Related species are grouped. Acoustical repertoire = patterns of: calling/courtship/ aggressive/ courtship interruption/ post-copulation/ "recognition" signals. For acoustical signals (-) indicates no signal known or suspected; (?) indicates signals suspected, but not known. In other parts of table, (-) indicates none; (?) indicates not known

Crickets	Geographic range	General habitat	Diapause stage	Adult season	Gen/yr	Acoustical repertoire
SUBFAMILY NEMOBIINAE						
43. <i>Nemobius griseus</i> Walker	NAmer.	Surface	Egg	Fall	1?	A1/A1-?/?/-/-/
44. <i>N. allardi</i> (Alex. & Thom.)	NENAmer.	Surface	Egg	Fall	1	A1/A1-B1-A3a/?/?/-/-/
45. <i>Nemobius tinnulus</i> Fulton	ENAmer.	Surface	Egg	Fall	1	A3a/B1-A3a/?/?/-/-/
46. <i>Nemobius funerals</i> Hart	SENAmer.	Surface	Egg	?	1?	A1/?/?/?/-/-/
47. <i>N. maculatus</i> Blatchley	ENAmer.	Surface	Egg	Fall	1	A3b/?/?/?/-/-/
48. <i>N. fasciatus</i> (De Geer)	NAmer.	Surface	Egg	Sum-Fall	1-2	B1/B1-F/B2/B2/-/-/
49. <i>N. sparsatus</i> Fulton	SENAmer.	Surface	Egg?	Fall	?	E1?/B1/?/?/?/-/-/
50. <i>N. confusus</i> Blatchley	NAmer.	Surface	Egg	Fall	1	E1/E1?/?/?/?/-/-/
51. <i>Nemobius</i> n.sp. (ESThomas)	NAmer.	Surface	Egg	Fall	1	E1/E1/?/?/?/-/-/
52. <i>Nemobius carolinus</i> Scud.	NAmer.	Surface	Egg?	Fall	1?	A3a-A3f/E1-E3/?/?/?/-/-/
53. <i>N. melodius</i> (Thom. & Alex.)	NAmer.	Surface	Egg	Fall	1	A3a/E1/?/?/?/-/-/
54. <i>N. bruneri</i> Hebard	ENAmer.	Surface	Egg	Fall	1?	A3a/?/?/?/?/-/-/
55. <i>Nemobius cubensis</i> Saus.	ENAmer.	Surface	Egg	Fall	1	A1/?/?/?/?/-/-/
56. <i>N. palustris</i> Blatchley	ENAmer.	Surface	Egg	Fall	1	A1/?/?/?/?/-/-/
57. <i>Nemobius</i> n.sp. (R.D.A.)	SWNAmer.	Surface	?	?	?	A1/?/?/?/?/-/-/
58. <i>Nemobius ambitiosus</i>	ENAmer.	Surface	Egg?	Summer	-	A2/?/?/?/?/-/-/
SUBFAMILY GRYLLEINAE						
59. <i>Miogryllus verticalis</i> (S.)	SENAmer.	Surf-Bur.	Egg	Summer	1	B2/B3/A1/A1/B2/-/
60. <i>M. saussurei</i> Scudder	SENAmer.	Surf-Bur.	Egg	Summer	1+?	B2/B3/A1/A1/B2/-/
61. <i>Modiocoryllus conspersus</i> W.	Hawaii	Surf-Bur.	None	-	-	B1/G1?/A1/A1/-/-/
62. <i>Gryllodes sigillatus</i> (W.)	Asia (cosm)	Surface	None	-	-	B3/G3/C/C/-/-/
63. <i>Acheta domesticus</i> (Linn.)	Asia? (cosm)	Surface	None	-	-	B1/G3/A1/A1/-/-/
64. <i>Teleogryllus commodus</i> (Walk.)	Austral.	Surf-Bur.	Egg	Fall	1	D/A1/A1/A1/-/-/
65. <i>Gryllus assimilis</i> Fab.	W. Indies	Surf-Bur.	None?	-	-	B2/G5/B2/B2/-/-/
66. <i>Gryllus</i> n.sp. (R.D.A.)	Mex.-SAM.	Surf-Bur.	None?	-	-	B2/G5/B2/B2/-/-/
67. <i>G. pennsylvanicus</i> Burm.	NENAmer.	Surf-Bur.	Egg	Fall	1	B1/G3/A1/A1/-/-/
68. <i>G. veletis</i> (Alex. & Big.)	NENAmer.	Surf-Bur.	Nymph	Spring	1	B1/G3/A1/A1/-/-/
69. <i>Gryllus firmus</i> Scudder	ENAmer.	Surf-Bur.	Egg	Fall	1	B1/G3/A1/A1/-/-/
70. <i>G. bermudiensis</i> Caudell	Bermuda	Surf-Bur.	None	-	-	B1/G3/A1/A1/-/-/
71. <i>Gryllus</i> n.sp.? (RD.Alex.)	SWNAmer.	Surf-Bur.	Nymph?	Spring	1	B1/G3/A1/A1/-/-/
72. <i>Gryllus campestris</i> Linn.	Europe	Surf-Bur.	Nymph	Spring	1	B1/G3/A1/A1/-/-/
73. <i>Gryllus bimaculatus</i> DeG.	Africa	Surf-Bur.	None	-	-	B1/G3/A1/A1/-/-/
74. <i>G. vernalis</i> Blatchley	ENAmer.	Surf-Bur.	Nymph	Spring	1	B1/G2-3/A1/A1/-/-/
75. <i>Gryllus fulvoni</i> (Alex.)	ENAmer.	Surf-Bur.	Nymph	Spring	1	B3/G2-3/C/C/-/-/
76. <i>Gryllus</i> n.sp. (R.D.Alex.)	WNAmer.	Surf-Bur.	?	?	?	B3/G7/C/C/-/-/
77. <i>Gryllus personatus</i> Uhler	WNAmer.	Surf-Bur.	Egg?	Fall	1?	B2/G3/B2/B2/-/-/
78. <i>Gryllus lineaticeps</i> Stal?	WNAmer.	Surf-Bur.	?	?	?	B2/G1?/B2?/B2?/-/-/
79. <i>Gryllus</i> n.sp. (R.D.Alex.)	WNAmer.	Surf-Bur.	?	?	?	B2?/G?/C?/C?/-/-/
80. <i>Gryllus</i> n.sp. (R.D.Alex.)	WNAmer.	Surf-Bur.	?	?	?	B3/G?/C?/C?/-/-/
81. <i>Gryllus armatus</i> Scudder	WNAmer.	Surf-Bur.	?	?	?	C/G3/C/C/-/-/
82. <i>Gryllus vocalis</i> Scudder	WNAmer.	Surf-Bur.	?	?	?	C/?/?/?/?/-/-/
83. <i>Gryllus rubens</i> Scudder	ENAmer.	Surf-Bur.	Nymph	S&F	2	A1-3a/G3/A2/A2/-/-/
84. <i>Gryllus integer</i> Scudder	WNAmer.	Surf-Bur.	Nymph	S&F	2	A1-3a/G3/A2/A2/-/-/
85. <i>Scapsipedus micado</i> Saus.	Asia (intr)	Surf.-Bur.	Egg	Fall	1	B1/A1/B1/B1/?/?/-/
SUBFAMILY BRACHYTRUPINAE						
86. <i>Anurogryllus muticus</i> De G.	SENAmer.	Deep Bur.	Nymph	Spring	1	A1/E1/A2/A2/A1/B2/
SUBFAMILY GRYLLOTALPINAE						
87. <i>Scapteriscus aetetus</i> (R. & H.)	SENAmer.	Subterr.	Ny&Ad	Sep-Jun	1-?	A1-3a/?/?/?/?/ B2/
88. <i>S. vicinus</i> Scudder	SENAmer.	Subterr.	Ny&Ad	Sep-Jun	1-?	A1-3a/?/?/?/?/ B2/
89. <i>S. abbreviatus</i> Scudder	SENAmer.	Subterr.	?	?	?	A1-3a/?/?/?/?/ B2/
90. <i>Gryllotalpa hexadactyla</i> P.	ENAmer.	Subterr.	Nymph	Fall	1	B2/B2?/A1/?/?/?/ B2/

sounds made by these two entirely different devices are operative in the same communicative system (Alexander, Moore, and Woodruff, in press).

The Structural Kinds of Cricket Sounds

A versatile communicative system not only effectively mediates a variety of life

situations for the species possessing it, but also can be utilized without confusion by a large number of species in the same region or habitat. It should be able to serve both long-range and short-range functions, and it should be usable under a variety of different environmental conditions. There is probably no system which fits these requirements quite as well as acoustical communication. Chemical signals can be transmitted across greater distances, and they can vary almost endlessly among different species; but they cannot be patterned so that the same signalling device and the same receptor can be utilized to transmit several different messages. Visual stimuli can be patterned in more complicated fashions than acoustical stimuli in most animals, and they can be effective across as great or greater distances. But if they consist of flashing lights, as in fireflies, then they are effective only during darkness; and if they are gestural or consist of patterns in action or color, then they are effective only during daylight. Tactile stimuli, while unsurpassed in their versatility at close range, obviously cannot be broadcast.

The stridulatory apparatus of crickets does not allow for the complicated frequency fluctuations or melodies that are so important to us vertebrates, and the tibial auditory organ is not a frequency-tuner, as are the auditory organs of most vertebrates. Long-continued, uninterrupted sounds cannot be produced by the oscillating forewings of a cricket. But the pulses that such an apparatus produces can be delivered at rates up to at least 155 per second, and they can be arranged in an almost infinite variety of patterns. Those produced by modern crickets are both simple and complex. They can be arranged in about 22 patterns under the two somewhat arbitrary headings of "chirping songs" and "trilling songs" (figs. 2, 3). Most of these patterns are reversible (essentially the same if played backward); a few are irreversible.

A CLASSIFICATION OF THE KINDS OF PATTERNS IN CRICKET ACOUSTICAL SIGNALS

- I. Reversible Patterns (essentially the same if played backward)
 - A. Trills (ungrouped pulse sequences and long groups of pulses)
 1. Irregularly broken
 2. Regularly broken
 3. Unbroken
 - a. One pulse rate, one intensity
 - b. One pulse rate, two intensities
 - c. Two intensities, one pulse rate
 - d. Two pulse rates, one intensity
 - e. Two pulse rates, two intensities
 - f. Two pulse rates, three intensities
 - B. Chirps (short groups of pulses produced in sequence)
 1. Intermediate-length chirps (3-7 pulses), delivered at intermediate rates (100-300 per minute) and somewhat irregularly
 2. Long chirps (6-15 pulses) delivered slowly (50-200 per minute) and regularly
 3. Short chirps (2-3 pulses), delivered rapidly (300-900 per minute) and regularly
 - C. Groups of chirps
 - D. Combinations of chirps and trills
- II. Irreversible Patterns (quite different if played backward)
 - E. Trills that change gradually in pulse rate and intensity
 1. Accelerating pulse rates and increasing intensities
 2. Decelerating pulse rates and decreasing intensities
 3. Accelerating then decelerating pulse rates and increasing then decreasing intensities
 - F. Groups of trills in which only the terminal trill changes in pulse rate
 - G. Soft, noise-like phrases (some reversible)

1. No intermittent loud pulses
2. Loud pulses following every two or three phrases
3. Loud pulses following every phrase
4. Several loud pulses between phrases
5. Several loud pulses in succession following every two or three phrases.

The most elaborate and obvious differences among cricket acoustical signals are in the rates and rhythms of pulse delivery. These are the principal kinds of differences that occur among the songs of related species, and they are the kinds of differences that we will discuss in greatest detail here. But in passing, it should be pointed out that frequency often differs considerably among species, ranging from 1,500 cycles per second in *Gryllotalpa* to 10,000+ cps in *Nemobius*. In general, smaller crickets have higher-pitched songs and faster pulse rates in their songs. These differences reflect structural differences in the stridulatory apparatus that undoubtedly follow rather than precede (in an evolutionary sense) the rate and rhythm differences which initially caused the songs to be specifically distinct. Gross frequency differences occur at the level of genus or subfamily and rarely occur among species within the same genus, where even differences in pulse rate are usually due either to wing strokes of shorter amplitude or to faster stroke rates rather than to structural differences in the stridulatory apparatus. Nevertheless, frequency differences probably do have some isolating value in an indirect fashion. Wever and Vernon (1959) showed that a *Gryllus* species (probably *pennsylvanicus* Burmeister) has a striking drop at about 5,000 cycles per second in the intensity required to stimulate the auditory nerve—in other words, at precisely the frequency of the sound produced by the males. This means that species in different subfamilies or genera which produce sounds of widely different frequencies may be almost deaf to one another's songs

even if they have the same pulse or chirp rate and rhythm, especially if intensity is reduced because the males of the two species are somewhat separated by ecological differences. One would expect that considerable overlap among the rhythms of calling in geographically sympatric species in different genera and subfamilies might be possible under these conditions without seriously affecting efficiency, and such overlap does in fact occur (tables 1, 2).

THE PHYLOGENY OF CRICKET ACOUSTICS

The Beginnings of Cricket Stridulation

The first cricket was without doubt a specialized stridulator. There are several reasons for believing this:

1. All modern and fossil crickets have the same stridulatory apparatus and the same auditory apparatus; furthermore, they share both of these specialized devices with the Tettigoniidae, a family that fossil evidence indicates diverged from the cricket line during the Jurassic.³ The auditory organ and the stridulatory apparatus are too much alike and too complex to have appeared more than once in their present forms.

2. All modern stridulating crickets—except for a few obviously degenerate species—produce the intense, clear sounds that only crickets among all animals are able to produce with a stridulatory device. The peculiar apparatus necessary to produce this kind of sound could only have appeared through a long process of evolutionary change.

3. The calling function is so widespread and so similar among Gryllidae and Tettigoniidae as to strongly suggest that it had appeared before these two families became

³ A few Gryllacrididae retain the tibial auditory organ, but have lost the tegminal stridulating apparatus and today possess only abdominal stridulating organs (Ander, 1938). One cricket, *Luzaropsis ferruginea* (Walker), appears to have additional auditory tympana near the apex of its femora (Chopard, 1926). Another, *Loxoblemmus equestris* Saussure, has developed an antenno-frontal stridulatory mechanism (Menon and Parshad, 1960).

separate evolutionary lines; and as I will show later, this calling song (at least as it occurs in modern species) could not have been the first signal in the system. The universality of "pure-frequency" stridulation in crickets is additional evidence that the calling function had appeared before crickets separated from Tettigoniidae, for the evolution of this intense characteristic could only have been associated with a long-range function such as calling.

The first acoustical signal in the cricket system was therefore not strictly a "cricket" signal at all, because it appeared in the common ancestor of the Tettigonioidae. It was almost surely a mediator of courtship, for the following three reasons:

1. The first sounds that actually carried auditory significance would have to have been low in intensity and operative only among individuals in close proximity, for the elaborate stridulatory (and auditory) devices of modern Tettigonioids could obviously not have appeared full-blown.

2. Lifting and fluttering of the forewings as visual and auditory stimuli, and also in association with exposing dorsal glands, occurs not only among many cricket subfamilies, but also among tettigoniids and cockroaches, the latter having diverged from other orthopteroids during late Paleozoic. In other words, either soundless or acoustical vibration of the forewings occurs today during courtship in the males of all orthopterans in which the female actively mounts the male in copulation, with the exceptions of: (a) wingless species in which the males have prominent dorsal glands (some Gryllacrididae and Phalangopsinae), and (b) a few winged species in which the males have tibial glands (some Nemobiinae). Among close-range interactions, only acoustical signals of a courtship nature are widespread among tettigonioids, and there is no other logical context for the origin of stridulation and auditory ability.

We can say with some confidence, then, that the first signal in the cricket (or the tettigonioid) acoustical system was a court-

ship signal, and that by the time crickets became a separate evolutionary line the system had either progressed to a two-signal stage or else the original courtship signal had been transformed into a calling signal. The evidence for this kind of beginning seems overwhelming; there is no reasonable alternative.

And so we are brought to the most difficult question of all, and the one which will occupy most of our attention: how have the six functional signals of modern crickets evolved from a beginning in a courtship context? At first, this question might seem unanswerable. But I think a structural-functional comparison of the acoustical behavior of many different cricket genera and subfamilies gives some rather convincing indications. We have not only the structures and functions of the sounds themselves—behavioral manifestations that are almost unparalleled in the ease with which they can be analyzed and compared—but we can also compare the nature of the stridulatory apparatus, the position of the wings during each kind of stridulation, the triggering stimuli, and all manner of directly and indirectly related material. In all of these characteristics, developmental variations in genetically similar individuals are negligible—certainly of little or no consequence in the comparisons of the complicated action patterns that need to be made to interpret general evolutionary pathways.

From Courtship Song To Calling Song— and Vice Versa

I have already suggested that the calling function arose as an outgrowth of the original courtship function. The evidence is as follows:

1. With respect to the male-female interaction, these two songs differ only quantitatively in their principal function: the calling song attracts the female from a great distance; the courtship song attracts her from a short distance.

2. The quantitative functional difference between courting and calling is related to quantitative structural differences. In

the species with the simplest (and apparently rudimentary) courtship songs—the Oecanthinae, which possess an important metanotal gland—courtship singing differs from calling chiefly in intensity and duration. The male trills continually when calling; he trills briefly, with erratic halts, when courting. Intensity and duration are characteristics which primarily affect range and redundancy, the two attributes that would need to be enhanced if a short-range signal were to be transformed or broadened to include a successful long-range function.

3. As Huber (1960) and Alexander (1961) have shown, and as can be partly learned from behavioral observations, calling and courting are physiologically linked in the male: a calling male is "primed" for courtship (requires a less precise or elaborate stimulus to begin courting than in other situations). He doesn't begin calling until he is ready to court and copulate, and a courting male will go over into calling very frequently if his courtship is interrupted by the departure of the female.

Therefore, I believe that there was selection for increased rhythmicity, intensity, and duration in the original courtship song (once or many times, it makes little difference) because these characteristics enhanced the courtship function itself, through increasing consistency, range, and redundancy. Eventually, through just this kind of change, this song must have become operative at such distances that it was sometimes advantageous (i.e., in some instances or in some species) for the male to be triggered into stridulation without contact with the female, and sometimes advantageous for the female to be attracted by hearing the sound when she was not otherwise in contact with the male. In this way the calling function, in the approximate form that it assumes today, could have evolved. But additionally, with the change in triggering of the male's song, the pathway would be opened for the evolution of two different signals that could go their own separate ways. It would only be necessary for the male to develop structurally

different signals, with slightly different effects, for the two different situations; or (perhaps originally) for the female to begin to respond differently to the original signal that served both calling and courtship, depending on whether or not she was in contact with the male through senses other than auditory. In all likelihood these changes did take place in many cases, with the resulting development of two separate signals. But there is also evidence that in some instances the courtship song was instead *transformed* into a calling song without a stridulatory replacement for the courtship situation, the advantage of having two different signals being accomplished by the elaboration of dorsal glands of one sort or another to mediate the courtship function—metanotal glands in Oecanthinae (Fulton, 1915), tibial and tegminal glands in Nemobiinae (Fulton, 1931; Gabbutt, 1954). This would result in the appropriate combination of a long-range acoustical signal and a short-range chemical signal, as is the case today in Oecanthinae and Nemobiinae, and very likely in several of the other subfamilies that have not been studied in these regards.

With respect to the functional origin of their present courtship acoustics, the Nemobiinae may represent a special case completely different from that outlined above. Their courtship songs are not only about as intense as their calling songs (in contrast to those of their relatives, the Gryllinae and Brachytrupinae), but there is in addition a different sort of relationship between the calling and courtship signals of closely related species. The *Nemobius carolinus* group and the *N. allardi* group are the best examples. The calling songs of *N. melodius* and *N. carolinus* are more or less continual trills, the former simple, the latter complex in nature. But the courtship songs of both species are short, complex trills that are very similar to the calling songs of *N. confusus* and an undescribed sibling (Alexander, 1957b). Likewise, *N. tinnulus*, *N. allardi*, and *N. griseus* have trilling calling songs; the song of the second has nearly

twice the pulse rate of the first, and the third nearly twice that of the second (Alexander and Thomas, 1959, and unpublished information). The courtship trill of each species has a pulse rate about half as fast as that in the calling song, so that *N. griseus* has a courtship song like the calling song of *N. allardi*, and *N. allardi* has a courtship song like the calling song of *N. tinnulus*. These courtship songs are not rudimentary, brief signals as in the Oecanthinae, and they do not resemble the soft, complicated courtship songs of the Gryllinae. During their production the tegmina are held neither in the 90° position nor in the lowered, roof-like position of *Gryllus*, *Acheta*, and *Gryllodes* courtship, but in the approximately 45° position characteristic of calling in both Gryllinae and Nemobiinae (table 3). The presence and absence of elaborate courtship in Nemobiinae is associated with the absence and presence, respectively, of tibial glands. The 75°–90° tegminal position is probably primitive because it occurs in Oecanthinae as well as Trigonidiinae, Eneopterinae, and presumably other cricket subfamilies—and also in cockroaches—and it most effectively exposes dorsal glands which were probably involved in early tettigonioid courtship.

It seems likely that if one traces the ground cricket line back to the common tettigonioid ancestor, he will have to account for a sequence of changes involving: (1) loss of some original dorsal glands that were exposed only by lifting the tegmina (this probably was associated with the production of an increasingly elaborate courtship sound and lowering of the tegmina during both calling and courtship), (2) subsequent loss of the courtship song and its replacement by tibial glands, (3) elaboration of a new courtship signal, this one derived from the calling song rather than vice versa, and (4) (in a few species) subsequent loss of the tibial glands. Although we cannot now explain such a sequence, it should be no more difficult than a similar one in connection with acridoid acoustics: why the Acridoidea lost or failed to elab-

orate the morphological and behavioral precursors of tettigonioid acoustics, later developed their own highly analogous acoustical system based on entirely different structures, and then several times lost stridulating ability and regained it later utilizing different appendages to make the sounds but retaining the abdominal auditory organs through it all (cf. Kevan, 1954; Alexander, 1960a).

Aggressive Sounds From a Calling Song

The second split that I have postulated is that aggressive signals appeared as outgrowths of the calling function. What is the evidence?

First, the aggressive signal mediates interactions between males. The calling song also has such a function—and the difference is essentially quantitative. The calling signal alone will elicit the complete aggressive repertoire of a hyper-aggressive male—and if the aggressive signal were completely eliminated from the repertoires of even the species in which it is most elaborate, the aggressive function would probably be changed only in a quantitative fashion: aggressive behavior would be elicited less often, fights would probably be shorter and less intense, and dominance and subordination following aggressive encounters would be less pronounced.

Second, the two signals differ structurally in a quantitative fashion, and this in turn is related in a quantitative way to the functional differences. In other words, the more aggressive the encounter, the more different from the calling song the aggressive chirps become. But even in the species with the most distinctive aggressive signals, some of the aggressive chirps are exactly like the calling chirps.

When the male calling song began to operate at long range, it seems inevitable that it should have eventually developed significance for the males—the other “kind” of individuals in the species—as well as for the females. First, we know that auditory feedback is involved in one of the earliest and most important attributes of calling

TABLE 3. Positions of the tegmina or forewings in males of 19 genera of crickets during stridulation in various situations and during copulation. Not all genera have been observed in all situations

Kind of situation	Approximate angle of tegminal elevation						
	75-90°	50-70°	40-50°	15-30°	5-15°	0° (at rest)	
	Maximum lateral tegminal tilt						
	20-40°	20-40°	20-40°	20-40°	50-70°	0° (at rest)	
Calling	<i>Neoxabea</i>	<i>Hapithus</i>	<i>Nemobius</i>				
	<i>Oecanthus</i>						
	<i>Orocharis</i>				<i>Miogryllus</i>		
	<i>Cyrtoxipha</i>				<i>Modicogryllus</i>		
	<i>Phyllopalpus</i>				<i>Grylloides</i>		
	<i>Paratrigonidium</i>				<i>Acheta</i>		
	<i>Anaxipha</i>				<i>Teleogryllus</i>		
					<i>Gryllus</i>		
					<i>Scapsipedus</i>		
					<i>Anurogryllus</i>		
		<i>Gryllotalpa</i>					
		<i>Scapteriscus</i>					
Fighting	<i>Neoxabea</i> ?		<i>Nemobius</i>				
	<i>Oecanthus</i>		<i>Miogryllus</i>				
	<i>Orocharis</i> ?		<i>Modicogryllus</i>				
	<i>Cyrtoxipha</i> ?		<i>Acheta</i>				
	<i>Phyllopalpus</i> ?		<i>Teleogryllus</i>				
	<i>Paratrigonidium</i>		<i>Gryllus</i>				
	<i>Anaxipha</i> ?		<i>Scapsipedus</i>				
			<i>Anurogryllus</i>				
		<i>Gryllotalpa</i>					
		<i>Scapteriscus</i> ?					
Courtship	<i>Neoxabea</i> ?	<i>Hapithus</i>	<i>Nemobius</i>	<i>Teleogryllus</i>	<i>Modicogryllus</i>		
	<i>Oecanthus</i>		<i>Miogryllus</i>				
	<i>Orocharis</i>					<i>Anurogryllus</i>	<i>Acheta</i>
	<i>Cyrtoxipha</i>						<i>Gryllus</i>
	<i>Phyllopalpus</i>						
	<i>Paratrigonidium</i>						
	<i>Anaxipha</i>						
Copulation	<i>Neoxabea</i> ?	<i>Hapithus</i>				<i>Nemobius</i>	
	<i>Oecanthus</i>					<i>Miogryllus</i>	
						<i>Modicogryllus</i>	
						<i>Grylloides</i>	
						<i>Acheta</i>	
						<i>Teleogryllus</i>	
						<i>Gryllus</i>	
						<i>Scapsipedus</i>	
						<i>Anurogryllus</i>	
						<i>Gryllotalpa</i>	
Post-Copulation	<i>Oecanthus</i>	<i>Hapithus</i>	<i>Miogryllus</i>			<i>Nemobius</i> ,	
			<i>Anurogryllus</i>			<i>Modicogryllus</i>	
						<i>Grylloides</i> ,	
						<i>Acheta</i>	
						<i>Teleogryllus</i>	
				<i>Gryllus</i>			

in the male—his ability to produce the song with relatively little interruption through long periods of time. A deaf male rarely sings normally for long periods, and it is questionable whether the calling function with its requirement of redundancy could have preceded the development of sensitive auditory organs in the male. Second, there are obvious selective advantages in interactions among the males of any animal in which the males and females pair off as a result of long-range communicative interactions, and all of the males of such species that I have studied do so interact, either grouping, or spacing, or both. Under these conditions it is doubtful that long-range acoustical communication could have been elaborated for long without the males becoming involved.

Today, the aggressive signal is triggered by contact with other males: this may be tactile or auditory contact, and the degree of ease in releasing the signal is generally related to the degree of aggressiveness exhibited by the species.

The interrelationships of calling, courting, and aggressive acoustical signals within the repertoires of different species of Tettigoniidae and Gryllidae appear to have been arranged in two different fashions. In the one case, exemplified by most *Gryllus* species, neither the courtship stridulation nor the aggressive stridulation is made up of pattern components that seem to be taken directly from the calling song as it exists now, but (as already pointed out) there are structural relationships associated with the functional relationships. The other case is clearly exemplified only in *Teleogryllus commodus* among the crickets studied. The males of this species have in their acoustical repertoires four different pulse rates; one is utilized for aggressive sounds, one is utilized for courtship singing, and three of them are combined in a unique fashion during calling (fig. 1). This interesting case suggests again the dual or multiple role of the calling song, and demonstrates that a single signal can broaden to involve more than one function in two obvious

ways: through the same signal having different effects in different situations or upon different kinds of individuals, or through the isolation of different functional units into different pattern components within the (in this case, calling) rhythm. This particular kind of complex calling song has apparently evolved in many Tettigoniidae, notably Conocephalinae and Phaneropterinae, and perhaps in Cicadidae and Acrididae as well (Alexander, 1960b; Alexander and Moore, 1958). It may exist in *Nemobius carolinus* Scudder in a form more rudimentary than in *T. commodus* (Alexander, 1957b; Walker, 1962).

Post-Copulatory Sounds From Calling or Courtship Songs

As I have said, acoustical signals are definitely associated with the post-copulatory situation in three subfamilies: Gryllinae, Brachytrupinae, and Oecanthinae. In the first two subfamilies, the signal is apparently inseparable from the calling song except that in *Miogryllus* it is slightly more irregular, and in Oecanthinae it is very much like the simple, apparently rudimentary, courtship singing of the different species. There is no other evidence as to the derivation of these signals.

The post-copulatory signal in *Miogryllus* and *Anurogryllus* is particularly interesting for two reasons. First, although the calling and post-copulatory signals are extremely similar in these two cases, they are triggered in two situations that are about as different as one can find in the sequence of sexual behavior—just before copulation and just after copulation. Huber (1955) has indicated that the male of *Gryllus campestris* will not call unless there is a spermatophore in the spermatophore pouch, but following copulation the spermatophore pouch has just been emptied, and still the male (in *Miogryllus* and *Anurogryllus*), in a sense, "calls."

The second point of interest involves the question of how the post-copulatory signal could happen to arise from the calling song,

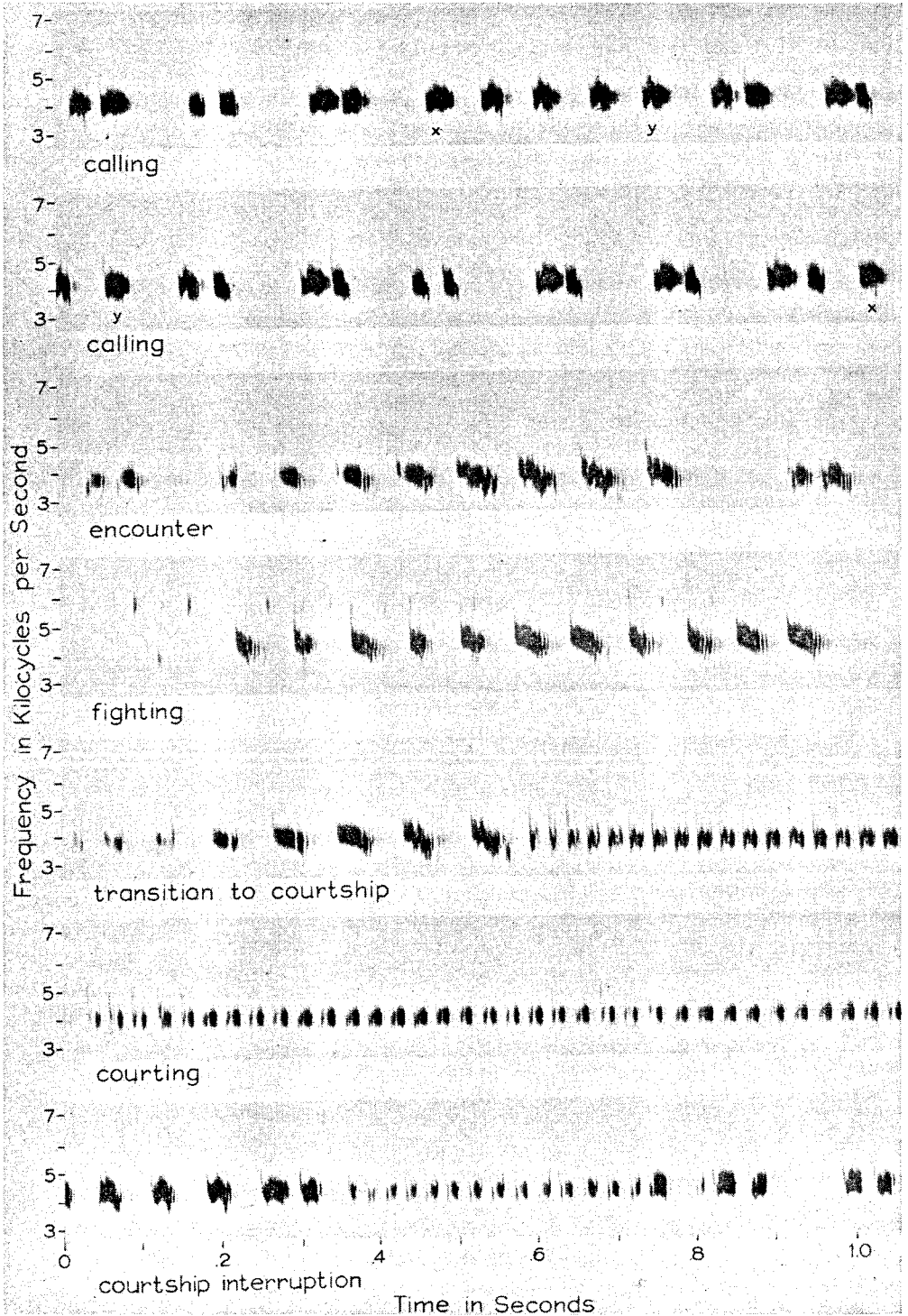


FIG. 1. Audiospectrographic samples from the acoustical repertoire of *Teleogryllus commodus* (Walker) illustrating a repertoire based on the most complicated calling song pattern known in crickets (pattern D, fig. 2).

perhaps two different times. It is not difficult to see how the courtship song might have been modified to mediate this situation, as is apparently the case in Oecanthinae. The second most likely candidate would seem to be the aggressive chirps. A male in post-copulatory behavior is in some senses more aggressive than in any other situation, and he is practically invincible (Alexander, 1961).

The reasons for elaboration or modification of the calling song to fit the post-copulatory function may be related to the effects of the signal rather than to its causes or triggers. When a responsive female attracted by a calling song has reached the area of greatest intensity, she becomes motionless; but a female responding to the courtship song keeps moving, apparently unable to remain immobile for long under this stimulation (Alexander, 1960b). These reactions would obviously make the calling song a more appropriate signal for the post-copulatory interaction, in which the male keeps the female immobile or nearly so in one location until he is ready to court again.

In several species of Gryllinae, the females are ready to copulate again considerably sooner than the males. This is revealed when two or more males are caged with a single female, and the female copulates with the second male while the first is still involved in the post-copulatory interaction and has not started to court again. I have observed this in *Miogryllus*, *Gryllobates*, and *Gryllus*. In *Gryllobates*, a female on one occasion copulated with a second male less than a minute after her first copulation, and the act required much longer than usual, apparently because the male could not attach the spermatophore as easily with the other male's spermatophore still in place. If a song structurally similar to courtship singing caused the female to mount before the male was ready to copulate again, obvious disadvantages would be involved. In this connection, it is noteworthy that the post-copulatory position of Oecanthinae differs from that of

Gryllinae in that the female is actually kept partially mounted on the male's back (Fulton, 1915), feeding at his metanotal gland. This could explain why a courtship signal could be utilized in the post-copulatory situation in these crickets but be inappropriate in Gryllinae.

At first there does not seem to be any logical way to eliminate the aggressive sounds as possible antecedents of the post-copulatory ones. They are produced in this context when another male intrudes, and also upon interruption of courtship. Their close-range effect upon a female in a normal encounter is probably to bring about immobility, especially in a sexually responsive female. But the post-copulatory situation is unlike either courtship or aggression in that it lasts a long time, during which there is little or no change in the external situation, except when the female starts to move away or another male or female interrupts the interaction. With either kind of interruption, the male stops his post-copulatory singing and shows aggressive behavior, only resuming post-copulatory stridulation when he has re-assumed the special post-copulatory position, which in *Miogryllus* and *Anurogryllus* is end-to-end with the cerci in contact. But the calling song is produced for long periods without change in external conditions, and this may be another reason why the post-copulatory signal bears a resemblance to calling. Again, we may note that the post-copulatory trills of Oecanthinae are produced when the female ceases to feed at the secretions of the metanotal gland and starts to dismount and move away—a situation analogous to courtship in Gryllinae in that the female, through her own movements or those of the male, is apt to continually shift her position with respect to the male's rear end and contact him repeatedly and in different locations.

"Recognition" Signals From Courtship Singing

The so-called "recognition" signals of crickets are so brief and simple, and so

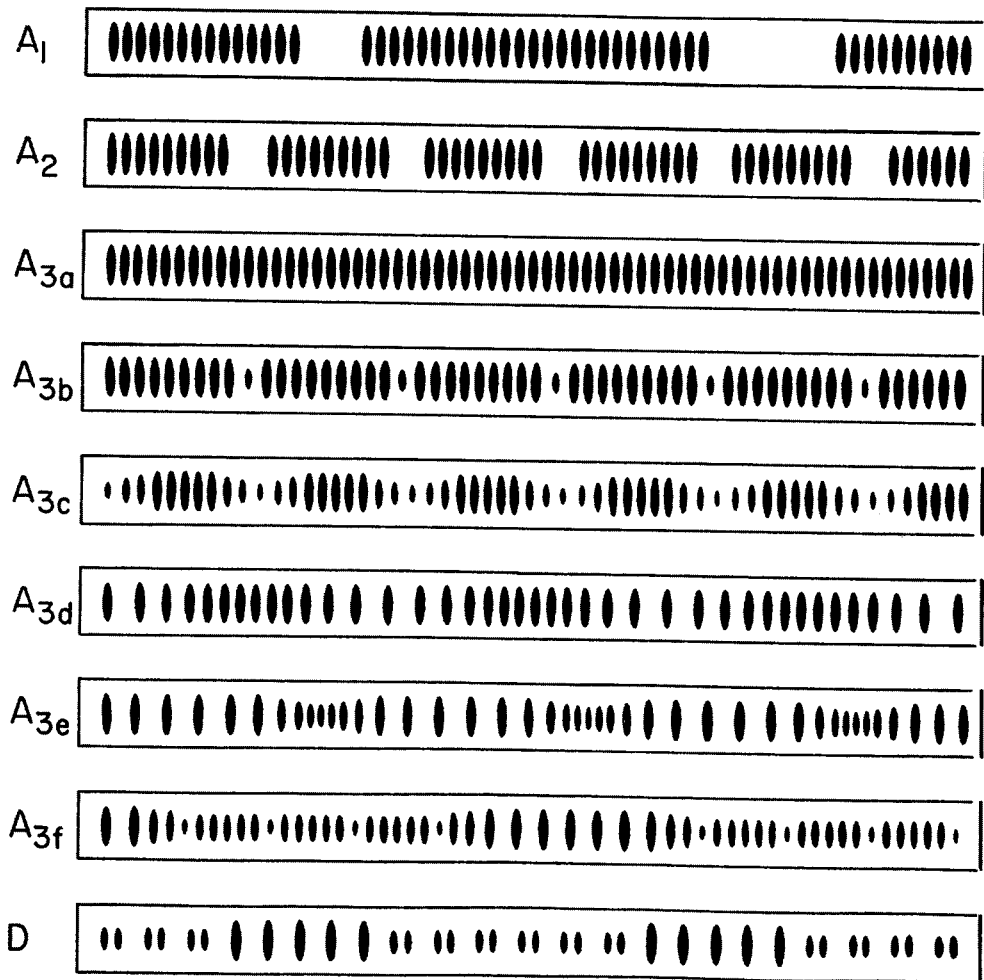


FIG. 2. Diagrams of trilling song patterns of crickets, arranged in approximate order of increasing complexity. Vertical width differences indicate intensity differences.

poorly known, that no satisfactory structural relationship with any other cricket signal has yet been established in the species of *Gryllotalpa*, *Scapteriscus*, and *Anurogryllus* where they have been heard and recorded (table 2). But one interesting functional clue has appeared. An *Anurogryllus* male that is producing this chirp while burrowing seems to be primed for copulation. That is, if he is merely touched from above by another cricket, he immediately extrudes his epiphallic hook and probes upward with the tip of his abdomen, an action that otherwise seems to be pre-

cipitated only when a courting male is touched from behind. Even a calling male usually goes briefly into courtship, regardless of how quickly the female responds.

The females of *Anurogryllus* probably mate but once. We have never been able to get an adult female collected in the field to mate in the laboratory, even after hours of courtship by several males. Only one female has mated in the laboratory, and she was collected as a last instar nymph. After her one mating, this female did not mate again although subjected to several hours of courtship. During this

time she showed only aggression toward males. This unusual situation suggests that males living together with fertilized females may produce the "recognition" sound in stimulus situations derived from contact that would ordinarily evoke courtship.

Evidence For Different Rates and Directions of Structural Change in Cricket Songs

Obviously, cricket sounds have changed structurally as well as functionally in the course of evolution. First, they have changed in connection with the simple enhancement of functions. As examples, a solitary desert or field cricket today inevitably has a clearer, more intense calling song than his relatives which aggregate in forest leaf litter; and a calling song is usually more intense than a courtship song. Second, whenever acoustical functions have multiplied, new sounds have developed in connection with keeping the different signals within repertoires distinctive, and yet compatible with the species' stridulatory, auditory, and other physiological and behavioral capacities. As we have already seen, a species rarely uses the same signal in different contexts, and the highly complicated signals are mostly possessed by the species that have large repertoires (tables 1, 2). Third, when species have multiplied, new sounds have developed, apparently in connection with keeping interspecific confusion at a minimum. Cricket species which live together never have the same calling songs—we still have to find the first exception to this old generalization. And the complicated calling songs—in crickets as well as in Tettigoniidae, Acrididae, and Cicadidae—occur in the regions where there are many species. It is probably not an accident that the Europeans have concentrated principally on acridid acoustics and the Americans on tettigoniid and gryllid acoustics; the Europeans have more acridids singing together, and most of the complicated acridid acous-

tics; the Americans have more gryllids and tettigoniids singing together, and nearly all of the complicated acoustics in these two groups. (It is probably also not an accident or a reflection of errors that investigators in these two different regions have sometimes come to different conclusions studying the same kinds of animals.)

If the distinctiveness of calling songs among species that live together is frequently cited as evidence of interaction, the point is generally neglected that related species which do not live together—and apparently never have—sometimes have not only identical calling songs, but nearly identical repertoires. This is true of at least two pairs of seasonally isolated species and one group of geographically isolated species, listed below:

1. *Gryllus veletis* (Alexander and Bigelow) and *G. pennsylvanicus* Burmeister—spring and fall field crickets in eastern North America that are practically indistinguishable morphologically, but cannot hybridize (Alexander and Bigelow, 1960).
2. *Scapsipedus aspersus* Walker and an unnamed sibling—seasonally isolated, morphologically similar or identical field crickets in Japan (Masaki, 1961).
3. *Gryllus campestris* Linnaeus, *G. firmus* Scudder, and *G. bermudiensis* Caudell—field crickets in Europe, eastern North America, and Bermuda, respectively. The last two are morphologically much alike, but greatly different from the first; the non-diapausing *bermudiensis* can hybridize with both of the other species, but a comparison of the results obtained by Cousin (1961) and Bigelow (1958, 1960) indicates that it is very unlikely that any nymph-diapausing species, such as *campestris*, can hybridize with any egg-diapausing species, such as *firmus* is in at least part of its range.

The fact that the entire four-signal repertoires of the *Gryllus* species compared above are very similar to one another reduces the likelihood that these are cases of

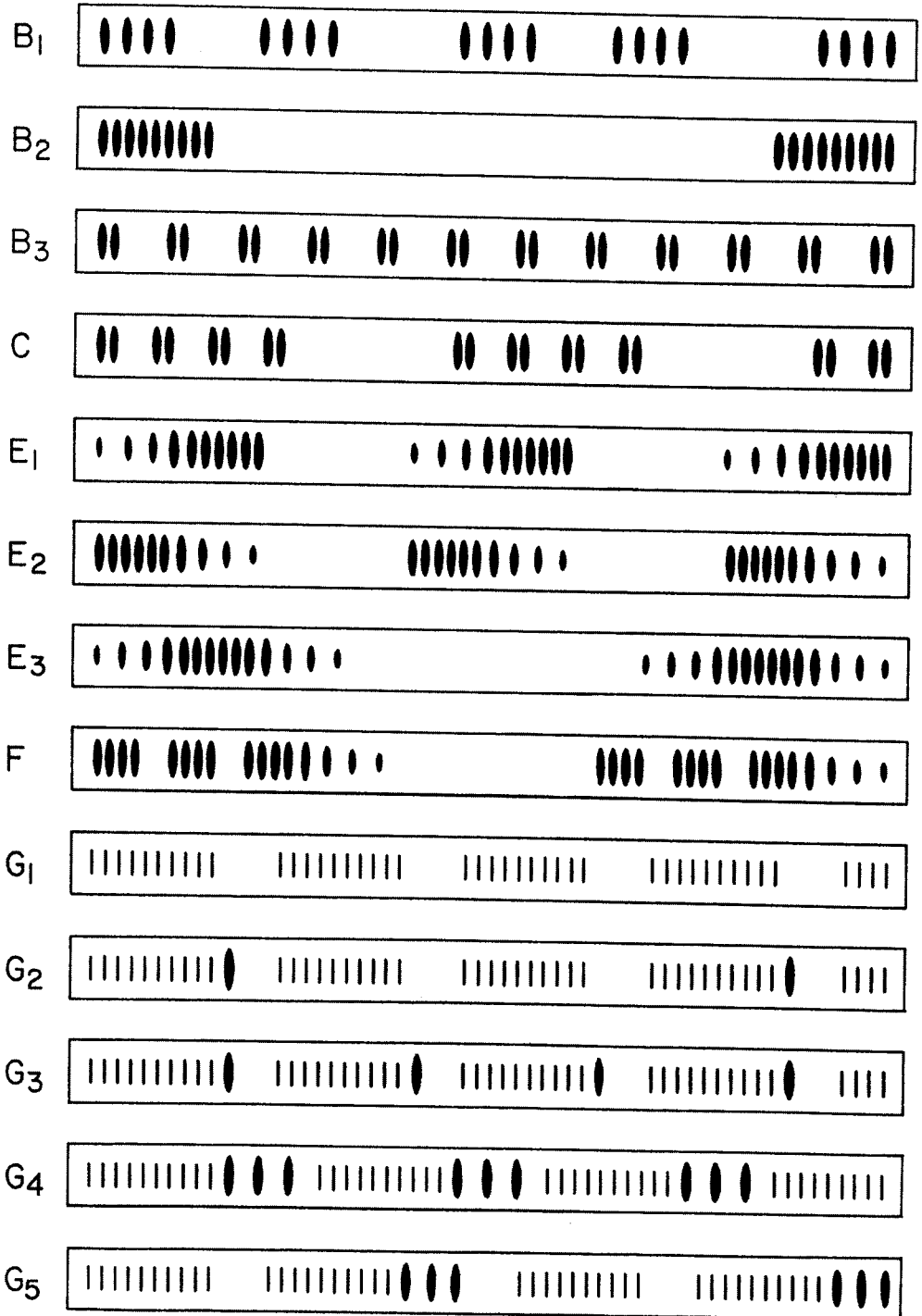


FIG. 3. Diagrams of chirping song patterns of crickets, arranged in approximate order of increasing complexity. Vertical width differences indicate intensity differences.

convergent evolution. We have to conclude that acoustical behavior is one of the slowest kinds of characteristics to change during evolution when it is not required to operate in an environment saturated with similar and potentially confusing signals of similar kinds of animals. It is probably significant that, in addition to the fact that the species mentioned above are not in contact with one another during the breeding season, *Gryllus campestris* lives alone throughout most of its range, *G. bermudensis* is apparently the only field cricket on the Bermuda Islands, and *G. firmus* lives chiefly with *G. rubens*, a trilling field cricket with a greatly different song.

It is also clear that the calling songs of field crickets in the genus *Gryllus* which live together are much more distinctive than their complex, but variable courtship songs. This too seems to be a case of different rates of evolutionary change, owing to the greater efficiency of the calling song as a reproductive isolating mechanism because it is ordinarily the first contact between sexually responsive male and sexually responsive female.

All of these facts taken together leave no doubt that the differences among the sounds of species living together are not accidental, any more than the differences among signals within species repertoires are accidental. The enhancement of existing functions, the multiplication of functions, and the multiplication of species have all contributed to fluctuating rates and directions of evolutionary changes in cricket song structure.

Song Structure and Species Relationships

There are many questions we would like to have answered concerning the song patterns shown in figs. 2-3. Here I will confine myself largely to deciphering some of the evolutionary pathways connecting them.

In the first place, we need to have some idea as to what the early or rudimentary cricket signals were like. In figs. 2-3, the various patterns have been arranged in apparent order of increasing complexity. The

most complicated signal has about seven discernible pattern components, the simplest only one. Some kind of continual trill (patterns A1, A3a) was probably the first kind of cricket signal, and there are several reasons for believing this. First, these are the simplest kinds of signals; and second, they are the most abundant kinds of signals found among crickets today. They are the simplest signals, not only from the information-carrying point of view, but also from the physiological and morphological points of view. Finally, they are the signals that are produced by activities most similar to flight movements in crickets.

But there are many evolutionary sequences in the diagrams in figs. 2-3 which might have begun with simple trills, as can be indicated by comparing calling songs among closely related species and by comparing signals within species repertoires.

Fig. 4 illustrates some probable pathways of evolutionary change in song patterns in three cricket subfamilies, based upon specific and generic relationships evidenced from all available data on morphology, behavior, physiology, hybridization, and distribution (cf. Fulton, 1931, 1933, 1937; Davenport, 1960, 1962; Alexander, 1957-1961; Walker, 1957, 1962, in prep.). It can be seen that all points of evidence suggest that certain kinds of changes are common to all three subfamilies. Although the evidence is largely circumstantial, its sources are sufficiently independent to indicate that at least some of these changes have taken place.

Song Structure, Information-Carrying Units, and Physiological Regulation

The final question I would like to explore in connection with rates and directions of evolutionary change in song pattern or structure is why particular directions of change occur rather than others which seem possible. Obviously, a good deal of the answer in specific cases is buried in problems of mode of inheritance and development. But some interesting questions and some possible answers arise when specific song

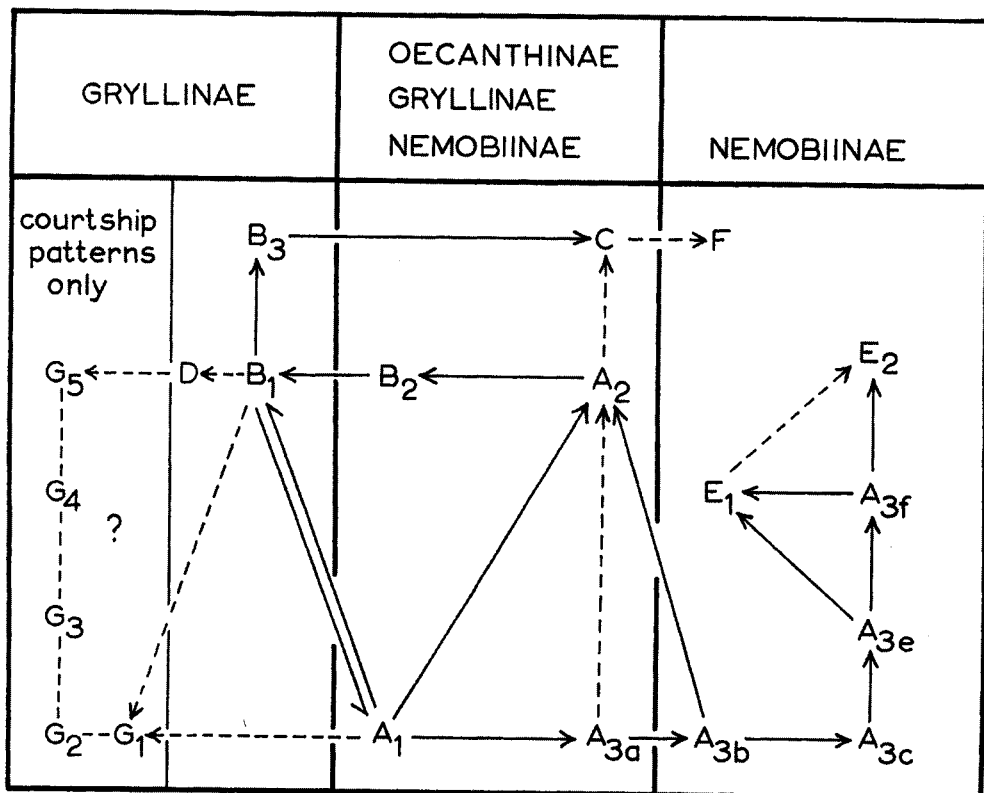


FIG. 4. Probable lines of evolutionary change in song structure in three cricket subfamilies, as indicated by all available evidence on species relationships combined with song similarities and differences. Dashed lines indicate doubtful relationships. See Alexander, 1956-1961, and text for further clarification.

patterns are compared among species in relation to: (1) the kind of sound the species makes in other situations, and (2) the variable elements in the song. One such case involves the chirping calling songs of Gryllinae (patterns B1, B2, and B3) in relation to the aggressive signals that go along with them.

Fig. 5 plots all of the available songs of chirping crickets on a scatter diagram showing increasing pulse rate along the horizontal axis and increasing chirp rate along the vertical axis. The numbers of pulses per chirp—in terms of the ranges of modes within the songs of individuals—are shown in the circles that represent each species. As chirps become longer, pulse rates (wingstroke rates) become much faster and chirp rate slower; and as chirp

rates become much faster, chirps become shorter and pulse rates faster; there are no intermediate songs on the right-hand side of the diagram. If only one genus were involved, this might suggest merely that three species groups of separate origin are involved. But several genera of Gryllinae, and several species groups in *Gryllus* alone, are included, and still the same picture emerges. Obviously it is impossible to produce a 15-pulse chirp 1,000 times per minute at the wingstroke rates available to crickets; but it is quite possible to produce an 8-pulse chirp 300 times per minute, and many other patterns that do not appear on the diagram.

The next interesting thing about this distribution of song patterns in chirping field crickets appears when we examine the kind

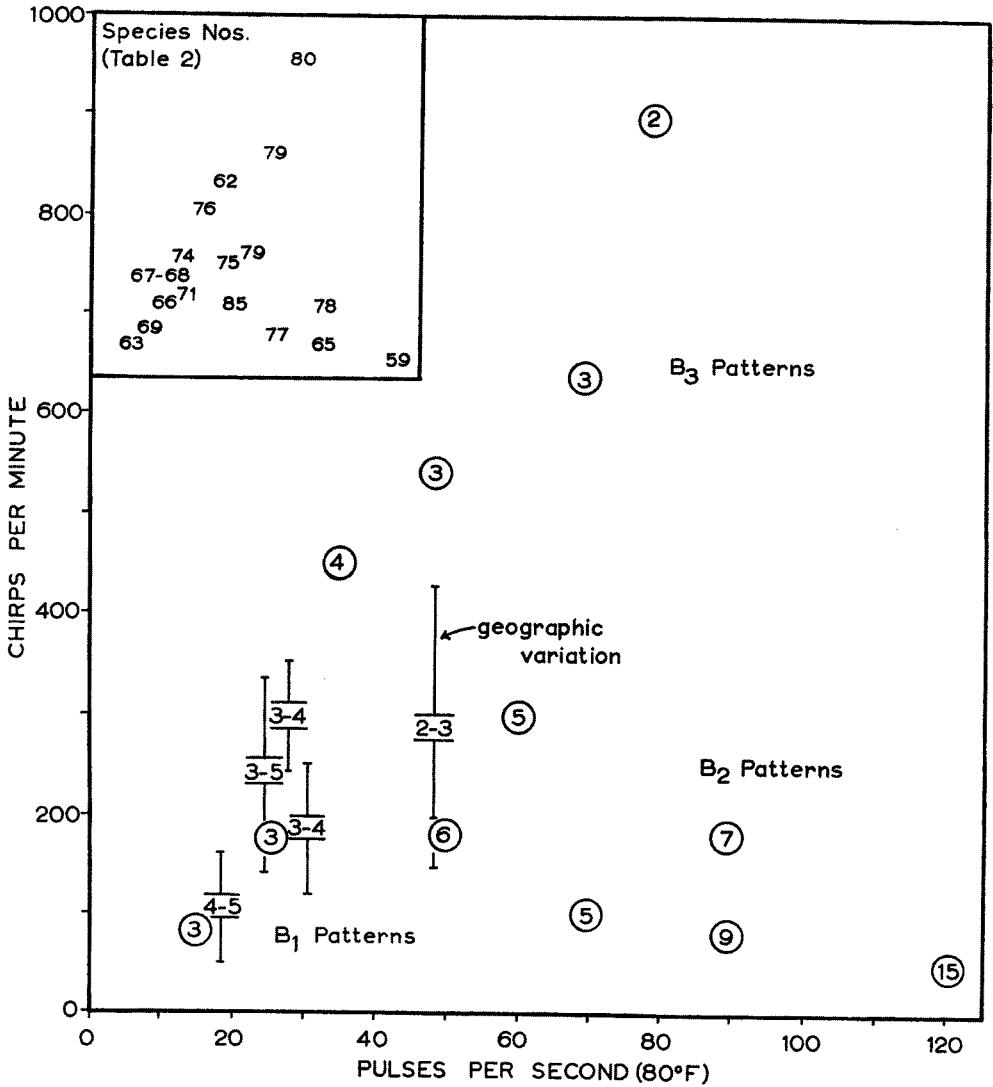


FIG. 5. Calling song structure and variability in Gryllinae with different kinds of chirping songs. Numbers indicate ranges in mode number of pulses per chirp in the singing of all recorded individuals of the species (location of species symbols on the diagram is approximate when variability is not indicated). Lack of chirp rate variability in B₁ songs indicates few recorded individuals; in B₂ and B₃ songs, all plotted characteristics are relatively invariable.

of aggressive chirp that goes with each kind of calling chirp. We have already seen that crickets with the *G. campestris* type of chirping song (pattern B₁, fig. 5) deliver very long chirps during fighting. But the crickets in the lower right portion of fig. 5 (pattern B₂) deliver aggressive chirps that are about the same length as the calling

chirps, but occur at faster rates; and the crickets in the upper right portion of the diagram (pattern B₃) deliver bursts of chirps—groups of pulse groups—during fighting. The “group of chirps” type of aggressive signal is the same pattern, incidentally, as occurs in the calling song of the sibling to the uppermost species in the

diagram in fig. 5. Trilling species similarly produce short bursts when fighting.

Thus, chirping crickets have three very different ways of making aggressive signals. The incompatibility of these three methods suggests that when a species with an elaborate aggressive signal for one reason or another begins the transition from one of the calling song types in fig. 5 to another, there may be accelerated change at the intermediate points where construction of an effective aggressive signal would be halfway between one method and another. This could be at least a partial answer to the question of why there are few intermediate song types in Gryllinae which have elaborate aggressive signals.

But what is it that is specifically different about these three kinds of calling songs from a functional point of view? The relationship between calling and aggressive signals and the extent and kind of the variability in each song suggests that it is the nature of the minimal information-carrying unit (the smallest unit that can carry any kind of information)—the morpheme or ceneme of the linguists (Hockett, 1960). In B_1 calling songs, the morpheme seems to be the short pulse group—a pulse group of minimal length that can transmit the pulse rate; this suggestion fits with all of Huber's findings as to the minimal signal in *G. campestris* that can cause a response. But in B_2 songs, the morpheme seems to be the particular chirp—its length an important aspect of its nature—and this fits with Walker's (1957) findings that the females of the snowy tree cricket respond to a pulseless chirp. The functional significance of the chirp in this song type also suggests that very fast pulse rates occur because this both increases the homogeneity of the chirp as a unit and removes the pulse rate from "accidental" communicative significance: in effect, pulse rate seems to be relegated solely to the role of a substructural unit. In B_3 songs, the morpheme is probably a chirp group of minimal length—one that can carry both the pulse rate and the chirp rate or length. The kinds of vari-

ations that occur between sibling species in the three groups are in accordance with these suggestions. Thus, chirp rate and length are variable in B_1 songs, and species differences are primarily in pulse rate. Chirp rate and length, on the other hand, are precisely the species-specific and invariable units in B_2 songs. Chirp rate and length, and eventually continuity or discontinuity in chirp sequences, are the differences among siblings in B_3 songs. In each case the characteristic which varies between species (the morpheme?) is also the one which is least variable within species repertoires and within the calling songs of individuals; this in turn suggests a correlation with the manner of physiological regulation. Huber (1960, 1962) has elaborated the probable mode of neurophysiological regulation of the pulse rate of *Gryllus campestris* and *A. domesticus* (song type B_1 in fig. 5). If there has been selection for correlation between the minimal information-carrying units and the maximal internally regulated or CNS-regulated units, then it is possible that in the other two song types shown in fig. 5, the kind of regulation that is involved with the pulse and its repetition rate in *G. campestris* has been extended to higher structural units such as chirp rate and length.

We cannot experimentally examine in great detail the particular informational nature of every cricket signal in every cricket species; and we cannot expect Dr. Huber to push electrodes into the brains of every different cricket species in order to figure out how its song is controlled. But perhaps with a little more information and correlation, we will be able to take two or more signals from the repertoire of any cricket, examine their structure in relation to general function as revealed by the context in which they are used and their variability within repertoires and between sibling species, and determine the nature of the information-carrying units and the mode of physiological regulation of the signal—in other words, to relate behavior,

neurophysiology, and evolution in this particular context.

A Possible Mechanism of Evolutionary Change in Communicative Systems

In the evolution of any communicative system, whenever change of any sort occurs, there must be a change in two respects: the signal and the receiver. In the case of cricket stridulations, this means that the song of the male and the ability of the female to respond to it (correctly) must evolve together as a unit. Actually, it means that the male's ability to respond must also change, for males do respond to their own and to other males' songs. But the kinds of differences that occur among the songs of closely related species usually do not in any way involve the structure of the stridulatory apparatus (at least externally). Likewise, the differences in the ability of females to *respond* (properly) probably do not in any way involve the auditory apparatus itself. In both cases the difference seems to reside in the central nervous system. Indeed, as is shown in tables 1-2, song differences among closely related species always (and usually only) involve those unalterable components of the patterns that must derive from the central nervous system. Is it possible that in some or many cases the genetic difference which causes the song difference—perhaps even the particular difference in the structure of the central nervous system itself—is exactly the same as the difference which causes the response difference? In this connection Huber's evidence (1962) that the components necessary for production of the song pattern reside (incompletely or completely) in the female's nervous system is particularly interesting. If there is a linkage—or an identity—here, it would represent an interesting simplification of the process of evolutionary change in a communicative system—something of an assurance that the male and the female or the signaller and the responder—really will evolve together, and possibly an increased likelihood through this that the

entire system will persist. The question has significance in connection with speciation as well as the evolution of communication, and possibly the relationship between temperature effects on signal response as well (Walker, 1957); if this situation exists in crickets, it may exist in many kinds of communicative systems in many kinds of animals.

CONCLUSIONS

Directions and rates of evolutionary change in cricket acoustical behavior are affected—in a kaleidoscopic fashion—by six principal aspects of the cricket's make-up, its mode of existence, and its history. These are:

1. The general kind of habitat that it occupies (surface-dwellers and subterranean species have evolved more kinds of acoustical signals than vegetation-inhabitants).
2. The particular number and sort of acoustical neighbors that it has (species that are sexually active in the same places at the same times never have the same acoustical behavior).
3. The behavioral complexities involved in its particular mode of life (the elaboration of particular contexts gives opportunity for incorporation of an acoustical mediator—for example, elaboration of particular kinds of post-copulatory behavior pre-adapts for development of a post-copulatory signal).
4. The number and kind of signals in its repertoire (as examples: calling signals have apparently always evolved as outgrowths of courtship signals, and the more signals a species possesses, the greater the complexity that will be necessary if any of them is changed).
5. The nature of the minimal information-carrying units in its signals (if the pulse is the phoneme, then species multiplication will result principally in songs with new pulse rates; if the phoneme is the chirp or pulse group, then chirp rates and lengths will be the principal specific variables). New morphemes will be the result in each case.

6. The kind of genetic and physiological regulation of its signals (species differences are associated with CNS-controlled, invariable units; signal differences within repertoires seem generally to depend upon more flexible units which can, for example, be adjusted by auditory feedback or other external stimuli).

Most of these effects could probably have been predicted, at least in a general way. But perhaps this discussion has clarified the importance of some of them, and the ways that they have interacted in particular cases.

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