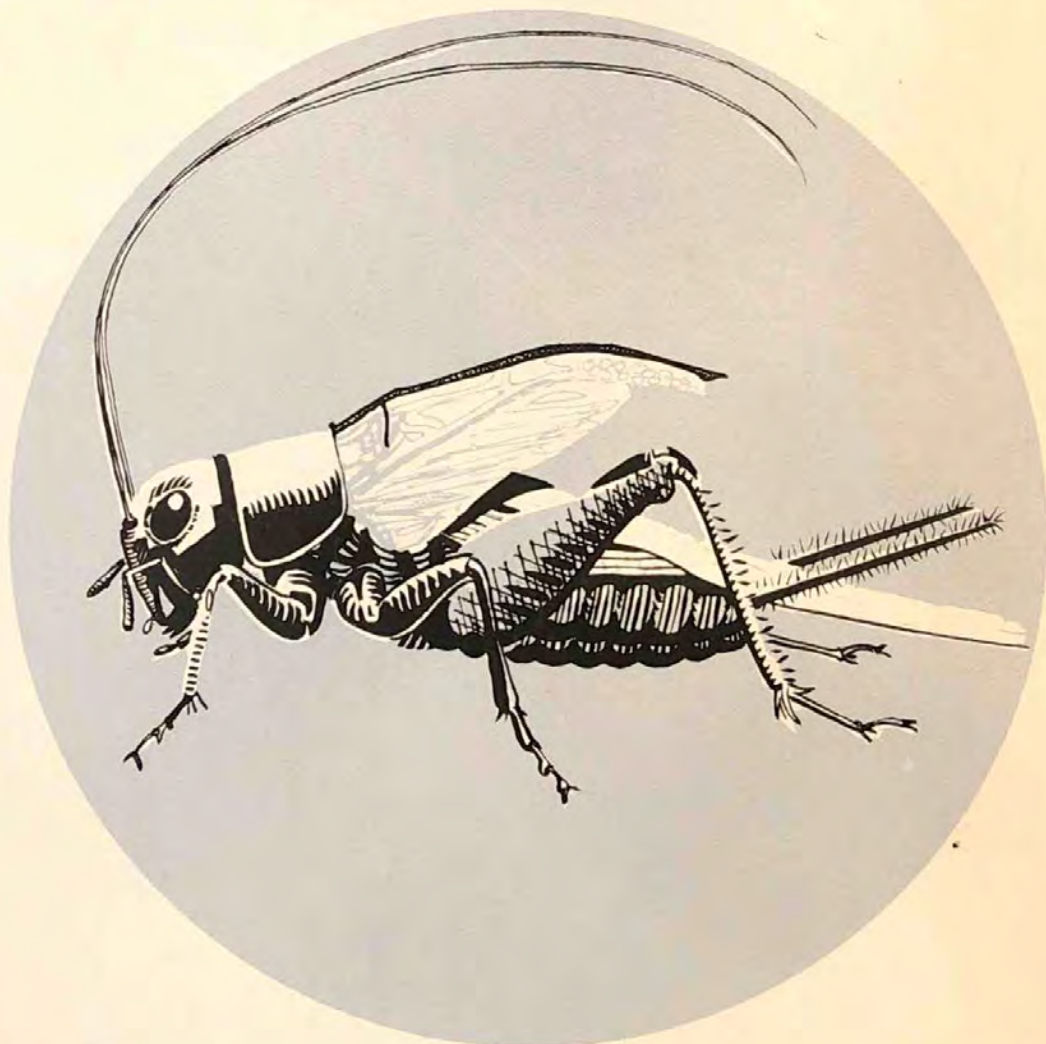


SINGING INSECTS

Richard D. Alexander

Rand McNally Patterns of Life Series



Patterns of Life Series

SINGING INSECTS

Four case histories in the
study of animal species

Richard D. Alexander

PROFESSOR OF ZOOLOGY
University of Michigan

Consultant: HAVEN KOLB
Baltimore County Schools, Maryland

Artist: Charles Moser
Evanston, Illinois

Rand M^cNally & Company / CHICAGO

RICHARD D. ALEXANDER

Dr. Alexander is a professor of zoology at the University of Michigan and curator of insects for the University Museum of Zoology. Since he received the degree of Doctor of Philosophy from Ohio State University in 1956, he has traveled widely throughout North America, studying the various species of singing insects. His many publications include not only scientific papers but also phonograph records of insect calls. In 1961 Dr. Alexander was awarded the AAAS-Newcomb Cleveland Prize, given in recognition of an outstanding contribution to science, for his paper, "The Role of Behavioral Study in Cricket Classification."



Copyright © 1967 by Rand McNally & Company. All rights reserved.
First Printing, 1967
Made in U.S.A.

Table of Contents

What Are Species and Who Studies Them?	5
The Field Crickets: What Sibling Species Are and How They Live Together	15
Regional Dialects in the True Katydid: Speciation Intercepted	44
Spring and Fall Field Crickets: A New Method of Speciation?	57
17-Year and 13-Year Cicadas: A Unique Problem in Species Origins and Interactions	63
Should We Plan to Study All the Species in the World?	82
Index	85

SINGING INSECTS

WHAT ARE SPECIES AND WHO STUDIES THEM?

This book is about animal species: what they are; how they originate; how they live together; and what the concept of species means to man in his attempts to explore and understand the world in which he lives.

Most people already have a general idea of what species are like—they are different “kinds” of things. But how different can two individual animals be and still belong to the same species? How much alike can two animals be and still belong to different species? How does *speciation*—or the formation of new species—come about, and how frequently does it happen?

Most people also have heard at one time or another that there are more than a million known species of animals and plants. But how many new ones are being discovered each year? What are the new ones like? Where are they being found? Are they newly *formed* or simply newly discovered? How many are becoming extinct each year? Is the total number getting larger or smaller? Does it make any difference to us?

How much do we really know about the million or so species that we already have discovered? How many of them are simply names associated with one or a few dead, dried specimens, “study

skins," or skeletons covered with dust somewhere in a museum, with little or nothing recorded about where and how they live and how they came to be?

How well do we need to study the species of the world if we are to continue to improve and develop human existence and make this into an ever better place in which to live? How well do we need to study them if we are merely to survive? Which ones can we do without? Which ones will we want back after they are gone?

How urgent are all these different questions? Who is investigating them? Who can give the answers?

SYSTEMATICS

Obviously, in a book as small and specialized as this one, so many problems cannot all be explored thoroughly. But together they give a general idea of the themes which run through a field of study in biology that is scarcely known at all outside universities and museums. This field is *systematics*—sometimes called taxonomy. It's the science of classification, but in biology it turns out to be a great deal more than just classification. For all living things on Earth have evidently come from one—or at most a few—beginnings. Living organisms are all interrelated, and to study their differences and similarities—to classify them—is to study their history and the history of the world. Of course, it is only through a knowledge of history, long-term and short-term, that we are able to predict; and prediction, in all its various guises, might be described as the ultimate goal of nearly every human enterprise.

The systematist is the student of animal groups. Unlike the physiologist or the geneticist or the embryologist or molecular biologist, he does not ordinarily look about for a principle or generalization to study and then decide upon the animal through which that principle can most easily or most appropriately be studied. Instead, he concentrates on understanding a group of animals or plants, searching out all the unconnected bits of information that have ever been discovered about his "pet" group. He studies the species one by one, perhaps discovering new ones, deciding upon relationships, filling in gaps in information wherever they exist, ferreting out details of prehistoric climatic changes, and using everything available from the fossil record to match up with how and where he thinks his group first appeared and how it evolved. He may construct a catalog of all the species known in his group, giving their relationships and geographic distributions all across the world. He decides what to do next by watching and studying the animals themselves and by developing files of information that contain everything that has ever been pub-

lished anywhere in the world in any language about his particular group of animals. One of the goals of almost every systematist is to publish eventually a monograph, or compilation, of everything worth knowing about his group—information of every kind, from every source.

Systematics, in a sense, is really where all biology begins and also is very close to its ultimate goals. This is where the names of animals come from, where the identification of species starts. It is the means by which the physiologists and geneticists and embryologists and other kinds of biologists are introduced to all the different kinds of animals that they must sort through in order to find the particular ones that are most likely to help them answer their special questions. Frequently the systematist's work also provides the focus that allows the experimental biologists to locate a significant problem, or a solvable one, to investigate. When all of the other kinds of biological investigators are finished with their particular studies, then back to the systematist goes practically everything they have discovered. All kinds of information are grist for his mill. He is, at his best, one of the ultimate synthesizers as well as the chief frontiersman.

It is, to one degree or another, around the work of the systematists that the term "natural history" has always had its most convincing meaning: systematics is, indeed, a methodical chronicling of the history of nature. The systematist, therefore, has to be a little more of a historian than most biologists, but he is also part detective and a little bit experimentalist. He usually has a great desire to explore—to describe and to compare. His endeavors are the kind that may involve not only traveling to the far corners of the world and living, at least briefly, under primitive and sometimes uncomfortable outdoor conditions, but also laboring patiently, hour after hour, in museums that most often are old, dark, and stuffy.

To understand the concept of species and the methods used in studying the species in any animal group, it is necessary to speak generally for a moment and consider the entire process of organic evolution and how it works. Every civilized human has an obligation to understand this process, for it is the most extraordinary event that we (as yet) know has occurred anywhere in the universe. We may speak of the strong possibility that life exists outside our own solar system; but even if this is true, that life is still inaccessible to us and likely will remain no more than an untested possibility for a long time to come. Within our solar system we have only the so-called "canals" and seasonal changes of color on Mars in which to place any hope that another kind of life has evolved. As a result, in this otherwise relatively simple and lifeless solar system that we inhabit, the process of organic evolution on Earth stands as the most remark-

able, most complex event in all history. Nothing is more fitting, as we humans continue to spread across the face of the earth and to increase our power and the extent of our organized knowledge, than that we spend an increasing amount of time and effort to understand the other living things upon which we wholly depend, not only for the "good life," but for survival itself.

MECHANISMS OF EVOLUTION

Organic evolution proceeds principally as the result of three phenomena: *mutation*, *selection*, and *isolation*.

Mutation is change. With regard to organic evolution, it is change in the hereditary materials—in the genes located on the chromosomes in the nuclei of the sperm and eggs and spores and other reproductive cells of animals and plants. Changes in nonreproductive (or somatic) cells may be important to the particular individual possessing them; but only changes in the reproductive cells, in individuals not yet past reproductive age, are of evolutionary significance.

Gene mutations are apparently changes in the chemical structure of the nucleic acid molecules that make up the genes. In a sense, they are all accidents; for they are not directed in any way toward making their possessor more fit to get along in the particular environment in which he lives. Even their rates of occurrence, at least in the vast majority of instances, seem to be totally independent of any "need" by the organism either to change or to remain stable. Mutations are caused by radiation, and—at least in artificial situations—by chemicals, heat, and other agents as well. Because modern animals are so complex, and because all the different parts of the genetic makeup of each animal are so intricately interadapted for the particular life it leads, most gene mutations actually prove to be harmful. But these accidents have to occur if evolution is to proceed. Even if only one in a million proves beneficial, it is still true that mutations alone provide the raw material of evolutionary change.

Natural selection sorts and arranges the mutations by a passive process of elimination and as a result causes their accumulation in what we might otherwise think of as extremely unlikely combinations. Selection operates through differential reproductive rates: some of those few mutations that are beneficial give their possessors a better chance to live long enough to reproduce, and others give their possessors a better chance of reproducing more abundantly.

It is easy to think that mutation and selection are enough to account for evolution, but with these two mechanisms alone there would be only a single species on Earth. The formation of new species involves *isolation* as well. When two populations of animals are sepa-

rated from one another by an accident of geography or climate or transport for a long enough period of time, they will become sufficiently different, through the action of mutation and selection on each of them, that they will never be able to merge or combine into one species again—thus destined forever to be separate evolutionary lines. The process whereby this kind of *irreversibility in evolutionary divergence between populations* comes about is called *speciation*, and its products are *species*. But to understand it we have to pause a moment and consider how and why isolated populations can become so different that they cannot amalgamate—why some of them do not speciate but instead re-amalgamate when they come back together.

Practically all animals are sexual. Usually this means merely that there are two or more kinds of individuals with different roles in reproduction: male animals produce sperm which fertilize the eggs of female animals, thus producing a zygote which develops into a new individual. This kind of animal is *bisexual* (has organisms of two sexes).

There are many other kinds of sexuality as well. Some kinds of animals, such as earthworms and leeches, are consistently *hermaphroditic*: each animal is both male and female, and during the mating of two individuals, the sperm from each fertilize the eggs from the other. In some cases, hermaphroditic animals may even fertilize themselves. In still other cases, a single individual may play the role of one sex during part of its life and transform to the other sex later on.

Many kinds of animals, particularly insects, have lost the male sex and are able to produce offspring from unfertilized eggs. Most of these *parthenogenetic* animals, however, either occasionally or regularly produce generations that are bisexual. Aphids, or plant lice, are a good example. Some kinds of animals, such as jellyfish and some parasitic worms, have asexual and bisexual generations produced in some kind of predictable alternation. A fertilized egg, for example, may develop into an individual which then reproduces by *fission*—dividing into two or more complete individuals. Humans occasionally reproduce asexually when a single fertilized egg or zygote, instead of developing into one individual, first divides completely into identical twins. Triplets, quadruplets, and even sextuplets can be produced by repeated complete division of a fertilized egg. In some animals, such as sheep, this process is fairly common, while in others it is the rule: A North American armadillo always gives birth to four identical offspring, all produced by double complete splitting of a single fertilized egg.

There may also be more than two sexes within a species. In some one-celled organisms there are several different "mating types"—for ex-

ample, in the tiny, slipper-shaped organisms frequently studied in biology classes and belonging to the genus (or species group) *Paramecium*. In paramecia, sexuality and reproduction are related in an unusual way. Reproduction is a matter of fission. And, as in most cells that divide by fission, the nuclear material is duplicated and distributed during *mitosis*. (This is essentially the same process as the one by which a one-celled fertilized egg becomes a many-celled animal.) In *Paramecium*, mitosis can occur without sexuality—at least for some time. Sexuality is exhibited during a process called *conjugation* when two individual paramecia come alongside one another, form a slender protoplasmic bridge between them, exchange some of their hereditary materials, and then go their separate ways without having produced any new individuals. Within a few hours following conjugation, however, reproduction by mitosis always occurs. In other words, sexual recombination does not occur simultaneously with reproduction, and reproduction without sexuality can also occur. But sexuality is nevertheless linked to reproduction, even in these strangely specialized little organisms.

The peculiar sexuality of *Paramecium* partly explains why I'm going to the trouble of describing different kinds of sexuality in connection with the process of speciation. During conjugation, essentially what happens is the exchange of hereditary materials (genes) by individuals. In other words, when two paramecia conjugate, neither goes away as the same animal it was before entering the act. Each one carries part of the other's hereditary material, just as the offspring of a normally bisexual animal carries hereditary material from both its father and its mother. This is the significance of sexual reproduction: it provides the species with the chance to shuffle its genetic materials into all possible combinations and thus to produce as many different kinds of individuals as are possible with its own particular "pool" of genes. This is how a group of individuals can maintain identity as a population. And it provides a clue for the question of how populations can become irreversibly divergent from one another.

The evolution of living things has been an increasingly complicated affair. It is also a rapidly changing one. Habitats and niches for particular kinds of organisms are here today and gone tomorrow, as species multiply and change and live together in ever greater numbers and ever more complex interrelations. If we consider sexual reproduction and recombination in this light, then it is not difficult to see what a tremendous advantage it must be to most kinds of animals that become capable of evolving it. Without the ability to shuffle and reshuffle the individual hereditary units that it has, a species or population would be doomed to producing only a small definite group of

different kinds of individuals. Each individual would really be a separate evolutionary line in itself, for it could never mix its genetic materials with any other. The only way that any particular set of hereditary materials could produce a new kind of individual, starting in one asexual individual and continuing only in its daughter organisms or offspring, would be through mutation. Furthermore, new mutations would only have one chance to confer their potential advantages: they would have to be advantageous as a component in the hereditary makeup of the particular individual in which they first appeared. They would have no chance to be shuffled into some other combination where they might prove to be more viable. And they would only be spread by happening to appear in the makeup of an individual that is going to have a large number of successful descendants. In some ways of life or some kinds of organisms, this condition must be advantageous, because unisexuality (or parthenogenesis) has evolved many times from bisexuality. The significance of bisexuality, on the other hand, is revealed by its prevalence throughout the animal kingdom.

Not so long ago biologists believed that a high proportion of the world's species are asexual; but when these species are studied carefully, most of them prove to be sexual organisms after all, though they may have many asexual generations for every sexual generation. Sexuality has been overlooked in some animals because, for one thing, it sometimes requires special conditions for its appearance. As a hypothetical example, a particular kind of single-celled organism might require a temperature between 20 and 25 degrees centigrade, a particular light intensity, and a shortage of food before it would conjugate or mate, before it would become sexual. As a result of such possibilities and the large proportion of species that have been revealed to have sexual periods in their lives, the burden of proof now falls more heavily on the shoulders of the investigator who believes that his animals are totally asexual. Are his animals truly asexual, or are they simply not being provided with the conditions that would allow sexuality to appear? All of this is important to the species concept because sexual reproduction lies at the very heart of the process of speciation; it is difficult to classify populations in a meaningful way at the species level in an asexual animal in which each individual represents a separate evolutionary line.

If you consult one of the better dictionaries or encyclopedias for a definition of species, you will usually find a phrase something like this: "actually or potentially interbreeding populations." According to such a definition, a species is a group of individual organisms sufficiently alike to hybridize, or interbreed successfully among themselves. Within

a species there may be much genetic variation. For example, hereditary differences may cause variations in color of hair or skin, size, mental capacity, shape of various body parts, behavior, or physiology.¹ Nevertheless, individuals with such variations will all belong to the same species because of their ability to interbreed and thus continually to mix up and redistribute these differences. Good examples of genetically different populations belonging to the same species are the different breeds of cattle, horses, sheep, or other domesticated animals which man has isolated from one another and purposely selected for differentiation.

As a point in passing, man still has probably not caused speciation among domestic breeds—even though he has often made breeds seem much more different than separate species are in nature. How do we account for this? Even two incompatible breeds of dogs (Chihuahua and St. Bernard, for example) would merge if they and all other dogs were released to make their own ways as wild animals. They would merge because there are breeds that are compatible with both of them, providing a “bridge” for the gap between them.

But suppose that we eliminated all dogs but St. Bernards and Chihuahuas from an island and then let these two breed as wild dogs. There is little doubt that, unless one of them became extinct, the Chihuahua and St. Bernard would go their separate ways on this island, behaving as perfectly good species—which is precisely what they would be in this situation! Where, then, and how must the tests of speciation take place? In the last analysis we must deal not with a theoretical question or “potentiality” but with the *actuality*—what really happens in the field.

I think you can see what difficult questions are raised by this example, particularly with our classification of populations that do not give us the “natural test” because they do not live together in nature. How do we decide how to treat such populations in our analysis of the evolutionary process? Clearly, we must find out whether or not there are “key” differences that will probably lead to incompatibility (that is, inability to keep on hybridizing until amalgamation has occurred) and thus indicate speciation even before the field test occurs. We can only find such key differences by knowing our animals thoroughly—how they live, where they live, and all the details of their existence in nature. We cannot rely upon laboratory or museum studies of animals alone to inform us accurately about their evolutionary status.

¹ Some of the same kinds of variations may exist among individuals of a species solely as a result of nutritional or other environmental differences, but here we are interested in variations resulting from hereditary differences.

To summarize, within each of two isolated populations, sexual reproduction results in the individuals continually mixing up the mutational differences that develop among them. Sexual reproduction also spreads any mutations that appear throughout the population, unless such mutations are so disadvantageous that they are quickly eliminated by selection. If the mutations that occur in two different isolated populations are different (and they almost always are, because the odds are so great against identical changes taking place independently), and if the selective action of the two different environments in which the populations find themselves are different (and it almost always is, at least slightly, in two different places), then divergence between the populations is bound to occur. But the critical question for speciation is: *When does such divergence become irreversible?* How can we predict that two populations which are very similar will nevertheless be unable to amalgamate because they have diverged in some important, though perhaps imperceptible, fashion?

WHY STUDY SPECIATION?

It is not difficult to see why the speciation process has always fascinated biologists: not only is there a great deal that we don't understand about it, but also its mechanisms lie at the very heart of evolution. Every separate evolutionary line, whether it be the entire animal kingdom, or all the mammals, or the insects, or any other group that has a single common ancestor, began in a speciation process.

We ought to expect, as a result, that some characteristics of every evolutionary line—however large or small—will have been determined by the events of one or more speciation processes. We cannot understand which parts, and to what extent, until we comprehend the nature of speciation.

UNANSWERED QUESTIONS

How long does it take for isolation to produce separate species? What kinds of isolation are sufficient to produce separate species? Have there been periods in the history of the world during which speciation took place very rapidly and other times when little was occurring, or is speciation going on around us all the time? Is speciation merely a matter of the number of differences that arise in isolated populations, or is it principally the result of *particular, critical kinds* of changes taking place? Is it quantitative, qualitative, or really both?

Which of the differences that we see in very closely related species today arose while they were still isolated from one another and were involved in their incompatibility when they came back together? Which arose after they came back together, perhaps being retained

as the result of the two species' interaction? Which of the differences that we see between populations that are isolated now, and thus undergoing divergence, might contribute to speciation, and which have no significance at all in this regard?

No man has observed the process of speciation from beginning to end. Apparently it takes much longer than a human lifespan for speciation to occur, at least in all the animals we know much about. Then how can we find the answers to the questions asked here? We study contemporary species and their interrelationships in all regards—geographically, ecologically, behaviorally, genetically, physiologically—and in any other way that can be found to make a significant comparison. We use the fossil record to “predict” backward in time. (We predict, in this sense, both ways in time—on the basis of partial information that will eventually be more complete, not only for future events but usually for past events as well.) We compare cases in which speciation has been intercepted at one stage or another with cases in which speciation is barely complete.

The systematist naturally has to be interested in studies of all animals. But for his own investigations, he is necessarily restricted to a group small enough for him to understand it. This is the systematist's particular brand of specialization in biology. If he is going to find out anything of sufficient importance to place into the scheme of things biological, then he must become at least temporarily “narrow-minded” in his pursuits. Only from relatively narrow and specialized investigations can significant new information be added to a field as complex and many-sided as biology.

On the other hand, it is also clear that there are generalizations to be made about species and speciation. Some things are the same no matter what group of animals one is examining. I am going to tell you about my own experiences in becoming acquainted with speciation—its novelties and its problems and its principles—in a rather heterogeneous group of insects, commonly referred to as the “singing” insects. These are the insects that make the noises that fill the night air, and sometimes the day air too, in most parts of the world. Their chirps and rasps and buzzes have always been a part of man's environment, and their influence is so prominent that they are still being used by the moving picture and television producers to create nocturnal atmospheres—even for modern city dwellers who otherwise seldom hear these sounds.

There are three insect families involved in the singing insects discussed here: the crickets (Gryllidae), the katydids (Tettigoniidae), and the cicadas (Cicadidae). The accounts are based chiefly on my

own personal study of these animals during the past ten years. Some of these stories are merely unusual, but others are without parallel anywhere in the animal kingdom. Each has been selected because it illustrates some of the particular questions I have raised in this introduction about what animal species are, how speciation occurs, and how we can be sure that we are correctly interpreting this part of the evolutionary process.

THE FIELD CRICKETS: WHAT SIBLING SPECIES ARE AND HOW THEY LIVE TOGETHER

Approximately three thousand species of crickets are known in the world. The field crickets make up a special group of about four hundred species which live on the ground and excavate shallow burrows. These are the crickets that “look like crickets” as far as most people are concerned—large, heavy-bodied, black, brown, or yellowish insects, perhaps best known for their rather loud, musical chirping.

It is appropriate to use field crickets to introduce the subject of species and speciation for two reasons. First, their classification has undergone some remarkable changes in the past few years as a result of changes in the ways that systematists have studied species and their relationships. Second, it is through a study of the field crickets that I first began to understand what species are really like and how they may form. Actually, there is a third reason which is somewhat incidental, and yet not trivial, and this is that field crickets occur almost everywhere. If you are really interested in understanding a species or two firsthand and in understanding its closest relatives as well, you can do this almost anywhere that you may live by going out and watching (and perhaps studying awhile in a cage) the field crickets that live in your area.

QUESTIONING AN OLD IDEA

My acquaintanceship with field crickets began several years ago when, as a graduate student just starting in research, I read an article in a scientific journal that excited my curiosity. A biologist in North Carolina, the late Dr. Bentley B. Fulton, had discovered that he could tell apart four kinds of field crickets just by listening to their songs. He could not get them to hybridize in the laboratory, and they lived in different kinds of habitats—but they appeared to be structurally identical, even when seen under a microscope.

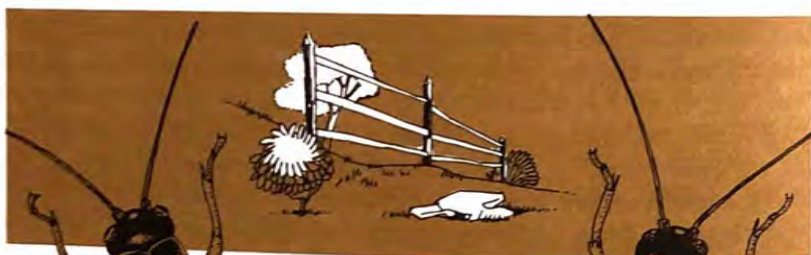
Dr. Fulton's discovery had a double interest for me because I was



A
veletis



B
pennsylvanicus



C
rubens



D
firmus



E

Northern *fulloni*



F

Southern *fulloni*



G

vernalis



H

assimilis



aware that the experts on field-cricket classification believed that all the field crickets found across North, South, and Central America, and across all the islands bordering these regions, belonged to a single species. This conclusion had been reached as long ago as 1915 through supposedly exhaustive studies utilizing all the methods systematists used in those days. Thousands of specimens had been examined, measured, and studied in the laboratory, and their characteristics had been plotted on scatter diagrams (see Figures 10-12) and otherwise examined statistically. Because no discontinuities could be discovered among them, it was decided that there were no distinct species among the New World field crickets.

Dr. Fulton's method—listening to the songs of crickets—could scarcely be described as an "orthodox" systematic procedure! But his paper raised some interesting questions. Perhaps the systematics of field crickets was not a closed book after all, and if not, what would be the result of looking at the field crickets from this new point of view? Of studying them as living populations rather than as specimens preserved in museum collections? Even though I had collected many field crickets for biology classes and had watched them as a youngster living in rural Illinois, I realized that I knew practically nothing about them, and it struck me that this was very much like the beginning of a fine adventure.

So I went out the first spring after reading Dr. Fulton's paper and collected a few black field crickets in a pasture in Ohio. They were quite ordinary looking crickets, but as I watched them in the laboratory and collected more of them in the field, the realization of my ignorance about them grew. I discovered that I didn't understand their ecological boundaries: I didn't know the kinds of places where they could live and where they could not. I knew scarcely anything about their seasonal life history—when the different developmental stages were present, where and how each lived, and how many generations developed each year. I didn't know whether these were the same crickets I also heard in the autumn or if they were always just spring chirpers. I didn't know the limits of their geographic distribution—whether they might be the same, for example, as any of the crickets Fulton had found in North Carolina. I wasn't even sure how I would know it if I did discover some other "kinds" or species of crickets living in Ohio!

A well-known biologist once compared a species to an island. It occurred to me as I became acquainted with my first field crickets that this is a good analogy, for one has to go all the way around an island if he is truly to understand it. He has to know which land masses lie

closest to it and on which sides of the island they lie, and he has to get a feeling for how that island was formed. If it broke off from some other land mass, when did it do this, and how? From which one? I realized that I couldn't answer any of these questions for this cricket.

I called this first field cricket the "pasture" cricket because that's where I collected it. Later, however, I discovered it was the same one that Fulton had called the "mountain" cricket because that was where he had collected it in North Carolina. Still later, after studying all the eastern North American field crickets, I decided that this one should be called the Northern Spring Field Cricket. Here I will always use such "final" names for the species in order to avoid confusion.

Fulton had discovered his different kinds of crickets by listening to their songs, and so I began to listen to the songs of crickets too and tried to decide if any of those I was hearing were different from the one that I knew to be my Northern Spring Field Cricket. Within a few weeks I had heard two additional songs. One was a coarse, soft chirp coming from the oak-hickory woods of central Ohio, and the other was a very rapid chirping coming from certain kinds of old abandoned fields in southern Ohio. When I collected the crickets that were making these different kinds of chirps, brought them into the laboratory alive, and allowed them to lay eggs and reproduce, I found that I could separate the three kinds of males by differences in size, color, and body shape. I could also tell the females of one kind from the rest, but the other two kinds of females were very difficult to separate. The differences in the males' songs were the most distinctive things about the three crickets. Each song could be recognized by several different characteristics.

When I tried to cross the first three kinds of Ohio crickets in the laboratory, I discovered that they ordinarily would not cross-mate but that occasionally a pair would be compatible and produce hybrids. The hybrids, however, were unusual in appearance; and I did not discover any of them in the field, even when I purposely collected every single cricket from a large area where two of these kinds of crickets were found together under leaf litter, debris, and stones.

SIBLING SPECIES

During that first season and subsequent ones, I discovered that there are seven different kinds of field crickets in eastern North America. They are listed on page 22 by their scientific and colloquial names. In Figure 1, males (left) and females (right) of all these crickets are drawn to the same scale. *Gryllus fultoni* is shown as it appears in Ohio (page 18) and in Florida (page 19).

<i>Gryllus veletis</i> (Alexander and Bigelow) ¹	Northern Spring Field Cricket
<i>Gryllus pennsylvanicus</i> Burmeister	Northern Fall Field Cricket
<i>Gryllus firmus</i> Scudder	Sand Field Cricket
<i>Gryllus vernalis</i> Blatchley	Northern Wood Cricket
<i>Gryllus fultoni</i> (Alexander)	Southern Wood Cricket
<i>Gryllus rubens</i> Scudder	Southeastern Field Cricket
<i>Gryllus assimilis</i> (Fabricius)	Jamaican Field Cricket

We can use the relationship of these seven species to show what "sister," or "sibling," species are, why they are often missed by the taxonomists, and how they can live together in the same areas without amalgamating.

All these species, as well as the rest of the New World field crickets, look very much alike, which was one of the reasons that the early systematists were confused when they tried to compare them structurally. Their songs, however, are in nearly all cases quite different from one another, and in this respect I had a distinct advantage over the biologists who had worked before me. Using battery-operated tape recorders and electronic sound-analyzing instruments (Figure 2), I could compare the songs objectively, study their rhythm patterns and their frequency (pitch) relationships, and discover precisely how they were alike and how they were different. Furthermore, because of the availability of a new sound analyzer called the audiospectrograph (Figure 3), I could reproduce the sounds on paper for illustration in a scientific publication. This would be much more convincing to other scientists than mere word descriptions of the chirp differences and similarities would be. Figure 4 is an illustration of samples from the sounds made by male crickets in each of these seven species in eastern North America.

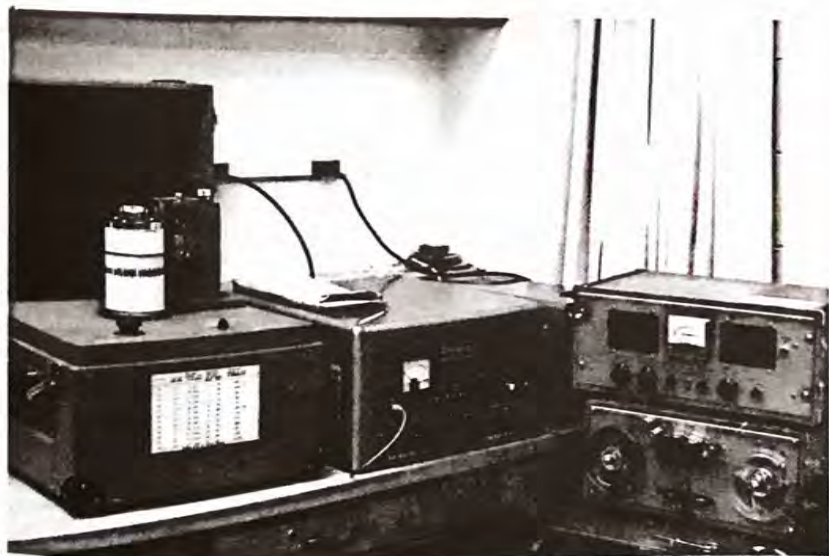
Using these *song differences* as my clues to which population I was dealing with, I was able to discover that there were also differences in *life history* among forms that had different songs. These are shown in Figure 5. As you can see, some of the species survive the winter, or *overwinter*, as partly grown juveniles and mature in the

¹ The proper names following the two-part scientific names are the authors who originally described the species. When they are placed in parentheses, it means that the species was placed in another genus at the time of its original description. The eighteenth- and nineteenth century investigators often gave a separate name to every preserved specimen that looked a little different from other specimens, and they sometimes did not keep up with the work of other taxonomists. As a result, some species recognized today have many old names available for them. In these cases, the oldest name is generally used.



Figure 2. Battery-operated tape recorder, microphone, and parabolic reflector used in making field recordings of insect sounds.

Figure 3. The vibralyzer: an instrument for making audiospectrographic pictures of sounds.



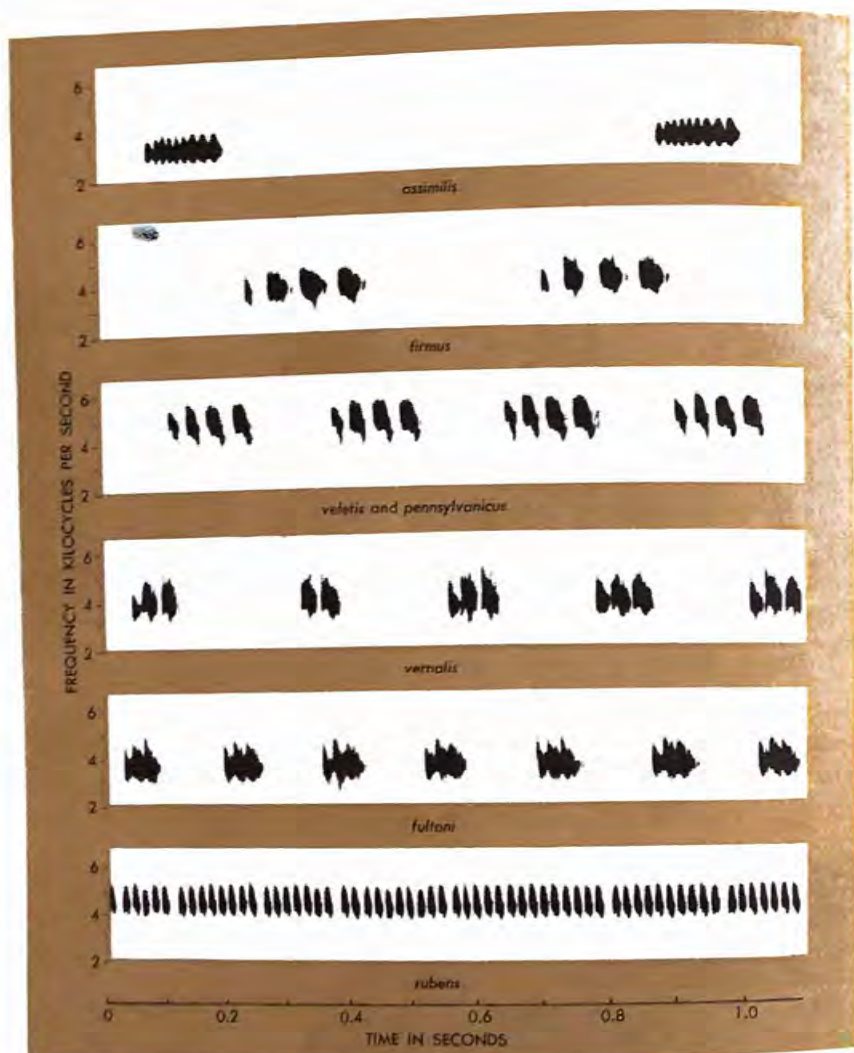


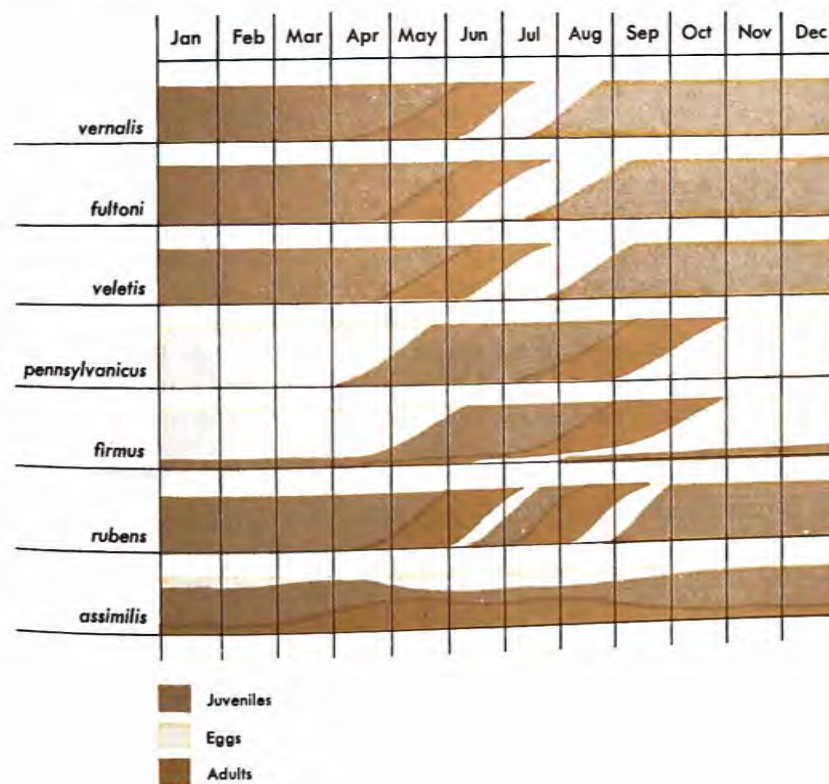
Figure 4- Audiospectrographic samples from the calling songs of the seven eastern North American field crickets. Time is read on the horizontal axis, frequency (pitch) on the vertical axis, and relative intensity within each graph by darkness of the mark.

spring. Others overwinter as eggs and mature in the fall. One species, the Southeastern Field Cricket, has two generations each year, overwintering as a juvenile and maturing in the spring, then immediately producing a fall generation of adults, which in turn produces the overwintering juveniles.

All these crickets that live far enough north to go through a real winter always pass it in the same stage, the *diapause*, or stage of arrested development. Diapausing insects cannot be reared easily in the laboratory because they stop developing when they reach the diapause stage, and, in the absence of a winter to "break" the diapause, most of them eventually die. The rest usually do not reproduce. If American field crickets turn out to be like some others studied in France and Japan, their diapauses are probably triggered by the day length or photoperiod, much as blossoming periods of some plants are timed.

Having a single diapause stage not only enables a northern species to concentrate all its physiological and behavioral winterhardiness into that single stage, but it also results in maximum synchrony in the appearance of the short-lived adults. It is not an illusion that field

Figure 5- Seasonal life histories of the seven eastern North American field crickets.



crickets and other noise-making insects seem to appear as adults almost overnight and to begin to chirp in great numbers all at once.

The Southeastern Field Cricket is an especially interesting species, for it diapauses only every other generation. Experiments show that this is because spring-day lengths prevent diapause in the first generation and fall-day lengths induce diapause in the second generation. Only one kind of life cycle additional to those shown in Figure 5 is known among field crickets: A European cricket evidently diapauses both in the egg stage and as a half-grown juvenile, thus always requiring two years to complete its life cycle.

Figure 6 shows still another difference among the seven field-cricket species—a difference in ecological distribution among the three spring species that occur in central Ohio. One species, the Northern Wood Cricket, occurs only in heavy leaf litter in oak-hickory and some other kinds of forests. Another, the Northern Spring Field Cricket, is widely distributed in the pastures and lawns and old abandoned fields that occur throughout central Ohio. A third species, the Southern Wood Cricket, occurs in this region only in old abandoned fields that have some particular kinds of plants growing in them. These old fields, it happens, resemble ecologically some prehistoric prairie habitats in Ohio; and this is apparently the only reason that this third cricket, which must have lived only in the true prairies prior to civilization, is able to exist in them today. In the South, this same species (the Southern Wood Cricket) lives in oak-pine woods, but we'll discuss this geographic variation later.

Two of the three Ohio species—the Northern Wood Cricket and the Northern Spring Field Cricket—overlap ecologically along forest borders. The broadest such overlap zone that I have ever found between them is about 15 yards wide, and there individuals of the two species are occasionally found together under stones or logs. On the other hand, the Southern Wood Cricket is thoroughly mixed with the Northern Spring Field Cricket across broad areas in abandoned fields in southern Ohio.

With such information one is able to keep the crickets with different habitats and different songs and different life histories separated in the laboratory, compare their structure and behavior, and attempt to cross them. Figure 7 combines the results of all the *interspecific* (between species) crosses that have been carried out by several investigators. There are many ways to attempt such crosses to determine the sexual interactions of different populations with one another. One way is to place together large groups of females of one kind with large groups of males of another kind. Another way is to isolate pairs in which the male and the female belong to different species. Still a

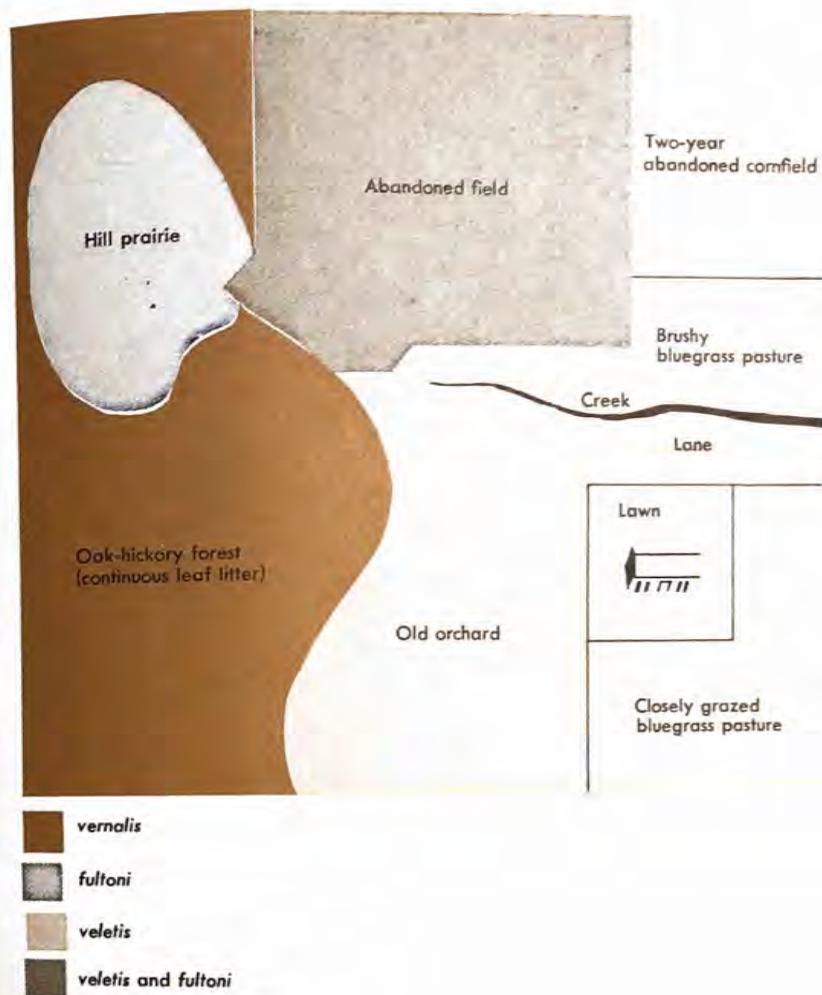


Figure 6. Ecological distribution of three Ohio field crickets in one locality in southern Ohio.

third is to place a male of A and a male of B with a female of A in one cage and with a female of B in another cage or vice versa, to place two females, one of each species, with a single male of one or the other species.

These three methods of trying crosses can be used to show different things. The third method is a selective mating test: one expects that individuals of the same species would be more likely to mate with

		MALES						
FEMALES		assimilis	rubens	firmus	pennsylvanicus	veletis	vernalis	fultoni
	assimilis	Hybrids almost always obtained.	Hybrids almost always obtained.			Hybrids never obtained in many tests.		
	rubens	Hybrids almost always obtained.	Hybrids almost always obtained.	Hybrids sometimes obtained.	Hybrids sometimes obtained.			
	firmus		Hybrids sometimes obtained.	Hybrids almost always obtained.	Hybrids almost always obtained.	Hybrids never obtained in many tests.		
	pennsylvanicus	Hybrids rarely obtained.	Hybrids sometimes obtained.	Hybrids almost always obtained.	Hybrids almost always obtained.	Hybrids never obtained in many tests.		
	veletis	Hybrids never obtained in many tests.		Hybrids sometimes obtained.	Hybrids sometimes obtained.	Hybrids almost always obtained.		
	vernalis					Hybrids rarely obtained.	Hybrids almost always obtained.	
	fultoni					Hybrids rarely obtained.	Hybrids rarely obtained.	Hybrids almost always obtained.

- Hybrids almost always obtained.
- Hybrids sometimes obtained.
- Hybrids rarely obtained.
- Hybrids never obtained in many tests.
- Not tried.

Figure 7. Results of attempts to cross the various species of eastern North American field crickets.

one another than they would be to mate with members of another species. The second method, that of pairing individual males and females that belong to different populations, is the one that makes it possible to discover whether or not there was some degree of incompatibility between the two. The first test, in which one puts together large numbers of males of one species with large numbers of females of the other, is used in an all-out attempt to secure hybrids. Thus, ten pairs of crickets placed together in one cage would give a total of

100, or ten-times-ten chances for the establishment of a compatible pair (each male would have ten chances of finding a compatible female, and each female ten chances of finding a compatible male). Placing one pair in each of ten different cages would yield only ten chances, but it would be easier to establish *relative* compatibilities of individuals taken from different populations.

Along with all interspecific pairings, one has to test an equal number of pairings within species—that is, between males and females of the same kind—to make certain that there's not something wrong with the entire setup. Under conditions that do not favor reproduction, not only incompatible males and females but also compatible ones will fail to produce offspring. This, of course, is known as the "control" for the experiment.

The tests illustrated in Figure 7 are the results of individual matings between males and females from the populations that have different songs and occur in different areas. It's clear that production of hybrids between these populations is very low. (I was also able to tell, just by watching the cages, that the incidence of mating between members of these different populations was greatly reduced, and in some cases there was probably no mating at all.) The few hybrids that were produced were peculiar animals. In all my research in the field I have discovered only one of these, a cricket collected in an abandoned field in central Ohio where, as I said earlier, both the Southern Wood Cricket and the Northern Spring Field Cricket occur in great numbers. This cricket seemed both in structure and in song characteristics to be hybrid between these two species.

You may be surprised that some species can produce hybrids when cross-mated—particularly hybrids that develop normally and, at least theoretically, could be perpetuated as a separate population or bred back with either parent species. Actually, this is not an uncommon situation in any kind of animal. Hundreds of interspecific hybrids have been reported in mammals and birds; in some groups, such as fish, species in widely different groups have been hybridized. The important point is that species do not hybridize frequently *in nature*. The fact that they will do so under unnatural laboratory conditions, however slightly altered from nature these conditions may seem to be, *has no direct significance for the recognition of species in the field*. Of course it does have great significance for the understanding of the speciation process, for it causes us to look again and wonder at the meaning of the phrase "actually or potentially interbreeding populations." What is the significance of the fact that many animal species can hybridize with others but do not when left alone in the field?

A final difference discovered among the seven species of Eastern United States field crickets was that they have *different geographic distributions* (Figure 8). This was one of the most important contributions of the study. The vast majority of animals are able to speciate only because they are *geographically* isolated from one another. This means simply that some kind of uncrossable barrier must appear between two or more segments of a population and prevent them from ever getting together at mating time. The barrier, furthermore, has to remain insurmountable long enough for divergence resulting in speciation to occur.

When groups of species are found to be related both geographically and structurally or behaviorally, certain questions arise. What was the location, nature, and timing (in geological history) of the barrier that originally kept the groups apart? What effect might that barrier have had on other organisms? The events of geological history, the requirements for speciation in the various animal groups, and the number, kind, and distribution of modern species in each group must eventually correlate; and all three kinds of information will probably be necessary for the puzzle of our planet's geological history to be unravelled.

RECONSTRUCTING THE FIELD CRICKETS' HISTORY

What are examples of barriers which can cause speciation? When a population gets to an island through some sort of rare accident and does not communicate again with the mainland, speciation can occur. If an animal cannot fly or swim, gradual division of its range by a river may separate its populations. Deserts, mountains, or any kind of area uninhabitable to the population involved can be a barrier permanent enough to cause speciation. Presumably the advance of glaciers can geographically fragment a species. Oceans, rivers, deserts—these are barriers whose appearance and disappearance must be measured in geologic time. They do not appear and disappear overnight. Even more important, they are radical changes—major events in the history of a continent.

If such events are necessary to bring about speciation, then to clarify the relationships of field crickets in North America constitutes an important step toward understanding the history of the continent. Whatever scientists propose as the course of events in North America during the past ten thousand years or so, on the basis of all kinds of evidence, must eventually agree with the fact that there are seven different field crickets on the continent, with particular life histories, habitats, geographic distributions, and *phylogenetic* (evolutionary) relationships. Surely it is clear that one "highly variable" and "widely

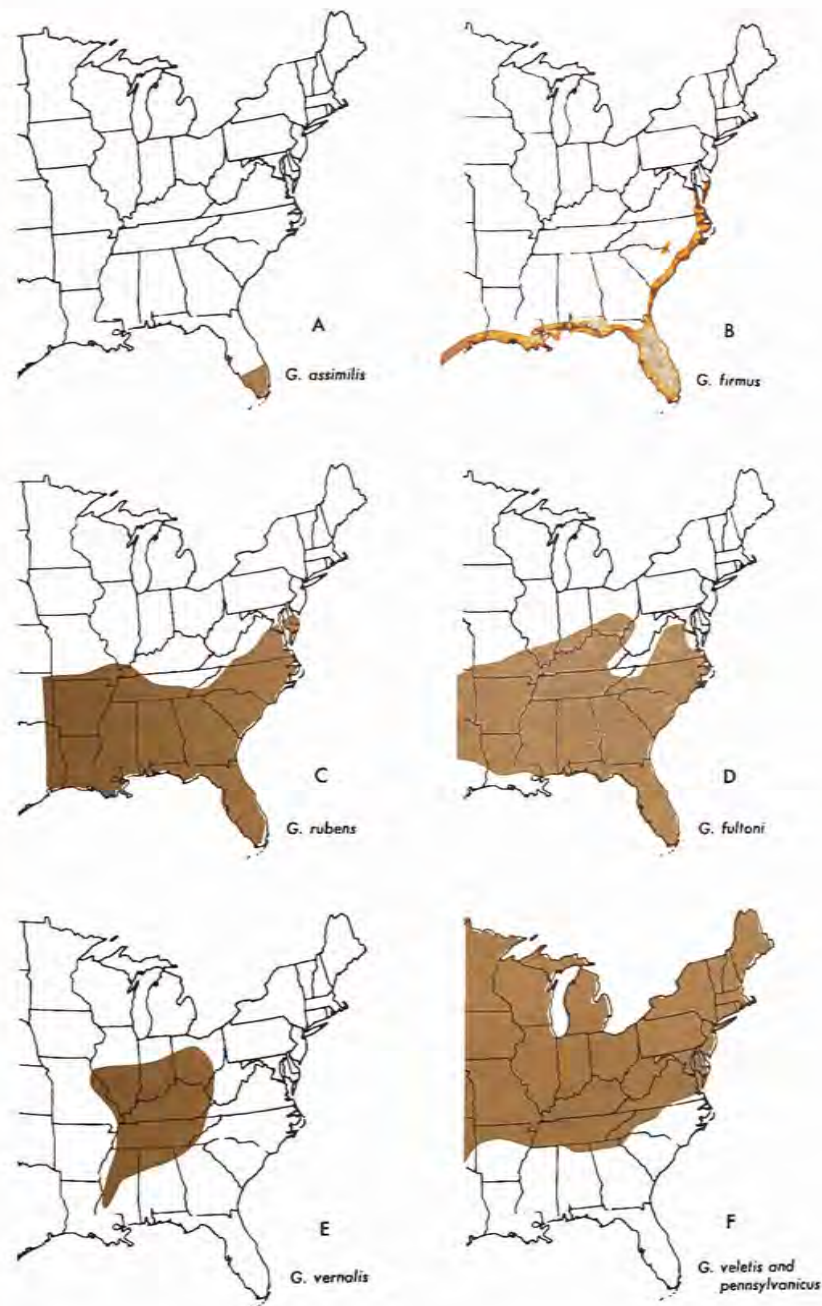


Figure 8- Geographic distribution of the seven eastern North American field crickets.

distributed" species—believed to be the case in American field crickets until a few years ago—is not the same as seven distinct species, each requiring geographic isolation from the others at some time in the past. As I will illustrate later, several of the distributional relationships between sibling field crickets occur also between other kinds of insects, and as a result we are slowly beginning to develop a picture of the succession of geographic barriers and climatic events that must have occurred during the last twenty thousand years or so in eastern North America.

During my study it became apparent why the early taxonomists could not distinguish the different field-cricket species. Of course, there was an occasional species, like the Southern Wood Cricket, that was sufficiently uncommon or peculiarly distributed in time or space as to be missed entirely by most or all collectors. But more interesting were those species that had found their way into almost every collection but had simply not been recognized as separate species. In some cases I have found these to be abundant species that live in such everyday places as lawns, vacant lots, or old fields! How could they be missed?

To understand this we must remember that the early taxonomists relied almost entirely upon structural characters in preserved specimens. After I had recognized the various field-cricket species by song, mating tests, and ecological distribution, I began to analyze differences and similarities in structural features, such as body length, *ovipositor* (egg-layer) length, and wing length—the same characters that the early investigators had used. Figure 9 illustrates what was discovered in one case of two species. If all the symbols on this graph were alike, it would be difficult to guess that there are two species rather than a single, variable species involved. However, as soon as one knows that the individuals plotted on one end of the graph had one kind of song and one kind of geographic and ecological distribution and those on the other end have another, then the *morphological* difference between them—even though overlapping—becomes significant.

Figure 10 also shows how putting together a large number of species on a single diagram causes differences between populations to be obscured. In this case other populations bridge the gap between the two being compared. In other words, if there were only two species involved, such as *Gryllus firmus* and *Gryllus vernalis*, it would be easy to distinguish them; but as soon as the other species are placed on the same diagram, then these two species appear to be merely the extremes of one variable species. In fact, that is the way they were described by an early statistician who studied these characteristics. He thought that crickets such as *G. vernalis* and *G. firmus* were like tall and short men—merely the extremes in a variable species.

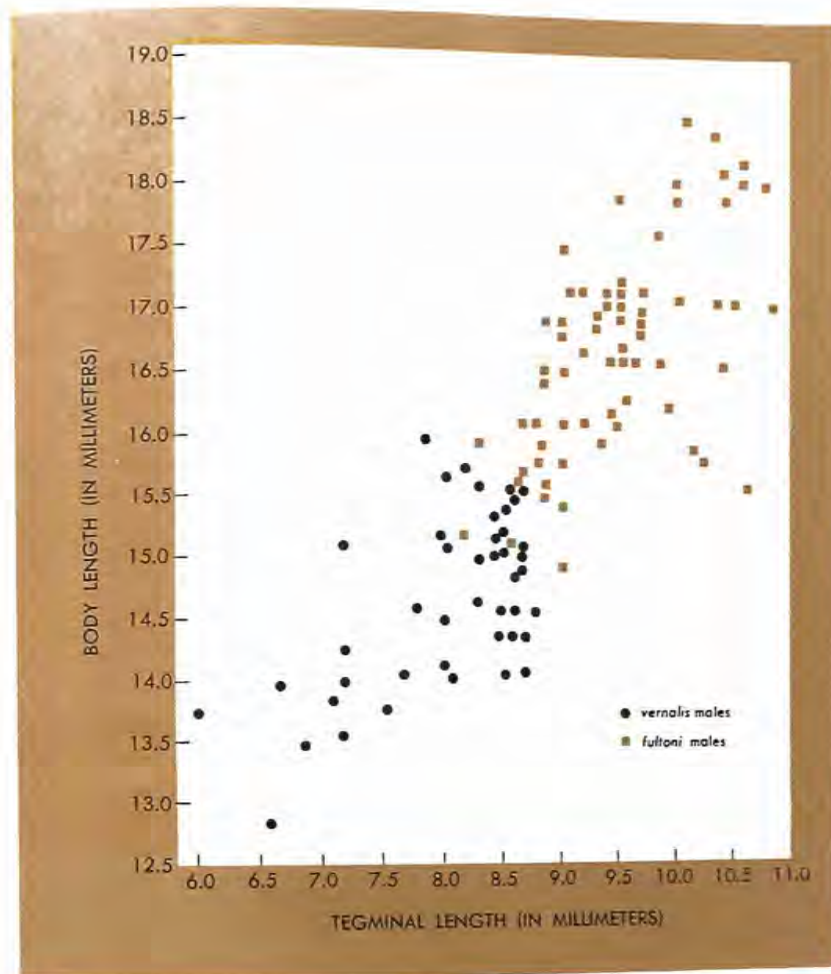


Figure 9. Wing-length and body-length ratios in the Northern Wood Cricket and the Southern Wood Cricket.

Figure 11 shows still another kind of situation. Here two groups of symbols clump separately—but one group contains two species, and the other contains four species. Furthermore, the two groups are bridged to some extent by one of the other six species. Small wonder that these species were not distinguished earlier!

The best structural character so far discovered for separating the species is correlated with their song differences. The males chirp (or

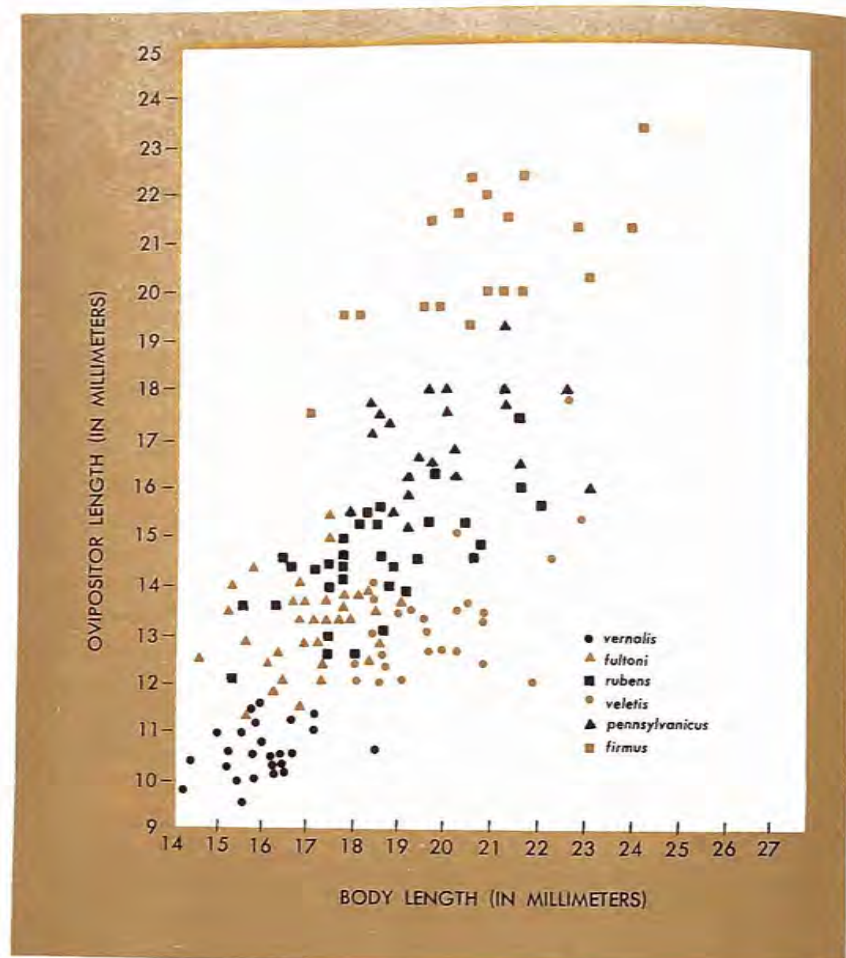


Figure 10. Lengths of the ovipositor (egg-layer) and body in females of seven eastern North American field crickets.

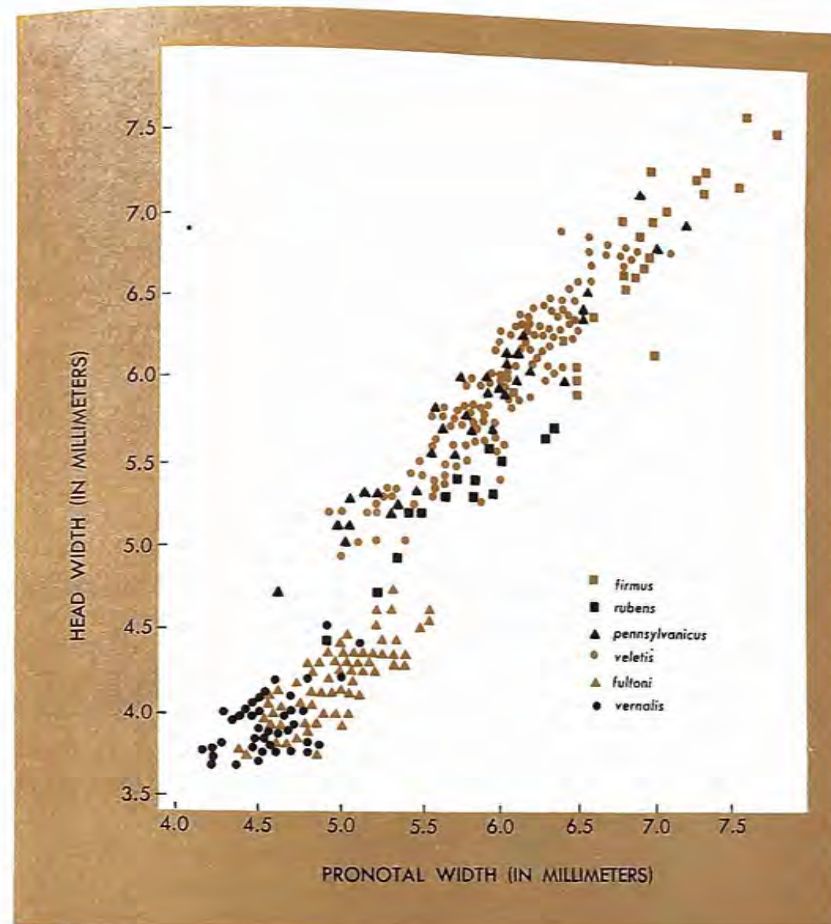
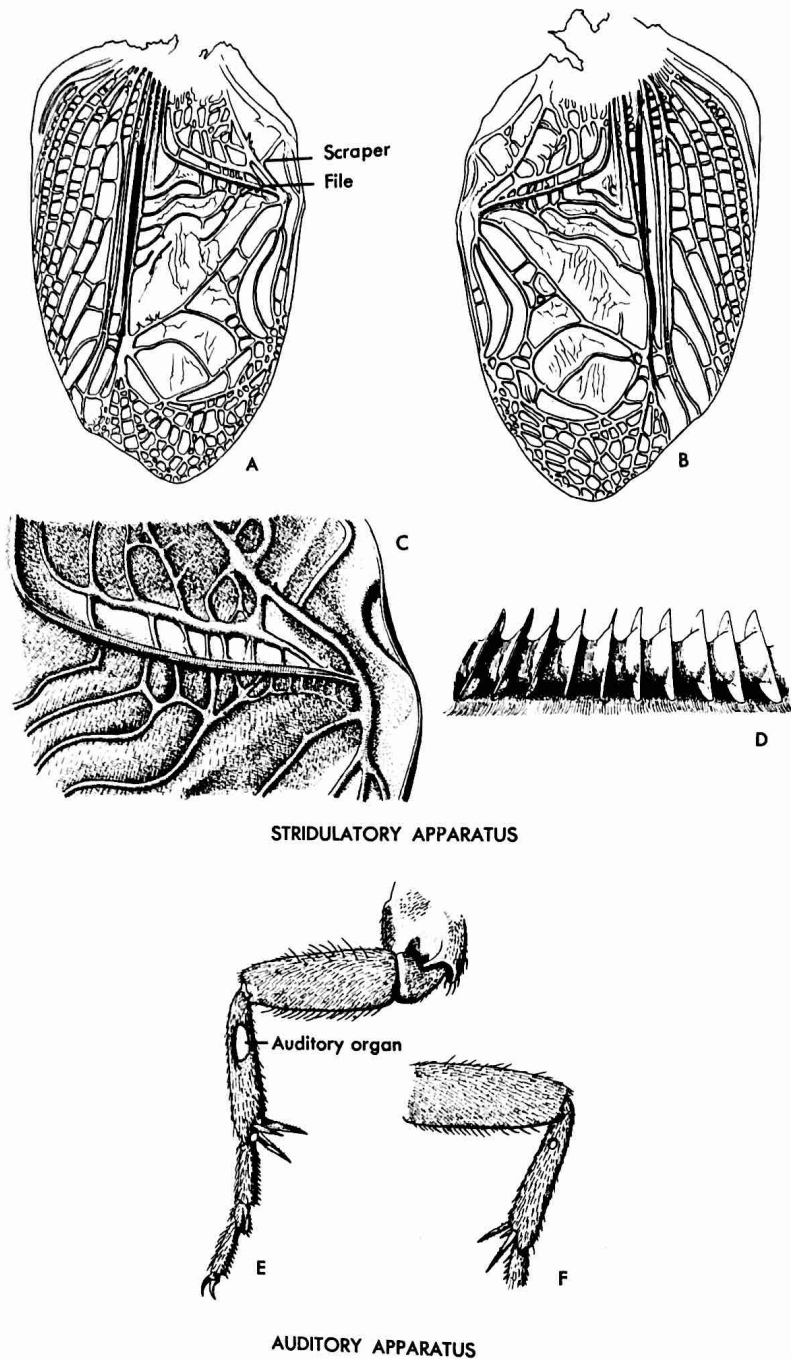


Figure 11. Widths of the head and pronotum (the part of the body just behind the head) in the seven eastern North American field crickets.

trill) by striking a row of tiny teeth (called the *file*) on the underside of the right (upper) fore wing with a scraper located on the inside edge of the left (lower) fore wing (Figure 12). Although certain pairs of species cannot be separated at all in this way, some pairs that are difficult to distinguish by other structural characteristics, such as *G. firmus* and *G. rubens*, and *G. rubens* and either *G. pennsylvanicus* or *G. veletis*, can easily be separated by differences in this one particular characteristic.

But now let us get back to the original question of what constitutes sibling species and how they live together. The term “sibling species” was developed to refer to species that are so similar that it is difficult for biologists to tell them apart. In general, as you can see, the term will also refer to what we might call “most closely related” species or “sister” species. Such species have an exclusive common ancestor and represent a “last fork” in the phylogenetic, or evolutionary, tree, having separated from one another fairly recently in evolutionary time.

Which of the field crickets being discussed here are siblings? Does



STRIDULATORY APPARATUS

AUDITORY APPARATUS

it make any sense to look for sibling species? If we examine all the different characteristics by which these species are distinguished, we will discover that in some cases a pair of species is much more similar to one another than either of the pair is to any other cricket. For example, *G. vernalis* and *G. fultoni* both occur in woodlands (woodlands of two different kinds, to be sure, but nevertheless woodlands); they are similar morphologically, and their songs are much alike. They also have the same life histories. This surely means that these two species are sister species or siblings.

You will also notice that *G. pennsylvanicus* and *G. veletis*—two species with differences in life history—are otherwise very similar in all structural characteristics, being almost impossible to separate by morphology. Further, they occur in the same habitats, and their geographical distribution is quite similar. It seems logical to assume that they also represent a pair of recently evolved species which have an exclusive common ancestor.

G. firmus seems to be quite similar to both *G. veletis* and *G. pennsylvanicus* in many characteristics.

Although *G. rubens* seems quite similar to both *G. pennsylvanicus* and *G. veletis* in superficial structural characteristics, both its life history and its song are distinctive, and along with *G. assimilis* we surely must assume that this species is somewhat apart from the others and not very closely related to any of them. A careful look reveals many structural characteristics, such as file tooth count (low in *G. rubens*), body pubescence (heavy in *G. assimilis*), head and thorax color (brownish in *G. assimilis* and often with light margins in *G. rubens*), as well as the behavioral and life-history characteristics, which these species do not share with any other member of this group of seven species. Thus, by comparing these different populations in many different ways, one begins to arrive at some hints regarding their origins and the sequence of separations by which they evolved.

Incidentally, my use of the phrase "closely related" brings up an important point. The degrees of difference between two populations or species depend not only on the length of time they have been separated but also on their rates of change or divergence from one another. One must always remember that two similar species may have been separated a long time with a relatively slow rate of divergence, while two strikingly different species may be more recently

Figure 12. The sound-producing (stridulatory) and auditory apparatus of a male field cricket. The number of teeth on the file varies among species.

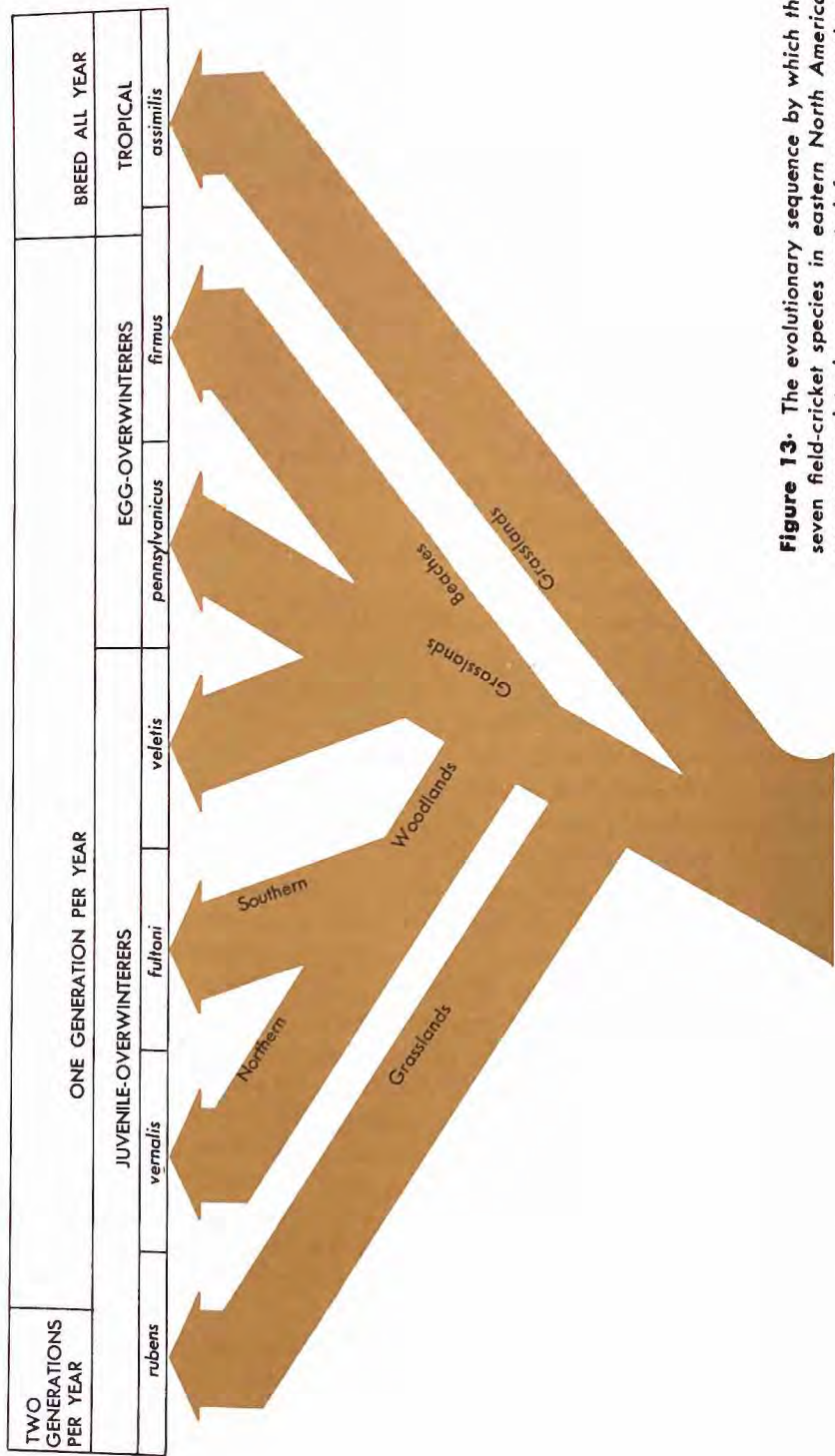


Figure 13. The evolutionary sequence by which the seven field-cricket species in eastern North America are presumed to have separated from one another.

separated but more rapidly divergent. One of the jobs of the evolutionary biologist is to attempt to discover how to “predict” which of these is the case. In other words, we search for a basis for generalizing about the conditions under which particular kinds of characteristics in different species diverge either rapidly or slowly. This is such a knotty problem that many biologists believe it is insoluble on the basis of the kinds of evidence we will have to use in most cases of evolutionary reconstruction. All this means, of course, is that we may not always be able to decide in what order species now in existence were formed. But the natural historian does not like any unfilled gaps in his reconstructions, even minor ones.

HOW THE SPECIES LIVE TOGETHER

In the case of the seven field crickets of eastern North America, we can draw up a tentative phylogeny as shown in Figure 13. Not only do the various structural, behavioral, ecological and life-history data confirm this arrangement but so does the information from geographic distribution. Thus *G. assimilis* appears to be a recent invader from the tropics with a history that was independent of the other species for a long time. *G. pennsylvanicus* and *G. veletis* have related (in fact, almost identical) distributions, as do *G. fultoni* and *G. vernalis*, confirming the suggestion that they separated recently. The distribution of *G. rubens* does not “pair up” with that of any other species, suggesting a more ancient separation.

I think you can see that the next step is locating specific causal events that occurred in the right places and in the right sequence to explain this phylogeny. This depends in part on analyzing many other species’ groups so that parallels in the necessary kinds of geological events can be established. Perhaps someday we can say when each separation of species occurred as well as what geologic event was responsible.

Now that we have seen the kinds of similarities and differences that exist between sibling species, we can go back to the question of how they are able to live together without amalgamating. What are their *reproductive isolating mechanisms*, and how do they avoid deleterious *competition*?

Let us take up reproductive isolation first. If the individuals of any population are to be able to interbreed freely with one another, then they must be adult at the same time of year—they must have the same breeding season. Any species that are not adult at the same time of year are therefore isolated, regardless of how the difference arose. You will notice that, today at least, *G. firmus* is largely sepa-

rated from *G. vernalis*, *G. fultoni*, and *G. veletis* by this kind of difference. *G. rubens* is isolated from neither spring nor fall species, however, because of its two-generation life cycle. Curiously, *G. veletis* and *G. pennsylvanicus* are the only *siblings* separated by a seasonal difference. This raises the question of how seasonal differences appear in the life histories of crickets. But let us defer that for now.

If two species have different geographic distributions, they cannot interbreed. We can see by this that *G. veletis*, for example, could not interbreed with *G. assimilis*, because these two species never meet anywhere in eastern North America; furthermore, these two species almost surely never did live together. *G. fultoni* and *G. vernalis* have different geographic distributions, but they overlap, while *G. veletis* and *G. pennsylvanicus* have almost identical geographic distributions. *G. rubens*, again, overlaps geographically with each of the other six species, just as it does seasonally.

Next, we can notice that any species living in different habitats could only interbreed in those cases where adult individuals came into contact in the region of overlapping between the two habitats. In southern Ohio we would guess that *G. vernalis* has relatively little chance to interbreed with either *G. veletis* or *G. fultoni*, which overlap ecologically with it only rather narrowly; but *G. fultoni* and *G. veletis*, which are individually intermixed across wide areas, would surely have a much greater chance to interbreed. As pointed out earlier, the only field hybrid we have so far discovered appears to be a hybrid between these last two species. Since the interspecific hybrids that have been produced in laboratories have distinctive songs, it is certain that if there were large-scale field hybridization between any species the extensive fieldwork of the past ten years would have brought it to light.

Continuing, we can see that *G. rubens* is again the only one of the seven species that overlaps ecologically to a rather large degree with most of the other species—with all but *G. vernalis*. These overlaps cause some question about the origin of the distinctiveness in some of the characteristics of *G. rubens*. We have to wonder, in other words, if this species has undergone rapid evolution in some characteristics because of its overlap with so many similar species and the possible competitive or confusing (at times of sexual activity) effects. Aside from this case, it would seem that most of the geographic, ecological, and seasonal differences described so far among these seven *Gryllus* species arose as a result of their original separation and divergence and not as a result of competition or some other inefficiency in the way they lived together. This must be so because

ecological and seasonal differences among the geographically overlapping species are not reduced where these species do not overlap geographically, as we would expect them to be if they had arisen as a result of interaction.

Ecological competition between species cannot exist when they are either geographically or ecologically separated. But if they live in the same places and merely have different life cycles, as in the case of *G. pennsylvanicus* and *G. veletis*, some competitive interactions must occur—adults and juvenile field crickets live in the same kinds of places and eat the same kinds of things. At this point, however, we have almost no data on the question of which species differences are associated with previous deleterious competition or on the extent to which overlapping species are affecting one another by competition now.

Leaving aside the question of competition, then, we may ask why there are no hybrids, even between the species which are not isolated geographically, seasonally, or ecologically? This brings us to *the single non-overlapping difference* among all of the seven species—their song differences. Here I can make a generalization: Among all the insects in the world in which pair formation and courtship are mediated by acoustical signals, there is no known instance of two species that are mature in the same times and the same places having the same acoustical behavior (the same songs and the same responses to the songs). Nearly a thousand species have been studied.

The significance of this statement, which cannot yet be made for any other single characteristic in any animal group, can be understood only if we know the functions of insect song. Among field crickets only the males make noises. They make three basic kinds of noises, one during fighting (the *aggressive* sound), one when alone—especially at the entrances to their burrows, and especially at night (the *calling* sound)—and the third only when in the presence of a female (the *courtship* sound). It has always been supposed that the males' sounds attract the females. As long ago as 1913, a German named Johann Regen demonstrated by playing the chirp of a male cricket through a telephone that the female cricket is indeed attracted by this noise, but only if she is an adult female which is sexually responsive—that is, one which has not copulated (mated) recently. The sound that has this female-attracting function is the calling song that the male produces when alone, the song that humans commonly hear. This sound has been termed a "song" because it is rhythmical and repetitious—actually resembling a human chant more than any other kind of song.

Since Regen's work, the fighting sound has been shown to affect the outcome of aggressive encounters between males, and the courtship song has been shown to influence the time required to enter into copulation. Only a few experiments have been performed to test whether or not one insect species can respond to the sound of another species, but thus far no females of any species have been shown to be capable of responding to the sound of the males of another species with which they live—even when the songs of the males of the two species sound fairly similar to humans.

In field crickets it is easier for us to separate different species by calling songs than it is by courtship songs. Very likely the calling songs are more distinct to the female crickets as well. In the field a large percentage of the male-female encounters occur as a direct result of the female hearing the male's chirps or trills while she is sexually responsive and moving toward his burrow or his calling station. Thus those song differences must be involved in keeping males and females of different species from encountering one another in the field even when they live in the same habitats and are adult at the same time of year. Consequently we may refer to the males' calling songs as *interspecific reproductive isolating mechanisms*.

There are unidentified mechanisms, in addition to the calling-song differences, that allow different species of field crickets to live together efficiently—even in addition to the differences in habitat and the differences in season and geography that have been described. The proof lies in the fact that there is inevitably much less interaction between males and females of different species than between those of the same species, even when they are kept together in a small cage where the calling song cannot affect pair formation. This may be a result of chemical differences between the species that they can sense at close range but that we have not yet discovered. There are detectable differences in the courtship songs, and these may also be significant to the females. But the consistency of calling-song differences among species which are adult at the same time and in the same places not only makes this the best clue to species recognition among animals which are otherwise difficult to tell apart, but also suggests that this is a very potent means by which the members of a species distinguish their own kind. Undoubtedly, this must be viewed as one of the major mechanisms for increasing the efficiency with which the two species can live together. If a female of species A reacts to the song of male B and yet cannot copulate with him or hybridize with him once she has been attracted to his burrow or his calling station, then she has wasted some time and energy in respond-

ing to his call. Consequently, those females which develop an ability to respond only to their own males and those males which develop a song to which only their own females will respond are more likely to leave offspring than those which are unable to discriminate their own species. In this way selection must have operated to produce the consistent song differences that we see now. And this is why song differences are such an extraordinarily good clue in distinguishing species of field crickets.

Incidentally, I have not yet said anything about the question of why it might be disadvantageous for two newly encountering populations to hybridize. All of the differences between siblings that I have talked about so far merely indicate that selection at some time in the past did operate to keep populations apart rather than to cause them to amalgamate. There are many possible reasons for disadvantage in amalgamation: the hybrids may be imperfect individuals; they may be unable to attract mates; or they may be of such a nature that there just isn't an appropriate place or way for them to live. This is an individual problem for each instance of speciation, and one that can be solved only by field study. We used to think that incipient (or newly forming) species are always so different genetically that hybridization is usually impossible, or that at least the hybrids would be defective. As a result, this problem was frequently left for the geneticists to solve. Now we know that such great differences between newly formed species are at least not the rule. The reasons for speciation must be much more subtle, and our understanding of them must depend upon detailed knowledge of the interaction of each pair of populations and their hybrids within the particular environment where the populations meet.

To summarize, then, we may say that field-cricket sibling species are able to live together efficiently because they can occupy different ecological niches and also because they can evolve differences in pair-forming mechanisms which reduce deleterious or wasteful sexual interactions. We can also generalize at this point that it is not only better to use a large number of characteristics to distinguish and to classify species in any animal group, but it is also fitting to locate those characteristics by which the animals themselves distinguish one another. There is an old verse which goes as follows:

Behold the happy, bounding flea,
You cannot tell the he from she;
The sexes are alike, you see,
But he can tell and so can she.

The moral of the story is that fleas don't use the same things that

we do to tell males from females. The verse can be extended to include the differences between species as well as differences between sexes. Someone has remarked that few bird species are referred to as siblings simply because birds use vision and hearing to a greater extent than, for example, insects; consequently, the kinds of differences that evolve as reproductive isolating mechanisms are often the same kinds of differences that we humans use to separate bird species—principally plumage color differences and song differences. The suggestion is that we can distinguish most of the closely related bird species more easily than we can distinguish closely related species in most other animals. If we paraphrased the flea verse, perhaps rather awkwardly, to make it apply to species differences instead of sexual differences, we might say:

Behold the happy, bounding fleas,
You cannot tell the A's from B's;
The species are alike, you see,
But the A's can tell and so can the B's.

REGIONAL DIALECTS IN THE TRUE KATYDID: SPECIATION INTERCEPTED

The field-cricket species that I have described so far have shown no significant tendency to hybridize in the field, and all of their characteristics are relatively unchanging, as individual species go. In other words, there is no question that speciation has been completed among all the seven field crickets; they are separate evolutionary lines which are destined to remain separate. But if evolution is proceeding continually, then whenever we look in on it at one time level, as we humans are doing now, we ought to be able to discover some populations that are just beginning to enter upon the process of speciation or are in some stage of divergence that leaves us unable to predict their future.

As I have already noted, humans probably do not live long enough ever to observe a case of speciation from the time that it starts to the time that it is completed (except possibly in rare cases such as some kinds of chromosome doubling). The only way we can study the speciation process directly, then, is through comparing forms that are in different stages of speciation. On the one hand, we examine sibling species, or most closely related species—instances in which speciation has just barely been completed. On the other hand, we study populations that have embarked upon, but not completed, the speciation process.

WHY BELIEVE IN GEOGRAPHIC SPECIATION?

There are several reasons for believing that most cases of speciation occur as a result of *geographic isolation* of populations. Briefly, these are: (1) practically all species today are fragmented geographically to one extent or another; (2) geographically separated fragments of species are often divergent from one another in various characteristics that can be related to species differences in other groups; (3) sibling species rarely have the same geographic distributions; (4) sibling species often differ more where they overlap geographically than where they do not; and (5) the geographic distributions of closely related or very similar species can be related to events such as glaciation, island formation, or the appearance of mountains or river barriers which we know could cause geographic separation between populations.

AN EXAMPLE OF GEOGRAPHIC VARIATION

Recognizing the central role of geographic isolation in initiating speciation, we might locate starts toward speciation by studying variations among geographically separated fragments of a species. In some cases we should expect to find relatively slight differences, and in other cases we ought to find great differences. Our question—and it is a difficult one, indeed—is the extent to which these differences are actually involved in the probability that the populations are developing some kind of reproductive incompatibility, or are proceeding toward speciation.

Let us take an example. One of the seven field crickets that I have just described shows considerable geographic variation across its range. This is *G. fultoni*, the Southern Wood Cricket, which extends from southern Ohio to Texas, northeast through the southern tier of states to about Maryland, and also down the Florida peninsula to the Keys (Figure 8). The closest relative of *G. fultoni* is *G. vernalis*, a highly uniform species all across its range. If one individual of *G. vernalis* were taken from any place in the species' range and placed in the middle of a large number of specimens from anywhere else in the range, you would be unable to pick out that misplaced specimen from the others. On the other hand, *G. fultoni* varies so greatly that, without knowing about what happens between different regions, one could very well believe that individuals put side by side from, say, Ohio and Florida belong to two entirely different species (Figure 1). In the northern part of its range, where it occurs in abandoned fields and prairie fragments, *G. fultoni* is a small brown species with a very fast, regular chirp. In the woodlands of southern Mississippi, Alabama, and Georgia, the same species becomes a large, black cricket, with

an irregular chirp, which lives in the oak-pine woodlands—frequently in fairly lush lowland forests. Perhaps most amazing of all, the males in this southern area climb trees and usually do their calling from six, eight, or ten feet up on tree trunks! This kind of behavior is quite bizarre for field crickets, which are normally surface-dwelling animals, and with rare exceptions it only happens in this particular part of the range of this particular species. There is no good explanation yet for such a strange variation in behavior, but there is no doubt that it exists. My intuition causes me to believe that this is a bona fide case of genetically-based geographic variation, no different from a variation in color, size, shape, song, or any other feature of the phenotype.¹

Additional geographic variation occurs in *G. fultoni* with regard to life history. In the north it is strictly a juvenile overwinterer which matures in the spring, but in northern Florida occasional individuals molt to adulthood in the fall. Consequently, one can hear both spring adults and fall adults in the Florida area. This variation, however, is likely not owing to a genetic difference between Florida and, say, Ohio individuals but to the difference between Florida and Ohio winters.

G. fultoni, therefore, shows geographic variation in ecology, behavior, song and structural features which probably reflects genetic variation. We may guess that these variations are owing to differences in selective action in the different areas in which *G. fultoni* occurs—partly because it has a wide range of distribution and partly because the habitat in which it lives varies across its range. An interesting question is whether the song differences between northern and southern *G. fultoni* are related to the fact that this species lives with its closest relative, *G. vernalis*, in the north but does not live with it in the south. We could reason as follows: if song is an important reproductive isolating mechanism, then one should expect to find not only that (1) species which are adult in the same place at the same time do not have the same song, and (2) some species which are not adult at the same time and in the same places still have the same song, but also that (3) overlapping species are more different song-wise where they overlap than where they do not overlap.

As I have already noted, no acoustical insect species that are reproductively active in the same places at the same times have yet

¹ Every animal and plant can be said to have a *genotype* and a *phenotype*. Genotype refers to the nature of its hereditary materials—its genes. Phenotype refers to the organism itself—the product of the interaction of its hereditary materials with its environment at any stage of development. Evolution depends upon correlation between variations in genotype and variations in phenotype. Such correlations may be extraordinarily complex and indirect, and a good deal of biology is actually concerned with little more than unravelling the connections.

been discovered to have identical acoustical behavior. On the other hand, three pairs of species that do not live together have been discovered to have the same song.

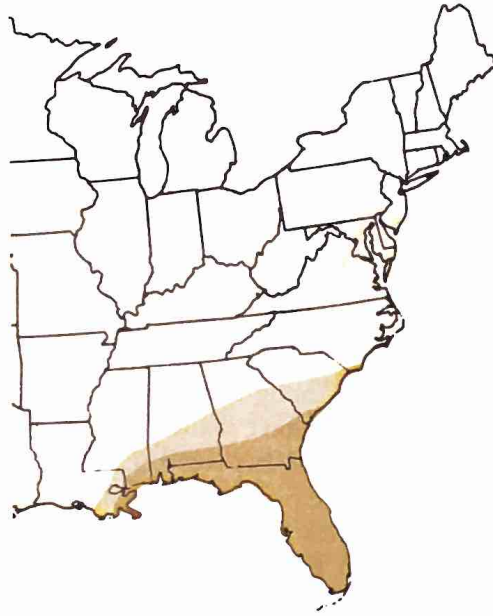
One of these pairs contains the northern spring and fall field crickets, *G. veletis* and *G. pennsylvanicus*, which occur in the same geographic areas but are temporally separated because they mature at different times of the year. All their sounds are identical.

A second case involves *G. firmus* and its close relative on Bermuda, *G. bermudiensis*, which undoubtedly was fragmented from the Atlantic coastal population of *G. firmus* at some time in the past. The calling song of *G. bermudiensis* is very nearly identical to that of *G. firmus*, even though specimens differ morphologically from those of *G. firmus*. We don't know whether these two species would be able to hybridize or not if placed in the same geographic area.

The third case of song identity between species involves the European field cricket, *G. campestris*, which lives in the same general kind of habitat in Europe as *G. veletis* does in North America and has the same life history. Surprisingly, this European cricket also has a song which is apparently not significantly different from those of *G. veletis* and *G. pennsylvanicus*. The basis for this similarity is not clear, but many other similarities among these species, now living on opposite sides of the Atlantic Ocean, make the possibility strong that their song identity dates from a time when European and American field crickets had a common ancestor.

Returning to the question of intercepting speciation, *G. fultoni*, in spite of its deceptive geographic variation, does not seem to represent such a case. Instead, it appears to illustrate how differences may arise between parts of populations that live in different regions in the *absence* of any special barriers. To carry this particular theme a little farther, Figure 14 shows the distribution of *Miogryllus verticalis* (Serville), known as the Little Field Cricket, which has a range similar to that of *G. fultoni*. A rather sudden change occurs in *M. verticalis* in morphology and also in the calling song, in the area of southern Georgia, Mississippi, and Alabama. This is very close to the region where *G. fultoni* changes. *M. verticalis* also occurs in approximately the same kinds of habitats that support *G. fultoni*. We don't know why variation occurs in this particular place in both of these species, but it is possible that a barrier did exist there at some time, causing divergence between northern and southern populations that was not sufficient to cause speciation in these animals. It is possible that some other animal groups will be discovered to have sibling species that overlap where *G. fultoni* and *M. verticalis* undergo rather sudden geographic change.

Figure 14. Geographic distribution of the Little Field Cricket, *Miogryllus verticalis* (Serville), showing a region of sharp geographic variation in song, color, and size.



THE TRUE KATYDID

Now let us turn to another kind of insect which is also very common across eastern North America and which does indeed represent a case of speciation intercepted—intercepted at such a point that it seems impossible to tell at this time whether the different populations involved are going to become more different from one another and more decidedly isolated, or if they will merge and become parts of the same species. The insects involved are usually referred to collectively as the *true katydids* of eastern North America (Figure 15). They are loud, raucous insects that sing from the treetops in almost all the deciduous (non-evergreen) forests of eastern North America. They happen to be the insects that are responsible for the coining of the word “katydid,” which is now the most widely accepted colloquial name for this worldwide family of several thousand species. Apparently their song sounded like this to someone back in the eighteenth or nineteenth century. There is an old tale in North Carolina to the effect that two sisters were in love with the same young man, and “Katy” was the one who didn’t win him. When the young man and the other sister later died mysteriously of poisoning, everyone said that the insects in the trees, by repeatedly announcing that “Katydid!” were accusing Katy of being responsible for the crime. But it seems as likely to me that the name arose as a convenient method of poking fun at some young lady—perhaps at a church supper or some

other kind of evening get-together back in early rural America. There are two groups of true katydids in eastern North America, but those of interest to us here belong in the genus *Pterophylla* (“leaf-wing”). In eastern North America, all the katydids in this genus are currently referred to under the name *Pterophylla camellifolia*. Apparently, Johann Sebastian Fabricius, a student of Linnaeus who named this species back in 1775, thought that the wing is not only like a leaf but more specifically a camellia leaf.

Figure 15. Katydid.



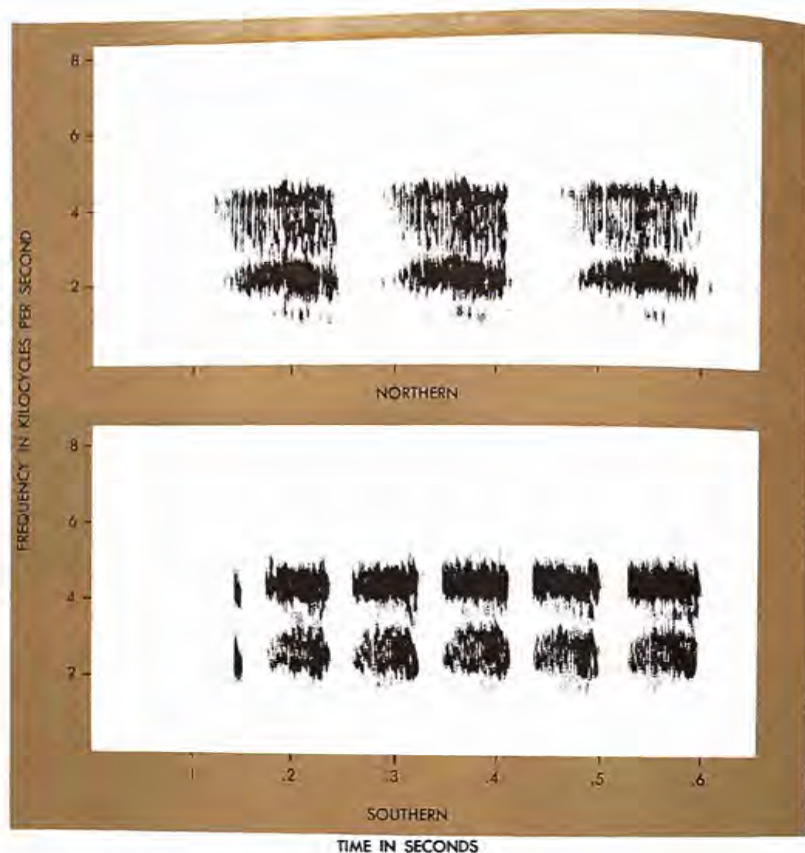


Figure 16. Audiospectrographs of phrases from the calling songs of the northern and southern katydids.

Because these katydids do not have functional hind wings (flying wings), they are much more frequently heard than seen. They live only in the tops of the taller trees and are almost never seen on the ground. Consequently one usually has to climb a tree to collect them. For these reasons, in spite of their wide distribution and loud, noticeable songs, there never have been very many of them in the entomological collections of North America.

The first time that I crossed the Appalachian Mountains after I had begun to study the singing insects of North America, I was aware of a change there in the nature of the song of the true katydid. On the northwestern side of the Appalachians, the song was a slow, two- or three-pulse phrase which I could easily paraphrase as "Katy" or

"Katy-did." On the southeastern side of the Appalachians, however, the sound had become a very rapidly delivered "Katy-she-did-she-did, Katy-she-did-she-did"—a five-, six-, or seven-pulse phrase (Figure 16).

My curiosity was aroused by this discovery, and I wondered how and where the song change took place. Was it a gradual change, geographically, or did the individuals with the two kinds of songs overlap somewhere and live together in the same woods? Because true katydids sing only at night, it would be necessary to travel at night through the mountains, listening to the katydids, and stopping to make tape recordings for further comparisons whenever a change seemed to occur.

A complicating factor was that the song of the katydid changes with the temperature in some of the same ways that the northern and southern katydids differ from one another. For example, when it is very cold in the mountains, a southern katydid with an unusually short phrase sometimes sounds like a northern katydid with an unusually long phrase. Although this is confusing to a human listener, it probably doesn't trouble the insects themselves. Dr. Thomas J. Walker has shown that in tree crickets when a male is cold and sings slowly, the female is also cold and responds only to the cold song of her own kind of male. In the case of the katydids, we still don't know if the song difference between populations is significant to the insects themselves, but we can be fairly certain that the temperature response is similar to that in tree crickets.

My initial discovery of the location and nature of the song change between northern and southern katydids took place at Droop Mountain Battlefield State Park in Greenbrier County, West Virginia, and this caused me some unnecessary confusion. In that particular locality, I discovered that the song change of northern and southern katydids took place gradually and slowly across a distance of about a mile, meaning that there must be hybridization between the two kinds of katydids. But the confusing thing was that no matter what direction I drove from Droop Mountain, there was a slow and gradual change from northern song to southern song! Later, we discovered that the northern katydids living on Droop Mountain belong to a colony that happens to be on the "wrong" side of the mountains and, therefore, is completely surrounded by southern katydids and interbreeding in all directions with them. This turned out to be a unique situation, but because of the confusion resulting from my encountering hybridization first in this particular place, my analysis of this situation was delayed several years.

Subsequent to these initial discoveries, Mr. Kenneth C. Shaw, a graduate student, and I discovered that the change from northern

katydid song to southern katydid song, except for the Droop Mountain oddity, occurs in a line extending from just south of New York City, west to Harrisburg, Pennsylvania, then south along the Appalachian Mountains west of Droop Mountain to western Georgia, and then through Alabama to the Gulf Coast in western Florida between the Choctawhatchee and the Apalachicola Rivers (Figure 17). Still later we discovered that the katydids in Louisiana and Mississippi are different from both the southeastern and the midwestern katydids. In other words, there are really three populations of katydids, which interbreed along a Y-shaped zone as shown in Figure 17. For the purposes of this discussion, however, I will only describe the hybridization which takes place across the Appalachian Mountains. This zone is a very remarkable one. In some places it is several hundred miles wide, and in others it is so narrow that one can stand in the middle of a road or in a stream bed and hear northern katydids on one side, southern katydids on the other, and a few hybrids in trees between them. In some parts of the Appalachians, northern and southern katydids do not meet at all because beech-birch-maple forests in which they cannot live persist directly between them. It seems likely that katydids were completely separated during some earlier period, and this isolation allowed the song divergence to take place.

Not only a song change but also a change in the structure of the male genitalia occurs in the Appalachian area. The strong likelihood that these two characters (song and genitalia) are based on independent variations in the genetic material (because they involve such different aspects of the phenotype) indicates that this is, indeed, a hybridization zone between different kinds of katydids.

The nature and location of this zone was traced very quickly by an unusual method never previously used for this kind of work. As I have emphasized before, these katydids are difficult to capture, so difficult that two collectors with nothing else in mind may spend an entire night capturing only three or four individuals. Females are not even represented in most collections because they don't sing and are almost impossible to find. All of the collections in all the museums in the world contain only a few hundred males. Yet in order to trace out the zones of hybridization shown in Figure 17, we had to sample the characteristics of literally hundreds of thousands of individuals. We did this by traveling at night up and down the Appalachian Mountains with tape recorders.

The main trip began in the area of Harrisburg, Pennsylvania, and extended almost to the Gulf Coast. During this trip we drove slowly through the mountains threading our way back and forth, beginning in a region of northern katydids, driving southeastward until we had



Figure 17. The area shown in color is the katydid-hybridization zone. Note the small circular zone in West Virginia, the Droop Mountain area.

crossed to the southern katydids, and then turning around on another road and driving back. Mileage was carefully marked on a detailed topographic map (one showing contours and landmarks) so that we would know exactly where we had been, precisely how wide the zone was, and how suddenly the intergradation in song took place.

In some cases we tape-recorded the songs of the katydids all the way across the zone of hybridization by walking along the road and pointing the microphone, fastened inside a parabolic reflector or "sound-gathering" device (Figure 2), at all the katydids in all the trees. These "transects" sampled almost the entire population in a way that has probably never been accomplished with any other kind of animal.

As already indicated, the song differences between northern and southern katydids comprise two sorts. First, there is a difference in "wingstroke" rate which produces the difference in pulse rate within phrases; and second, there is a difference in the number of "wing-strokes" per phrase or pulses per phrase (Figure 16). Both characteristics vary gradually in the zones of hybridization.

THE NATURE OF THE HYBRIDIZATION ZONE

Now let us examine in some detail the location and nature of the zone of hybridization from Harrisburg to the Gulf Coast. Perhaps we should begin in the Monongahela National Forest, located in the central Appalachians in Pocahontas County, West Virginia. In this

area there is in the high mountains a 20-mile strip of beech-birch-maple forest which true katydids do not inhabit. On one side are the southern katydids and on the other side, the northern katydids. As I have already said, at one point—Droop Mountain Battlefield State Park—there is a small population of northern katydids on the southern side of this “inhospitable” forest. How they got there is unknown, but human transport may have been involved. Aside from this unique situation, the two kinds of katydids are still completely separated from one another in this general region—and only in this region. Because strips of beech-birch-maple forest extend northward in the Appalachians, we must expect that only in scattered places do the northern katydids and southern katydids meet—through breaks in this inhospitable forest. Just south of Pocahontas County—in Greenbriar County and other more southern counties—the two kinds of katydids do meet, and there the zone of hybridization is extremely narrow.

Whenever a wide river such as the Susquehanna River in Pennsylvania or a forest such as the beech-birch-maple forest in Pocahontas County provides a barrier, this is called a *pre-civilization barrier*, one which we may assume has existed since before the katydids reached this region. In these cases the katydids on each side are usually pure northern and pure southern, with no evidence of interbreeding. There are some exceptions, however. I have already mentioned one in connection with Droop Mountain Battlefield State Park. Similarly, at a narrow place in the Susquehanna River above Harrisburg, we discovered that a small population of the southern katydids has somehow got across to the west side of the river and formed a small peninsula of southern katydids, extending into the northern katydid population and intergrading with it.

Whenever inhabitable forest is cleared, the katydid population is also destroyed; and whenever a forest that was cleared in the Appalachian Mountains happened to lie in the zone of hybridization between northern and southern katydids, a *post-civilization barrier* between northern and southern katydids was erected. We found several such cases. If the field happened to be cleared at just the right place, one finds pure northern katydids on one side and pure southern katydids on the other side; but if the cleared zone was a little to one side or if the zone of hybridization was wider than the cleared field, then only a little influence of the pre-clearing interbreeding might show on one or both sides.

In the southern Appalachians, the northern and southern katydids have apparently been in contact for a much longer time, and their zone of hybridization is several hundred miles wide. Still farther south, however, in Alabama and Florida, the zone of hybridization

becomes narrow again. Near the small town of Marianna, Florida, it is only a few miles wide. Actually there is even less hybridization in this area than this narrow width of the zone would suggest. It is important to understand the reason for this, if we are to predict whether these katydids are likely in the future to become separate species or to merge. These particular katydids can rarely survive in lone trees, except in very large ones such as sometimes occur around farmsteads and residences in the eastern United States. In the region where the hybridization zone approaches the Atlantic coast near New York City, there is so much human habitation that one finds very few katydids. Here it is almost impossible to discover what the zone of hybridization was like before civilization. There is very little hybridization in this location because we have created a barrier between the remaining northern and southern katydids by clearing the land and building cities. In the southern part of the hybridization zone (in northern Florida) there is also very little interbreeding because the uplands are covered with pine trees, which are completely unacceptable for katydids. This means that in this region there are only two kinds of areas where katydids can exist: moist stream bottoms where deciduous trees line the creeks and rivers and around residences and along roadsides where people have purposely left deciduous trees. As a consequence, northern and southern katydids hybridize in northern Florida only where the tributaries of the Apalachicola River flowing eastward approach near their headwaters the headwaters of westward flowing tributaries of the Choctawhatchee River.

WHAT WILL HAPPEN TO THE KATYDIDS NOW?

Even though there is a wide zone of hybridization between northern and southern katydids in the southern Appalachian Mountains, it is still possible that the growth of human populations will so reduce the interbreeding between these two populations that they will again take up the path of divergence—towards speciation—upon which they undoubtedly embarked once, a long time ago. When did they start on this path? How long were they apart? Which of the characteristics by which they now differ might be important factors in their remaining apart, and which ones will be unimportant? Are there any intrinsic (genetic) differences between northern and southern katydids now which are making it disadvantageous for them to hybridize?

These are still questions we cannot answer completely. We don't know yet if the song differences are significant to females. We don't know whether the hybrids have any advantage or disadvantage. It would seem that the last time the Appalachian Mountains could have

been a barrier to katydids would have been when the climate in this region was affected by the advances of ice in the Pleistocene epoch, about ten thousand years ago. Does this mean that these katydids, which apparently have a life cycle of either one or two years, require more than ten thousand years to speciate? It seems possible. At any rate, this is certainly one case of speciation intercepted, and one that gives us some clear starts toward understanding how species are formed by geographic isolation and divergence of populations.

My studies of several hundred species of singing insects in North America have so far revealed only one case like this—populations meeting and reacting to one another in such a way that we honestly cannot predict whether they are going to continue to diverge and become two different species or amalgamate and form a single one. This might cause us to wonder if speciation is proceeding at a very slow rate at this particular time in history. But the speciation rate is a function of two things: the number of isolated populations and the rate of change (and therefore divergence) in the isolated populations. It is possible—even probable—that certain times in geological history were considerably more favorable to speciation in North America than is the present. For example, during the Pleistocene epoch, when populations were not only repeatedly and continually isolated by the effects of the advances and retreats of the glaciers but also subjected to extreme conditions under which selective action must have caused wholesale annihilation and rather rapid evolutionary change, speciation must have occurred at a much faster rate than now. Otherwise there does not seem to be any compelling reason to believe that this moment in history is one of slower speciation than any other.

There is another aspect to the question of what is going to happen to true katydids—one which clearly illustrates how complicated the problem of isolation and its effects can be. Not only do we reduce gene exchange between northern and southern katydids as we continue to clear forests and build houses, but we also reduce gene exchange between individual populations *within* both the northern and the southern katydids! Will this lead to eventual extinction or possibly to the production of a whole host of separate species? It does not seem likely that we will create a more effective barrier in the Appalachians than elsewhere. The future of true katydids is much more difficult to predict, even, than it would seem.

To return to the problem of the infrequency with which we find cases of “partially completed” speciation, there are still other ways of looking at it. First, consider the great similarities between many sibling species that live together. Some populations which are isolated geographically now and are considered to be parts of a single species

because they are so much alike may be divergent enough that when and if they ever come together they will not merge. Instead, they will begin to develop more efficient reproductive isolation and thus prove to be distinct species. Such might be the case, for example, with the populations of *G. fultoni* on Key Largo, Florida; Hunting Island, South Carolina; Tybee Island, Georgia; or Ossabaw Island, Georgia.

Second, it is possible that the time of interaction between populations which have just come back together geographically, during which we would be unable to predict outcomes, is usually so brief that at any one time in history there are few of these cases to be examined. In other words, it is possible that the evolutionary “decision” is usually made quickly as to whether or not hybridization is disadvantageous between two populations that have just started living together again. This would be the case, for example, if any tendency not to interbreed upon initial contact had a quick reinforcing effect on the reasons for that tendency. If the first crop of hybrids was at a great disadvantage, the suppression of crossbreeding could happen quickly. Conversely, if hybrids were not at any disadvantage, amalgamation might occur quickly. My saying these things in a speculative way reflects our ignorance concerning this question.

The case of the true katydid reveals that nothing short of extensive and intensive field study can answer the questions we must answer to understand speciation—particularly in view of (1) the complex factors involved in analyzing the effectiveness of the geographic and ecological barriers between katydids at the two ends of the zone of hybridization, and (2) the wide variation in the width and nature of the zone of hybridization.

SPRING AND FALL FIELD CRICKETS: A NEW METHOD OF SPECIATION?

I indicated earlier that geographic isolation of populations is one of the most important ways that speciation is initiated or caused. Actually, this remark can be made stronger: geographic isolation is the *only* method widely acknowledged among biologists today to account for speciation. Some evolutionary zoologists believe that the process of speciation always occurs in this fashion in sexually reproducing animals. Others simply do not believe that any of the alternatives so far proposed represent better explanations than geographic separation.

Here I am going to describe for you a case which Dr. Robert S. Bigelow (now of Christ College, Auckland, New Zealand) and I

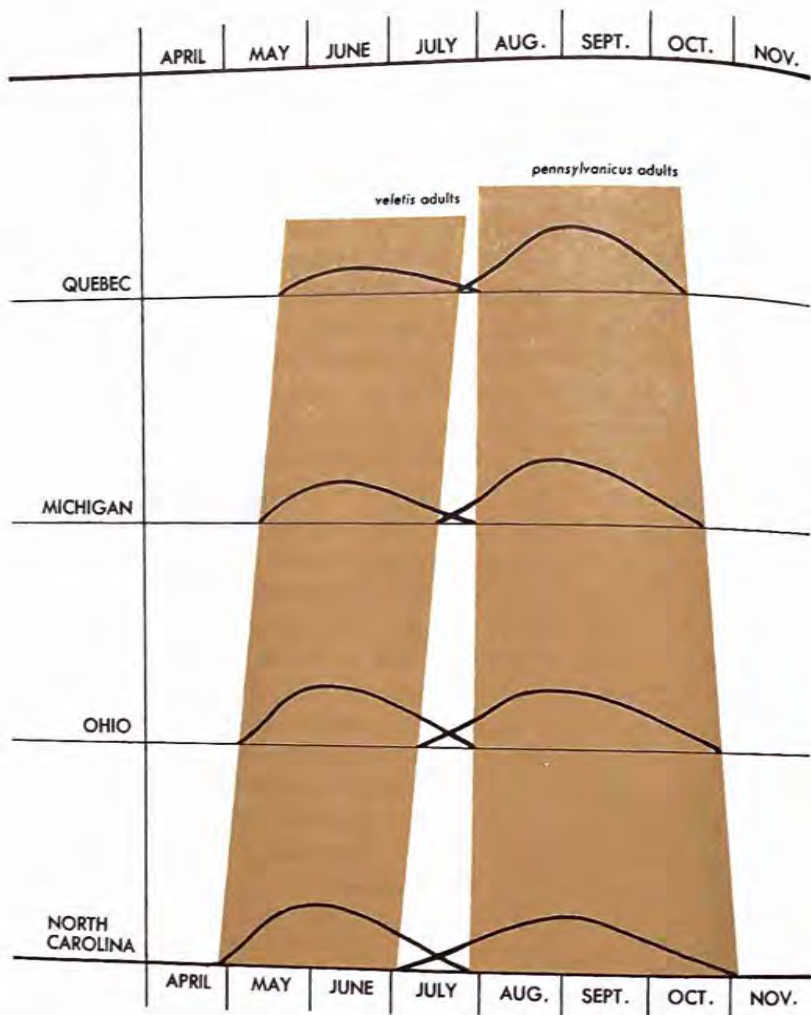


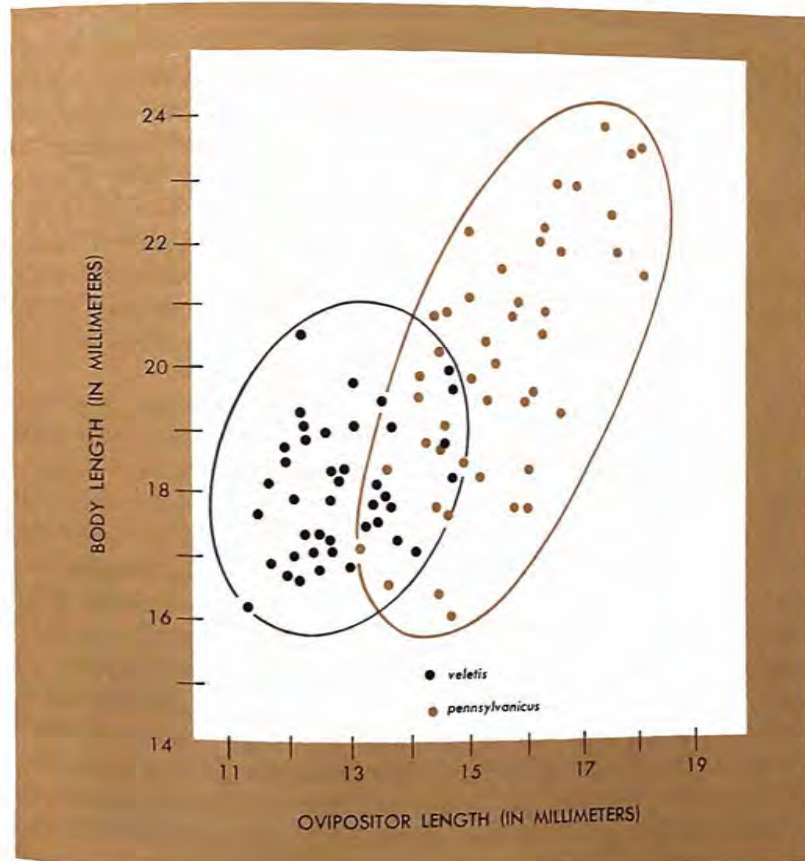
Figure 18. Seasonal relationship of the adult populations of *Gryllus veletis* and *Gryllus pennsylvanicus*.

believe represents speciation by *temporal* rather than by geographic or *spatial* isolation. I must preface this story by telling you that only a few zoologists have yet accepted our hypothesis. I present it as an example of the kind of unusual, new phenomenon that can be uncovered in the analysis of common, widely distributed, and seemingly well-known animals.

You may remember some peculiarities of one of the pairs of field-cricket species that I described. *G. veletis* and *G. pennsylvanicus* are

two extremely similar species, each of which has a one-year life cycle. However, *G. veletis* overwinters two molts from adulthood and matures in the spring, chirping from mid-May until mid-July. *G. pennsylvanicus*, on the other hand, overwinters as an egg and matures in mid-July, taking up just as *G. veletis* is leaving off and chirping until frost (Figure 18). The songs of these two species are identical, so far as we have been able to tell. The two species look exactly alike, except that females of *G. pennsylvanicus*, the egg-overwintering species, have longer ovipositors and apparently deposit their eggs a little deeper in the soil. This difference is not complete enough, however, to separate all the females of one species from all the females of the other (Figure 19).

Figure 19. Ovipositor and body-length ratios in *Gryllus veletis* and *Gryllus pennsylvanicus* females from a single locality in Michigan



You may say: How do you know, then, that they are different species? In this case the answer is also unusual. These two very similar species are unable to produce hybrids under any circumstances—even if we juggle their life cycles in the laboratory so that they are mature at the same time, and even if we put together great numbers of males of *G. veletis* with females of *G. pennsylvanicus*, or vice versa. Like the difference in life history, this is a peculiar circumstance for such similar species. And there is still a third peculiarity: these two siblings have almost identical geographical ranges, with the exception that *G. pennsylvanicus*, the egg-overwintering species, extends a little farther north in Canada and occurs in Nova Scotia where *G. veletis* does not (Figure 8).

The uniqueness of the relationships between *G. veletis* and *G. pennsylvanicus* caused Dr. Bigelow and me to believe that these two species may have been formed as a result of some process other than initial geographic separation, or "allopatric" speciation.

A third species assisted us in the development of this hypothesis, a species which seems to be most closely related to *G. pennsylvanicus* and *G. veletis*. This species is *G. firmus*, the Sand Cricket, which occurs principally on the beaches of the Atlantic and Gulf coasts but also inland in some sand hills extending from North Carolina to Georgia (Figure 8). In southern Florida and Texas, this species breeds continuously—that is, there are adults the year around. From North Carolina south to northern Florida and west to northern Texas, however, most individuals overwinter as eggs, with a small proportion overwintering as juveniles. As a result, *G. firmus* produces both spring and fall adults in most of the northern parts of its range, each belonging to a population which has a one-year life cycle.

It is obvious that a cricket which matures in the spring cannot interbreed with a cricket which matures in the fall unless they overlap temporally. There would have to be sufficient overlap for females from the spring population to be sexually responsive until males of the fall population were ready to mate, or, vice versa, males of the spring population would have to live long enough to overlap the onset of sexual responsiveness in females of the fall population. Male crickets don't live as long as the females, and the males also mature a little ahead of females. Thus we would expect interbreeding of "spring" and "fall" species to be between spring females and fall males.

Such interbreeding can't happen with *G. veletis* and *G. pennsylvanicus* at the present time because, of course, they cannot hybridize. We have not yet found the reason for the inability of these two species to hybridize, but it seems significant in our hypothesis. Of the thirty-five cases of hybridization that have been attempted between

species in this genus—involving seventeen species from several different parts of the world—there have been only four complete failures. Two of these have involved two pairs of species in eastern North America that have differences in their overwintering stage—*G. rubens* and *G. pennsylvanicus*, in addition to *G. veletis* and *G. pennsylvanicus*. As a result, we believe that some kind of special incompatibility is associated with the development of overwintering hardiness in different stages.

An additional factor that appeared as we searched among the crickets for evidence concerning this hypothesis was that, except for mole crickets which live underground almost entirely, there are only two overwintering stages among all crickets all over the world. One of these is a juvenile stage, a molt or two from adulthood, and the other is the egg stage. Overwintering of the egg stage is easy to understand. Besides being buried in the soil, insect eggs are protected, hardy life-stages. The juvenile stage at first seemed more difficult to understand, but then it occurred to us that this stage is also buried in the soil, for the juvenile begins to dig its shallow burrows, and to spend time in the burrow, about two or three molts from adulthood. The juvenile is as protected from the winter as the egg, for it is in a burrow several inches deep.

The adult also lives in a burrow—or at least the males do—while the females rove about and locate the more or less stationary males by their songs. Why shouldn't adults overwinter? The adult, however, only lives about thirty days; and if an individual started a northern winter as an adult, it is very unlikely that it would live through to the spring unless it could develop a special diapause, as have nearly all overwintering stages of northern insects. Only rare species among crickets and their relatives overwinter as adults, and these are always southern or subterranean species.

In any area where there are inhospitable seasons, such as winter, the short adult life of an insect species must be synchronized with climatic conditions if efficiency in reproduction is to be maximized. For example, if there were no special method of synchronizing the appearance of adults in an insect, such as crickets, in which the adult stage lasted only about thirty or forty days, then only a small number of adults would be present at any particular time during the year. Thus it would presumably be more difficult for a high proportion of them to find mates. As the species would also have to maximize winterhardiness in many different stages, it is not difficult to see why the appearance of diapause stages would be expected in every species that lives where there are severe winters. Even in regions where severe winters do not occur, there is some timing of the life cycle among

insects with short-lived adults, based on such events as dry and wet seasons.

We still don't know why field crickets have a dual winterhardiness, but it is interesting and significant that they do. The two hardy stages are located in time on completely different "sides" of the life cycle. That is, the time required to go from the juvenile stage of a cricket to the egg stage of its offspring is about the same as that required to go from the egg stage to the juvenile stage in one individual. This is why, among species with a one-year life cycle, there can be spring adults and fall adults that are temporally isolated from each other.

Our hypothesis for temporal speciation in field crickets can be summarized as follows. We believe that the ancestor of *G. veletis* and *G. pennsylvanicus* extended either northward or southward into an area of mild winters such as now occur in the sand hills from North Carolina to Georgia. We think that in this area there were populations broken off from the major part of the species, which extended into Florida where there was breeding the year round, and that at least some of these fragments continued both the spring and the fall-maturing components of the northern population.

If both life-cycle components persisted successfully in such a region, it would be possible for them to be temporally isolated for an indefinite period of time before they became different enough that they couldn't hybridize with one another. Even if they lived in exactly the same places during this time, they wouldn't be able to hybridize very much—perhaps not at all—because the adults would be seasonally separated. While they were temporally isolated, the two populations would undoubtedly diverge from one another in just the same way that two geographically isolated populations would diverge. Furthermore, their developing what we call *obligate diapause*—an inescapable period of suspended development—in their two different overwintering stages (which would increase the proportion of individuals in each of the two populations entering the winter in the hardest stage) would cause them to diverge even more rapidly. Since *G. veletis* and *G. pennsylvanicus* and other species with different diapause stages cannot hybridize, this particular diverging (or "disruptive") selection may have been keyed to an incompatibility, and as a result to accelerated speciation.

In short, we believe that *G. veletis* and *G. pennsylvanicus* may have speciated without any geographic isolation because (1) crickets have a double winterhardiness, which tends to temporally isolate populations within a species like *firmus* where the species extends into a northern climate, (2) *G. veletis* and *G. pennsylvanicus* present the

unusual picture of sibling species with nearly identical ranges and habitats but with different life cycles, (3) differences in overwintering stages seem to be tied to reproductive incompatibility, and (4) *G. firmus*, *G. pennsylvanicus*, and *G. veletis* have certain geographic and phenotypic relationships.

Although it is necessary to separate a northern fragment of *G. firmus* from the continually breeding populations farther south to bring about this kind of speciation, the geographic separation itself would not be directly involved in the speciation if the northern fragment contained both the spring and the fall components. It happens that *G. firmus* shows between Florida and North Carolina both the postulated geographic variation in seasonal life history and the postulated geographic separation of a northern component. We are studying this species in the field and under different temperature and photoperiod regimens in the laboratory to determine how many geographic fragments have both life cycles and if there are the beginnings of both egg and juvenile diapause in these populations. Our object is to keep crickets taken from both life cycles under identical conditions of temperature, humidity, and day length and to see if any evidence of genetic difference between them can be detected—for example, differences in length of the egg or juvenile stages. In addition, the questions brought up by this case have caused us to start a systematic review of sibling species all through the insects. Life histories, diapause relationships, and geographic distributions are clues that will help us determine the extent to which *allochronic* speciation, or speciation by temporal isolation alone, may occur in this very large group.

17-YEAR AND 13-YEAR CICADAS: A UNIQUE PROBLEM IN SPECIES ORIGINS AND INTERACTIONS

So far I have illustrated a variety of things related to speciation and used several groups of crickets and katydids to do so. We have seen how alike sibling species can be, what kinds of characteristics can be expected to be most different between them, how they manage to live together without gross inefficiency, what kinds of geographical and seasonal relationships they may have to one another, and how one can discover them in the first place. We have examined the phenomenon of geographic variation, both in instances where it appears to have no relationship to specification and in instances where it appears to reflect a previous geographic separation that almost resulted in speciation, or may still result in speciation. We discussed geographic separation (allopatry) as being nearly always the initiator of specia-



Figure 20. Left: the 13-year cicadas. In each pair the female is at the left—(top) *tredecula* Alexander and Moore; (center) *tredecassini* Alexander and Moore; (bottom) *tredecim* (Walsh and Riley). Right: the 17-year cicadas—(top) *septendecula* Alexander and Moore; (center) *cassini* (Fisher) (bottom) *septendecim* (Linnaeus).

tion and the possibility that allochrony might also cause the divergence of populations of some kinds of animals. We have talked about the kinds of characteristics which seem to diverge while populations are still separated and the kinds which diverge only after intrinsically different populations come back together and begin to interact.

"MAGIC" CICADAS

One group of singing insects in eastern North America is unique because it illustrates all these different phenomena in one way or another. This is a group of cicadas belonging to the order Homoptera. Cicadas are insects with sucking mouthparts instead of the chewing kind of mouthparts that katydids and crickets possess. Juvenile cicadas live underground, sucking juices from roots, and the adults are flying, noisy insects which characteristically sing in the daytime, in contrast to the chiefly nocturnal singing of crickets and katydids.

There are about 165 species of cicadas in North America. The group that is discussed here contains only six species. All of these are members of a single genus that William T. Davis, of the Staten Island Museum, named *Magicicada* because of the incredible life history of its members.

Until very recently it was believed that there was only one species of *Magicicada*, and in college and high school biology classes all over the United States, films and lectures were presented on the story of *The Periodical Cicada*. The discovery by Dr. Thomas E. Moore and me that there are actually six species, living together in a fashion otherwise unknown anywhere in the animal kingdom, makes the story so much more complex as to be almost unbelievable.

Three of the six species of *Magicicada* require seventeen years to mature, and the other three require thirteen years (Figure 20). The juveniles spend all this time beneath the ground before emerging to molt to adulthood on tree trunks; this is the longest period of sexual immaturity known in any kind of animal. The adults emerge in the month of May and live only about thirty days, which is a very short period in proportion to the total life span—equivalent to about two days in an insect with a one-year life cycle. By the first of July, they have laid their eggs and died. The eggs hatch in August and September, and the juveniles drop to the ground and burrow, there to remain for another thirteen or seventeen years. This amazing life cycle is so rigid that the 17-year cycle had been verified as early as 1633 by the New England settlers, and the 13-year cycle by the early nineteenth century in the South.

The range of 17-year and 13-year cicadas extends from New England south to northern Florida, west to Louisiana and eastern Texas, north to Wisconsin, and east through southern Michigan (Figure 21). Interestingly, this is about the same distribution that the katydid, *Pterophylla camellifolia*, has, including all of its geographically varying populations. In the southern part of this range, all of the cicadas in this group are 13-year cicadas, while in the northern part, all have 17-year life cycles.

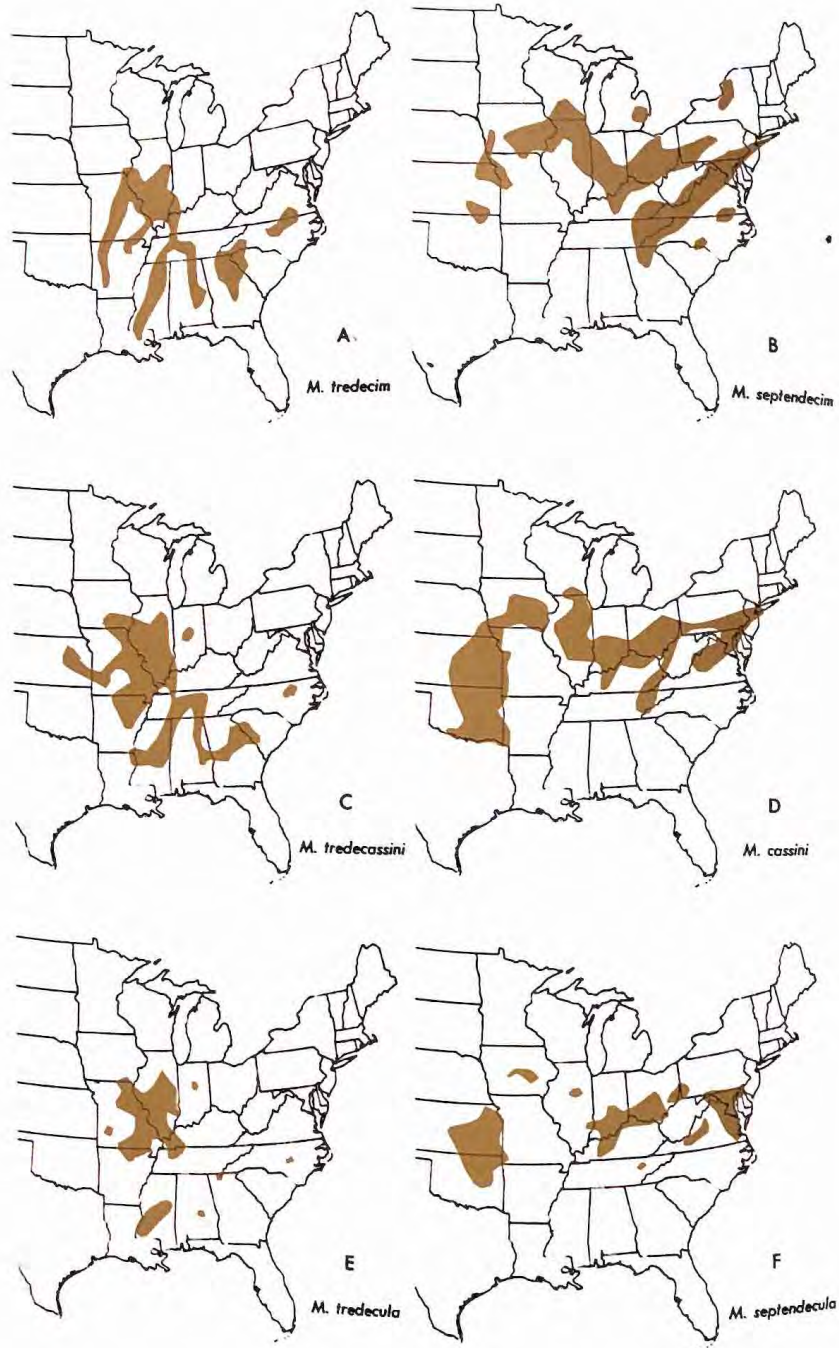


Figure 21. Overall distribution of 17-year and 13-year cicadas—all broods combined.

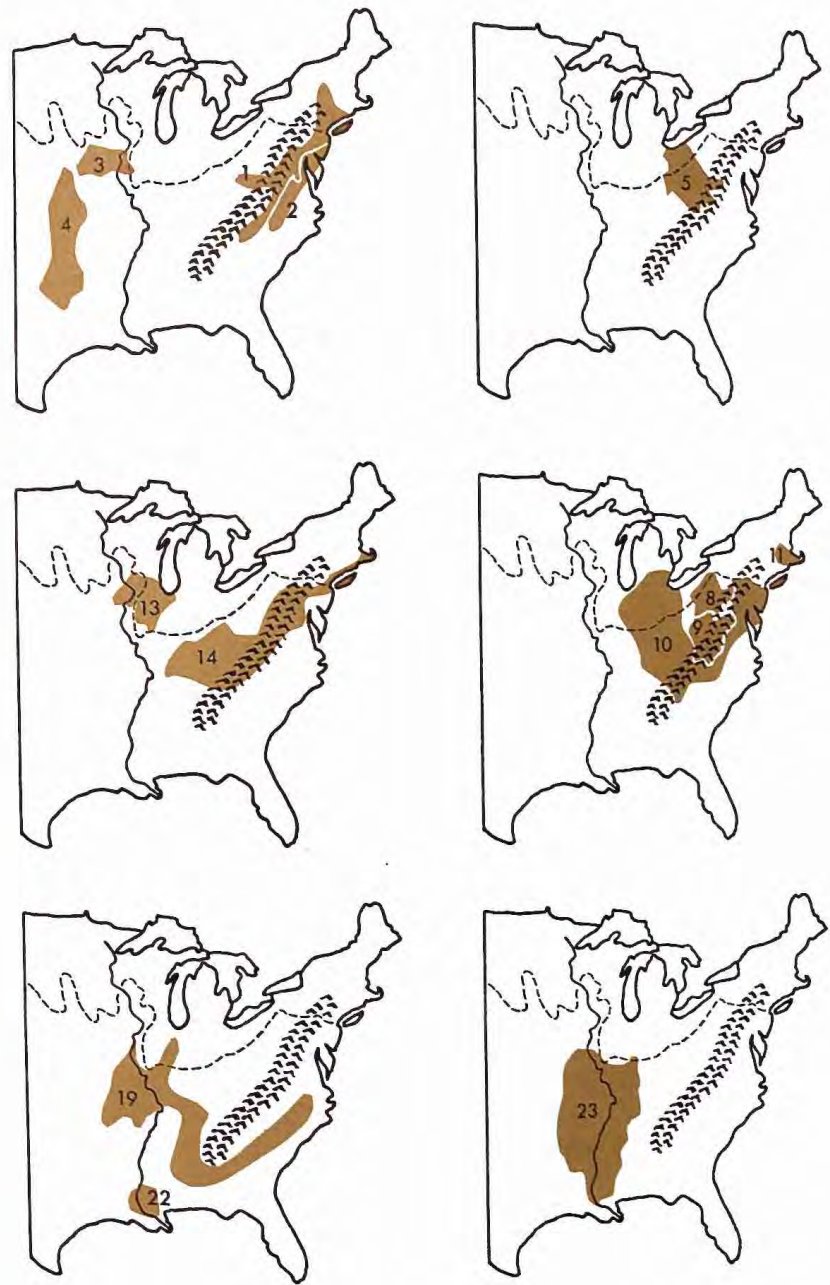


Figure 22. Approximate distributions of major broods of 17-year and 13-year cicadas. Dashed lines represent approximate limit of Wisconsin glaciation.

Within both northern and southern regions there are several different broods of cicadas, which appear as adults in different years. Almost every year there are 17-year or 13-year cicadas, sometimes both, emerging somewhere in the United States. These broods that emerge in different years, of both 17-year and 13-year cicadas, became separated from each other in an unknown fashion some time in the past. Obviously, the different broods are now not only temporally isolated from one another but also, to some degree, geographically isolated, except for the rare instances when off-year "stragglers" provide opportunity for hybridization between broods. The numbers of these stragglers are very low at the present time, and because large broods almost never come out in successive years in the same locality, the chance of their bridging the gaps between broods is almost nonexistent. There must have been more straggling in the past to allow the development of the different broods, but at the present time, such interbreeding is either rare or completely absent. In typical large emergences, adult cicadas are so thick that in cities one can sweep them up by the bushel beneath street lights, and the trunks and branches of trees in the forest are literally covered with them. Yet in the preceding and following years, one is likely to see and hear no cicadas whatsoever in the same regions—or he may hear just one or two individuals calling for a few days. From this, and from the brood distribution maps, one can also see that the 17-year and 13-year cicadas are largely separated geographically, and the different broods within each of them are isolated both geographically and temporally from one another (Figure 22).

Finally, it is necessary for us to describe the relationships among the three species within each of the two life-cycle groups of *Magicalcicada*. Each major brood of 17-year cicadas and each major brood of 13-year cicadas has three species within it. The individuals of these three species are mixed thoroughly, both as juveniles and as adults. They have slight differences in their ecological distributions, so that an occasional dry woods may lack one species and an occasional damp lowland woods may lack another, but, in general, all three species are found together across most of the range of each brood. They emerge as adults at the same time of year, usually precisely together, although in some places there may be slight differences in the proportions of species emerging on successive days. There are no temporal or geographic differences among the species, on either a yearly or a seasonal basis, that do not overlap.

DIFFERENCES IN ACOUSTICAL BEHAVIOR

There are definite differences in the behavior of the three species

that live together in each brood. One of our first discoveries was that there is no cross-mating between them. This was confirmation, following discovery of song differences and then color, genitalic, and overlapping size differences among them, that they are indeed different species.

Acoustical behavior is perhaps the principal item in our attempts to examine what the relationships are among the species and how the species came to be the way they are. First, the periodical cicada males produce four sound signals (Figure 23). These are (1) the *calling song*, produced either by individuals or in chorus to activate and assemble both males and females; (2) and (3) two *courtship songs*, produced by the males near the females just prior to copulation; and (4) what we call a *disturbance squawk*, made when an individual is held or captured or disturbed into flight. The function of the disturbance squawk is not yet known, but it may sometimes cause predators to release cicadas. It may also cause other cicadas to fly when one individual is captured by a predator. The courtship song either shortens the time necessary for copulation to take place after a male and female have met, or it may facilitate copulation in some cases where it could not occur without the courtship sound. But these possible functions have not been tested experimentally.

EXPERIMENTS WITH SONG FUNCTION

Some experimentation has been done on the calling or *congregational song*. This sound functions in quite a different way from those of the crickets and katydids that we have been discussing.

There are two general methods by which pair formation may occur as a result of acoustical behavior in crickets, katydids, and grasshoppers. The first and most common is that the male simply stays in one spot and produces the sound continually during certain periods of the day or night. The females are active during that period and are attracted to the male's sound, especially since it is a stationary target. Females can locate individual males across considerable distances, even if it requires two or three nights to reach the male.

The second method, common in many katydids and most grasshoppers, is that both the male and the female are capable of making noises. The male first makes a noise which causes the female to make a noise. When the male hears the female, he changes to a second noise and moves to the female, who keeps replying to his sound and in this way enables him to locate her. In these kinds of species, the males that are producing sound and are sexually responsive move around while singing. This is a contrast to the instances where the male stays in one location and attracts the females.

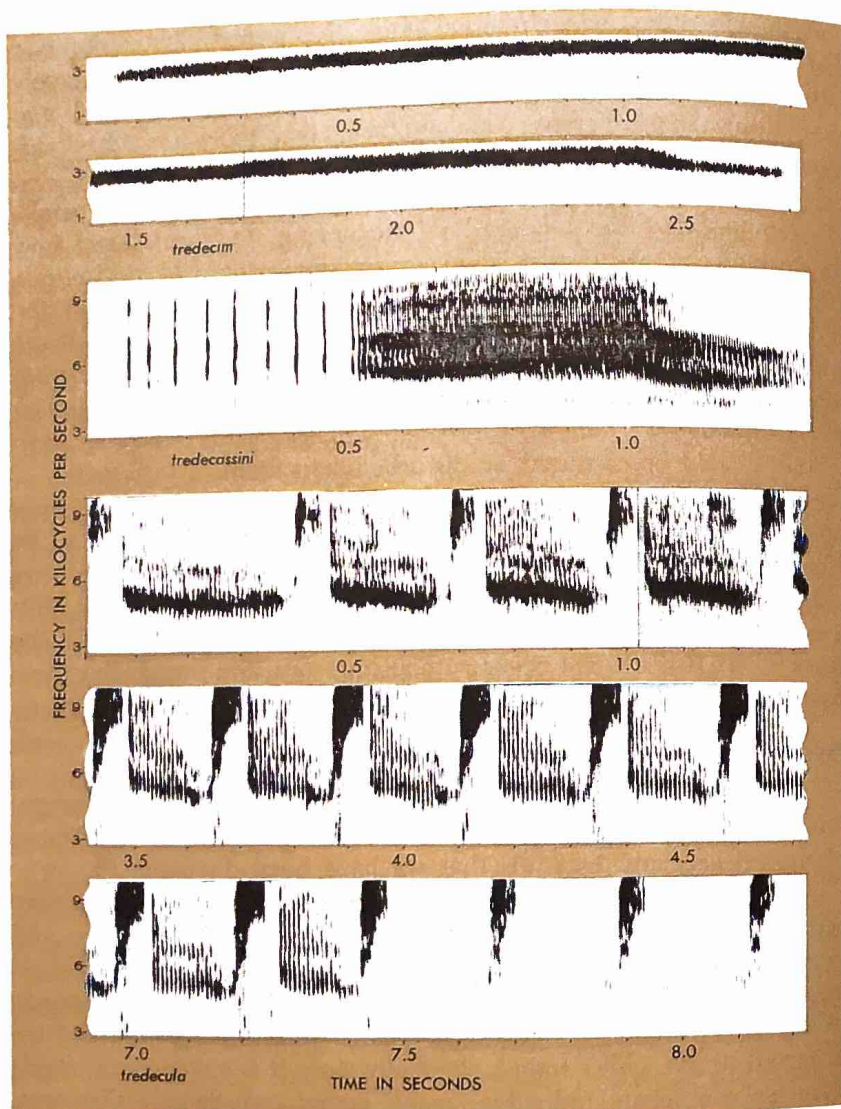


Figure 23. Audiospectrographs of the acoustical signals of the 17-year and 13-year cicadas.

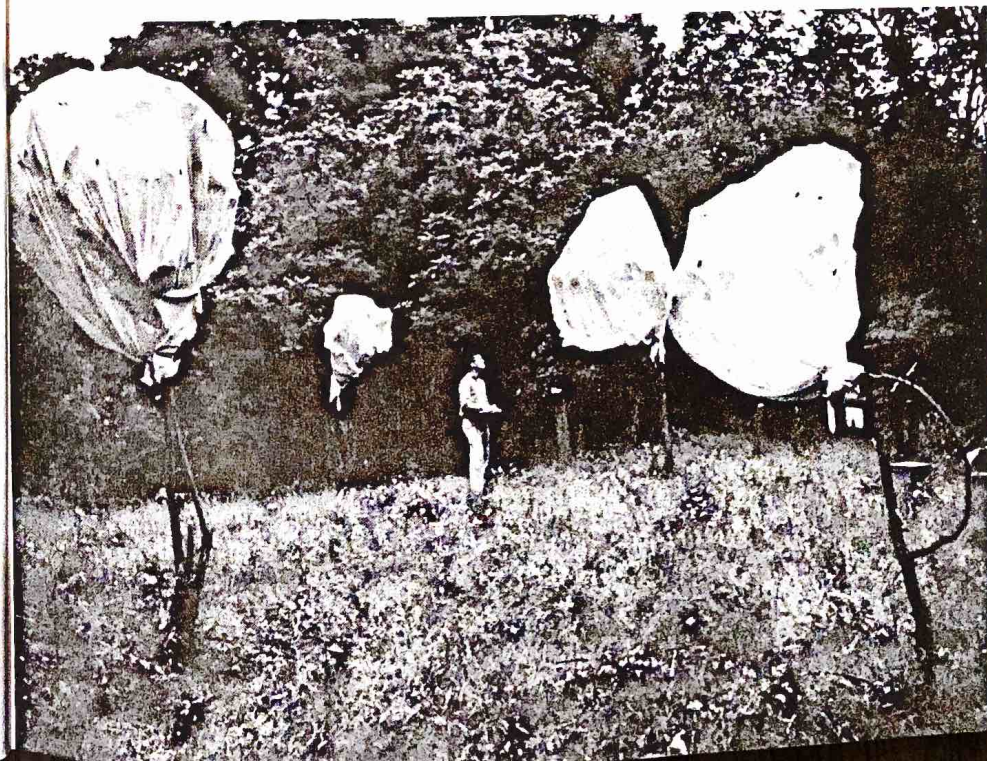
The periodical cicadas display a third method of pair formation through song. Our first study of these animals in the field showed that the male sings a few phrases, flies a short distance, sings a few more phrases, flies, and so forth. This means that during the maximal time of sound production there are large numbers of cicadas flying and

singing. At first it was very difficult for us to decide how this could cause pair formation. The females are silent, so how could a male increase his chances of locating a sexually responsive female by moving about all the time? How could a female locate a moving male?

We tested these questions in a small clearing in a woods, where *Magicicada septendecim* and *Magicicada cassini* lived together (Figure 24). Four small trees were left in the clearing and covered with cheesecloth cages. The cages were then filled with cicadas of different kinds. In one cage we put normal *cassini* males and *septendecim* males that had been silenced by destroying their sound-producing organs. In another we put normal *septendecim* males and silenced *cassini* males. In a third cage we put normal *septendecim* females, and in a fourth we put normal *cassini* females. The silenced males eliminated the possibility that chemical or visually perceived differences between the species might be of significance to females. Females were placed in the cages to determine whether females would attract more males from the woods than singing males would. Thus one cage was producing the normal *septendecim* sound, another the normal *cassini* sound, and two were silent.

Our test results were not as clear as we would have liked, but one thing was certain: *septendecim* males and females from the woods

Figure 24. Clearing with cheesecloth-covered trees for field tests on the function of *Magicicada* calling songs.



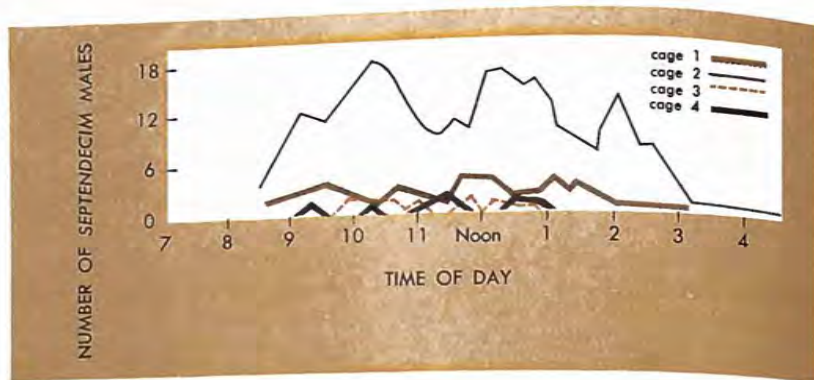


Figure 25. Numbers of males of *Magicicada septendecim* at each cage at intervals throughout each of the test days. Cage 2 was the only cage emitting septendecim sounds.

Figure 26. Proportions of individuals of *Magicicada septendecim* and *Magicicada cassini* at cages 2 (septendecim sounds) and 3 (cassini sounds) at intervals throughout each of the test days (all zeroes are treated as ones).

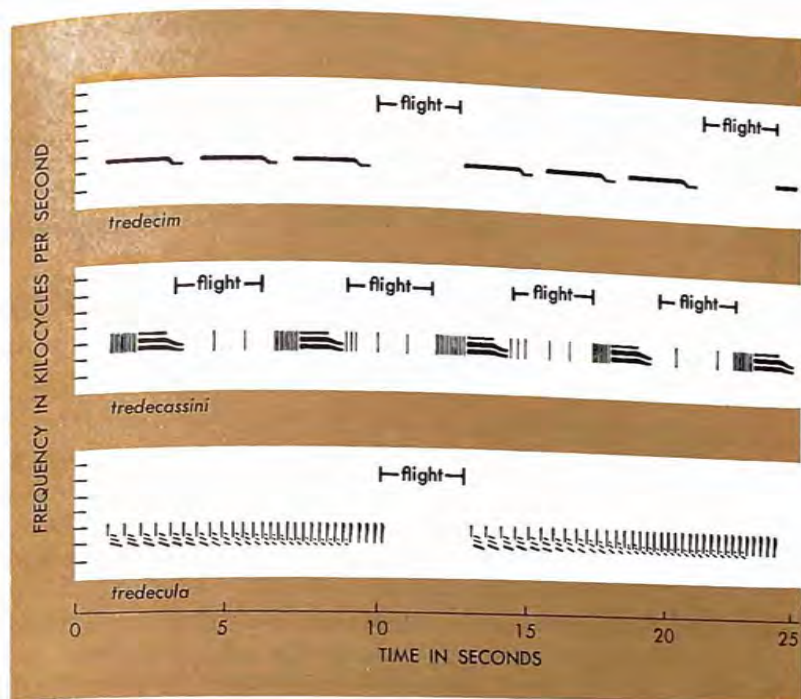
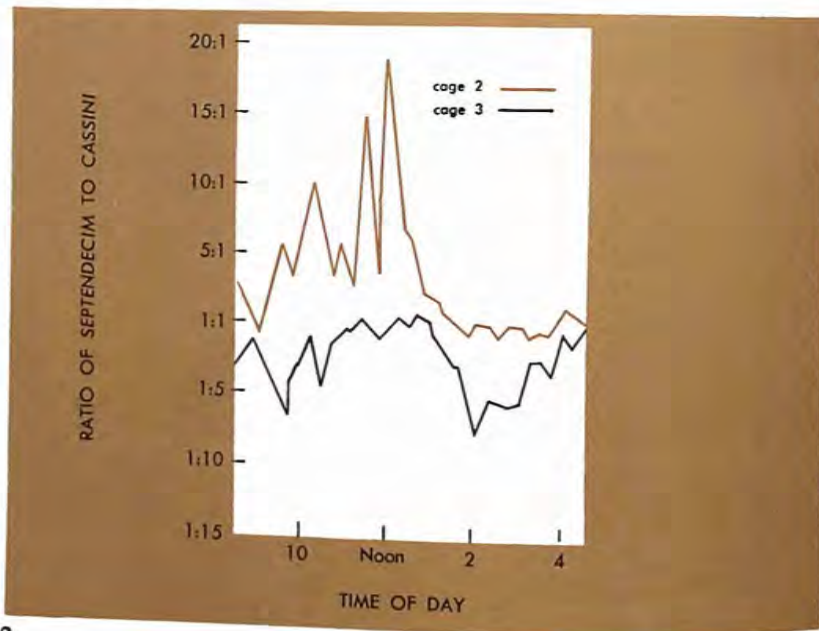


Figure 27. Diagrams of the manner of chorusing in males of the three 13-year (or 17-year) cicadas.

were both attracted to the sound of *septendecim*, and (less clearly) *cassini* males and females were both attracted to the sound of *cassini*. This indicates that, as we suspected, the songs of these cicadas function by bringing together large numbers of males and females. Pair formation must take place inside these aggregations. Results of the tests are shown in Figures 25 and 26.

Pair formation and copulation do, in fact, seem to be largely restricted to such congregations or aggregations or choruses of males and females, and as a result song differences, with their associated behavior, also reduce interspecific encounters between sexually responsive males and females. Females are attracted to the loudest colonies of males, and an individual male has a reasonable chance to copulate, and thus pass his genetic materials on to the next generation, only if he becomes a conformist and enters a group of singing males. Females that are sexually responsive fly into the chorus and there perch motionless on a branch, enabling the males to distinguish

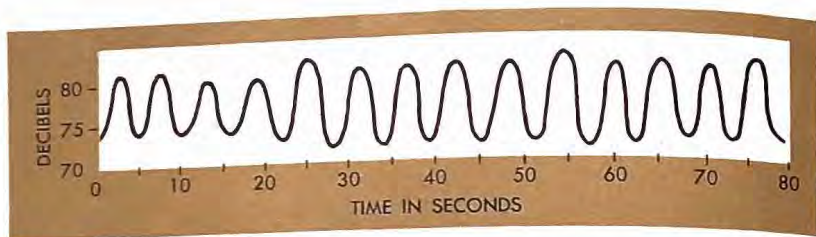


Figure 28. The degrees and regularity of fluctuations in sound level produced by a synchronized chorus of *Magicicada cassini*, diagrammed from timed, successive readings of a sound-level meter on the ground in the forest.

them from the active, performing males. These songs, then, as with the cricket songs, do indeed function as "reproductive isolating mechanisms" for cicadas.

It happens that not only the patterns of sound are different among the three species but also the method by which they are produced (Figure 27). *M. tredecim* and *M. septendecim* both sing two or three phrases, fly briefly, produce two or three more phrases, fly briefly, and so forth. *M. tredecula* and *M. septendecula* produce only one of their long phrases between flights. *M. tredecassini* and *M. cassini* perform like *M. tredecim*, except when weather conditions are optimal and when there are very dense populations of the cicadas. In these instances there is a fantastic synchrony among individuals of a population, in which only one phrase is produced between flights and all the males in the population sing and fly at the same time (Figure 28). This is probably the most remarkable case of synchronized behavior in the animal kingdom. It is difficult for us to determine its functional significance at this time, but one thing that this behavior accomplishes is to make the performance of song by these cicadas even more different from the performances by the other two species with which they live.

OTHER BEHAVIOR DIFFERENCES

There are some differences in behavior among *Magicicada* species besides those in song pattern and in methods of chorusing. One of these is a difference in the time of day during which chorusing is at its maximum (Figure 29). In *M. tredecim* and *M. septendecim*, maximal chorusing and maximal sexual activity occur in midmorning. *M. tredecula* and *M. septendecula* chorus maximally about midday and *M. tredecassini* and *M. cassini* chorus maximally in early afternoon and midafternoon. This means that the three species, living

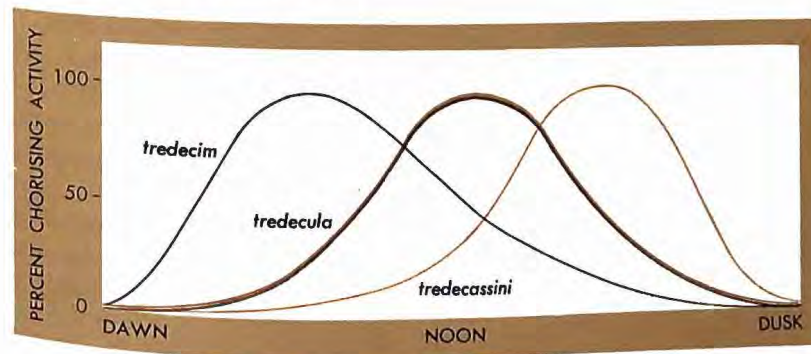
together seasonally, annually, geographically, and ecologically, have exploited almost every means imaginable for efficiency of operation under such amazing conditions of sympatry and synchrony.

This raises the next puzzling question: Why have these species continued to live together? Why haven't they diverged more than they have with respect to habitat? Surely, the broad range of forests they inhabit collectively provides the possibility of specialization that could almost completely separate them spatially. Likewise, why haven't they diverged, at least to some significant degree, in the times of their emergences? Collectively, the eastern North American cicadas use the entire summer, from *Magicicada* time until late fall, to carry out their adult activities. Just a couple of weeks difference in emergence time between species would seem to be an effective way for *Magicicada* to reduce breeding confusion. Certainly, some combination of incomplete spatial and incomplete temporal separation could almost entirely separate these species. But the very slight and very broadly overlapping differences in emergence time and habitat concentrations that have been observed in some regions give us little confidence that selection has ever acted to bring this separation about. Such separation has occurred in every other case of sibling species studied through the animal kingdom. We are almost led to believe here that a *reverse* selection has occurred instead—that these species have been *kept together!* If so, this is a unique situation. How could it happen?

INTERACTIONS AMONG SPECIES

First, we may ask how efficiently these species can live together. There are two kinds of harmful interaction that we might consider. One of these takes place during the juvenile stages, when there would

Figure 29. Approximate times of maximal chorusing activity in the 13-year (or 17-year) cicadas.



be competition for food. The other takes place during the adult stages, when there would be possible confusion in connection with reproduction. We know practically nothing about the first possibility, so let us discuss the second. Only a few cases of cross-copulation have been encountered in the field, in peculiar and apparently heavily overcrowded areas of small trees, even though tens of thousands of matings have been examined to attempt to discover cross-mated individuals. However, when Dr. Moore and I placed the three 13-year species in cheesecloth cages over trees, we were amazed to discover that all kinds of interspecific copulation took place in just a few hours. This suggested that only a slight adjustment of external environmental conditions would be necessary to break down whatever it is that allows these species to live together without cross-copulating.

We still do not know what prevents copulation between species under natural conditions. Of course, the periods of maximum sexual activity are at different times of the day; also, the congregational songs are different, so that during the weeks that the insects are adult there is a slow clumping of the different species in different trees within the forest. Yet we know that in any chorus of a given species many individuals of the other species will be present. Why don't they cross-copulate? We have observed that female cicadas reject the advances of males of other species (or of their own species when they are not sexually responsive) by walking away, by flying away, or by pushing out the wing on the side next to an approaching male so as to dislodge him or push him away. The females also reject males by walking or flying when a male has mounted. We believe that males were able to copulate with females of other species in our cheesecloth cages simply because the cheesecloth surface reduced the females ability to reject males.

But what stimulus causes females to reject males of the other species? We don't know the answer to this question. Perhaps there is an odor or a visual reaction; at any rate the stimulus is a subtle one that we have not yet been able to test.

In the spring of 1963, we transported several hundred individuals of the 13-year species into a region where 17-year cicadas were adult that year. We found that cross-matings between the 13-year and 17-year cicadas occurred only between the species which were most alike, that is, between *tredecim* and *septendecim* and between *tredecassini* and *cassini*. This is not particularly surprising; but it is significant that the apparently free cross-mating between these two largely geographically isolated forms suggests that there has been no development of special efficiency in reproductive isolation between

them, as has definitely occurred among the three species which live together in each brood. Perhaps this is because they have not interacted long enough for selection to operate on premating devices and cause them to diverge. In fact, we are not certain that the 13-year and 17-year cicadas ever do live in the same areas, because we have not yet discovered them together. The overall distribution map from all literature records (Figure 26) suggests that they overlap, but we discovered by fieldwork that in some places the map is wrong, and the broods involved approach to within only a hundred miles or so of one another.

Even if they do overlap somewhere, however, 17-year and 13-year cicadas could only come out together every 221 years. Because of this infrequent mixing, it is possible that the development of reproductive isolating mechanisms has been so greatly retarded that it has not yet occurred. A bit of calculating reveals that since the glaciation of eastern North America ten or fifteen thousand years ago, periodical cicadas have undergone only about as many generations as a *Drosophila*, or fruitfly, population would have undergone if it had been cultured continuously in the laboratory for the last twenty-five or thirty-five years! This is quite instructive for any question we might have relative to the rate of evolutionary change in 17- and 13-year cicadas.

In view of their abundance and mixing as adults, the periodical cicadas surely represent an unparalleled case of efficiency in mating separation among closely related species. It is worth emphasizing, therefore, that the actual barriers are combinations of behavioral characteristics. Selection for behavioral incompatibility has apparently been intense and affected several characteristics.

Complete structural incompatibility, or inability to cross-mate because of structural differences, is absent in every case, as was proved by the interspecific copulations obtained in cheesecloth cages. Such incompatibility in structure can probably now develop only through chance divergence. Genitalic differences may not at all be brought into play now in mating separation among the species, even if they were once; and if so, there is no chance now for selection to operate upon them.

The obvious efficiency of behavioral incompatibility (because it happens sooner in any series of male-female interactions) as compared with structural incompatibility makes it likely that this kind of situation occurs throughout the animal kingdom. To say it another way, if song differences could prevent pair formation between males and females of different species, then practically no selection for courtship

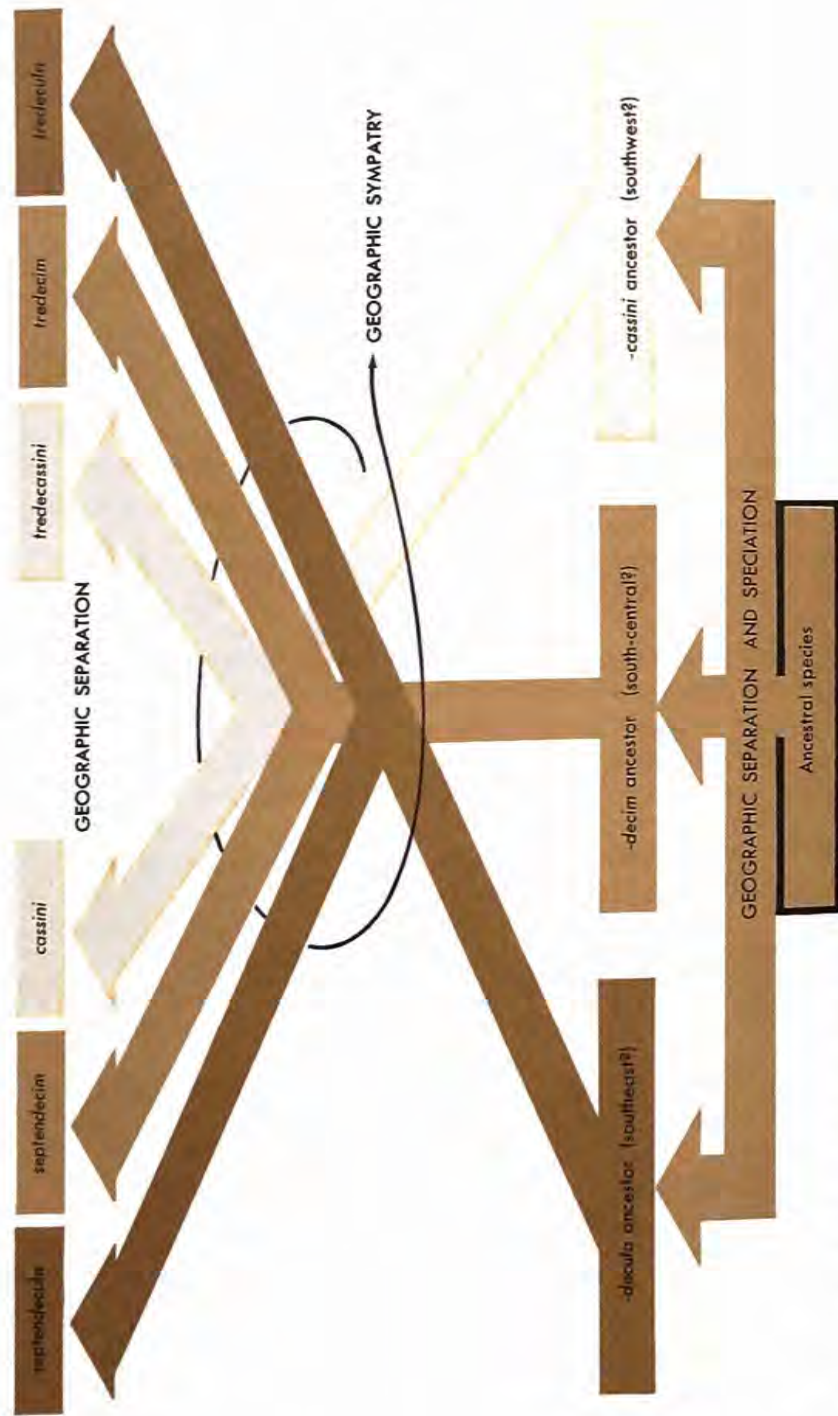


Figure 30. The probable phylogenetic relationships of 17-year and 13-year cicadas.

differences, genitalic differences, or for anything else that would happen only after pair formation had taken place, could occur. Structural incompatibility could function only after a wrong pair had been formed—could only develop as a result of chance, and not as a result of direct selection. (Actually, because there are always some cicadas of the non-chorusing species sitting quietly in the chorusing tree of an active species, there are always a few starts toward interspecific copulation by chorusing males that react to such individuals as if they were females of the chorusing species. So the exact nature and extent of selective action on reproductive isolating mechanisms is not as simple as it might be.)

HISTORY OF MAGICICADA

We believe that the three cicada species in each life-cycle group diverged from one another during geographic isolation and suppose that the sequence of events went something like this. At first, when they came back together, there must have been selection for divergence in many characteristics associated with mating—morphological, physiological, and behavioral characteristics (both efficient and inefficient barriers to copulation in terms of fruitless expenditures of time and energy).

But when behavioral barriers—that is, the song differences and whatever difference causes the female to reject the male of the other species before mating—began to become effective, then selection for divergence in other respects, such as in genitalia or other structural variation, would more or less come to a standstill.

Our reconstruction of the probable evolution of the different kinds of periodical cicadas is shown in Figure 30. We believe that there must have been geographic separation along three lines producing the ancestors of the species pairs that now exist. Then all three of the populations must have come back into contact geographically, leading to their striking differences in song now.

Still later, the 17-year and 13-year life cycles were developed in two different geographic locations—probably northern and southern—each one of them containing all three species. But now an even more perplexing question arises: How could all three 17-year species hit upon the same odd life cycle or all three 13-year species hit upon the same one, depending on which one (if either) was not the same as the original life cycle? This question is not yet answered. It is easy to see that our original discovery of six species instead of just one or two has made the understanding of the evolution of periodical cicadas a much more difficult task than it had seemed to be.

Subsequent to the development of differences in life cycle, or perhaps accompanying it, there was a splitting of the groups from one another, producing the geographically and temporally isolated broods.

One of the questions that arises in attempting to reconstruct the history of the periodical cicadas is their relationship to the Ice Age in North America. If we study the distribution of broods relative to the "maximum extent" of the glaciers, we discover, first, that no brood is completely within the most recently glaciated area and only two broods are completely outside it. Second, groups of broods are related both geographically and temporally—that is, the broods that come out in different years neighbor each other or overlap geographically: Broods 1 and 2 are in the eastern Appalachians, Broods 3 and 4 in the west central states, Broods 5 and 6 in the central and southern Appalachians. Broods 8, 9, 10, and 11 in the Appalachian region, and Broods 13 and 14 in the central and southern Appalachians. This suggests that each group arose from a single ancestral brood which occurred in the same general area that the group occupies today. It suggests further that there were at least two major periods of brood formation.

Now there must have been a major climatic fluctuation to upset the emergence times of significant portions of a brood and to set the life cycle as it is today. The life cycles must have been fixed prior to any brood formation to allow the appearance of the many broods that occur today, each containing the same three species. So we have assumed that some major climatic upsets were indeed necessary for the formation of the broods. The most likely candidate for this period of major climatic upsets would have been the Pleistocene epoch, or the period of glaciation, in eastern North America.

MUTUAL BENEFIT

Our final question is perhaps the most intriguing and difficult: Why have the different species of 17-year and 13-year cicadas failed to separate ecologically, either in habitat or in seasonal time of emergence, as have practically all other closely related species in the animal kingdom?

Our observations on predation by birds on newly emerged adults have led us to believe that a kind of mutualism may exist among these species. There are no parasites or predators with 17-year or 13-year life cycles, so the enemies of these cicadas must always be opportunistic in their predation. Birds have completely wiped out experimentally displaced populations of hundreds or thousands of cicadas in only a few days, and we have observed that they are able to keep up with

straggling emergences, killing the cicadas as fast as they mature. Bird predation may have been a critical influence in the evolution of the sudden, overnight emergences for which these cicadas are famous.

Just as one or two individuals have a greater chance of surviving if they emerge at the same time as many others, so is a small species population more likely to survive if it emerges along with one or two other more abundant species. Not only that, but the sparse species' ability to survive predation actually increases as the number of individuals in its population decreases, for predators will then kill proportionally more individuals of the other species in the same area. But if the species' population emerged alone each time, then the "safety in numbers" principle would work against a small population: a small population would be preyed upon more, proportionally, than a larger one.

We might then suppose that those populations of species which came to live alone were decimated when they were for some reason low in numbers, whereas species which have stayed together have persisted. This might be the reason that we find three species living together almost everywhere that any periodical cicadas are found.

This "cushioning" of one population by another is dramatically illustrated when one of the species is quite sparse. In such cases one often finds the sparse species chorusing in only a single tree in the forest, with the other one or two species filling the rest of the forest. Predation on the sparse species, "hidden" within a forest full of cicadas of another species, would be almost nil.

But what happens during the juvenile stages, when there must be interspecific competition for food? Perhaps the three different species of periodical cicadas, as juveniles, react to one another as if they were all members of the same species. This would mean that competition between individuals of the different species would be roughly equivalent to competition between members of the same species. It suggests that there has been selection for "ecological identity" (a tendency to use exactly the same things in the environment—to behave as members of the same species) among the juveniles. Perhaps the juveniles of, say, species A that were so much like species B that they were able to compete against individuals of species B were more likely to survive than those that became different. Then at any one time the sparse species is a kind of ecological parasite on the other, finding an advantage in resembling it as a juvenile and living in the same place as an adult. In this case, instead of the species evolving ecological differences which would allow them to occupy different niches as juveniles and might also force them into different habitats

during the adult stage, they may have undergone selection in the opposite direction, becoming more and more alike as juveniles. This would allow them to emerge in the same areas as adults and to be more likely to survive through the adult stage, when they possess the peculiar chorusing that causes intensive predation.

THE UNIQUENESS OF MAGICICADA

At least five aspects of the *Magicicada* story represent unique or extreme events in biology: (1) the extremely long life cycle and short adult life, (2) the extreme mixing and apparent mutualism of closely related species, (3) the strange temporal relationship between 13-year and 17-year siblings, (4) the incredible synchrony in the chorusing behavior of the males of *M. cassini* and *M. tredecassini*, and (5) the special significance of brood distributions for the question of the effects of Pleistocene glaciation on deciduous forest animals. We are a long way from solving these problems, and much of what is said in this book must be recognized as almost purely speculative. But for a commonplace, abundant, supposedly well-known group of insects, the periodical cicadas have managed to turn up for us some rather intriguing questions, with potentially great significance in the study of animal species and their evolution.

SHOULD WE PLAN TO STUDY ALL THE SPECIES IN THE WORLD?

Answering the question of whether we need to study all the species of the world is a bit like answering the question of whether we need "pure" research. Pure research can be defined as the uncovering of new knowledge in any area where we have no way of knowing beforehand whether any practical applications to human existence may be involved. As long as we don't have such knowledge, we cannot say how trivial the results of such pure research might be, but neither can we say how startlingly *important* they might be. One of the best contemporary examples is the exploration of outer space. The following remark has been repeated so many times that it is almost trite: "We should settle our problems on the earth before we attempt to go to the moon." Surely if mankind had always operated on that thesis, he would have cheated himself of some extraordinary opportunities, just because of his own ignorance. It is not only very difficult to know just what our "problems" are and how to solve them, but unless we are adventuresome, we may forego many chances to reduce them to insignificance in ways that we had not dreamed possible.

Many people believe that going to the moon is a trivial enterprise.

One prominent scientist has remarked that it may be an adventure, but it's not "science." Aside from the question of whether science and adventure can ever be synonymous (I think they usually are), and aside from the question of whether going to the moon is or is not a good introduction to the problems and possibilities in the further exploration of outer space (which we know will *not* be trivial), it seems as impossible to be sure that a man landing on the moon would itself have only trivial results, as it is to predict certainly what the maximal usefulness in terms of additions to our knowledge might be. The result in changes in our outlook, either with regard to the Earth with its climate and its future or with regard to the exploration of the rest of the universe, might well be far in excess of any present expectation. This is the way of all "pure" research. One is unaware, at the time that he begins, either of the potential practical applications or of the potential triviality of the investigations.

Perhaps you can see by now that this is the way it is with the study of the animal species of the world. About a million have been formally described, but most of these are known only to a very slight degree. It's not easy for us to predict what leaps in understanding with regard to the history and the future of life on Earth—and the question of the nature of life elsewhere in the universe—will be answered only by studying many more of the species on Earth in much more detailed fashion.

To go back to questions asked in the introduction, we still don't know which species we will need or will want to keep among those that live with us on the earth. Until we know which species are which, how they live together, and what they do in the scheme of things, we can never answer such questions. And yet, in view of the increasing rate of expansion of human populations across the earth and our increasing simplification of the human environment by the elimination of species after species, these are questions that we must answer, and that we must answer soon. No one could have predicted the discoveries that you have just read about in this book, or their general usefulness in biology. The species studied were all believed to be well understood. Yet our ignorance of them concealed some important surprises. So long as we continue to be utterly dependent upon the other animals and the plants of the earth, I think there is a strong likelihood that we humans will, in fact, have to study all of the species of the world if we are to be able to do the kinds of things that we will want to do at the rates that we will want to do them.

REFERENCES

Most of the material in this book has been brought up to date from the following technical articles.

Alexander, Richard D. "The Taxonomy of the Field Crickets of the Eastern United States (Orthoptera: Gryllidae: *Acheta*)." *Annals of the Entomological Society of America*, Vol. 50, No. 6 (1957), pp. 584-602. Contains 19 figures, 1 table.

———. "Sound Communication in Orthoptera and Cicadidae." *Animal Sounds and Communication* (editors: W. E. Lanyon and W. N. Tavolga), AIBS Publication, Vol. 7 (1960), pp. 38-92. Contains 16 figures, 5 recordings.

———. "Aggressiveness, Territoriality, and Sexual Behavior in Field Crickets (Orthoptera: Gryllidae)." *Behaviour*, Vol. 17, No. 2-3 (1961), pp. 130-223. Contains 63 figures, 31 tables.

———. "The Role of Behavioral Study in Cricket Classification." *Systematic Zoology*, Vol. 11, No. 2 (1962), pp. 53-72. Contains 19 figures, 1 table.

———. "Rates and Directions of Evolutionary Change in Cricket Acoustical Communication." *Evolution*, Vol. 16, No. 4 (1962), pp. 443-467. Contains 5 figures, 3 tables.

———. "Animal Species, Evolution and Geographic Isolation." *Systematic Zoology*, Vol. 12, No. 4 (1963), pp. 202-204.

———. "The Evolution of Cricket Chirps." *Natural History*, Vol. 75, No. 9 (1966), p. 26.

———, and R. S. Bigelow. "Allochronic Speciation in Field Crickets and a New Species, *Acheta veletis*." *Evolution*, Vol. 14, No. 3 (1960), pp. 334-346. Contains 5 figures.

Alexander, Richard D., and T. E. Moore. "Studies on the Acoustical Behavior of Seventeen-Year Cicadas (Homoptera: Cicadidae: *Magicicada*)." *Ohio Journal of Science*, Vol. 58, No. 2 (1958), pp. 107-127. Contains 16 figures.

———. "The Evolutionary Relationships of 17-Year and 13-Year Cicadas and Three New Species (Homoptera: Cicadidae: *Magicicada*)." *University of Michigan Museum of Zoology Miscellaneous Publications*, Vol. 121 (1962), pp. 5-59. Contains 10 figures, 2 tables.

Alexander, Richard D., and T. J. Walker. "Two Introduced Field Crickets New to Eastern United States (Orthoptera: Gryllidae)." *Annals of the Entomological Society of America*, Vol. 55, No. 1 (1962), pp. 90-94.

INDEX

Audiospectrograms, 22-23

of cicada songs, 70
of cricket songs, 24
of katydid songs, 50

Auditory apparatus, 36

Barriers, 30, 47
post-civilization, 54
pre-civilization, 54

Bigelow, Robert S., 57, 60

Cicadas, 14, 63-82
broods of, 66-68, 80

Competition, 39-41

Crickets, 14
ecological distribution, 26-27
field, 15-47, 57-63
geographic distribution, 30-32, 45-47

Jamaican Field, 19, 22
life histories, 22-26, 46, 58-63
Little Field, 47-48
Northern Fall Field, 17, 22
Northern Spring Field, 16, 21, 22, 26, 29

Northern Wood, 18, 22, 26
phylogeny, 38-39
sand, 60

Sand Field, 17, 22
Southeastern Field, 16, 22, 24, 26
Southern Wood, 19, 22, 26, 29, 32, 45

Davis, William T., 65

Diapause
in crickets, 25-26, 61-63
defined, 25

Divergence, 9, 13, 75

Ecological identity, 81-82

Evolution
of cicadas, 78-80
of crickets, 38-39
of katydids, 54-57
mechanisms of, 8-13, 39-45, 60-63

Fabricius, Johann Sebastian, 49

Fulton, Bentley B., 15, 20-21

Genes, 10, 46

Genotype, 16

Gryllus

assimilis, 19, 22, 37, 39-40
bermudiensis, 47
campestris, 47
firmus, 17, 22, 37, 39, 47, 60, 62-63
fultoni, 18-19, 22, 37, 39-40, 45, 47, 57
pennsylvanicus, 17, 22, 37, 39-41, 47, 58-63
rubens, 16, 22, 37, 39-40, 61
veletis, 16, 21, 22, 37, 39-41, 47, 58-63
vernalis, 18, 22, 37, 39-40, 45

Hybrids, 26-29, 41, 51-55

Ice Age, 56, 77, 80

Incompatibility, 77, 79

Insects, singing, 14

Isolation, 8-9
geographic, 30, 32, 45, 56, 63-64, 75, 77, 80
reproductive, 39-44, 76-77
temporal, 58-63, 75, 79-80

Katydids, 14, 44-57

Magicicada, 63-82
cassini, 64, 71-74, 76
septendecim, 64, 71-74, 76
septendecula, 64, 74
tredecassini, 64, 74, 76
tredecim, 64, 74, 76
tredecula, 64, 74

Moore, Thomas E., 65, 76

Mutation, 8

Mutualism, 80-82

Over-wintering, 22

Paramecium, 10

Phenotype, 46

Pterophylla camellifolia, 44-57, 65
Regen, Johann, 41
Scatter-diagrams, 32-35, 59
Selection, 8
Sexuality, 9-11
 and speciation, 10-13
 types of, 9-10
Shaw, Kenneth, 51
Sibling species, 21-30, 35, 37-44
Songs
 aggressive 41
 calling, 41, 69
 cicada 69-74
 courtship, 41, 69
 cricket, 15, 20-22, 24, 41-43,
 46-47
 disturbance squawk, 69
 katydid, 50-53
Speciation, 5-6, 13-15, 44-47,
 56-57
 defined, 5
Stridulatory apparatus, 34, 36
Synchrony, 25-26, 74
Systematics, 6-8, 14
 defined, 6
Taxonomy, 6
Variation, 11-12
 geographic, 45-47
Walker, Thomas J., 51