Patterns of Life Series

SINGING INSECTS

Four case histories in the study of animal species

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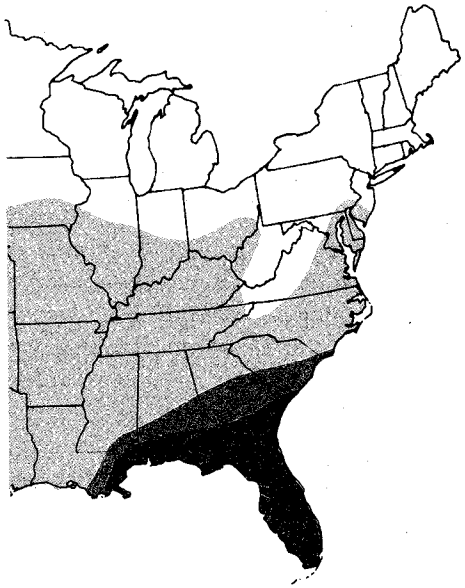


Figure 14. Geographic distribution of the Little Field Cricket, *Miogryllus verticalis* (Serville), showing a region of sharp geographic variation in song, color, and size.

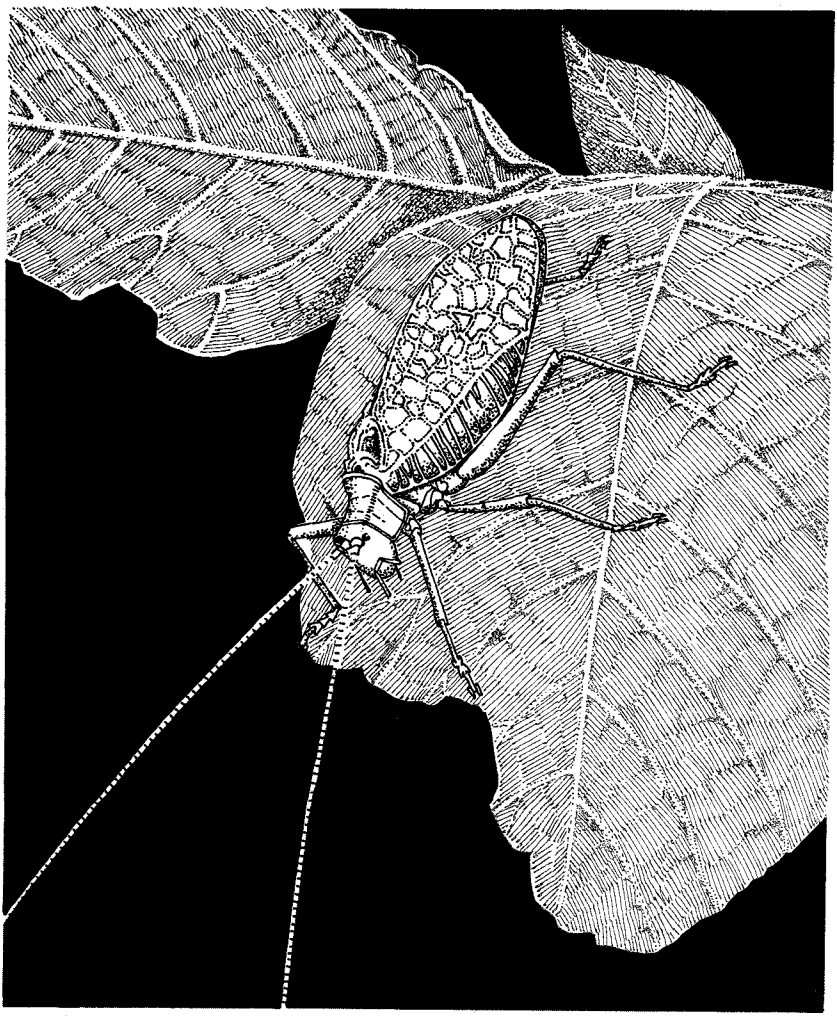
THE TRUE KATYDID

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.



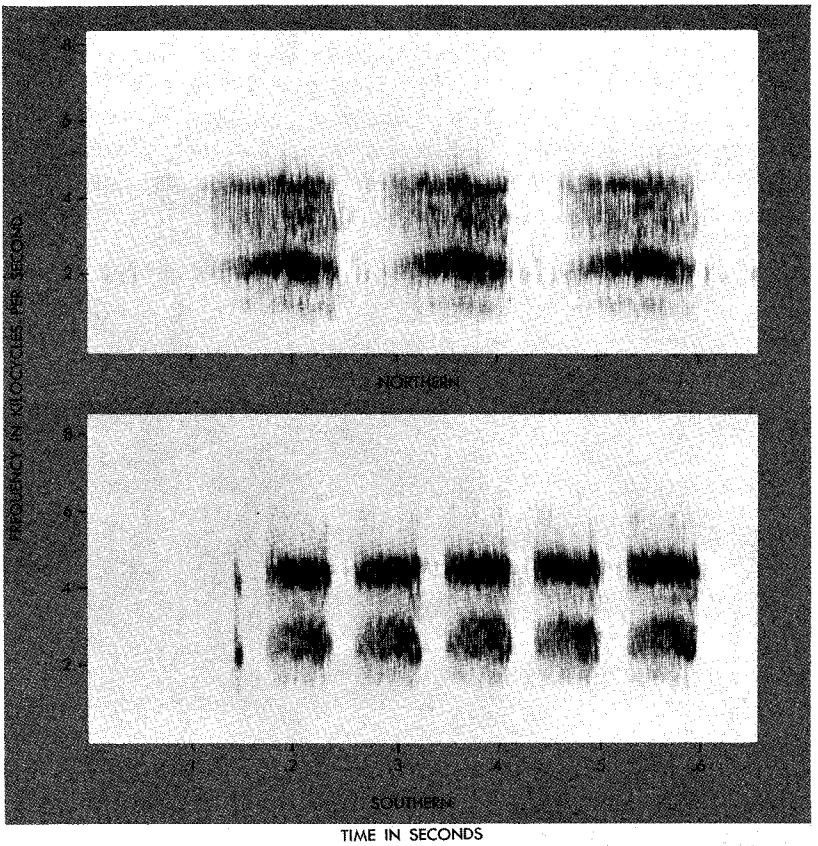


Figure 16. Audiospectrographs of phrases from the calling songs of the northern and southern katydids.

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 paraphase 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 Greenbriar 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

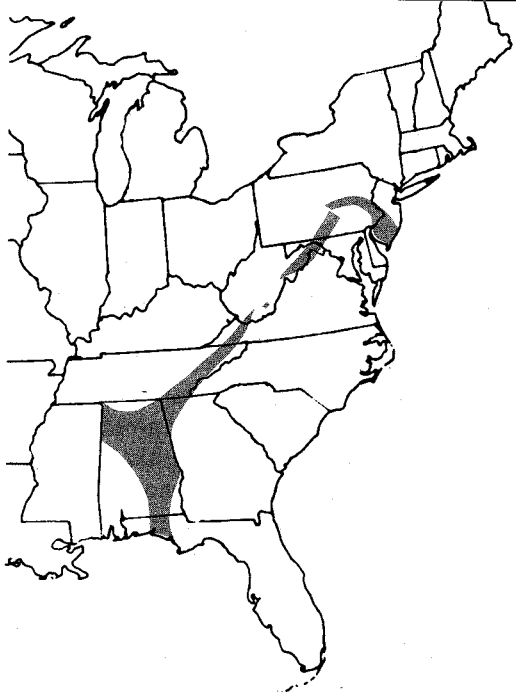


Figure 17. The area shown in color is the katydid-hybridization zone. Note the small circular zone in West Virginia, the Droop Mountain area.

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 "wingstrokes" 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