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SPECIATION, WITH SPECIAL REFERENCE TO THE SINGING INSECTS OF NORTH AMERICA

Anyone who sets out to understand a group of organisms necessarily has to understand species. You have to have a species concept. Otherwise you can't even think about the group. And it has to be a real species concept -- one that works. It has to satisfy you as you keep looking at those animals or plants or whatever they are. You can't learn about a group unless you know how to separate the different kinds. You can't get by with just recognizing one or two species well enough to use them in a laboratory experiment or some kind of behavioral or ecological work. The problem, of knowing what species are, is faced not only by every academic taxonomist and systematist and cladist and phylogeneticist, but also by every person, amateur or not, who wants to know something significant about any group of organisms. And this everyday problem supercedes all the complicated theoretical and philosophical arguments about species in the entire history of biology. Those arguments don't even matter when you're out there in the field.

Most people who set out to learn a group do it by adopting what somebody has called the Local Naturalist Approach. This just means you start out in a small place and expand. When you start out in a small place -- like a woods or a field, or your own farm -- learning the species of birds or mammals or singing insects or whatever, is pretty easy. And you don't usually get into big problems right away. The species are pretty obvious.

But the more you expand your area of study, and the more you begin to know about those species you're looking at, the more likely you are to encounter problems. "Problems" just means that there are some populations that puzzle you. You feel as though you can't be sure whether they represent one species or more than one. Are they really species, or just some slightly different populations that haven't made it yet. This problem is most acute when populations don't live together, at least when they reproduce.

When you start running into problems, you being to get interested in speciation, or how species have come about. That's because you start noticing the particular kinds of differences that exist between species in your group: which differences are always there, or nearly always, and which are unique to two or a few species. And it's also because you begin to wonder how to tell whether those populations that you can't really be sure about are really on their way to being what people call "good species" or not.

I knew a little about species when I went in the Army in 1951 because I did a master's thesis on the insects that inhabit woody fungi. They didn't belong to just one group, but that thesis got me thinking about species. In the Army I was an entomologist supposedly locating breeding places of malaria-carrying mosquitoes, and I got to explore some caves on Fort Knox, in Kentucky. I found several different kinds of blind carabid beetles in these caves, and it dawned on me that cave environments are pretty stable, and usually pretty much alike. So what causes the divergence that yields species, I wondered. I wrote to Northwestern University to see if I could work with Allee, Emerson, Park, Park, or Schmidt, the authors of the big ecology text of that time, whom we called the GREAT AEPPS. Unfortunately, they were all retired, or nearly so, and so I went back to Ohio State. There my advisor gave me one of the battery-operated field tape recorders and suggested I find out what I could about singing insects. I read Ernst Mayr's paper in the first issue of a new journal called Evolution and another paper in the same journal by an old man in North Carolina named Bentley B. Fulton. Fulton had found several field crickets he could distinguish only by song. I spent the first winter studying the acoustical repertoire of the house cricket, which was used in labs at Ohio State, and gave a paper in the spring at the Ohio Academy meetings called Songs of the House Cricket.

In May 1954 I went into the field, collecting in a pasture near Blendon Woods in Franklin County, Ohio. And I got a shock. Unlike most local naturalists, I began with a huge problem: a cricket that was overwintering as a juvenile and maturing in the spring that I didn't know about, and as it turned out, no one had ever named. The shock was that I couldn't find a single way except its life cycle to tell it from its fall counterpart in the same geographic region and the same habitats. So I logically began to wonder two things: Did these two species form quite recently -- hence their similarity? And did they form by suddenly shifting their life cycle -- hence, the surprising life cycle difference?

They did not have a song difference. And when I looked at Bentley B. Fulton's paper again, I discovered that he treated these two populations, which turned out to be seasonally isolated as adults, as a single species. But several of us found they couldn't hybridize. Later, Richard Harrison would discover allozyme and mitochondrial DNA differences that would cause him to say they were just about the most distantly related among all the six other species of field crickets they lived with in eastern United States.

I also found, that first summer, that when different singing insects live together they always have different songs, and when they don't live together they may not; that at least half of all the species of singing insects in eastern United States -- and all of the field crickets -- hadn't been discovered, or named, yet; or else they hadn't been accepted as species by succession of the systematic experts in the museums. And I also found that you can trace geographic, seasonal, and ecological distribution faster in the singing insects than in any other group of organisms; and that there are a whole lot of species "problems" in the singing insects, like that first one that had confronted me.

I was instantly hooked on species and speciation, and it has always been the academic topic I loved the most. Even though many of my colleagues don't know it, I never stopped working on species problems in the singing insects. Next year, when I have said my final say in a book on the human species, and stopped being director of this institution, I will devote myself almost full-time to completing a volume on the topic of my talk today. David Marshall, who is already working on three of these problems with me -- and by himself as well -- has agreed to work as a postdoc, and promised to do all the really hard and technical work. John Cooley and Andy Richards are also involved. My wife, Lorraine, deserves enormous credit because she has been my faithful field assistant virtually every single year since 1954, traveling more miles, writing more field notes frantically by flashlight, and taking more temperatures than everybody else who has worked with me in North America put together.

Gradually I have become quite chauvinistic and arrogant about species problems in the singing insects. I decided, along the way, that I am actually studying the best group from which to understand species and speciation on the best continent to do that, and that every year I do it is a little better than the last one. Let me explain.

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Outline of Talk

1. There are three grand sets of questions in evolutionary biology (BOARD)

a. species and speciation

(1) generating a consistent, useful species concept
(2) discovering how do species form most of the time
(3) discovering how they form the rest of the time

b. phylogeny: determining the historical sequences of speciation

c. adaptation: finding out what determines which genes survive and explains the incredible complexity and hierarchical organization of life.

2. The 3 groups I've studied and their numbers of North American species: (Gryllidae: 150-200 species, Tettigoniidae: 250-350 species (Orthoptera), Cicadidae:150-200 species (Homoptera). (U.S. vs. North America) (BOARD)

3. Two sets of ten reasons for studying <u>singing insects</u> in <u>North America</u> <u>(HANDOUTS)</u>.

4. Compare the continents of North America and Australia: Every continent is unique. If a continent is used as a sample of the world fauna, it needs to be compared to at least one other continent:

a. Australia has over 500 known species of <u>crickets</u>, North America about 150. Other places in the world (New Caledonia; Malaysia)

b. North America is a temperate-climate continent with intruding glaciation maybe 15,000 years ago, Australia a largely tropical and subtropical one that has been relatively unaffected by major upheavals for an indefinite period: the five glacial periods during the past 350,000 years appear (from pollen, carbon) mainly to have cooled it and temporarily increased its continental size. Some call that larger Pleistocene continent, connected to New Guinea and Tasmania, Sahul.

c. In northern Queensland, in the wet tropics nearest New Guinea, <0.5% of the land mass has 25% of the species. By comparison, Ohio, with 1% of the area of continental U.S., has 25% of the U.S. species (the meaning of this comparison escapes me).

d. The U.S. has about as many cricket species audible in one spot (28 in southern Ohio versus 23, 26, etc. in various tropical locations -- except Malaysia, Peru). The reason, however, is different: extensive ranges and much sympatry rather than many tiny allopatric ranges and overall many more species. The U.S. has generally species with (a) larger ranges, (b) lower percentages of allopatry within genera, (c) higher percentages of macropterousness (more vagility: reflecting recent re-invasion?).

(1) Biologists think speciation usually occurs when islands (real ones or habitat ones) are created (or inhabited) sufficiently far apart to prevent transfer of individuals. They probably must last hundreds or thousands of generations to yield speciation. Cricket and katydid generation times are 1/2 to 2 years; the cicadas I'll discuss, 13- or 17-years. (Biologists, however, usually don't specify the actual or required degree and duration of allopatry . . .)

(2) On continents with stable climates and patchiness in soil, rainfall, and topography, islands of habitat, once formed, can persist almost indefinitely -- long enough for speciation to occur between them.

(3) During long-term stability, interpatch vagility will tend to disappear because emigrants will have no place to go. Allopatry will tend to become more emphatic, and speciation more likely.

(4) If stability is great and long-term, tiny populations are more likely to make it; bottlenecks can hasten speciation. Consequences will be larger numbers of species with smaller ranges, more allopatry, less vagility.

(5) In North America habitat islands may have not been isolated long enough since the last glaciation to allow speciation. The consequence is lots of undifferentiated allopatric populations that may never speciate (e.g., if stability doesn't last).

(6) Illustrate with the distribution of *Gryllus fultoni* and *G. vernalis*, and the potential vegetation of U.S. and the current and 1820 oak-hickory woods of southern Illinois.

(7) Compare the Australian map and the Ohio map. Note that because of the location of the glaciers we expect species to appear to have expanded north or east since glaciation. Species pairs that seem to have done this may or may not have formed as a result of recent glaciations.

[It's appropriate to ask, then, whether greater species density in the tropics is partly a result of habitat-fragmenting events correlated with long periods of stability while species were fragmented and speciating.]

5. When we study speciation we are working on the three "layers" of phenomena on top of the existing phylogeny or species lists (BOARD):

a. previously undetected sympatric and synchronic species (known reproductive corporations);
b. diagnosable allopatric or allochronic species;
c. all kinds of situations involving populations that might represent speciation in progress.

6. Speciation biologists usually begin with a "local naturalist approach" (*G. veletis*:): I seem to have been perversely thwarted in this approach by always finding an odd case first! I started in central Ohio and immediately found a surprising life cycle difference between two populations inseparable by all other means. I couldn't at first convince myself these were different species, but Richard Harrison later concluded from allozyme work that they're not even closely related. Note that 8 of 12 *Gryllus* species from the Great Plains east are juvenile-overwinterers, but only a tiny fraction in the PANS collection used by Rehn and Hebard in a prior comprehensive study of *Gryllus* were spring adults.

7. Distributions of cognate species in U. S. form a few patterns.

8. Slide of special cases of species multiplication in North America.

9. The Oecanthus quadripunctatus complex:

a. quadripunctatus, nigricornis, argentinus (Note that we do not expect species to be as widely distributed as quadripunctatus initially appeared to be). First findings: 3 previously undetected species, in this case hinted at before: songs helped us tell them apart and locate morphological differences.

b. Some cogante species have different life cycles. Selection strongly divergent where they approach one another. Explain how voltinism changes might happen: continuous distribution or some emigrant crickets make a big geographic leap.

(1) Day lengths are different for different stages (affect wing length, rate of growth, body size, and diapause stage and obligateness).

(2) Selection for development time is dramatically different across the line.

(3) Selection for body size is opposite across the line.

(4) Diapause every generation (obligate) or alternate generations (non-obligate).

(5) Diapause is most stringent in the southern part of the range of a northern species and in the northern part of the range of a southern species.

c. Some cognate species occur on different hosts: explain theory.

(1) If a newly encountered host is abundant and similar enough to the existing host it might be entered successfully.

(2) As the insect adapts to the new host it can spread rapidly.

(3) There is likely to be no predator with an appropriate search image there (predators are important, as shown by cricket's ability and tendency to mimic pine needle).

(4) It will surely be more difficult for a cricket specialized to one host to move on to another unless it is quite similar.

(5) To work out the history of these cases one has to know the geographic history of the host plants.

10. Use the quote from Alexander and Moore.

11. The last set of cases I have discussed appear to involve:

a. some degree of isolation, but not necessarily, or even probably, complete isolation.

b. strong divergences of selection at the border between incipient species (adaptation is involved in speciation).

c. special evolved features of the organisms (such as life cycle).

d. They all appear to represent speciation taking place right where they exist today, suggesting that 10-15,000 generations may be sufficient for speciation in crickets with 1-2 generations per year (Klicka and Zink in *Science* 277:1066, 12 Sept 97, conclude from molecular evidence that cognate bird species in North America are more likely to be 1-2 million years old . . .)

I regard the above four conclusions (a-d) as general for the fauna of North America I have been studying; maybe they are even more general.

TEN REASONS WHY NORTH AMERICA IS THE BEST PLACE IN THE WORLD TO DO SYSTEMATIC WORK

1. Most of the continent, the U.S., is the biggest, most complex, most diverse region in the world where one can travel end-to-end without passports, visas, customs or language problems, malaria, yellow fever, hepatitis, climbing scabies, creeping modock, jungle rot, lions, tigers, collecting permits, water or fuel problems, eternally exploding bowels, or serious threats of multiple deadly snakes and bandits. Canada and Mexico are available with few added problems.

2. Considering travel to and from as well as living expenses, fuel costs, collecting permits, immunizations, bribes, and general nightmares, it's the least expensive and least harrowing place, and the most directly and quickly available place, in the entire world, in which to do research.

3. There are maps of everything: soils, climate, weather, current and past drainage, physiography, and vegetation today, years ago, and even prehistorically.

4. There are roads everywhere. You can sample and record distributions on unmatched and unprecedented micro- as well as macro-scales.

5. Other fauna and flora are known better than anywhere else in the world.

6. Property is privately owned, so that you can ask to use it and obtain permission without having to schedule times for spending half the night drinking foul, muddy, brown, alimentary-tract-anesthetizing fluids from wooden bowls into which everyone in the village has already slobbered.

7. There are innumerable all-night motels and radio shacks, sometimes almost anywhere you need them, for repair, replacement, and recharging of bodies and minds as well as electronic equipment.

8. Intriguing problems are endless, and when you get absolutely sick of them you can arrive home quickly and drop into your own fine bed (or ride your own horse through your own woods. . .) before you go out again.

9. Compared to the rest of the world, every year North America gets better, even relatively, in nearly all of the above respects:1997 is the best year ever.

10. Because of all these considerations of time, expense, and research aids, you can spend an immensely larger amount of immensely more effective research time, at immensely less cost, on this continent than on any other. You can do it as a hobby, just for the fun of it, as part of your vacations, and, best of all, you may not even need an NSF grant.

It is indeed time to look at the bees across the road.

TEN REASONS WHY SINGING INSECTS ARE THE BEST GROUP FOR STUDYING MANY GENERAL PROBLEMS OF SPECIES AND SPECIATION:

1. As with many insect groups, they include relatively large numbers of species, perhaps 25,000 known species world-wide, up to 30-50 audible in one spot, as many as 500 or 1000 on a single continent, and in some locations, such as Malaysia or Peru, hundreds in a few square miles.

2. They form pairs using loud, easily recorded and analyzed songs that (a) are invariably distinct among microsympatric, seasonally synchronic species, (b) can be heard and even taped while driving at speeds of 30-50 miles per hour, (c) possess recognizable heritable differences between species that give predictable patterns and ratios in hybrids produced in the laboratory or in the field, (d) are unaltered by learning experiences, and (e) can be used to trace geographic and ecological distributions and patterns of life history. Therefore (f), easily analyzable samples unmatched in size and completeness can be amassed quickly and inexpensively and (g) the faunas of islands or entire continents can be examined relatively swiftly in unmatched detail. Singing insects, unlike many birds and amphibians, also (h) perform continually across long periods each day or night for their entire adult lives, giving immensely longer and more reliable periods in which to sample them. Because in many species females mate but once, operational sex ratios are typically extremely male-biased, this contributing to the typical situation of (i) large numbers of males calling more or less continually. Moreover, unlike plants, some of which can be easily seen but only in the daytime and only along the edges of habitats like forests, singing insects not only can be sampled acoustically throughout the night, but in many species single individuals can be heard at considerable distances, meaning that (j) they can be detected, and often taped, even if they are deep inside a forest that is not entered.

That seems to be eleven reasons. Maybe there are more . . .

Someone suggested to me that bird lovers might argue with the contention that singing insects are the best groups in which to study speciation because birds also have distinctive songs. It seems to me, however, that, among other things, the small numbers of bird species make them poultry by comparison. Amphibians also are not nearly as useful as insects, not only because of the small number of species (apparently, amphibians have largely forgotten how to speciate), but also because some species sing so briefly and unpredictably, during day or night as well as season (e.g., those in the Rana pipiens complex), that they cannot reliably be located and traced across large areas that might entail days or weeks of travel.