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Richard S. Cowan, Head, Office of Systematics, Smithsonian Institution

Robert P. Higgins, Wake Forest University, Co-director, representing American Society of Zoologists

Ellis L. Yochelson, U. S. Geological Survey, Executive Co-director, representing Society of Systematic Zoology

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ANIMAL BEHAVIOR AND SYSTEMATICS

Richard D. Alexander

Museum of Zoology and Department of Zoology
The University of Michigan, Ann Arbor

Introduction

I have thought about this lecture all the way down here, and I still cannot imagine that at eleven thirty I'm still going to be standing here talking and you're still going to be sitting out there listening! I have never talked for two and a half hours straight. I have always thought I was pretty lucky in teaching if I got fifty minutes ahead of the students, which is an absolute minimum. Furthermore, I realized on the way here that I couldn't think of anyone that I would like to listen to for two and a half hours!

After having these thoughts, I decided to make some changes in my talk. The principal one is that it is really going to be a series of short talks, each ten or fifteen minutes long. I'll try to pause between these for questions and I hope that you'll also interrupt me at any time you want.

I don't know most of you, and I don't think that most of you know me. My topic is supposed to be animal behavior and systematics. I decided that staying precisely with that subject is probably the least important thing I can do. Instead I will try to emphasize those things in which I at least feel that I have some special competence or special information. It seems only fair, therefore, that I should tell you a bit about my background so that you'll understand how I happen to be here, and why I tend to emphasize the things I do. I got a degree in entomology at Ohio State University, where I became a systematist more or less indirectly through the influence of my advisor there, Donald J. Borror, and also because of a paper on cricket speciation that I read in my early graduate student days, written by Bentley B. Fulton of North Carolina State University. I spent my graduate student days proclaiming that one place I would never be found working is in a museum. But then I left Ohio State, went directly to work in a museum, and have been in a museum ever since!

In the United States, animal behavior was almost non-existent as a subject in zoology curricula in the early 1950's. Partly as a result, I nearly became a psychologist. But somewhere along the way I got diverted into biology. When I went to Michigan I taught introductory zoology for five years. My interest in animal behavior grew during this time, and I eventually started teaching a course in insect behavior and a graduate seminar in evolution. Finally these two courses became combined into a course called animal behavior and evolution, which I have been teaching the past four years.

So I am really a systematist with a special interest in behavior, and I'm still studying the same insects that I started to work on as a graduate student: the crickets, katydids, and cicadas--three families containing about a thousand species in North America. My chief ambition at this moment is to finish a monograph on these species, along with Thomas E. Moore at The University of Michigan and Thomas J. Walker at the University of Florida.

If I have any special knowledge about behavior, then, it is a result of coming in more or less through the back door. I am quite serious when I express the hope that Dr. Eisenberg, who did not come through the back door, but, more recently than I, through one of the big open front ones, will not hesitate to straighten out any important errors that I might make.

Some General Comments on Classification

First, I want to give a brief discourse on something I got to thinking about as a result of the systematics conference we had at Ann Arbor three weeks ago, and which has only a very indirect relationship to behavior.

I consider myself a systematist and a taxonomist--in both the broadest and narrowest senses of those terms. I mean by this that I am not willing to admit that taxonomists engage in any worthwhile activities that I don't carry out in my own biological work. I don't claim the same for systematics in the broadest sense, but at least I do believe that systematists, collectively and individually, are not likely to be interested in anything in biology that is not directly of interest and concern to me too.

Nevertheless, I am one of those many taxonomists, or systematists, who never has worried too much about higher categories. I think I always have had some sort of vague feeling that when the proper time arrived, or when the necessity of dealing with them became sufficiently urgent, they would either fall into place or I could at least work something out on a provisional basis.

I have been noticing, of course, the steady increase in the number of papers dealing with the arrangement of higher categories, particularly those published in <u>Systematic Zoology</u>, and, I might add, the steady increase in the complexity of their discussions; and I include in this growth of complexity the writings and suggestions of philosophers, logicians, statisticians, and numerical pheneticists (whatever they may be).

But I stopped trying to keep up with these papers because I never could develop the intensity of concern I seemed to need to go to the trouble of trying to understand all of the arguments. I think I have had some kind of sneaky hope that these people would argue around among themselves until they figured it all out, and then I could just read the summary!

After I had sat through the first day or two of the Ann Arbor conference, I was actually beginning to wonder if I am a systematist after all! Because here all of these people were, right in front of me, arguing the same issues vocally that I had been sort of skipping over when they were published in <u>Systematic Zoology</u> and other journals. I might add that a lot of other people to whom I talked were also wondering out loud if they were systematists. This made me feel a little better.

As I listened, it struck me that there were two kinds of people present at that conference: first, those behaving as though classification is something you do so that you can proceed with biology--or even something that you do more or less independently of the growth of biological knowledge in general; and, second, those who act as though they believe that classification is something that proceeds <u>out of</u> biological knowledge in general, or is possible as a <u>result</u> of the general growth of biological knowledge--something that is dependent upon general biological knowledge, contributes directly to it, and in fact is involved in a kind of reverberating feedback with it.

The first category includes some investigators that all of us would call the old-fashioned variety of taxonomist, and some who are bound and determined, it would seem, to think of themselves as the most new-fangled of all taxonomists.

Someone in a discussion following the conference asked a question that I think ultimately bears on my feeling that there are two kinds of people talking about classification. He said, "Well, why do we need classification anyway?" What struck me from the answers he got immediately was that when you start listing reasons--say, you need classification for biogeography, for understanding evolutionary mechanisms, for working out geological history, or for understanding the evolution of some particular characteristic--then you begin suddenly to realize that all of these reasons are not equally urgent at any stage in the development of biology. Furthermore, classification at the different levels in the taxonomic hierarchy does not contribute equally to these different problems to which classification in general contributes.

And so, the question, "Why do we need classification?" suddenly becomes "How much classification do we need when?" Someone suggested that some of the numerical pheneticists saw a lot of taxonomists behaving as though they wanted the "complete and correct" classification right now, said, in effect, "Oh, if that's what you want, I can show you how best to do it!," did it, and cannot figure out now why the systematists don't really want the technique.

The reason, I think, is that a classification is not something that one sets up completely so that he can then proceed with the rest of biology. It is something that, at first, in its most provisional, rudimentary state, assists beginning efforts toward the collection, arrangement, and understanding of biological information, and thereafter is alternately adjusted and refined by, and then used to test the significance and validity of, biological information of all kinds and in all stages of development. It is something that contributes continually to the growth of biological knowledge in general and yet can never be complete as long as biological information is still coming in. This is why the systematist, at his best, has to be not only the chief pioneer in biology but as well one of the ultimate synthesizers.

I have been wondering since that meeting if it is not possible that lack of agreement on this point underlies every major disunity in systematic biology? And that failure to understand it, or agree with it, is responsible for many of the trivial, inadequate, and mis-directed efforts in systematics? I include here those people who, when involved in some big biological project, go out and "hire" a taxonomist--and who then take the taxonomist's word as gospel on classification and work everything else around what he says, not realizing that every piece and kind of biological information they discover is also taxonomic information.

Construction of a classification, then, does not proceed independently of the growth of biological knowledge in general; indeed, it must neither run too far ahead nor lag too far behind the development of other aspects of biology. But how do we decide what is "too far ahead" or "too far behind?" I think we do it by asking again that same question: "What do we need classication for?"

Classification at any level or in any group might be construed to have "fallen behind," hence, deserve more effort (Could we say that special effort toward it would be more rewarding, useful, and effective?) when its absence or its imperfections are retarding progress on questions pertinent to the groups of organisms or the evolutionary events involved.

Adequate classification is not going to proceed on its own. On the other hand, is it not possible to work so hard at classifying at any point in the development of knowledge about a given group (or at a given level in the classification hierarchy) that the effort necessarily will be trivial? Is this perhaps a part of the background for the exaggeration of efforts at weighting and selecting "characters'? Don't the relative costs of these efforts increase with the intensity of efforts at classification relative to the extent of biological information available?

The "level" of classification" which comes closest to being justified regardless of what else is known is that "level" needed for identification or repeatability which, of course, is the essence of science. Most often this is the one we call the "species." This is especially true, and easy to understand, when the species has what we call the "biological" meaning--or is clearly synonymous with the smallest, or most truly separate evolutionary line--in at least bisexual organisms.

I have sometimes believed that some of the decriers of the biological species concept have just been unable to figure out what species are in their groups, and they'll be damned if they're going to let anybody else think he's done it in his group!

But, look how inappropriate, in this light, is the idea that "species" don't <u>have</u> to be biological species even when they can be! I'm referring now to the idea that one can handle this level of classification without dealing with biological entities--that he needs only to identify groups of look-alike specimens. I would ask those people who challenge the biological species concept whether they do not need it as badly as some of us who are convinced that in our organisms we can cause it reasonably to represent the forking of the phylogenetic tree--the origin of discontinuity? I would ask them if they are sure they have not been using it all the time as a standard against which to compare and understand their own organisms when they may think don't evolve that way at all? I agree that it is unfortunate that populations of asexual and parthenogenetic and other non-bisexual organisms have not been studied enough to understand the significance of their similarities and differences, cohesiveness or lack of it; but I do not think we should blame the biological species concept for this particular area of ignorance, or do away with it because we don't know whether or how universally it can be applied.

I think we need to find "biological" species wherever they exist, and perhaps we need to find distinct evolutionary lines as analogous to biological species as they may be, in all kinds of organisms.

But, going back to higher categories, we really don't need the family as badly as the species, nor do we need, say, that badly the order or the tribe. Perhaps we ought to talk about degrees of antiquity rather than taxonomic levels: in general, the more recent the evolutionary divergence, the more likely we are to need the classificatory effort at that level earlier in the growth and development of general biological knowledge concerning that group.

If I can inject one more comment on this general theme, I have been serving on a panel on which we have been admonished continually to "describe the problem-solving methods of your field." At first I didn"t really think this assignment was appropriate with regard to systematics, but I finally decided it is a very valuable one. For one thing, pondering it caused me to realize that in a field with as much history as biology, classification itself is one of the most crucial problem-solving methods! I'm sure that many of you already know this, and you may have specific and personal examples to demonstrate it. But let me explain what this remark means to me, for I feel that I have only recently become aware of its real significance.

A couple of weeks ago, I found myself explaining to a novice that two look-alike Gryllus species with quite different chirps are "not even in the same species group." Suddenly, my own remarks caused me to realize that all of the field crickets of North America (about 40 species) fall into just three species groups. This realization caused distributions, habitats, life histories, behavior, and morphology to fall suddenly into place in my mind. What had been a confusing tangle of data became an orderly, reasonable, exciting story, and partly as a result when Ashley Gurney (sitting in this audience) next asks me: "When are you going to finish the field crickets of North America?" I think I can say "Right away!"

As soon as I gained the realization of species group identities, I knew that if my idea was correct then certain subtle morphological differences ought to exist between the two specimens I was holding. Each was present: (1) more pubescence on the head and pronotum of one cricket, (2) a bigger head on the other, (3) a more prominent light line along the tegminal margin in the first cricket, (4) tan spots on the inside of the hind leg of one cricket and orange or reddish ones on the other, and (5) certain subtle differences in body shape and wing glossiness. Yet I noticed none of these differences until I had placed the crickets in different species groups by their songs--going a little beyond my own inclinations because I was trying to explain something to a novice and was exaggerating somewhat to make a point. Here I must acknowledge that my classification of field crickets needed to "catch up" with my general information.

I ought to point out here that what I had done in this case was something that everyone insists cannot be done: I was, in effect, using a reproductive isolating mechanism (song) to classify "higher" categories (species groups). I want to come back to that after discussing reproductive isolation a little more thoroughly, and argue that the people who say you can't use reproductive isolating mechanisms to group species into higher categories are misleading biologists in a very important way. They are right in the sense that the differences actually responsible for reproductively isolating particular pairs of species must usually be of recent origin, and change must be rapid in such characteristics. They are wrong in supposing that there are not some features of such phenomena which do not change rapidly. A cricket song, for example, is not one character--it is a whole constellation or hierarchy of characters, some of which are not any longer changing with every case of speciation; and some of which reveal generic and even subfamilial relationships. Part of the reason for the evolution of hierarchial complexities yielding such useful characteristics is that speciation and reproductive isolation force species specificity and overall rapidity in evolutionary change. I will give an example when I take up reproductive isolation later this morning.

The History of Behavioral Study

I doubt that any area or field within zoology has had a more curious history than the study of animal behavior. None of the characteristics of animals are more broadly interesting than those which we lump under this term "behavior," and there is ample evidence that men have been intensively preoccupied with behavior, and skillful interpreters of it, for many thousands of years. Nevertheless, throughout the history of zoology as a formal discipline there never has been a very long period during which behavioral study was able to maintain a consistent respectability. At times it has seemed that the mere acquisition of formal training in zoology was almost synonymous with the suppression of any active interest in behavior. No field has seemed more devoid of a cumulative growth of knowledge, and it is not surprising that in the early part of this century the zoologists more or less just gave up and turned the entire subject over to the psychologists. As recently as 1956, when I was still a graduate student, it was virtually impossible to obtain a Ph.D. in this country with animal behavior formally given as a major field of concentration. There was a mere handful of courses concerned with behavioral topics. In zoology, they were practically all moribund hangovers from the old "anatomy and development" themes of the 1930's, and in entomology they were almost exclusively concerned with social life in ants, wasps, bees, and termites.

This has always been a most puzzling phenomenon to me, because I have been impressed with the idea that "behavior" is almost a part of the definition of "animal." Is there anything that more clearly sets animals apart from plants than the evolution of complexity in behavioral phenomena? Anything that more clearly analogizes on a broad scale the independently followed evolutionary pathways of such anciently divergent animal groups as the vertebrates, the molluscs, and the arthropods?

I was reminded of the attitude toward behavior that I have been describing only last week when I gave to a taxonomist a copy of a key to the flashing patterns of the 13 species of fireflies flashing right now in the swamp behind his house, a key made up by James E. Lloyd of The University of Florida. In the first couplet, the genera <u>Photuris</u> and <u>Photinus</u> are distinguished, and in addition to color of flash and the behavior of captured males in one's hand, Dr. Lloyd included the difference in striping on the elytra. This zoologist's only remark about the key was a somewhat triumphant one to the effect that he noticed that morphology "had to be used" in the very first couplet. He had already forgotten the main reason that I gave him the key, which was that one year before he had told me that there were only three species of fireflies in his swamp!

Behavioral Study and the Development of Zoology

When men began formally to study animals, they started with <u>anatomy</u>, in the contexts of <u>medicine</u> and <u>classification</u> (or taxonomy). At first the mere acknowledgment that an animal can be divided up into namable parts or units (<u>descriptive</u>, <u>gross</u> <u>anatomy</u>), the study of anatomy became comparative with the realization of <u>similarity</u>, which in turn led to the development if not the immediate distinction and clarification, of the concepts of homology and analogy.

Anatomy, or morphology, is quite a different thing from behavior. It is something that is permanent, not fleeting. You can study it, think about it, draw pictures of it, and write about it; and all the time it stays there in one place so that you can check and re-check whenever you wish. One man could easily check another's results, and individualistic interpretations were not so easily defended. A true accumulation of knowledge could take place.

Anatomy has continued as a basic form of study in zoology for the reasons that (1) it has become increasingly repeatable (with better methods of preservation) (Repeatability, you will note, is at the heart of what has been called the scientific method, (2) it has been subject to finer and finer analyses (with the development of better and better microscopes), and (3) it forms the best link with past, extinct life through fossil remains.

The early anatomists seemed principally to be interested in animals similar to man, and the rise of medicine is intricately involved in early anatomical work. A second great usefulness appeared when Linnaeus developed his system of classifying and naming animals and plants, using principally structural or anatomical features that he could describe from dead specimens. Linnaeus never travelled far from the place of his birth, but he named thousands of animal and plant species from the far corners of the earth--brought to him dead and in various stages of preservation and decay.

With the rise of morphological study and the desire to classify and arrange the animals of the world, came the museums--places to store collections and type specimens. With the rise of museum work came the museum "expeditions"--trips by groups of collectors with the goal of bringing back well-preserved specimens of every animal species possible. The success of the trip was measured by the number of specimens brought back, for amount of information were usually equated with numbers of specimens.

On such expeditions, little or no time was spent observing the activities of animals--such things as how they lived, what they ate, or which ones mated with one another. Time taken from collecting was time wasted, and to take the chance of losing a specimen just so you could see what it was going to do next was considered to be a blunder of considerable proportion. The locality was recorded, often in a most exact and detailed fashion, so that later expeditions could come to exactly the same spot if they wished to check on a particular specimen. Still later, it became evident that the habitat of a specimen was important in determining its identity and the significance of finding it in a particular place. Long lists might be made of the plants and animals noticed where a particular species was found--especially if it looked like a new species. The studies of zoogeography and systematics--where animals live, how they got there, and how they are related to each other--were developing together.

Still more recently, biologists have become increasingly aware that the activities of species are often the best clues as to their distinctness and their relationships with one another. Frog calls, firefly flashing rhythms, bird songs, butterfly flight patterns, moth odors, ant swarms, dragonfly territorial flights, and cricket chirps are samples of the kinds of behavior that taxonomists have found to be important in identifying and classifying species. But not until recently have taxonomists been willing to admit that they use such things in taxonomy. B. B. Fulton, the man who originally inspired me to work on crickets, wouldn't describe his new species that he found by their chirps. He told me he "didn't want to incur the wrath of the museum taxonomists." Although he, W. S. Blatchley, and Harry A. Allard are the only old-time North American orthopterists whose work stands with few or no alterations, none of the three, except probably Blatchley, considered themselves systematists, and neither did the "professional" orthopteran taxonomists.

When I have used a tape recording to plot distributions, I have on occasion been challenged by fellow taxonomists who ask me "Where is the specimen?" I say that the tape is the specimen, but this is not satisfactory. Why is a piece of a carcass more adequate than a song record? Each is a part of the animal's phenotype, and each is subject--perhaps equally subject--to errors of labelling and identification.

Recent increases in emphasis on the nature of animal activities have brought about startling changes in the activities of taxonomists. Less time is spent making exhaustive analyses of the measurements of dead specimens or skins, and more time is spent recording and describing what the animals do while they are alive. Biologists on expeditions for museums sometimes are as frequently found studying the activities of their animals as they are actually collecting or preserving them, and when they return from the trip their principal loads sometimes are cages of live animals. Taxonomists have been assisted in this important shift in their activities by the development of some really important tools. Complex photographic equipment, high fidelity portable tape recorders, and other means have been developed for preserving behavior patterns for later analyses and comparisons. One of the most dramatic of such tools in my experience is the electronic "eye" that Jim Lloyd can point at fireflies in flight and obtain a tape-recorded beeping pattern corresponding to the flash pattern, set at any frequency he desires. Remarkably effective methods for keeping animals alive in the laboratories, observing their activities, and hybridizing different species have been developed. Perhaps most important of all are the modern means of travel available to taxonomists. No longer must they rely upon the whims of wealthy explorers or the occasional, laborious, and unwieldy expedition. A New York biologist with special interests in a group of animals in Trinidad can step aboard a jet plane and be out in the field hard at work in a few hours. Taxonomic biologists can be found in all parts of the world. I happen to believe that the days of proxy collectors are about over. Few top-notch systematists are going to settle for someone else sifting through the habitats where their animals live and bringing back the fragments they find.

Going back to the early days of formal zoology again, just as Aristotle's "body of facts" became more important during the early Christian era when authoritarianism was the sign of the times than the spirit of inquiry which developed them, so morphology, or anatomy, became, at times and to many biologists, particularly the taxonomists, more sacred than the repeatability originally responsible for its special value.

The study of anatomy has been followed by the development of a series of disciplines in biology that are well-known to all of us; descriptive embryology, physiology, genetics, and so forth. These are respectable portions of biology, well written up in all the introductory zoology textbooks.

But what has been happening to the study of behavior while all of this was going on? No one has ever denied that there is something definite called behavior, but, say, ten years ago, who had seen its history traced or its contributions welded into the developing pattern of zoology? A good argument can be made that it is the behavior of animals that characterizes them more than any other attribute--that, for example, sets their evolution off from that of plants. Why hasn't the study of behavior been at least cumulative enough to merit a tracing when zoological history is reviewed?

Actually, a variety of things had been happening to behavioral study during these first two centuries or so of zoology, and altogether they make a complex and interesting story.

A resurgence of anecdotal behavioral study occurred when Darwin's books were published. The idea of physical continuity inspired a search for mental continuity--evidence of "reason" in animals as well as "instinct" in man. Another began in the 1930's with the development of Lorenzian ethology, which we shall take up in some detail later.

C. R. Carpenter (1950:N.Y. Acad. Sci.) points out, with regard to the study of social life in animals:

"The prevailing 'climates of opinions,' including scientific value systems and attitudes of the majority of our research colleagues, are of such a character as to impose an unusual burden of proof on us for the professional status of our efforts and achievements. Those of us who are interested in comparative behavior, naturalistic behavior, and interactions of organisms are required to accumulate, and even dramatically to present, an overwhelming weight of evidence on very significant theoretical problems for these areas of research effort to be accepted and duly accredited. Our work is put into a disadvantageous position by the historic flood of poor natural history writings in our fields of interest. At the same time, the prestige of our work is not greatly enhanced by excellent qualitative writings during this quantitative-laboratory age."

Two nineteenth century trends in behavioral study were associated with anecdotalism, anthropomorphism, and natural history, which we ought to note. A strong feeling best termed anti-anthropomorphism set in in the late nineteenth century. Morgan's canon was illustrative of this trend; part of William Morton Wheeler's tirades were against it; Loeb's tropism theory, and the battle between mechanists and vitalists, carried on right up to the present arguments between people like Konrad Lorenz and Daniel Lehrman, and J. S. Kennedy and W. H. Torpe, are outcomes of it.

The connections with religious feelings and attitudes in behavioral study was not so surprising, for clerics worked hard to broaden the gap between man and animals, doubly so following the evolution backlash in post-Darwinian times. And underlying any evolutionary study of behavior is the eventual question of how man became a man, and in what way his mental evolution was a continuous process. One thing I must mention as an entomologist.

The entomologists never were too much disturbed by "anti-anecdotalism." They kept right on describing in detail how insects lived--species after species after species--but they called it bionomics, biology, life history, and almost anything but behavior. Fabre, Wheeler, the Peckhams, von Frisch, and many others--J. P. Scott (1958, Animal Behavior) a mammalogist, put it, "for a while social behavior was little more than a branch of entomology."

The Rise of Ethology

The development of the particular branch of behavioral study now known as "ethology" began to flourish following the Second World War, but it had its origins much earlier. One of the important individuals involved has been a German zoologist named Konrad Lorenz, who wrote his first influential paper in 1935, titled: "Der Kumpan in der Umweld des Vogels" (The Companion in the Bird World). The ethological "movement" probably has to be described as the first sustained effort by zoologists to analyze animal behavior on a wide scale. The history of its development and its impact on psychology and zoology is both fascinating and instructive, and I am going to trace it here in some detail.

This story is one of the most interesting in all of biology because it has involved not only personalities and biological issues, but religious, philosophical, racial, political, and ideological differences as well. Perhaps it has revealed again man's inability to examine objectively the characteristics of animals that lie closest to the bases for his own ability to introspect and calculate and contemplate. In the history of ethology we will find, in succession, pre-World War II writings by a German accused of supporting Nazi views of racial superiority and of writing anti-semitic articles--more vehemently by a succession of Jewish comparative psychologists in America. A highly religious British zoologist has been accused, along with most of the other ethologists, by a British member of the communist party of being vitalistic, dualistic, and Freudian in his behavioral theories. I have said these things bluntly, but I believe there is something both surprising and enlightening about discovering how many of the emotion-provoking and even internationally critical issues of a few decades can be woven into a story of this sort--on the surface seeming to deal with a purely "scientific" subject, somehow removed from the problems of human relations. Perhaps, it only shows how inseparable are the study of man and the study of the rest of life--at least animal behavior.

The word ethology comes from the Greek word ethos. According to Mayr (In Schaffner, 1955), there are two Greek words which translate as ethos in English, one meaning "habit" or "custom" and the other meaning "character" (Mayr wonders if "ethics" did not come from the latter word). John Stuart Mill (1943) used the word to mean "the science of character," and A. F. Shand (1920) continued this use. But apparently the first zoologist to use the word to refer to animal behavior was our old friend William Morton Wheeler, who in 1903 wrote a paper titled: "Ethological observations on an American ant (Leptothorax emersoni Wheeler)," which he published, interestingly enough, in the Journal für Psychologie und Neurologie. Oskar Heinroth (1910) used "ethology" in a paper on ducks, and Lorenz then used it in his writings, probably causing the first widespread use of the term with his 1950 paper on "The comparative method in studying innate behaviour patterns." Lorenz himself has defined ethology as "that branch of research started by Oskar Heinroth." Thorpe (1961) says: "The word ethology in English originally meant 'the interpretation of character by the study of gesture.' Some 35 or more years ago (1926±) it came into general use among zoologists to signify the comparative study and analysis of the instinctive or stereotyped movements of animals. It came to mean, in fact, the comparative anatomy of gesture of animal species. This zoological use was actually a narrowing from a wider scientific use prevalent in the early years of the century, when the term ethology was sometimes used to mean simply the scientific study of animal behavior. The present writer is convinced that this wide use is the right, indeed the only logical, use for today, and the term as so defined has great convenience for the zoologist as a complement to the term ecology."

One of the reasons that it is so difficult to give a discussion of ethology that will satisfy everyone involved is the intensity and emotionality of the arguments that have surrounded it since the Second World War. So many specific connotations have grown up around the word "ethology," and so many different opinions have been held by its proponents, that like comparative psychology it will probably be viewed by students in the future as another temporary sub-discipline in the study of animal behavior. If so, it will have failed in one way in the effort to bring behavioral study back to the zoologists, although, regardless of the name that zoologists choose to apply to this field (it is increasingly called merely "animal behavior," "behavior biology," or "behavioral ecology"), the ethological movement will probably have to be considered most important in its genesis.

It is possible to consider ethology in terms of:

1. the reasons for its appearance.
2. the methods espoused by its proponents
3. the neurophysiological, hereditary, developmental, and evolutionary ideas generated by it and attributed to it.

With regard to the first, I think we can say that the zoologists had begun slowly to realize that psychology, by splitting off entirely from biology and perpetuating itself solely through association with human pathologies and problems, had forfeited its chances of ever solving a significant number of the zoologists' problems regarding animal behavior. It had become not only largely non-evolutionary, but on occasion even <u>anti</u>-evolutionary.

It is not surprising that the ethological movement began in Europe. In America, comparative psychology was much more prominent than in Europe, where psychologists had concentrated more completely on the direct study of humans. One has to believe that the complexity of the methodological and theoretical aspects of comparative psychology in America has constituted a considerable deterrent to zoologists who might otherwise have become involved in behavioral study. Perhaps it is significant that the behavioral study of insects and other invertebrates didn't suffer from the same relegation to amateurs and anecdotalists that plagued vertebrate zoology in America during the early 20th Century.

I think Tinbergen's (1963) remarks describe well the effects of the continual frustrating drifting of zoology away from behavioral problems:

"One thing the early ethologists had in common was the wish to return to an inductive start, to observation and description of the enormous variety of animal behaviour repertoires and to the simple, though admittedly vague and general question: "Why do these animals behave as they do?" Ethologists were so intent on this return to observation and description because, being either field naturalists or zoo-men, they were personally acquainted with an overwhelming variety of puzzling behavior patterns which were simply not mentioned in behaviour textbooks, let alone analyzed or interpreted. They felt, quite correctly, that they were discovering an entire unexplored world. In a sense this 'return to nature' was a reaction against a tendency prevalent at that time in Psychology to concentrate on a few phenomena observed in a handful of species which were kept in impoverished environments, to formulate theories claimed to be general and to proceed deductively by testing these theories experimentally. It has been said that, in its haste to step into the twentieth centruy and to become a respectable science, Psychology skipped the preliminary descriptive stage that other natural sciences had gone through, and so was soon losing touch with the natural phenomena.

"Ethology was also a reaction against current science in another sense: zoologists with an interest in the living animal, overfed with details of a type of comparative anatomy which became increasingly interested in mere homology and lost interest in function, went out to see for themselves what animals did with all the organs portrayed in anatomy handbooks and on blackboards, and seen, discoloured, pickled, and 'mummified' in standard dissections."

I think that the principal reason psychology has not answered the kinds of questions that zoologists must have answered about animal behavior is that it was never comparative, and in general, it is not comparative now, in the zoological sense of involving the identification of homologies and the study of relationships among organisms. "Comparative" in psychology is very much like "comparative" in physiology has been: it involves comparison of selected types without any particular reference to the question of relationship. The phylogenetic variable is simply ignored.

Animal Behavior and Systematics

In 1905, four years after publication of De Vries' book, "The Mutation Theory," William Morton Wheeler delivered a lecture entitled: "Ethology and the Mutation Theory" in which, as he put it, he was "asked to consider the question as to whether the theory will apply also to the behavior or ethological, as well as to the morphological aspect of organisms."

Wheeler said several things in this paper that could have been said today, and I am going to quote a few of them, as illustrations of what entire lectures on the topic assigned me could be made up of. Ultimately I will get to what I think was the most important topic in his paper.

Wheeler said the following:

". . .in the field of possible observation the ethological tend to outstrip the morphological characters. We observe great differences in habits and behavior between genera of the same family, between species of the same genus, and what is most significant, between individuals and even twins of of the same species. At the same time we may be utterly unable to point out the corresponding structural differences.. . . It is clear that the prestige of morphology has been artificially enhanced by a continual appeal to complex invisible structures. . . . What bold man, for example, will undertake to show us the morphological characters corresponding to such striking differences in behavior as are manifested by the horse and ass, by cats and dogs of the same litters, or children of the same parents. . . ? Whatever may be the truth concerning such structures, it is undoubtedly a matter of considerable theoretical and practical importance that we are able to detect ethological where we cannot detect morphological differences or characters."

Wheeler is telling us systematists, students of diversity, that behavior is the most diverse level of organization in living things; that it is the most diverse level of expression of the phenotype. I would like to make an additional point. Systematists are concerned, not only with kinds of characteristics likely to reveal differences but also with those likely to reveal similarities, relationships, and common ancestry.

Although it may not seem obvious, if Wheeler is right, as I believe he is, and ethological characters do indeed tend to outstrip morphological characters "in the field of possible observation," then they should be more useful in detecting relationships, homologies, and common ancestry as well as in distinguishing species, populations, and other genetically different entities.

Wheeler continues:

"We are certainly justified in regarding ethological characters as very important, as belonging to the organism and as being at least complementary to the morphological characters. If this is true, our existing taxonomy and phylogeny is deplorably defective and onesided. To classify organisms or to seek to determine their phylogenetic affinities on purely structural ground can only lead, as it has led in the past, to the trivialities of the species monger and synonym peddler. . . . The fact that the morphologist has so consistently either neglected or opposed the use of ethological characters in classification shows very clearly that in his heart of hearts he has never very earnestly concerned himself with the parallelism of structure and function. He is inclined to regard function, especially psychical function, as something utterly intangible and capricious. For does it not seem to make its appearance in the embryo or young after structure has developed, and to depart at death before the dissolution of visible structure? And are not our museums largely mausoleums of animal and plant structures which we can forever describe and redescribe, tabulate and retabulate, arrange and rearrange, without troubling ourselves in the least about anything so volatile as function?

"It is, indeed, not only conceivable, but very desirable, that a taxonomy should be developed in which the ethological will receive ample consideration, if they do not actually take precedence of the morphological characters. It is certainly quite as rational to classify organisms as much by what they do as by the number of their spines and joints, the color of their hairs and feathers, the course of their wing-nervures, etc. To regard our existing purely structural classifications as anything more than the most provisional of makeshifts, is to ignore the fact that the vast majority of organisms are known only from a few dead exuviae."

If all that is any less pertinent today than when it was written in 1905, than I am unaware of the fact.

Wheeler is now telling us that we cannot have a "whole" taxonomy which does not include functional as well as structural characteristics. No one would disagree with him--not even the thousands of systematists who wouldn't be caught dead including behavioral characteristics as integral evidence for their classifications and their hypotheses.

These arguments have not changed in the last 62 years. But I am interested in why they can be as appropriate today as then--in why zoologists turned behavior over to the psychologists decades ago, and have never clearly succeeded in recovering it in spite of repeated efforts and even when faced for a long time with the fact that psychologists have not been answering the kind of questions zoologists need to have answered about behavior. I want to know why, within zoology, the systematists have tended to leave the paltry amount of behavioral understanding that has developed largely to the "experimental" zoologists.

In his book, "<u>Adaptation</u> <u>and</u> <u>Natural</u> <u>Selection</u>," George C. Williams (1966) suggested that the problems of understanding selection, behavior and adaptation are not going to be solved by the methods of systematists. I take issue with this statement in one regard. There is a lot of narrow-minded systematic work which will not solve such problems. On the other hand, I really doubt that these problems are going to be solved until the systematists get heavily involved in them.

Now what's a systematist? I think a systematist is anyone who carries out broadly comparative work that includes phylogenetic relationships as a significant variable, or anyone who takes as his specialization in biology a group of organisms rather than a set of problems such as the nerve impulse or muscle contraction of something similar.

I am reminded by this of the Wigglesworth Law and the Inverse Wigglesworth Law. V. B. Wigglesworth is reputed to have said that for every problem in biology there is a group of organisms most admirably suited for its study. The Inverse Wigglesworth Law which followed quickly must have been formulated by a systematist, for it says: For every group of organisms there is a set of problems, for the study of which that group is most admirably suited!

Wheeler seems to me to have been speaking of a related problem when he said:

"There are, of course, enormous difficulties in the way of constructing ethological classification, quite apart from the fact that our knowledge of behavior is even more fragmentary than that of structure, as anyone will realize who tried to write an ethological description of some common animal or group of animals. In morphology the elements of description can be treated as parts of an orderly and traditionally respected routine, but in ethology we still lack the necessary preliminary analysis of the more complex instincts, and are therefore unable to construct uniform and mutually comparable descriptions. One great desideratum in ethology at the present time is a satisfactory and sufficiently elastic working classification of the instincts and reactions, like that of the organs and organ systems of the morphologist. Such a classification can be developed only by comprehensive, comparative study of behavior in a number of genera and families and not by any amount of intensive study of a few reactions in a few species."

Wheeler's remarks lead to three conclusions with which I agree:

1. Behavior is the most diverse aspect of the phenotype, and systematists are the biologists most emphatically concerned with diversity.

2. Behavior is the most directly selected aspect of the phenotype. Recently, a botanist put me on the spot by suddenly demanding an answer to the question: "Well, what is animal behavior anyhow?" I didn't want to show any hesitation in front of a botanist, so I just blurted the first thing that appeared in my mind, and it came out: "Behavior is what animals have interposed between natural selection and the other (morphological, physiological) aspects of their phenotypes."

I have thought a lot about that definition a good deal, and I don't think I want to change it.

3. Behavior is the aspect of the phenotype most indirectly and complexly related to the genotype.

It is in this third statement, I suspect, that we can find a most prominent reason for the reticence of systematists concerning the use of behavioral characteristics. They want to know that the variations they use have a genetic basis, and so they have believed the experimental biologists who have told them that they must know all about the development of a behavior pattern before it can be trusted. They know how much they can change their own behavior, and so they are suspicious of variations in animal behavior, and they find it easy to believe the psychologists that all behavior is "learned," one way or another, without going to the trouble of figuring out what this actually means.

This dichotomy, incidentally, between learned and unlearned behavior, is in my opinion one of the most troublesome things in the study of animal behavior. It never has disappeared, from the time of the Greeks. Instinct and learning, innate and acquired, learned and unlearned--and the last attempt to make it respectable by cloaking it in new terms is in a recent textbook of animal behavior where it is called "endogenous and exogenous." I am going to say more about this later if I have time.

A few weeks ago I sat on a committee in which a group of behaviorists reported a list of problems in animal behavior that they thought are important today. I put down this set of problems so that I could read it, to give an idea of what the behaviorists think is important about their field:

1. Ontogeny of behavior

2. Behavioral genetics

3. Neural bases of sensory coding and coordinated movements
4. Biological rhythms
5. Behavioral neuro-edocrinology
6. Physiological bases of motivation
7. Emotionality and stress
8. Alertness, attention, sleep, wakefulness, etc.
9. Learning, conditioning, memory.
10. Higher neural functions.
11. Biology of mental deficiency, mental disease, and behavioral aberrations
12. Spatial orientation of animals, taxes, migrations, homing behavior
13. Ecological and evolutionary relations
14. The problem of the relationship between human and animal behavior

Of these items, the second and the thirteenth, I think are of most interest to us. Ultimately, all of them must be of interest to systematists, for, as I have stressed, systematics cannot ignore any kind of data in biology.

The ecological and evolutionary aspects of behavior are of most direct interest to systematists, and this group of behaviorists broke this topic down further into: the role of behavior in differentiation of the species and in isolating mechanisms; the comparative anatomy of behavior ("Not an active area but needs doing"); the ethogram as an important part of the data on comparative relations ("The natural history of behavior is in the same state that comparative anatomy was in 150 years ago"); changes in the gene pool as a result of selection; population density and behavior; habitat selection; migration; social organization; and some others.

Pause for Questions

Question: Hasn't some of the technology of the last fifty years been extremely important in the study of animal behavior--for example, the equipment that makes it possible to analyze crichet chirps?

RDA: Yes, and that's a good point to bring up. Sound recording and analyzing equipment, for example, is only about 20 years old. A man now at The University of Florida, James E. Lloyd, has just figured out how to translate firefly flashes into sounds and then tape-record them for later analysis. He is using the sound-analyzing technologies, in other words, to solve the problem of analyzing firefly flashes. The people working with chemical communication are still somewhat behind, but are beginning to use gas chromatography. Many of the techniques and equipment used by behaviorists are very new and very important. But just plain watching has not gone out of style, either.

Question: I realize that your purpose is to emphasize behavior, but isn't it true that use of behavioral characters by systematists involves the same problems that are involved with morphological characters? That is, one still has to deal with such things as convergence, and even worse, . . .

RDA: Yes, that's true, but, after all, that is the way evolution works . . .

Question: Yes, I understand, but unfortunately behavior is frequently very plastic. People working with arthropods don't have the same kind of problems that people working with vertebrates have, but . . .

RDA: Well, let me ask a question to that: Do you know of any species differences in behavior in any organism that you have some reason to suspect, or that anyone at all seems to have a reason to suspect, do not have a genetic basis?

Question: I don't suppose there is any aspect of any animal that doesn't have a genetic basis.

RDA: No, I said any difference that does not have a genetic basis. Let me give an example of what I mean. In 1961, in the symposium on vertebrate speciation held at The University of Texas, Lester Aronson and Ernst Mayr got into an argument concerning use of the word "innate"--or one of the words in that general category--in discussing behavior. Mayr finally said something like this: "When you have taught one species of spider to spin the web of another species, then I will give up using the word 'innate!'" I think this remark has some significance in connection with my question to you. A while ago a behaviorist remarked to me that studies on the genetic background of behavioral differences among species are largely trivial and useless efforts. When they involve rather nebulous things like whether an animal requires, on the average, say, 30 trials or 40 trials to learn a maze, then I would agree. But there are many areas of investigation in the realm of "transmission" genetics involving behavioral differences, particularly between species, that are by no means trivial, for they involve some of the best clues concerning the extent and nature of developmental influences on behavior, hence, the nature of selective action on behavioral development.

[Note added in proof: Recently, Jerry Hirsch (In Spuhler, 1967) has pointed out that if all the data concerning differences in intelligence between variously related humans are assembled, they make up a picture that looks just as it should if differences in intelligence were strictly genetic in their basis. He goes on to point out that our efforts to improve the educational environments of humans across the world mean that in the future observed differences in intelligence are going to be increasingly owing to genetic differences and less and less owing to environmental differences. I can't think of an example that would illustrate my point here any better.]

Just after I first brought up this question I happened to think of a species difference in behavior which may possibly have no genetic basis. The spring and fall field crickets, Gryllus veletis and G. pennsylvanicus, usually have sparse and dense populations, respectively. Density of population affects aggression: crickets reared in dense populations are non-aggressive, those in sparse populations become highly aggressive. One observes differences of the predicted sort between field-collected individuals of these two species, but the differences can be erased by reversing the densities in laboratory populations. Thus, it is at least possible that the consistent difference in aggressiveness between field-collected individuals of these two species may not be related to any genetic difference at all.

Question: Well, since you brought up spiders as an example, I will use them too. When one tries to solve a problem in systematics, of course he uses every characteristic he can locate. Behavior has been useful in spiders, at the species level and at all levels, but it also gives some trouble. For example, there are two groups of spiders which build orb webs, and anyone just looking at the webs would think that these are the same types of spiders. But a look at the morphology of these two groups reveals rather basic differences. And after synthesizing the two kinds of information one comes to the conclusion that these are two different evolutionary lines. An orb web is just the most efficient way of catching prey, and these two lines have converged, now having almost identical web forms.

RDA: And if you looked back at the webs a little more closely, you would probably find something about the differences between them that would tell you that they are independently evolved.

Question: Yes, I'm sure of that--for example, you might find that there is a basic difference in the protein structure of the silk. But what I wanted to say is that it is really the synthetic approach that yields the most appropriate answers.

RDA: I certainly agree. That's why my phylogeny, if I may call it that (which I showed you on a slide a while ago), for the field crickets of eastern North America included life histories, songs, morphology, behavior, habitat, and other things. You remind me of something that happened as a result of one of the first papers I published, titled "The taxonomy of the field crickets of the eastern United States." Many people who read it said I should have titled it the taxonomy and biology of the field crickets because it contained much information that was not taxonomic in nature. I was stubborn, and I believed that all the information used was indeed taxonomic and didn't need any other name (One result of that was that no one wanted the reprints!). But a curious opinion has been expressed regarding that paper, to the effect that I am "that guy who describes new species on the basis of song alone." In fact, I have never done that. In the particular paper I mention, one can find considerable information on morphology (in fact, a repeat of all those morphological features studied by all of the previous taxonomists dealing with this group) as well as on song, life history, ecology, geographic distributions, and even crossing experiments. Yet in 1961 an orthopteran taxonomist published a paper revising the genera of Gryllinae and when he came to those species I discussed he referred to them as "species or subspecies, whatever they may be"--or in words very similar. At first I gave him credit for acknowledging the possiblility that they at least might be different species, then I realized that this man has described practically all of his species on the basis of one or a few pinned specimens, most often brought to him by someone else!

I have wondered often if the kind of attitude that I have been characterizing is not related just to the fact that behavior is used at all in the papers involved. This is something like drumming individuals out of systematics not because of what they don't do, taxonomically speaking, but because of what they do in other fields or areas. B. B. Fulton, Harry Allard, and William T. Davis used behavior--but they avoided using it in their more taxonomic work. Fulton and Allard contributed mightily to the systematics of the Orthoptera through their behavioral observations, yet they have on occasion been omitted entirely from the ranks of orthopteran taxonomists. I have suspected for a long time that Scudder used song differences to distinguish North American field crickets, for he had them nearly correct away back in the nineteenth century, although his morphological distinctions are impossible to use or understand. I wonder if he left song out of his species descriptions because of the "prevailing climate of opinion" among taxonomists about such things? His classification was swept completely under the rug and has been there for more than fifty years now. Sometimes I think we have with our museums and collections built a monster which has been a terrible deterrent to systematic advance. Too many taxonomists have wielded their collections as weapons against the budding systematist rather than encouragements. Too often we have forgotten that the job of systematics is to solve certain kinds of biological problems, and collections were developed solely as a means to that end and have no other biological significance.

Question: Relative to the title of your paper, there is of course a problem of recovering the information in published papers, and the title should reflect as much as possible of the contents of the paper.

RDA: Oh yes, I agree.

Speaking of recovering biological information brings up an important point concerning behavioral study. I think that many of the old-time natural historians who worked out the natural history of wasps and other insects one hundred or more years ago knew as much about their animals then as anyone knows now, or can know. This bothers me very much, for it is an indication that behavioral study is not as cumulative as many other branches of biology. How do we make the study of the biology of animals a cumulative science? How do we record the behavioral characteristics of organisms in such a way that an accumulation of knowledge can occur? One of the current investigators who is really doing great work in this regard is Howard Evans in his studies on the comparative ethology of wasps. He is probably as closely focused on the kinds of things that interest me in regard to the relationship between behavior and systematics as anyone in the world. I noticed that someone reviewed his last book and lamented the fact that there were not more experimental studies in it. I think this lament is symptomatic of an illness in modern biology--the tendency to argue that there is some qualitative distinction to be made in biology between data derived from descriptive and comparative work and data derived from experimental work. There is not. Data are data, and descriptions, comparisons, and experiments are not different in kind.

Question: But we have had trouble with the anecdotal nature of many observations.

RDA: Yes, largely because of anthropomorphism.

I will give another example along the lines of comparative and descriptive biology before stopping for coffee, and for it I would like to use man. I gave this example at Ann Arbor and someone said he was surprised that I "emphasized" man so much. I don't wish to emphasize man, but use this merely as an example.

We know that man evolved from apes. As George Simpson says, we always want to say, well, not really from apes but from the cousin of apes or something like that. But, he says, if what we evolved from was walking around today it would be called an ape, so we should really stop pussy-footing around.

What we don't know about man's evolution is how he evolved from an ape. We don't know what the selective action was that caused man's brain suddenly to enlarge. What caused men with larger brains to outreproduce men with smaller brains? How did man's brain make its dramatic departure from the general kind of brain possessed by other apes across the relatively short period of a million years or so? What was the nature of the selective action? We don't know. How will we find out? You say, well, we will have to scrape around at fossils. But we don't have many fossils, and I don't think, relatively speaking, we'll ever find out very much from fossils. But I do think we will find out. And I think the way we'll find out will be by comparative study. I think, furthermore, that we would have discovered by the same kind of evidence, in the absence of a single bit of fossil evidence, that man did indeed evolve from apes. We would have discovered this by comparative study that would have gone on long enough that we would have figured out on the side how evolution proceeds--its mechanics. The knowledge of inheritance, selection, mutation, isolation, and other evolutionary forces, together with information from comparative study of men and other animals, would surely have led us to the firm conviction that man evolved from apes. [Note added in proof: Desmond Morris' new book "The Naked Ape" points up the kind of comparisons I mean--whether or not one thinks any of the particular interpretations he makes are most reasonable.]

I think we can use comparative study to find out much about the history of selective action during man's evolution. For example, there seem to be four possible kinds of intraspecific competition or four different levels of intensity at which selection can operate on alternative genetic elements:

1. Indirect "competition": differential reproduction without direct interaction, and no confrontation between competitors.

2. Partial or complete exclusion of competitors from the best (or only) sources of food, mates, and shelter through aggressiveness and territoriality.

3. Elimination of competitors or potential competitors by killing them.

4. Intraspecific predation: cannibalism, or the elimination of competitors with food being obtained without additional risk or energy expenditure.

Of these four kinds of intraspecific competition, the first would usually result in the slowest evolutionary change, the others, in order, in increasingly rapid change. I think it is important for us to ask, with regard to man's evolution: (1) which kinds of competition were involved, (2) which were most likely predominant, and (3) what were the sizes and compositions of the units among which each kind of competition operated? That is, which operated only among individuals and which among social groups, such as families, of different sizes and complexities?

When I say that I think we can use the comparative method to solve problems such as this, it raises in the minds of some people the question: What is the comparative method in biology, anyway? Not long ago, an anthropologist expressed a not uncommon opinion in a discussion when he said that he wasn't quite sure what this comparative method is all about, but he didn't see how it could be very accurate or very useful. Someone should have been there to point out to him that it represented essentially the only source of evidence available to Darwin!

There is nothing mysterious about the comparative method as I am referring to it. Yet I am convinced that many systematists and other biologists who use it all the time scarcely know what they are accomplishing with it, are not sufficiently prepared to explain and defend its problem-solving value, and in any case could not give a clear exposition of its usefulness to systematics or to biology in general.

When I was trying to think of a good example to use to illustrate the comparative method this summer, I remembered a little discussion that I had gone through with myself relative to the question of speciation. After Bob Bigelow and I published our hypothesis that the two sympatric sibling field cricket species, <u>Gryllus</u> <u>veletis</u> and <u>G</u>. <u>pennsylvanicus</u>, had speciated without geographic separation by a process of accidental seasonal separation of adults, we got involved in some great arguments about the likelihood of this possibility. Some of the people in those arguments obviously had a great reluctance to admit that speciation might be possible without geographic separation even before they heard the hypothesis explained. It occurred to me that, even though I firmly believe that the vast majority of speciation occurs through geographic separation, I never had sat down and listed the reasons for my having this belief. When I tried to do it, they came out as follows. Unless I miss my guess, many of you would also have been unable to come up with this list of reasons, which reveal that essentially all that we know about speciation comes from comparative study.

We rely in the study of speciation, almost entirely upon information derived from the comparative study of a vast number of fragments of the speciation process. A bit of this one, a bit of that one, and the whole taken collectively, give us a composite picture that we can construct into a process from which we can predict rather precisely what must happen in any given individual case.

The picture that we construct, of course, (in over-simplified form) is that speciation in bisexual organisms usually occurs when populations become geographically separated and undergo divergence through divergent selection and differential mutations until they are sufficiently different to make hybridization either impossible or sufficiently disadvantageous that amalgamation is impossible. The evidence from comparative study which gives us this picture, I believe, can be summarized in five statements, as follows:

1. Practically all species are geographically fragmented. Geographic fragmentation, in other words, happens on a wide scale, and is likely candidate to permit much speciation.

2. These geographic fragments, taken collectively, show every possible degree of divergence from scarcely measurable up to what seems to be complete speciation. Geographic isolation, in other words, does lead to divergence of apparently the right sort, and in a great many cases.

3. Most sibling pairs or groups of species have a particular kind of geographic relationship: they are either allopatric or have relatively narrowly overlapping geographic ranges. This suggests that they were geographically separated in the recent past.

4. Cognate species are sometimes more divergent in the area where they overlap, suggesting that the contact there has occurred following geographic separation.

5. Pairs and groups of species that are not related--say, a pair of bird species, a pair of insect species, and so forth--often overlap in the same regions, suggesting a common geographic barrier that caused all of them to speciate. Often the probable barrier can be postulated with considerable confidence.

I predict, and I have some personal experience upon which to base this prediction, that no alternative to this process of geographic speciation will be widely accepted among biologists unless and until it can be documented in the same fashion--that is, until comparative study can establish sufficient replications of the individual steps in the postulated process to indicate the likelihood that it has gone all the way in one or more cases. In a paper in press in the Quarterly Review of Biology, I have tried to present such evidence for speciation by accidental seasonal separation of adults, postulated by R. S. Bigelow and me to have occurred in certain crickets.

This means, in part, that I think it is time we stopped fooling around with more theories, and more elaborate theories, about how sympatric speciation might occur, or could occur. Such theories are by now almost a dime a dozen, and can even be dreamed up by beginning biology students. The real question, as Ernst Mayr has pointed out, is the likelihood of their occurrence, and that question can only be answered if we get out into the field and accumulate the kind of comparative information that alone will tell us whether any particular postulated process does occur, and to what extent.

I would make one additional point about speciation and the kind of evidence from comparative study that I have just described. Many investigators seem not to realize that the list of facts I gave also represents a set of "criteria"--criteria against which one may in fact test whether any particular case of speciation that he wishes to examine is likely to have occurred as a result of geographic isolation. To take the extreme example, if none of the five statements I have just given seems to apply to, or coincide in any way with, the status of some particular pair of species, then I suggest that the investigator not only has an excellent reason for taking a closer look, but that he also has no right to assume that speciation in that case occurred as a result of geographic isolation without taking a closer look.

Ernst Mayr has said, and I appreciate the implication, that speciation is the most important single event in evolution. I have just argued that essentially everything we know about speciation has been learned from the classical kind of comparative study. I have also suggested that information from broadscale, even though relatively shallow, comparisons not only can enable us to predict with high confidence concerning specific cases, but also can provide criteria by which to test the significance of specific information about individual cases. This, I believe, is one of the best kinds of documentation of the power and usefulness of the comparative method in biology.

The kinds of evidence I have just been describing, incidentally, are those whose significance and validity are denied by anti-evolutionists--on a much wider scale than most people realize, I am afraid--and, further, whose significance is often downgraded and misunderstood, not only by physical scientists, but by many experimental biologists as well. Yet we rely almost wholly upon information from such kinds of comparative study for a wide variety of our concepts in evolutionary biology. It behooves us to understand this method thoroughly, and to be able to use and defend it facilely.

Life Cycle Changes and Sympatric Speciation in Crickets

(this section taken from notes)

Bigelow (1958) and Alexander and Bigelow (1960) postulated that Gryllus veletis and G. pennsylvanicus may have originated when a tropical species developed both egg- and juvenile-overwintering populations along its northern border. Masaki (1961) described a juvenile-overwintering population in the southern part of the range of the otherwise egg-diapausing species, Scapsipedus aspersus, sympatric with the parental population but with the adults of the two populations seasonally separated. In the eastern United States there is a temporally isolated, fall-adult population in the southern part of the range of G. fultoni, a species which farther north overwinters only in the juvenile stage and is adult only in the spring. Fulton (1951) and Alexander (1957) described temporally isolated, spring-adult populations in the northern part of the range of G. firmus. None of these temporally isolated populations is geographically isolated from the rest of the species.

These four cases all imply a connection between the appearance of a new life cycle and the multiplication of species. In fact, the presence of sibling species with radically different life cycles, such as G. veletis and

G. pennsylvanicus, is enough to raise the question whether the life cycle change contributed to the speciation process or was merely incidental to it. This question is particularly interesting with crickets and their relatives (1) because both of the common temperate life cycles occur within species as well as between siblings, (2) because no genetic difference is necessary for essentially complete temporal isolation of the relatively short-lived adults, and (3) because no case is known of spatial isolates with the two different life cycles, either sibling species or conspecific populations.

The next question seems to be: to what extent is it necessary or reasonable to postulate that geographic isolation was in some way involved in the development of life cycle differences between closely related species or populations of the same species? Alexander and Bigelow (1960), referring to G. veletis and G. pennsylvanicus, maintain (p. 477): "It is doubtful that the possibility of allopatric speciation could ever be completely ruled out, but the evidence suggests that geographic isolation is both unlikely and unnecessary in this particular case." Mayr (1963a), on the other hand, believed (p. 477): "It would be altogether unlikely for a population to adapt itself simultaneously to two different breeding cycles. Where a species evolves two such cycles it does so in different, geographically segregated, populations . . ." [and] "It is rather probable that the difference in breeding cycle of [G.] pennsylvanicus and [G.] veletis was not yet complete, when they first met, after emerging from their geographic isolation. If so, competition eliminated any tendencies for spring breeding in pennsylvanicus and of fall breeding in veletis." Alexander (1963) discounted the likelihood of Mayr's interpretation, pointing out that certain species have in fact evolved two cycles in one locality, but Mayr (1963b) responded (p. 206): "To me, at least, it would be far simpler to have the ancestral species of the veletis-pennsylvanicus group split into at least two border populations, one let us say east and another one west of the Appalachians, furthermore, to assume that in one of these egg-overwintering was more advantageous, in the other one, juvenile-overwintering, and that with the post-Pleistocene improvement of the climate, the two populations could overlap and coexist, owing to their previously established seasonal separation." Mayr concluded by repeating his earlier conclusion that "in not a single case is the sympatric model superior to an explanation of the same natural phenomenon through geographic speciation."

Mayr's (1963a) postulate that seasonal separation was completed because of competition following establishment of sympatry brings up some points evidently requiring clarification. Two kinds of competition could be meant: (1) between adults at mid-season, particularly in connection with reproductive activities, and (2) between juveniles of the two populations, or between juveniles of one and adults of the other, particularly in connection with food. It is difficult to imagine how either of these kinds of competition could be eliminated by shifts in life cycle. First, adult and juvenile crickets (possible excepting very tiny juveniles) live in the same places and eat the same things. Competition of the second kind, therefore, probably still exists between veletis and pennsylvanicus, and seemingly could not be changed by any possible shift in their life cycle. Second, competition (or interference) between adults of the two species also could not easily be construed to shift the life cycle, though it might adjust slightly the timing of the adult periods. The cycle itself is evidently restricted by possible over-wintering stages; there are no known intermediate overwintering stages between eggs and late juveniles and, therefore, no seasonally intermediate periods of adulthood. The only possible "intermediacy" is represented by late adults of veletis or early adults of pennsylvanicus, but veletis and pennsylvanicus currently have about the same adult periods as other univoltine crickets overwintering respectively as juveniles and eggs, and lacking seasonally different, sympatric siblings. No evidence exists, therefore, that competition between veletis and pennsylvanicus has materially affected their life cycles.

Because of the history of the discussion about the significance of seasonal isolation in speciation, and the general attitude among biologists toward the possibility of speciation without geographic separation, it seems useful to account for other disagreements between Mayr (1963a, 1963b) and Alexander and Bigelow (1960) and Alexander (1963).

Mayr (1963b) (1) says that it is not stated how the northern and southern populations of a species such as the ancestor of G. firmus might have been geographically separated so that a process of allochronic speciation could occur within the northern segment (which Alexander and Bigelow suggested it may illustrate in part for this particular case of veletis and pennsylvanicus), (2) believes that not one but a series of peripheral isolates would have been involved, (3) suggests that there may have been an east-west split between two such border populations (contrasting this with a north-south split), and (4) believes that one isolate became solely juvenile-overwintering and the other solely egg-overwintering, and that speciation occurred allopatrically between them.

Concerning the first point, geographically isolated populations of G. firmus in the inland sand hills of North Carolina were first described by Fulton (1952), and later discussed by Alexander (1957), who noted that they hybridized with coastel populations (unpubl. tests by Fulton) and had the same song. Additional inland populations in Alabama have been found since then, some of which contain individuals with different life cycles. The example of a north-south split is, therefore, already before us in the proper species group, the right geographic locations, and (at least today) the right climate.

Second, the number of successful peripheral isolates does not seem to be important in assessing the significance of seasonal isolation in causing speciation. In fact, the more isolates there are, the more likely it is that allochrony was involved in this case, and the less likely it is that allopatry was more than incidental to the speciation process. The reason for this assertion is the following: if a species tends to produce populations with two kinds of life cycles, as, for example, G. firmus does, then an increased number of isolates will mean it is less likely that none contains both life cycles. The almost universal success of breeding tests among related Gryllus species that overwinter in the same stage, and the absence today of song or ecological (habitat) differences between veletis and pennsylvanicus, indicate that any persistent, double-cycled, ancestral population would have contributed genes to both incipient species. Accordingly, the significant isolation would still have been temporal from the start, and whatever geographic isolation occurred would have been quite incidental. In other words, speciation would have occurred in the north even if every isolate had been doubled-cycled. Furthermore, unless the temporal isolation were effective as an extrinsic separator (in fact, capable of causing speciation), double-cycled populations would tend to destroy the effects of prior geographic separation when they became sympatric with geographic isolates (incipient species) that had developed different, single cycles while living in different places. In other words, even if there were evidence that geographic isolates sometimes develop different cycles (and there is none), we are not free to consider the fact by itself until we can eliminate the likelihood that double-cycled populations will also persist.

Third, whether the split, or separation of double-cycled northern populations from southern non-cycled populations, is "east-west" or "north-south" does not matter as long as it took place somewhere in the northern part of the range of the species--or in the region where there are mild winters, as there are today in the sand hill region of North Carolina where an "east-west" split is known to have occurred in G. firmus. Mayr's postulate of an east-west split on either side of the Appalachians is not unreasonable, but it confuses the issue since the only important point is that the involved populations must be separated in some fashion from the continuously breeding populations farther south in Florida; otherwise the latter would provide a means of indirect gene exchange between sympatric northern spring- and fall-maturing populations. This required break has no relevance to the question of geographic isolation between the two northern populations, which need never be allopatric during their speciation; three species, not two, would result from the one geographic discontinuity. Likewise, the particular timing of the geographic break relative to the genetic divergence of the sympatric northern populations from one another is of no relevance.

Mayr's fourth point of concern--whether life cycle differences now existing between siblings arose during allopatry or during sympatry--is evidently the only critical one.

First we should check natural populations for evidence. The four cases I have already mentioned are pertinent: Gryllus firmus, G. fultoni, G. campestris, and Scapsipedus aspersus. In all four cases populations with the two kinds of life cycles coexist in the same regions, in the southern part of the range of the three more or less northern species and in the northern part of the range of G. firmus, the only southern species. Recourse to natural situations, therefore, does not support Mayr's argument, for in no cricket, and to my knowledge in no other arthropod, are there allopatric populations with seasonally staggered life cycles correlated with different overwintering stages.

This finding is no surprise. The kind of life cycle shift it would involve can occur in three possible ways: (1) a continuously breeding population moving north in two or more locations could develop one kind of life cycle in one place and another in the other place, (2) one or more populations already having a single life cycle could make a complete shift in one generation to the other cycle, or (3) one or more single-cycled populations could develop a double life cycle and then lose the original cycle through extinction (shift slowly from one cycle to the other).

No case is known of the first of these three possibilities, which has already been discussed. But we should note that if it is used to account for the origin of species such as G. veletis and G. pennsylvanicus, two problems are introduced. First, if a third (southern) derived species is involved, such as G. firmus in this case, then the near-identity of veletis and pennsylvanicus in a variety of regards in which they differ from firmus, such as chirp rate and pulse rate in calling, number of file teeth on the tegmina, and general size and body form, must be accounted for by parallel evolution or divergence solely by firmus from the common ancestor. Second, we must wonder why, in species like firmus and fultoni, all populations with one of the two possible cycles are inevitably small, sympatric portions of a large population with the other cycle; likewise veletis has never been found without pennsylvanicus, though pennsylvanicus occurs without veletis in Nova Scotia.

The second possibility above, a sudden shift in one generation of an entire population from one life cycle to another, seems too far-fetched to consider seriously. Only slightly less likely is the third possibility that some individuals would shift cycles and those with the old cycle would subsequently disappear leaving only the new cycle. But if we must involve allopatry this seems to be the only possibility. Requiring allopatric development of life cycle differences when sympatric duality in life cycles is known is to require not only a more complex hypothesis than is necessary, but a more complex one that is suggested by the facts.

Suppose allopatry is not required. Can the pairs of seasonally different populations persisting today, completely sympatric with members of the larger (parent) population still possessing the other (original) cycle, fail to diverge, over-wintering as they do in different stages and being subjected to different temperature and photoperiod regimes during the various parts of their life cycle? I believe that selection strongly favors divergence between such populations from the start, particularly in regard to overwintering behavior and physiology. Even if some gene flow occurred at mid-season between sympatric, differently cycled populations, or because of repeated shifting back and forth between the two life cycles, divergence would surely continue if only because of the selective advantage in the acquisition of different kinds of special overwintering characteristics, owing to the difference in the life stage that repeatedly enters winter.

One question that might be raised, and perhaps was involved in Mayr's objections, concerns the problem of survival of newly off-cycle individuals in the face of competition from the established population. Lewis (1966), for example, raises this question in attempting to describe how chromosomal reorganization may result in speciation without geographic isolation. That this problem is probably not pertinent to allochronic speciation in crickets is indicated by the coexistence of seasonally different populations within species.

If no gene flow at all occurs between seasonally cycles populations, then speciation would occur almost exactly as if the separation were geographic. If gene flow persists, however, then divergent selective action (roughly equivalent to a combination of disruptive selection and partial extrinsic separation) will result in speciation only if overwintering differences in some way eventually become linked to incompatibility.

Here an unexplained phenomenon enters the picture, at least with regard to *veletis* and *pennsylvanicus*. Among some 40 attempts to hybridize different cricket species, of which about half have been really intensive efforts, four of the five complete failures known to me have involved northern crickets with different over-wintering (diapause) stages. No hybrids have even been produced between species with different diapause stages, even though three investigators in North America (Fulton, 1952; Bigelow, 1958, 1960; Alexander, 1957, and unpubl.) have tried several cases. This is almost the only generalization about incompatibility between *Gryllus* species that can be erected at this time. Both copulation and oviposition (less frequent in the interspecific matings) occurred in all crosses tried by me, but no eggs hatched. Since populations of crickets consistently entering winter in different stages ought to develop appropriate diapause rather quickly, any strong reduction of gene flow between populations with different over-wintering stages could, therefore, cause an irrevocable shift toward total inter-sterility. This kind of divergence seems appropriately described in crickets as a "short route" to speciation, for total sterility is actually rare among sibling species of most or all kinds of animals. But early inter-sterility is not a required part of the process of speciation by seasonal separation outlined here.

Both spring and fall adults of *firmus* have repeatedly produced hybrids in matings with *pennsylvanicus*, but neither has hybridized with *veletis*. This may be an indication of ancestral northern affinities in *firmus*, and along with the more northward extension and greater northern abundance of egg-overwintering populations of *firmus* suggests a close relationship with *pennsylvanicus*. Because of this information, the possibility cannot be eliminated that *firmus* is a derivative of a *pennsylvanicus*-like ancestor, rather than vice versa. This would mean that, considering present distribution and sterility barriers, spring-adult *firmus* may be independently derived. It could also mean that *veletis* and *pennsylvanicus* may have diverged by production of a double-cycled population in the southern part of the range of a northern species rather than vice versa. This question affects the relative probability of the two models for allochronic speciation in explaining the origin of *veletis* and *pennsylvanicus*, but it does not reduce the likelihood that seasonal separation rather than geographic separation was the cause of speciation.

In summary, it would seem difficult to prevent genetic divergence between persisting seasonally different populations, even if they were sympatric, even if some gene flow persisted, and even if hybrids were not adult at the wrong season and did not enter winter during other than the two winter-hardy stages. The eventual result of such divergence would be two species that overwintered in different stages and were adult at different seasons, but had essentially the same habitats and occupied, at least initially, the southern portion of the parental range in the case of a northern species and the northern portion of the parental range in the case of a southern species.

There does not seem to be any easy way to derive *veletis* and *pennsylvanicus* except by one of the two possible variations of this scheme, which Alexander and Bigelow (1960) termed "allochronic" speciation in reference to the central role of extrinsic temporal separation. "Allohoric" speciation is a more specific term referring directly to seasonal separation.

It seems impossible even to gain an inkling concerning how frequently allochronic speciation may have occurred in various kinds of insects until intensive systematic-biological work has been carried out on a large number of temperate insect groups by investigators who are at least aware of the possibilities and know how the process can work. Such studies obviously have not yet been accomplished, for the possibility had not been considered prior to presentation of this case and that of Ghent and Wallace (1958). For at least three reasons I believe a large number of additional cases may be discovered:

1. Multiple-year life cycles and univoltine life cycles with short-lived adults are widespread among temperate insects (Pickford, 1953; Brooks, 1958; Alexander and Moore, 1962). Both involve potential temporal isolation of adults. As Walker (1964) points out, there is less expectation of rapid divergence in the case of multiple-year life cycles; geographic isolation of populations emerging on different years is also more likely, and is known in various cicadas (Alexander and Moore, 1962).

2. Unexplained variations in overwintering stage are prevalent in all major groups of temperate insects, both within and between species as presently recognized. Except for species with many generations per year, or long-lived adults that reproduce during successive seasons or cause overlap of generations, when such variations are intraspecific they lead either to multiple-year life cycles or to seasonal separation of adults. As an example of the possibilities, Brooks (1958) presents evidence that populations of a grasshopper, _Arphia conspersa_ Scudder, in Alberta, Canada, contain some individuals that mature in two years, overwintering first as eggs and then as juveniles and producing spring adults, and other individuals than mature in one year, overwintering only as eggs and producing fall adults. Walker (1964) described two populations of a coneheaded grasshopper, _Neoconocephalus triops_ that overwinter, respectively, as eggs and sexually immature adults and are sexually active during different seasons.

3. Cryptic species are abundant in every well-studied insect group, and most insect groups (tens of thousands!) have not yet been well enough studied to detect them. Every life cycle change that occurred within a temperate region could have involved allochronic speciation, and every pair of sibling species with different adult seasons and overwintering stages may properly be suspected of having speciated allochronically.

Even geographic speciation can only be inferred in the vast majority of cases. As a consequence there will never be a successful argument against those who insist that no alternative is possible. It does not matter whether this insistence takes the form of a flat statement of simply the rejection of all alternative hypotheses through construction of a geographic one that is continually altered and defended as more likely in the face of any and all evidence to the contrary. Speciation by other than geographic isolation may justifiably be inferred whenever sibling species are not geographically related in the ways common to sibling species, and when they simultaneously exhibit a striking ecological difference (such as a host difference or a life history difference) that separates their adults and does not appear to have arisen through competition or other interaction between the species. Such facts are not only inconsistent with a geographic hypothesis, they may cause the necessity of accounting for a geographic difference to become an onerous complication. If, under the above conditions, an alternative to geographic speciation exists that is reasonable in its totality, based on the characteristics of the organisms under consideration, and if intermediate steps in such a presumed alternative process are found in natural populations, geographic speciation may be an extremely unlikely possibility.

In view of the importance of explaining rates and distribution of speciation, I think it will be unfortunate if attention to extrinsic temporal isolation is delayed by lumping it with some of the more outlandish attempts to explain speciation without extrinsic isolation of any kind, or discouraged by pronouncements deriving from previous arguments over the old specter of "sympatric speciation" in the sense of no extrinsic isolation. On the other hand, even if field crickets were so peculiar that allochronic speciation turned out to be trivially infrequent, I think we would still want to understand it in this case.

Pause for Questions

Question: Have you any evidence to show whether behaviorally, either *veletis* or *pennsylvanicus* is more like *firmus*?

RDA: No. I would like to see if northern spring *firmus* are less likely to cross with fall *pennsylvanicus* than with fall *firmus* and, vice versa, fall *firmus* with *pennsylvanicus* more likely with spring *firmus*.

Question: Can you break the diapause so as to synchronize adults?

RDA: It is easy to synchronize them by manipulating temperatures.

Question: Can you rear them easily?

RDA: No, the cultures weaken and die out after a few generations.

Question: What do you mean by "hybridize?"

RDA: I mean, just the production of offspring. We get cross-mating between *veletis* and *pennsylvanicus*, and oviposition, but no offspring.

Question: Do the embryos develop at all?

RDA: I don't know. Bigelow has some information on that but I can't remember what it is.

Question: Does the song of one attract the other?

RDA: Yes, it should. They are identical.

Host Shifts and Sympatric Speciation

Now I would like to describe another possible case of "sympatric" speciation involving host shifts in host-specific insects. I suppose that if I ever publish this I will have to use a pseudonym or I will indeed be labelled as another "sympatric speciation nut!"

In the summer of 1966, I travelled through parts of western United States tape-recording, collecting, and studying the ecological and geographic distribution of crickets, katydids, and cicadas. My chief aim was to complete as satisfactorily as possible a survey of North American crickets. The western tree crickets had been treated recently by Walker (1962, 1963), using methods similar to mine, so I was not expecting new discoveries in the Oecanthinae. In western Nebraska, however, in the Wildcat Hills of Banner County, I tape-recorded and collected a tree cricket on Ponderosa Pine. Its dark green color and non-descript trill, together with its occurrence on a conifer, indicate that this cricket is related to two eastern species not known to occur within 2000 miles of the Wildcat Hills in Nebraska: Oecanthus pini Beutenmuller, taken from several species of pine and balsam fir and known from New England to Florida, west to Arkansas and north to Ohio; and O. laricis Walker, known only from tamarack (larch) in southeastern Michigan and hemlock in northwestern Ohio (Walker, 1963). Indeed, Ponderosa Pine is known east of the Rocky Mountains only in western Nebraska and eastern Wyoming, several hundred miles east of the rest of its range.

This discovery caused me to pay more attention to Ponderosa Pine as I continued west. Sure enough, in the western Rockies and the Sierras, I heard a non-descript trill from Ponderosa Pine. For several nights I simply tape-recorded the song and made casual searches for specimens. I expected that this cricket was the same one I had collected in Nebraska, and at the least had no doubt that it was distinct from all the other western tree crickets. This opinion was based partly on my knowledge of eastern crickets, specifically the failure of any species to live on both coniferous and deciduous trees, and the relative host-specificity of those living on conifers. I was not disturbed that its song was not distinct from other trills, such as those of O. quadripunctatus Beutenmuller and O. californicus Saussure, for simple trills of this sort differ only in pulse rate and often sound very much alike to the human ear, especially in mountains as regions where temperature variations are often considerable from one collecting spot to another. I cannot distinguish by ear the trills of O. laricis, O. pini, and O. quadripunctatus.

The geographic distribution of the "western pine tree cricket," as I was thinking of it, also reinforced my assumption of its distinctness, for it did not correlate with any other cricket in the area. I heard this cricket only in fairly large pine trees, usually well out of reach (as with eastern pine tree crickets), and only at certain altitudes, it seemed, within the altitudinal range of Ponderosa Pine on the western slopes of the Sierras. The other trilling tree crickets in this area included O. californicus, abundant across most western states on a wide variety of deciduous shrubs and scrubby trees, both above and below the altitude of the pine cricket and always in the low vegetation several feet beneath the tall pines containing the "mystery" species. Walker (1962) records O. californicus from oak, almond, chaparral, juniper, piñon pines, and "small spruce-like conifers in a scrubby area in New Mexico." But at that time I had not carefully read his description of hosts.

Near Mariposa, California, I climbed a succession of Ponderosa Pines and spent most of one night collecting, finally one male, one female, and one juvenile. The male was the second seen, and he was taken from a pine branch extending from a clump of pines full of this cricket into the foliage of a group of Gambel's Oak trees containing no singing tree crickets. As is common in such close intertwining of deciduous and coniferous branches, I needed only to trace the limb carefully to find the male, surrounded by oak branches, but perched on the single pine limb near its tip. I caught him by means of a ten-foot extension on my net handle.

I was astonished upon seeing these pine tree crickets, for they looked exactly like *O. californicus*, yellow-brown and broad-winged, and did not at all resemble the eastern pine cricket which are all more slender and greenish.

At this point I was convinced that the "western pine cricket" was a sibling of *O. californicus*, and was immediately intrigued by the ecological and geographic relationships of the two. The pine cricket seemed confined to a region wholly inside the geographic range of the more abundant *O. californicus*. It was more host-specific, lived on conifers, and was almost restricted to tall trees rather than shrubs and scrubby trees. Across more than two weeks of work, encountering both crickets nightly, it did not occur to me that they might be other than two different species.

I returned to the laboratory and made the interesting discovery that the songs of the two "kinds" of crickets are identical. Having a virgin female of *O. californicus* taken from oak and a male taken from Ponderosa Pine, I put the two together and watched their behavior. The male courted the female upon contact and she copulated with him within a few minutes, and repeatedly. There was no indication of incompatibility of any sort.

I am sure that these crickets are not different species. But this only makes their ecological separation all the more intriguing. There is no doubt that cross-mating between them is restricted by their ecological relationship. I am convinced that any individual is most likely to remain on pine or some deciduous tree, but not to travel freely from one kind of host to another. This bimodality, partly because of the host species difference and partly because of the difference in height from the ground, largely separates the breeding adults of the two populations, perhaps almost entirely separates them.

When I had been considering them as distinct species, and trying to figure out how they might have separated, I had started drawing parallels with the eastern conifer-inhabiting crickets and their relatives. *O. pini* and *O. laricis* are most similar to *O. quadripunctatus*, a species with the same ecological and geographic relationship to *O. pini* and *O. laricis* as *O. californicus* has to the western pine cricket. Further, in the East, pine trees are the first trees to appear in *quadripunctatus* habitat and they grow in clumps that increase in size and eventually contain massive center trees with no low foliage and are bordered by smaller seedlings. I reasoned, in fact, that the ancestor of *pini* and *laricis* could have separated from *quadripunctatus* in the same way that the pine relative of *californicus* diverged from *californicus*. It was difficult for me to see how this could have happened geographically, first because in all of these cases the host-specialized forms are well inside the geographic ranges of the host-generalized forms, and I didn't see how one could easily postulate the host shift in an allopatric form so as to leave no crickets on the general large array of non-coniferous hosts. Moreover, in view of what I had discovered to that point, an alternative, sympatric hypothesis seemed highly reasonable. If individuals of *O. quadripunctatus* or *O. californicus* occasionally got on low coniferous trees, stayed there successfully, and they and their progeny were inclined to remain on pine, then as the pines grew and lost their lower branches, ecological isolation from the parent species would be enhanced. If dispersing individuals favored pine, exchange between pines could occur. Life on conifers would cause divergent selection, evidently because of predation since *O. pini* and *O. laricis* are colored so precisely like pine and larch needles, respectively, and probably also in association with food, host-finding, and other characteristics. The great ecological separation of pine crickets and their close relatives is indicated by the confusingly similar songs of *O. pini*, *O. laricis*, and *O. quadripunctatus*, which may not even be distinctive to the crickets themselves (Walker, 1963).

Finding out that the western pine cricket is not a distinct species does not reduce the likelihood that sympatric speciation has occurred between tree crickets. By demonstrating that habitat bimodality can appear without allopatry, it instead increases the plausibility of sympatric speciation in these insects through a spatial-mosaic separation of adults by host preference.

Tree crickets eat both plant materials and other insects, particularly aphids. The next steps in understanding this situation of course, are to test individuals taken from each kind of host for host preference and mate preference, and if host preference exists to see how it is established, whether by genetic differences or effects of the host on juveniles. Hybridization tests may be useful, and geographic distribution of each form, including possible variations in range of hosts, need to be worked out. Some attention must also be paid to hints of peculiarities in host-specificity and morphological and song divergence of populations in other species such as with *O. nigriconris* F. Walker, (Walker, 1963). Additionally, I have found that near Provo, Utah, there is a "form" of *O. quadripunctatus* on sagebrush foliage yet interspersed with normally green individuals on grasses and weeds. The trills of the two forms are slightly different. Again, a host difference is associated with a divergence that occurs now, at least, well inside the geographic range of the more widely distributed, more abundant form.

These cases warrant further attention, specifically in regard to the question of whether or not speciation without geographic isolation is occurring. The possible process is a variant of that originally outlined by Thorpe (1930), involving infrequent shifts between specific host, with host preferences based on some kind of early experience, and breeding and oviposition of individuals restructed to the host on which they developed. The means of separating gene pools is thus clear; the geographic relationships of siblings are unusual; and intermediate steps in the postulated process occur within species in the same genus. Perhaps there is not enough evidence to argue that sympatric speciation is more likely than allopatric speciation in any case of tree cricket siblings. But there is enough to indicate that it could happen, may have happened, and may be happening and that special attention to this question is warranted in this case.

Pause for Questions

Question: Do these things have a one-year life cycle, only?

RDA: Yes.

Question: How do you figure the relationships among these species?

RDA: Morphologically and by song; they have the same color pattern, the same size and shape, and the same songs.

Question: Is the color confused by the matching of host color?

RDA: No, we use only the pattern--for example, the patterns of black spots on the antennae. Species groups in the Oecanthinae have similar patterns of spots.

Again, the only way we can solve the problem of the origin of host-specific pine tree crickets is by comparing all of the related species that occur on different hosts, or are variously host-specific, and, for example, by finding out whether any species are fragmented reproductively by host differences. In other words, our only recourse is to comparative study.

Raven: I certainly agree that sympatric speciation is a reasonable possibility and I also agree that this is a good way to approach it, but I want to ask you a couple of questions about the examples. First, how could you ever tell whether two species with life cycle differences arose in one place or two different places?

RDA: That's a good question, and I've often thought about it. One of the questions I've asked myself as a result is whether I have any evidence in any of the animals with which I deal that it is better to overwinter in one stage in one place and in another stage in another place? I can't find any such evidence.

Raven: Maybe it's a paradaptation . . .

RDA: Well, one also has to ask the question why there are no cases in which a species has geographically separated populations that overwinter in different stages when there are several that do show two overwintering stages in the same place and only one in another place.

Raven: Doesn't firmus have that in part? Aren't there some populations that are only juvenile-overwintering and some that are only egg overwintering?

RDA: There are only some that are solely egg-overwintering--none that are solely juvenile-overwintering. What happens is that the juvenile-overwintering population disappears as one goes north--as does the veletis population. I suppose that the ability of eggs to overwinter farther north than juveniles is one indication of what I'm looking for, when you come right down to it.

Raven: Well, it seems that allopatry and allochrony are equally likely, in this case, but it is interesting to distinguish the two.

RDA: They are not equally likely.

Raven: They seem so to me.

RDA: I wish I could figure out how to explain to you that they are not. You don't need geographic separation and there is not reason to introduce it here.

Raven: No, I don't say you need it; I just don't know how to exclude the possibility.

RDA: I can't exclude the possibility. That would be like proving that speciation occurred this way. You can't do that. Prove how any pair of species formed.

Raven: Yes. We have examples very comparable in the subgenus Diadrena where oligolectic species occur sympatrically and have differentiated. For instance, one is a spring-blooming plant and another one is an early summer-blooming plant closely related to it. These seem very parallel and equally likely to have diverged sympatrically. But I don't know how to prove it.

RDA: I don't know about that case, but one of the things that have been introduced here and has done nothing but add to the confusion is the question of species that are adult at different stages but overwinter in the same stage. For example, Orchelimum gladiator is adult in spring and early summer, overlapping only a little with it very close relative, O. vulgare, adult in late summer and fall. This could well be a result of interaction, with some kind of competition between the species causing gradual divergence having nothing to do with speciation itself and occurring only after allopatric speciation. This is an entirely different kind of situation.

Raven: But there could be some advantage to blooming at a different time, or in the case of your grasshoppers to being adult at different times if they were using the same food source. And in your second case, involving host specificity, you have to assume that something like that is happening for them to get from one plant to another. You have to assume disruptive selection.

RDA: With regard to veletis and pennsylvanicus, they could still be competing very much with regard to food, but the juveniles and adults--especially the late juveniles--eat about the same things. [Note added in proof: But in the case of host-specific species, it's not necessary to have disruptive selection except after the fact of accidental isolation by moving to different hosts and then staying there because of some kind of response to the host on which the animal grew up or has been feeding--independent of any advantage or disadvantage as such. Disruptive selection need not be involved until after this happens. If the populations are already separated, then the selection causing their divergence would be no more "disruptive than that occurring between two populations that happened to get on different islands--except, in my opinion, it would be more likely to be intense and effective between two populations on different hosts or with different life cycles than between two populations on different islands.]

I went through all that material on speciation partly because I wanted to promote the comparative method and argue for the need for more comparison in the study of behavior, and partly because I like to talk about speciation.

Behavior and Reproductive Isolation

An approach similar to that used in the analysis of speciation, and one that concerns behavior and also has been of great usefulness to alpha taxonomy in a few groups, has involved the study of reproductive isolating mechanisms. Reproductive isolation is so clearly the best understood liaison between behavioral and systematic work that I will go to some trouble to express some opinions that do not seem to jibe with much of the published, and evidently influential, literature, and to describe some of the arguments that underlie these opinions.

Although reproductive isolation is a relatively young subject, it has been discussed so extensively that one would suppose our ideas concerning it to be fairly well crystallized. Unfortunately, this is not the case. Presently, I think all of the good analyses of the actual reproductive mechanisms between pairs of species, in animals at least, can probably be counted on the fingers of one's hands. I say this in full awareness that some authors have been telling us that the literature on reproductive isolation is massive--so massive as to be almost not reviewable. This is not true. There is indeed a great deal of published information on courtship and mating behavior, and this is what our guides have been telling us is information on reproductive isolating mechanisms. But most of this information cannot be applied easily to questions about reproductive isolation. This is one of the ways that the study of animal behavior is currently out of focus; this would not be so if systematists were more involved in it.

I feel the same way about descriptions of mating behavior and their usefulness for studies of reproductive isolation as I do regarding descriptions of behavior in general and their usefulness for the analysis and understanding of behavior in general. One cannot just describe, sort of *in vacuo*: he must know what he's doing--what he is seeing in terms of life functions--before his descriptions are likely to make much sense or have much significance.

A few years ago, Paul Ehrlich said something in front of me that I sort of resented at the time. He didn't say it to me, but I resented it because of what I thought about it. He said, "You would never catch me studying the courtship of an animal unless I knew exactly what I was going to do with the information when I got done with the study." Frankly, I sometimes think Paul doesn't apply the same criteria to the study of morphological characteristics, but I understand what he meant. I think that as a result of carelessness in this regard of putting behavior into the proper life or selective contexts, what we are going to have to do in regard to much of the material being published in the behavior journals now is to start all over again.

You cannot go out and simply describe what you see in the courtship and mating behavior of a species, independent of where it lives, where and when it mates, with whom it lives, and to whom it seems most closely related, and expect to discover very much of significance to anyone interested in reproductive isolation.

To illustrate this point, I will use the example given us by the extensive and elegant work of Tinbergen (1953, 1960) on gull behavior. While Tinbergen has provided much fine information on displays associated with courtship and mating, and some questions and speculations about probable isolating mechanisms, I believe that he fails entirely to comment on possible species differences in eye ring color. Yet, as a result of extensive field study, Neal Smith (1966) has presented data to show that merely changing eye ring colors among species that are sympatric is enough to break up pairs that are already formed, or to cause pair bonds between individuals belonging to different species, which apparently does not otherwise happen in the area where he studied them. Smith and Tinbergen did not study exactly the same group of gull species. But I suggest that anyone wishing to account for reproductive isolation in Tinbergen's species would now want to examine eye ring differences; and so would anyone wishing to use reproductive isolation to explain species distinctiveness in the displays of Tinbergen's gulls.

Species-specificity can evolve in many contexts other than reproductive isolation. Some of the interspecific variations Tinbergen has described may once have been reproductive isolators, but are not any longer. Or they may be involved in one of the other two possible functions of what we call courtship behavior--either the selection of superior or more compatible mates within the species or the synchronization of behavioral and physiological events between the male and female in connection with parenthood. Both functions are more likely to be prominent in animals like gulls, which have long-term pair bonds, or strict monogamy in some cases, and complex parental behavior. Mere species-specificity does not in itself mean isolating mechanism.

The chief point I want to make is simply that a tremendously important species difference evidently had been overlooked because reproductive isolating mechanisms as such had never previously been investigated among gulls.

[Remainder of this section taken from RDA's notes]

Let me dwell a moment on the succession of questions Neal Smith asked about reproduction isolation among gulls, for I think this is a good model for any of us to use when we attempt to investigate specific cases. Here is the succession of questions he asked: (1) to what extent do the different species overlap geographically; (2) to what extent do they overlap ecologically; (3) to what extent do they overlap temporally (seasonally); (4) to what extent do they interact (behaviorally) where they do breed together; (5) what is the significance of any morphological differences among them; and (6) what is the significance of their genetic differences for hybridization and hybrids? Now, of course, this is just the old familiar list of possible isolating mechanisms; but it's the order that is important. Anyone who does not ask these questions more or less in this order will not know whether or not he is studying isolation mechanisms among his species, even if he does prove that, say, genitalic differences or gametic incompatibility prevent or partially prevent hybridization when sexually responsive individuals are brought together. If the chance of mating has never occurred in the field, then such differences may arise without ever having the opportunity to function in reproductive isolation. Under such circumstances they are neither isolating mechanisms nor isolating differences. They are just differences.

Many authors behave as though they think that any differences they find between species that breed in the same general area at the same general time are functional isolating differences or, even, evolved "mechanisms." In conjunction with this line of reasoning, it has become popular in recent years to speak, often glibly in my opinion, of "chains of partially effective reproductive isolating mechanisms." This casual approach misses the important point that some differences between species may never have been involved in their inability to interbreed or merge, or even in their living together without reproductive interference or competition. To use an extreme example, this is like saying that genitalic differences are reproductive isolating mechanisms between the Blue Jay and the White Oak, which happen to be sympatric, synchronic species that do not interbreed with one another. To take less "far-out" but equally ridiculous examples, it is like saying that genitalic differences are reproductive isolating mechanisms between two species of Drosophila that have always mated in different habitats, or between two species of cicadas that have never emerged as adults on the same year, or between two species of mammals that have never attempted cross-copulation.

A paper by Clark, Aronson, and Gordon (1954) on mating behavior in xiphophorine fishes has been referred to as a classic example of the study of reproductive isolation. But these authors did not investigate the interactions of the species of concern in the field; if the species do not even interact sexually there, then Clark, Aronson, and Gordon, too, may have been studying differences, but not isolating differences, and not isolating mechanisms in the sense of evolved isolating differences selected in the context of reproductive isolation.

Much discussion has been published on the question why, if selection works as I have just outlined, so many species that have never lived together have perfectly good pre-mating isolating differences already developed. The argument has been presented, evidently with much effectiveness judging from published references to this topic, that differences in pre-mating behavior between species living together usually arise not in the context of reproductive isolation at all, but in other contexts, and that they function only incidentally in reproductive isolation.

I believe that this argument (which sometimes seems related to a belief that sterility usually occurs before establishment of secondary contact between populations destined to remain separate) ignores the likelihood that, as reproductive isolation in the sense of minimal wastage of time and energy causes a focus on a few specific aspects of pre-mating behavior (such as calls in crickets, frogs, and birds, or odor in moths, or vision in butterflies), shifts in these characteristics in the context of reproductive isolation will be going on continuously. The result is that a species may be changed in a way that incidentally results in isolation from more than just the species causing the selective effect. A large proportion of species falling into this category must shift their most important pre-mating isolators a little almost every time any change occurs in the complement of species with which they live. Two unrelated species, after all, may have confusingly similar signals. I suspect, therefore, that many of what we might call "incidental" isolating differences are owing directly to selection for isolation between (1) one or both of the two involved species and (2) additional species with which one or both of them formerly lived. If this is true, we would expect to find that species in groups which have come to rely chiefly upon one or two kinds of isolating differences (such as calls), would be more likely to be different in those characteristics upon first meeting than would species in groups that rely upon several kinds of differences (such as, say, chemicals, vision, host specificity) in different sub-groups. On the other hand, if reproductive isolating differences ordinarily arise in other contexts, differences between these two kinds of groups would not be so obvious.

If all this is true, one should expect to find in acoustical insects and anurans:

(1) few cases of identical pair-forming signals among allopatric or allochronic species. I know of only five or six cases among the approximately 1000 known calling signals of insect species (Alexander, 1967).

(2) few cases of character displacement. I know of only two probable or possible cases among the same 1000 insect species (Alexander, 1967).

The next pertinent comparison, obviously, would be between groups like the calling insects or anurans, and other groups in which one particular kind of signal or behavioral unit is not universally involved in reproductive isolation. Unfortunately, the information needed to make such a comparison is not readily available.

The Comparative Method and Reproductive Isolation

I have been talking chiefly about experimental studies, and about detailed observations on individual cases. How is the comparative method used in studying reproductive isolation, and what are its special values? A most striking parallel can be drawn between the results of studies on the calls of anurans and various insects (specifically crickets, katydids, and cicadas), and, I might add, the work of H. S. Barber (1951) and James E. Lloyd (1966, other papers) on fireflies. I don't think there is a single finding on anurans that does not have a close parallel in these insect groups, and I don't believe that any results on anurans, or insects, conflict with any results on the other group. What I want to emphasize, though, is one specific point: There are now experimental demonstrations that call differences between sympatric, synchronic, closely related species are sufficient to enable the males and females both to distinguish their own conspecifics; at least one demonstration exists for anurans, and one for each major insect group in which calls are prominent in breeding behavior (Alexander, 1967). For a long time, however, there were no such demonstrations at all. Yet we knew even then, or I should say were highly confident, that the calls indeed do function in reproductive isolation, and we used them successfully and accurately as if they did. Our evidence, like that used in understanding speciation, was derived from broad-scale comparisons. It can be summarized in the following group of statements which to some extent parallel those I gave earlier for speciation:

1. The calling (or pair-forming) signals of species that breed at the same times and in the same places are never the same, except in a few newly established situations. This fact, based on comparison of nearly 1000 insect species alone, including essentialy all of the North American crickets, katydids, and cicadas, and many of the grasshoppers and fireflies there, suggests that, in these groups, no two species breeding together are exempt from selective action on reproductive isolating mechanisms until their calling pair-forming signals are specifically distinctive. This, I believe, is a critical bit of evidence, for it indicates that no one can effectively study reproductive isolation in any group without being specific about whether the species involved breed together, and for how long they have been doing so. I would point out that many studies on Drosophila mating behavior, even those supposedly dealing with reproductive isolation are either vague about geographic, ecological, seasonal, and daily overlaps in breeding, or they do not mention them at all. No wonder it sometimes seems easiest to behave as though the origin of reproductive isolating mechanisms only incidentally has anything to do with living together!

2. Calling signals of species that breed in different places, or at different times in the same places, are sometimes the same. This fact, based on six known cases in insects, four of geographic isolation and two of seasonal isolation (Alexander, 1967) makes the previous statement even more significant. This is interesting in itself. Why aren't there more cases?

Question: How many have been looked for?

RDA: Oh! How can I answer that question? My first thought is to say thousands! In the groups that Tom Walker, Tom Moore, and I have studied, we have certainly been looking for displacement in every instance in which we have recorded geographic variation in calls.

I will give you an example in which we expected to find it and did not. E. S. Thomas and I studied three meadow grasshoppers comprising the Orchelimum concinnum group, which provide an almost ideal model for the expectation of character displacement. They all have linear ranges, two forming semi-circular ranges and overlapping only at their ends in Michigan and Louisiana and the third extending between the circle formed by the linear ranges of the other two and also overlapping with both of them geographically, ecologically, and seasonally, yet the songs are no more different in the overlap zones than outside them. The songs, however, are quite different so perhaps the differences arose during sympatry in one place a long time ago, perhaps in Louisiana.

I think that in species like these, using acoustical signals, when there may be up to 50 such calling species in one area, any slight shift in the species complement may cause slight song adjustments. The species involved may not even be closely related if there are enough of them sympatric and synchronic. Perhaps this would cause much song divergence between cognate species during allopatry.

Let me go back to my list of statements.

3. Calling signals of closely related species that overlap narrowly are occasionally more different in the region of overlap than elsewhere, suggesting reinforcement of differences owing to competitive interaction. Two cases have been suggested in North American crickets (Alexander, 1967).

4. Calling signals represent the earliest unit in sexually significant encounters between males and females. From an a priori viewpoint, therefore, these signals are the most efficient possible part of the sexual encounter for the function of reproductive isolation.

5. Calling signals are more species-distinctive than any other aspect of the mating sequence, and there is a progressive loss of species-distinctiveness as one considers events that occur later and later in the mating sequence. This statement is based on our knowledge of call distinctiveness in several hundred (all known) insect species with pair-forming calls, plus a study of courtship, genitalic structure, and mating behavior in some ten subfamilies, 22 genera, and 50 species of crickets (Alexander and Otte, 1967).

Call differences are behavioral differences, and reproductive isolating mechanisms in established situations must be behavioral nearly all of the time, even if the behavior involved is associated with locating the habitat or host to which mating activity is restricted, or with being active only at certain times of the day, as in some fireflies. Behavioral differences, if available to selection, will always be more efficient isolators, in terms of wasted time and energy, because they operate before morphological or physiological, or late-operating behavioral differences will, I suggest, always be replaced by behavior as functional isolators as selection continues between species that remain sympatric and synchronic. This argument indicates that no one interested in reproductive isolation can avoid studying behavior, and I believe that no one interested in species and speciation can avoid studying reproductive isolation.

A writer using almost exactly the same title as mine today said last year that there is no argument that behavior should replace morphology as the main tool of alpha-taxonomy in distinguishing species. But it already has, for groups containing, collectively, somewhere between 25 and 50 thousand species (Anura, Ensifera, Caelifera, Auchenorrhyncha, Lampyridae) and in the case of acoustical and visual signals it has proved to be of enormous (I would say, unparalleled) value, not only in distinguishing species but also in locating and collecting specimens and in tracing geographic and ecological distributions and seasonal life histories. This approach is, of course, not applicable to all kinds of organisms, for reproductive isolating mechanisms of certain sorts may be very difficult to identify and measure. Further, this method does not help us with forms that have never lived together. But the advent of new techniques and instruments suggests that anyone serious about alpha-taxonomy in any group of organisms cannot really afford to assume that his organisms automatically fall into a category of being inaccessible taxonomically from this approach. After all, 15 years ago we couldn't study sounds objectively, and only five years ago there were no gadgets to record the subtleties of firefly flashes.

The Problem of Instinct

[This section from notes]

To this point I have said nothing about what has undoubtedly been the knottiest problem in the study of animal behavior, and the one responsible, I suppose, for deterring the advance of comparative study of behavior more than any other. We could call this the "problem of instinct," and most people would have a good idea what is meant. It would be more descriptive to term it the problem of the extent and nature of hereditary influences on behavioral variations, both between species and among the individuals of each species.

Adaptation is a result of selective action on alternative genetic phenomena. Therefore, it is a critical question for my topic which behavioral variations at least do correlate with genetic variations. Few people challenge the idea that species differences in frog and insect calls, or firefly flashes, or any other behavioral characteristics identified as reproductive isolating mechanisms in any kinds of animals, have genetic bases. Of course, we know from hybridization experiments now that insect and anuran cell differences do indeed have genetic bases, and in fact results from crossing experiments on crickets and frogs are probably cited more frequently in reviews concerning transmissibility of behavioral variations than any others from any other kinds of animals.

The systematist wants to know more about this. He wants to know he can be sure that he is not examining some behavioral difference that has nothing to do with hereditary differences. Some systematists and other biologists have gotten involved in long, bitter, and futile arguments about how much influence heredity has in contrast to how much influence environment has in determining the characteristics of particular behavior patterns.

Concerning this topic, we are pursued now by a whole string of admonishments: "To ask how much a given piece of behavior depends upon genetic factors and how much upon environmental factors is like asking how much of the area of a field depends upon its length and how much upon its width." "Nothing is inherited but the genotype and a little cytoplasm." "Heredity is particulate, but development is unitary." "Instead of speaking of this or that trait as genetic or environmental, the correct way is to ask yourself which differences in which characters, and to what extent, are due to environment on the one hand and to heredity on the other."

Konishi (1966) has recently written a paper which, I think, clarifies several of the issues that have been involved in this problem. He points out that one of our shortcomings has been that we have acted as though the formula is always true that, in behavior, stereotype = species-specificity = inheritance = central coordination = spontaneity = self-differentiation. These things are not strictly correlated, and, as with learning, what has been called "instinctive" behavior is therefore not really a unitary phenomenon, and it should not be treated as if it is.

But these issues are not all of great or immediate concern to the systematist or evolutionary biologist interested in behavior. What is of concern is predictability. And the likelihood is great that significant increases in predictability can be attained sooner in many cases by insightful, properly directed, broad-scale (even superficial) comparisons than by detailed studies of development of specific patterns of behavior in individual animals or species. The comparative anatomists, as many ethologists have emphasized, have already shown us that this is true. It would seem that we systematists have allowed ourselves to be led into being somewhat overly concerned about precisely how individual patterns of behavior develop. As a comparison, we do not know a very great deal, even in 1967, about the development of morphology in a wide variety of animals, but we do know a very great deal about speciation, adaptation, and phylogenetic history--all of it learned directly, almost solely, from comparisons of those very features of anatomy for which we still do not understand development.

When we have carried out broad-scale comparative studies of behavior similar to those available in anatomy and begin to acquire the glimmers of understanding that will come from predictiveness based on such studies, then those investigators concerned chiefly with the developmental bases of phenotypic differences will indeed have something to think about and work with. Since the question then becomes how to know <u>how much</u> genetic variation is involved, a considerably sharper focus should be provided for the investigations of many biologists who are now skeptical that broad-scale comparisons can be made in the absence of extensive information on developmental pathways and stimuli for particular behavioral units.

I expect this remark will raise some eyebrows, but I suggest that behavioral variations which look at first glance as though they might be useful to systematists, particularly those working at and above the species level, may rarely lack correlation with specific genetic variations. For example, as I asked before, would anyone here like to describe a species difference in behavior--that he has some cause to suspect does not have a genetic basis? Further, and of great importance, the extent and nature of correlations between behavioral variations and genetic variations, or their absence, is to a large extent predictable.

One aspect of such predictability can be exemplified by cricket calls. A slight understanding of cricket biology reveals that in most temperate species, only the eggs pass the winter. The auditory organs are not functional until maturation or near maturation. With only this information we can predict confidently that selection (at least usually) favors insulation from influences by environmental sounds in the establishment of the pattern of the call. For there can be no appropriate sounds available to copy.

On the other hand, only a little knowledge of passerine bird biology allows the reverse prediction: that most young birds probably have evolved specific ways of being influenced by their parents' song patterns. There are at least two reasons: the overlap of the young and adults each generation, and an apparent premium on individuality in song pattern, promoted by having part of the pattern learned, and associated with parental behavior and tendencies toward monogamy. Critical periods of song learning and imprinting of following behavior in precocious birds, are both predictable on this same general bases. Even the indiscriminateness of suitable stimuli for imprinting of following behavior is predictable, for the situation is such that unsuitable stimuli are not likely to be available, and selection will therefore have no chance to focus on a restricted group of them.

Likewise, we would predict that different populations of birds within species should sometimes have song differences that lack genetic bases, as with human languages.

The psychologists who chastised ethologists for erecting dichotomies with regard to learned and unlearned behavior were right, for many ethologists had their dichotomy out of focus. But when this argument took the form of rejecting all implications of important dichotomies in the manner of development of behavior patterns, it became a source of confusion rather than clarification. An important dichotomy can be identified in the examples I have just given: the question whether selection favors the use of a given stimulus, say, sound, in the establishment of a pattern in the same modality as the stimulus, or whether it specifically favors insulation from all stimuli in that particular modality. This is a dichotomy in direction of selection, and it leads to extreme differences in certain relationships between genetic phenomena and behavioral characteristics. We identify it and discover its significance by studying adaptation and natural selection in relation to behavioral development.

I would suggest that consistent selective action on any kind of behavioral variation, regardless of its original basis, will usually result in the presence, ultimately, of genetic variation relating directly to the behavioral variation. This would mean that the more ancient a behavioral difference is, the more likely that it has some genetic basis. Let me emphasize that I do not mean to imply by this any special kind of selection simply that selection will work on both genetic and non-genetic variations, but evolution will occur only when genetically-based variations become available.

No broad-scale attempt has been made to study adaptation in behavioral terms by the kind of comparison and prediction method of Darwin that I have just been describing. Yet such attempts should be fruitful if what I have just argued is true, even in dealing with the behavior of man, the most "labile" of all organisms in the functioning of his phenotype.

To show what I mean, let me use a simple example cited by Williams (1966). He notes that the females of many kinds of animals are usually described as being more "coy" or discriminating or reluctant in copulation than the males (or one could turn it around and say that the males are more "aggressive" in courtship), and he notes that this is predictable because the female invests a greater proportion of her total reproductive potential in each copulation or fertilization than does the male. If this argument is correct, then, as Williams points out, the situation should be reversed in parental animals in which the male is solely responsible for the zygotes, or more involved in parental behavior. Such reversals have indeed been reported in pipefishes in the genus Syngnathus, in which the males carry the fertilized eggs (Fiedler, 1954) (though not in all such fish: Breder and Rosen, 1966; Straughan, 1960), and also in birds, such as some tinamous and phalaropes, in which the males incubate the eggs and protect the young (Bent, 1927; Tinbergen, 1935; Höhn, 1967).

Similarly, reversals in which of the two sexes behaves territorially, fights off intruding individuals, and courts more aggressively, have been reported in some species such as the Ornate Tinamou (Pearson and Pearson, 1955), the Red Phalarope, the Northern Phalarope, and Wilson's Phalarope (See

Tinbergen, 1935; Höhn, 1967; Bent, 1927). Polyandry is more likely to be prominent in such animals and strict polygyny ought to be rare, although polygamy (or promiscuity on the part of both sexes) and monogamy have both been reported (Lancaster, 1964; Höhn, 1967). Polygyny, on the other hand, is prominent among species in which the females carry most or all of the parental responsibility, and polyandry is almost non-existent. Some of the disagreements in the literature (e.g., see Höhn, 1967) may result from differences in sex ratios among demes studies by different investigators. In some cases, what happens when sex ratios are locally or temporarily uneven may be important in understanding how selection has operated.

The relationship between reproductive effort and proportion of reproductive potential involved in any circumstance or event can be extended to include not only the proportion of eggs or sperm used per copulation, but also the proportion of the breeding season used per clutch or pregnancy, and the total probable reproductive life involved in each season, as Don Tinkle demonstrated on this program. Such considerations of proportions must also include the likelihood of changes in reproductive possibility, such as improvements through learning about one's mate or about the food and predators in one's territory, and the likelihood of improvement in weather conditions. Williams (1966) and Lack (1966) have pointed out that this means that longer reproductive lives, and that clutch sizes will increase with age. We should expect that, especially in long-lived, monogamous animals with specialized parental behavior, selection will continually maximize the slope of a line depicting the increasing reproductive ability of individuals and pairs.

Hereditary, Developmental, and Neurophysiological Basis for Cricket Stridulations

Someone asked me about plasticity in behavior, so I'd like to describe what we know about the genetics, ontogeny, and neurophysiological background of cricket songs. I think it's one of the more complete stories of this kind for any sort of behavior in any animal.

Acoustic insects not only grow up with little or no chance to hear the calls of their own species, they are also surrounded by a multitude of other sounds that bear little or no resemblance to signals they must eventually produce. A high percentage of the individuals in such species probably hear only totally foreign or inappropriate noises, and their own signals, during most or all of their lives, particularly during that portion of their lives when their ability to make the right noises in the right situation is developing.

It is not surprising that, in general, the communicative signals of arthropods do not depend in any way for their structure on perception of the signals of other individuals, of either the previous or the same generation.

The next question one is inclined to ask is: To what extent is a signaling individual influenced by his own signals? Do arthropods improve with practice or repetition of signal-producing movements?

Several investigators have deafened old adult male crickets and noted that their ability to stridulate normally was not affected. Except for loss of ability to alternate or synchronize with other individuals, the only effects hinted at have been tendencies to stridulate for either longer or shorter periods than nondeafened individuals, results which could be obtained if auditory feedback has a stimulative effect and if other noises picked up by the auditory organs are sometimes interruptive.

To my knowledge, no one has previously reported destroying an insect's auditory organs before they had become functional, thus before it could have heard any sound, and subsequntly obtaining a song pattern from it. I tried this experiment unsuccessfully for several years with the snowy tree cricket (Oecanthus fultoni) because its chirps are so complex, and delivered at such an unvarying interval, and because the well-known mass synchrony of males in colonies suggests that auditory stimulation and auditory feedback are important. In August 1965, I was finally successful in obtaining two sequences of chirps (208 and 272 chirps, respectively) from a male defeaned as a juvenile (by cutting off its forelegs) before chirping began outdoors, and one sequence (too far from the microphone to analyze) from another deafened while still soft after molting to adulthood. Chirps were recorded by using an automatic recording device in operation twenty-four hours a day for eight days. They were produced in sequences, at least as long and uninterrupted as those of normal males. Wingstroke rate, chirp length, and chirp interval were all normal, and chirp intervals following occasional short chirps were shorter, as in the singing of normal males. The chirps of the male in which individual pulses (wingstrokes) could be analyzed were abnormal in one unexpected regard: the stridulatory apparatus was in contact during both opening and closing strokes of the wings, rather than just the closing strokes. This defect did not disappear from this male's song during several hundred chirps. Intrachirp variation, however, are common in this species, the known ones including pulse groupings and pulse omissions or weak pulses; Walker (1957) found that females and males respond to pulseless electronic chirps if they are the right length and properly spaced. I doubt that the abnormality of this chirp would greatly reduce its communicative value to males or females and I further suspect that it was not owing to the male's deafness but to thoracic damage caused by handling.

The most we can say of a positive nature about developmental influences on communicative signals in arthropods is that, with a few minor and doubtful exceptions, not a single one has been discovered; no one has found any way, short of actual mutilation or gross physical deformity, to alter the communicative signals of any arthropod. Wherever the internal environment of the structures responsible for the ultimate patterns of these acoustic and visual signals may be, the variable inputs of the developing individual's external environment must be translated into an essentially constant, species-specific milieu before they reach it. In what ways has selection brought this about?

Fulton (1933) conducted perhaps the first experimental hybridization of two species with different songs, and his study is still the most careful and detailed analysis available. He hybridized two North American ground crickets, Nemobius allardi and N. tinnulus, sibling species that are adult at the same time and overlap both geographically and ecologically, the former an inhabitant of grassy areas, the latter a woodland species. Fulton was able to analyze the songs of F_1 and F_2 hybrids and F_1 backcrosses with both parental species.

Fulton's results are in most regards straightforward: pulses in the songs of F_1 hybrids were delivered at intermediate rates, those in the songs of backcross progeny were generally somewhat more like the parent used in the backcross when compared with one another. There are some puzzles, however. The pulses in both backcross hybrids seem too slow; two of them are slower than most recorded tinnulus, and all but one of both kinds of backcross hybrids have slower pulse rates than the F_1 hybrids. The F_2 hybrids also seem to have pulse rates that are a little too slow--nearly all slower than the songs of the F_1 hybrids.

Two possible sources of error in the analysis could explain this discrepancy. First, Fulton had no method of counting pulses except by ear and by using a vibrating clamp that he could set by ear to correspond with the speed of pulse delivery in the insects' songs. As he cautioned, his counts above six pulses per second are probably somewhat inaccurate, and many of the hybrid songs were evidently heard only at higher temperatures and therefore were more rapid and difficult to analyze.

The second possible source of error involves the relationship between courting and calling sounds of N. allardi and N. tinnulus. One of the courtship sounds of both species is simply a slowed version of the calling sound. The particular courtship sound in allardi is quite similar to the calling sound of tinnulus, so similar that the insects themselves are probably unable to distinguish them. Some of the crickets whose songs Fulton analyzed may have been courting, not calling; he could have no way of telling certainly under all circumstances, and the possibility is especially great when large numbers of crickets are caged together as they evidently were in this case. With intermediate hybrid songs involved, the possibility of confusion is even greater.

Bigelow also crossed females of G. assimilis (a chirping species) with males of G. rubens (a trilling species). The hybrid males chirped and had wingstroke rates intermediate between the two parents (90 to 105 per second for assimilis at 70° F, 60 per second for rubens at 80° F, 75 per second for hybrids at 75° F). Bigelow concluded that the genes responsible for causing a field cricket to chirp are probably located on the X chromosome (♂XO, ♀XX). Those responsible for wingstroke rate variations are obviously not located on the sex chromosomes, since there was segregation of variations in these two characteristics as well as a probable difference in the number of genes involved in the differences between pulse rates and those between chirping and trilling. There is a suggestion here that song characteristics which stem from pacemakers located in different parts of the central nervous system have been altered by replacing genes located on different chromosomes. Since the differences between a chirping and a trilling song is simply a very long wing-hold interval which becomes the chirp interval, an interesting relationship exists with the findings of Fulton (1933) with trilling Nemobius songs having a very long pulse interval.

In all species treated so far, wingstroke rate differences between species seem to depend on a number of genes, while differences in patterning of wingstrokes (chirp patterns) may depend on a different gene or genes located on another chromosome (Bigelow, 1960). It is within reason that discovery can be made of the number of genes involved in pulse rate differences between species and the quantitative effect of single gene replacements on pulse rate. Such information, together with studies of variation within species, is needed to elucidate how overlapping genetic differences between incipient species become effective in selective divergence.

In a series of publications, Huber (1955-1956) has discussed his findings that certain of the sounds in a field cricket's repertoire, and also a more or less nonacoustic wing-whirring prominent in some Gryllus species (preflight behavior), can be produced by stimulating the cricket brain and that brain stimulation in different regions causes different kinds of sound or wing motion.

The parts of the brain Huber stimulated, the mushroom bodies, receive fibers from the antennal lobes, and, presumably, imput from the antennae. The stimulation points eliciting aggressive stridulation, although not easily separated geographically as a group from those eliciting first transition to courtship, are generally somewhat peripheral to the latter. Since those eliciting aggressive stridulation are associated with effects of violent antennal stimulation and the others with effects of mild antennal stimulation, it seems at least possible that variations in the sounds elicited reflected variations in the size of the region stimulated that are related to normal variations in the intensity (and perhaps duration) of antennal stimulation.

The precise portions of the patterns involved above depend for their nature upon postulated "pacemakers"--either single neurons or small groups of neurons--located in the mesothoracic ganglion (wingstroke rates), possibly the prothoracic ganglion (wing-hold or chirp intervals), and in courtship stridulation, possibly the cercal ganglion. The postulated prothoracic ganglion pacemaker, most interesting to us at this point, evidently fires continually at specific, temperature-dependent rates unless specifically inhibited. Only light-dark cycles, contact with other crickets, extreme temperatures, and disturbances are known to affect the calling cycles of males with spermatophores, and the effect in all three cases is evidently inhibitory. The only stimulative effects which might be suggested are (1) stridulation of other males--known to be stimulative (Alexander, 1961) and (2) the effect of the presence or absence of a spermatophore in the spermatophore pouch (Huber, 1955). But crickets call without acoustic stimuli, and undisturbed crickets with spermatophores do not call continuously; the latter effect is not specifically known to be stimulative rather than inhibitory.

Pause for questions

Question: How do the physical characteristics of the stridulating organs affect the sound?

RDA: They don't affect the pattern. They only affect dominant frequency (cps) and the intensity.

Question: Is there no variation in those respects?

RDA: Yes, there is both individual variation and variations between species. But you could probably play Yankee Doodle with a cricket's song and if you didn't change the rhythm or pattern you wouldn't change the cricket's response. The effect would be only to change the intensity. Crickets of grossly different sizes (say, Nemobiinae and Gryllinae) have such different frequencies in their sounds, and such different tunings of their auditory organs, that they can evolve pattern independently because they are not likely ever to hear one another. I think there's a point to be made here concerning the use of reproductive isolating mechanisms to arrange higher categories. The point is that when something like an acoustical system becomes prevalent in many species, there will ultimately be a hierarchy of patterns. Some aspects of the pattern can be used to identify genera and subfamilies.