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Comparative Animal Behavior and Systematics

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Behavior is probably the most diverse aspect of the animal phenotype—at least, as William Morton Wheeler (1905) put it, "in the field of possible observation." On this basis alone, behavior should be fascinating to the systematists because they are always looking for characters. Furthermore, among biologists, systematists are, more than any other group, the real students of diversity. Comparison is their chief method of exploration, and the comparative method, of course, depends upon and thrives upon diversity.

On the other hand, to some extent the diversity of behavior results from its being, in general, more directly and probably more complexly related to the genotype than to any other aspect of the phenotype. This particular feature discourages the systematists. They are not interested in getting involved with phenotypic variations that might be due solely to variations in the developmental environment. After all, morphology is troublesome enough in that regard.

Behavior has some other special features. In general, it is more strongly selected—or perhaps I should say more directly selected—than morphology or physiology. By this I mean that in any representation of the chains of cause-effect relationships between gene action and selective action in animals, behavioral characteristics nearly always would be placed directly next to selective action.*

* A botanist asked me abruptly in a phone conversation recently, "What *is* animal behavior, anyhow?" I tried to answer him unhesitatingly, and my reply came out: "Behavior is what animals have interposed between natural selection and the other (morphological and physiological) aspects of their phenotypes." Even with an indefinite amount of reflection, I think it might be difficult to improve on the emphasis in that definition.

The systematist's concern with adaptation should prevent him from passing this off too lightly. On the other hand, behavior is often difficult to document or to communicate to others. As Dr. Wagner stressed in his paper, repeatability is the essence of science, and to many taxonomists this traditionally has meant that morphology alone is sacred. Very little behavior is evidenced by preserved specimens or fossils.

BEHAVIOR AND MAN'S EVOLUTION

The facts I have outlined above suggest some of the problems and possibilities in using behavior to understand the history of life. I think one of the best illustrations of these problems and possibilities comes from the evolution of man himself. We surely would all agree that the most important thing we could possibly discover about man's transition from the nonhuman state to the human state would be how he behaved during that period—the details of what he did and how he lived while he was evolving into a man. We know positively that he did make the transition from ape to man. What we do not know is precisely *how* he did it. By that I mean we do not know what the selective forces were, and, for example, why such forces seem to have been relatively strong and unidirectional for a while—at least in regard to changes in size of the brain case—and then to have slacked off, perhaps rather abruptly, some tens of thousands of years ago. We speak (vaguely, I think) of tools and communication, and of growing food and fighting off predators, but the truth is we still have no really good notion how and why men with bigger brains once outreproduced those with smaller brains and then stopped doing so. A wide range of possibilities still exists, and the answers could very well turn out to be more startling than most of us might suppose. As one example, we do not really know what kinds of predators, if any, might have been involved in the steady increase in man's brain size, and, as much as we may dislike the idea, I believe the possibility still exists that man himself is the only one that could have done the job.

Perhaps I can explain what I mean, and demonstrate some of our ignorance about man's evolution, by posing a question. Intraspecific competition, in connection with natural selection, may be said to

occur in three possible forms. Sometimes different individuals simply compete indirectly, without direct interactions, for whatever food, mates, shelter, or other commodities may be in short supply. In other cases, some kinds of individuals may partially or completely exclude others from the best sources of food, mates, and shelter through territoriality of one sort or another. There is another possibility, less often recognized. Superior individuals might sometimes actually pursue and destroy competitors, or potential competitors, thus removing them and their descendants from the possibility of competing. Such a superior individual might, in addition to removing competition, actually derive direct benefit from the slaughter, through cannibalism. Which of these three kinds of intraspecific competition operated during the evolution of humans from nonhuman primates, and how significant was each? The question has certainly not been answered; I do not think it has even been clearly posed before. Yet the different possibilities could scarcely fail to produce widely different attitudes among men trying to understand themselves and their behavior through knowledge of history. [Since submission of this manuscript the ideas involved here have been discussed and extended in a book review coauthored by D. W. Tinkle (Bioscience 18:245–248).]

Sometimes I have thought that to understand the selective action that made a nonhuman primate into a man could be the most important question in all of biology. It could change man's attitude toward nearly everything he does or tries to do—in education, politics, religion, and all the rest—for it could tell him more precisely what he is, and therefore why, in one sense, he persists in doing some of the things he does, and why he still fails to accomplish some of the things he seems to want to do. Any adult who has tried to explain to a child the pre-eminence of things sexual in so much of human affairs (as well as in the lives of other organisms) without using natural selection in his explanation surely will understand what I mean. To use another example, it is possible that we should be taking the history of selective action upon man much more directly into account in our attempts to deal with overpopulation and its consequences.

In other words, we cannot learn how man became a man, and therefore, in a sense, what a man really is, without knowing some things about the history of his behavior. Yet, it seems that the only thing we can do about this problem is to dig and scrape around at a

few fossils that reflect his morphology and represent a few indirect traces of his behavior.

THE COMPARATIVE METHOD IN BEHAVIOR

It *seems* as though this is all we can do; but my theme here is that such an idea about evolution is false. I suggest that we can find out how man's behavior evolved and the kinds of selective action that were involved. More fossils will help, of course, but we can do it without fossils if we have to; in any case, the most important advances in understanding man's history may not come from fossil evidence, and I consider it unlikely that satisfactory progress will come from the efforts of humanists who are not simultaneously first-rate evolutionary biologists. I believe that we will make the significant advances in this area in the same way that we eventually would have arrived confidently at the conclusion—even without the help of a single fossil—that man and the other living primates have diverged from common ancestors. We would have done this, of course, through extensive, intensive, and perceptive comparative study over a period of time long enough for us to have developed—on the side, from direct observation and experimentation—an understanding of the steps and the mechanics of the process of evolution.

It should be clear by now that I am not arguing simply about the role of behavior as a tool for taxonomists. I want to argue instead for the establishment of a reasonable relationship between those biologists interested primarily in behavior and those interested primarily in systematics in the broadest sense—a relationship that will result in the kind of reverberating feedback between these fields that both need, and have needed, for a long time. I think the key to this relationship—perhaps the only key—lies in applying the comparative method to behavior on a much wider scale than has been the case. I realize that I am one small voice in a long line of people carrying this particular argument to the zoologists. But I do think the point has not yet been properly made.

To some zoologists—though perhaps not to those here—to argue for a rejuvenation of comparative study must sound a little old-fashioned. Nowadays biologists are calling for precise, quantitative results and for more and more experimentation. Comparative study

and the broad-scale, observational-descriptive work that undergirds it are often viewed as outdated, trivial pursuits. The need for more experimental work, however, and the possibility of more precise experimentation do not reduce the need for good, evolutionarily oriented, comparative investigations. Rather, though it may surprise some biologists, the need for comparative study is thereby increased, for it is a central role of comparison to tell us which experiments to do, and which ones to do first.

In his recent book on adaptation and natural selection, Williams (1966a) argued that systematists never will prosecute the study of adaptation the way it ought to be prosecuted. All of us will agree that there is a lot of shortsighted, narrow-minded systematic work going on but, contrary to Williams' argument, I believe that the methods of systematists represent a great potential contribution to the study of adaptation, beginning at the point where we find ourselves today. And I refer specifically to the comparative study of behavior, which Williams himself employed effectively in his book. Comparative study is the stock-in-trade of the systematist. It has never been the stock-in-trade of any other group of biologists in a very extensive, persistent, or pertinent fashion—least of all, perhaps, the behaviorists.

One of my favorite psychologists argued recently that molecularly oriented biologists are on the wrong track when they believe they can predict everything of significance about the biological world through a knowledge of structure and function at molecular and submolecular levels. He noted that, while theoretically this may be possible, it is unreasonable or impractical unless one knows beforehand what it is that he must be able to predict. I suggest that the same criticism can be leveled at many people studying behavior. They expect to be able to predict from precise, quantitative, laboratory experimentation without having any idea of the complexity, the variety, or even the nature of the things they will have to predict.

Zoologists left behavior largely to the psychologists, long past the time of knowing that psychologists in general do not answer the kinds of questions that zoologists must have answered. And systematists, in turn, have left zoological studies of behavior to the experimental zoologists, despite the fact that certain questions about behavior that are of importance to everyone are not going to be answered for a very long time using the methods generally conceded to experimental biology.

There is nothing mysterious about the comparative method. 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.

THE COMPARATIVE METHOD AND SPECIATION

I will cite an example from a field familiar to this audience—the study of speciation, which I rank as one of the three general problem areas of chief concern to evolutionists, the other two being adaptation and phylogeny.

I am sure that everyone in this audience believes he has a good idea how speciation usually occurs, at least in sexually reproducing, gonochoristic or dioecious organisms. But how many are prepared to list and defend, as of this moment, the specific points of evidence that allow us to argue convincingly on the question of how speciation *usually* or *generally* occurs?

One thing is certain: None of us would get very far if he were asked to rely solely upon experimental studies or upon direct observation of complete speciation processes, witnessed from beginning to end.

Instead, we rely, as Darwin did, 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.

Of course, the picture we construct (in oversimplified 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 that gives us this picture can be summarized, I believe, in five statements.

1. Practically all species are geographically fragmented. In other words, geographic fragmentation occurs on a wide scale and is likely to permit much speciation.

2. Taken collectively, the geographic fragments show every possible degree of divergence—from scarcely measurable up to what seems to be complete speciation. So, geographic isolation does lead in a great many cases to divergence of apparently the right sort.

3. Most cognate pairs or groups of species have a particular kind of geographic relationship: either they are allopatric or their geographic ranges are narrowly overlapping. This suggests that they were geographically separated in the recent past. [Murray Littlejohn pointed out to me recently that use of the term "cognate species" for species believed to share an exclusive common ancestor (most closely related species, or species representing last forks in the phylogenetic tree) eliminates the confusion in the dual meaning of sibling species. Henceforth, I will use the term "sibling species" to mean simply species that are especially difficult to distinguish by conventional means.]

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

5. Pairs and groups of species that are not related—for example, a pair of bird species and a pair of insect species—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 the prediction—that no alternative to this process of geographic speciation will be accepted widely 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 recent paper (Alexander, 1968) I have tried to present such evidence for speciation by accidental seasonal separation of adults, postulated by Alexander and Bigelow (1960) to have occurred in certain crickets.

I believe it is time we stopped concerning ourselves with more theories, and ever more elaborate theories, about how sympatric speciation *might* or *could* occur. Such theories are, by now, almost a dime a dozen and can be dreamed up even by beginning biology students. The real question is the likelihood of their occurrence, and that question can be answered only if we go into the field

and accumulate the kind of comparative information that alone will tell us whether, and to what extent, any particular postulated process occurs.

There is an additional point to be made 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" against which one may test whether any particular case of speciation 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 also that he 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. Also, I have suggested that information from broad-scale—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.

Incidentally, the kinds of evidence I have just been describing are those whose significance and validity are denied—on a much wider scale than most people realize, I am afraid—by antievolutionists and, further, whose significance is often downgraded and misunderstood not only by physical scientists but by many experimental biologists. Yet, we rely almost wholly upon information from such comparative studies 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.

BEHAVIOR AND REPRODUCTIVE ISOLATION

An approach similar to that used in the analysis of speciation, one that concerns behavior and has been of great usefulness to alpha

taxonomy in a few groups, involves the study of reproductive isolating mechanisms. Dr. Littlejohn has discussed this topic extensively on this program, and I agree with essentially everything he said; so I will attempt to make my comments complementary to his. Reproductive isolation, however, is so clearly the best-understood liaison between behavioral and systematic work that I will go to some trouble to express certain opinions that do not seem to jibe with much of the published—and evidently influential—literature and to describe some of the arguments underlying these opinions.

Although reproductive isolation is a relatively young topic of study, it has been discussed so extensively that one would suppose that our ideas concerning it would be fairly well crystallized. Unfortunately, this is not the case. One point of confusion, I believe, is that two quite different things commonly are considered under this topic without being adequately distinguished. These are (1) those differences that, initially, make it disadvantageous or impossible for two populations newly in secondary contact to hybridize or merge and (2) those differences that, in situations of long-established sympatry and synchrony, enable two species to live together with a minimum of deleterious sexual interaction. Failure to make this distinction at the proper times and in the proper ways seems largely responsible for the somewhat clouded discussions—to which Dr. Littlejohn alluded—as to whether reproductive isolating mechanisms are, as one writer has put it several times, "an incidental by-product of the genetic divergence of isolated populations or the result of natural selection."

In some ways it is appropriate to concern oneself first with phenomena in the second of these two categories—those species differences that prevent or reduce sexually significant encounters between species that have been breeding together for a long time. This approach focuses attention on both major questions concerning reproductive isolating mechanisms: (1) their specific identity and nature, and (2) their origins. Both questions, in my opinion, are being approached in awkward fashion by many investigators.

As with speciation, we can study reproductive isolating mechanisms either experimentally or by comparison of situations known only fragmentarily. Experimental studies are actually few and far between. Hopefully, they will increase in the future, for they can be

carried out with greater success than can experimental studies of speciation. Presently, I think all the good analyses of the actual reproductive isolating mechanisms between pairs of species, in animals at least, can probably be counted on one's fingers. I say this in full awareness that some authors have been telling us that the literature on reproductive isolation is massive—so massive as almost to defy review. This is not true. There is indeed a great deal of published information on courtship and mating behavior, and this is what we are told 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 in which the study of animal behavior is currently out of focus; and it would not be so if systematists were more involved in it.

One cannot go into the field and simply describe what he observes 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 has posed some questions and speculated 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 already formed or to cause pair bonds between individuals belonging to different species, which apparently otherwise does not happen in the areas 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 now would 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.

Some of the interspecific variations Tinbergen has described may have been reproductive isolators once 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 such as gulls, which have long-term pair bonds, or strict monogamy in some cases, and complex parental behavior. Mere species specificity does not itself mean isolating mechanism.

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

I will dwell a moment on the succession of questions Neal Smith asked about reproductive isolation among gulls, for I think his model is a good one for any of us to use when attempting 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 temporarily (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?

Of course, this is just the old familiar list of possible isolating mechanisms; but it is the sequence that is important. Anyone who does not ask these questions in this general order will not know whether he is studying isolating mechanisms among his species even if he does prove, for example, that 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, such differences may arise without having had an opportunity to function in reproductive isolation. Under such circumstances these differences 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 breeding in the same general area at about 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 each other. To use equally, but perhaps less obviously, 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 in the same year, or between two species of mammals that have never attempted cross-copulation.

A paper by Clark *et al.* (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 never interact sexually there, then Clark and her co-workers 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 isolation.

There has been much discussion on the question of why, if selection works as I have just outlined, so many species that have never lived together have perfectly good premating isolating differences already developed. The argument has been presented—evidently very effectively, judging from published references to this topic—that differences in premating behavior between species living together usually arise in contexts other than that of reproductive isolation, and that these differences function only incidentally in reproductive isolation.

I believe that this argument (which sometimes seems to derive from a belief that sterility usually occurs before establishment of secondary contact between populations destined to remain separate*) ignores the likelihood that, as reproductive isolation

*I believe this idea to be false, and that, instead, intersterility is rare between members of the same species groups. This hypothesis appears to be supported by all of the information available on hybridization: Blair (1963) for *Bufo;* Alexander (1967) for Gryllidae; Miller (1960) for American freshwater and marine fishes; and Gray (1954, 1958) for mammals and birds. Nearly every intensive effort at hybridization seems to reveal widespread interfertility among congeneric species.

in the sense of minimal wastage of time and energy causes a focus on a few specific aspects of premating 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 premating 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 the direct result of 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 so, we would expect to find that species in groups that have come to rely chiefly upon one or two kinds of isolating differences (such as calls) more likely would be different in those characteristics upon first meeting than would species in groups that rely upon several kinds of differences (e.g., chemicals, vision, host specificity) in different subgroups. On the other hand, if reproductive isolating differences ordinarily arise in other contexts, differences between these two kinds of groups should 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 1,000 known calling signals of insect species (Alexander, 1967); and (2) few cases of character displacement—I know of only two probable (or possible) cases among the same 1,000 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?

Murray Littlejohn has introduced this topic, and he and Frank Blair, in particular, have illustrated through their studies on the calls of anurans, the usefulness to taxonomists of the comparative approach. As Dr. Littlejohn has indicated, 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 results of studies by H. S. Barber (1951) and James E. Lloyd (1966, other papers) on fireflies. I do not believe there is a single finding on anurans that does not have a close parallel in these insect groups, and I do not believe that any results on anurans, or insects, conflict with any results on the other group. However, I want to emphasize one specific point. There are now experimental demonstrations that call differences between sympatric, synchronic, closely related species are sufficient to enable both the males and females to distinguish their own conspecifics; at least one demonstration exists for anurans (see Littlejohn, this volume, page 471) and one for each major insect group in which calls are prominent in breeding behavior (see Alexander, 1967). For a long time, however, there were no such demonstrations at all, but we knew even then—or I should say we were highly confident—that the calls do indeed function in reproductive isolation, and we proceeded successfully and accurately on this basis. 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 my earlier statements regarding speciation.

1. The calling (or pair-forming) signals of species that breed at the same times and in the same places are almost never identical (the exceptions are newly established situations). This fact—based on comparison of nearly 1,000 insect species alone, including essentially all crickets, katydids, and cicadas in North America and many 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 or 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, if so, for how long. I would

point out that many studies on *Drosophila* mating behavior, even those supposedly dealing with reproductive isolation, either are vague about geographic, ecological, seasonal, and daily overlaps in breeding or 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, sometimes are the same. This fact, based on six known cases in insects—four cases of geographic isolation and two of seasonal isolation (Alexander, 1967)—makes the previous statement even more significant.

3. Calling signals of closely related species that overlap narrowly occasionally differ more 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 all known (several hundred) insect species with pair-forming calls and on a study of courtship, genitalic structure, and mating behavior in some 10 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 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 conserving time and energy, because they operate before morphological or physiological differences. The only exception seems to be differences in seasonal life history that effectively keep the adults of two species from inter-

acting. Differences in habitat or daily times of breeding generally involve behavioral differences, and allopatry is rarely evolved as a result of species interactions. Partially or completely effective morphological, physiological, or late-operating behavioral differences, I suggest, will always be replaced by behavior as functional isolators as selection continues between species that remain sympatric and synchronic. This suggestion 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.

Last year a writer who was using almost exactly the same title as I am said there is no valid argument that behavior should replace morphology as the main tool of alpha-taxonomy in distinguishing species. But it has already done so 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 afford to assume that his organisms are taxonomically inaccessible from this approach. After all, 15 years ago we could not study sounds objectively, and only five years ago we had no instruments to record the subtleties of firefly flashes.

THE PROBLEM OF INSTINCT

So far, I have said nothing about what undoubtedly has been the knottiest problem in the study of animal behavior, and the one responsible more than any other, I suppose, for slowing the advance of comparative study of behavior. If we call this the "problem of instinct," most people have a good idea what is meant. It would be

more descriptive, however, to term it the problem of the extent and nature of hereditary influences in 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 critical for my topic to determine which behavioral variations correlate with genetic variations. Few people challenge the idea that certain species differences, such as frog and insect calls, firefly flashes, or other behavioral characteristics identified as reproductive isolating mechanisms in any kinds of animals, have genetic bases. And, we know from hybridization experiments that insect and anuran call differences do indeed have genetic bases. In fact, results from crossing experiments on crickets and frogs probably are cited more frequently in reviews concerning transmissibility of behavioral variations than are any experiments with other kinds of animals.

The systematist wants to know more about this. He wants to know whether 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 whether heredity or environment has greater influence 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 aspect 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, and the extent to which, differences in characters are due to environment on the one hand and to heredity on the other."

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

But not all these issues are of great or immediate concern to the systematist or evolutionary biologist interested in behavior. What is of concern is predictability. And it is very likely that significant increases in predictability, in many cases, can be attained sooner 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 this to be true. We systematists seem to have allowed ourselves to be overly concerned about precisely how individual patterns of behavior develop. We do not know a great deal 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 which knowledge was gained directly, almost solely, from comparisons of those very features of anatomy whose development we still do not understand.

When we will have carried out broad-scale comparative studies of behavior similar to those available in anatomy, and when we 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. Because the question then would concern *how much* genetic variation is involved, a considerably sharper focus should be provided for the investigations of many biologists now skeptical that broad-scale comparisons can be made in the absence of extensive information on developmental pathways and stimuli for particular behavioral units.

This remark may raise some eyebrows, but I suggest that behavioral variations that at first glance appear useful to systematists—particularly to those working at and above the species level—rarely lack correlation with specific genetic variations. For example, is anyone here in a position to describe a species difference in behavior—any species difference in behavior—that he has 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 predictable to a large extent.

*Alexander and Bigelow (1960) have given a possible example. Males of *Gryllus veletis* generally are much more aggressive than those of *G. pennsylvanicus*. They also occur more sparsely, and the difference can be erased, or even reversed, if males of *G. veletis* are crowded in the laboratory and males of *G. pennsylvanicus* are isolated.

One aspect of such predictability can be exemplified by cricket calls. Examination of cricket biology soon reveals that in most temperate species only the eggs pass the winter, and that the auditory organs are not functional until maturation or near-maturation. With this information alone we can predict confidently that (at least usually) selection favors insulation from influences by environmental sounds in the establishment of the pattern of the call (R. D. Alexander, "Arthropods" *in* T. Sebeok, *Animal Communication,* to be published by Indiana University Press), for there can be no appropriate sounds available to copy.

On the other hand, even a limited 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 young and adults in each generation, and an apparent premium on individuality in song pattern; the latter is associated with the presence of specialized parental behavior and tendencies toward monogamy and is promoted by having part of the pattern learned.

In precocious birds both the critical periods of song learning and the imprinting of following behavior are predictable on the same general basis. 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, therefore, will have no chance to focus on a restricted group of stimuli. Likewise, we would predict that different populations of birds within a given species should sometimes have song differences that lack genetic bases, as is the case 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 dichotomies out of focus. But this argument became a source of confusion rather than clarification when it took the form of rejecting all implications of important dichotomies in the way behavior patterns develop. An important dichotomy can be identified in the examples I have just given: Does the selection favor the use of a given stimulus (sound, for example) in the establishment of a pattern in the same modality as the stimulus or does it specifically favor insulation from all stimuli in that particular modality? This is a dichotomy as to 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 suggest that selection acting consistently on any kind of behavioral variation, regardless of its original basis, will usually result in the presence, ultimately, of genetic variation that relates directly to the behavioral variation. This would mean that the more ancient a behavioral difference, the more likely it is to have some genetic basis. By this I do not mean to imply any special kind of selection, I simply mean that selection will work on both genetic and nongenetic 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 that I have just described. Yet, if what I have argued is true, such attempts would be fruitful, even those dealing with the behavior of man, of all organisms the most "labile" in the functioning of his phenotype.

I will use a simple example cited by Williams (1966a), who notes that the females of many kinds of animals usually are 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 in each copulation or fertilization the female invests a greater proportion of her total reproductive potential than the male invests of his. 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 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 such birds, as some tinamous and phalaropes, in which the males incubate the eggs and protect the young (Bent, 1927; Tinbergen, 1935; Höhn, 1967).

Similar reversals as to which sex behaves territorially, fights off intruding individuals, and courts more aggressively have been reported in the ornate tinamou (Pearson and Pearson, 1955), red phalarope, northern phalarope, and Wilson's phalarope (Tinbergen, 1935; Höhn, 1967; Bent, 1927). Polyandry is more likely to be prominent in such animals, and strict polygyny ought to be rare,

although both polygamy (or promiscuity on the part of both sexes) and monogamy have 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 nonexistent. Some of the disagreements in the literature (e.g., see Höhn, 1967) may result from differences in sex ratios among demes studied 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 proportion of the total probable reproductive life involved in each season, as Dr. Tinkle demonstrated on this program. Such considerations of proportions must include also 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 (1966b) and Lack (1966) have pointed out that this means that longer juvenile lives will correlate roughly with longer reproductive lives, and that clutch sizes will increase with age. We should expect, especially in long-lived, monogamous animals with specialized parental behavior, that selection continually will maximize the slope of a line depicting the increasing reproductive ability of individuals and pairs.

Since man's plasticity in behavior seems for a long time to have been a major reason for our reluctance to discuss the general problem of behavior in relation to heredity and, therefore, a major reason for the reluctance of systematists and other biologists to use behavior in comparative work, it is appropriate that I conclude by referring to the possibility of heredity in an example of variation in man's behavior. I will use the previously mentioned theory of female "coyness," or difference between male and female, and suggest that what we frequently and sometimes jokingly refer to as the "double standard" in man's sexual behavior is, in part, a reflection of differences in selective action on male and female behavior during man's evolutionary history.

In general, in both polygynous and monogamous animals with specialized parental behavior selection should favor females that

promote monogamy and should favor males that promote polygyny. Even in evolutionary lines in which monogamy is never actually realized, tendencies toward it in females would be favored consistently if the male's cooperation in any way promoted the female's reproductive success. Likewise, even in a monogamous line polygynous tendencies in males often would be favored because in a species in which the female is responsible for the fertilized eggs a male is much more likely to benefit from, shall we say, "stealing" copulations with his neighbors' females than is the female who indulges in the same kind of behavior. Tendencies toward polyandry in man are evidently rare, but tendencies toward polygyny are not nearly so rare.

Is it reasonable to argue that there likely are no genetic correlates underlying even subtle intraspecific differences of this sort in an organism as plastic as man, when selection on man's breeding system has probably been consistent in the ways I have described all through man's evolutionary history? I think not.

CONCLUDING REMARKS

I have dealt in this paper with a few points that I believe will be useful in making the analysis of behavior more important in systematic work than it has been in the past, in searching for both similarities and differences among organisms. To bring these two fields into closer cooperation, I believe we need, chiefly, to be (1) more aware of the role of the comparative method in biology and in behavioral analysis, (2) more thoughtful in our searches for behavioral variations likely to be correlated with genetic differences, and (3) as systematists, more cognizant than we have been of the significance of studying adaptation directly, both by experimentation and by comparison.

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REFERENCES

Alexander, R. D. 1967. Acoustical communication in arthropods. Ann. Rev. Ent. 12:495–526.

Alexander, R. D. 1968. Life cycle origins, speciation, and related phenomena in crickets (Orthoptera: Gryllidae). Quart. Rev. Biol. 43(1):1–41.

Alexander, R. D., and R. S. Bigelow. 1960. Allochronic speciation in field crickets, and a new species, *Acheta veletis*. Evolution 14(3):334–346.

Alexander, R. D., and D. Otte. 1967. The evolution of genitalia and mating behavior in crickets (Gryllidae) and other Orthoptera. Univ. Michigan Misc. Pub. 133:1–62.

Barber, H. S. 1951. North American fireflies of the genus *Photinus*. Smithsonian Inst. Misc. Coll. 117:1–58.

Bent, A. C. 1927. Life histories of North American shore birds, Order Limicolae. I. U.S. Nat. Mus. Bull. 142.420 p.

Blair, W. F. 1963. Evolutionary relationships of North American toads of the genus *Bufo:* A progress report. Evolution 17(1):1–16.

Breder, C. M., and D. E. Rosen. 1966. Modes of reproduction in fishes. Natural History Press, Garden City, New York. 941 p.

Clark, E., L. R. Aronson, and M. Gordon. 1954. Mating behavior patterns in two sympatric species of xiphophorin fishes: Their inheritance and significance in sexual isolation. Bull. Am. Mus. Nat. Hist. 103:135–226.

Fiedler, K. 1954. Vergleichende Verhaltensstudien an Seehadeln, Schlangennadeln und Seepferdchen (Syngnathidae). Zeit. Tierpsychol. 11(3):358–416.

Gray, A. P. 1954. Mammalian hybrids: A check-list with bibliography. Commonwealth Bur. Anim. Breed. Genet. Edinburgh, Tech. Comm. 10. 144 p.

Gray, A. P. 1958. Bird hybrids: A check-list with bibliography. Commonwealth Bur. Anim. Breed. Genet. Edinburgh, Tech. Comm. 13. 390 p.

Höhn, E. O. 1967. Observations on the breeding biology of Wilson's phalarope (*Steganopus tricolor*) in central Alberta. Auk 84(2):220–244.

Konishi, M. 1966. The attributes of instinct. Behaviour 27(3–4):316–328.

Lack, D. 1966. Population studies of birds. Clarendon Press, Oxford. 341 p.

Lancaster, D. A. 1964. Biology of the brushland tinamou, *Nothoprocta cinerascens*. Bull. Am. Mus. Nat. Hist. 127 (6):271–314.

Lloyd, J. E. 1966. Studies on the flash communication system in *Photinus* fireflies. Univ. Michigan Mus. Zool. Misc. Pub. 130:1–95.

Miller, R. R. 1960. Records of natural hybrids among American freshwater and marine fishes. (Mimeographed.)

Pearson, A. K., and O. P. Pearson. 1955. Natural history and breeding behavior of the tinamou, *Nothoprocta ornata*. Auk 72(2):113–127.

Smith, N. G. 1966. Evolution of some Arctic gulls (*Larus*): An experimental study of isolating mechanisms. Am. Ornithol. Union Ornithol. Monogr. 4. 99 p.

Straughan, R. P. L. 1960. 100 seahorses spawn. Aquarium J. 31(6):302–308; 325–326.

Tinbergen, N. 1935. Field observations of East Greenland birds. I. The behavior of the red-necked phalarope (*Phalaropus lobatus* L.) in spring. Ardea 24(1–2):1–42.

Tinbergen, N. 1953. The herring gull's world. A study of the social behaviour of birds. Collins, London. 255 p.

Tinbergen, N. 1960. Comparative studies of the behavior of gulls (Laridae): A progress report. Behaviour 15(1–2):1–70.

Wheeler, W. M. 1905. Ethology and the mutation theory. Science 21(536): 535–540.

Williams, G. C. 1966a. Adaptation and natural selection. A critique of some current evolutionary thought. Princeton University Press, Princeton, New Jersey. 307 p.

Williams, G. C. 1966b. Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am. Natur. 100(916):687–690.