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NATURAL ENEMIES AND INSECT SPECIATION¹

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In this last month of 1959, one hundred years after the publication of *The Origin of Species*, it is fitting that this Society give some acknowledgment to the Darwin Centennial. Biologists all over the world have paused to recognize this important anniversary, to consider the impact of the theory of evolution on the thinking and culture of mankind, and to pay tribute to the man whose name has become almost synonymous with the theory which he proposed. However, it should be mentioned parenthetically that while we think of Darwin when evolution is mentioned, Darwin apparently never used the term evolution, which in its modern sense is due to Herbert Spencer (Ford, 1956).

During the past eleven months of the Darwin Centennial many scientific groups, far more elegant and famous than ours, have scheduled commemorative lectures, symposia, and appropriate exhibits. These have all been properly dignified, impressive, and praiseworthy. While few of us have been actual participants in these events, we do, nevertheless, identify ourselves with the spirit of the occasion and from it tend to derive some vicarious satisfaction. However, I think there is a much better way to commemorate Darwin's contribution. I think that each biologist, each one of us who is a student of living organisms, should take time to view from our own particular vantage point the theory of evolution and the factors that influence speciation.

It is true that our own vantage point may not offer a very superior view; there may not be much to be seen from it, or, if it does command a spectacular view, we may suffer from some intellectual myopia so that we are unable to take advantage of it. But, however handicapped we may be, I think the honesty of the effort makes it worthwhile and that it would please Charles Darwin. He was not always sure of his own position, but was frequently puzzled and confused by what he observed. It is this fact which has given me the courage to speak to you on a subject

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in which I have few qualifications. It is this fact which makes me willing to risk the charge of being presumptuous in talking to you about insect speciation when I really am not conversant with the subject. I merely wish to tell you what I see from my vantage point as a worker in biological control and accordingly one who is interested in population dynamics and the role of parasites and predators.

We must start from firmly established principles, and I do not intend to depart very far from them. The great truths in biology are always immediately before us; they are not cryptic and obscure phenomena that only a few are privileged to see. For example, Darwin's Galapagos finches were seen by people before Darwin went ashore from the Beagle, and the influence of these birds even on Darwin was apparently delayed and retrospective, for it was ten years before he made any significant comment on them (Lack, 1947). I am certain that Darwin's finches have their counterparts in many phenomena that we entomologists probably see but do not recognize yet as being significant. Now I am not suggesting that I have found some new significance in rearranging some frequently observed phenomena in insect populations. Instead, I am inviting you to join me in viewing these phenomena from a novel and perhaps slightly unconventional aspect, and I further ask you to consider them in the light of the twentieth century notions about insect speciation.

THE EQUILIBRIUM POSITION OF A SPECIES AND THE BALANCE OF NATURE

One good starting point is the basic fact that there is a balance of nature, which means simply that barring any major changes in any given environment the resident insect species over a period of time maintain a fairly constant quantitative relationship to one another. (Smith, 1935). In this situation no single species continually increases or decreases in relation to the others. For example, consider for a moment the insect species that exist outside this hall in Golden Gate Park. If we had taken annual surveys of these insects for the past 25 years we would have found that year after year some species were always fairly abundant, others less so, and finally some species were so rare that we would have considered them to be collectors' items. We would have found this to be true because each of the species has an equilibrium

position which it maintains in relation to the other species in its environment. Of course at the same time each species fluctuates both positively and negatively from this equilibrium position because of the changing seasons, or its reproductive cycle, or to any one of many other causes, but these are short term departures only. The species population always tends to return to its normal level of abundance. This reflects the general truth which was known to Darwin and his predecessors, that, on the average, only one progeny per parent can survive, otherwise the species would increase to infinity or decrease to extinction. This, then, is the static aspect of populations; it is the seeming paradox of stability in the midst of constant change. It can be compared to sea level which furnishes us a zero basis for altitude and one of the standard conditions in the most precise of physical sciences, and yet the sea is never level but is always in motion by waves or tides.

There are entomologists who see only the dynamic aspects of populations and not these static characteristics. They are so impressed by the fluctuations of insect populations that they are inclined to deny the existence of any equilibrium position in a species. To them its existence is contrary to facts and a denial of organic evolution. My contention, on the contrary, is that this equilibrium position does indeed exist; that it is just as universal a phenomenon among insect species as sea level is among the oceans of the world. Furthermore, I believe that the tendency of a species to keep this balance is absolutely essential to the maintenance of the species because it prevents the disastrous over-exploitation of the limited requisities in the environment. I endorse the view of my colleague, Dr. C. B. Huffaker, who believes that the measure of success of a species is the relative stability of its ecological position and that any adaptation which gives increased security of ecological position will tend to be perpetuated. In other words, natural selection is involved in the maintenance of balance in populations, and this has survival value. This is, of course, difficult to prove, for as Dr. Huffaker points out, these balanced relations, as such, do not fossilize (Huffaker, in press).

By adhering to our biologists' store of well established and basic facts perhaps we can find among them persuasive evidence to support this hypothesis. For one thing, it is evident that the equilibrium position of each species is determined by the regu-

latory factors in the environment. What do we mean by regulatory factors? These are mortality agents, usually biotic, which operate in a density dependent manner. That is, as the population grows above its equilibrium position the probability of survival of any individual member of that population becomes increasingly less. In our empirical work in biological control we have demonstrated repeatedly that these regulatory factors acting on insect populations may commonly be entomophagous organisms such as predators, parasitoids, and pathogens. These natural enemies frequently regulate the abundance of the host species in any given habitat, and their action prevents wildly fluctuating host densities that could lead to the exhaustion of all the requisites of food and space in the environment and through this, absolute depletion to the ultimate extinction of the species. Instead we find that through their regulatory action the natural enemies maintain the host populations in a stable sort of existence in the environment. They are very often responsible for the balance of nature as we see it among the species of insects.

It might appear at first glance that this tendency to evolve toward a stable system would cause variability to be at a minimum and to lead to fewer and fewer species. Actually the reverse is true. For example, the results achieved over the years in biological control projects sometimes appear to be a product of latitude, for the chances of quick and effective control by importing natural enemies seem to improve the closer we approach the tropics. This merely reflects the fact that the biotic mortality factors of the environment are comparatively much more effective in tropical than in temperate latitudes. At the same time, the numbers of species are far greater in the tropics. Coupled with this great complexity in the tropical biota is the fact that the populations tend to be very stable. It is only as we go toward the higher latitudes that we find the wildly fluctuating populations. It seems evident that where there is intense inter-specific competition the course of evolution is toward greater diversity of species and greater stability of this increasingly diverse and complex system. It is my suggestion that natural enemies are very often protagonists in this evolutionary drama.

What I am suggesting is that in many insect species it is an advantage to them to have effective natural enemies. By effective

natural enemies I mean those which are quickly responsive to changes in host density and increase the intensity of their action as the population increases. Probably most of us are not accustomed to thinking that mortality factors which are increasingly severe on a growing population can actually be beneficial to the survival of that species. The notion nevertheless appears to be true that an efficient entomophagous organism or high degree of pathogenicity in a parasite or pathogen may indeed work to aid the survival of the insect host or prey species.

The predators and parasitoids that we use in biological control are fatal to their hosts, and yet there is a widely published hypothesis, which indicates an equally wide acceptance, that an organism which kills its host is, comparatively speaking, a newcomer to the ranks of parasitism. The hypothesis is that a parasite which does not tend to kill its host is a more completely adapted type which reflects a host-parasite relationship of long standing. I am not competent to judge the validity of this theory when applied to the conventional types of parasites, but it is completely erroneous when one applies it to insect parasitoids, the parasitic Hymenoptera and Diptera. With these groups I am convinced that there is a preponderance of evidence to the contrary. The morphological and physiological adaptations exhibited by endo-parasites for their life within the host individual are far from being primitive. The psychological selection of hosts by female parasitic wasps and their general searching behavior and ovipositional responses do not fit the ordinary criteria that define primitive characteristics. These facts, I think, give very strong support to the belief that insect species tend to evolve toward stable balanced relationships and are aided in this by very effective natural enemies, which are themselves well adapted species, although fatal in their action on their respective hosts or prey.

THE FRAGMENTATION OF HOST POPULATIONS BY NATURAL ENEMIES

Although still largely based on theoretical grounds, there is a belief that a very efficient parasite or predator, particularly one that tends to be host-specific, tends to break a host population up into small isolated units. These small and separated colonies are often exterminated by the natural enemy, but in the meantime there have been a few escapees or emigrants that have started

new colonies of the host. We see evidence of such a colonial distribution in many of the sessile hosts such as diaspine scales. These small and somewhat isolated populations have been termed "demes" by some geneticists and it is rather generally agreed that the division of a species into a number of partly or temporarily isolated populations of various sizes gives the conditions most likely to result in rapid evolution (Sheppard, 1956). Of course, the demes are not completely isolated, but selection, with the deme as its unit, takes the form of more rapid growth of populations of the better adapted ones and their more extensive dispersion into territories of the less adapted with consequent grading up, or even replacement of the latter (Wright, 1956).

Quite probably there are a number of factors which lead to this colonial type of distribution in insects, but I am suggesting that natural enemies can play a very important role. Whenever extrinsic factors cause an interruption or retardation in gene flow between portions of a species, then these subdivisions of the species tend to drift apart genetically (Mayr, 1948). If then a very efficient parasite can fragment the populations of its host, it is precluding absolute randomness of mating and is creating a condition in which greater variability of the host species will be possible.

NATURAL ENEMIES AND THE PHENOTYPIC EXPRESSION OF INSECT SPECIES

While the most important role of natural enemies of insect species is in maintaining balance by regulating the equilibrium position of the given species, it has long been evident to biologists that natural enemies may play a very important part in determining which phenotypes in a species survive. In other words, without natural enemies many of our insect species might look very different. This view is, of course, based on the phenomenon of mimicry and protective coloration that we so often observe in insects.

For example let us consider a butterfly which may in the adult stage mimic a species that is distasteful to birds. We generally consider the outstanding function of such mimetic resemblance to be protection, and yet in the population dynamics of Lepidoptera we believe that the predation on the adult stage is of minor importance, whereas by contrast the attack by natural enemies on the lepidopteran eggs, larvae, and pupae is very intense.

Certainly there are abundant data to show the important part played by parasites in destroying eggs, larvae, and pupae. Furthermore, general field observations show that caterpillars are heavily attacked by predators such as birds and wasps. Yet at the same time, adult butterflies are seldom seen to be attacked by birds. So it follows that protection from attack in the adult stage can be of little, if any, importance to a species of butterfly. Therefore, if a perfect mimetic pattern appeared suddenly in a non-mimetic species, giving complete immunity from attack, it would not increase the success of the species, which would be just as successful without the mimetic pattern. At first glance this would appear to render natural selection of the mimetic pattern impossible, but actually this is not so (Nicholson, 1927).

Imagine a hypothetical situation where a perfect mimetic pattern offering complete immunity from attack appears suddenly in adults of a non-mimetic species which is subject to attack by birds capable of discriminating between the two color patterns. All the possessors of the mimetic pattern would survive to lay eggs, while a proportion of the non-mimetic adults would be destroyed by birds. Therefore the proportion of the mimetic to the non-mimetic individuals would be greater when the insects laid their eggs than it was when the adults emerged. The parasites of the developmental stages of this generation would operate to regulate the equilibrium position at the same level it was previously, but in their attack they would not operate selectively and would therefore destroy, on the average, an equal proportion of the mimetic and non-mimetic stocks. Consequently, the proportion of the mimetic to non-mimetic individuals surviving to the adult stage would theoretically be the same as that proportion which existed in the egg stage. Again the birds would act selectively against the non-mimetic adults, but the parasites would in turn act without selective action on the succeeding generation of eggs, larvae and pupae. The selective action on the adults, although perhaps very slight, would nevertheless be cumulative generation after generation until finally the mimetic form would completely replace the non-mimetics. The result would be not an increase in the numbers of the species but a species composed of phenotypes of very different appearance from the original stock.

This theory would apply to cryptic coloration equally well,

and it is in these species which have built up complicated patterns suitable for concealment on lichenized tree trunks, rocks, and posts that we see the phenomenon of industrial melanism. It has been reported that of the 780 species of *Macrolepidoptera* which occur in the British Isles, about 70 are in the process of replacing their populations with dark or black individuals in the vicinity of soot-laden industrial areas (Kettlewell, 1956).

It is of extreme interest that such a change in gene frequency in one species will alter the amount of predation on other species in the same habitat. Accordingly industrial melanism is suggested as being an auto-catalytic process by Sheppard (1956) who also points out that the evolution of mimicry will lead to mimicry in other species with the same mode of life and living in the same area. Thus parallel evolution in mimicry tends to be produced in insects living in the same area and with similar ecologies. Consequently, it is a noteworthy but not surprising fact that where mimicry is found usually a large number of species are involved, while in other places mimicry is rare or absent.

For a long time the idea has been prevalent in biological control circles that in general vertebrate predators do not regulate the population density of any given insect species. It has been thought that birds are not quickly responsive to changes in numbers of any one insect species and are therefore not density dependent in their action. However, there are data on a few bird species, at least, which show that birds can be very important. Brower (1958) has generalized that the behavior of birds which eat phytophagous insects is such that the probability of discovery of a food item of a particular shape, color-pattern, and size is increased if the one previously found is of similar appearance and is palatable. The birds thus form a "searching image" or a "visual image" of the prey. This kind of behavior could easily lead to density-dependent predation in nature.

Experiments were conducted by de Ruiter (1952) in which twig-like geometrid caterpillars and the twigs they specifically resembled were scattered on the floor of an aviary. Individual jays were then admitted and characteristically began to hop about looking for food but in each case ignored both the twigs and the motionless caterpillars. However, after birds finally found and ate a larva then both twigs and larvae were pecked at, which

resulted in nearly all the larvae being eaten. Tinbergen (1957) discussed these experiments and said that when caterpillars outnumbered twigs, the birds went on hunting for caterpillars, but if they picked up more twigs than caterpillars, they gave up searching. From this it can be seen that the time interval between successes can not be too long if the bird is to continue searching, and in nature this interval would bear a direct relationship to how well the prey was spread out.

Brower (1958) believes that this phenomenon of persistent and successful searching after the bird has found the first prey plays a role in the food plant specialization of phytophagous insects. Brower suggests that in a situation where two closely related, pro-cryptic species are feeding together on the same plants slight genetic differences in the two species would result in them being cryptic to a slightly different extent on any one food plant species. Therefore the selection pressure by birds concentrating on the common prey image would favor those individuals of each species which were on mutually exclusive plants, and in this way the common food plant diet originally shared by all would come to be divided among them. Brower suggests that the reason that food plant specialization is so prevalent is probably because the selective advantage of being on separate plants is greater than that conferred by the initial stages of a divergence in appearance which would ultimately be different enough to be overlooked by the birds.

So far I have stressed the positive role of natural enemies in being responsible for the phenotypic expression of a species population, but there are cases where just the opposite is true and the phenotypic expression is due to the absence of biotic pressure. In this connection one can consider some of the flightless endemic species in Hawaii. As Zimmerman (1948) points out "The flightless insects of Hawaii are the descendents of cripples which survived only because in these insular environments biotic and environmental pressures are reduced to a minimum, and conditions have been favorable for their survival. They are 'hopeful monsters' arisen under circumstances in which there is hope."

"Some of these flightless species which were successful under primitive Hawaiian conditions have recently succumbed to new

biotic pressure brought about by the introduction of predators which are foreign to the Hawaiian biotal balance. Some of us have searched intensively under the very trees where Dr. Perkins procured a series of the flightless fly *Emperoptera mirabilis* Grimshaw but have never been able to find a single example of the species. It appears that this remarkable fly is now extinct—at least in the type locality—because it was unable to withstand the new pressure created by the invasion of its environment by immigrant predaceous ants.” (Zimmerman, 1948.) Therefore it appears from these observations that non-adaptive radiation can take place relatively easily where there is an absence of predators or where the predator pressure is low.

NATURAL ENEMIES AND INSECT BEHAVIOR

Not only may the phenotypic expression of morphological characters in a species be influenced by natural enemies, but certainly the behaviouristic characters of the species may also be the end result of the pressure of natural enemies. All entomologists are aware of the behavior of certain insects when startled, such as beetles immediately dropping from plants, insects taking flight, or perhaps feigning death.

The power of flight in insects may originally have evolved because it gave a great advantage to the insects in escaping predators, and it has been suggested that this in turn led to the development in other animals of the ability to fly. It is apparently a system of measures and counter-measures, for, while bats through echosounding locate flying insects, there are moths which have the ability to detect the ultrasonic emanations from the bats and characteristically respond by immediately ceasing flight.

Many insects, particularly in the Orthoptera, locate mates by the sound made by one of the sexes. It would seem that this might also notify vertebrates of the insect's location, but actually the sound is of such frequency that vertebrates have difficulty in locating the source. This is due to a basic difference in the manner of hearing. Each sound wave has two basic properties, one the displacement of the particles or molecules of the medium and the other the change of pressure with which this is associated. Vertebrate ears perceive pressure changes while the hearing organs of insects register particle displacement. It was pointed out by Pumphrey (1940) that since any sound involves particle displace-

ment, and particle displacement involves direction, grasshoppers can locate sounds of all types equally efficiently as long as they are within the audible range. The situation is quite different in vertebrates.

Marler (1959) reminds us of the common experience that many Orthopterans are difficult to track down by their songs. "As has already been pointed out, the 'displacement' hearing organs of insects locate sound sources in a different way from vertebrate ears, and the efficiency is unaffected by the frequency of the sound, as long as it is audible. Insects therefore are freer than vertebrates in their choice of frequency. It is interesting to note that most of them, nevertheless, lie between about 6 and 14 kilocycles per second (Busnel, 1953). In the absence of breaks to serve as time clues, this is probably a quite difficult frequency range for those birds which prey on grasshoppers to locate. One may speculate on the possibility that some insect songs are adapted so that they are both easy for insects to track down, but difficult for vertebrates. It is noteworthy, too, that crickets, with songs which are often broken and lower-pitched, around 2 to 4 kilocycles per second and therefore easier to locate, are largely crepuscular and nocturnal. Because of this, and their cryptic and often subterranean habits, they may be less exposed to predators than some other species."

INSECTS AS PLANT PARASITES

Although the title of this address indicates that emphasis is being placed on the role of natural enemies in insect speciation, I think it is profitable to digress for a moment and consider the role of insects as parasites of plants. As natural enemies of plants, the insects may well have played a very important part in determining at least the quantitative balance that we find among our plant species. As you are aware some of the most spectacular results in biological control have been in the control of weed pests by imported phytophagous insects. In California, for example, Klamath weed has been cleared from hundreds of thousands of acres of range land by the imported chrysomelid beetles, and the plant now exists as a roadside inhabitant or a plant that grows on the marginal areas of clearings. Couple with this demonstration the result of the destructive scale insects on the junipers in

Bermuda, and it is evident that insects can play a very important role in determining the quantitative composition of the flora.

SPECIATION IN ENTOMOPHAGOUS FORMS

The whole subject of speciation in the entomophagous forms themselves is far too large to take up in detail in an address such as this. It is, however, one of great interest, and it is possible that a few isolating mechanisms exist among the parasitic groups that are not encountered in other insect species. I like to think of an internal parasite as living in a host that is sort of a physiological island. Thorpe (1945) reports that there is considerable presumptive evidence of the isolating effect of host conditioning in parasitic insects. He believes that the conditioned response will give momentum to and set the direction for the selective processes tending to bring about genotypic isolation. Thorpe concludes that it would seem best to regard geographical and topographical and ecological isolation as three different scales of spatial isolation. In fact it has been said by Allee, *et al.* (1949) that living organisms, as hosts to parasites, form one of the three major habitats on earth, comparable to the aquatic and terrestrial habitats in which the hosts themselves dwell. Therefore, with each host as a kind of physiological island, it is not surprising that speciation has apparently occurred frequently among the parasitoids. It is not difficult to see how extrinsic factors associated with the host might set up isolating mechanisms in parasite populations attacking it. If these were sufficient to interrupt gene flow between portions of the parasitoid species and lasted for any substantial period of time, then perhaps a new species would evolve.

There is one contribution which a study of parasitoids can make to the general subject of insect speciation and that is the disclosure of races or biological species among host insects through the differential behavior of the parasite complex. There have been a number of examples where a single morphological host species has been proved to consist actually of several distinct forms because the parasites of one form were unable to develop in the other. On the other side of the coin one finds cases where a single host may actually have several morphologically indistinguishable but biologically very different parasites attacking it. These facts arise because of the necessity in biological control of studying in detail the biological and behaviouristic characters of the host and

parasite respectively. To me the discovery of these biological entities within a well established morphological species is no criticism at all of conventional taxonomic procedures. Instead I view it as the next logical step, another dimension to insect taxonomy. This is a refinement that can be accomplished only after the basic morphological taxonomic foundation has been laid. This is, then, the expected progress and evolution in insect taxonomy toward a degree of sophistication in systematics that we now only dimly see, and it is my suggestion that insect parasites can assist us in reaching this goal.

SUMMARY

The relative stability of an insect species in its ecological position is due to regulatory factors which are often predators, parasites, or pathogens. Through the action of such density dependent agents, the evolutionary tendency is to develop increasingly complex but stable biota. The phenotypic expression of morphological characters as well as the development of certain behavior patterns in insects is often due to the selective pressure of natural enemies. The speciation of insect parasitoids is discussed in relation to modern systematics.

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TENTH PACIFIC SCIENCE CONGRESS

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