

A MODEL FOR SYMPATRIC SPECIATION IN *MEGARHYSSA*
(HYMENOPTERA: ICHNEUMONIDAE):
COMPETITIVE SPECIATION

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Sympatric speciation is like the Lernaean Hydra which grew two new heads whenever one of its old heads was cut off [Mayr (1963)].

The mechanism(s) by which sexually reproducing organisms form new species has long been a subject of controversy (see Mayr 1942, 1963, 1970; Dobzhansky 1937, 1951, 1970). Realistic alternatives to the classical, allopatric model of speciation (where diverging populations are geographically separated) have recently been presented for a number of animal groups (e.g., White 1968; Bush 1969, 1975*b*; Ford et al. 1973; Tauber and Tauber 1977*a*, 1977*b*.) Other workers (e.g., Sokal 1974; Ghiselin 1975) have pointed out that problems involving the origin of species are closely related to those concerned with species definition and species concept.

The criteria used in defining species have also been controversial. The morphological species concept which so dominated animal taxonomy in the nineteenth and early twentieth centuries has been largely replaced, at least for evolutionary biologists, by biological species concepts (e.g., Dobzhansky 1937; Mayr 1942), which stress the importance of reproductive isolation as the mechanism by which species maintain their distinctness. A species could thus be defined as a group of naturally occurring populations that can actually or potentially interbreed while maintaining distinctness from other such groups through reproductive isolation.

In the past decade the biological species concept (*sensu* Mayr) has come under attack from several authors (Ehrlich and Raven 1969; Sokal and Crovello 1970; Sokal 1974; Scudder 1974; Ghiselin 1975), but alternative definitions seem to present more problems than they solve. I have therefore taken reproductive isolation as the major criterion in distinguishing species in the case model presented below. However, reproductive isolation itself may break down under changed environmental conditions. The word *species* thus has spatial, temporal, and ecological connotations and does not depend solely upon the intrinsic prop-

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erties of individuals and populations. It seems to me that within a given biological community the various species represent different adaptive peaks of resource utilization, while niche width varies according to the degree of specialization (see Van Valen 1965). The process of speciation thus involves not only the establishment of a group of individuals reproductively isolated from its parental or sister species, but also the occupation of a new portion of niche space in all areas of sympatry. In fact, if sympatry does not occur then it is most difficult to determine whether speciation has actually taken place.

Bush (1975a), in his comprehensive review of the different modes of animal speciation, has described three broad patterns in which new species of animals can arise: allopatric, parapatric, and sympatric modes of speciation. Of these three, allopatric speciation has been extensively described and accepted elsewhere (Mayr 1963). Parapatric speciation has been regarded as a special case of sympatric speciation by some biologists (Bush 1975a), and this standpoint is taken here. This paper is mainly concerned with the sympatric model of speciation; however, the actual mechanism proposed is quite distinct from any of those in the various models noted by Bush.

Sympatric speciation could be defined as the origin of two or more reproductively isolated daughter populations within the dispersal area of a single parental group. It is important to note that the kind of reproductive isolation envisaged is the pre mating form and that the formation of hybrid zones separating parental types is precluded. Several authors (e.g., Maynard Smith 1966; Basykin 1965) have developed realistic mathematical models of sympatric speciation. Such theoretical models have been criticized by Mayr as either being unsound or unlikely to represent natural conditions, and are therefore in themselves of limited value as evidence in favor of sympatric speciation. The four models proposed by Maynard Smith each included, as a first stage, the development of a stable polymorphism in a heterogeneous environment. The first model—differential habitat selection by the two morphs followed by a reduction in gene exchange and the acquisition of reproductive isolation—resembles those of Bush (1969, 1975a) and Tauber and Tauber (1977a, 1977b). Of the other models proposed by Maynard Smith, pleiotropism, modifier genes, and assortative mating genes, the last is somewhat similar to the one described here for *Megarhyssa*. Recently, Rosenzweig (1978) has developed a theoretical model of “competitive speciation” which closely parallels the ideas expressed in this paper (see below).

Attempts have been made to simulate sympatric speciation in the laboratory under different regimes of artificial selection and isolation. In attempts with *Drosophila melanogaster*, only Thoday and Gibson (1962) successfully produced reproductively isolated daughter populations. However, the results of this experiment are puzzling since A. Manning (personal communication) found no indication of any isolation between the high and low lines in Thoday and Gibson's stocks after they had been sent to him in Edinburgh, nor could the authors repeat their work after a number of other laboratories failed in attempts to replicate it (e.g., Scharloo 1964, 1971; Robertson 1970; Thoday and Gibson 1971). However, in several of these experiments it was shown that considerable genetic divergence can occur even in the face of massive gene flow between lines.

Mayr (1963, 1970) criticized the design of these laboratory experiments on the basis that a situation of extreme and consistent selection against intermediates (disruptive selection) was unlikely to occur in nature. More important, many authorities (G. L. Bush excepted) have tended to conceive of the sympatric model of speciation as invariably involving disruptive selection as a prerequisite to assortative mating and the acquisition of full reproductive isolation. It is therefore unfortunate, in discussions on the existence of sympatric speciation, that so much emphasis has been put on the contentious results of a single laboratory experiment. The model presented below does not involve disruptive selection, but relies on directional selection to explain divergence and the development of reproductive isolation; nor does it require immediate and complete termination of gene flow between parent and daughter species.

Though nobody has yet observed the entire process of development of a new species in nature, there is now good evidence that new host races (species) of insects have arisen sympatrically on introduced and native plants of the United States within the last 150 yr (Bush 1969). In the fruit fly genus *Rhagoletis*, the rapid formation of new host races has probably been greatly assisted by the planting of massive monocultures of introduced plants such as apples and cherries (Bush 1975*b*). According to Bush, this mode of speciation is probably restricted to phytophagous and zoophagous parasites and parasitoids on account of their specialized way of life. Mate selection in these groups depends on host selection, since the host is used by many parasites as a rendezvous for courtship and mating. The principal isolating mechanism in these groups is therefore ecological, not ethological. A shift to a new host can therefore have a profound effect on mate selection and provide a strong barrier to gene flow between parental and daughter populations. Host selection has a genetic basis and the number of genes controlling host selection may be relatively few, while a single locus can control host recognition (Huettel and Bush 1972). In summary, this model adequately explains host race formation and resembles the mathematical model of Maynard Smith (1966) in that host selection is, in fact, a special form of habitat selection and the barrier to gene flow arises as a result of the two allelic forms (the normal and the mutant) seeking, and subsequently mating, on different host plants. As Maynard Smith has pointed out, this might be regarded as a form of allopatric speciation in which isolation is behavioral rather than geographic.

Bush's model does not include the possibility of sympatric speciation among nonparasitic animals, nor does it account for the common occurrence of several sympatric sibling species of parasite present together on a single host. The model presented attempts to explain the latter phenomenon, although the principles involved apply equally well to free living animal groups (see below). In order to overcome the highly theoretical nature of earlier models, I have chosen three species of the genus *Megarhyssa* (Hymenoptera: Ichneumonidae) to illustrate the processes involved.

The model is unusual because (1) no spatial isolation is involved, (2) no extrinsic environmental change is required for the process to operate to completion, (3) the evolutionary force is intraspecific competition, and (4) the final outcome is the formation of three species separated by premating isolation. Prior to describing

the model itself, a fairly detailed but relevant account of the biology of *Megarhyssa* is given.

THE BIOLOGY OF *Megarhyssa*

Townes and Townes (1960) in their bulletin on ichneumon flies of North America and Mexico, describe the species *Megarhyssa atrata*, *M. macrurus* and *M. greeni*, "All three of these are dependent on the same host, in the same geographic area (N.E. and Central U.S.A., S.E. Canada), and frequently in the same tree or log, yet each one remains moderately common and is not eliminated by competition with its cogeners." Further study of the species was carried out by Heatwole et al. (1963, 1964) and by Heatwole and Davis (1965) working in beech-maple forests in Michigan.

The overt life histories of the three species are virtually identical (Heatwole and Davis 1965). All three parasitize the wood-boring larvae of the pigeon tremex *Tremex columba* (Hymenoptera: Siricidae). A female *Megarhyssa* detects a host larva or pupa in a dead log or stump, inserts her ovipositor full length into the wood, and deposits an egg on the host. Upon hatching the parasitic larva feeds on the host and finally pupates in the host's burrow. After metamorphosis the adult chews out of the wood. Males detect an emerging female by her chewing noises, which sound rather like "a person eating a raw carrot" and they aggregate at the site of her future emergence (Heatwole et al. 1964, p. 376). Copulation takes place immediately after she emerges. Although mixed species aggregations form at the emergence sites, only males of the same species as the emerging female attempt copulation with her (Heatwole et al. 1964). Heatwole et al. (1964) were unable to determine the method by which males recognized conspecific females but suggested that it might be olfactory (e.g., pheromonal). Visual stimuli were ruled out because males showed no interest in emerged (mated) conspecific females, and males of other species lost interest and left the area as soon as the emergent female opened a small hole in the surface of the log. No auditory differences could be detected between females of the three species in the 50–30,000 cycle/s range.

Heatwole and Davis (1965) were chiefly interested in the comparative ecology of the three *Megarhyssa* species. Adults of the three species are strikingly similar in all aspects of their ecology and behavior. Both sexes of each species tend to return repeatedly to a particular log or stump, with only limited movement between sites. During periods of inactivity adults rest on the under-sides of beech and maple leaves, which are so numerous that there is no possibility of competition for shelter. Furthermore, the adults feed very sparingly, if at all (Townes, personal communication in Heatwole and Davis [1965]), so that competition for food seems most unlikely.

Competition for host larvae might be expected to be keen since all three species are restricted to the same host and occur together. In this context, investigation of oviposition behavior of *Megarhyssa* females and the burrowing behavior of the host larvae is important. In regard to the former, Heatwole et al. (1964) found that: females detect the location and depth of the host larvae and direct their ovipositors to them; (2) they select only those larvae which are at a depth in the

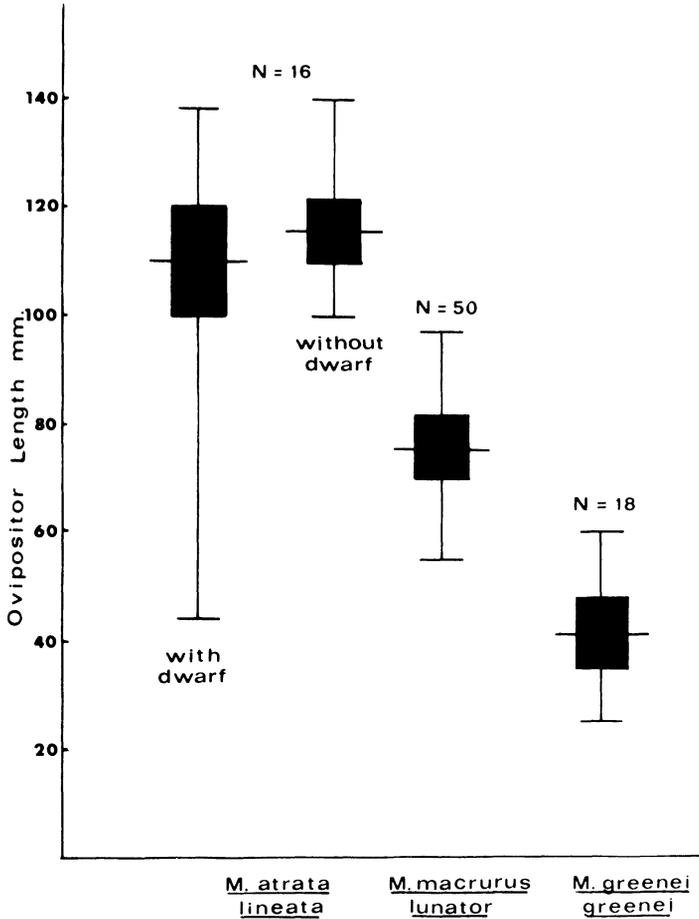


FIG. 1.—Comparison of ovipositor lengths of three species of *Megarhyssa*. Vertical lines represent ranges; rectangles represent the mean (horizontal line) ± 2 SE. From Heatwole and Davis (1965).

wood so that the ovipositor just reaches them when fully inserted and at right angles to the surface, i.e., all ovipositions involve complete insertion of the ovipositor. Thus, if the ovipositors of the three species are of different lengths and the host larvae maintain a constant depth from the surface during their tunneling in the log, the *Megarhyssa* would be parasitizing different segments of the total host population.

To test these conditions, ovipositors of insects captured in the field as well as those of local (Mich.) museum specimens were measured. Figure 1 is taken from Heatwole and Davis (1965) and shows that the lengths of the ovipositors of the three species (distinguished on minor morphological differences—see Townes and Townes 1960) were significantly different. *Megarhyssa atrata* had the longest ovipositors and, with the exception of one unusual dwarf, their length range did

not even overlap with those of the medium length species *M. macrurus* in the same study. Even including this dwarf, the differences between the two species are significant as indicated by the nonoverlap of the rectangles which represent twice the standard error on either side of the mean. Similarly, significant differences exist between *M. macrurus* and *M. greenei*, although some overlap in the length range of ovipositors was found to occur.

To test the second condition—that host larvae do not change their depth from the surface during their tunneling in the log—tremex infested logs were opened and examined. The path which one tremex larva followed was traced through the wood. After hatching near the surface of the log, it burrowed in at an angle of about 45° to the surface and then leveled out and followed the grain of the wood. Logs sawed in cross sections showed tremex larvae and burrows scattered at various depths in heartwood and sapwood. All followed the tremex grain of the wood except the very smallest, which represented newly hatched tremex moving inward. The pattern of burrowing noted seems to be general, with tremex larvae leveling off at variable depths. Once this has taken place the larvae maintain a relatively constant depth in the wood until they are ready to emerge (Heatwole and Davis 1965). Thus the conditions for ecological segregation are largely met, and the parasites do not appear to compete for host larvae except perhaps to a limited extent due to (1) the small overlap in ovipositor length between *M. macrurus* and *M. greenei*, and (2) the possibility of slight changes (not mentioned by Heatwole and Davis) in the effective vertical depth of oviposition as a result of peeling bark or unequal growth at the surface of the trunk, or depth of host larvae due to internal factors such as knotting which affect the grain of the wood.

Unfortunately Heatwole and Davis' attempts to identify or culture the parasite larvae were unsuccessful, so they were unable to directly check the spatial distribution of the three *Megarhyssa* species with respect to depth. However, they were able to provide some indirect evidence that larvae of the three species occurred at different depths as follows. A brief study was made of different logs to determine if the ratios of the different species might change in space or time. Here, a definite change in species composition was observed with *M. greenei* predominating in younger wood and *M. atrata* in older, rotting wood. Three stages were arbitrarily defined denoting this succession of *Megarhyssa* species on logs. Stage I represented freshly fallen, firm wood. In a fallen tree which was studied *Megarhyssa* was absent at first (1959), but in 1960 the parasites began to appear with *M. greenei* predominating. In stage II there was a shift in numerical dominance from *M. greenei*, to *M. macrurus*, to *M. atrata* associated with ageing of the logs. (This stage may take many years and thus all three species may be present together for several seasons.) During this time the logs were characterized by decay and the presence of fruiting fungi. Finally, in stage III *Megarhyssa* disappeared from the log as it reached late decay.

Heatwole and Davis suggested that the shift in numerical predominance from *M. greenei* through *M. macrurus* to *M. atrata* is related to the presence or absence of *Tremex* at various depths in the wood, and hence to ovipositor length. In a process which takes several years, fungal attacks on newly fallen logs begin at the outer surface and proceed inward, rendering conditions suitable for *Tremex*. At

first the depth distribution of *Tremex* is most suited to *M. greenei* and later to *M. macrurus*, and later yet to *M. atrata*. As advanced decay sets in from the outer regions of the log conditions become unsuitable first for *M. greenei*, whose numbers therefore decline before those of *M. macrurus* and *M. atrata*. Heatwole and Davis concluded that the major factor responsible both for ecological segregation and for the succession of species was the difference in ovipositor length between species.

Predation and the proportion of host larvae parasitized are also important. Ovipositing females are at a disadvantage because they are unable to fly away when their ovipositors are inserted. Heatwole et al. (1963) found that *M. atrata* takes more than 1 h for oviposition, and they observed frequent instances of bird predation in this species. The time is shorter in *M. macrurus* (12 min) and even less in *M. greenei* (7 min). Evidently the benefits accruing to *M. atrata* by having a long ovipositor, and thereby avoiding competition with species having shorter ovipositors, outweigh the increased chances of predation.

Finally, the extent of parasitism on the host population is important. In a sample of 86 hosts Heatwole and Davis found that 23 (27%) were parasitized. In all cases only a single parasite was found within a given host, suggesting that a female can detect whether or not a larva has been previously parasitized when her ovipositor reaches it.

THE MODEL

Assumptions

Distribution of Host Larvae.—Though the data are scant it can be readily inferred from Heatwole and Davis' (1965) results that tremex larvae occur fairly uniformly in rotting wood between depths of 20 mm and 140 mm, the extreme limits of ovipositor length in the three *Megarhyssa* species. It is true that this situation is complicated by a biological succession of decay in fallen tree trunks, but by considering the whole population of such trunks in a given area this effect can be overcome. It may also be valid to suggest that there will be slight, though uniform, decreases in total numbers of host larvae with depth owing to the decreased cross section of the trunk.

Nevertheless, in a population of such fallen tree trunks a plot of host abundance versus vertical depth in wood can be expected to produce an approximately straight line distribution. Thus Heatwole and Davis (1965) noted *Tremex* larvae and burrows scattered at variable depths without any noticeable patterns in both heartwood and sapwood. For the sake of simplicity and clarity in the model a hypothetical depth distribution of *Tremex* larvae in a population of logs is shown in figure 2, and superimposed upon subsequent figures.

Distribution of Parasitized Larvae.—Since all ovipositions involve the full insertion of the ovipositor, the vertical distribution of host larvae available to each species of *Megarhyssa* must closely correspond to that given for ovipositor length of figure 1. Figure 3 represents a hypothetical depth distribution of parasitized *Tremex* larvae within the total host population (which in Heatwole and Davis'

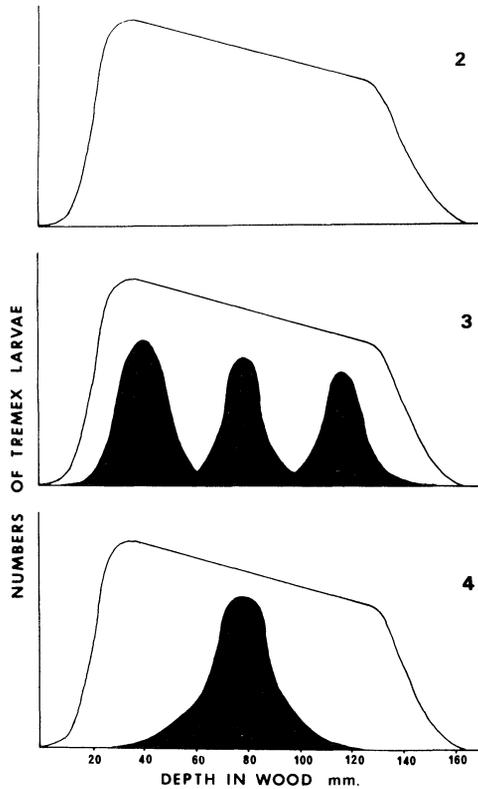


FIG. 2-4.—2, Hypothetical depth distribution of *Tremex* larvae in a population of logs based on Heatwole and Davis (1965). 3, Hypothetical depth distribution of parasitized *Tremex* larvae (solid) within total host population (open); present situation, based on Heatwole and Davis (1965). 4, Hypothetical depth distribution of parasitized *Tremex* larvae (solid) within total host population (open); situation for ancestral *Megarhyssa* species.

sample represented 27% of the total). This distribution is in part inferred from Heatwole and Davis' data on ovipositor lengths.

Distribution of Ovipositor Length of Ancestral Megarhyssa Species.—According to contemporary evolutionary theory it is probable that the three species of *Megarhyssa* have evolved from a single common ancestor and that this ancestor had an ovipositor and parasitized *Tremex* larvae. Natural selection would favor an ovipositor distribution which enabled this ancestral species to parasitize the maximum possible number of host larvae. This could be achieved through genetic changes affecting the mean and standard deviation of ovipositor length, as well as the shape (skew) of the curve itself. Less likely, but possible, is the selection for linkage producing a bimodal distribution for this character. However, linkage would tend to produce a discrete rather than a continuous distribution if more than a few alleles were involved.

The result of such an ancestral ovipositor distribution would be a corresponding depth distribution in the wood of parasitized *Tremex* larvae. Figure 4 represents a

possible example of the pattern of parasitization. Although the number of alternative distributions is legion, it remains highly probable that the proportions of host larvae parasitized at extreme depths in the wood were smaller than those at intermediate levels. It is also probable that a single generalized (with respect to ovipositor length) form of *Megarhyssa* could never achieve as high a percentage of host parasitization as the three extant specialist species combined (fig. 3; see below).

There are five other important assumptions in the model.

1. In the present situation, intraspecific competition among females for host larvae is strong, while interspecific competition is weak. This is supported by the relatively high overall percentage of parasitized larvae (27%) coupled with the virtually contiguous distribution in the ovipositor length ranges (fig. 1).

2. Ovipositor length is determined genetically and is therefore dependent upon the genotypes of the parent male and female. Probably many genes are involved (polygenic), as is the case for bristle number in *Drosophila melanogaster* (Thoday and Gibson 1962).

3. Both host abundance at different depths and ovipositor length show continuous variation.

4. There is a premating isolating mechanism with a genetic basis that must be complementary in the two sexes to be fully operational.

5. With the haplodiploid genetic system, genes responsible for isolating mechanisms in the male are passed on to all female offspring.

Applications

Formation of a New Species.—It has been noted that mate selection in *Megarhyssa* is accomplished by some cue, probably olfactory, emanating from the female which attracts only males of the same species (Heatwole et al. 1964). If this isolating mechanism has evolved in sympatry rather than as a by-product of genetic divergence in allopatry, then the critical question is, By what process and under what selective forces can divergence be achieved? The model attempts to show that under certain ecological conditions selection for the isolating mechanism will indeed occur.

From figure 4 it immediately becomes apparent that those females with ovipositors which are very long or very short relative to the mean length of the population face far less intraspecific competition for host larvae. Therefore they enjoy increased reproductive success. In a system of random mating their offspring will, on average, have ovipositor lengths more closely approaching the mean, and therefore be less successful. The genotype for ovipositor length is expressed phenotypically in the female only, but in the population of *Megarhyssa* one would expect complementary gene frequencies for this character in the two sexes. For the ancestral population a hypothetical distribution of the phenotype for ovipositor length is given in figure 5. Let this distribution have a mean μ and a standard deviation σ .

As mentioned above, it seems likely (Heatwole et al. 1964) that species recognition in *Megarhyssa* is achieved by means of specific pheromones produced in the

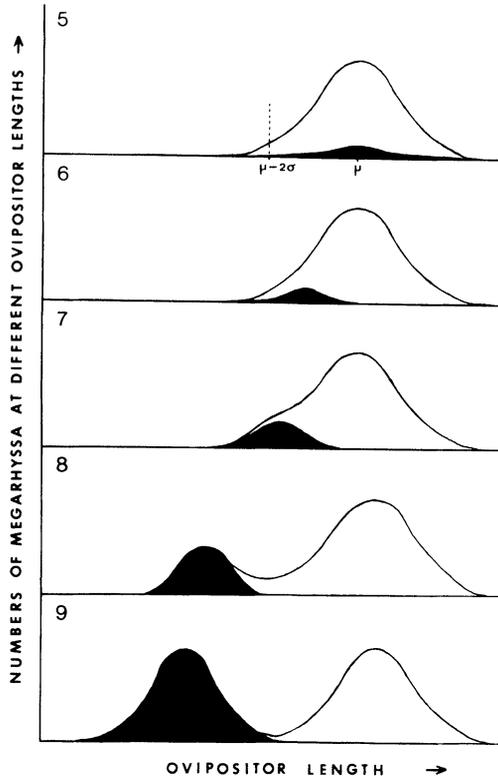


FIG. 5-9.—Ecological divergence of daughter group from parental population in terms of ovipositor length. Solid areas represent individuals containing allele *y*, open areas individuals homozygous for *Y*. 5, Situation at generation 0; females homozygous for *b* have phenotypes for ovipositor length even when heterozygous. 6, Situation at the end of generation 1 after *By* and *by* males from generation 0 have assortatively mated with *bbYY* females. 7, Situation after generations 3 and 4 when “left-shifted” *By* and *by* males mated with *bbYY* and *bbYy* females. Alleles *y* and *b* have increased in frequency owing to the increased reproductive success of individuals with very short ovipositor lengths. 8, Situation in subsequent generations. Alleles *y* and *b* have shown further increases in frequency and become closely associated. Individuals in solid areas are now highly homozygous for these two alleles, particularly *y*. Gene flow between the two groups is low. 9, Reproductive isolation has been reinforced as a by-product of the (polygenic) divergence in ovipositor length. Speciation is now complete.

female. Suppose in the ancestral population that allele *B* is responsible for the mating attractant, while *b*, when homozygous, gives rise to a different pheromone unattractive to males. In males (which are haploid) suppose that the pheromone receptor is determined by allele *Y*, and that a mutant *y* occurs, which is strongly attracted to *bb* rather than *BB* or *Bb*. For clarity in further discussion, let allele *b* be associated through linkage and by chance with alleles for short ovipositor length, with *bb* occurring in individuals whose mean ovipositor length is $\mu - 2\sigma$ when expressed phenotypically.

It might appear improbable that both mutant types *bb* and *y* should occur in a

relatively small local population. Certainly allele y would be rapidly eliminated without bb , being selected against in all males. But b could persist without y for a long time, perhaps indefinitely at low to medium frequency, as follows. Genotype Bb has, on average, a shorter ovipositor length than mean for the population and, for the reasons mentioned above, will therefore enjoy slightly increased reproductive success compared with BB . This success will be offset, perhaps even balanced, by the failure of any bb offspring to reproduce. In effect, allele b is thus behaving like a lethal gene when homozygous, while being associated with high fitnesses when heterozygous. Such genes are known to occur, even in man (e.g., sickle cell anemia, see Ford 1975).

One would be also justified in wondering what sort of probabilities might be involved in a y male meeting a bb female. If there were a mutation rate of between 10^{-3} and 10^{-5} for y and a probability of 10^{-2} for genotype bb , then the probability of the two meeting in all random encounters between males and females would be between 10^{-5} and 10^{-7} . If the average population size in *Megarhyssa* were 2×10^3 one might expect the mutant types to be present together in every .01-.0001 population, assuming a 1:1 sex ratio. It is true that the above figures do not take into account the probability of genes for ovipositor length being at loci close to those for pheromone production, and this may be a weakness of the model. If the loci were close then the mutant b would have to be associated with divergent ovipositor length genotypes of high fitness in order to persist in the population. As Dawkins (1976) has stressed, genes may be considered good or bad, but their success or lack of it depends very much upon the company they keep.

Having made all of the above assumptions, the stage is now set for the operation of the model. At generation 0 a small number of mutant males (a single individual will suffice), designated y males, show a high preference for females with bb . In order not to introduce bias, let the initial y allele be associated with genotypes for ovipositor length like that of the rest of the population, i.e., with a mean μ and a standard deviation σ (fig. 5).

In generation 1 (fig. 6) the population distribution of genotypes pertaining to ovipositor length will remain unchanged (in females) since the initial distribution of the genotype in y males in generation 0 was no different from that in the rest of the population. However, since y males mated assortatively with $\mu-2\sigma$ females (bb), allele y will become predominately associated with ovipositor lengths far to the left (short) of the mean; this process will be duplicated in generation 2 by other y males. In both generations the y mutation may well be disadvantageous since $\mu-2\sigma$ females are scarce (see below). To some extent there is compensation in the increased reproductive success gained by mating with such a female.

However, by generations 3 and 4 (fig. 7) the (female) offspring of y males which mated with bb females in generations 1 and 2 will have significantly shorter ovipositors than the rest of the population. They can now enjoy greatly increased reproductive success as a result of reduced intraspecific competition for *Tremex* larvae at shallower depths in the wood. The population distribution for ovipositor length has become skewed and there is an increase in the number of individuals with short ovipositors.

In subsequent generations (fig. 8) the following developments will take place.

1. The *bb* females (which mate assortatively with *y* males) will produce, on average, daughters with shorter ovipositors than equally short *BB* or *Bb* females (which mate with *Y* males) due to the left-shifted genotype of *y* males. Such offspring will enjoy increased fecundity as a result of decreased intraspecific competition at extremes of length distribution.

2. Alleles *b* and *y* will therefore greatly increase in frequency in the population, and in the process, become closely associated genetically.

3. The gene frequency of *y* will approach zero in all genotypes other than those at the extreme left (very short ovipositors). Divergence to the left of individuals with allele *y* from the rest of the population will continue to occur so long as the advantage of reduced intraspecific competition, and therefore increased food supply, at shorter ovipositor lengths is maintained.

4. As the *y* males increase in number and divergence proceeds, less and less gene flow will occur between *Y* males and females with very short ovipositors for reasons mentioned above and to follow. The genotypes of the two diverging groups will now be: daughter (short) group, almost entirely *bbyy* females and *by* males; parental group, mainly *BBYY* in females with a smaller number of *BbYY* and even fewer *bbYY* females, males *BY* or less commonly *bY*. It therefore follows that only very limited gene flow could now occur between the two groups, restricted to *bbYY* females from the parental group mating with males from the daughter group, i.e., *by*. Their offspring would have the genotype *bbYy*. Such diploid offspring would give rise to genotypes *by*, *bY*, *bbYy*, and *bbyy*. Of these, *by* and *bbyy* would be harmoniously absorbed into the daughter population, and *bY* into the parental population. However, *bbYy* would continue to supply genetic material to both populations so long as allele *Y* was maintained in its diploid offspring.

5. Genetic divergence between the daughter and parental population will occur in characters other than ovipositor length (polygenic) as a by-product of assortative mating and the shift to the left of the *bbyy* group. Also, the parental group may show a slight shift to the right for reasons complementary to those mentioned in (1), and as a result of increasingly strong competition with the *bbyy* group at short ovipositor lengths. Reproductive isolation between the two groups will be perfected and reinforced as further divergence proceeds. Speciation has by now been effectively achieved.

6. Once full reproductive isolation has been achieved the *bbyy* group can become completely separated from the parental population in terms of ovipositor length (fig. 9). High frequencies of short individuals can now be maintained without the polluting effects of gene flow from parental types (i.e., from the rare *bbYY* individuals).

7. Following the perfection of reproductive isolation, the *bbyy* group will reach a peak level in numbers regulated by intraspecific competition for *Tremex*. In the parental population allele *b* will now be selected against owing to the reproductive failure of the homozygote *bbYY*. The two gene pools can now evolve in total independence and much genetic divergence can take place. Allele frequencies in parental and daughter groups, previously similar because of continued gene flow during early stages of divergence, may become dissimilar. A "genetic revolution"

(Mayr 1963) could take place in either group, so that in the present situation reproductive isolation might have a highly polygenic basis.

8. Most important, the proportion of the total host population parasitized is now significantly larger with two specialist species than it was with a single generalized ancestral population.

Formation of a Second Daughter Species.—Subsequent to, or concomitant with, the formation of the first daughter species described above, and for identical reasons, divergence may occur on the right (i.e., at long ovipositor lengths). Females with very long ovipositor lengths will face far less intraspecific competition than those at medium lengths. Mirror images of figures 5–9 could well represent the stages in such a process of divergence. The end result will be a population of individuals with extremely long ovipositors separated from parental types by reproductive isolation. The present situation of three ecologically segregated species has now been achieved.

Alternative Directions of Divergence.—In the process of divergence described above, an ancestral species of *Megarhyssa* of intermediate ovipositor length resembling *M. macrurus*, gives rise to two daughter species, one of short length like *M. greenei* and the other long, like *M. atrata*. This may not have been the direction of divergence: A short species could have given rise to an intermediate species, which in turn produced a species of extreme ovipositor length. Nevertheless, the mechanism of speciation would not be different in detail from the one already described. The second alternative, that the species with a very long ovipositor (like *M. atrata*) gave rise to the other two species is, however, most unlikely. Extreme length is a very specialized feature and renders the ovipositing female much more susceptible to predation than in the two shorter species. Indeed, extreme length is probably only maintained as a result of interspecific competition at shorter lengths (Heatwole and Davis 1965).

Validity of Assumptions Used in Model

In presenting this model of speciation, I have attempted to cut the Gordian knot encountered in using mathematical models or the results of laboratory experiments as evidence for or against sympatric speciation by selecting field data from known species of animals. Thus, the situation renders itself open to further research, and the stalemate imposed in using purely theoretical examples can be overcome. The validity of the assumptions used in the model are now discussed in terms of present and possible future knowledge.

The depth distribution of host larvae in wood and the distribution of different species of *Megarhyssa* within the total host population remain open to further investigation, but H. Heatwole (personal communication) has expressed no objection to my interpretation of his data. The same comments apply to the method of species recognition. There seems no valid reason for supposing that ovipositor length is not determined genetically, but the degree of phenotypic plasticity remains an open question. In the model the genotype for ovipositor length (assumed to be polygenic) is associated through interaction with the gene responsible for the mating attractant. Though the genetic system of *Megarhyssa* is not well

known, a similar type of interaction has been shown for *Drosophila melanogaster* where the number of sternopleural chaetae is associated with several other characters (see Thoday and Gibson 1962). Furthermore, the genome size of parasites and parasitoids tends to be small (Bush 1975a) so the chances of interaction might be expected to be high in these groups.

One should know the conditions in related species of the genus *Megarhyssa* and in related genera before one can reconstruct the ancestral condition. Although I have no data from North America, two subspecies of *Megarhyssa nortoni*, *M. n. nortoni* and *M. n. quebecensis*, have been introduced to Australia to help control the sirex wasp *Sirex noctilio* (Hymenoptera: Siricidae), a pest of *Pinus radiata* plantations in Tasmania and southeastern mainland Australia. *Sirex* was accidentally introduced from Europe, and has a similar ecology to *Tremex*. R. McKimm of the Forest's Commission of Victoria informs me that each subspecies of *Megarhyssa nortoni* shows a fairly high degree of ovipositor length variation, which is mainly a function of body size. Both *M. n. nortoni* and *M. n. quebecensis* have now become established as wild populations and hybridization may be taking place. Data from Tasmania indicate parasitization rates of *Sirex* may be as high as 40%, although in Victoria this figure is closer to 20%. Intraspecific competition for host larvae would therefore appear to be keen. In North America, *M. nortoni* seems to be a more variable and generalized species than any of the three described here and has a wide geographic range (Townes and Townes 1960).

It appears likely that there would be a high selective premium on the development of an intrapopulational polymorphism in the ancestral *Megarhyssa*. In studies of the polymorphism of butterfly mimics, P. M. Sheppard and his colleagues have encountered such a solution. In natural populations of some butterfly species highly colored mimics, some resembling species A while others mimic species B, are common and crossbreed freely; yet intermediates are exceedingly rare. Although the phenotypic difference between two morphs has a highly polygenic basis, the alleles (i.e., cistrons) involved have all become so closely linked on the same chromosome that crossing-over is very infrequent. The end result is that two or more "super-genes," corresponding to peak levels in fitness, become established in the population (Ford 1975); but the situation in *Megarhyssa* is quite different. Whereas in the butterflies fitness has a very well defined discrete distribution at two or more adaptive peaks (as a result of bird predation), fitness in *Megarhyssa* is nondisjunctive and density dependent along an array of phenotypes. Individuals in the *Megarhyssa* population are fit or unfit on the basis of the absolute frequency of their phenotype rather than on some predetermined extrinsic selection pressure. There would therefore be no selective premium on the development of an intrapopulational polymorphism, since rarer intermediate individuals would then be of high fitness, in contrast to the butterflies. For the gene pool to exploit more niche space a different evolutionary strategy would have to be adopted. The model described above is a possible solution.

Perhaps the most important assumption in the model is that only two allelic differences are required for reproductive isolation to be effective. The first is in the enzyme used by the female to produce the mating attractant, the second in the protein receptor cells of the male. Such a situation is known to exist in several insect groups. For example, two pheromone "races" are known to occur in

populations of the European corn borer *Ostrinia nubilalis* now resident in North America (Kochansky et al. 1975). Males of the eastern population are attracted to a pheromone consisting of *trans*-11-tetradecenyl acetate (96%) and *cis*-11-tetradecenyl acetate (4%). Males of the western strain are attracted to the same isomers but in reverse concentrations (3% and 97%). Since the two forms, which have slightly different biological traits, occur sympatrically in Pennsylvania without interbreeding, they can be regarded as distinct species. As Bush (1975a) points out, such a change in responsiveness could have arisen by only two independent mutations, one altering a *trans* receptor protein to a *cis* receptor in the male, the other occurring in the enzyme used by the female to produce the *cis* rather than the *trans* form of the pheromone, irrespective of the origin of the two species in North America. The model for *Megarhyssa* shows that such an oligogenic system of reproductive isolation would be most likely to arise at the center of abundance of a large population, since the two independent mutant forms would be unlikely to occur at the same time in small peripheral isolates. For other examples of reproductive isolation being achieved by slight differences in molecular structure of pheromones see Wilson (1971).

In summary, most of the assumptions in the model have either been shown to be real phenomena in other species or possibilities for investigation in further studies of *Megarhyssa*. The chances of two independent mutations being present at the same time seem fairly good in terms of the moderately large populations and relatively short generation times of this genus (see Townes and Townes 1960). Furthermore, allele *b* could persist for many generations as the heterozygote *Bb* without being expressed in the phenotype or being selected against in the haploid males. It is only allele *y* that comes under immediate and rigid selection.

Finally, it must be pointed out that genotype *bb* for the mutant type of pheromone was arbitrarily assigned to be associated with ovipositor lengths with a mean of $\mu - 2\sigma$, but the same pattern of divergence might be expected to occur for any such association as long as the mean for ovipositor length in the mutant group was far enough removed from the population mean, μ , to be at a selective advantage. The same process of divergence would still occur even if some of the original *bb* genotypes were associated with ovipositor lengths of μ or longer, for the following reasons. First, such genotypes would enjoy less reproductive success than other *bb* genotypes which were associated with ovipositor lengths further removed (to the left) from μ . Second, *bb* offspring of these genotypes that survived would, in subsequent generations, become left-shifted owing to matings with left-shifted *by* males. The greater their divergence from μ , the greater their reproductive success. Equally plausible is the idea that allele *y* rather than allele *b* could originally have been associated with genotypes for short ovipositor length. Whatever the case, the same inevitable process of divergence would proceed.

DISCUSSION

Alternative Model of Speciation

If the present situation in *Megarhyssa* was achieved through allopatric speciation, then in the past the species must have been split up into a number of

geographically isolated populations which subsequently invaded each other's territory. Reproductive isolation would have been acquired as a by-product of (ecological and genetic) divergence in allopatry, so that when the populations met they would rank full species status. Indeed, Mayr (1963) has presented such a model for sympatric sibling species of parasite. For example, in the case of the louse (*Pediculus*), he proposes that the human head louse could have evolved on races with much head hair and little clothing, such as the Melanesians, while the body louse probably evolved on well-clothed races, such as the Eskimos. By the time the two forms reestablished contact they were reproductively isolated. In the case of *Megarhyssa* this model of allopatric speciation seems difficult to explain for three reasons. First, all three species now occupy virtually identical geographic ranges and there is no evidence that they were ever geographically isolated. Second, since they all parasitize the same host, *Tremex* itself would be most likely to have been split up into a number of isolates in the past, but there is no suggestion of any speciation in *Tremex*. Finally, the dispersal ability of *Hymenoptera* in general seems to be good, so that it is difficult to see how major geographical barriers to dispersal could arise. This problem has been discussed in more detail by Askew (1968) for chalcidoid wasps. In other examples of insect-host parasitoid communities, the gall forming midge *Rhopalomyia californica* has at least 10 species of hymenopteran parasitoids, while Askew (1975) notes cases of 30–40 parasitoids per host species. The idea that each parasitoid evolved as a geographic isolate without the host also speciating seems most difficult to accept. If this were so, the high ratio of parasitoid to host species can only be explained in terms of different groups of organisms having highly unequal speciation rates.

Competitive Speciation

The model of speciation in *Megarhyssa* is novel because it depends uniquely on competition for the production of new species, whereas all other modes of speciation depend on competition only for the elimination of excess species after they have been produced. Such a process was envisaged in theoretical terms by Rosenzweig (1978) and termed "competitive speciation." Competitive speciation invokes at least three concepts: disruptive selection, niche discreteness, and density-dependent selection. Each of these on its own seems unlikely to account for sympatric speciation, but when all three concepts are applied together the result seems more favorable (see below). The last mentioned, density-dependent selection, should not be confused with frequency-dependent selection, a process which depends on relative abundance of different phenotypes rather than absolute abundance (see Clarke 1975).

Disruptive selection (Mather, 1955) is one means by which speciation could occur in the absence of geographic isolation. If a species contains a spectrum of phenotypes and intermediate phenotypes become unfit, then extreme phenotypes will enjoy enhanced fitness if they practice homogamy. The end result would be sympatric speciation. Although some laboratory experiments and field studies (see Antonovics 1971) have confirmed this potential under stringent regimes of

selection, it seems most unlikely that the middle range of phenotypes would suddenly become unfit in a natural population. On the contrary, one might expect the middle range of the spectrum to be the most fit and most adaptable to environmental change.

Hutchinson (1968) has put forward the idea that the members of a given species are often easily definable because they occupy an island in niche space. If a way could be found for a species occupying a discrete niche to colonize a neighboring island in niche space, then intermediate phenotypes between it and the daughter colony would be unfit. This might produce selective pressure for the evolution of homogamy and the production of a new species. The speciation models of Bush (1975a, 1975b) and Tauber and Tauber (1977a, 1977b) discussed below explain how such islands of discrete niche space could be colonized. However, the *Megarhyssa* case seems different because a continuous array of phenotypes is fit and occupies undivided niche space in the ancestral species. Disruptive gaps do not seem to exist.

Rosenzweig (1978) explains how intermediates might become unfit, and how colonists arrive at tenable niche islands in terms of Wrightian surfaces (Wright 1932) which are the representation of adaptive landscapes of genotypes. A fitness of zero implies steady generation by generation replacement and is equivalent to an arithmetic fitness of 1.0. Rosenzweig points out that, in the absence of environmental change, the adaptive landscape had previously been thought to be fixed in altitude because fitnesses were assumed to be constant properties of phenotypes. But this situation exists only in that magical world where resources are infinite. In the real world, fitness declines as resources become scarce and reaches zero when density achieves carrying capacity (Fretwell 1969). Thus fitness of a genotype is density dependent and the rigid topography of adaptive landscapes becomes a dynamic surface.

Rosenzweig's analogy of comparing a Wrightian surface to a sphagnum bog is of value in understanding the *Megarhyssa* model. The floating island of interconnected moss will vary in thickness, and therefore varies in the weight it will support at any given point, before that point and a neighboring portion of the mat of moss sink below the surface of the water. In this analogy weight is like density, position like phenotype, and the water level symbolizes the zero fitness level. The mat's thickness is related to abundance of resources for the various phenotypes. With this graphic image of what a Wrightian surface might be like, one can describe the situation in *Megarhyssa* in these terms.

With zero density supported everywhere, most or all of the mat is above water, while the limits of the mat represent extreme depths in the wood (i.e., very shallow or very deep). In the ancestral population the center of the mat supports so much weight that it may sink below the surface producing a disruptive gap. The data on *Megarhyssa* cited above support the idea that density (percentage of hosts parasitized) of phenotypes is relatively high. Each phenotype exploits its own special subniche, and diffuse intraspecific competition may occur between similar phenotypes. High weight at one point will thus depress other nearby areas on the mat. Diffuse competition is a helpful concept in understanding the model, since the solid areas drawn in figure 3 may be much flatter and overlap to a greater

degree than I have indicated. This is likely since at each ovipositor length *Megarhyssa* could probably parasitize a narrow depth range of host larvae. Also, the larvae might themselves show slight changes in effective vertical depth.

The reason why intermediate or very common genotypes become unfit can be explained equally well in terms of density-dependent selection. To my knowledge, Gustafsson (1953) was the first to argue that intraspecific competition might be the usual agency for such selection. In field trials using barley he found that mixtures which included inferior yielding strains could produce greater yields per unit area than a single superior strain alone. This result was dependent, however, on density of sowing. At high densities the mixture produced greater yields, but at low densities the situation was reversed. As Gustafsson stressed, density-dependent selection explains how "the co-operation of fit and less fit makes the population, the entirety, fitter than the partaking constituents themselves and alone." This is in contrast to the rude method of stamping out of the unfit which still forms a central theme in classical Darwinian evolution. Until recently (Rosenzweig 1978), the importance and evolutionary significance of density-dependent and frequency-dependent selection (Clarke 1975) as causes of intraspecific variation seems to have been completely overlooked by most biologists. Instead, environmental instability has been cited as the major cause of heterozygosity in many texts (e.g., Williams 1966). It is probably for this reason that competitive speciation has not previously been proposed.

Finally, one might ask under what circumstances competitive speciation might or might not occur in nature. One reason why disruptive gaps may prove insufficient for speciation is that a species faced with such a gap may respond with a classical discrete polymorphism rather than homogamy. The type of selective regime that would favor polymorphism has been noted above for butterfly mimics. Second, for competitive speciation to occur the environment would have to be sufficiently stable to support a continuous and broad array of phenotypes with strong intraspecific competition for resources at intermediate positions. If the environment was so unstable that one of the subniches disappeared for a while (as a result of lack of resources, etc.) one might expect a single heterozygous, generalized species. J. M. Cullen (personal communication) has envisaged such a generalized species, and has expressed the view that speciation is unnecessary to fill vacant niche space in ancestral *Megarhyssa* populations. Instead, divergent types, which enjoy greater reproductive success than mean phenotypes, would simply cause the standard deviation of ovipositor length to become greater. Suppose in the ancestral population this value diverged far beyond that illustrated in figure 4. More niche space would be filled, but it seems to me that this situation would result in the production of individuals with ovipositor lengths so long or so short (most likely the latter) that they could no longer parasitize *Tremex* larvae. Stabilizing selection would cause the standard deviation to revert back to a size that resulted in a balanced level of reproductive success between the mean and extremities of the population, and vacant niche space would once again exist at the extremities.

If competitive speciation had taken place, one might expect the various species

members to have extremely specialized resource requirements. For coral reef communities, for example, this specialization seems true for some gastropods (e.g., for *Conus*; Kohn 1971 and several other papers), but not for many reef fishes (Sale 1977). In the latter group much overlap occurs in food and habitat requirements, and suitable living space seems to be the resource most likely to be in short supply. Sale has developed the argument that interspecific competition for space among reef fishes is a lottery which no species can consistently win. Diversity of reef fish communities is directly correlated with small scale, unpredictable disturbances, including predation. However, lotteries have probabilities and predation itself may have a frequency-dependent basis. Such an idea has been proposed to account for the number and density of tree species in a tropical forest (Janzen 1970). Competitive speciation might therefore operate where susceptibility to predation or some other disturbance directly influenced the fitnesses of the competing genotypes. What I am trying to stress here is that species represent adaptive peaks of resource utilization, and such adaptation includes not only efficiency of feeding, nesting, etc., but also the ability to withstand the constellation of disturbances, notably predation and physical changes, which may occur from time to time.

Affinities with Other Models of Speciation

In many respects, apart from those noted above, the process of divergence in *Megarhyssa* closely resembles the genetic model of speciation proposed by Bush (1975*b*) for phytophagous parasitic insects. Phytophagous parasites tend to mate on or near the host plant, and one or a few closely related plant species may be attacked. The adult female selects the host, mainly on the basis of odor, and the larvae have no choice. Both host selection and larval survival in different hosts are under genetic control, and these are the most important genetic factors in the model. If a population of fruit flies (genus *Rhagoletis*) is polymorphic for an allele pair S_1S_2 , where each allele confers the ability to survive in one host plant, and is also polymorphic for a second allele pair H_1H_2 causing positive assortative mating (H_1H_1 selects host A, H_2H_2 selects host B), then two reproductively isolated populations can evolve. As an example of this model Bush cites the shift of *R. pomonella* from apples to cherries in Wisconsin.

A host shift is initiated by mutations which introduce new host selection ($H_1 \rightarrow H_2$) and survival genes ($S_1 \rightarrow S_2$) in the original apple-infesting population. A major problem is how S_2 and H_2 could be retained in the ancestral population. Bush suggested that each could be retained at low level by chance, either through close linkage to a beneficial gene or through overdominance, and this is the same solution I have adopted for the retention of allele *b* in ancestral *Megarhyssa* populations.

Though gene flow would still occur through H_1H_2 individuals ovipositing on both plants, induction and allochronic isolation would inhibit random mating between the two races. Cherry tends to come into fruit earlier than apple, and allele S_2 would become strongly associated with H_2 . Gene flow would be further

inhibited as a result of a shift to an earlier emergence of the cherry race once it was established, and be reduced to an insignificant trickle of H_2H_2 from apples as a stronger coadapted gene pool evolved in the cherry race.

Tauber and Tauber's (1977a, 1977b) model of speciation in green lacewings (Neuroptera) is genetically very similar to that for *Rhagoletis*. It involves, as a first stage, establishment of stable polymorphism based on color matching. *Chrysopa carnea* is light green and found on grasses; *C. downesi* is dark green and found on coniferous trees. Each is camouflaged in its own habitat. The two species are interfertile, and a single pair of alleles was found to control this difference. Individuals homozygous for the semidominant autosomal allele *G* are exhibited in the dark green phenotype of *C. downesi* adults, whereas the recessive *g* alleles produce the light green phenotype. Color is intermediate in *Gg* heterozygotes. The second stage in the model involves the development of asynchronous breeding cycles in the two ecotypes. Tauber and Tauber found that single allele differences at each of two autosomal loci could produce this result. They concluded that though the two species may now differ in many characters, as few as three gene substitutions could have led to their speciation.

In both of the above models there may be only a narrow window in time and space when such factors as adult emergence, food abundance, and the insects' genetic constitution are suitable for a successful host or habitat shift. Bush (1975a) also points out that attempts at colonization of a host plant probably occur more frequently than we now realize. The vast majority of the beachheads established on new host "islands" are probably doomed to failure either by chance extinction, competition, lack of genetic diversity, or other factors. The same comments would equally well apply in the formation of a daughter species of *Megarhyssa*. Recall that in the model this process begins with *y* males mating with *bb* females. Suppose such females have a five times greater chance of parasitizing larvae than the mean for the population. In the first generation the allele frequency of *y* would be greatly increased (in females). In the second generation more *y* males would be produced than in generation 0, but *bb* females would at best be only slightly more common than previously, and might be absent altogether. It is only when allele *y* becomes associated with *b* after a few generations that large numbers of *bb* females can be produced and the process of divergence really picks up momentum.

Functional Significance of Haplodiploidy

There is one special condition in hymenopterans. That is, with the haplodiploid genetic system, the males are hemizygous and therefore any (male) assortative mating or host selection genes come under immediate and rigid selection. As shown in the model, ecological divergence can still occur in the face of massive gene flow when the genetic system is haplodiploid. In many other animal groups, males, while not being haploid, are hemizygous for characters on the *X* and *Y* chromosomes, and the same process could operate if the assortative mating gene of the male was carried on these chromosomes.

The Hymenoptera contain many parasitoids, a large number of which occur as

species groups living on a single host. In groups such as the *Chalcidoidea*, host specificity is high and mating frequently occurs on the host. Sib mating and inbreeding are common, and females usually mate only once (Askew 1968). All this would facilitate rapid adaptation to a new host.

The haplodiploid genetic system has received much interest in connection with the evolution of insect social behavior (Hamilton 1964; Wilson 1971). Yet haploid-diploidy is probably a much more ancient phenomenon than insect eusociality, and therefore must have other evolutionary significance. It has arisen independently in several diverse and very successful groups of arthropods including mites and some beetles, as well as in the hymenopterans (Wilson 1971). My suggestion is that haplodiploidy is of adaptive value for rapid speciation in groups with narrow niche requirements.

CONCLUSIONS

If we have learned anything about the process of speciation in the last 40 yr, it is that we cannot generalize too broadly. Until recently, arguments on speciation have been based on evidence derived from studies of nonparasitic animals such as birds, fishes, mammals, and insects such as *Drosophila*, which are quite different in their ecology, behavior, and genetic structure from many parasitic insect species with narrow niche requirements. Knowledge of the mechanisms of the latter group has great significance in studies of applied evolutionary biology, particularly in the control of economically important pest species.

Given the causes of variation within species, one might expect the maintenance of genetic variability to have a high selective premium. For this reason assortative mating is remarkably rare in most species and, in fact, as investigations have shown, there is often a preference for different genotypes. However, given the appropriate selective forces, stable environmental conditions, and a suitable genetic potential, the time may be ripe for sympatric speciation.

SUMMARY

Three species, *Megarhyssa atrata*, *M. macrurus*, and *M. greenei* are dependent on the same host, larvae of the wood-boring *Tremex columba* (Hymenoptera: Siricidae) in the same geographic area (Townes and Townes 1960). Adults are extremely similar in their ecology and behavior but do not appear to compete for food or shelter. Three factors permit larvae of the three species to be segregated ecologically by parasitizing different segments of the host population. (1) The adults select a host larvae at a depth in the wood so that complete insertion of the ovipositor at right angles to the surface of the wood will just reach it. (2) The ovipositors of the different species are of different lengths. (3) The host larvae maintain themselves at about the same depth in the wood for most of their larval period (Heatwole and Davis 1965).

A mechanism is proposed whereby the ancestral *Megarhyssa* species diversifies and divides by several stages to achieve its present condition. The model is unusual because (1) no geographic isolation is involved, (2) the evolutionary

force is intraspecific competition, and (3) the final outcome is the formation of three species separated by premating isolation.

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