

Points of View

Animal Species, Evolution, and Geographic Isolation

The review by Throckmorton and Hubby (1963, *Science*, 140[3567]:628–631) leaves the correct impression that a major theme in Ernst Mayr's important new book, *Animal Species and Evolution*, is the universality of geographic isolation as a prerequisite to speciation in sexually reproducing animals. This topic is discussed in nearly every part of the book, with Mayr finally concluding (p. 477) "In not a single case is the sympatric model superior to an explanation . . . through geographic speciation." The attitude with which Mayr views geographic isolation is probably no better illustrated than by his first reference to it (p. 2): ". . . Darwin . . . often went too far in compromising . . . one can find support in Darwin's writings for almost any theory of evolution: speciation with geographic isolation or without it. . ."

Mayr's book is a landmark in evolutionary synthesis which will be the "bible" of neophytic and experienced zoologists alike for years to come. Therefore, I feel obliged to put on record the errors and inadequacies in his treatment of some particular investigations on this topic with which I am familiar.

Twice (pp. 475, 476), Mayr indicates that Young (1958) explained origin of "the various broods and sibling species of the periodical cicadas (*Magiccada*)" through geographic separation, and both times he discusses this finding as an alternative hypothesis under "Speciation by seasonal isolation." However, all 20–30 broods and all six species of *Magiccada* are *seasonally synchronous*. Mayr has confused, perhaps for himself and certainly for all readers, Young's discussion of the origin of the spring adulthood of the genus *Magiccada*, and his discussion of the origin of broods

and species *within* the genus which appear in *different years*. Curiously, Mayr has omitted from the book any reference to this question of accidental annual separation by rare climatic events among populations with life cycles requiring two or more years. Do such *extrinsically* isolated (and *initially identical*) populations always become reunited unless all but one are exterminated? Such an argument can scarcely be defended, and the fact is that tens of thousands of species of arthropods alone are involved (for example, all of the approximately 1,500 world species of Cicadidae may be "periodical"). Even the fact that climatic events causing accidental annual separation of periodical cicada broods were geographic in their effect (and this is by no means a new idea) does not erase the certainty that "wrong-year" emergences must have occurred in only parts of some continuously distributed populations, leaving areas of either complete contact or, more likely, rather broad geographic overlap between affected and unaffected (and thus annually separated) populations. This is *not* geographic isolation.

In particular, periodical cicadas can in no way be used as parallels to seasonal separation between populations that overwinter in widely different stages (such as egg and late juvenile), as Mayr does use them (p. 476), referring to: "The same model of breeding-season differences. . ." His attempt to further the parallel by referring to an "older model of allochronic speciation" is very misleading. To my knowledge, no one has ever suggested that *Magiccada* species or broods arose by either seasonal or annual separation "through mutation," and the reference cited (Mayr, 1947:277) does not even mention periodical

cicadas; it only describes objections to a hypothetical scheme for allochronic seasonal speciation.

Mayr discusses recent work on field crickets rather extensively (pp. 45, 52, 99, 476). On p. 476, he inadvertently uses two different generic names for the same two species within the same paragraph. The illustration he reproduces on p. 46 from Fulton (1952) includes four of the seven eastern North American field crickets, and gives only colloquial names that are either incomplete or no longer in use. Nothing tells the reader how to find out which species are actually involved, that part of the figure is now known to be in error, or that Mayr discusses some of the same species in other places under different names. Thus, the reader cannot discover that the "Mountain Cricket" in Fig. 3-2 is really *two* species—indeed, the same two species discussed by Mayr on p. 476 as *Gryllus veletis*, the "Northern Spring Field Cricket," and *G. pennsylvanicus*, the "Northern Fall Field Cricket." The spring adult population of *Gryllus firmus*, described by Fulton (1952) and Alexander and Bigelow (1960), and important to the hypothesis of allochronic speciation discussed on p. 476, is not shown in the figure. The legend says the figure considers four sibling species, when actually three or four different species groups are now known to have been represented (Alexander, 1957; Alexander and Bigelow, 1960). One might as well refer to all the eastern North American *Drosophila* species as siblings—just because they look alike. I recognize the possibility of confusion owing to the rapid changes resulting from new information on this group, but all of the necessary publications to straighten out these points are in Mayr's bibliography, and all are mentioned more than once. Too much is said about these species for these kinds of errors and omissions to be justifiable.

On p. 476, Mayr analyzes Bigelow's (1958) and Bigelow's and my (1960) hypothesis of allochronic (in this case, seasonal) speciation in field crickets. He says that only

one of his three objections is met: that seasonal climatic events usually would not eliminate the mid-season breeders (apparently he agrees that they would, in this case, because two stages completely separated in the life cycle are clearly superior to all others for overwintering). His other objections are: (1) ". . . the existence, in an area with pronounced seasons, of a species with such a long breeding season but only one generation per year is altogether unlikely. Prolongation of the breeding season is invariably achieved by having several successive generations or broods per year" and (2) ". . . if there were such a species it would have a wide geographic range and it is improbable that the extermination factor would affect all the populations in a like manner." Mayr has missed the point completely. As postulated, our ancestral species *did* have successive generations across the total available season, and it *did* have a wide geographic range. But only along its (advancing?) northern border would the separation into juvenile-overwintering (spring-maturing) and egg-overwintering (fall-maturing) populations take place. Even if this northern "border" were eventually separated geographically from the rest of the species, geographic separation between the incipient spring and fall species *would never be involved*. Furthermore, almost certainly the exterminating factor *would* affect all parts of the border populations in a like manner. All over the world in temperate climates, field crickets are known to overwinter in only two stages, and thus several independent origins for at least the juvenile diapause stage are certain. It is critical that extensive crossing tests have indicated that diapause differences alone appear to be sufficient to prevent hybridization among field crickets, congeneric species of which are otherwise almost universally interfertile.

Mayr omitted any mention of Bigelow's and my discussion (1960) of *Gryllus firmus*, the southern relative of the northern spring and fall field crickets, which shows across its range precisely the intermediate steps

and variations which Mayr says could not occur. This species, which we believe may actually represent the southern remnant of the ancestral species involved here, all by itself meets both of Mayr's objections. In the south, adults have been taken the year around; in the northern parts of its range it becomes principally an egg-overwintering, fall-maturing species, but with a small part of the population overwintering as juveniles and maturing in spring (Fulton, 1952; Alexander and Bigelow, 1960).

Mayr concludes the field cricket discussion (p. 476) with two completely unsupported remarks. First, he says that the spring and fall species probably separated seasonally because of ecological competition after developing different overwintering stages while geographically isolated. But all of the evidence suggests otherwise. All juvenile-overwintering species of related Orthoptera are spring adults, and all egg overwinterers are summer and fall adults. Why believe that these two lived together in the past as adults with their present life cycles, when no other species with different overwintering stages and life cycles of similar length, with or without potentially competitive siblings, do so? The identity between these two species in all aspects of acoustical behavior, unique among sympatric insect species anywhere in the world (with the probable exception of a parallel case of two seasonally separated Japanese siblings in another genus), also militates against this idea.

Finally, Mayr says, "Related species, not in competition with a close relative, are rarely as narrowly specialized." There is absolutely no basis for this statement, and in fact the exact opposite is true. *Gryllus campestris* in Europe lives alone across most of its range and has a life history and ecology almost identical to that of *G. veletis*. *G. vernalis* has the same life history, and so does its sibling, *G. fultoni*, which is often individually intermixed with *G. vernalis*. Narrow seasonal specialization occurs in every northern field cricket for which the life history is known. In fact, it occurs in the vast majority of all insects in northern climates. It also occurs *only in the northern part of the range* of southern field crickets. Mayr may have been thinking of *Gryllus rubens*, but this is a rigidly two-generation species in the north, always maturing both in spring (together with three ecologically overlapping species) and in fall (with two ecologically overlapping species), and overwintering *only* in the late juvenile stage. It is in no way relevant to this argument. Nor is any other cricket.

I have used no new information in this discussion, and all of the references cited appear in Mayr's bibliography. The unfortunate thing is that most people will read only Mayr's book on these subjects, and they cannot derive an accurate picture from it.

RICHARD D. ALEXANDER

The University of Michigan
Ann Arbor, Michigan

Reply to Criticism by R. D. Alexander

No one can write a book of 813 pages with 1,800 literature references and numerous generic and specific names quoted on almost every page and not expect to make an occasional mistake. However, I hope that matters are not quite as bad as Dr. Alexander would seem to make them.

(1) Alexander is quite right when he says that it might have been better not to include *Magicicada* in the discussion of "Speciation

by Seasonal Isolation." Perhaps the section should have been entitled "Speciation by Isolation in the Time of Breeding." Periodical cicadas breed, of course, at the same season, but related broods may be out of step with respect to the particular year in which they emerge.

I am afraid Alexander did not get the essential point of my discussion, and I must take the blame for not having made this