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AN EVALUATION OF NARROW HYBRID ZONES IN VERTEBRATES

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ABSTRACT

A review of the literature on vertebrate hybridization reveals the existence of a number of narrow hybrid zones. Three hypotheses have been suggested to explain the occurrence of these zones. The ephemeral-zone hypothesis states that hybridization will end either in speciation or fusion of the hybridizing taxa by means of introgression. The dynamic-equilibrium hypothesis allows the possibility that narrow hybrid zones might be stable: where hybrids are confined to a small area by steep selection gradients, "crystallization" of an antihybridization mechanism might be prevented by naive immigrants from the parental populations even though hybrids are selected against. The hybrid-superiority hypothesis states that hybrids are more fit than parental phenotypes in some environments.

The ephemeral-zone hypothesis fails to explain the antiquity and apparent stability of several hybrid zones. The dynamic-equilibrium hypothesis does not adequately explain the persistence of hybrid populations that do not receive a substantial influx of genes from both parental populations. The hybrid-superiority hypothesis is consistent with the various sizes, shapes, and positions reported for stable hybrid zones because, under this hypothesis, the range of a hybrid population is determined by the range of environmental conditions within which the hybrids are superior.

Although there are exceptions, most vertebrate hybrid zones are, in fact, narrow. The hybrid-superiority hypothesis must accommodate this fact. The additional hypothesis is offered that hybrids, in some cases, can succeed in environments where competition from parental phenotypes is weak. Thus, hybrid populations are often found in areas devoid of stable ecological communities. Ecotones are one such area, and I suggest that stable hybrid zones are often narrow because they tend to occur in ecotones which are themselves narrow.

INTRODUCTION

THE EVENTS which ensue secondary contact between two morphologically and presumably genetically distinct vertebrate populations are obscure. Certainly, hybridization is to be expected if the taxa in question have not diverged too far, but the final outcome is unpredictable. It is widely believed that natural hybridization is ephemeral, leading ultimately to either speciation — i.e., the perfection of reproductive isolation — or to fusion of the two races through introgressive hybridization (e.g., Dobzhansky, 1940; Sibley, 1957; Wilson, 1965; Remington, 1968). This hypothesis no longer seems tenable, however, because there are several examples of hybrid zones which appear to

be stable (see Short, 1970, and below — p. 266 ff.).

Short (1969) made a distinction between a hybrid zone and a zone of overlap and hybridization; both are subcategories of zones of secondary intergradation. Although this could be an important distinction, it can rarely be made with regard to published reports of secondary intergradation zones. In this article I have used the term hybrid zone interchangeably with zone of secondary intergradation in order to reduce verbiage.

The hypothesis that hybrid zones are always ephemeral is based on two concepts: the concept of coadapted gene complexes; and the concept that gene flow is a strong cohesive force

in maintaining the unity of a species. It can be reasonably argued that an organism's phenotype is a singular manifestation of the synergistic actions of numerous gene loci. A successful organism must, therefore, have an integrated genetic system whose component genes work harmoniously to produce a physiologically homeostatic organism capable of reproduction. When a species population is divided, differential mutation and coadaptation would be expected to cause divergence between the isolates. If divergence progressed to the extent that hybridization would disrupt the harmony of the distinctly coadapted gene complexes, secondary contact would lead to speciation because natural selection would eliminate those individuals prone to hybridization. On the other hand, if divergence and differential coadaptation had not progressed to the extent that hybrids were less fit, fusion of the races would be expected, because the viable and fertile hybrids would serve as a bridge for introgressive hybridization. In fact, Wilson (1965) said that when two Mendelian populations with imperfect intrinsic isolating mechanisms come into contact, one of these two outcomes is inevitable and no other equilibrium state seems possible.

Another hypothesis, which I will refer to as the dynamic-equilibrium hypothesis (or model), reconciles the existence of narrow stable hybrid zones with the concept of coadapted gene complexes. Given that two populations had diverged to the point that hybrids suffer depressed fitness, Bigelow (1965) postulated that gene flow through the hybrid zone into the parental populations would be inhibited by selection. Where selection gradients were steep, intergradation would be restricted to a narrow zone between the parental populations. Although hybrids might be inherently less fit than parental phenotypes, only a few individuals in or near the zone of secondary contact would be exposed to selection disfavoring hybridization, while a much larger proportion of the parental phenotypes would never experience this selection pressure. Gene flow from the parental populations into the zone of secondary intergradation could "swamp" alleles which cause individuals to avoid hybridizing and, thus, hinder the evolution of an antihybridization mechanism.

A third hypothesis which, like the dynamic-

equilibrium hypothesis, could account for stable hybrid zones is that the hybrids are actually more fit than the parental phenotypes in the restricted regions where they occur. This hypothesis has been espoused by botanists for years (e.g., Anderson, 1949; Muller, 1952; Grant, 1971), but it is not often given serious consideration as an alternative to the ephemeral hybrid zone and dynamic-equilibrium hypotheses by students of vertebrate hybridization. Hagen (1967), however, argued in favor of hybrid superiority as an explanation of the narrow hybrid zones between the anadromous form "*trachurus*" and the freshwater form "*leirus*" of three-spine sticklebacks (*Gasterosteus aculeatus*). More recently Short (1970) pointed out that ephemeral hybrid zones are the exception rather than the rule in avian hybrids and concluded (Short, 1972) that these hybrids are more fit than parental phenotypes in zones of antiquity, although strong selection against alien genes is occurring in the parental populations. And, finally, Littlejohn and Watson (1973) concluded that the most likely explanation of a stable narrow hybrid zone between two closely related anurans *Geocrinia laevis* and *G. victoriana* in Victoria was that the hybrids were more fit than either parental species within a restricted region at the interface of the ranges of the two species populations.

The hybrid-superiority hypothesis has largely been ignored because the occurrence of adapted hybrids would be inconsistent with the central dogma of animal speciation theory, namely, that the integrity of a species, at least in its infancy, is maintained by coadaptation of the species gene pool. That coadaptation exists is unequivocal (e.g., Wallace and Vetukhiv, 1955), but its universal importance as a cause of speciation is a presumption and not a demonstrated fact.

My present purpose is, first, to advocate the hypothesis that hybrids between morphologically, genetically, and ecologically distinct phenotypes are in many cases more fit than either of the parental phenotypes; and, second, to develop a hypothesis which explains the occurrence of stable hybrid zones. My argument is premised primarily on the common properties of several such zones which have been described in the literature, but my initiative to explore this literature was prompted by an in-

vestigation of fitness components in unisexual fishes (Moore, 1976). The basis of this initiative will be briefly presented also.

THE CASE OF *Poeciliopsis monacha-occidentalis*

P. monacha-occidentalis is an all-female fish species. As is characteristic of unisexual vertebrates, it is also a hybrid; that is, a population of *P. monacha-occidentalis* is genetically equivalent to a population of female F₁ hybrids between *P. monacha* and *P. occidentalis* (see Schultz, 1969, 1971, 1973 for reviews of unisexuality in *Poeciliopsis*). Moore (1976) analyzed the fitness of this hybrid in the context of a mathematical model. The results indicated that the broad distributional success of *P. monacha-occidentalis* is

primarily attributable to the simple fact that it produces approximately twice as many female offspring as does *P. occidentalis*, with which it is sympatric (Fig. 1A). When all-femaleness is discounted, however, *P. occidentalis* is better adapted than the hybrid over the entire range of sympatry with the exception of a narrow zone (the Rio Mayo), where the ranges of the parental species overlap slightly, and of a single locale in the next northerly drainage.

The model can also be used to deduce the distribution of *P. monacha-occidentalis* under the hypothetical condition that assumes it to be not a unisexual species but, rather, a *P. monacha* × *P. occidentalis* bisexual hybrid. This distribution is illustrated in Figure 1B.

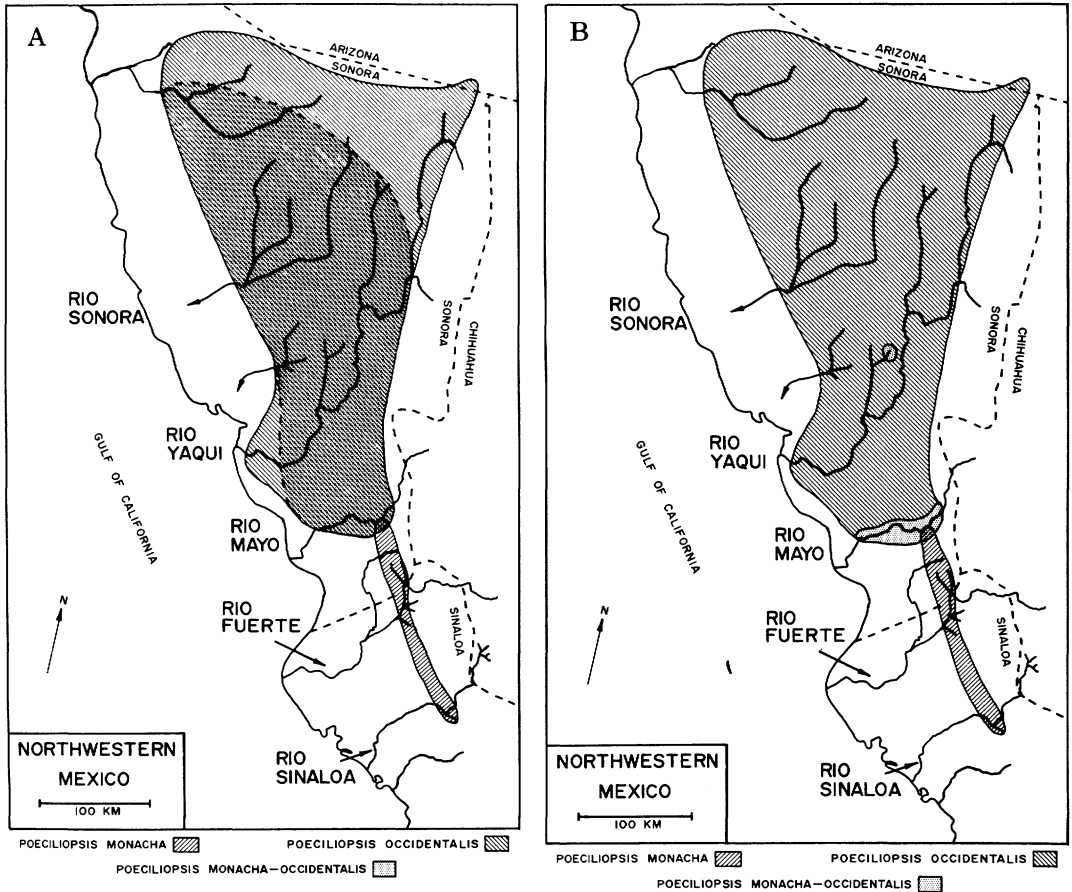


FIG. 1. DISTRIBUTION OF THE COMPLEX *Poeciliopsis occidentalis* — *P. monacha-occidentalis*

A, the actual distribution of the component species; B, the predicted ranges of the component species if *P. monacha-occidentalis* were an independent, sexually reproducing hybrid.

Although some reservations need to be registered regarding the applicability of this result to the problem of narrow hybrid zones, two features of the hypothetical distribution are remarkable — viz., that the hybrids are more fit than one of the parental species anywhere, and that the region of hybrid superiority is, in the main, restricted to a narrow zone at the interface of the ranges of the parental species.

The major reservations are twofold. First, the result was obtained from a mathematical model, and therefore, the inference can be no more valid than the set of simplifying assumptions made when the biological problem was translated into a set of mathematical relationships. Second, all *P. monacha-occidentalis* individuals are F₁ hybrids, whereas a population of bisexual *P. monacha* × *P. occidentalis* hybrids would consist of numerous recombined phenotypes. Although heterosis does not appear to be an important component of fitness in *Poeciliopsis* (Thibault, 1974; Moore, 1976), it is possible that the adaptive superiority of *P. monacha-occidentalis* in the Rio Mayo would be lost if the F₁ hybrid condition of this species were eroded by recombination.

These reservations notwithstanding, the situation in *P. monacha-occidentalis* provides the insight that hybrids between some vertebrate species may be more fit than the parental species, under some circumstances. In any case, discarding the presumption that hybrids are invariably inferior allows one to explain readily much of the otherwise enigmatic and inexplicable data on hybrid zones.

HYBRID ZONES IN OTHER VERTEBRATES

The hypothesis that all hybrid zones are ephemeral is untenable because several ancient zones do exist. In addition to the often cited zone of hybridization between the Hooded and Carrion Crows, *Corvus corone* and *C. cornix*, which traverses central Europe (Mayr, 1963), it has been reasonably argued that the following hybrid zones are stable and of remote origin: domestic mice, *Mus musculus musculus* × *M. m. domesticus*, on Jutland (Hunt and Selander, 1973); iguanid lizards, *Sceloporus woodi* × *S. undulatus undulatus*, in Florida (Jackson, 1973); and warblers, *Dendroica coronata* × *D. auduboni* in Alberta and British Columbia (Hubbard, 1969). The domestic mice were thought to have

been hybridizing for 5000 years, *Sceloporus* for up to 100,000 years, and *Dendroica* for “several thousand years” (5,500-6,500 — Hubbard, 1969). There is no evidence of assortative mating in any of these hybrid zones nor evidence of introgression beyond the narrow confines of the zones.

In addition, there are numerous reports of hybridizing specific or subspecific pairs where stable hybrid zones are at least indicated. These reports variously include evidence of hybrid fertility, backcrossing, morphological intermediacy, hybrid viability, constancy in historical times, and random mating in the secondary contact zone. In some cases, inferences based on geological data or events recorded in historical times, were made as to the time when secondary contact was established. These complexes include two ecologically distinct morphs of sticklebacks, *Gasterosteus aculeatus*, in British Columbia (Hagen, 1967); toads, *Bufo woodhousei* × *B. fowleri*, in Texas (Meacham, 1962); anurans, *Geocrinia laevis* × *G. victoriana*, in Victoria (Littlejohn, Watson, and Loftus-Hills, 1971; Littlejohn and Watson, 1973, 1974, 1976); anurans, *Litoria ewingi* and *L. paraewingi*, in Victoria (Watson, Loftus-Hills, and Littlejohn, 1971; Watson, 1972; Gartside, 1972; Littlejohn, 1976); whiptail lizards, *Cnemidophorus tigris gracilis* × *C. t. marmoratus*, in Arizona and New Mexico (Zweifel, 1962; Dessauer, Fox, and Pough, 1962); leopard lizards, *Crotaphytus wislizenii* × *C. silus*, in California (Montanucci, 1970); chromosomal races of the *Sceloporus grammicus* complex of iguanid lizards in Mexico (Hall and Selander, 1973); orioles, *Icterus galbula galbula* × *I. g. bullockii* (Sibley and Short, 1964; Rising, 1970, 1973), flickers, *Colaptes auratus auratus* × *C. a. cafer* (Short, 1965), and towhees, *Pipilo erythrophthalmus erythrophthalmus* × *P. e. arcticus* (Sibley and West, 1959), on the Great Plains; grackles, *Quiscalus quiscula quiscula* × *Q. q. versicolor*, in eastern and southeastern United States (Huntington, 1952; Yang and Selander, 1968); titmice, *Parus bicolor* × *P. atricristatus*, in Texas (Dixon, 1955); towhees, *Pipilo erythrophthalmus* × *P. ocai*, in Mexico (Sibley, 1954); cactus wrens, *Campylorhynchus rufinucha humilis* × *C. r. nigricaudatus*, in Mexico (Selander, 1965); toucans, *Pteroglossus torquatus torquatus* × *P. (t.) sanguineus*, and jacamars, *Galbula ruficanda ruficanda* × *G. (r.) melanogenia*, in Colombia (Haffer 1967); and pocket gophers,

Thomomys bottae and *T. townsendii*, in California (Thaeler, 1968).

Whereas the hybrid-superiority hypothesis accommodates all of these stable hybrid zones, circumstances in some of the zones appear to be inconsistent with predictions made by the dynamic-equilibrium hypothesis. To see the discrepancies, it is necessary to explore in greater depth the latter hypothesis and its implications.

An implicit requirement for stability in the dynamic-equilibrium hypothesis is that the zone be sandwiched between the parental species populations, or at least so situated that the hybrid population receives a substantial influx of genes from both parental species. Imagine that species A and B come into secondary contact and begin to hybridize. Although the hybrids are less fit than either A or B, a hybrid zone is established and maintained according to the dynamic-equilibrium hypothesis. Now, suppose that the range of species B contracts, thus breaking contact between the hybrid population and species B. As the remnant genes of species B combine with species A genes they are eliminated by selection from the hybrid population. There is no longer a source to replace dwindling species B genes, and the hybrid population would be swamped by species A.

Narrowness also has been implied to be a necessary condition for stability in the dynamic-equilibrium model. Bigelow (1965) posed the question: "If selection can maintain effective reproductive isolation for several thousand generations despite interbreeding in a zone of contact, one might ask how selection could fail to perfect ethological or (other) mechanisms to prevent interbreeding in that zone of contact" (p. 454). Later he answers this question as follows: "Actually, the evolution of mechanisms that prevent interbreeding is not likely to occur in a narrow hybrid zone. The 'zones of contact' cited by Mayr and others usually involve but a small fraction of the total range of the component populations. In every case the vast bulk of each population lives *outside* [Bigelow's italics] the zone of contact and is derived from a long line of ancestors that have seen neither the zone nor an individual from the population beyond the zone. . . . The evolution of mechanisms to inhibit interbreeding appears to have taken place as a direct result of selection *in a narrow hybrid zone of contact*

[Bigelow's italics] rather infrequently" (p. 454). Jackson (1973) echoed this view when he interpreted the hybrid zone in iguanid lizards: "Continuance of hybridization between *undulatus* and *woodi* probably results from the very sharp boundary between the two plant associations. This sharpness allows such a small part of each species population to be sympatric with the other that gene flow to the ecotone swamps any tendency toward development of ethological reproductive isolating mechanisms" (p. 67). This also seems to be the implication of the following statement from Watson's (1972) abstract: "The presumed antiquity of the contact, and the narrowness of the zone suggest a stable situation" (referring to the *Litoria* hybrid zone).

The postulate that stable hybrid zones must be narrow actually supports the position I advocate, namely, that the dynamic-equilibrium model does not explain the observed variation in breadth of some of the zones cited above. Nevertheless, I am uncertain that narrowness is, in fact, a necessary condition for stability in this model. Suppose that a hybrid zone has gained considerable breadth relative to the dispersal capabilities of the species involved. "Naive" migrants from allopatric portions of the parental populations would rarely reach the center of the hybrid zone. Presumably in each generation of random mating, however, a few nearly pure parental genotypes would segregate in this central hybrid swarm. These would be strongly favored by selection, particularly if they were also fortuitously endowed with a complement of genes that caused them to mate with similar genotypes, thus reducing the number of maladapted hybrid offspring produced. Since the central portion of the zone would be effectively isolated from "naive" migrants, an antihybridization mechanism might "crystallize" there. Crosby (1970) actually simulated a comparable situation. Crosby's plant "subspecies" were defined by eight independent loci; in addition, the two "subspecies" were identically polymorphic at three loci that determined flowering time and two loci that determined duration of flowering. Hybrid genotypes were selected against in proportion to their admixture of genes. When the hybrid swarm was initiated, the identity of the parental phenotypes was rapidly lost. By generation 44, however, bimodality was again apparent, and

by generation 80 "speciation" had occurred. A marked divergence in flowering time between "species" concomitant with reductions in flowering duration in both species effectively prevented miscegenation by generation 80. In theory, then, re-segregation of parental genotypes should occur in a hybrid swarm or, equivalently, near the center of a broad hybrid zone, and it follows that narrowness is, indeed, a necessary condition to prevent the evolution of reproductive isolation in a zone where hybrids are less fit than parental phenotypes. Whether these events would occur in reality is uncertain. It would depend upon the probability of parental, or near parental, genotypes re-segregating. This, in turn, would depend on population size, the number of loci that distinguish the parental genotypes, and the number of loci that determine an antihybridization mechanism. Data of these sorts are yet to be collected.

To summarize these predictions of the dynamic-equilibrium hypothesis: it is clear that a hybrid zone in contact with one parental species would be unstable, and it seems likely that a broad hybrid zone would be unstable also. Furthermore, if Crosby's (1970) result is generally true, speciation would be expected in a hybrid swarm if the hybrids were maladapted.

A comparison of the predictions of the dynamic-equilibrium hypothesis with the list of apparently stable hybrid zones cited above reveals several discrepancies. The hybrid populations of leopard lizards, *Crotaphytus wislizenii* × *C. silus*, apparently are in contact only with *C. silus* at some locales, and with neither parental species at others. Thus, the persistence of these hybrids does not depend upon an influx of genes from both parental populations. Furthermore, not all of these hybrid zones are uniformly narrow. For example, the zone of hybrid mice in Denmark flares in width along the west coast of Jutland; the zone of grackles is as much as 320 km wide in the southern Appalachians (Huntington, 1952) although it is much narrower in Louisiana (Yang and Selander, 1968). The narrow hybrid zone between the anurans *Geocrinia laevis* and *G. victoriana* also has a feature that is not adequately explained by the dynamic-equilibrium hypothesis. Littlejohn and Watson (1973) reported a salient protrusion of the range of *G. laevis* into that of *G. victoriana* near the northeastern end of this hybrid zone. The protrusion is sufficiently narrow that gene

flow from the clearly allopatric portion of the *G. laevis* population to the tip of the protrusion ought to be very limited. Since the flow of genes to the distal region of the protrusion would not be expected to be of sufficient magnitude to disrupt the evolution of an antihybridization mechanism, the dynamic-equilibrium model would predict that reproductive isolation would be more highly developed at the tip of the protrusion than in other parts of the hybrid zone where the parental populations interface along a broad front. Littlejohn and Watson (1973), however, reported that hybridization at the tip of the protrusion was not discernibly different from that occurring elsewhere in the zone.

A final piece of evidence that casts doubt on the validity of the dynamic-equilibrium hypothesis also comes from Crosby's (1970) simulation studies. Crosby simulated the essential circumstances of the dynamic-equilibrium hypothesis (see Crosby, 1970, pp. 288-289, *Centrifugal* gene flow), and the outcome was "speciation" rather than stabilization of the hybrid zone. Again, there is some doubt as to whether Crosby's result can be generalized, but it does raise the possibility that the postulates of the dynamic-equilibrium hypothesis do not lead to an equilibrium at all, or if they do, the equilibrium is an unstable one.

Implicit in the hypothesis that hybrids can be more fit than parental phenotypes is the postulate that ecological factors are primary in determining the fitness of these hybrids. Accordingly, the breadth of a zone is determined by the geographical range of ecological conditions to which the hybrid is adapted — or more plausibly, to which the parental phenotypes are less adapted. The complex array of hybrid populations of towhees in Mexico is readily accommodated by the hypothesis that ecological factors determine the relative fitness of hybrid phenotypes. At some locales, *Pipilo erythrophthalmus* and *P. ocai* are sympatric and do not hybridize. Elsewhere, however, partially isolated populations comprised entirely of intermediates are known. At still other locales step clines in hybrid index occur (Sibley, 1954; Sibley and West, 1958; Sibley and Sibley, 1964).

Although the hybrid-superiority model can account for irregularities in the structure of secondary intergradation zones, the fact remains that most of these zones are narrow and occur at the interface of the ranges of parental

populations. To survive, the hybrid-superiority hypothesis must account for this fact. A simple explanation is suggested by the zoogeography of primary fitness values in *P. monacha-occidentalis*, viz., hybrids are better adapted than parental species in narrow geographical regions. This explanation, however, only raises the question: why would hybrids be more fit in such restricted areas?

A plausible answer is suggested by the botanical literature on hybridization and, again, by the unisexual vertebrates. Systematic botanists have long recognized that natural plant hybrids are often restricted to man-disturbed environments; i.e., they are weeds in an ecological sense (e.g., see Grant, 1971, Chap. 11). Wright and Lowe (1968) borrowed this concept and the term "weed" habitat to describe collectively the habitats that support parthenogenetic species of *Cnemidophorus*. Under this rubric they included ecotones, disclimax communities, marginal habitats, and perpetually disturbed habitats. The common property of these habitats is that there is no bisexual analogue with which the parthenospecies must compete. Now, there is substantial evidence that the parthenogenetic species of *Cnemidophorus* have hybrid phenotypes (Lowe and Wright, 1966; Neaves and Gerald, 1968; Fritts, 1969; Neaves, 1969; McKinney, Kay, and Anderson, 1973; Parker and Selander, 1976). So the question is: are parthenogenetic whiptail lizards relatively well adapted to "weed" habitats because they are parthenogenetic, or because they are hybrids?

Most of the stable hybrid zones appear to occur in ecological conditions which conform to Wright and Lowe's (1968) definition of a "weed" habitat (see below). Since both sexual and asexual hybrids share a common type of habitat, it is probable that hybridity and not asexuality is the adaptation to these habitats. Particularly relevant is the frequent ecotonal occurrence of unisexual *Cnemidophorus* as opposed to bisexual species which occupy more stable widespread habitats. For example, the bisexual species *C. inornatus* occurs in grassland communities whereas the unisexual *C. uniparens* occurs in desert-grassland ecotones.

Most of the better documented narrow secondary intergradation zones occur in ecotones also. The two subspecies of grackles, *Quiscalus quiscula quiscula* and *Q. q. versicolor*, have diverged ecologically. In Louisiana, the more

northerly *Q. q. versicolor* inhabits pine forest and mixed pine-hardwood forest where *Q. q. quiscula* inhabits cypress-tupelogram swamp and coastal marshes (Yang and Selander, 1968). The narrow zone of hybridization between these subspecies occurs along the interface of the two vegetational zones. The zone is 24 km wide where the two associations are in contact, but it is 64 km wide where they are separated by disturbed bottomland forest.

The hybrids of Audubon's Warbler and the Myrtle Warbler occur in ". . . the meeting and mingling place of the northern boreal forests, and the western, or cordilleran forest" in Alberta and British Columbia (Hubbard, 1969). The antiquity and narrowness of this zone imply that selection gradients inhibit gene flow through the zone. Although the precise nature of these gradients is obscure, the Myrtle Warbler is favored in boreal forest while Audubon's Warbler is favored in cordilleran forest (Hubbard, 1969).

The Eastern Tufted and Western Black-crowned Titmouse hybrid zone occurs in a narrow ecotone between an eastern deciduous forest assemblage and a more xeric woody assemblage including live oak, juniper, and mesquite. The abrupt floristic and faunistic transition is correlated with a humidity gradient and with changes in edaphic conditions (Dixon, 1955).

Bufo fowleri and *B. woodhousei* are parapatric and hybridize freely in a narrow south-north zone slightly to the east of that involving titmice in Texas. *B. fowleri* and *B. woodhousei* are ecologically quite distinct. *B. fowleri* has a proclivity for forested regions and sandy soil; *B. woodhousei* occurs in a wider range of habitats including blackland prairie and oak-hickory forest, but not pine-oak forest which is inhabited by *B. fowleri*. The hybrid populations occur primarily in the narrow belt of transitional oak-hickory forest sandwiched between pine-oak forest to the east and blackland prairie to the west (Meacham, 1962).

Zweifel (1962) noted that the narrow secondary intergradation zone between *Cnemidophorus tigris gracilis* and *C. t. marmoratus* is correlated with the specific and subspecific range limits of several forms with which these two lizards are geographically and ecologically associated. Lowe (1955) described the general vicinity of these hybrid populations as a complex ecotone

between the Sonoran Desert and more eastern biotas.

Montanucci (1970) described the occurrence of natural hybrids between *Crotaphytus wislizenii* and *C. silus* in a narrow ecotone between the California Steppe and Great Basin pinyon-juniper woodland and noted that the distribution of hybrids closely coincides with the limits of the ecotone.

Several subspecific pairs of woodland birds hybridize on the Great Plains. Three pairs which are of particular interest here are the orioles, *Icterus galbula galbula* and *I. g. bullockii* (Sibley and Short, 1964; Rising, 1970, 1973); the flickers, *Colaptes auratus auratus* and *C. a. cafer* (Short, 1965); and the towhees, *Pipilo erythrophthalmus erythrophthalmus* and *P. e. arcticus* (Sibley and West, 1959). The congruence in position and width of the secondary intergradation zones in orioles and flickers is remarkable (see maps in Sibley and Short, 1964, p. 131; Short, 1965, p. 325). Particularly striking is the similarity of plots of the respective hybrid indices along the Platte River transect (Sibley and Short, 1964, p. 138; Short, 1965, p. 327). Rising (1970) noted that hybrid index in the orioles is correlated with precipitation and suggested that the western *I. g. bullockii* is adapted to a warmer, drier environment than is the eastern *I. g. galbula*. The potential vegetational map of Kansas (Kuechler, 1974) shows a transition from bluestem-grama prairie to northern grama-buffalograss prairie where the oriole and flicker hybrid zones cross Kansas, but a correlation between the center trace of these zones and a vegetational transition is not apparent in northern Nebraska and South Dakota (Kuechler, 1964). Whether a grassland ecotone could be a causative factor in the occurrence of hybridization in woodland birds is doubtful. Sibley and West (1959), however, noted that the riparian woodland becomes narrower and drier, cottonwoods more scattered, and the understory thinner, west of the junction of the North and South Platte rivers. It may be significant that this is where the sharp transition in hybrid indices begins for both orioles and flickers.

The center trace of the secondary intergradation zone in towhees is somewhat more to the east than those of the orioles and flickers, particularly along the Niobrara River where the western flora extends further to the east. The distributions of the Spotted (*Pipilo eryth-*

rophthalmus arcticus) and the Unspotted (*P. e. erythrophthalmus*) Towhees appear to be determined by vegetational patterns. Both races require a dense woody undergrowth, but the Spotted Towhee usually occupies a chaparral formation of woody shrubs without an arboreal cover as is more typical of the western plains, whereas the Unspotted Towhee occupies the understory shrubbery of the eastern deciduous forest. Sibley and West (1959) suggested that the spotting pattern affords camouflage in chaparral habitats where the absence of an arboreal canopy allows sunlight to dapple in low dense shrubbery.

It is likely that all three zones on the Great Plains resulted from secondary contacts (see Short, 1965, pp. 407-411, for a discussion of Pleistocene climatic conditions on the Plains) and that these zones originated with the recession of the Wisconsin Glaciers. Although European man has altered the availability of habitat for orioles and flickers (Sibley and Short, 1964; Short, 1965; Anderson, 1971), Rising (1970) has argued that the oriole zone is stable. Although introgression may be more extensive in the flickers, the zone within which birds are undoubtedly hybrids is little, if any, wider than the oriole zone. In view of the antiquity of the flicker zone, it is likely that it is stable also. The shrubby undergrowth inhabited by towhees has not been increased significantly by man (Sibley and West, 1959). If man's activities have not increased the opportunity for hybridization in towhees, this zone is also probably stable.

To summarize the situation on the Great Plains: It is likely that at least three subspecific pairs of birds hybridize in stable secondary intergradation zones. The occurrence of the zones appears to correlate with a change in climatic conditions, viz., precipitation. It is also possible that this region represents an interface between distinct floristic assemblages, i.e., an ecotone. In any case, it seems possible that hybrids are more fit than parental phenotypes in these zones.

Perhaps the sharpest ecotone supporting a stable hybrid zone is that between sand-pine and sandhill plant associations where the iguanid lizard hybrid, *Sceloporus woodi* × *S. undulatus undulatus*, occurs in Florida (Jackson, 1973). The antiquity of the *Sceloporus* hybrid zone is intriguing. It is likely that these species have been hybridizing for 100,000 years, and

yet there is no evidence of reproductive isolation nor extensive introgression into the parental populations. Obviously selection gradients must inhibit introgression, but an explanation for the failure of a premating reproductive isolating mechanism to evolve is not obvious. It is possible that the two species lack the genetic basis for the evolution of a premating reproductive isolating mechanism, but this seems very unlikely since such mechanisms are known in congeneric species (Jackson, 1973). The dynamic-equilibrium hypothesis could explain the situation in *Sceloporus* and cannot be discounted. The equally viable and more parsimonious hypothesis that I advocate is that the hybrids of *Sceloporus* are not inferior in the ecotonal areas, as was presumed by Jackson (1973).

Littlejohn, Watson, and Loftus-Hills (1971) and Littlejohn and Watson (1973) described the region in Victoria where *Geocrinia laevis* and *G. victoriana* hybridize as a subtle ecotone. The hybrid zone is not correlated with any "man-made ecotone," but it does seem to be correlated with a steep precipitation gradient and with the periphery of the pristine range of a forest since obliterated by the activities of European man. Littlejohn and Watson (1976) subsequently described this hybrid zone as occurring near the ecotone between dry sclerophyll eucalypt forest and open grassland of the basaltic plains of southwestern Victoria.

Another anuran hybrid zone, this one involving *Litoria ewingi* and *L. paraewingi*, occurs approximately 300 km northeast of the *Geocrinia* zone (Watson, Loftus-Hills, and Littlejohn, 1971; Watson, 1972; Gartside, 1972; Littlejohn, 1976). The *Litoria* zone is clearly associated with a forest-grassland ecotone. When the considerable data on this zone are synthesized, however, the picture that emerges does not clearly favor one hybrid-zone hypothesis over the other two.

Watson (1972) thought it probable that the *Litoria* zone was established at the end of the last period of Pleistocene glaciation (about 12,000 years B. P.). Genetic incompatibilities between the parental species are manifest in developmental aberrations when *L. ewingi* females are crossed to *L. paraewingi* males, but offspring from the reciprocal cross develop normally (Watson, Loftus-Hills, and Littlejohn, 1971). Surprisingly, there is no evidence that mating call has diverged between these species in terms of characteristics which are known to effect

mate discrimination within the *Litoria ewingi* complex (Littlejohn, 1976), nor do females of either species demonstrate any ability to discriminate between the mating calls of allo-specific and conspecific males (Watson, Loftus-Hills, and Littlejohn, 1971). Littlejohn (1976) did discern a slight displacement in scatter plots of two call parameters when near-allopatric and distant-allopatric males were compared. The displacement was slight, however, and did not involve the critical parameter of pulse repetition rate which effects mate discrimination in at least some congeneric species.

The *Litoria* hybrid zone, more than any other, does satisfy the dynamic-equilibrium model: it is narrow, it is probably stable, and there is clear evidence of fitness loss in hybrids. Furthermore, both developmental (Watson, 1972) and mating-call (Littlejohn, 1976) studies indicate the presence of significant numbers of the parental species in the hybrid zone. The latter fact is important because a postulate of the dynamic-equilibrium model is that there are enough "naive" individuals moving into the hybrid zone to prevent crystallization of an anti-hybridization mechanism. The dynamic-equilibrium model is unclear with regard to the association of narrow hybrid zones with ecotones. Bigelow (1965, p. 452) recognized that coadaptation of a species gene pool is, at least to a slight extent, forged by an intricate pattern of ecological factors. It is possible, then, that distinct ecological communities on either side of a hybrid zone act as the selection gradients which are postulated to prevent fusion in the dynamic-equilibrium model. In this model, a disturbed habitat is perhaps a sufficient condition for the establishment of a narrow hybrid zone; but it is not a necessary condition, since a disruption of physiological homeostasis could also serve as the selection gradient against gene flow.

In the case of the *Litoria* hybrid zone, the observed fitness loss is physiological in nature, and therefore it is unlikely that this has caused the zone to occur in an ecotone. It is possible that the association of this zone with an ecotone is coincidental, but it is also plausible that the hybrids are more fit than the parental phenotypes in the ecotone despite some developmental aberrations (Littlejohn, 1976). For example, a very large portion of *Poeciliopsis monacha-occidentalis* eggs go unfertilized in Rio

Mayo populations, and yet this hybrid is immensely successful there (Moore, 1976). High survivorship of *P. monacha-occidentalis* in the Rio Mayo is apparently more than enough to compensate for the large number of unfertilized eggs. By analogy, it is plausible that high survivorship beyond metamorphosis in *Litoria* hybrids compensates for a high level of larval mortality. Finally, since the observed developmental abnormalities manifest themselves only in crosses between *L. ewingi* females and *L. paraewingi* males, it is possible that they are caused by a cytoplasmic reaction and that hybrids suffer no fitness loss once this initial hindrance is cleared.

The most thorough genetical analysis of a hybrid zone is that of *Mus musculus musculus* × *M. m. domesticus* in Denmark (Hunt and Selander, 1973). This zone traverses central Europe from south to north and extends across Jutland. *M. m. musculus* and *M. m. domesticus* have diverged morphologically to the extent that they probably would be classified as distinct species by typological criteria. Allozyme analysis shows a genetic similarity index comparable to sibling species of other rodents. Allele frequencies at six of seven enzymatic loci studied formed step clines centered along or near the same line. Hunt and Selander (1973) concluded, as had Ursin (1952), that the zone lies in a region where climatic gradients, particularly in precipitation, create environments to which *M. m. domesticus* and *M. m. musculus* are equally well adapted. They also concluded that selection pressures resulting from disruption of the internal genetic environment must be a factor because the major shift in allele frequencies for all loci studied occurs along the same line.

The latter conclusion is perplexing because there is no evidence of reproductive isolation or assortative mating between the two subspecies. Coadaptation of gene complexes means that alleles which substitute at a given locus interact with alleles which substitute at other loci in such a way as to produce fit phenotypes. It is impossible to have coadaptation in gene pools of parental forms without the production of less fit phenotypes by hybridization. It is difficult, therefore, to reconcile the postulate that *M. m. domesticus* and *M. m. musculus* have gene complexes coadapted to distinct internal genetic environments with the facts that the hybrid zone is old and a premating isolating mechanism has not evolved.

Alternatively, the congruent step clines could be caused by a change in a common environmental variable. To test this hypothesis, Hunt and Selander (1973) did a step-wise multiple linear regression of hybrid index for a limited sample taken from the center of the hybrid zone on several climatic and geographical variables. The only good predictor of hybrid index was latitude, although July precipitation seemed weakly associated with hybrid index also. In spite of no clear correlation between hybrid index and environmental variables in the limited sampling region, there is evidence that the positions and slopes of these step clines are environmentally determined. First, the clines are invariably more gradual and have a more northerly center along the western edge of Jutland. Second, the allele frequencies on the islands of Fyn and Als are invariably more similar to the corresponding frequencies on northeastern Jutland than on more proximal southern Jutland. Precipitation levels on these islands are comparable to that of northeastern Jutland but less than those on nearby southern Jutland. Soil type on Als and Fyn also resembles that of northeastern Jutland. When all of Jutland and the adjacent islands where data were collected are considered, hybrid index does appear to be related to precipitation, although the relationship is not linear.

To summarize the situation in *Mus*: *M. musculus musculus* and *M. m. domesticus* have diverged to the level of distinct species by morphological and enzymatic criteria. Natural hybrids occur in a narrow stable hybrid zone in Jutland. Overall, hybrid index appears to correlate with precipitation and soil type, although a linear correlation analysis on a limited sample from the area where allele frequency clines were steepest did not detect a good environmental predictor of hybrid index. No correlation analysis was made between hybrid index and biotic variables; so, it is unknown whether this region is an ecotone.

DISCUSSION

Exploring the ramifications of coadaptation in a gene pool requires that we distinguish coadaptation to an endogenous regime of selection pressures from coadaptation to an exogenous regime of selection pressures. Minimally, the alleles at all loci in a fit organism must interact in such a way as to produce a physiologically

homeostatic individual capable of reproduction. In nature, a homeostatic phenotype must also be successful in the ranges of physical parameters it encounters (e.g., temperature, humidity, soil type) as well as in its biotic interactions in an ecological community if it is to survive to reproduce. The latter set of demands constitutes an exogenous regime of selection pressures, whereas the demands for physiological homeostasis are endogenous. When an allele enters a natural population it is not only selected against if it perturbs physiological homeostasis but also if it renders its carriers less successful in terms of intraspecific and interspecific competition, predator avoidance, pathogen resistance, and the like.

When hybridization ensues secondary contact, a large infusion of new alleles into the parental populations is initiated. If the gene complexes of the parental populations were distinctly coadapted to endogenous regimes of selection pressures, hybrid offspring would be selected against and the evolution of an antihybridization mechanism would be expected regardless of ecological conditions. On the other hand, if the gene complexes of the parental phenotypes were coadapted to distinct exogenous regimes of selection pressures, the outcome of hybridization would depend upon ecological conditions. If hybridization occurred in a zone of marginal habitat for both parental phenotypes, the hybrids would not have to overcome rigorous competition from parental phenotypes and they could, therefore, persist if physiologically homeostatic.

I suggest that the several evidently stable hybrid zones cited and discussed above are the result of coadaptation of parental gene pools to distinct exogenous selection regimes. Introgression is limited and fusion prevented by ecological selection gradients. Antihybridization mechanisms do not evolve because the hybrids are physiologically homeostatic and because they occur in regions where the parental phenotypes are no better adapted than the hybrid phenotypes. The narrowness common in stable hybrid zones is attributable to the fact that the hybrids often occur in ecotones which are themselves narrow. Hybrids are probably not preadapted to these zones but, rather, their success depends on the parental forms being less adapted. When geographical barriers divide the gene pool of a species it is obvious that it remains but one species in a whole ecological

community divided into isolates. It is thought that during prolonged isolation coadaptation of specific gene pools occurs. It is logical to recognize that whole communities must undergo divergence and coadaptation also. Because all species interact in a community through food webs, competition, patterns of protective coloration, commensalism, mutualism, and the like, a simple change in species structure should alter the regimes of selection pressures operating on many species in the community. Consequently, allele frequencies which are sensitive to biotic selection pressures would adjust in many species in the community. As an interpretation of vertebrate hybrid zones this is a novel idea; however, it is far from original. Grant (1971, p. 158) summarized the belief held by many botanists regarding the occurrence of natural plant hybrids as follows:

The explanation of the correlation between hybridization and habitat disturbance which is favored by most students is an extension of one proposed by Kerner in 1891. In a closed stable community no habitat is available for such hybrid zygotes as are formed from time to time. Stabilizing selection eliminates them from the scene almost as soon as they arise. But, where the natural community has been broken into by road building, overgrazing, or the like, so that new open habitats are created, the hybrids can and do become established. In other words, environmental isolation operates to suppress hybridization between intercompatible species in a stable, closed community, but ceases to be fully effective in an open habitat.

The subspecific occurrence of spotting patterns in towhees is a simple example of adaptation to distinct communities. If the spotting pattern is camouflaging, as Sibley and West (1959) suggested, then hybrid phenotypes would be more susceptible to predation in either deciduous forest or chaparral than the parental phenotypes, regardless of the vigor or fertility of the hybrid. In an ecotone, however, the intermediate phenotype may be no less cryptic than the parental phenotypes and would not be selected against.

Sceloporus woodi and *S. undulatus undulatus* occupy similar niches but in distinct ecological communities. The two have diverged in morphological characteristics that are apparent adaptations to their respective communities. Although speculative, alternatives to the hypothe-

sis that hybrids of *Sceloporus* are inferior should be considered. For example, it is possible that hybrids, because of their intermediacy, are able to compete moderately well in either community whereas the more specialized parental phenotypes compete well in their own community but poorly in the other. The success of a parental phenotype at the ecotone depends upon finding habitat available in its specific community. The hybrid, in contrast, might be an opportunist utilizing whatever habitat is available at least moderately well. Presumably, a large number of genes contribute to the ecologically adaptive morphology of both the towhees and *Sceloporus*. The important point is that a regime of ecological and not physiological selection pressures enforces the integrity of this kind of adaptive gene complex.

To cast this analysis in a final perspective, it is useful to recall the method of deductive testing described by Popper (1959). If a theory withstands a scrutiny "... then the theory has, for the time being passed its test: we have found no reason to discard it. But if the decision is negative or in other words, if the conclusions have been falsified, then their falsification also falsifies the theory from which they were logically deduced" (p. 33). The hybrid-superiority hypothesis has been subjected to less scrutiny than the other hypotheses, and this may well account for its vigor at this juncture. An a priori assumption of most hybrid-zone studies is that the hybrids are inferior to parental phenotypes; as a consequence, the kinds of data that could falsify the hybrid-superiority hypothesis have usually not been sought. The hybrid-superiority hypothesis does make predictions that are testable. The prediction which, if invalidated, would directly falsify this hypothesis is that hybrids should be more fit than parental phenotypes in stable hybrid zones. Predictions that would less directly test the hypothesis but are more testable from a practical standpoint include the following: (1) all stable hybrid zones should be restricted to regions devoid of, or at least at the periphery of, stable ecological communities; (2) mating should be random in stable hybrid zones; (3) there should be no character displacement associated with a stable hybrid zone, particularly in features that could effect reproductive isolation (such as mating call). In addition, the genetic structure of the population through the hybrid zone would probably

manifest some distinctive features; however, these are difficult to deduce without the aid of a mathematical model. Mathematical modelling would be very useful at this juncture to generate predictions about genetic structure, and, also, to test the internal consistency of the hypothesis. That is, would a geographical region of hybrid superiority suffice to cause the stabilization of a hybrid population between the ranges of the parental populations, given some reasonable assumptions about the genetics of the parental differences and of a potential isolating mechanism?

Comprehensive studies of individual hybrid zones thought to be stable could test the "mettle" of the hybrid-superiority hypothesis and further test the other two. These studies should include comparative data on survivorship, fecundity, fertility, mating behavior, gene frequencies, ecology, and zoogeography. Several recent studies are commendable in this respect. But, these data would be of little consequence if they were not used to choose between plausible hypotheses. Popper (1959) expressed part of his method in a metaphor borrowed from the late 18th and early 19th century philosopher Novalis. Popper: "Theories are nets cast to catch what we call the 'world': to rationalize, to explain and to master it." Novalis' germinal thought seems an apropos terminus to this discussion: "Hypotheses are nets: only he who casts will catch."

SUMMARY

Three alternative hypotheses have been proposed to explain the occurrence of vertebrate hybrid zones: (1) the ephemeral-zone hypothesis states that hybridization following secondary contact will lead to either speciation or fusion of the populations. Speciation is to be expected if the populations have diverged to the extent that the hybrids are less fit than the parental phenotypes; otherwise, the hybrids would serve as a bridge for introgressive hybridization. (2) The second hypothesis accounts for the evident stability of some hybrid zones despite selection against hybrids. Bigelow (1965) proposed that stable narrow hybrid zones might result from a dynamic balance between gene flow into the hybrid zone and selection against hybrids. He suggested that steep selection gradients might inhibit introgression and that the evolution of

an antihybridization mechanism in the restricted zone of contact might be disrupted by migrants moving into the contact zone from the more extensive areas of allopatry. (3) The third hypothesis states that hybrids are actually more fit than the parental phenotypes in the restricted regions where hybrid zones occur. The latter hypothesis has not gained strong advocacy because it is inconsistent with the concepts that hybridization disrupts coadapted gene complexes and that the unity of a species is maintained by gene flow.

Neither of the first two hypotheses explains the full range of observed hybrid-zone phenomena. The failure of the ephemeral zone model is that there are several zones which are old and evidently stable. The dynamic-equilibrium model requires that the hybrid zone be sandwiched between the parental populations, or so situated that genes flow from both parental populations into the hybrid zone. Since some apparently stable hybrid zones do not satisfy these conditions, the dynamic-equilibrium model does not adequately explain all stable hybrid zones.

The geography of fitness in the unisexual hybrid fish *Poeciliopsis monacha-occidentalis* supports the hypothesis that hybrids are in some circumstances more fit than parental phenotypes. Furthermore, to discard the presumption that hybrids are invariably less fit allows one to explain readily much of the otherwise inexplicable data on hybrid zones.

Although the hybrid-superiority model can account for a stable hybrid zone of almost any shape or size, the fact remains that most stable hybrid zones are narrow. The nearly universal association of stable hybrid zones with ecotones suggests that ecological factors are often important in determining the success of hybrids. It is suggested here that coadaptation within a species gene pool can be a response to two regimes of selection pressures, one endogenous, the other exogenous. Hybrids between races

that have gene complexes distinctly coadapted as responses to endogenous selection regimes are likely to be selected against in any environment because disruption of the coadapted gene complexes would perturb physiological homeostasis. In contrast, hybrids between races that have gene complexes distinctly coadapted as responses to exogenous but not endogenous selection regimes might survive in nature provided they did not have to compete in a stable community with species that were well adapted to that community.

Ecotones probably provide marginal habitats for many of the species that comprise the ecological communities on either side of the ecotone. Homologous species or races which have diverged in response to the peculiar exogenous selection regimes exerted by the respective communities may produce hybrids which are physiologically homeostatic and are no less adapted to the transitional habitat than are the parental phenotypes. In this circumstance, a stable hybrid population would be established in the ecotone. Selection gradients exerted by the distinctly integrated ecological communities on either side of the ecotone would prevent expansion of the hybrid zone; and reproductive isolation would not evolve because, where the opportunity to hybridize occurs, there is no selection against hybrids.

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