

TAXONOMIC ASPECTS OF AVIAN HYBRIDIZATION

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INSTANCES of natural hybridization frequently pose difficult taxonomic problems. A decision regarding the taxonomic status of hybridizing forms should be based upon an evaluation of all available biological information concerning their relationship. The paucity of available information usually hampers taxonomists treating hybridization among the higher vertebrates. Also it is difficult or impossible to subject such animals, and particularly animal populations, to experimental study. Nevertheless taxonomists must render decisions that reflect current available knowledge. I offer the following discussion and definitions in the hope of facilitating such decisions by taxonomists, especially those working with terrestrial vertebrates. Examples forming the framework for the discussion are drawn from the literature of avian hybridization, including some work of my own.

The widely divergent treatment of hybridizing forms evident in the recent ornithological literature demonstrates the need for some guidelines. At one extreme this divergent treatment appears to reflect a hold-over of typological thinking (e.g. Godfrey, 1966; Sutton, 1967), while the opposite extreme (e.g. Phillips et al., 1964; West, 1962) results from an overly strict interpretation of the biological species definition in that different species do not interbreed, and hence interbreeding forms must be conspecific. The results of such divergent treatment are taxonomic oversplitting in the former case, and overlumping in the latter.

I define hybridization as the interbreeding of individuals of morphologically and presumably genetically distinct populations, regardless of the taxonomic status of such populations (see Anderson, 1949: 61; Short, 1965: 360). This definition of hybridization, essentially that of Mayr (1963: 110), does not differ fundamentally from its broader genetic meaning, in which it can even include interbreeding of genotypically different individuals; I have simply restricted its usage. Included are both sympatric and allopatric hybridization; the latter includes secondary intergradation, but not primary intergradation (see Mayr, 1963: 368-369). Secondary intergradation is distinguished, occasionally with difficulty, from primary intergradation by the increased variability of populations within compared with those outside the area of intergradation, contrasted with the normal variability of populations within and outside an area of primary intergradation. I define "hybrids" as the products of sympatric and allopatric hybridization (including secondary intergradation), and "intergrades" as the products of primary intergradation. The practice of defining hybridization on the basis of the taxa involved should be dis-

couraged, because it requires a taxonomic decision before "hybridization" can even be employed (see Mayr, 1963: 111; Bigelow, 1965), and it unnecessarily limits the use of this word. I cannot see the need for encumbering taxonomically a term that is fundamentally nontaxonomic.

How distinct must populations be to warrant considering their interbreeding as "hybridization"? The populations ought to be sufficiently distinct to permit recognition of a hybrid as such. I suggest that their distinctness ought to approach, equal, or exceed the level of distinctness of subspecies. Criteria for subspecies are a purely taxonomic matter, irrelevant to this point, the idea being that the populations are about as distinct, or more so, than subspecies. For example, designation of an area of primary intergradation depends on the distinctness of the populations involved. These populations are usually considered as subspecies, but that depends on the criteria of the taxonomist viewing the situation. I have designated as intergrades above the products of interbreeding through an area of primary intergradation, but this does not preclude the possibility of true hybridization occurring between individuals of the same two populations. Wandering birds from one population occasionally may traverse the area of intergradation and mate with birds of the other population, producing true hybrids. Of course one might obtain individuals of the two populations and mate them under captive conditions to produce offspring that are F^1 hybrids, not intergrades.

While the framework for the consideration of hybridization presented herein is novel, most of the basic ideas are drawn, some insensibly, from the vast literature on speciation and population genetics. Especially helpful have been the important works of Mayr (1942a, 1963), Anderson (1949, 1953), Dobzhansky (1951), Stebbins (1959), and Sibley (1957, 1959, 1961).

The biological information forming the basis for a taxonomic decision in cases of hybridization should ideally include: 1) knowledge of the occurrence and/or lack of occurrence and the place of occurrence of hybrids; 2) knowledge of the distribution and habitats of the parental forms and hybrids; 3) knowledge of the relative frequencies of hybrid and parental phenotypes in the area of hybridization; 4) knowledge of the type of crossing (F^1 , F^2 , backcross) that is occurring; 5) knowledge of the occurrence and the extent of any introgression (introgression is gene flow resulting from hybridization; for discussion and definition see Short, 1965: 360); and 6) knowledge of the population dynamics (especially of the spatial distribution of individuals and the population structure) of the forms involved. Although full data are often unavailable for some of these items, there may exist inferential bases for their consideration permitting a tenta-

tive taxonomic evaluation. Other (behaviorial, genetic, ecological) data are of course desirable; their availability greatly aids in the taxonomic evaluation, and strengthens the decision that is ultimately reached.

Hybrids produced under captive conditions are not discussed in this paper. I agree with Mayr (1963: 112) that "the mere possibility of hybridization in captivity proves nothing as far as species status is concerned." Artificially induced hybridization proves only the existence of considerable genetic similarity and compatibility. Of course studies of hybridization under captive experimental conditions are a useful adjunct to the study of natural hybridization in those animals that can be maintained and bred successfully, and in sufficient numbers.

The several categories of natural hybridization are discussed in the order from rare hybridization to frequent hybridization and more complex interactions.

INFREQUENT AND RARE HYBRIDIZATION

Single instances of hybridization are generally of limited taxonomic usefulness, although they may provide clues to relationship. Many intergeneric avian hybrids involving taxonomically valid genera have been recorded. Other purported cases involve species of overly split genera that should be congeneric, for example hybrids among species of North American hummingbird "genera" (Short and Phillips, 1966). Recently reported unique intergeneric hybrids include a flycatcher *Contopus sordidulus* × *Empidonax traillii* (Short and Burleigh, 1965), a wood warbler *Dendroica striata* × *Seiurus noveboracensis* (Short and Robbins, 1967) and a hummingbird *Cynanthus latirostris* × *Eugenes fulgens* (Short and Phillips, 1966). In the first two of these cases the occurrence of the hybrid tends to corroborate generally accepted generic relationships and the current adjacent placement (A.O.U., 1957) of the genera involved. Study of the third case led to the suggested close relationship between *Cynanthus* and *Eugenes*, which previously had not been considered closely related. Thus, lone hybrids between species representing valid genera may corroborate relationships determined by other studies, or they may suggest comparisons not previously considered. The occurrence of several unique intergeneric hybrids involving different species of the same two genera is more strongly suggestive of generic relationship. I have elsewhere (Short and Phillips, 1966) noted as inconsistent with modern phylogenetic and evolutionary concepts the suggestion (Banks and Johnson, 1961: 26) that intergeneric hybridization might occur more frequently than intrageneric hybridization. Aside from serving a taxonomic function, these hybrids may help to elucidate the pattern of evolution of a group, or they may aid in establishing the patterns of evolution of a trait or traits within a group.

Unique intrageneric hybrids vary in their taxonomic significance. Generally they are of little significance in groups in which hybrids are uncommon. Miller (1955) suggested the evolutionary history of certain North American woodpeckers of the genus *Dendrocopos* mainly on the basis of a single hybrid *D. scalaris* × *D. villosus*. Recently, I have found (Short, MS) numbers of hybrids of *D. scalaris* × *D. nuttallii*, and two hybrids of *D. nuttallii* × *D. pubescens*. The new evidence from these specimens necessitates considerable modification of Miller's views. Hence a lone intrageneric hybrid is of limited use as a basis for inferring relationships. The amount of hybridization may suggest or corroborate relationships in genera such as the duck genus *Anas*, that exhibit, for reasons elucidated by Sibley (1957), a great deal of hybridization (Johnsgard, 1960). Important here is the rare occurrence or absence of hybrids between certain species, contrasted with more frequently occurring wild hybrids among other species of a genus. One must, of course, evaluate these occurrences on the basis of the opportunity of the various species to hybridize, i.e. the degree of sympatry of potentially hybridizing species. More distant relationship is implied if few, one, or no hybrids occur, while closer relationship is suggested by occurrence of crosses involving several to many hybrids (Johnsgard, 1960).

Hybrids more frequent than the unique or rare hybrid, yet less frequent than sporadic, i.e. up to 10 or so, may assume greater taxonomic significance. If the species represent different genera close relationship is suggested, possibly including the merging of the genera. Recently reported cases in this category are those of North American hybrid sparrows *Junco hyemalis* × *Zonotrichia albicollis* (Short and Simon, 1965) and hummingbirds *Archilochus alexandri* × *Calypte costae* (Short and Phillips, 1966). When considered with other kinds of evidence in the light of instances of intergeneric hybridization between certain of these and other species of the genera mentioned, their hybridization suggests generic merger. Another interesting case is the hybridization between the ducks *Mergus cucullatus* and *Bucephala clangula* (Cockrum, 1952; in the U. S. National Museum is an additional subadult hybrid male). Although these species represent different genera sometimes placed in different "subfamilies" (A.O.U., 1957), behavioral study (Johnsgard, 1961a) has indicated their close relationship. The existence of several hybrids and a morphological comparison of the two species, and especially comparison of the females, lead me to concur with Johnsgard. The divergence in morphological specializations among the ducks (subfamily Anatinae) seems to belie their fundamentally close relationship and the recentness of their origin and adaptive radiation (Delacour and Mayr, 1945).

Existence of several intrageneric hybrids between two species may be evidence for their relatively close relationship. In groups where hybridization is rare, several hybrids between sympatric species may suggest that they formerly comprised a superspecies, a superspecies being a "group of entirely or essentially allopatric taxa that were once races of a single species but which now have achieved species status" (Amadon, 1966). This may be obvious, as in the case of the meadowlarks *Sturnella magna* and *S. neglecta* (Lanyon, 1966), which have recently come broadly into sympatry. A few hybrids have occurred at scattered points within the area of sympatry. Sympatric intrageneric hybrids tend to occur where one species is at the border of its range, encouraged by restricted mate choice where that species is uncommon. Such special circumstances usually are involved because sympatric species normally are effectively reproductively isolated, which is partly responsible for their sympatry. The woodpeckers *Dendrocopos nuttallii* and *D. pubescens* are broadly sympatric in California, which comprises almost all of *nuttallii*'s range. Two of their three known hybrids (Short, MS) are from the southern extreme of the range of *D. pubescens* in California; the locality of the third hybrid (Ridgway, 1887) is unknown. South of the range of *pubescens*, *nuttallii* replaces *pubescens* in riparian vegetation like that occupied by the latter where they are sympatric. These two woodpeckers probably formerly comprised a superspecies. The former existence of a superspecies may be less obvious, as perhaps in the broadly sympatric and sporadically hybridizing tanagers *Thraupis palmarum* and *T. virens* (Haverschmidt, 1966). Likewise in a group prone to hybridize like the grouse (Tetraoninae; see Sibley, 1957), even more numerous hybrids in sympatry may suggest the former existence of superspecies. An example is the case of the Eurasian capercaillie (*Tetrao urogallus*) and black grouse (*T. tetrix*), which interact ecologically and hybridize occasionally in their extensive area of sympatry, although each today comprises a superspecies of its own with related Asian species (Short, 1967). Existence of a superspecies may be directly inferred from the occurrence of two to several hybrids in a contact between allopatric congeneric species. An example is the case of two hybrids of the tanagers *Piranga ludoviciana* and *P. olivacea*, respectively, of western and eastern North American (Tordoff, 1950; Mengel, 1963).

When discussing the numbers of natural hybrids, one must recognize the vastly greater opportunity to recover hybrids of waterfowl and other gamebirds, compared with other birds. Fully half the population of certain game species may be killed yearly by hunters, and hence a considerable portion of obvious hybrids (mainly males) are recovered. The discussion herein is mainly concerned with nongame species.

ZONES OF OVERLAP AND HYBRIDIZATION

The term "hybrid zone" has been loosely used to designate any area of secondary contact in which hybrids occur. I restrict a "hybrid zone" (see below) to include an area of hybridization where only hybrids occur, as distinguished from a "zone of overlap and hybridization." I prefer to include both of these categories within the category of secondary intergradation, thus retaining the latter general term for all situations involving hybridization and backcrossing between allopatric forms in a secondary contact. A zone of overlap and hybridization is an area of secondary intergradation occupied by numerous hybrids and both parental forms as well. The parental phenotypes must occur in numbers sufficient to preclude their representing extreme hybrid phenotypes (recombinants). I arbitrarily consider the occurrence of both parental phenotypes in numbers greater than 5 per cent, taken together, of the population in the zone of overlap and hybridization as indicating that at least some parental phenotypes normally comprise a part of this population. The use of 5 per cent has no function other than to insure the presence of parental phenotypes; if these otherwise can be demonstrated, their per cent occurrence is unimportant. A zone of overlap and hybridization has two taxonomically significant features. The existence therein of numerous parental phenotypes should result from impediments to gene flow, presumably the action of partial isolating mechanisms (Short, 1965: 418; Bigelow, 1965). Immigration of parental phenotypes from outside the zone also may take place when hybrids are at a selective disadvantage. Secondly, phenotypes of the parental forms are sympatric in this zone; their reactions can include primary (F^1) hybridization, competition, and reinforcement or breakdown of isolating mechanisms (Table 1.)

Other than the indirect evidence for partial isolating mechanisms provided by the existence of a zone of overlap and hybridization, there appears to be no logical basis for deciding the taxonomic status of the interacting forms. The amount of hybridization and the relative proportion of hybrids and parental phenotypes in the zone do not provide useful, nonarbitrary criteria for a taxonomic decision, for both may be influenced by factors such as the size of the contact; hence neither necessarily is correlated with the efficacy of partial isolating mechanisms. The presence and maintenance of parental phenotypes in the zone of overlap and hybridization appears to constitute a nonarbitrary basis for a taxonomic decision. The taxonomic value of this phenomenon is enhanced by the direct relationship it seems to have with functioning reproductive isolating mechanisms.

I restrict the term "semispecies" (Amadon, 1966) to those forms actually or potentially capable of forming a zone of overlap and hybridization.

TABLE 1
A CLASSIFICATION OF SOME HYBRIDIZING FORMS

Forms involved	Distribution	Interactions
Subspecies, or subspecies groups of polytypic species	contiguously or strictly allopatric	primary intergradation, or potentially capable of so doing
subspecies, or subspecies groups of polytypic species	strictly allopatric	hybridize in <i>hybrid zone</i> (or potentially capable of so doing)
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semispecies (allospecies)	basically allopatric, but some sympatry evident or possible	form <i>zone of overlap and hybridization</i> (or potentially capable of so doing); competition; reinforcement of isolating mechanisms
allospecies of a superspecies	basically allopatric; some or no sympatry	rare, inconsequential or no hybridization; effective isolating mechanisms, rarely breaking down; competition if sympatric
related, but not allospecific species	Sympatric or allopatric	rare or no hybridization; effective isolating mechanisms, very rarely breaking down; competition or not when sympatric

These semispecies truly combine attributes of populations at both the species level, such as morphological distinctness and reproductive isolation, even if only partial, and at the intraspecies level, such as the ability to interbreed. On the basis of suggestive evidence for existence of partial isolating mechanisms in situations involving semispecies, I recommend that semispecies be considered taxonomically as species (Table 1). Semispecies are one type of allospecies comprising a superspecies (Amadon, 1966). Other superspecies are comprised of allospecies that infrequently or never hybridize in areas of secondary contact or limited areas of sympatry, or of allospecies that are completely allopatric. All types of allospecies are geographically representative forms taxonomically considered species (Amadon, 1966).

Zones of overlap and hybridization may be stable, but often they may change dynamically, either on a broad level or locally. The frequency of such changes suggests a need for continuing analysis and reexamination of all zones of overlap and hybridization. In his discussion of the invasion by the woodpecker *Dendrocopos syriacus* of the European range of its close relative *D. major* from southeastern Europe earlier in this century, Bauer (1958) shows that hybridization occurred in a narrow belt along

the advancing zone of overlap and hybridization as *D. syriacus* expanded its range to the northwest. As the front passed a given area, hybridization diminished, then ceased, and the two species came to exist in sympatry. Hybridization in this case seems due to restricted mate choice among immigrants of *D. syriacus*; interbreeding diminishes as its population reaches sufficient size to make available enough conspecific mates. A similar case involves the titmice *Parus caeruleus* and *P. cyanus* (Vaurie, 1957). Late in the past century the Asian *P. cyanus* massively invaded the east European and west Asian range of the largely European *P. caeruleus*. Since the 1880s the range of *P. cyanus* has receded somewhat, but a vast area of overlap still exists. Hybridization, apparently widespread during the period of expansion, has diminished and now takes place only in the northern part of the zone of overlap (Vaurie, 1957). In these two cases the zone of overlap and hybridization has become greatly restricted, while the former region where the zone occurred is now an area of sympatry, or simply a zone of overlap. The gulls *Larus argentatus* and *L. hyperboreus* are sympatric without interbreeding over much of the northern Holarctic region. Iceland was formerly occupied by *L. hyperboreus*, but not by *L. argentatus*. The recent arrival of the latter as a breeding bird in Iceland has resulted in widespread hybridization (A. Ingolfsson, pers. comm.), despite their sympatry elsewhere. All these examples are special cases of zones of overlap and hybridization—they might also be considered cases of combinations of situations, as shown below. As the forms involved are basically reproductively isolated, they are species. I would not designate them as semispecies; they are former semispecies, able to coexist over large areas without interbreeding.

Large, broad zones of overlap and hybridization are not infrequent. (The adjectives "large," "small," and "moderate" herein pertain to the overall extent or area of the zone, while "broad" and "narrow" describe the width of the zone at a specified point, or the average width of the zone if no point is specified.) The warblers *Vermivora pinus* and *V. chrysoptera* extensively overlap and hybridize in eastern North America. Parental phenotypes apparently are maintained throughout the zone of overlap and hybridization, and introgression is taking place (Short, 1963). In the same region the ducks *Anas platyrhynchos* and *A. rubripes* broadly overlap and hybridize, with parental phenotypes remaining more common than hybrids (Johnsgard, 1961b, 1967). Likewise, the kingfishers *Ceryx erithacus* and *C. rufidorsus* interbreed and overlap over a large area including most of Sumatra, Borneo, and the Malay Peninsula (Sims, 1959). In most cases of this type the parental phenotypes and recombinants closely resembling them comprise a majority of the population in much of the area of over-

lap and hybridization. These forms are semispecies that I believe should be accorded the taxonomic status of species.

Moderate zones of overlap and hybridization exist in many areas. In central North America broad zones of overlap and hybridization exist between the grosbeaks *Pheucticus ludovicianus* and *P. melanocephalus* and the buntings *Passerina cyanea* and *P. amoena*. Although broad, the zones are limited in extent because these species inhabit only river valleys within the vast central Great Plains area the zone encompasses. The maximum width of the grosbeak zone is about 200 miles (West, 1962; Short, unpublished data from recently collected Nebraska specimens). Within this zone both parental and hybrid phenotypes are encountered. Slight introgression is detectable immediately adjacent to the zone of overlap and hybridization. The buntings overlap and hybridize along river valleys in the same region (Sibley and Short, 1959a), but the zone is broader, about 400 miles wide. The eastern semispecies, *P. cyanea*, recently has bred sporadically far within the range of *P. amoena* in California, Arizona, and Utah (some citations are in Sibley and Short, 1959a). Significantly, most pioneer birds were apparently phenotypically pure *P. cyanea*, and some individuals secured mates of their own species despite being far beyond the species' normal range.

Examples of small and narrow zones of overlap and hybridization are provided by semispecies of gulls (*Larus glaucescens* and *L. argentatus*) and chickadees (*Parus atricapillus* and *P. carolinensis*). The gulls meet in southern Alaska where they sometimes occur in mixed colonies. In at least some colonies considerable hybridization occurs, although parental phenotypes apparently are maintained despite interbreeding (Williamson and Peyton, 1963). The ranges of the chickadees are sporadically contiguous from the Mississippi River to the Atlantic Coast of North America. Known contacts mainly involve no overlap (Tanner, 1952; Brewer, 1963), but slight overlap with limited hybridization occurs in southern Illinois.

HYBRID ZONES

A hybrid zone is an area occupied by a hybrid population connecting two parental gene pools (Short, 1965 and above). The parental phenotypes together comprise less than 5 per cent of the hybrid zone population, i.e. they occur so infrequently that they might be due to chance recombination. Occasional immigrants or wanderers from the range of one or the other parental form could account for some occurrence of parental phenotypes, which are virtually or actually lacking from most hybrid zones. Parental phenotypes do not occur together in the hybrid zone; rather, each is limited usually to that edge of the hybrid zone appropriate for its adjacent

distribution. Each border of the zone is marked by an increase in the parental phenotype of the immediately adjacent form, and a decrease in hybrid and introgressant individuals.

A significant feature of the hybrid zone is that the hybrid population simultaneously both connects and separates the parental populations; the latter hence are completely allopatric (Table 1). The opportunity for primary (F^1) hybridization is lacking because individuals of the parental forms are no longer directly in contact, as they were when the secondary contact initially was established. Reproductive isolating mechanisms are nonexistent or ineffectual. Analysis of populations adjacent to the hybrid zone usually will uncover evidence of introgression. The genetic contact between the hybrid population and the parental form insures occurrence of introgression, whether or not it is detectable. Forms connected by a hybrid zone are considered conspecific because of lack or ineffectiveness of reproductive isolating mechanisms.

One is often reluctant to accept conspecificity of two forms interbreeding in a hybrid zone when one or both of the forms are polytypic. As free interbreeding and lack of reproductive isolation demand conspecificity of the forms involved, use of the term "subspecies groups" is helpful (Table 1). Subspecies can vary tremendously in their degree of morphological divergence. Also, they may be entirely allopatric, broadly connected through areas of primary intergradation involving gradual or step-clines, or connected through hybrid zones. A group of slightly or moderately differentiated clinal races may comprise a subspecies group having a hybrid zone with another such group, as in the flickers (Short, 1965) discussed below. Of course polytypic species with numerous races may have subspecies groups even without hybrid zones.

The often considerable morphological differences between forms interbreeding in a hybrid zone is no reason for reluctance to merge them, for the morphological features by which they differ have no significance with regard to their reproductive isolation. Why should we question the conspecificity of two morphologically divergent forms, when individuals of these forms accept each other as conspecific? When this acceptance results in the formation of a hybrid zone, the hybrid population becomes a connecting link between the parental forms, which are thereby buffered from direct contact. The formation of an intermediary hybrid population attests to the success of the interbreeding, the lack of reproductive isolation of the parental forms, and the insignificance of the morphological differences between the parental forms with regard to reproductive isolation. Because the evolution of reproductive isolating mechanisms is related only indirectly to morphological divergence, the level of morphological distinct-

ness of interbreeding subspecies groups can approach, equal, or occasionally exceed that achieved by semispecies.

The best test for the existence of reproductive isolating mechanisms is a large contact between two populations. When a large contact ensues, there is a direct threat of genetic swamping of the parental gene pools through hybridization and introgression. Any existing incipient isolating mechanisms should be enhanced under these circumstances. Sibley (1961) discusses the reinforcement of isolating mechanisms through selection acting against hybrids; reinforcement is a part of Brown and Wilson's (1956) "character displacement."

Large and broad avian hybrid zones are evident on most of the continents. The morphologically divergent *auratus* and *cafer* subspecies groups of the North American flicker (*Colaptes auratus*) form a vast mid-continental and northwestern hybrid zone (Short, 1965). Introgression affects parental populations as far from the zone as the east and west coasts of North America. Likewise two forms of grackle (*Quiscalus quiscula*) form a large hybrid zone over much of eastern North America (Chapman, 1940; Huntington, 1952). The flowerpeckers *Pardalotus melanocephalus* and *P. "uropygialis"* form such a zone in northern Australia (Salomonsen, 1961); for several other fine examples of this phenomenon see Keast (1961). The forms involved in these hybrid zones are obviously conspecific, as no isolating mechanisms exist and the parental gene pools are firmly connected. This does not mean that these forms necessarily will merge completely. Very often, as in most continental hybrid zones, the large parental populations occupy an immense area, allowing for isolation by distance and gradual filtering (see below) of introgressed genes away from the hybrid zones. Just as variable clines often are evident in cases of primary intergradation, the differential sorting action of natural selection will fashion variable clines for introgressant genes and gene combinations. In the flickers mentioned above, some features by which the hybridizing forms differ are sharply clinal within the hybrid zone (e.g. nuchal patch; see Short, 1965), while others (e.g. shaft color) are step-clinal within the hybrid zone; these clines assume a gradual slope outside the hybrid zone.

Narrowness of a hybrid zone is not related necessarily to any basic genetic incompatibility of two hybridizing forms. Narrower zones occur when differences between the parental forms are few. Genetic gradients for various characters across and beyond the hybrid zone inevitably will vary with the selective forces regulating gene flow, as noted above. This differential action of natural selection operating with respect to introgression out of a hybrid zone, which Bigelow (1965) ignored in his contrary

view of the narrow hybrid zone between *Corvus corone* and *C. "cornix"* (below), has no bearing on reproductive isolation of the two forms; hence it has no bearing on their taxonomic status. When individuals of two forms can interbreed, and their hybrid offspring and successive hybrid populations are genetically connected with both forms, then these forms patently are not reproductively isolated species.

There exist a few large or moderately large but narrow hybrid zones, notably the famous case of the Eurasian crows *Corvus corone* and *C. "cornix"* (Meise, 1928; Vaurie, 1954). These crows form a narrow hybrid zone across central and northwestern Europe; little introgression is apparent beyond the zone. A third crow (*C. "orientalis"*) occupies northeastern Asia and forms a broader hybrid zone with *C. "cornix"* in West Siberia (Mayr, 1942a; Vaurie, 1954). Previous workers discussing this problem generally overlooked the great morphological similarity of these crows in virtually all traits except the one color feature by which they differ strikingly, and upon which we have had to depend for evidence of introgression. The narrowness of this hybrid zone simply may reflect the dearth of morphological characters available for analysis. Even with free interbreeding through a hybrid zone selection may fashion a sharp step-cline (see above) for certain genes and gene combinations, perhaps including those responsible for the gray versus black backs of the two crows. Advantageous genes and genes not strongly disadvantageous may pass unimpeded through the hybrid zone. For example, morphological analysis of a hybrid zone in lizards (*Cnemidophorus*) of southwestern North America indicated very limited introgression, but use of biochemical techniques proved that introgression was actually extensive (Dessauer et al., 1962). As the crow populations are connected by a totally hybrid population, and there is no evidence of isolating mechanisms acting to limit the hybridization, we are obliged to consider them conspecific.

A broad hybrid zone of moderate extent is found in the Great Plains of North America between the *galbula* and *bullockii* groups of orioles (*Icterus galbula*) (Sibley and Short, 1964). The zone is roughly 200 miles wide, but as it occurs principally along river valleys its extent is limited. Introgression is evident immediately adjacent to the hybrid zone. A moderate, narrow hybrid zone is that connecting the *bicolor* and *atricristatus* groups of titmice (*Parus bicolor*) in east-central Texas (Dixon, 1955). A true hybrid zone 25 to 50 miles in width occurs in five areas of contact between them. Marked introgression is not evident.

Hybridization in small areas of secondary contact inevitably places less stress on the parental populations than occurs in situations involving massive contact. Small hybrid zones hence pose more difficult problems

for the taxonomist than do large hybrid zones. A small hybrid zone involving extensive hybridization but little introgression may result from chance topographical or habitat conditions, restricted mate choice, or other special local factors. Thus a small contact may not test effectively the parental forms' capacity to interbreed. The existence of a small hybrid zone demonstrates that reproductive isolating mechanisms are not fully effective, but the presence or absence of partial isolating mechanisms often remains a moot point.

Small hybrid zones may persist indefinitely. This simply may reflect their small size and limited genetic effects. There is a possibility that minor genetic contact may benefit populations, whether or not partial isolating mechanisms exist (Anderson and Stebbins, 1954; Stebbins, 1959; Short, 1965). Counter selection from this source could balance the effects of weak isolating mechanisms or even negate them (Stebbins and Daly, 1961), producing a stalemate.

The problem of establishing the presence or absence of isolating mechanisms in situations involving small hybrid zones is a serious one. Nevertheless, when no evidence of isolating mechanisms exists in such situations we are obliged tentatively to consider the interbreeding forms as conspecific. Conversely the demonstration of isolating mechanisms functioning in small contact situations supports consideration of the interbreeding forms as species.

A small, narrow hybrid zone exists in Colombia between the tanagers *Ramphocelus flammigerus* and *R. "icteronotus"* (Sibley, 1958). The hybrid zone is but 10 or 12 miles wide, and a total change from one "pure" parental population to the other takes place within about 50 miles. A hybrid zone about 16 miles across connects the wrens *Campylorhynchus rufinucha humilis* and *C. r. nigricaudatus* in Chiapas, Mexico (Selander, 1964, 1965; see also Short, 1966). The Colombian toucans *Pteroglossus torquatus torquatus* and *P. t. sanguineus* form a hybrid zone only about 12 miles across (Haffer, 1967). Finally a very small hybrid zone connects the birds-of-paradise *Astrapia stephaniae* and *A. "mayeri"* (Mayr and Gilliard, 1952). Introgression was detected in a population of the latter about 15 miles from the hybrid zone. Regardless of the size of these hybrid zones, they are indicative of free interbreeding; the forms involved therefore should be considered conspecific.

HYBRID SWARMS

Hybrid swarms are hybrid populations of small to large size that are nearly or actually genetically isolated from populations of the parental forms. Their lack of contact with the parental stock hampers evaluating these populations taxonomically. It is usually impossible to establish

whether the swarm resulted from breakdown of isolating mechanisms under the exigencies of local selective forces, or whether such mechanisms simply were lacking. On one hand the occurrence of several hybrid swarms involving the same two forms suggests that their isolating mechanisms are weak and probably ineffective, or nonexistent. On the other hand, populations which are partly sympatric or occur adjacently without interbreeding may form a lone hybrid swarm; this would suggest local breakdown of extant isolating mechanisms as the cause of the hybrid swarm.

Evidence for the occurrence of introgression should be sought in populations of the parental forms nearest the hybrid swarm. The existence of introgression may be used as a basis for considering the forms involved as conspecific, while lack of introgression would be inconclusive. Evidence for the stabilization of a single hybrid swarm also would warrant conspecific status for the parental forms. The basis for this conclusion is that stabilization proves the parental genotypes are sufficiently compatible and alike to permit selection of adaptively satisfactory genotypes from their recombinants, at least in one region. Isolated single instances of hybrid swarms not exhibiting stabilization remain a problem. A hybrid swarm does prove that the forms involved can interbreed, at least in certain circumstances. Lacking other concrete evidence, especially sympatry elsewhere, for the presence or absence of reproductive isolating mechanisms, I suggest that the lone instance of a hybrid swarm provides a tentative, albeit weak, basis for merging the forms in question. This action is more justifiable than assigning each of them full species status, because existence of the hybrid swarm proves that they have not achieved complete reproductive isolation, or at any rate had not at the time the swarm became established.

Various insular populations of the highly polymorphic *Pachycephala pectoralis* of the Southwest Pacific (approximately 70 races) comprise hybrid swarms (Mayr, 1942a; Galbraith, 1956). These apparently resulted from colonization of certain islands by individuals representing two races. Most of these hybrid swarms have retained the high variability typical of hybrid populations. Solomonsen (1950) regarded the Iceland population of redpolls as a stabilized hybrid swarm of *Carduelis flammea* × *C. hornemanni*, although the two species are sympatric elsewhere. Other examples (*Colaptes auratus*, *Pipilo erythrophthalmus*) of hybrid swarms are discussed below.

COMBINATIONS OF SITUATIONS

Various combinations of situations sometimes occur between populations, including different types of hybrid reactions. These combinations occur

because of genetic differences among various populations of two forms, reflecting the simple fact that evolution does not proceed at the same rate in all populations of a species. The often difficult taxonomic problems presented by these combinations ought to be solved on the basis of the extent of reproductive isolation. Thus, existence of a large hybrid zone would more than offset the presence elsewhere of a small area of overlap. Conversely a large area of sympatry without interbreeding would override existence elsewhere of a hybrid swarm or a small hybrid zone. Nevertheless instances occur, like those of circular overlap discussed below, that involve both a large area of overlap and a large hybrid zone. Each case must be decided after careful analysis of every situation and an evaluation of the sum of the reactions. Combinations of situations are sufficiently complicated to merit discussing several examples.

Miller's (1941) intensive study of the North American juncos led him to recognize a number of species, notwithstanding hybridization among them. The eastern *Junco* "*hyemalis*" forms a large hybrid zone with the western *J.* "*oreganus*." Miller attempted to show that the hybrid population is a stable hybrid race ("*cismontanus*") affiliated with *hyemalis*. The parental populations mainly involved in the interbreeding are virtually identical in those mensural characters that Miller used to demonstrate the supposed stability of the hybrid race. A hybrid population should not show increased variability in features not differing in the parental forms; hence the supposed stability of "*cismontanus*" is spurious. Miller's analysis of "*cismontanus*" was based on only two samples from the vast area ascribed to that form. He admitted (1941: 342-343) that "actual" hybrids cannot in fact be distinguished from individuals representing "*cismontanus*." Critical examination (Short, MS) of large numbers of northwestern juncos, many taken after Miller's study, indicates that "*cismontanus*" actually represents a vast hybrid zone population, and that considerable introgression occurs beyond this zone. Since Miller's (1941) work, Dickinson (1953: 128-131) and Phillips (1961: 372-377) have studied the interbreeding of *hyemalis* and *oreganus* through "*cismontanus*"; both concluded that the interbreeding of these forms shows them to be conspecific. The Southern Rocky Mountain *Junco* "*caniceps*" forms isolated hybrid swarms with the race *thurberi* of *J.* "*oreganus*" in eastern California and Nevada, and a moderate hybrid zone with *mearnsi* of *J.* "*oreganus*" in Wyoming, Idaho, and Utah. Finally, although *Junco* "*aikeni*" of the Black Hills region is geographically isolated from other junco populations, several hybrids (*aikeni* × *mearnsi*) were obtained from the population of *aikeni* geographically nearest to another junco (*J.* "*oreganus*" *mearnsi*). I concur with the suggestions of Mayr (1942b), Dickinson (1953), and

Phillips (1961; and in Phillips et al., 1964) that the *oreganus*, *caniceps*, *aikeni*, and *hyemalis* groups (= subspecies groups) of juncos should be considered conspecific (= *Junco hyemalis*). The genus *Junco* actually appears to be a superspecies, a view Mayr (1942b: 379) suggested; the component species are *J. hyemalis*, *J. phaeonotus* and *J. vulcani*. These are probably congeneric with *Zonotrichia* (Short and Simon, 1965).

Three morphologically divergent forms of North American flickers (*Colaptes auratus*), considered by some as separate species, hybridize in North America (Short, 1965). The eastern *auratus* and western *cafer* subspecies groups form a large hybrid zone across North America, as mentioned above. The third form (*chrysoides* group) inhabits the south-western desert region, and it forms both variable and semi-stabilized hybrid swarms with the western *cafer* group in Arizona and Baja California (Short, 1965; Short and Banks, 1965). In addition, it forms a single tenuous narrow hybrid zone with flickers of the *cafer* group along one river valley in Arizona. The existence of the *auratus* × *cafer* hybrid zone, the narrow *cafer* × *chrysoides* hybrid zone, and evidence for some stabilization in a hybrid swarm of *cafer* × *chrysoides* justify conspecific status of these forms.

The towhee (*Pipilo erythrophthalmus*) of most of North America and the towhee (*P. "ocai"*) of the Mexican highlands interact in the following three ways (Sibley, 1950, 1954; Sibley and West, 1958; Sibley and Sibley, 1964): 1) they form semiconnected, variable hybrid swarms that almost constitute a hybrid zone in western Mexico; 2) they form two small but moderately broad hybrid zones in south-central and eastern Mexico; and 3) they are sympatric with little or no interbreeding in several parts of Oaxaca and one area in eastern Mexico. Introgression is evident about the hybrid zones and is affecting populations in at least one of the three areas of sympatry. When hybridization and introgression affect major populations of two forms, these cannot be considered fully reproductively isolated. It is not fitting to designate two forms as species when the extent of their interbreeding and introgression outweighs the extent of their sympatry. Hence the towhees are best considered as conspecific.

The bulbuls *Pycnonotus cafer* and *P. leucogenys* broadly overlap in India and Pakistan. Scattered hybrids occur in the overlap area near the western end of *cafer's* range, while two local hybrid swarms also occur in that region (Bannu and Kohat in northwestern Pakistan; Sibley and Short, 1959b). These bulbuls are evidently species exhibiting occasional breakdown of reproductive isolation, probably only where one species is uncommon and the choice of mates is therefore limited.

Chapin (1948) reported different reactions between the African paradise

flycatchers *Terpsiphone rufiventer* and *T. viridis*. The subspecies *T. r. nigriceps* and *T. v. viridis* occur sympatrically without interbreeding in some areas, but in Gambia and Portuguese Guinea they formed a hybrid zone that apparently has become a relatively stabilized hybrid population, designated as *T. r. rufiventer*. Other races of these species (*T. r. somereni* and *T. v. ferreti*) form a zone of overlap and hybridization in Uganda, where the hybrids appear less numerous than individuals of the parental types. It seems best to consider these flycatchers as separate species.

The sparrows *Passer domesticus* and *P. hispaniolensis* are broadly sympatric in Spain, northwestern Africa, the Balkans, Asia Minor, and south-central Asia. Yet they have formed a large stabilized hybrid population in Italy, *P. d. italiae*, considered a race of *P. domesticus* because of its hybrid zone with that form (Meise, 1936; Vaurie, 1956, 1959), small stabilized and nonstabilized hybrid swarms in central Algeria and southern Tunisia, and a zone of overlap and hybridization in northern Algeria (Meise, 1936). Although genetic exchange between these forms indicates that they comprise a single evolutionary unit, the great area over which they coexist without interbreeding merits assigning specific status to each.

Three taxa of sapsuckers, once regarded as separate species, were merged in *Sphyrapicus varius* following studies by Howell (1952). The three forms are: the northeastern *S. "varius,"* the Rocky Mountain *S. "nuchalis,"* and the western and northwestern *S. "ruber."* Two races of *ruber* (*ruber*, *daggetti*) hybridize with *nuchalis*. In one case (*daggetti* × *nuchalis*) a small, narrow zone of overlap and hybridization has resulted, with parental phenotypes as numerous as the hybrids. The other case (*ruber* × *nuchalis*) involves a moderate, narrow zone of overlap and hybridization with few hybrids. *Sphyrapicus "nuchalis"* and *S. "varius"* make contact in Alberta, but little is known of their reactions except that hybrids are few and interbreeding apparently is limited. *Sphyrapicus "ruber"* and *S. "varius"* overlap in British Columbia, where hybrids rarely are produced despite the considerable extent of the area of overlap (Howell, 1952; Dickinson, 1953). Thus in every situation involving these sapsuckers gene exchange is limited; barriers seem to prevent free interbreeding. As no basis for merging them exists, I consider the sapsuckers *S. varius*, *S. nuchalis* and *S. ruber* as species. These semispecies comprise the superspecies *S. varius*.

CASES OF CIRCULAR OVERLAP

These situations are very complex and all known cases require further study before even tentative taxonomic decisions can be rendered. It is crucial that all reactions between two forms be documented before undertaking a full taxonomic evaluation. For example Vaurie and Snow (1957)

mention evidence of interbreeding between the terminal populations of the *major* and *minor* groups of *Parus major*; the terminal forms involved in this famous case of circular overlap thus do *not* overlap without interbreeding, as previously had been supposed (Mayr, 1942a: 182).

Cain (1955) and Keast (1961) discussed a case of circular overlap in *Platycercus* parrots of Australia. A terminal form *Platycercus elegans elegans* intergrades with *P. e. adalaidae*, which in turn hybridizes with the other terminal form *flaveolus*. One hybrid exists between *flaveolus* and *P. e. elegans*; otherwise these forms contact or overlap slightly without interbreeding. The crux of the problem is a need for analysis of the *adalaidae* × *flaveolus* interbreeding. If a zone of overlap and hybridization exists, *flaveolus* should be considered a separate species. This would not involve circular overlap. Should free interbreeding occur through a hybrid zone, circular overlap would exist. I would then consider the three forms conspecific on the basis of the genetic exchange among the populations and relatively small overlap of *flaveolus* and *elegans*.

The circular overlap involving gulls of the *Larus argentatus* group is exceedingly complex, despite the recent work of Smith (1966) and others (cited by Mayr, 1963: 508–510). There is not even agreement on which forms comprise the complex. Mayr (1963) includes *L. glaucoides* in the *argentatus* complex, but excludes *L. glaucescens* and *L. schistisagus*. Recent studies (Williamson and Peyton, 1963; Vaurie, 1965: 735) have shown that the latter two forms hybridize with and are closely related to *L. argentatus*. Stresemann and Timoféeff-Ressovsky (1947) demonstrated that gaps exist between Eurasian populations of this complex that previously were thought (Mayr, 1942a) to be continuous. Any taxonomic decision in this case will be premature until there is further documentation of all existing reactions.

Other cases of circular overlap Mayr (1963) cites also are fraught with problems. These especially involve the continuity of links in the circle, and the exact reaction of the terminal populations. When true circular overlap is demonstrable, I would consider the terminal forms as conspecific if their genetic connection is continuous through areas of primary intergradation and hybrid zones. Major gaps in the continuity of the chain, including the existence of zones of overlap and hybridization, would necessitate designation of several species; the situation would not be one of true circular overlap.

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SUMMARY

Instances of natural hybridization in birds provide the framework for a discussion of guidelines for taxonomically appraising various phenomena of hybridization. Hybridization and semispecies are defined, and the superspecies concept is related to hybrid situations.

The occurrence of unique hybrids is generally of little taxonomic consequence, but these may corroborate or suggest relationships. Several hybrids between species of different genera suggest generic relationship, while several intrageneric hybrids may suggest the existence of superspecies or former superspecies.

Zones of overlap and hybridization occur between semispecies that are taxonomically species. The occurrence of parental phenotypes with hybrids indicates the operation of partial isolating mechanisms restricting gene exchange. In such cases the parental forms are actually sympatric. On the other hand, hybrid zones contain only hybrids, and they connect as well as separate conspecific populations (subspecies or subspecies groups). The fact that the hybrid population both connects and separates the allopatric parental forms attests to their lack of reproductive isolation. Unique hybrid swarms pose serious problems that are discussed.

Combinations of relationships, including hybridization, are discussed and examples are provided. In such cases the extent of hybridization and introgression is weighed against the degree of reproductive isolation and the amount of sympatry exhibited by the populations involved. Instances of circular overlap are complicated and they seem to require further study before they can be taxonomically resolved.

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