The classification of avian species and subspecies

*A lucid presentation of the bases on
which species are lumped or split*

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INTRODUCTION

RECENTLY, THERE HAVE BEEN a number of changes in the classification of bird species approved by the Committee on Classification and Nomenclature (American Ornithologists' Union Check-List Committee 1973, 1976). Nearly all changes involve two or more closely related species or subpopulations of a species. Thus, the systematist rarely has difficulty separating species from different orders or families, and challenges in proper classification usually involve populations of the same genus or species. Such changes are casually referred to as "lumping" (combining two or more species into a single species) or "splitting" (separating a species into two or more species) and often generate confusion and misunderstanding among amateur ornithologists and some professional biologists. To eliminate this confusion one must study and consider past and present concepts of speciation. The following brief review may be helpful in this regard. Some readers may wish to review the glossary of technical terms in the Appendix.

THE SPECIES CONCEPT

MOST SPECIES OF BIRDS currently recognized were described on a morphological basis, *i.e.,* classification of species according to consistent size, structure, and color differences. When dealing with extinct species and fossil records, we are forced to base classification on morphological characteristics. However, most modern systematists disfavor the morphological species concept because it may lead to incorrect classification (of subspecies or failure to recognize the separate species status of sibling species). These problems will be discussed later with examples. Selander

(1971:99) reported that ornithologists have "universally adopted" the biological species concept, defined by Mayr (1969:20) as "groups of interbreeding natural populations that are reproductively isolated from other such groups." Strictly and simply, this definition states that if two populations occur in the same region (sympatric) and do not interbreed, they are separate species regardless of phenotypic (appearance), morphological, or ecological *similarities.* On the other hand, if two sympatric or adjacent populations frequently interbreed, they are the same species (conspecific) regardless of phenotypic, morphological, or ecological *differences.* Consequently, "reproductive isolation" is the key to the biological species concept. However, this does not mean that closely related valid species never hybridize. Isolating mechanisms are often imperfect, and Mayr (1951:102) noted that "I understand the occasional interbreeding of two otherwise well-delimited sympatric species. There is no conceptual difficulty in regard to this type of hybridization." Speciation is regarded as essentially complete if, during sympatry, interbreeding is reduced to a level that prevents genetic swamping by the parent species (Mayr 1959, Bigelow 1965). An example may be helpful at this point. Because two species of indigo birds of Africa, *Vidua chalybeata* and *V. purpurascens,* were morphologically indistinguishable, their status as separate species was questioned (White 1962, Payne 1973). To clarify the problem, Payne (1973) studied the degree of reproductive isolation; pair observations revealed 71 *chalybeata* x *chalybeata,* 5 *chalybeata* x *purpurascens,* and 73 *purpurascens* x *purpurascens.* Although a small number of hybrids was observed, these data, along with phenotypic differences, were reported to provide "direct

evidence that these two indigo birds locally behave as distinct biological species" (Payne 1973:175).

ISOLATING MECHANISMS

IN THE PARAGRAPH above I referred to "isolating mechanisms." This concept should be discussed before considering evolution of species. Populations of birds that occur in the same general region, yet fail to interbreed, are said to have isolating mechanisms— "properties of individuals which prevent interbreeding" (Mayr 1970:56). Mayr (1970) classified isolating mechanisms as "premating" or "postmating." Premating isolating mechanisms include seasonal and habitat isolation, behavioral isolation, and mechanical isolation. Postmating mechanisms include gametic mortality, zygotic mortality, hybrid inviability, and hybrid sterility. Avian isolating mechanisms are commonly reported to be behavioral premating mechanisms associated with species-specific recognition of song, color patterns, courtship displays, and similar mechanisms that may be reinforced by conditioning or imprinting by newly hatched chicks (Beach and James 1954, Marler 1957 and 1961, Hinde 1959, Immelmann 1975a and 1975b).

Smith (1966) found contrasting color patterns near the eye and wingtip pattern to be the isolating mechanisms among four species of gulls (*Larus* spp.). Jehl and Bond (1975) described a similar situation with murrelets of the genus *Endomychura* and suggested that facial patterns near the eye and bill shape both function as isolating mechanisms between these closely related species. Song and/or call notes have been identified as isolating mechanisms for sympatric meadowlarks (*Sturnella* spp.), Australian Wedgebills (*Psophodes* spp.), flycatch-

ers (*Empidonax* spp.), and indigo birds of the sub-genus *Hypochera* (Szijj 1966, Ford and Parker 1973, Stein 1963, and Traylor 1966, respectively). Combinations of song and color pattern have been identified as isolating mechanisms by Gill and Murray (1972) and Brown (1967) while Payne (1973) reported the combination of song and behavior.

Selander and Giller's (1961:77) study of the Great-tailed (*Quiscalus mexicanus*) and Boat-tailed grackles (*Q. major*) reported the primary isolating mechanism to be female recognition of male "behavioral differences, both at the time of nest site selection and at time of mating." Many other isolating mechanisms are reported, including habitat (Brewer 1963) and seasonal isolation (Smith 1966).

An important part of isolating mechanisms and speciation is reinforcement (Mayr 1970). For example, a population having color patterns as an isolating mechanism may have a fractional portion of members that will readily hybridize. However, if the hybrid offspring (F$_1$) express an intermediate color pattern, they may be selected against by the majority in their attempt to find a mate. This negative selection will eventually minimize or completely eliminate hybridization.

THE SPECIATION PROCESS

MAYR (1970:247-277) discussed various modes of speciation with examples from several taxonomic groups (birds, plants, insects, etc.), but ornithologists agree that geographic divergence best explains this evolutionary process for birds.

Geographic, or allopatric, speciation is a process that typically involves the subdivision of a large, widely distributed parent population (species) into two or more populations. The sub-populations are isolated genetically from each other by some extrinsic barrier, *e.g.*, an ocean or mountain range. While separated, the populations diverge either randomly or via selective forces of their respective environments. Divergence by the respective populations may yield differences in one or several factors, such as color pattern, size and structure, song, feeding habits, habitat selection, and behavior. These or other divergent factors may function as isolating mechanisms which will prevent widespread interbreeding when and if the populations expand and overlap. Initially, the populations may

occasionally interbreed. If hybridization is frequent, the populations will quickly lose any differences evolved during isolation, and their species status will be unchanged. However, if isolating mechanisms prevent interbreeding, or only allow for occasional hybridization, then a new species will have evolved (Dobzhansky 1937, Lack 1944, Miller 1947, Mayr 1951 and 1970, Sibley 1961, Selander 1971, Stebbins 1971, and Bush 1975). Speciation is usually a long-term process and likely involves thousands of years of evolution. Figure 1 was constructed to offer a graphic review of geographic speciation.

At this point one should carefully consider the following note of caution. Divergence and development of isolating mechanisms are not mutually dependent; many populations are known that have diverged morphologically in allopatry but possess no isolating mechanisms in zones of sympatry. These populations are usually called subspecies. Conversely, some populations evolve effective isolating mechanisms, become sympatric, but fail to diverge morphologically or in general appearance. Such populations are called sibling species.

Mayr (1970:278) noted that, given the overwhelming acceptance of geographic speciation, "the basic problem of speciation consists in explaining the origin of the gaps between sympatric species." With the exception of founder species (to be discussed), extrinsic barriers promoting speciation result from large-scale environmental change, such as continental drift, glaciation, or climate shifts (Selander 1965, Cracraft 1973, Croizat *et al.* 1974). A commonly proposed geologic event responsible for recent North American avian speciation is Pleistocene glaciation. Evidence or hypotheses for speciation by Pleistocene glaciation are presented by Rand (1948), Sibley (1950), Brewer (1963), Selander (1965), Mengel (1970), Heusmann (1974), and many others. On a more regional scale, the emergence of mountain ranges or the transition of a grass plain to desert could easily segregate widely distributed populations.

A special form of geographic speciation has been called founder effect. The founder effect is explained as a small number of birds ("founders") becoming established in an area highly isolated from the parent population, such as an island. Darwin's finches (Lack 1947) of

the Galapagos Islands and Hawaiian Honey Creepers (*Drepanididae*) are dramatic examples of founder species. Mayr (1951:98) suggested that founders may speciate by double invasion. Where "an island is repeatedly invaded by colonists from a distant mainland, it may happen that the descendants of the first wave of colonists have changed so much that they are reproductively isolated from new arrivals."

SUBSPECIES

BECAUSE SPECIATION is such a long-term process, some populations cannot be classified as simply belonging to one species or another. Certain populations are in intermediate stages of speciation or have special morphological characteristics (Mayr 1951, 1963, and 1970, Selander 1971, Stebbins 1971).

The taxonomic category of subspecies is assigned to distinct subpopulations of the same species. This category ranges from populations having barely perceptible morphological differences to those that appear sufficiently distinctive to have been classified as separate species. In each case, the populations so classified have discrete geographic ranges, have morphologically diverged, but have not developed sufficient isolating mechanisms to maintain reproductive isolation should their ranges overlap. Consequently, most bird populations that undergo geographic speciation likely evolve through a period when they would be recognized as subspecies (Figure 1). Hence, we do not expect to observe subspecies that are sympatric (especially during the reproductive season) because subspecific characters will quickly be lost via frequent interbreeding, *i.e.*, subspecies by definition cannot be sympatric.

Canada Geese (*Branta canadensis*) provide one of the well-known cases of avian subspeciation in North America. There are 10 subspecies of Canada Geese recognized by the American Ornithologists' Union. Each subspecific population has isolated breeding grounds (Hine and Schoenfeld 1968) and the birds range in size from the 3 1/2-pound Cackling Canada Goose (*B.c. minima*) to the 12 1/2-pound Giant Canada Goose (*B.c. maxima*) (Bellrose 1976:141). Although the subspecific populations have evolved significant morphological differences, there is no evidence to indicate they have developed isolating mechanisms.
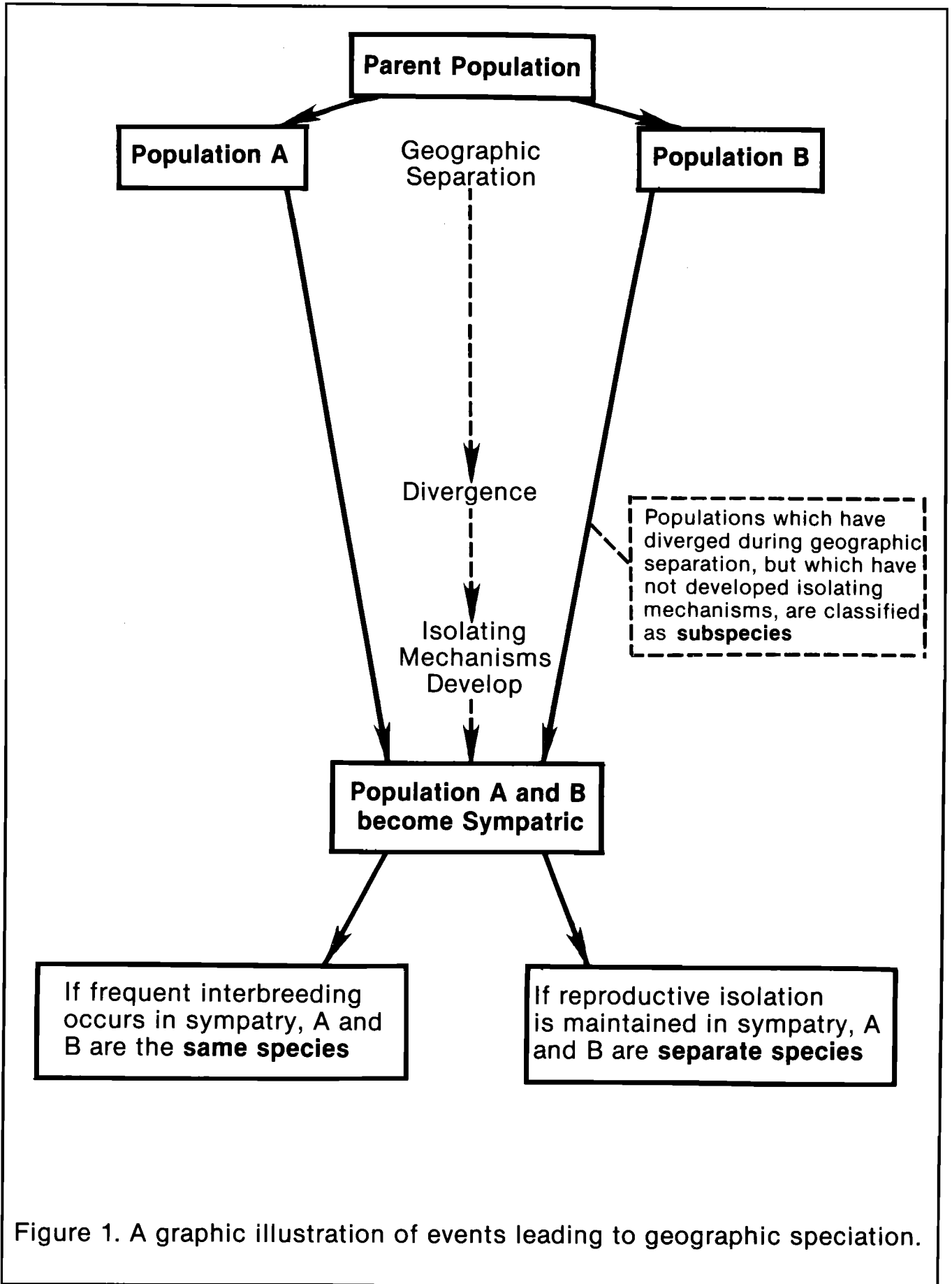
Figure 1. A graphic illustration of events leading to geographic speciation.

THE SPECIES-SUBSPECIES CON—TROVERSY

APPLICATION OF THE SUBSPECIES concept creates some controversy among systematists. Stebbins (1971:99) noted "there are many allopatric, completely separated populations which are obviously related to each other, but between which no intermediate individuals exist. These populations have never had a chance to take the 'test of sympatry' and so could be either species or subspecies." The problem is somewhat paradoxical in that species evolve during geographic isolation, yet cannot be classified as species (via the biological concept) until they lose their isolation and become sympatric with their parent species. When "allopatric populations are so different morphologically or otherwise that reproductive isolation between them can be assumed" they are classified as superspecies (Mayr 1970:286, also see Amadon 1966). Mayr (1970) noted that over 30 percent of the breeding birds in North America meet the classification criteria of superspecies. Therefore, often with "allopatric populations, phenetic data are evaluated and a prediction is made as to whether or not interbreeding would occur if the forms were in contact" (Selander 1971:100). It is quite understandable that "predictions" will lead to disagreement, controversy, and error. Equally understandable is Mayr's (1970) contention that the biological species concept, when applied to sympatric populations, is "unambiguous."

HYBRIDIZATION

ISOLATING MECHANISMS seldom are perfect between closely related species, and the breakdown of isolating mechanisms results in hybridization. Hybridization was defined by Mayr (1970:69) as "the crossing of individuals belonging to two unlike populations that have secondarily come into contact." Unlike populations usually refer to populations that are separated by discrete, contrasting characters such as color pattern, and are separate species. Hybridization occurs commonly; Mayr and Short (1970) noted that 10 percent ("at least 52") of North American nonmarine avian species have been reported to hybridize. Mayr (1970) was careful to point out the "erroneous" notion among many naturalists that hybrids are always "sterile mules."

Several hypotheses have been proposed to explain the occurrence of hybridization. Prevett and MacInnes (1973) suggested that the probable factor causing hybridization between Blue Geese (*Anser caerulescens*) and Canada Geese (*Branta canadensis*) is egg-dumping. This results in chicks hatched by, and imprinted to, geese of the other species. When reproductively mature, these birds are probable candidates to seek members of the other species for mates, and thus, hybridize. Several groups of birds, such as waterfowl, experience "brood mixing" when broods from separate species meet during use of common habitat. Occasionally chicks end up with the wrong parent of a different species, which provides an opportunity for imprinting to the wrong species, as with egg-dumping. When a rare species inhabits the range of a common, closely related species, hybridization is likely to occur. Sibley (1961:76) hypothesized that when conspecific mates are in short supply "the intrinsic mating drive eventually overcomes the inhibitory effect of incorrect species recognition signals and a mixed pair is formed."

Hybridization among some species is well known. The Golden-winged and Blue-winged warblers (*Vermivora chrysoptera* and *V. pinus*) have recognized hybrid forms known as the Brewster's and Lawrence's warblers (Parkes 1951, Gill and Murray 1972). Trauger et al. (1971) reported that hybridization is so common among Snow (*Chen h. hyperborea*) and Ross' geese (*Chen rossii*) that approximately 1400 hybrids have been produced annually in recent years. In one or both of these cases, hybridization may become more frequent and systematists may consider "lumping," consistent with the biological species concept. However, in numerous cases, hybridization is occasional or stable, and does not threaten species status of the respective populations. Numerous other accounts of hybridization are discussed by Short (1969). A full review of avian hybridization is beyond the limits of this manuscript, and the following list of selected references of reported avian hybridization is certainly incomplete: Dixon (1955), Sibley (1957), Johnsgard (1960), Selander (1964), Smith (1966), Szijj (1966), Gurr (1967), Short (1969), Ingolfsson (1970), Mayr and Short (1970), Patten and Weisbrod (1974), and Jehl and Bond (1975).

DISCUSSION

MANY OF THE RECENT species changes by the American Ornithologists' Union Check-List Committee have been reviewed by Arbib (1973). In the following paragraphs I will comment on only a few of the recent changes and relate them to the previous discussion of concepts.

At this point, it should be fairly obvious why some of the classifications of avian species have been changed and why more changes will occur in future years. The biological species concept demands years of careful field study to determine the relationship of populations. Recalling that I began this paper noting that most species presently recognized were classified on a morphological basis, it should be understandable that errors from this approach will be disclosed.

Two well-known species of warblers, the Myrtle Warbler (*Dendroica coronata*) and Audubon's Warbler (*D. auduboni*), have been merged into a single species, the Yellow-rumped Warbler (*D. coronata*). The two populations were originally considered to occupy separate ranges and to show distinctly different color patterns. However, study of overlapping populations has revealed widespread interbreeding—evidence that sufficient isolating mechanisms have not evolved to consider these forms as separate species (Hubbard 1969).

Several species of flickers, known to hybridize for nearly a century, have recently lost their species status. The Yellow-shafted Flicker (*Colaptes auratus*), Red-shafted Flicker (*C. cafer*), and the Gilded Flicker (*C. chrysoides*) are now considered to be the same species—the Common Flicker (*C. auratus*). Again, widespread interbreeding by overlapping populations indicated that classification as separate species was an error (Short 1954). The three populations are now considered subspecies

A third example of "lumping" involves the Tufted Titmouse (*Parus bicolor*) and the Black-crested Titmouse (*P. atricristatus*). Head markings are the chief differences between the two forms (Dixon 1954). "The evidence suggests that these forms diverged from a common ancestor, but that the morphological changes which developed were not accompanied by the evolution of mechanisms which would ensure reproductive isolation. Since free inter-

breeding between Black-crested and Tufted titmice occurs, the suggestion is made that they be considered conspecific" (Dixon 1954:190). In 1976 this suggestion was adopted and both forms are now considered to be the Tufted Titmouse (*P. bicolor*).

Each of the above errors was due to earlier classifications based on morphology in the absence of information on interbreeding. The morphological differences were considered to reflect reproductive isolation and the presence of effective isolating mechanisms. Similar errors, based on the same morphological approach, have been disclosed resulting in "splitting" of several species into two separate species. An excellent example is the Boat-tailed Grackle and the Great-tailed Grackle. Prior to the 1973 changes, the Great-tailed Grackle was considered to be a subspecies of the Boat-tailed Grackle. "These two grackles are so similar morphologically that museum systematists have generally accepted without question their designation as subspecies" (Selander and Giller 1961:29). However, study of a 100-mile-wide zone of sympatry showed that they failed to interbreed and are separate species.

Species such as the Boat-tailed and Great-tailed grackle are called sibling species. Sibling species are populations that are morphologically very similar, or identical, yet are reproductively isolated. Sibling species are often sympatric, and because they are nearly indistinguishable, they go unrecognized as separate biological species. Mayr (1970:23) acknowledged the importance of sibling species for they permit "us to test the validity of the biological versus the morphological species concept." Five species of flycatchers of the genus *Empidonax* are classified as sibling species in North America. The species are only recognized in the field with certainty by their song, and the song is considered to be the primary isolating mechanism and means of the species recognition (Stein 1963). In 1973, the Traill's Flycatcher (*Empidonax traillii*) was reclassified as two sibling species populations; the Willow Flycatcher (*E. traillii*) having the vocalization "fitz-bew," and the Alder Flycatcher (*E. alnorum*) having the vocalization "fee-bee-o."

Another phenomenon causing changes in the classification of avian species is polymorphism. Gardner (1975) defined polymorphism as "the existence of two or more genetically different classes in the same interbreeding population." The genetics of polymorphism will not be discussed here, but are well presented in most standard genetics texts (Srb *et al.* 1965, Levine 1969, Gardner 1975). The objective here is to note how polymorphism is diagnosed in an avian population and to provide some examples. Studies of polymorphism in birds frequently deal with phenotypic polymorphism, or what Mayr (1970:89) defined as "the occurrence of several strikingly different discontinuous phenotypes within a single interbreeding population." One well-known example of polymorphism is the red-phase and grey-phase Screech Owl (*Otus asio*). Mayr (1963) and Traylor (1966) reported that polymorphism is best demonstrated by random interbreeding and by both color types occurring in a single nest.

Among recent changes in classification are two species that were lumped when polymorphism was demonstrated. The Great White Heron is now considered conspecific with the Great Blue Heron (*Ardea herodias*). This change was made after Meyerriecks (1957) reported interbreeding by the herons and both color types occurring in the same nest.

One of the best-known cases of a color phase of a polymorphic species masquerading as a separate species is the blue phase of the Snow Goose (*Chen caerulescens*). Blue and snow phases of the Lesser Snow Goose were considered to be separate species prior to a study by Cooch (1961). The two color phases were found to readily interbreed and mixed color phase broods were observed. Cooke and Cooch (1968) have studied the genetics of this polymorphism and reported the color phases represent a single pair of alleles, the blue phase being BB or Bb and the snow phase being bb. Other cases of polymorphism in birds were reported by Cooke and Ryder (1971), Johnson and Brush (1972), and Bengston and Owen (1973); Mayr (1970) noted that over 100 cases are known of morphs originally considered separate species.

Although numerous cases of polymorphism were unrecognized for many years, some species may have been prematurely classified as polymorphic. Dark- and light-phase Western Grebes (*Aechmophorus occidentalis*) have been described by Storer (1965) with the main differences being color pattern near the eye, bill color, and flank color. The Western Grebe has been classified as a polymorphic species (Mayr and Short 1965). However, three years of recent field study (Ratti 1979) have shown that sympatric populations of dark- and light-phase Western Grebes rarely interbreed. Surveys of mated pairs in 1975, 1976, and 1977 from California, Oregon, and Utah revealed 577 dark x dark pairs, 432 light x light pairs, and only 5 dark x light hybrid pairs. These data indicate that dark- and light-phase Western Grebes are separate biological species.

In conclusion, many avian species have been "lumped" or "split" because recent field studies have provided sufficient information to disclose errors in classification. Future research will certainly generate additional changes, and this knowledge should be welcomed, for it furthers our understanding of avian evolution.

APPENDIX

The following selected terms and definitions are from the glossary in Mayr (1970:413).

ALLOPATRIC. Of populations or species, occupying mutually exclusive (but usually adjacent) geographical areas.

ALLOPATRIC SPECIATION. Geographic speciation.

BIOLOGICAL SPECIES CONCEPT. A concept of the species category stressing reproductive isolation and the possession of a genetic program effecting such isolation.

CONSPECIFIC. Individuals or populations of the same species.

ETHOLOGICAL. Behavioral, particularly with reference to species-specific components of behavior, the phenotypic expression of which is largely determined genetically.

ETHOLOGICAL BARRIERS. Isolating mechanisms caused by behavioral incompatibilities of potential mates.

F_1. First filial generation.

FOUNDER PRINCIPLE. The principle that the founders of a new colony (or population) contain only a small fraction of the total genetic variation of the parental population (or species).

GAMETES. Functional germ cells (= eggs and spermatozoa).

GEOGRAPHIC BARRIER. Any terrain that prevents gene flow between populations.

GEOGRAPHIC SPECIATION. The acquisition in a population—while it is geographically isolated from other populations of its parental species—of characters that promote or guarantee reproductive isolation after the external barriers break down.

HYBRIDIZATION. The crossing of individuals belonging to two unlike natural populations that have secondarily come into contact.

IMPRINTING. A process of rapid learning of highly specific information (like the parent image) during a critical period in the life cycle.

ISOLATING MECHANISMS. Properties of individuals that prevent successful interbreeding with individuals that belong to different populations.

MECHANICAL ISOLATION. Reproductive isolation owing to mechanical incompatibility of male and female genitalic structures.

MORPHOLOGY. The description and study of structural characteristics, particularly those on the surface of the body.

PHENOTYPE. The totality of characteristics of an individual (its appearance) as a result of the interaction between genotype and environment.

POLYMORPHISM. The simultaneous occurrence of several discontinuous phenotypes or genes in a population with the frequency, even of the rarest type, higher than can be maintained by recurrent mutation.

SIBLING SPECIES. Morphologically similar or identical populations that are reproductively isolated.

SPECIATION. The splitting of a phyletic line; the process of the multiplication of species; the origin of discontinuities between populations caused by the development of reproductive isolating mechanisms.

SPECIES. A reproductively isolated aggregate of interbreeding popula-tions.

SPECIES RECOGNITION. The exchange of appropriate (species-specific) stimuli and responses between individuals (particularly during courtship).

SUBSPECIES. An aggregate of local populations of a species inhabiting a geographic subdivision of the range of the species and differing taxonomically from other populations of the species.

SUPERSPECIES. A monophyletic group of entirely or essentially allopatric species that are either morphologically too different to be included in a single species or demonstrate their reproductive isolation in a zone of contact.

SYMPATRY. The occurrence of two or more populations in the same area; more precisely, the existence of a population in breeding condition within the cruising range of individuals of another population.

ZYGOTE. A fertilized egg; the cell (individual) that results from the fertilization of an egg cell.

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