

THE EVOLUTIONARY AND TAXONOMIC SIGNIFICANCE OF SEXUAL DIMORPHISM AND HYBRIDIZATION IN BIRDS

By CHARLES G. SIBLEY

INTRODUCTION

Some of the most difficult problems in avian systematics concern the generic level of classification in groups with a high degree of sexual dimorphism. The hummingbirds, manakins, birds of paradise, pond ducks, grouse and pheasants provide examples. In all of these groups there are two lines of evidence which provide indications of relationship, but which, frequently, appear to conflict with one another. On the one hand the male plumage characters of related species are highly diverse and, judged on a "degree of difference" basis, argue for wide taxonomic separation. At the same time the female plumages may be very similar. Viable, often fertile, hybrids may result from interbreeding between species with extremely different looking males.

When the taxonomist attempts to evaluate these various pieces of evidence he is faced with the decision as to the proper emphasis to be accorded to each. Which is more important: the secondary sexual characters of the males, which seem to argue for the separation of certain species into different genera, or the similar females and viable hybrids which seem to indicate a closer degree of relationship? Most taxonomists have tended to search for, and to emphasize, differences. The result has usually been that the characters of the diverse males have been utilized as the principal criteria while the similarities among the females, and the evidence from hybrids, have often been ignored. In all of the groups previously mentioned this has led to a high degree of generic splitting and has resulted in an inordinately large proportion of monotypic genera. Within the past few years, due mainly to the work of Ernst Mayr and Jean Delacour, this situation has been largely remedied in the ducks, pheasants, and birds of paradise, but the other groups still bear an excessive burden of generic names in current usage. Many avian taxonomists will agree that some groups of birds are overly split generically, but even a widely held opinion is insufficient grounds upon which to advocate or undertake the extensive revisions of hummingbird genera, for example, which some believe are needed (see Van Tyne, 1945).

The first requirement is a conceptual basis upon which to evaluate the taxonomic significance of sexual dimorphism and hybridization. To arrive at this in turn requires an understanding of the origin and function of the characters used in taxonomy and of the selective forces which determine their evolution. The reasons for, and results of, interspecific hybridization must be understood before its significance in systematics will be clarified.

It is the purpose of the present paper to review the process of speciation, especially as it pertains to the evolution of secondary sexual characters; to consider the results of secondary contacts which permit hybridization; to establish the relationship between different pair-bond patterns and the degree of sexual dimorphism, and to relate these various subjects to one another and to the taxonomy of certain groups of birds.

THE PROCESS OF SPECIES FORMATION

It is generally agreed that the process of speciation, at least in most animals, is accomplished through the interaction of heritable variation, natural selection, and spatial isolation. The first step in the process is the splitting of a single, interbreeding population into two spatially isolated populations. Since mutation, recombination and selection will be different in each of these daughter populations, they will diverge genetically from

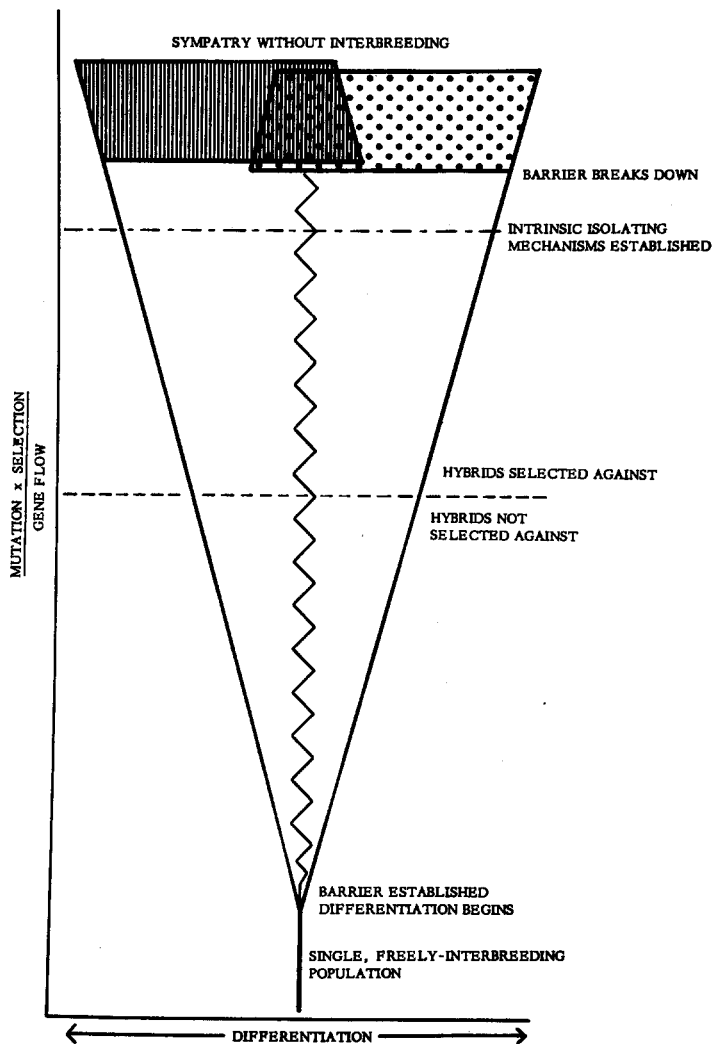


Fig. 1. Diagram of the process of speciation according to Muller.

each other and from their common ancestral type. Muller (1939, 1942) has postulated that the gradual accumulation of genetic differences in such isolated populations eventually results in the establishment of intrinsic isolating mechanisms which prevent interbreeding if the extrinsic barrier breaks down. Figure 1 diagrams the process of speciation according to Muller's hypothesis.

Since speciation is gradual there exists the possibility that the extrinsic barrier may break down before intrinsic isolating mechanisms have become fully effective. If this occurs the two partially differentiated populations are presented with the opportunity to interbreed. The extent and results of such hybridization will largely depend upon the degree to which they have diverged genetically during the period of spatial isolation.

In the present paper the term "hybridization" will be used to indicate interbreeding between populations in secondary contact regardless of their taxonomic rank. Mayr

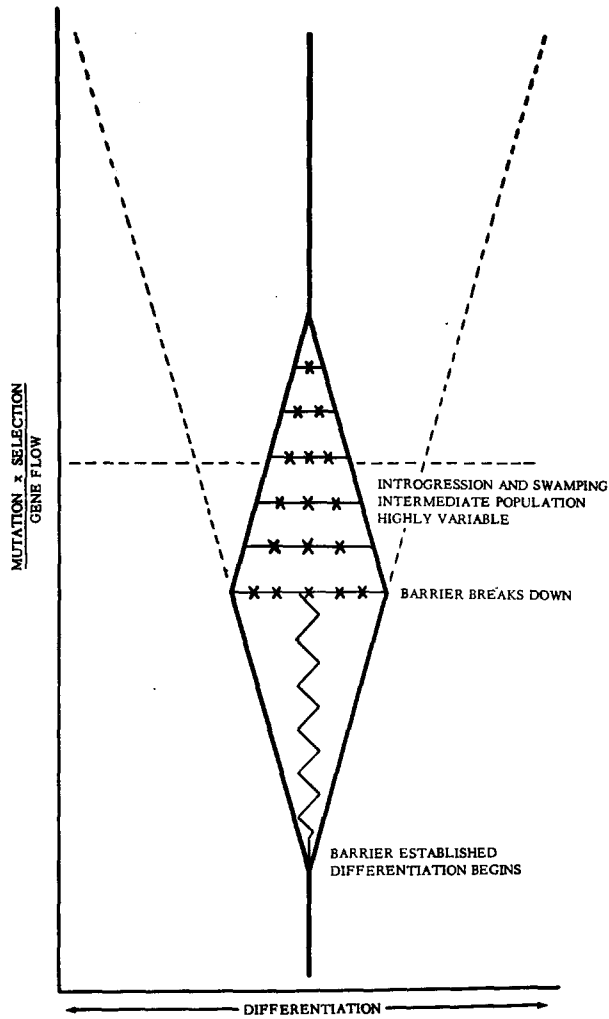


Fig. 2. Diagram of the results of breakdown in spatial isolation when hybrids are not selected against.

(1942:258) and Miller (1955:11) have discussed certain problems of definition and the recognition of secondary contacts. Miller's justified objection to the use of hybrid segregation and recombination patterns as indicators that contacts are primary or secondary is avoided here by specifying the condition theoretically and by choosing examples which appear undoubtedly to be secondary in nature.

INTROGRESSION AND SWAMPING

If the extrinsic barrier between diverging populations breaks down before marked ecological, morphological or physiological differences have accumulated, the hybrid individuals resulting may be fully fertile and viable. If they have as high a reproductive potential as the parental types they will be at no selective disadvantage in comparison with the parents and will form a bridge between the parental gene pools. For a time this

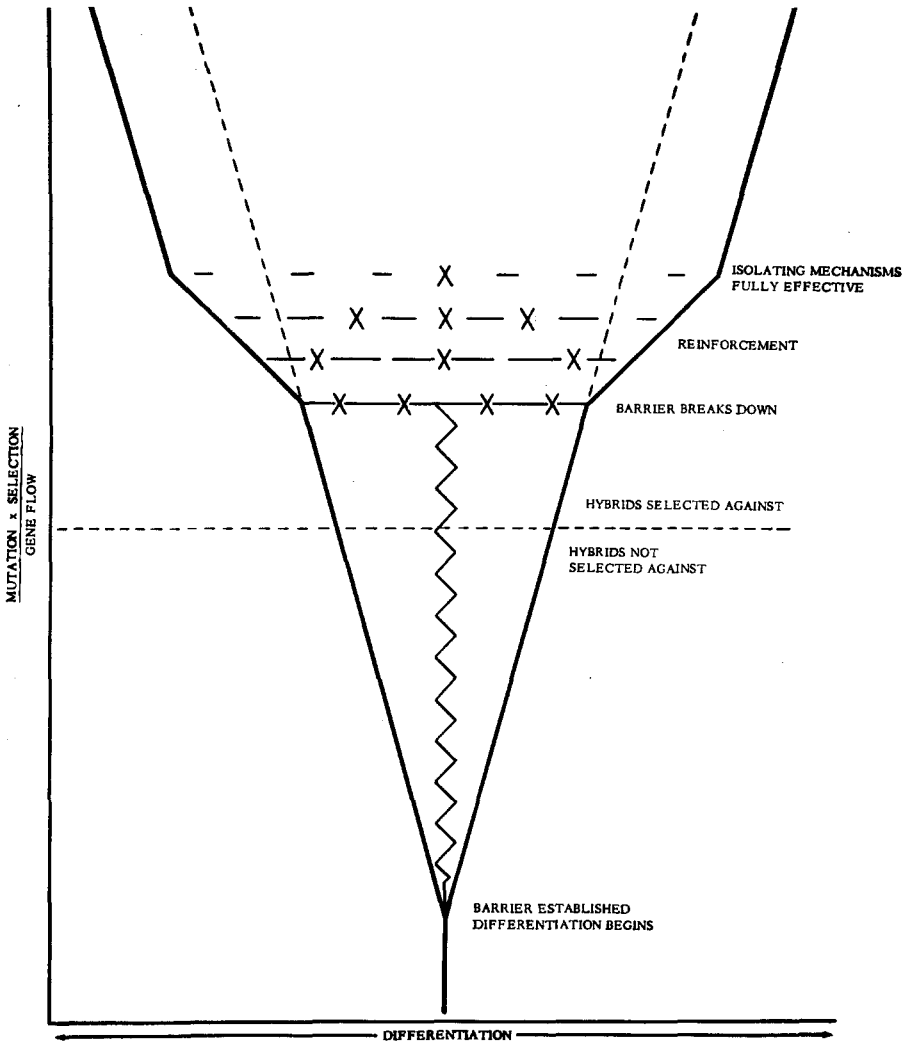


Fig. 3. Diagram of the results of breakdown in spatial isolation when hybrids are selected against.

will result in an increase in the variability of the rejoined populations due to the new recombinants present. As selection fashions a new adaptive peak the variability will decrease to a normal amount. Figure 2 diagrams this situation.

HYBRIDS SELECTED AGAINST—REINFORCEMENT

If, on the other hand, by the time the extrinsic barrier fails, sufficient differences have accumulated to render the hybrids less fertile or less viable than the pure parental individuals, a source of selection against the individuals entering into hybridization has been attained.

This hypothesis was first proposed by Fisher (1930), further discussed by Sturtevant (1938) and elaborated by Dobzhansky (1940). As described by Dobzhansky

(1951:208), "This hypothesis, which is complementary to Muller's, starts from the same premise, namely that the genotype of a species is an integrated system adapted to the ecological niche in which the species lives. Gene recombination in the offspring of species hybrids may lead to formation of discordant gene patterns. This decreases the reproductive potentials of both interbreeding species." The result is that the individuals in each parental population which enter into hybridization produce fewer offspring than those which do not. Thus the genotypes of the non-hybridizing individuals are at a selective advantage. The genetic basis for the better isolating mechanisms thereby increases its frequency, and any mutation which provides an additional basis for inter-specific sexual isolation will be selected for. Through this process the isolating mechanisms of each of the participating populations will be reinforced relative to the other until gene exchange between them is virtually or entirely stopped. Figure 3 illustrates this hypothesis.

A convincing proof of this idea has been provided by Koopman (1950) utilizing *Drosophila pseudoobscura* and *D. persimilis* in a population cage experiment. Inter-specific matings were selected against by eliminating all hybrids in each generation. In one series the percentage of hybrids dropped from nearly 50 per cent in the first generation to one per cent in the fourth generation and, except for single generation fluctuations, remained below three per cent for the remaining eight generations of the experiment.

Further, but less direct, evidence that selection against hybrids can reinforce isolating mechanisms has been provided by Dobzhansky and Koller (1939) in their study of sexual isolation between *Drosophila pseudoobscura* and *Drosophila miranda*. Strains of the two species from areas of sympatry, or near sympatry, show greater sexual isolation than those from areas far removed from the region of overlap. Similarly King (1947) found that sexual isolation between the two sympatric Brazilian species, *Drosophila guarani* and *D. guaru*, was much better than between either of the Brazilian species and *D. subbadia* of México. Huxley (1940:15) has also commented on this point.

Additional examples and a discussion of the genetics of isolating mechanisms have been provided by Dobzhansky (1951), who summarizes (pp. 210-211) as follows: "It is important to remember that the formation of reproductive isolation . . . requires time. The first vestige of the isolation develops . . . in allopatric populations. Inviability of F_1 hybrids, and low average adaptedness of the F_2 and of backcross products are probably by-products of the genetic differentiation of allopatric populations. Here the mechanism suggested by Muller is probably most important. The hybrid inviability and breakdown provide, then, the stimulus for natural selection to build up other reproductive isolating mechanisms. Reproductive isolation diminishes the frequency of the appearance of hybrids, prevents the reproductive wastage, permits the populations of the incipient species gradually to invade each other's territories, and finally to become partly and wholly sympatric. It is during the latter stages of this process that the selection pressure bolstering the reproductive isolation becomes strongest, helping to complete the process of speciation."

INTERMEDIATE SITUATIONS

Between the extremes of swamping when hybrids are not selected against and reinforcement of isolating mechanisms when hybrids are selected against, there exist situations in which selection is neutral or in which the hybrids are able to thrive in an ecological situation intermediate between those required by the parental types.

An interesting example is found in the narrow hybrid zone which exists between the European Hooded Crow, *Corvus cornix*, and the Carrion Crow, *C. corone* (Meise, 1928).

The width of this hybrid zone "is from 75 to 100 kilometers, and there is no evidence that it has broadened materially within the last 5,000 years" (Mayr, 1942:265-266). In this situation the isolating mechanisms have not become reinforced to the point of preventing hybridization nor has introgression caused swamping. Apparently alien genes are selected against in each of the parental populations but the hybrids are favored in the ecologically intermediate area. Some evidence for this explanation comes from the facts that with the well-known climatic shift occurring in the northern hemisphere the two species of crows are shifting their ranges and that the hybrid zone, although maintaining its width, is shifting in accordance.

ISOLATING MECHANISMS

The useful term "isolating mechanism" was proposed by Dobzhansky (1937) to describe agents which curtail or prevent gene exchange between populations. Classifications of isolating mechanisms have been proposed by several authors (see Dobzhansky, 1951:181-182; Stebbins, 1950, chapt. XI).

The nature of the isolating mechanisms which evolve will depend upon the means by which the organisms involved achieve recognition and/or fertilization. In wind-pollinated plants gametic incompatibility or hybrid sterility are possible mechanisms. Insect-pollinated plants may utilize the visual and olfactory senses of the insect pollinators as isolating mechanisms as Mather (1947) found in *Antirrhinum*. Some insects have evolved isolating mechanisms dependent upon chemoreceptors (probably olfaction) as determined by Miller (1950) in his study of *Drosophila affinis* and *D. algonquin*. Mayr (1950) found that sexual isolation between *D. pseudoobscura* and *D. persimilis* depends upon olfactory stimuli received via the antennae of the females. Removal of the antennae of the females greatly reduces sexual isolation between these species. Spieth (1952) has studied a large number of species of *Drosophila* to determine the species-specific differences in mating behavior which function as isolating mechanisms. The subgenus *Drosophila* utilizes contact stimuli while members of the subgenus *Sophophora* have developed signals such as movements and olfaction which function without physical contact.

Crane (1941) studied the behavior of fiddler-crabs (*Uca*) in Panamá. The males of each of the twenty-seven species present have a species-specific pattern of claw structure and display movement which function to warn off other males and to attract females of the same species. In spiders (Kaston, 1936), recognition is by sight in some groups, by both visual and tactile stimuli in others, and by touch alone in still others. Frogs and toads utilize species-specific vocal calls, pre-amplexic behavior patterns, and reactions during amplexus as isolating mechanisms (Jameson, 1955). Nocturnal mammals apparently utilize olfaction and hearing in species recognition; diurnal species depend more upon vision and less upon hearing and scent. Further examples are given by Dobzhansky (1951, chapt. VII).

In birds the senses of vision and hearing are especially acute while the sense of smell is totally or nearly absent in most birds. Diurnal species possess ranges of color vision and hearing similar to those of man. It is therefore to be expected that isolating mechanisms in birds will be primarily dependent upon visible and auditory characters in the form of colors, structures, display movements, and sounds. These signal characters function as "releasers" (Lorenz, 1935, 1937; Tinbergen, 1948, 1951) which activate innate patterns of response in other individuals, usually of the same species. The signal characters which function in species recognition and in pair formation are most important as isolating mechanisms. It is these which will be reinforced by selection against hybrids in a secondary contact.

Before signal characters can be fully utilized in taxonomy, it is necessary to determine their *function* and, for display movements and sounds, their *motivation* or drive, or "the complex of internal and external states and stimuli leading to a given behaviour" (Thorpe, 1951, 1954). Behavior patterns which function as interspecific isolating mechanisms will have a different taxonomic significance from those which function as signal characters in intraspecific responses. Furthermore, there are many stereotyped, innate behavior patterns connected with comfort movements such as scratching, preening, and stretching or with feeding behavior or sleeping postures which have phylogenetic significance at the familial or ordinal level (Heinroth, 1930). A behavior pattern called "courtship" may actually function both as an isolating mechanism and also as a hostile display. It may have been derived from a completely hostile pattern and be motivated by internal drives of escape, attack, and sex in varying relative and actual intensities. The isolating mechanism component may be of taxonomic value at the species level while the hostile component may have generic value. In their excellent revision of the ducks (Anatidae), Delacour and Mayr (1945), believing that genera should reflect similarities, were more impressed by the similarities between species in "courtship" patterns than by the differences which also exist. It seems logical to expect that the hostile components will be similar in a group of species like the anatine ducks while the isolating mechanism components will be specific and hence dissimilar in sympatric species. By using the similar components, which probably function in hostile responses between as well as within species, Delacour and Mayr found the "courtship" behavior patterns to be of generic significance.

The discussions of ethological isolating mechanisms by Mayr (1942:254), Lack (1945:62) and Huxley (1938, 1940) are of interest. Marler (in press) has investigated the taxonomic value of certain signal characters.

INTERSPECIFIC RESPONSES

There is another point which is significant in organisms having ethological isolating mechanisms. Hybridization is the proof that members of different populations have interbred and, as noted, if selection is against the hybrids, isolating mechanisms are reinforced. However, any expenditure of time, energy or gametes which fails to produce offspring will be selected against and will contribute to the reinforcement of isolating mechanisms. Hybridization should therefore be looked upon as the proof that interspecific pairing responses have occurred, but lack of hybridization does not prove that such responses are absent. In birds, which use vision and hearing in species recognition, it is apparently this source of selection which has been important in producing diversity in visible and/or audible characters among sympatric species. Such selection is effective between any two species which interact, regardless of their phylogenetic relationship. If, for example, individuals of two unrelated species are mutually attracted to one another for even a short period they will reduce their chances of successful breeding with members of their own kind. Presumably they were so attracted because of imperfections in their isolating mechanisms, hence any reduction of their reproductive success increases the incidence of those genotypes with the better isolating mechanisms.

This type of selection becomes especially intense when the length of time during which the members of a pair are associated before copulation occurs is very short. A short pair bond places a greater premium upon rapid and correct species recognition. Selection against errors in recognition will act to reinforce the characters used in recognition. Such characters are, by definition, isolating mechanisms.

SEXUAL DIMORPHISM

To this point the discussion has been sufficiently general to apply to most or all groups of animals. Our principal concern, however, is with the generic concept in those groups of birds having a high degree of sexual dimorphism.

In the foregoing discussion of hybridization evidence has been presented which indicates that the degrees of difference in the isolating mechanisms of sympatric species may be increased if selection is against interspecific responses pertaining to pair formation. This, obviously, can function only if two or more interacting species are in contact. A second source of selection, tending to increase the degree of difference between the sexes of a species, is derived from the competition among individuals for mates. This selective pressure is independent of the presence of other species, hence is always present. It is this source of selection which has long been known as "sexual selection."

The theory of sexual selection was proposed by Darwin (1871) to explain the origin of such secondary sexual characters as the bright colors, displays and songs of male birds, the antlers of male deer and similar structures which result in sexual dimorphism. Sexual selection was conceived by Darwin as resulting from the competition among males for mates, hence any heritable variation which gave an individual male an advantage in securing mates would increase in frequency in succeeding generations. Darwin's theory fell into disrepute for a period because it seemed to require a conscious ability on the part of female animals to discriminate among the small degrees of individual variation in the males. With the better understanding of instinctive behavior, which has accompanied the relatively recent rise of the science of ethology, it has become apparent that this objection is specious. With but slight modification in wording Darwin's concept may be shown to apply with special significance to certain groups of animals and to be of great importance in several families of birds.

In most birds it is the males which possess the species-specific colors, structures, sounds or displays ("releasers") which function as the basis for instinctive species recognition. Females, presumably, possess an innate perceptory pattern ("innate releasing mechanism") which matches and responds to the signal characters of the male. Pairing responses of the female depend upon the encountering of the male when her physiological thresholds are at certain levels. In species which are monogamous, or which pair for life, there will be but limited competition among males for mates. However, in polygamous species with a short pair bond a higher selective premium is placed upon any character in the male which more strongly stimulates the instinctive pairing responses of the females. It is this which Darwin called sexual selection, and it may be defined as *the reproductive advantage accruing to those genotypes which provide the stronger heterosexual stimuli*. It seems certain that the intensity of this source of selection reaches its maximum in those species in which several males gather to display on a "lek," or "booming ground," to which the females come for fertilization. In such species the pair bond lasts only for the period of copulation and an individual female has a "choice" of several males.

The result of sexual selection is sexual dimorphism. In species utilizing vision in recognition it will be visible characters which are affected. The genetic basis for such characters may, and probably does, involve but a very few genes and these may control only relatively superficial characters of plumage and display movements. This seems to explain why species with very different looking males and similar females can produce viable, often fertile, hybrids. The complete process appears to be as follows.

In polygamous species sexual selection produces high degrees of sexual dimorphism by action upon a few genetic factors in the males. When such species become separated into geographically isolated populations the secondary sexual characters of the males,

in each population, evolve more rapidly than other characters. Because available mutations will, by chance alone, be different in these separate populations, the males of the two groups come to look and/or sound extremely different and may evolve different "courtship" displays. The external characters of the females differentiate much more slowly because they are evolving at approximately the same rate as those characters of the male which are not affected by sexual selection. When such populations rejoin, they can produce hybrids because, in all essential factors, they are still genetically compatible.

The reduction or absence of sexual dimorphism in monogamous species in which the males participate in brood care is, apparently, due to two factors. In such groups sexual selection is less intense than in polygamous species and, since both adults accompany the young, the effects of predation on the male become as important as those on the female.

TAXONOMIC IMPLICATIONS

The reasons for the high incidence of monotypic genera in polygamous groups are now clear. Birds are visual animals, hence develop visible signal characters. Taxonomists utilize visible characters and emphasize differences. The degrees of difference among the males in polygamous groups are relatively large, hence the morphological taxonomist accords them generic rank.

The taxonomic significance of hybrids in polygamous groups also becomes clear. They prove the genetic compatibility of the interbreeding species, hence they prove their close relationship. Hybridization should be given far more weight as an indicator of close relationship than is given to secondary sexual characters as evidence of diversity.

If the foregoing theoretical explanation is correct, we should find highly specialized signal characters (color, pattern, voice, display) in those species which (1) are polygamous and do not form lasting pairs, and which (2) occur in sympatry with one or more related species, and which (3) occasionally form mixed pairs with one or more such related species.

Conversely, highly specific signals should be reduced or absent in species which (1) are monogamous and form a lasting pair bond and which (2) occur in isolation from species of sufficiently close relationship ever to form mixed pairs.

With these several theoretical considerations in mind we may examine some examples which appear to illustrate them.

THE BIRDS OF PARADISE (PARADISAEIDAE)

It has been suggested that the most pronounced signal characters should be found in a group of polygamous birds wherein there are several related sympatric species having short pair bonds and forming occasional hybrids. In such a group the combined effects of selection against hybrids and of sexual selection should produce a high degree of species diversity and development of signal characters in the males. These conditions are found in the birds of paradise of New Guinea.

The males of many of the 39 species of this family have long been famous for their highly specific displays, brilliant colors, plumes, and other modified feathers. Their popularity as decorative material for the millinery trade resulted in the importation of large numbers of "trade skins" to European markets. More than 100,000 were exported from New Guinea between 1870 and 1924 (Mayr, 1942:260). Among these, most of the known hybrids; some "two or three dozens," were discovered. Mayr (1945) estimates the ratio of hybrids to pure types as 1:20,000. Stresemann (1930) identified a number of hybrids which had been named as "species" and Mayr (1941) gives the parentages of known hybrids and (1942:260) discusses their significance.

In most birds of paradise the males call and display in a particular place. The females, when ready for fertilization, go to the display area, copulation occurs, and the female departs to build the nest, to incubate, and to raise the young alone. The pair bond is thus virtually non-existent since it exists only for the time required in copulation.

Ten "genera" of New Guinea birds of paradise have been involved in hybridization (Mayr, 1942:260). These apparently are the result of a female being attracted to the display ground of a male of another species. All of the hybridizing species are sexually dimorphic and all are polygamous. Three genera, *Manucodia*, *Phonygammus*, and *Macgregoria* have *not* been found to hybridize and are not sexually dimorphic. The solution was discovered by Rand (1938) who found that *Manucodia* forms lasting pairs and the males participate in brood care.

Evidence that sexual selection is an important factor in the evolution of male signal characters comes from at least two sources among birds of paradise. The first has been noted, namely, that the polygamous species with short pair bonds tend to be strongly sexually dimorphic, while the monogamous manucodes show a reduction of sexual dimorphism. The second piece of evidence is found in the existence of a strongly dimorphic species, Wallace's Standard Wing (*Semioptera wallacei*), living in isolation from related species in the northern Moluccas.

THE HUMMINGBIRDS (TROCHILIDAE)

The pattern of pair formation in the hummingbirds is similar to that of the birds of paradise. In most of the approximately 300 species no lasting pair bond is formed and the males are polygamous. In many species the males defend territories in which they display and to which the females come for fertilization. Species-specific displays are directed toward other males, females, and often toward other animals. The displays thus appear to be motivated primarily by hostile tendencies, that is, by escape and attack (Hinde, 1955; Moynihan, 1955), but by their specificity they can, and probably do, function as species recognition signals and hence as isolating mechanisms.

Sexual dimorphism tends to be highly developed in the species in which solitary males defend territories (Pitelka, 1942). It is certainly significant that the reduction of sexual dimorphism in the genus *Phaethornis* is accompanied by a highly vocal group display in the males. In *Phaethornis superciliosus*, for example, Nicholson (1931) and Davis (1934) have described the "singing assemblies" where several males gather to perch and call loudly in proximity to one another. Similar assemblies have been reported in *Phaethornis ruber* (Davis, 1934), *P. longuemareus* (Chapman, 1894; Skutch, 1951), and *P. guy* (Brewster and Chapman, 1895). In *Colibri thalassinus*, another species in which the sexes are alike, Wagner (1945) has described similar assemblies. In one instance 27 males were noted in an area approximately 500 meters long and 100 meters wide; sometimes two were in the same tree.

If sexual selection is operating upon these lek species of hummingbirds as, apparently, it does upon many birds of paradise, we should expect to find evidence of its effects. The sexes in *Phaethornis* and *Colibri* tend to be alike in plumage and, compared with many other genera, plumage characters are not strongly specific. There is some evidence that the pattern of the breeding biology may be of importance in this regard. In many of the species of *Phaethornis* the singing assemblies of males congregate in low, dense second-growth or thickets. In *P. longuemareus* Skutch (1951) describes a typical courtship assembly in which each male sits upon a low perch in dense cover. The tail is "wagged" while the song is repeated over and over. The assemblies of *P. superciliosus* and *P. ruber* (Nicholson, 1931; Davis, 1934) are basically similar in that the males perch for long periods and sing loudly and continually.

In these species of dense cover it appears that the vocal signals have been enhanced while in the males of genera such as *Calypte* and *Selasphorus*, which display in the open, visual signals have evolved. It is in open country species that iridescent gorgets and elaborate flight displays are most highly developed.

In most hummingbirds the females build the nest, incubate, and care for the brood alone. In two species, however, there is evidence that the males participate in brood care. Moore (1947) and Schäfer (1952) have shown that the male in *Colibri coruscans*, apparently regularly, participates in incubation and brood care; and Davis (1945) found an incubation patch in a male of *Eupetomena macroura*. In both of these species the sexes are similar in plumage.

The occurrence of hybrids in hummingbirds contains several points of interest. Of 37 hybrid combinations, recorded in the papers cited below, 25 are "intergeneric" and only five are between species of the same genus. The remaining seven are doubtful for various reasons. In these 37 hybrid combinations 28 genera are involved. Of these, 21 are sexually dimorphic, in seven the sexes are alike. Furthermore, no species of any of the so-called "hermits" (*Eutoxeres*, *Phaethornis*, *Glaucis*, *Threnetes*, *Ramphodon*) is involved (Berlioz, 1929, 1930, 1937; Butler, 1927; Hartert, 1900; Huey, 1944; Peters, 1945).

The ratio of intergeneric to intrageneric hybrids (5:1) is itself a strong indication that many of the so-called "genera" are invalid. Hummingbird genera are based largely upon the secondary sexual characters of the males (see Peters, 1945; Van Tyne, 1945). If male plumage characters have evolved originally under the impact of sexual selection, while isolated from closely related forms, it is possible that species having very different looking males are actually closely related. Their ability to hybridize should be taken as proof of close relationship, not regarded as proof that "genera" can hybridize! Hybridization may, in turn, result in further reinforcement of the male characters which function as isolating mechanisms. It is entirely possible that the ultimate result could be a pair of closely related, sympatric species with remarkably different looking males, and similar females, which occasionally produce viable hybrids.

The abnormally high incidence of monotypic genera in all classifications of hummingbirds is now understandable. Even the most recent treatment (Peters, 1945) recognizes 123 genera, of which 73 are monotypic, for 327 species. In addition, it is significant that the larger genera tend to contain groups of species in which sexual dimorphism is absent or reduced, for example, *Phaethornis* with 22 species and *Amazilia* with 29. As already suggested by Peters (*op. cit.*) the remedy for this taxonomically unsound situation is a generic classification based upon female plumages or other characters which do not function primarily as specific recognition signals. As long ago as 1909 Taylor called attention to the fact that many hummingbird genera are based upon the same characters used to differentiate species. His viewpoint was disputed by Ridgway (1909) and, unfortunately, found no protagonists. Recently Zimmer (1951:3), in a paper on Peruvian hummingbirds, has united a number of monotypic genera whose characters appear to be "of not more than specific value."

THE PHEASANTS (PHASIANIDAE)

The tribe Phasianini of the family Phasianidae is a group of 16 genera containing 49 species (Delacour, 1951). The center of distribution is southeastern Asia where up to 10 species may be sympatric. Hybrids of many combinations have been produced in captivity (Delacour, 1927, 1951) and several have been recovered in the wild (Delacour, 1948). In Europe and North America the introduced Ring-necked Pheasant (*Phasianus colchicus*) has hybridized with various native species. For example, in Europe, it has

hybridized with the Black Grouse, *Lyrurus tetrrix* (Jourdain, 1912) and with the Capercaillie, *Tetrao urogallus* (Clarke, 1898; Wynne-Edwards, 1950) and in North America with the Prairie Chicken, *Tympanuchus cupido* (Lincoln, 1950) and the Ruffed Grouse, *Bonasa umbellus* (Bump *et al.*, 1947:268). Many other hybrids involving members of this family have been reported (Peterle, 1951; Hopkinson, 1926).

The degree of sexual dimorphism tends to be high, the males usually being brightly colored, the females concealingly colored in dull browns and grays. As a rule the pair bond is not a lasting one although the sexes may remain together for a longer period than that required for copulation.

Exceptions to these rules parallel the situation in *Manucodia* and *Colibri coruscans*. In the Eared Pheasant (*Crossoptilon*) the sexes are alike and the males participate in the care of the young (Delacour, 1951:188, 195), and in the Cheer Pheasant (*Catreus wallichi*), which is monogamous, sexual dimorphism is greatly reduced.

THE GROUSE (TETRAONIDAE)

The 17 species of grouse are currently contained in 10 genera, six of which are monotypic. Hybrids are frequent, all but one genus (*Centrocercus*) and at least 10 of the 17 species have hybridized with another (Peterle, 1951; Jollie, 1955). Hybrids between the Sharp-tailed Grouse (*Pedioecetes phasianellus*) and the Prairie Chicken (*Tympanuchus cupido*) are common enough to be observed with a moderate degree of frequency in the field. The hybrid between the Capercaillie (*Tetrao urogallus*) and the Black Grouse (*Lyrurus tetrrix*) is of frequent occurrence in northern Europe. The male parent is usually the Black Grouse and, according to Millais (Witherby *et al.*, 1944), the hybrids result when pioneering Capercaillie females invade a new area occupied by Black Grouse before males of their own species arrive. Westerskov (1943:43) believes hybridization between these species is due to the fact that when male Capercaillie are shot out locally the females, left without mates of their own species, are attracted to the display grounds of the Black Grouse.

In most grouse the pair bond is short and the males are polygamous. In *Tympanuchus*, *Pedioecetes*, *Lyrurus*, and *Centrocercus*, the males display in a group (lek) while in *Bonasa*, *Lagopus*, and *Dendragapus* the males usually display singly. The Capercaillie may gather in loosely organized groups or display singly. In *Lagopus* the males are monogamous, remain near the nest, and participate in brood care and incubation.

The degree of sexual dimorphism is apparently correlated with the intensity of sexual selection. In the monogamous ptarmigan (*Lagopus*) the sexes are most alike. In the polygamous, but solitary, *Bonasa* and *Dengragapus* the sexes differ more than in *Lagopus* but less so than in the polygamous lek species of the remaining genera. In these sexual selection should be especially intense. It seems probable, therefore, that the strongly specific male secondary sexual characters in the five lek genera have evolved primarily under the influence of sexual selection. The frequent hybridization between the sympatric pairs of species is indicative of their close relationship and argues strongly for the congeneric status of *Tympanuchus* with *Pedioecetes*.

THE MANAKINS (PIPRIDAE)

The manakins include approximately 59 species usually placed in some 20 genera ranging from southern México to Argentina. In all species where life-history data are known the sexes meet only for copulation after which the female builds the nest, incubates, and cares for the young alone. The females of all species tend to be concealingly colored in shades of brown or green. Color patterns in the males are of two principal types and, in the few species for which data are available, the coloration is correlated

with the pattern of courtship and, presumably, with the intensity of sexual selection.

In the species with brightly colored males the males form courtship assemblies at certain places where they display and to which the females come for fertilization. In the Gould's Manakin, *Manacus manacus* (Chapman, 1935), the Yellow-thighed Manakin, *Pipra mentalis* (Skutch, 1949), the Blue-backed Manakin, *Chiroxiphia pareola* (Lamm, 1948), and the Lance-tailed Manakin, *C. lanceolata* (Friedmann and Smith, 1955), two or more males have been observed to display either immediately adjacent to one another (*Chiroxiphia*) or in individual "courts" spaced several feet apart.

In the Brown Manakin (*Schiffornis turdinus*), a species in which the similar sexes are dull greenish-brown in color, the males are solitary. Skutch (*in litt.*) notes that the male repeats over and over a ventriloquial, tripartite whistle as he clings to a stem in the undergrowth. Aside from this whistle there is no display. As in other manakins the male appears to take no part in the nesting or brood care.

Only one hybrid has come to my attention. This is between *M. manacus* and *Pipra erythrocephala* (Hellmayr, 1929:75). It is of interest that the males in these two species, although differing in many plumage characters, both have areas of orange-yellow on the head. It is tempting to speculate that such similar characters may have been the basis for the "mistake" in identification by the female which led to this instance of hybridization. The females of these species are extremely similar.

It is significant to the taxonomy of this group that the genera of the sexually dimorphic species have often, partly or entirely, been based upon the secondary sexual characters of the males. Examples from Hellmayr's (1910) generic diagnoses include the following genera: *Machaeropterus* Bonaparte, *Masius* Bonaparte, *Antilophia* Reichenbach, *Chiroxiphia* Cabanis, and *Chiomachaeris* Cabanis. Such characters as modified feathers, crests, color pattern, and tail length have been used as generic characters. It seems quite certain that a re-evaluation of generic limits in this family is justified.

THE GENUS ANAS

The surface-feeding ducks of the cosmopolitan genus *Anas*, as defined by Delacour and Mayr (1945, 1946), comprise 36 species which are restricted mainly to fresh water.

A pattern of pair formation somewhat different from that of preceding groups is found in this genus. Although they are monogamous, pair formation, at least in Northern Hemisphere species, occurs while the birds are in flocks during the fall, winter, and early spring. Mixed flocks of both sexes, and often of several species, congregate on the wintering ponds or lakes. Beginning as early as September, in the Mallard (*A. platyrhynchos*), the drakes perform the "courtship" displays which are associated with the formation of pairs. Sexual selection under these circumstances should be of considerable importance although possibly not as intense as in the polygamous lek groups.

In most Northern Hemisphere species there is strongly marked sexual dimorphism in plumage color and pattern but in many Southern Hemisphere species, and in all solitary forms on the smaller islands, there is little or no sexual dimorphism. The plumage patterns and colors of the females of Northern Hemisphere species tend to be composed of mottled browns, grays, black, and white which produce a cryptic pattern. The survival value of such coloration to a ground-nesting bird is obvious and has undoubtedly evolved under the selection pressure provided by predation. Only the females, as a rule, incubate and care for the young. In most species the males desert their mates when the clutch is partly complete.

In all species of *Anas* there are two molts each year. In some species the pre-nuptial molt occurs within a month or two following the post-nuptial molt. The winter plumage, which is assumed between these two molts, resembles the female plumage and is com-

monly designated the "eclipse plumage." This brings the males into nuptial plumage in the fall when pair formation begins. It seems clear that sexual selection has been an important factor in the evolution of this molt schedule.

There is fairly good evidence that the isolating mechanisms between sympatric species of *Anas* depend, at least in part, upon the female's instinctive "choice" of a male of her own species. This "choice" must depend upon innate responses because the males leave their mates before the eggs hatch, thus removing the possibility that "imprinting," or other primitive learning processes, could offer a method by which the females could learn to recognize males of their own species through early contact with their own male parent. It is likely that the combination of colors, sounds and displays (Heinroth, 1911; Lorenz, 1941, 1951) provide the basis for this innate recognition system. Males will court the females of any species. Seitz (1948) has described a similar situation in certain cichlid fishes. The males of *Tilapia heudeloti* and *T. natalensis* will direct courtship displays at the females of either species. The females, however, normally will pair only with a male of their own species. The females apparently discriminate instinctively between males on the basis of color and display movements.

Interspecific hybrids are well known in *Anas*. Their frequency and occurrence will be noted under the geographic groups of species which will follow. It will become apparent that hybrids occur with the greatest frequency between species which have a high degree of sexual dimorphism and that, on islands occupied by a single species, sexual dimorphism is reduced or absent. Where one species occurs alone the selection pressure of hybridization is absent but, presumably, sexual selection should still operate to increase sexual dimorphism. This might be interpreted to mean that the non-migratory island birds form lasting pair bonds and hence sexual selection is not sufficiently important to produce sexual dimorphism. However, at least one continental Nearctic species, the Black Duck (*A. fulvigula*), is migratory and shows a very low degree of sexual dimorphism. The correlation between lack of related sympatric species and reduction of sexual dimorphism seems to apply to the Black Duck as to the island forms. Until recently, and due to man-made habitat disturbances, the Black Duck, except for local contact with the Blue-winged Teal (*Anas discors*) was not sympatric with other species of *Anas*. The evidence thus suggests that, in *Anas*, male plumage characters function importantly as the basis of recognition by the females and are, therefore, functional as isolating mechanisms. The relative roles of sexual selection and hybridization in the evolution of plumage characters are not yet entirely clear. More information on pair bond duration in tropical and insular populations should help to clarify this problem.

THE NEARCTIC SPECIES

Nine species of *Anas* occur in North America. They are the Mallard, Pintail (*Anas acuta*), Gadwall (*A. strepera*), Green-winged Teal (*A. crecca*), Shoveller (*A. clypeata*), Blue-winged Teal, Cinnamon Teal (*A. cyanoptera*), Baldpate or American Widgeon (*A. americana*), and the Black Duck. The first eight are sympatric in the western part of the continent.

Plumage characters.—The males of each of the nine Nearctic species differ markedly from one another. The differences are especially striking among the eight widely sympatric species. Colored illustrations of these species are readily available (see Kortright, 1942; Peterson, 1947) so that detailed descriptions seem unnecessary. Since the females all look much alike, the specific characters of the males result in a high order of sexual dimorphism. From the point of view of isolating mechanisms it is important to keep in mind that it is *differences among males of sympatric species* which are significant, not merely the differences between the sexes of each species.

Hybridization.—Figure 4 indicates the extent of natural and captive hybridization among the nine Nearctic species. Captive hybrids are indicated only between species where wild hybrids are not known. Hybrid records are primarily from Phillips (1923), Delacour (1927), Rothschild and Kinnear (1929), Cockrum (1952), and Sibley (1938). Hybrid fertility is high in the crosses indicated in figure 4. The Baldpate forms sterile hybrids with all except the Gadwall. The Gadwall is thus interfertile with all of its sympatric species; the others are fertile *inter se*, except with the Baldpate.

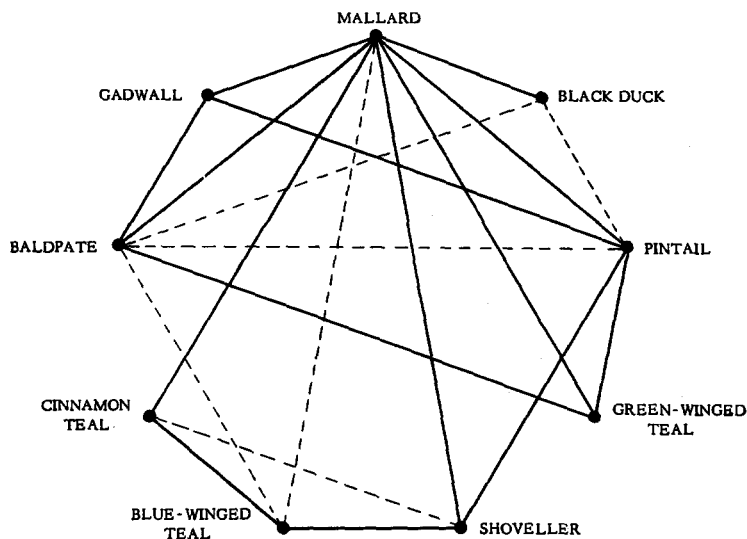


Fig. 4. Hybridization among the Nearctic species of *Anas*. Solid lines connect the parental species of wild-taken hybrids; broken lines connect the parents of hybrids bred in captivity only.

Although many specimens of hybrid ducks have been reported, their incidence is very low when the total annual hunters' kill of waterfowl is considered. Reliable data are difficult to obtain but, as one example, Hochbaum (1944:40) found one hybrid Mallard x Pintail among 1662 Mallards in checking hunters' bags at Delta, Manitoba. This is not a reliable index since hybrid females are seldom detected but it seems safe to assume that hybrid ducks, although among the more frequent natural avian hybrids, are still of uncommon occurrence. This in turn suggests that they are at a selective disadvantage in comparison with the pure parental types, even though fertility is high. Although what follows is only speculation, it may be that one reason for reduced reproductive success in the hybrids lies in the fact that their signal characters, which are utilized in pair formation, are intermediate between those of two species and hence do not "fit" either. In competition for mates the hybrids are thus placed at a disadvantage.

Nuptial display or "courtship."—Under this heading may be included all species-specific activities which, in any way, relate to pair formation. Such activities may function as intraspecific releasers in hostile encounters and also as recognition signals. For example, in most "song birds" (order Passeriformes) the males defend an area of suitable breeding habitat (= "territory") against other males of their own species. Song and

display of species-specific plumage characters and movements function both to repel other males and to attract unmated conspecific females (see Nice, 1941; Lack, 1939; Howard, 1920; Tinbergen, 1951). Tinbergen (1954) lists four functions of "courtship," namely, (1) synchronization of sexual activities in the members of a pair, (2) orientation, such as guidance of female to the song of the male, (3) suppression of non-sexual responses in the partner, such as escape and attack, and (4) reduction of interspecific mating, that is, as an isolating mechanism.

Lorenz (1941, 1951) has described the courtship movements of the males of the Mallard, Pintail, Green-winged Teal, Gadwall, and Shoveller. The displays of the Blue-winged and Cinnamon teals have been under observation by Helen Hays (personal communication). The European Widgeon (*Anas penelope*) is a close relative of the Baldpate and its display movements have been studied by Lorenz. From limited observations of Baldpate display the two appear to be very similar in their courtship movements. The Black Duck seems to be virtually identical to the Mallard in its displays.

When the courtship displays of these species are compared, it is apparent that, among sympatric species, there are differences even though the more closely related groups show strong similarities. The Mallard, Black Duck, Pintail, Gadwall, and Green-winged Teal are alike in many ways but each species (possibly excepting the Black Duck-Mallard combination) differs from the others in one or more patterns of display. The Cinnamon Teal, Blue-winged Teal, and Shoveller are similar to one another and differ widely from the Mallard type. The Baldpate is different from all of the others.

The "eclipse" plumage and time of pair-formation.—In the males of the sexually dimorphic species the plumage which follows the postnuptial molt closely resembles the plumage of the adult female. Thus it is, in general, a mottled brown pattern lacking the specific male signal characters. The flight feathers of the wing are shed simultaneously, leaving the drake flightless until they are regrown. This "eclipse" plumage is retained for periods, varying with the species, of from two to six months. A partial molt (= prenuptial) then occurs and the characteristic male plumage comes in once more. The "eclipse" plumage is thus actually the "winter plumage." What makes it special is that in some species, for example the Mallard, it is retained for only the shortest possible period of time. Thus, the drake Mallard may leave his mate in June, molt into the eclipse plumage in July, then begin the prenuptial molt in early September, regaining his nuptial plumage by October. Courtship displays begin as early as late September, even while the drakes are in the eclipse plumage. Pair bonds in the Mallard are formed by December or January (Kortright, 1942:150; Phillips, 1923:29).

There is considerable variation in the plumage and molt cycles of the males of the nine Nearctic species. The Mallard is the first to begin its courtship in the fall while the Shoveller and Blue-winged Teal do not form pairs until late winter or early spring. The other species are intermediate. Although the differences in the time of pair formation are not always pronounced, they may function as isolating mechanisms and the differences may have been enhanced through selection against hybrids. The only North American *Anas* with which the Mallard has not yet been found to hybridize in the wild is the Blue-winged Teal. The difference in the time of pair formation may be an important factor in preventing these two species from forming wild hybrids for they interbreed readily in captivity.

The "eclipse" plumage is thus simply the winter plumage which has been reduced in its duration. This has been accomplished by the shift in the occurrence of the prenuptial molt from the normal time in the spring back, in some species, to the early fall. The source of selection pressure is associated with the necessity for the drakes to be in nuptial plumage at the time of pair formation. Stresemann (1940:315) has commented

on this aspect of the plumage cycle in *Anas*. As previously noted sexual selection would tend to favor the males which regained their nuptial plumage first and would act to shift the time of the prenuptial molt. Selection against mixed pairings would tend to do the same thing since species recognition seems to depend upon the nuptial plumage characters of the males. An additional advantage is secured by the lengthening of the pair-formation period since more time is available in which to correct the mistake if mixed pairs are formed. The simultaneous shedding of the flight feathers is a mechanism which speeds up the molt cycle and returns the drakes to nuptial plumage as soon as possible. Flightlessness is not selected against since, being aquatic, the drakes are able to feed and escape from predators in the water. The desertion of his mate before the hatching of the clutch allows the drake more time to molt and, in addition, removes the non-cryptically colored drake from association with the vulnerable incubating female and flightless downy young.

ISOLATING MECHANISMS IN ANAS

It has been suggested that specific differences in (1) male plumage characters, (2) courtship display movement, and (3) the timing of the pair-formation period may function as interspecific isolating mechanisms in the sympatric Nearctic species of *Anas*. Proof of the function of plumage characters is to be sought where the hypothetical factor producing species differences is absent, namely, where only one species occurs, thus removing the selection pressure of hybridization.

In the Hawaiian Islands and on Laysan Island there occur subspecies of the Mallard. On Kerguelen Island and Crozet Island there are resident subspecies of the Pintail. The Mallards and Pintails of North America, Europe, and Asia are sexually dimorphic but in these solitary insular races the males have lost their distinctive plumage characters and both sexes have the female type of plumage. Thus, it appears that when the selection pressure afforded by the disadvantages of hybridization is removed, both sexes are able to take advantage of the selective factors producing cryptic coloration. In sympatric groups, therefore, the males are impinged upon by at least two sources of plumage-pattern-determining selection. One is predation, the other is hybridization. The first is direct, the second is via the instinctive "choice" mechanism of the female. Thus, when the female need not choose, there being no closely related sympatric species, she cannot make a mistake; the selective pressure of hybridization (interspecific responses) is removed and the male becomes cryptically colored or "feminine" under the still present and now unimpeded selection pressure from visual predators.

Mayr (1942:49, 261) has called attention to several similar situations in other insular species of birds. For example, on Rennell Island and Norfolk Island the widespread and geographically variable Whistler (*Pachycephala pectoralis*), which is usually sexually dimorphic, has evolved "feminine" races. As Mayr notes, such situations occur only where no similar species exist. The identity of the interacting species in this instance has not been determined. There is no way to predict how it will look or sound, except that it must be different from the species which it affects by its presence. Its identity may be revealed by a study of the species which are present or absent on various islands in relation to the distribution of the "feminine" races. Lack (1945:62-63) cites other examples.

Vaurie (1951) has described an interesting situation which illustrates this same principle. *Sitta neumayer* and *Sitta tephronota* are rock nuthatches occurring in southwestern Asia. Each species has a large distribution and over most of the ranges they are allopatric. At the extremes of their respective ranges, where each is far removed from the other, the two are remarkably similar in facial markings and bill size. In one region

the two species are sympatric. In this area of sympatry each has diverged, in opposite ways, from the similar pattern they possess when allopatric. One has developed a black facial "mask," in the other the facial area has become paler. The bill size is similar in the allopatric forms but in the area of overlap one has evolved a larger bill and the other a smaller bill. The facial markings apparently function in species recognition; the difference in bill size is advantageous in reducing competition for food.

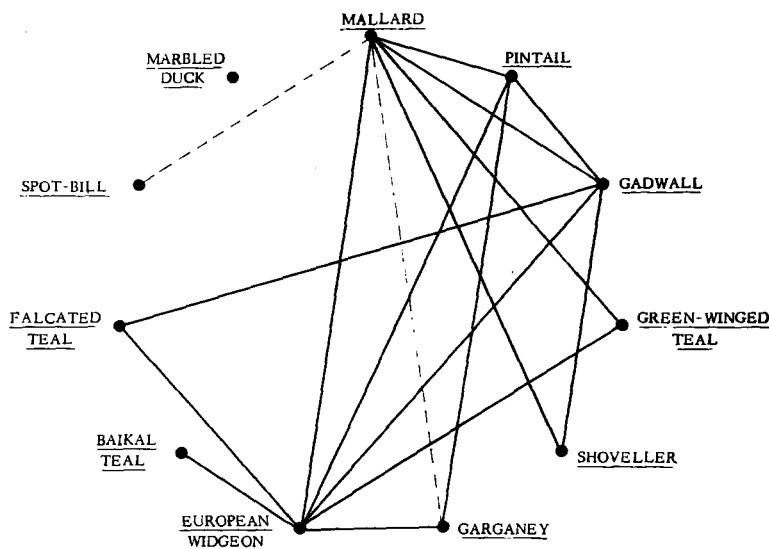


Fig. 5. Hybridization among the Palearctic species of *Anas*. Solid lines connect the parental species of wild-taken hybrids; broken lines connect the parents of hybrids bred in captivity only.

There is no direct evidence to prove that "courtship" movements function as isolating mechanisms. The fact that they vary specifically in sympatric groups of species suggests that they do so. However, the fact that they are most similar in the most closely related species such as Mallard, Pintail, Gadwall, Cinnamon Teal, Blue-winged Teal, and Shoveller suggests that the movements *per se* may function importantly in hostile responses between males and that the patterns of color and structure revealed or brought into prominence by the movements are more important as isolating mechanisms. The timing of pair formation, in its role as an isolating mechanism, has been discussed previously.

Palearctic species.—In the Palearctic there occur 11 species of *Anas*. Figure 5 indicates the known occurrence of hybrids. As in the Nearctic species the male plumages and nuptial displays are species-specific and the timing of pair formation is variable. The Mallard is the earliest in forming pairs and the Garganey (*A. querquedula*), a close relative of the Blue-winged Teal, is the latest. It appears that the Palearctic group of sympatric species is similar with respect to isolating mechanisms to the Nearctic group.

Southern-hemisphere species.—In the course of this study the South American, African, and Australasian species of *Anas* were investigated. Information on many aspects

of the problem is lacking and, from some areas, reports are conflicting. It is, therefore, difficult to assess the significance of variational patterns but several items are of interest.

In many species in South America and Africa there is a tendency for sexual dimorphism to be slight or lacking. If our premises are correct this condition may indicate that both interspecific reactions (hybridization) and intraspecific reactions (sexual selection) are reduced in intensity. Such reduction in these sources of selection could be achieved by an increase in the degree of ecological isolation among seemingly sympatric species and in the establishment of a permanent pair bond. Skutch (1940:502) has suggested that the existence of permanent pair bonds in tropical species may account for the reduction in sexual dimorphism in some instances. There seems to be no proof that this is a factor affecting tropical species of *Anas* but, at least in non-migratory species, pairs may remain together more than in the strongly migratory Holarctic species. Information on this problem is needed.

South American species.—The nine species of *Anas* in South America are the Bronze-winged Duck (*A. specularis*), Versicolor Teal (*A. versicolor*), Bahama Duck (*A. bahamensis*), South American Pintail (*A. georgica*), Yellow-billed Teal (*A. flavirostris*), Chiloe Widgeon (*A. sibilatrix*), Cinnamon Teal (*A. cyanoptera*), South American Shoveller (*A. platalea*), and the Ringed Teal (*A. leucophrys*). Two species (*specularis* and *leucophrys*) are somewhat aberrant; the other seven are typical *Anas*.

Each of the nine species overlaps with one or more of the others in some portion of its range. As many as eight species occur sympatrically in certain parts of the continent.

The information on wild hybrids is extremely meagre. The only record is of a Bahama Duck x South American Pintail (Phillips, 1923:338) taken near Buenos Aires in 1914. Hybrids between the similar species might well go undetected and the paucity of informed hunters, "bag checks" by game wardens, and other factors which act to bring hybrids to the attention of scientists in North America make it likely that this is not a ratio comparable to that for North America.

In captivity the following hybrids have been recorded. Versicolor Teal x Baikal Teal; Bahama Duck x Mallard; Bahama Duck x Brazilian Teal (*Amazonetta brasiliensis*); Bahama Duck x South American Pintail; South American Pintail x Wood Duck (*Aix sponsa*); Yellow-billed Teal x Mallard; Yellow-billed Teal x Chestnut-breasted Teal (*Anas castanea*); Chiloe Widgeon x Mallard; Chiloe Widgeon x European Widgeon; Chiloe Widgeon x Wood Duck; Ringed Teal x Brazilian Teal.

These hybrids indicate that at least these six species are capable of forming mixed pairs under certain conditions. The Cinnamon Teal of South America may be assumed to be similar to the North American populations in this respect, making seven of the nine South American *Anas* which have been known to form hybrids with some other species.

The Cinnamon Teal, South American Shoveller, and Ringed Teal are strongly sexually dimorphic. In the Chiloe Widgeon and Bronze-winged Duck both sexes are brightly colored. The other four species exhibit a tendency toward reduction of sexual dimorphism, the males being less, the females more, brightly colored than in most Northern Hemisphere species. The Bahama Duck and the Versicolor Teal are similar in color pattern but differ greatly in body size and bill color. The South American Pintail resembles the Yellow-billed Teal in coloration but Lorenz has found that the courtship movements are extremely different in the two. The display of the Versicolor Teal has not been studied but that of the Bahama Duck includes the most highly specific "head-up-tail-up" movement of any of the species of *Anas* which have been investigated.

Solitary insular forms again provide evidence of the loss of signal characters in isolated species. In the Galapagos Islands subspecies of the Bahama Duck (*A. b. galapag-*

ensis) and the South Georgia Island race of the South American Pintail (*A. g. georgica*), the species-specific markings are reduced as compared with the mainland populations. The Galapagos Bahama Duck has the white facial area reduced in size and brightness and the South Georgia Pintail has a gray bill in marked contrast to the bright yellow bill of the continental races. They thus exhibit the same tendency toward a "feminine" coloration as in the Hawaiian Mallard, Kerguelen Pintail, and others. This is interpreted as evidence that these characters function as "recognition signals" and hence are isolating mechanisms in areas of sympatry with close relatives.

African species.—In Africa the genus *Anas* is found primarily in the southern and eastern portions of the continent. The species are the Cape Teal (*A. capensis*), Hottentot Teal (*A. punctata*), Red-billed Duck (*A. erythrorhyncha*), Madagascan Teal (*A. bernieri*), Meller Duck (*A. melleri*), Yellow-billed Duck (*A. undulata*), African Black Duck (*A. sparsa*), and the Cape Shoveller (*A. smithi*). Two species (*bernieri* and *melleri*) are confined to Madagascar and two others (*punctata* and *erythrorhyncha*) occur both on the mainland and on Madagascar. The other four species occur only on the mainland. Thus there are four species on Madagascar and six on the mainland.

The tendency for sexual dimorphism to be reduced is extremely pronounced. The Cape Shoveller is the only African species which is dimorphic and it is but weakly so. The other species show no important degree of difference between the sexes in plumage color or pattern and all tend toward a cryptic plumage pattern.

In Africa not more than six species may be sympatric. Of these the African Black Duck is a solitary stream-dwelling species which is thus ecologically well separated from its congeners. The other five species are separable from one another by plumage patterns but to a lesser degree than in the males of Holarctic species. There is, however, apparently a tendency for these species to segregate ecologically to a greater degree than do the Holarctic sexually dimorphic species. Phillips indicates that the Cape Teal is partial to the larger lakes, the Hottentot Teal is most common in the mountains, the Red-billed Duck inhabits swamps and rushy pools, and the Yellow-billed Duck is most abundant on lakes and rivers in open country.

Thus, in comparison with the Holarctic species, there are in Africa fewer sympatric species and these are to some degree isolated ecologically from one another. These factors act to reduce the opportunity for the formation of mixed pairs. This in turn has apparently reduced the pressure of selection from this factor and permitted the various species to respond to the forces of selection producing concealing patterns of color. The result is a group of species with a tendency toward a plumage type in both sexes such as is found in the females of Northern Hemisphere species and which reaches its extreme development in insular species where no congeners are present. Information on the duration of pair bonds is not available.

No wild-taken hybrids have been recorded. In captivity the Meller Duck x Mallard produced fertile offspring (Phillips, 1923:128). The Yellow-billed Duck has been crossed with Mallard, Red-billed Duck, North American Black Duck, and Spot-billed Duck (*A. poecilorhyncha*). A female African Black Duck in the London Zoo formed a pair with a Spot-bill but reared no young (Delacour, *in litt.*).

Lorenz has studied the Meller Duck and the Red-billed Duck. The Meller Duck is extremely similar to Mallards but more pugnacious. It is of interest that in this sexually monomorphic species, females are especially prone to mate with drakes of other species in captivity, even when their own drakes are present. This, as Lorenz (1951) points out, is certainly connected with the lack of a distinctive male plumage. The females of this insular species, which presumably evolved as an isolated population of ancestral Mallard stock, apparently have their pair-formation responses adjusted pri-

marily for patterns of movement. It may be that the strong colors and patterns of Holarctic drakes function as "supernormal releasers" (Tinbergen, 1951), that is, they stimulate the innate responses of the females more strongly than the "normal" releasers contained in the plumage patterns of drakes of their own species.

There are additional situations in *Anas* which merit attention but these few will serve to illustrate some of the aspects of the problem. Information about Australasian species is difficult to assess. Perhaps resident ornithologists in that region will know of situations which parallel those noted herein.

DISCUSSION

The examples which have been cited were chosen to illustrate groups in which sexual dimorphism is present, hybrids are occasional, polygamy is usually present, and genera are often based on male signal characters. These various conditions do not invariably accompany one another and, to be complete, such groups as the sunbirds (Nectariniidae), wood warblers (Parulidae), and tanagers (Thraupinae) should be considered. In these sexual dimorphism is often pronounced but monogamy is the rule and the males tend to participate in brood care, although not in incubation. It is obvious that other sources of selection, possibly associated with inter-male competition for territories, are important.

I have tried to show why, at the generic level, taxonomists have tended to oversplit groups with a high degree of sexual dimorphism in visible characters. The opposite effect is demonstrable in groups having little or no sexual dimorphism in such characters. In birds which are nocturnal, or which live in dense cover, visual signals are of less value while sounds become more so. In such groups there is a tendency to evolve highly specific songs or calls but to reduce the specific diversity in plumage characters. This is reflected at the generic level by a decrease in the number of monotypic genera and an increase in the number of species per genus in such groups. The following are examples.

The owls (Strigidae), which seem to utilize sound more than sight in species and sexual recognition, have 27 genera for 123 species (4.5 species per genus). The goat-suckers (Caprimulgidae) have 19 genera and 67 species (3.5 species per genus). The genus *Caprimulgus* alone contains 39 species. The ant-thrushes (Formicariidae) are mostly thicket-dwelling birds; the family contains 221 species in 53 genera (4.2 species per genus). The wrens (Troglodytidae) with 16 genera and 63 species (4.0 species per genus) are also a group which apparently utilizes sound more than sight in species recognition.

In comparison consider the number of species per genus in the following groups: Hummingbirds (Trochilidae), 2.6 species per genus; grouse (Tetraonidae), 1.6 species per genus; manakins (Pipridae), 3.0 species per genus; and birds of paradise (Paradisidae), 2.4 species per genus. These data are derived from Peters (1945), Hellmayr (1929), and Mayr and Amadon (1951).

In the Anatidae, Peters (1931) recognized 62 genera for 167 species (2.7 species per genus). In their revision of the Anatidae, Delacour and Mayr (1945) reduced the genera to 40 and the species to 144 (3.6 species per genus). In the process a considerable number of "intergeneric" hybrids became intrageneric.

SUMMARY

The process of speciation is accomplished through the accumulation of genetic differences in spatially isolated populations. If intrinsic isolating mechanisms evolve before the extrinsic barriers break down, the secondarily rejoined populations can exist in sympatry as good species. If the extrinsic barrier fails before intrinsic barriers are fully established the resulting hybridization will have different effects, depending upon the relative biological success of the hybrids. If the hybrids are not at a selective disadvan-

tage compared with the parental populations, the result will be introgression leading to ultimate swamping and, following a period of increased variability, a new adaptive peak will become established.

If the hybrids are selected against, they function as a selective force against the individuals of both parental populations which enter into hybrid pairs. Any mechanism which reduces the incidence of mixed pairs is thus selected for with the result that, as long as the hybridization continues, the isolating mechanisms of the parental species are reinforced relative to one another. Reinforcement ceases when interspecific reactions relative to pair formation cease. This may be some time after hybrids are no longer produced.

The reinforcement of isolating mechanisms in animals which utilize visual signal characters in pair formation results in the enhancement of visible structures and associated behavior patterns. Birds are especially fine subjects for study in this connection. In most birds the females instinctively "choose" males of their own species as mates. The choice mechanism depends upon the stimulation of the innate releasing mechanisms of the females by the species-specific signal characters ("releasers") of males of their own species. It is these signal characters, or isolating mechanisms, which are enhanced by the reinforcement which occurs when interspecific hybrids are selected against.

In groups of closely related species where hybridization occurs, but is selected against, the males develop "exaggerated" signal characters. In certain instances the males of insular populations, which occur in isolation from any closely related interacting species, have lost their signal characters and become "feminine." This is due to the fact that the females cannot make a mistake in mate choice, there being only one species present, and thus the selective effects of hybridization are removed.

A second source of selection which increases the development of signal characters is derived from the competition for mates. This "sexual selection" is an intraspecific phenomenon and is especially important in polygamous species. Since only the secondary sexual characters of the males (in most groups) are affected, the result is an increase in sexual dimorphism. The males of related species tend to diverge rapidly while the females remain similar. Secondary contacts between such pairs of species may result in hybridization because the degree of relationship is actually very close.

The high incidence of monotypic genera in groups of sexually dimorphic visual animals is due to erroneous human evaluation of the taxonomic value of signal characters. Morphological structures evolved under the selection pressure of deleterious hybridization and/or sexual selection seem highly "specialized" to the intelligent discrimination of the human taxonomist who therefore accords them generic rank on a "degree of difference" basis. This is a coincidental result of the fact that we too are visual animals and hence can and do utilize visible characters in taxonomy. It is significant that "intergeneric" hybrids are found almost exclusively in visual animals, principally birds and, to some extent, fish. It is apparent that genera in such groups should not be based only upon secondary sexual characters nor upon characters which have been reinforced by selection against hybrids since these, inevitably, are *species* characters.

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Department of Conservation, Cornell University, Ithaca, New York, December 31, 1956.