

V. ISOLATING MECHANISMS

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In the first article of this series, What is a Bird Species? (BIRD OBSERVER, Vol. 1, No. 5, pp. 104-108), a species was defined as "an evolved or irreversibly evolving aggregate of natural populations, actually or potentially freely interbreeding, genotypically distinctive as a group, and reproductively isolated from all other species." The mechanisms which serve to isolate a species reproductively are the subject of the present article; they have been known since 1937 as isolating mechanisms.

That there is a whole set of special devices, both physiological and behavioral, by which the gap between closely related species is maintained was not at first realized by biologists. Charles Darwin considered the species to be a conceptual construct, arbitrarily delimited, and he consequently neglected the question of the nature and origin of the species gap. Later biologists likewise ignored the problem, or else over-simplified it considerably by assuming that reproductive isolation was synonymous with cross-sterility. Toward the beginning of the twentieth century, however, naturalists began to realize that there were a great many mechanisms other than cross-sterility which tended to prevent the interbreeding of closely related sympatric species.¹ These mechanisms invariably have at least a partially genetic basis, although certain components may be affected by forms of conditioning (especially imprinting).

It is important to realize that each species maintains a whole spectrum of such factors---ecological, behavioral, and physiological---which safeguard its species identity. Interbreeding is prevented, as it were, by a series of hurdles, of which one may be dominant and the others subsidiary. The cross-sterility barrier, when present, is by definition quite effective. Yet it is usually a subsidiary mechanism, for it is rarely tested. Of what importance is it that Cardinals may be cross-sterile with Gray Catbirds, if in fact neither species can be induced to try to mate with the other?

Conversely, cross-fertility is no proof of a common species identity. As Mayr (1963: 90) says,

"the mallard, Anas platyrhynchos, and the pintail, Anas acuta, are perhaps the two most common fresh-water ducks of the Northern Hemisphere. The total world population of these two species may well exceed 100,000,000 individuals...[In] captivity these two species are fully fertile with each other and...there is no reduction of fertility in the F_1 , F_2 , or F_3 , or in any of the backcrosses.² One would therefore expect a complete interbreeding of these species in nature, as their world breeding ranges largely coincide. In northern Europe, Asia, and North America they nest side by side on literally millions of ponds, sloughs, or creeks; yet the number of hybrids found among the many birds shot every year is on the order of one in several thousand. Nor is there evidence of backcrossing between these hybrids and the parent species. Obviously, then, the two species are being kept apart not by a sterility barrier but by some other factors."

Before beginning the investigation of isolating mechanisms in detail, it is important to point out that geographical isolation is NOT considered an isolating device. This may seem paradoxical at first, for surely it must be of significance in understanding why American and European Robins do not interbreed to note that they never occur together, never meet. To the biologist, however, geographical separation is too ephemeral a condition, too extraneous a factor, to be considered a candidate for inclusion in the list of isolating mechanisms. The argument is best made, perhaps, by analogy: Life-term inmates of a penitentiary are quite effectively segregated spatially from the other members of the human species and are thus reproductively isolated. Yet none of us would think of arguing that these individuals constitute a separate species. Again, toy poodles are usually forcibly segregated from other house dogs in breeding condition by pedigree-conscious breeders. They do not form a separate species either. Or again, the San Lucas Robin breeds in an area which is totally disjunct from the breeding range of the other American Robins; it is regarded as a geographical subspecies of the American Robin, not as a separate species.

It is precisely to emphasize the irrelevance of this particular complication (geographical isolation) that isolating mechanisms are currently defined as "biological properties of individuals which prevent the interbreeding of populations that are actually or potentially sympatric." (Mayr, 1963: 91--*Italics mine.*)

What then does constitute a legitimate isolating mechanism in the eyes of the biologist? I shall not take up the various devices in order of strength or effectiveness, for this may vary from species to species. Rather, following the analogy of the sequence of hurdles used above, I shall discuss these various mechanisms in the order in which they would occur as part of the breeding cycle.

A. Factors limiting all contact: Habitat isolation

Among the more sedentary lower animals, habitat isolation can be a most effective isolating mechanism. Edaphic isolation, or the adaptation of a species to a particular soil substrate coloration is one of its more exotic forms. Certain grasshoppers, for example, acquire a coloration which conceals the adult on certain soils. An individual passively transported to a differently colored substrate becomes very agitated until he can find another background with which he can harmonize. Needless to say, it is quite unlikely that individuals from two distinct soil substrata would ever hybridize.

This same color-consciousness seems to be characteristic of certain South African larks. Reddish-colored larks (such as the Fawn-coloured Lark, *Mirafra africanoides*)³ alight consistently on the redder sands, such as are to be found in the Kalahari Desert. These birds cannot be chased onto or over darker soils. Conversely, the darker-backed Small-billed Sabota Lark (*Mirafra sabota*)³ flies above and rests on the darker, humus-rich soils exclusively. Since both species are ground-nesting birds, they clearly will not interbreed even in those areas where the two soil types meet along an edge. (Mayr, 1963: 570)

Habitat selection among birds is more commonly a question of vegetation. Birds of the forest will typically not intermingle with species of the open grasslands, even in those places where the forest forms an edge with the more open area. Many avian species are associated with vegetation of a certain height, with the presence of a particular species of plant (e.g., cattails), or with the presence or absence of standing water, etc. Some species require a certain vertical contour to the terrain if they are to find the habitat acceptable. Peregrine Falcons nest exclusively on cliff ledges or on the window ledges of skyscrapers, except for a few of the more remote subspecies inhabiting desert areas or parts of the northern tundra. (Brown and Amadon, 1968: 854)

Neal Smith (1966) found that Glaucous and Kumlien's Gulls preferred to nest "in coastal colonies, usually on cliffs overlooking tidal inlets. Herring Gulls predominated in tundra valleys and flat, marshy regions where they nested on islets in lakes." Glaucous Gulls preferred ledges with greater surface area; Kumlien's utilized the smaller ledges.

A pair of species, each associated with a distinct, albeit neighboring, habitat, will remain reproductively isolated so long as these two habitats remain undisturbed; but therein lies the rub. For man has a great propensity for disturbing natural habitats and for producing new ecosystems of a somewhat more intermediate nature. In so doing, he often affects the bird populations inhabiting the given area. Most frequently, this results in the complete substitution of one set of species for another. Occasionally, however, two or more species which originally preferred distinct habitats both remain, each adapting to the new intermediate habitat and, in the process, coming into contact with each other. Several cases of this sort which have resulted in hybridization between species are discussed below.

B. Factors limiting breeding contact: Seasonal isolation.

Unlike humans, who are sexually willing and able year round, birds have a definite annual reproductive cycle, and each species has its own more or less well-defined breeding period. What better mechanism can there be for preventing interbreeding between species than a lack of synchronization in the periods of peak sexual activity? Indeed, in most multi-species colonies that have been studied carefully, ornithologists have found differences between the respective peak egg-laying periods of the co-resident species. Smith (1966) found, for example, that on Baffin Island, Glaucous Gulls initiated copulations on May 15 with the peak frequency occurring on May 27. Kumlien's Gulls mated between May 23 and June 4, and Herring Gulls copulated first on June 5.

In spite of evidence of this sort, however, Smith and other authorities feel that seasonal isolation is not in and of itself a strong isolating mechanism. There are

several reasons for this opinion:

1. Sharply delimited non-overlapping breeding periods among co-resident species are characteristic principally of colonial nesters. They apparently serve mainly to reduce competition for vital resources (e.g., for food for the chicks). In nearby colonies, if one of the competitive species is lacking, the breeding period of one of the other species will be extended. In colonies where Thayer's Gull and the Herring Gull both nest, Thayer's Gull finishes mating before the Herring Gull starts; in colonies of Thayer's Gull which contain no nesting Herring Gulls, the egg-laying period extends throughout the period utilized elsewhere exclusively by Herring Gulls.

2. Northern European species introduced into Australia promptly shifted their reproductive cycles by six months in order to re-coordinate their breeding with the onset of spring in the Southern Hemisphere. In most of these species, the shift was surely completely involuntary, for the reproductive cycle in birds is closely tied to the lengthening of the daylight hours in the spring. In this sense, these birds would have little "choice" as to when they would breed, and distinct species might well continue to have separate and non-overlapping breeding periods.

The deterministic nature of the "choice" of breeding period is well documented for a few species. Lowery (1974, p. 127) points out that Brown Pelicans transplanted from Florida to Louisiana have a high nesting mortality because they have brought with them the annual rhythm of their ancestors, and thus nest at a season inappropriate to their new home. At the other extreme, however, are those species (such as our cuckoos) which are opportunistic breeders, waiting to nest until they find conditions precisely suited to the raising of their young. (Cuckoos often wait for an outbreak of caterpillars.)

The consensus seems to be that most species can delay the breeding period when forced to do so by inclement weather or other external factors. Since reproduction has at least this modest flexibility to it, authorities feel that seasonal isolation is important only as a secondary mechanism. Seasonal isolation serves to enhance the isolating effect of the other devices, but for most species it is too weak a characteristic to prevent hybridization by itself.

There seems to be one major exception to this rule, however: seasonal isolating factors are particularly potent when they arise in conjunction with factors having to do with water temperature. For instance, the six members of the whale bird genus Pachyptila have breeding ranges in the Southern Hemisphere which are arranged in concentric circumpolar rings. Mayr (1964: 251-252) says, "Different subspecies of the same species in this genus are always found...in the same hydrological zones. But once a population becomes adapted to a new zone of ocean water, it adopts a new mode of life, including a different breeding season, and becomes permanently separated."

C. Morphological species-recognition factors

The importance of color and color pattern in the reproductive life of visual animals has been recognized since antiquity. Red-winged Blackbirds raise their flashy epaulets during courtship. Female redwings discriminate against males whose epaulets have been dyed black. Gulls, as a group, seem particularly conscious of the color of the eye-ring of any potential mate. Females will not mate with a male having an eye-ring of the wrong color (BIRD OBSERVER, Vol. 1, No. 5, p. 126). Ross' Goose probably identifies conspecifics by the contour of the feathers about the upper mandible.

Since a large portion of the bird brain is given over to visual centers, it is not surprising that individual female birds should rely heavily on the visual appearance of the male to identify prospective mates correctly. The bright nuptial plumages of the male bird are already well-known to us birders, who also have a well-developed sense of sight, and we need no further convincing that the visual patterning of the male spring bird may well serve the female as her primary means of identifying conspecifics. A few side comments on these plumages, however, may be of interest:

1. Visual stimuli usually work in conjunction with auditory identification clues among birds. Naturalists have at times suggested that when visual stimuli are predominant and well-developed, the other stimuli tend to be less well-developed; but this generalization admits of far too many exceptions to be useful. Cardinal-grosbeaks, New and Old World orioles and many cardueline finches are both beautiful to see and lovely

to hear. Conversely, Henslow's Sparrow is totally insignificant in song and in appearance.

2. A more accurate generalization is this: brightly-colored males do not as a rule take any part in the nesting activities. But this is putting the cart before the horse. Stated more accurately, elaborate plumages, gaudy coloration and other striking forms of "sexual dimorphism have evolved in birds usually only in species in which the male does not participate in the raising of the young, and consequently does not endanger his brood by his conspicuous presence." (Mayr, 1963: 108)

3. Among phalaropes, all of which practice sex role reversal with a vengeance, it is the female that is gaudily colored. It is she who actively courts the male until he is ready to mate, and, true to the above generalization, it is the dull-colored male alone that attends to all of the nesting duties, while the sporty female cavorts in the harbor with the drake ducks.

4. Among those species which mate promiscuously without the formation of a pair-bond, striking male plumages are the rule. The Ruff, hummingbirds, pheasants, grouse, manakins and birds of paradise all fall into this category. Hummingbird species have developed highly distinctive pendulum aerial displays which serve to identify the male's species to the female (and to us). Ruffs, pheasants and birds of paradise, on the other hand, utilize an unusual mating procedure. Males of these species assemble on a lek, or display ground, to perform pre-mating rituals. The female is attracted to these leks, and mating takes place there after the shortest of acquaintances. Obviously, a distinctively colored male is of high selective value in such species, and the color patterning in these groups is quite remarkable.

It is the reliance of the female on visual clues that results in this strange evolutionary development. Apparently she is attracted not only to males of the proper coloration, but more specifically to that male who is the gaudiest and most elaborately plumaged of the group. Since mating is promiscuous, it is this male who stands the best chance of impregnating the greatest number of females, and it is his genes that will be passed on to the majority of his population's offspring. As Mayr (1963: 199) says, "This is the reason for the almost absurd ornaments of the males in many of those bird groups in which a single male may fertilize many females."

5. Quite surprisingly, certain species in which the male is quite distinctively colored have developed races in which this coloration is lost. Mayr (1964: 48-50) cites "the species Petroica multicolor [a flycatcher]. This Australian species has colonized many of the South Sea Islands, where it occurs in thirteen races... Normal sexual dimorphism characterizes the Australian parent race and eight races of the South Seas. In two places, however, the males have lost their bright plumage and wear a feminine one, while on San Cristobal in the Solomon Islands and in Samoa the females have become masculine and wear a plumage which resembles that of the male... It is important to emphasize the fact that loss of sexual dimorphism through feminization of the male plumage seems to develop only in well-isolated and rather small populations... It might also be mentioned that such a breakdown of the male nuptial plumage seems to occur only in localities where no other similar species exists, i.e., where a highly specific male plumage is not needed as a biological isolating mechanism between two similar species."

D. Auditory species-recognition factors

Among birds the two most strongly developed senses are sight and hearing. So it is not surprising that most bird species have developed songs which are quite distinctive. In fact, in certain families (for example, Tyrant Flycatchers, the species of which are extraordinarily similar in appearance), the nature of the territorial song constitutes the diagnostic field mark par excellence. Apparently, the female of many species is just as reliant on auditory clues as we are. Ornithologists believe that she will not mate with a male who does not sing her the correct song. This belief is, however, currently under investigation and revision. Bird-song constitutes the first and most important category of behavior which may serve as an isolating mechanism, and all such ethological patterns are difficult to analyze or assess, for they are usually multivalent in their signification. The territorial song of the Red-winged Blackbird has, for example, at least three major functions:

- 1) It identifies the singer as a Red-winged Blackbird.
- 2) It identifies the singer as a male.

- 3) It advertises the singer as a holder of a breeding territory.

Each of these functions is also served by other clues. The red epaulets serve for species-recognition, and certain aggressive behavioral patterns would identify the individual as a territorial male. Recent experiments seem to suggest that the female uses all available information to recognize the male of her own species, and no one datum functions pre-emptively. (She will mate with a male lacking red wing patches if he sings correctly, or with a male unable to sing if he has the correct wing pattern and maintains a territory.) On the other hand, females of other species fail to respond to males having either the Red-winged Blackbird visual pattern or song. Both coloration and song function, therefore, as isolating mechanisms.

E. Non-auditory ethological isolating mechanisms

The males of every bird species have specific courtships or displays to which usually only females of the same species are receptive. Isolating mechanisms that are based on behavioral incompatibilities are now referred to as ethological barriers. Mayr (1963:95) describes them thus:

"In most animals it is the male that actively searches for a mate. He is usually somewhat easily stimulated to display to objects, sometimes quite inappropriately. When he does not receive adequate responses from his display partner, or is actively repulsed, his display drive soon becomes exhausted. Consequently, if such a displaying male encounters an individual of a different species, or a male of his own species, he will break off his courtship sooner or later. If the male is displaying to a nonreceptive female, the same will happen, perhaps after a longer interval. However, if the male encounters a receptive female of his own species, he will be sufficiently stimulated by her to continue his displays until the female has passed the threshold of mating readiness. This threshold is on the average much higher in females than in males. 'Species recognition,' then, is simply the exchange of appropriate stimuli between male and female, to insure the mating of conspecific individuals and to prevent hybridization of individuals belonging to different species."

It is these ethological mechanisms which account for the extreme rarity of hybridization in those species which form a pair-bond. After all, pair-bonding is, in essence, an extended "engagement" period during which mutual behavioral incompatibilities are almost sure to surface. Species that do not pair-bond are far more subject to interbreeding. Females have less of an opportunity to "recognize" the species of the prospective mate, and "mistakes" are made. Mayr (1963: 126) estimates that there were as many as 50 hybrids among the 100,000 specimens of the birds of paradise collected in New Guinea during the period 1870-1924.

Ornithologists are just beginning to study intensively ethological barriers, and, although the literature is vast and rapidly growing, many species have yet to come under scrutiny. Here are a few examples to illustrate some of the variety of the patterns which have been observed:

1. During courtship, Boat-tailed Grackles (Cassidix major) fluff the feathers of the head and neck, giving them a rather thick-headed appearance. Great-tailed Grackles (C. mexicanus) slick down the feathers of the head, giving them a thin-headed appearance. (Lowery 1974: 547)

2. Laysan Albatrosses almost invariably touch bills when they first come near each other. Black-footed Albatrosses tend to use this gesture later on in the courtship dance, only rarely initially. Blackfoots dance intensely, with much more vigor than Laysans. They dance on tiptoe, whereas Laysans rise on tiptoe only to pose statue-like. Blackfoots elevate both wings simultaneously and only occasionally tuck the bill under the wing as part of the same gesture. If they do bill-tuck, both birds do so at the same time and on opposite sides of their bodies (as if one were the mirror image of the other). Laysans invariably bill-tuck after a wing-lift, and a pair characteristically wing-lift and bill-tuck alternately. Blackfoots clap bills rapidly, both members of the pair performing the motion simultaneously and with the bill held next to the mate's head. A Laysan pair clap bills alternately and with the bill held low, away from the partner's head. (Fisher 1972)

Readers who are interested in courtship displays, many of which will automatically function quite successfully as isolating mechanisms, are urged to consult Palmer (1962), whose descriptions of behavioral patterns are quite modern and thorough.

F. Mechanical Isolation

When insects were first carefully studied under the microscope, it was discovered that the males of many species sported an elaborate genitalic armature, the shape of which was characteristic of that species. It was assumed that it would be mechanically impossible for the male of one species to mate with a female of another species. Biologists coined the term "mechanical isolation" for this situation. Birds have only a most rudimentary copulatory apparatus, and mechanical isolation is thus meaningless for them. (In fact, biologists have since concluded that mechanical isolation is not an important factor among insects either.)

G. Post-mating Mechanisms

Let us consider now a pair of birds for which none of the above isolating mechanisms are effective. So they mate. However, there are still many more hurdles to be surmounted before hybridization can occur:

1. Gametic mortality: the male sperm may die from an antigenic reaction of the female.
2. Gametic impotency: the sperm may fail to penetrate the egg.
3. Zygotic mortality: even if the egg is fertilized and laid, the mebro may not survive.
4. Hybrid inviability: if the embryo does hatch as a chick, this F_1 -individual may not survive to reproductive age.
5. Hybrid sterility: the F_1 -individual may prove to be sterile.

These five forms of reproductive isolation seem to form, as a group, a natural unit in our minds. We speak of any one of them as an instance of cross-sterility. The layman finds it difficult not to believe that the sterility barrier is pre-eminent among isolating devices. He might argue as follows:

1. All five of these forms of reproductive isolation are especially distinguished in that they have a largely genetic basis.
 2. All five are totally effective in their action, at least as described above.
- A great many pre-mating mechanisms admit of exceptions.
3. None of these five isolating devices are subject to human meddling, at least not yet.

In rebuttal to these points let me observe the following:

1. All forms of reproductive isolation among birds have a largely genetic basis. We humans are born with a most meager set of instincts; our attitudes and behavioral patterns are largely acquired through learning and socialization. In this, humans are unique. A bird's behavioral patterns and his habitat preferences are far more likely to be the result of genetic pre-programming. The Alder Flycatcher cannot be taught to sing the song of the Willow Flycatcher. To the female Mallard, the drake Mallard's nuptial plumage is invariably "in style."

2. Quite obviously, in the great preponderance of individual instances, the five isolating devices above are either inoperative or else totally effective. However, we can reach a characterization of the sterility barrier as an on-or-off attribute only by viewing interbreeding as an activity of individual pairs of birds; and this is an incorrect viewpoint. Hybridization is a population phenomenon, not an individual pastime. Between two closely related species, the more usual situation might be this: of every 10,000 attempts at interbreeding, in perhaps 10 cases the fertilized egg will hatch. The unthinking amateur says, "These birds can interbreed, for hybrids have been found; they are the same species." The trained ornithologist says, "These two species are quite effectively isolated reproductively by, say, different habitat preferences and numerous ethological barriers. In addition, zygotic mortality is an isolating mechanism which is 99.9% effective."

3. The behavior of caged birds is irrelevant to the species problem for two reasons. First, this behavior is unnatural and in no way representative of the

behavior of these same individuals in the wild; and second, the population of caged birds normally represents only a very tiny percentage of the total species population. Humans can effectively meddle with only one type of isolating mechanism on the population level --habitat isolation. A few cases of this are discussed in subsequent paragraphs, and the ornithologist does recognize that perhaps 10 times within recorded history, man has jeopardized the species integrity of a pair of closely related species. But this outcome is quite rare. Man's interference with the ecology all too frequently results in the extinction or local extirpation of a species; only in the most exceptional cases does this meddling cause a merging of distinct species.

H. Introgressive Hybridization

We are now ready to consider a few unusual cases in which the isolating mechanisms separating two species are unusually weak, so that interspecific pairs do form on a more regular basis. Before attempting to classify these exceptional situations into different categories, I must digress to point out one well-known and thoroughly studied phenomenon: certain genetic difficulties inherent in interbreeding often remain hidden in the first generation (the F_1 -individuals). Hybrid sterility or inviability, for example, may not show up until the second or third generation. A thorough analysis of a case of hybridization must necessarily, therefore, give prime attention to the progeny of the hybrids. Since F_1 -hybrids are ordinarily fairly rare, the prospective mate of such a bird will quite often be an individual from one of the parent species. Their offspring are referred to as backcrosses.

Many cases of hybridization are known for which backcrossing does not occur, but backcrossing is part of the picture in the more serious cases of hybridization. The importance of the phenomenon lies in the potential for the transmission of a gene from one of the parental species through first-generation hybrids into individuals of the other parent species. This transfer of characters from one species to another is referred to as introgression, and there are several well-studied cases of hybridization the effects of which include limited or massive character introgression.

Among North American species pairs, Mayr and Short (1970) list only one case of sympatric species which hybridize introgressively: Prairie Chickens (Tympanuchus cupido) and Sharp-tailed Grouse (T. phasianellus)⁴ interbreed in Wisconsin and Ontario. There is a high initial interbreeding rate resulting in populations which are 5-25 percent hybrid. Hybrid males are, however, apparently less successful in their courtship, and the over-all population effects are thereby reduced. (Mayr, 1963: 117).

I. Semi-species

Pairs of species which are so closely related that they cannot normally co-exist in the same geographical area may nonetheless meet along a narrow zone of overlap. Often they hybridize there with backcrossing to produce a whole range of intermediates. In each of the cases below, however, mating is non-random with the result that the two parental types continue to be found in some numbers as part of the hybrid population. Such pairs of species are often referred to as semi-species to emphasize that they have barely separated, and their mutual reproductive isolation is as yet imperfect. Mayr and Short (1970) list the following instances of hybridization between largely allopatric semi-species for which backcrossing has been confirmed:

1. Mallard and Black Duck
2. Herring Gull and Glaucous-winged Gull
3. Semipalmated Plover and Ringed Plover
4. Ladder-backed Woodpecker and Nuttall's Woodpecker
5. Eastern Wood Pewee and Western Wood Pewee
6. Black-capped Chickadee and Carolina Chickadee
7. Golden-winged Warbler and Blue-winged Warbler
8. Rose-breasted Grosbeak and Black-headed Grosbeak
9. Indigo Bunting and Lazuli Bunting
10. Common Redpoll and Hoary Redpoll.

Absence of significant backcrossing in the hybrid zone will probably be part of the basis for arguing that the following should be split:

- A. Arctic Loon (Gavia arctica) and Pacific Loon (Gavia pacifica).
- B. Yellow-bellied Sapsucker (Sphyrapicus varius), Red-breasted Sapsucker (S. ruber) and Red-naped Sapsucker (S. nuchalis).

J. Complete Intergradation

If isolating mechanisms between two adjoining populations are non-existent or extremely weak, these populations will meet along a hybrid belt and produce a full range of intermediate forms. Within the hybrid zone individuals conforming to the parental types (recombinants) should be almost non-existent (less than 5 percent), and introgression will be detectable at some distance from the edge of the zone of contact.

Most of these cases have been recognized now for some time, and the contiguous populations have already been lumped into a single species. Other instances (potential future lumpings) are the following:

1. Brant and Black Brant
2. Mallard and Mexican Duck
3. Common Crow and Northwestern Crow
4. Tufted Titmouse and Black-crested Titmouse
5. House Wren and Brown-throated Wren
6. Mourning Warbler and MacGillivray's Warbler
7. Gray-crowned Rosy Finch and Black Rosy Finch
8. Dark-eyed Junco and Gray-headed Junco.⁵

The following may be split for lack of evidence of random interbreeding and failure to intergrade completely:

- A. Canada Goose (Branta canadensis), Richardson's Goose (B. hutchinsii) and Cackling Goose (B. minima).
- B. Eastern Screech Owl (Otus asio) and Western Screech Owl (O. kennicotti).

The Breakdown of Isolating Mechanisms

Hybridization between Blue-winged and Golden-winged Warblers was discussed recently in an article in BIRD OBSERVER (Vol. 2, No. 3, pp. 70-73). These two species diverged from each other, probably during the Ice Ages of the Pleistocene in areas which were geographically isolated from each other. For many centuries their breeding ranges west of the Appalachians remained separated from each other by an arm of the Great Prairie. However, this prairie peninsula has been eliminated as a result of man's activities in the Northwest Territory states, and both species were able to extend their breeding ranges so that they now overlap. The two species now hybridize quite frequently in the Great Lakes region.

Hybridization also occurs in the New England area. Ornithologists have suggested that until some 200 years ago, these two species were isolated by habitat preferences in the Northeastern states, even though they were in contact geographically along the southern border of the region. Man's systematic deforestation of the area and his introduction of agricultural activities have brought the two species into contact much more generally, with the result that hybrids are fairly common throughout our area also.

The theory that it was alteration of the habitat that induced this hybridization is strengthened by evidence from a much more recent case from tropical Africa. There, three species of Paradise Flycatchers have quite recently begun hybridizing. Two of these species, Terpsiphone rufiventris and T. rufocinerea, live ordinarily in the rain forest, but in different parts of Africa. The third species, Terpsiphone viridis, inhabits second-growth woods and second-growth savanna forest. In most regions where these various species come into contact, they co-exist with each other side by side without any evidence of interbreeding, each species being restricted to its own preferred habitat. Recently, however, African natives have begun clearing parts of the rain forest, and in these areas T. viridis now interbreeds freely with each of the other two species. Areas which have been cleared for some years have evolved stabilized hybrid populations. (Mayr, 1963: 119-121).

In another similar case, that of the Malayan kingfishers Ceyx erithacus and C. rufidorsus, hybridization has progressed so completely that authorities now consider these two species to have merged. (Sims 1959) Note that this is not a case of "lumping" in the usual sense of the word, i.e., it is not a case in which ornithologists have decided that they had formerly inappropriately separated two natural populations into separate categories, giving each its own individual species name. Rather, this is a

case of two valid species whose isolating mechanisms have been broken down as the result of man's ecological disturbance which are now hybridizing so freely as to merge completely into a single species.

Another case of this type may be closer at hand, at least in its incipient stages (Trauger, et al. 1971). The population of the Lesser Snow Goose, as estimated from counts of wintering birds in North America, has grown from 641,000 in 1956-1957 to 966,400 in 1966-1967. During the same period, the population of Ross' Goose increased from 7,930 to 31,400. These population increases occurred during a period of general climatic improvement in Arctic Canada and may be the result of a series of extremely favorable breeding seasons. Concomitant with these increases, the breeding ranges of both species have apparently been extended, and they are now sympatric over a broad area in the Canadian Arctic.

Beginning in 1962, white geese with morphological characteristics intermediate between these two species have been captured or collected, and biologists are sure that these birds represent hybrids of Lesser Snow and Ross' Goose. In the early 1960s most intermediates conformed rather closely to the original description, suggesting that these were all F_1 -individuals (first-generation hybrids). More recent observations have included individuals deviating significantly from this original pattern, suggesting that backcrossing with the original species is occurring on a wide basis.

Let us consider a possible explanation for this more recent case of hybridization. During the Pleistocene era, the two species were separated geographically, and, in fact, they may have re-established contact only within the past two decades. Historically, Ross' Goose wintered exclusively in central California. Around 1955, however, Lesser Snow Geese shifted their major migration route eastward, and shortly thereafter (around 1960) Ross' Goose likewise diverted its route to the east. As a consequence of this shift, 200 to 400 Ross' Geese now winter each year with the large flocks of Lesser Snows in Louisiana, Texas and New Mexico.

The birds that winter in the southern and southwestern states will be somewhat isolated from the main concentration of wintering conspecifics and will presumably find difficulty in pairing with another bird of the correct species. Since courtship, pair formation and copulation among Ross' Geese takes place on the wintering grounds and during spring migration (Ryder 1967), the absence of a conspecific mate may allow the mating drive to intensify to such a degree as to overcome the inhibitory effects of incorrect species recognition and permit the formation of mixed pairs. (Mayr 1963: 127-128) This phenomenon of hybridization occurring at the edges of a (winter) range expansion will be examined again below. Undoubtedly it is a factor promoting the interbreeding of these two species, for all of the intermediate geese have appeared in the United States on the wintering grounds in the South; none, in California.

The thesis that hybrid formation is related to the scarcity of appropriate mates is also supported by more recent observations. For instance, Ryder (1973) reports that in 1972, Ross' Goose began nesting at La Pérouse Bay, Manitoba, near Churchill. Of those breeding birds observed, there were a single pair of Ross' Geese, three pairs that consisted of one Ross' Goose mated with a Lesser Snow, and one pair consisting of a male Lesser Snow mated to an intermediate female.

But there may be more to the story. Apparently the spring of 1967 was quite late in the Arctic, and inclement weather delayed the arrival and nest initiation of both species at Karrak Lake, Northwest Territories. When the snow melted exposing the nesting habitat, Ryder noted considerable interaction between these species as nests were established. Later he found 16 nests containing eggs of both Ross' Geese and Lesser Snow Geese...[and] Trauger and J.B. Gallop found four additional mixed clutches on another island...With the exception of one nest, the incubating female of these clutches was a Lesser Snow. Apparently Ross' Geese were displaced by Lesser Snows from nests established in preferred habitat...Dump nesting⁶ by both species also may have occurred." (Trauger, et al. 1971: 865).

The significance of these observations is easy to elucidate: The courtship displays of all geese are remarkably similar. Hence, there are few instinctual ethological barriers to inhibit interspecific hybridization. Geese are, moreover, subject to two phenomena not characteristic of birds in general. First of all, true geese imprint, i.e., during a certain critical period, the gosling "learns" his parent, accepting for the model any animal of appropriate height which emits goose-like

sounds. Konrad Lorenz and his associates succeeded in imprinting Greylag Geese to human models by waddling about in a squatting position at the head of a line of goslings and imitating the honking of the true parent. Second, geese maintain the family structure throughout the first winter. They migrate south together and continue to socialize on the wintering grounds until such time as pair-formation for the new year begins. An egg dumped in the nest of the wrong species will thus hatch a gosling that will (1) imprint to the wrong species, and (2) migrate to the incorrect wintering grounds, there to bond with an individual from the incorrect species. At present, intermediate geese are occurring in the Central Flyway in the ratio of one intermediate to approximately 200 Lesser Snow Geese, or one intermediate to 171 Ross' Geese. Trauger, et al. (1971) estimate that hybrids account for 4.8% of the Ross' Goose population, indicating a fairly high rate of hybridization. They state (pp. 870,873), "If the present trend of hybridization and introgression continues, several valid reasons suggest that Ross' Goose, one of the rarest North American geese, may be in serious jeopardy as a species...Because of its relatively small gene pool, the rare Ross' Goose may be vulnerable to eventual genetic swamping by the Lesser Snow Goose."

Temporary Hybridization

We have seen above how hybridization may on occasion spontaneously begin as an after-effect of climatic amelioration, or be brought about as a result of man's interference in the ecology. But just as interbreeding may start more or less spontaneously, so also may it stop abruptly.

The range expansion of a species will often bring it into (secondary) contact with certain other species from which it is imperfectly isolated. As a result, hybridization begins and will be particularly frequent along the advancing frontier of the expanding species (where conspecific mates are rarest). Biologists feel that introgressive hybridization is potentially dangerous in that it tends to weaken both species by allowing "foreign" genes to be imported into the "pure" gene pools of the parent populations, as perfected by natural selection. In some cases, these foreign genes may alter the habitat preferences of the parent species or yield such other side-effects as would tend to increase the frequency of contact between them. Thus, interbreeding is accelerated, and the two species may even eventually merge.

However, this is not the inevitable scenario. More frequently, in the case of an ongoing range expansion, interbreeding increases and reaches its peak just after the edge of the expanding population first reaches a given locale. Later, as that area becomes part of the interior of the zone of sympatry, both species will find it relatively easy to locate conspecifics with which to mate. They will begin to reassert their special mating preferences, and hybridization will taper off.

Moreover, in at least one case involving a non-ongoing range expansion, hybridization has practically vanished. In the period 1870-1900, the Blue Tit (Parus caeruleus) and the Azure Tit (P. cyanus) mutually expanded their ranges so as to overlap in Western Russia. At first, there were numerous hybrids, but now, some 60 years after the original expansion, interbreeding has greatly decreased, and the isolating mechanisms separating the two species have apparently been strengthened. (Mayr, 1963: 562)

Concluding Remarks

In the decades before the twentieth century, biologists relied almost exclusively on the cross-sterility barrier to explain the species gap. Ornithology was simpler to understand then, but to me it was far less interesting and much less exciting. I have sampled in this article some of the rich variety of devices (as recognized by modern ornithology) that tend to assist a species in the maintenance of its own species integrity. Although the subject is both complex and technical, it is one which the average birder can and should come to appreciate, for the subject matter is in truth nothing more nor less than the sum total of the complete life histories of all the various separate species, together with an analysis of their similarities and incongruities. Look at it this way: the more we learn of the methods by which the bird itself identifies others of its own species, the better our own field work will become.

Footnotes

1. Sympatry = the occurrence of two or more populations within the same area during the breeding season. The populations may be separated according to habitat provided that individuals in breeding condition from one population lie within the cruising range of individuals of the other population.
2. Hybrids produced by two individuals each from a different parent population are referred to as F_1 -individuals. The offspring of two such F_1 -individuals are referred to as F_2 -individuals, etc. The offspring produced by an F_1 , F_2 , etc., and a member of either of the two parent populations is referred to as a backcross.
3. These two species are illustrated in Machworth-Praed, C.W., and C.H.B. Grant. 1962. Birds of the Southern Third of Africa. Longmans, Green and Co., Ltd. Plate 36, before p. 561.
4. Pediocetes phasianellus in the A.O.U. Check-List. Mayr and Short argue that any two species that hybridize as regularly as these two do should never be placed in separate genera; hence, their change of name.
5. These are not the only potential lumpings which listers have to fear. Several geographical isolates may also be lumped. Mayr and Short combine the Greater and Lesser Prairie Chickens, for example, and they consider the Golden-cheeked Warbler to be but a well-marked geographical race of the Black-throated Green Warbler.
6. Dump-nesting = the laying of one or more eggs by a species which normally constructs or appropriates its own nest in the nest of another bird. The term is used most frequently of a bird of one non-parasitic species which lays in the nest of another species. Intraspecific dumping may be quite common, but it is much more difficult to detect, for the laying female must be "caught in the act."

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