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COMMENTS ON "SPECIES RECOGNITION" WITH SPECIAL
REFERENCE TO THE WOOD DUCK AND
THE MANDARIN DUCK

BY WILLIAM C. DILGER AND PAUL A. JOHNSCARD

IT is well known that closely related, sympatric species have evolved species-specific features which serve to minimize the possibility of "wrong" choices being made during pair formation. The amount of evolution of such species-specific features is roughly proportional to the deleterious effects of the "wrong" choices made in species recognition. Of course, if upon initial contact, the forms interbreed too freely panmixia will occur and both will eventually lose whatever genetic identity they may have had. On the other hand if, by the time of contact, the forms have incidentally developed differences sufficient to serve automatically as isolating mechanisms from the outset, then the further evolution of such characters will not occur as a result of "mistakes" being made. Thus, it would seem that the post-contact evolution of species-specific features which serve as isolating mechanisms depends upon rather particular conditions involving contacts between forms which find themselves neither impartially interfertile nor completely isolated at the start (see Sibley, 1957, for a thorough discussion of these phenomena).

The species recognition features evolved in birds are mainly visual and/or vocal in nature. Either may predominate, depending on the nature of the selection pressures involved and upon the nature of the genetic variability available upon which the selection can exert its influence. Visual recognition will tend to be emphasized by selection in those species in which visual features are most advantageous, and the same may be said for vocal features. The relative advantage or disadvantage is probably determined largely by the ease in which either may be perceived in the physical environment in which pair formation typically takes place (Dilger, 1956). Ducks of the genus *Anas*, many trochilids, paradiseids, phasianids, etc., probably rely largely on visual species recognition (Sibley, 1957); and thrushes of the genus *Catharus* have been shown to rely most heavily on vocalizations for their species recognition (Dilger, 1956).

The process of evolution of a signal character (visual, vocal, etc.) from a nonsignal origin is termed "ritualization." This term is used because it is rather descriptive of what happens to a movement as it evolves into having a greater and greater effect as a signal. Ethologists employ this term for the evolution of motor patterns (Blest, 1957 MS), but it should also apply to the evolution of associated structural features (shape, color, texture, etc.) which the motor patterns accentuate and which accentuate the motor patterns. This course seems reasonable because structural changes toward increasing signal

function exhibit the same phenomena characteristic of the ritualization of motor patterns.

It is necessary to emphasize that the same selective pressures which are responsible for ever refining and rendering more "unmistakable" the male signal characters are also working equally on the releasing mechanisms (RM's) of the female. These RM's are responsible for receiving (via the sense organs) the sign stimuli emanating from the male and, depending on the circumstances, translating these signals into varying combinations of effector (muscular and glandular) actions. Thus the females exhibit as much sexual "dimorphism" as the males do only it is not visible. The evolution of the RM ideally "keeps pace" with the continuing refinements of the signal to which it is attuned. In most cases it seems likely that the male signal characters and the female RM's do evolve roughly apace although it is unlikely that they evolve *exactly* together because of the probable disparity in the amount of genetic variability in the systems controlling the signal characters and the RM's.

Investigations into the mechanisms of species recognition should not only include consideration of the innate releaser-sign stimulus-RM features briefly discussed above, but should also include a consideration of possible effects of early experience in regard to various learning processes such as "imprinting" (*Pragung*) and allied phenomena. These are undoubtedly of great importance in some instances even though they may not always be as directly controlled genetically as are the purely innate mechanisms. If the critical features of the normal environment which serve as releasers, and which make up the *Umwelt* for each species, are rather rigid and "predictable" then the animal can "afford" to have its responses "built in," so to speak, in a rigid manner exemplified by the common releaser-sign stimulus-RM type of response. If, on the other hand, the animal's *Umwelt* is a rather plastic one in any regard, then the responses to this type of situation are likely to be learned in some fashion. Different types of learning (see Thorpe, 1951) will prevail, depending on the nature of the situation. Imprinting, characterized by a short "sensitive period" and relative stability once established, seems to be a type of learned response close to a purely innate type of response.

It has been long known that if hybrids are desired under laboratory conditions it is easier to obtain them if individuals of one of the two species with which one wishes to work are raised by the other species. Individuals thus reared seem to behave as if they had become imprinted on the foster parents and form pair bonds with members of the foster parent species much more easily than otherwise. The senior author has data indicating that this may be true within the genus *Agapornis*, for instance. Whitman (1919) utilized this technique with various pigeons and may have been the first to

discover this principle. It is equally well known, however, that in some species this early experience has apparently no effect on future behavior as far as "choosing" a mate is concerned. The Brown-headed Cowbird (*Molothrus ater*) and the Cuckoo (*Cuculus canorus*) are two examples in which the young are regularly raised by foster parents and which, as adults, have no trouble in choosing mates of the proper species. If imprinting is involved in such cases it would mean that the sensitive period does not occur until the young normally have contact with their own species. At any rate it seems that species recognition, like other behavior features, is dependent upon both innate and learned elements in various relative strengths and combinations, depending upon the nature and the amount of the selective pressures brought to bear. This would naturally vary from species to species. However, it does seem probable that parasitic species are the only ones in which early experience is likely to play no part in rendering the adults more likely to "choose" mates of their own species (see also Cushing, 1941).

The source of selection in developing species recognition features and their attendant RM's may be *any* of the many and biologically disadvantageous events attendant upon the formation of interspecific pairs (Dilger, 1956). In addition, it may be of importance to consider the circumstances under which "mistakes" may be made. There seem to be at least two such circumstances. One is a situation where a female is located geographically in such a manner that her own species is relatively rare and a closely related, or even a merely similar appearing or sounding, species is rather abundant. This is a situation that is common where two related species share a rather narrow zone of overlap. This female will display the usual appetitive behavior associated with a "search" for a mate. The longer she searches in vain the lower her threshold to respond becomes. This threshold may become so lowered that she will eventually respond to the suboptimal stimuli afforded by the next most similar set of sign stimuli, which will most likely be a male of the next most closely related species. Selection may work on such species as this to either restrict its range to areas in which the conflicting stimuli do not exist or to further refine the male signal characters and the female RM's to function in a signal spectrum even farther from that of the related species. In this latter case, the related species will also evolve its signal characters and RM's farther away from its "competitor." The other situation is where a female has an unspecific set of RM's resulting from an unfortunate genetic recombination or, possibly, because of a mutation causing her to react unspecifically to male signals. Males may also have unspecific signals caused by the same phenomena. This situation, of course, will be selected against possibly even more strongly as these birds would be prone to make "mistakes" chronically in the case of females or be not as likely to attract mates in the case of males.

It has been suggested (Sibley, 1957) that those sympatric, closely related species which are polygamous and exhibit short term pair bonds demonstrate the most pronounced species recognition signal characters. The reason suggested is that "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" (and a high degree of species diversity and development of the RM's in the females). This is quite likely to be true. However, there are many closely related and sympatric species (such as some parrots, for instance) which are not polygamous and which form pair bonds of long duration—perhaps for many years. These species also evolve highly diverse species characters. If a "mistake" is made by individuals of these species it will tend to be of long duration and will likewise tend to cause a consequent high degree of "damage" to the gene pools involved. Hence, selective pressures brought to bear in these cases would also be very strong ones and would also result in a high degree of species diversity in regard to signal characters and RM's. The parrot genera *Amazona* of the New World and *Psittacula* of the Old World provide likely examples of this.

Not only does the length of the pair bond seem to have an influence upon the nature of the selective pressures brought to bear, but the time it takes the bond to form is probably of importance as well. Some thrushes, which have a seasonal pair bond, take three to four days to form their pair bonds (Dilger, 1956), and ducks commonly require several months to form their pair bonds, but Budgerigars (*Melopsittacus undulatus*), which have pair bonds lasting for years, take but a few hours to form them (Morris, 1956). Budgerigars do not have the problem of existing sympatrically with closely related species, but the thrushes and ducks considered do. In some cases it might be an advantage to have evolved behavior patterns which cause the pair bond to be formed rather slowly where mistakes are likely to be made.

The most effective species-recognition insurance may occur in species having strong parental imprinting overlying innate behavior, militating for a long pair bond formation period and highly evolved signal characters with their associated RM's. These modifications which may evolve as isolating mechanisms probably occur in various combinations and strengths depending again on the vicissitudes of the selection pressures involved and upon the genetic variability available.

From our human viewpoint we naturally tend to think of these as problems of species recognition. However, if we try to project ourselves into the bird's *Umwelt* and regard these problems from its "viewpoint," a slightly different slant is obtained which may be of use to our thinking. Birds apparently are incapable of having concepts of any kind, including those of "sex," "species," "male," "female," etc. The bird's "problem" becomes one of culminating a

period of appetitive behavior with the perception of sign stimuli which, in a broad sense, triggers the initiation of a "satisfactory" sexual association. It is of value if we are aware of this "bird's eye view" because it may give us a much better idea of what is important to the animals concerned and thus may give us a better idea of how and where selection is working. The major reason why birds, like most other animals, make "mistakes" is that they do not react to the total environment but only to those features to which they have evolved to react under particular circumstances. This is why they are so easily misled experimentally by what may seem to many as totally improbable objects (see Tinbergen, 1951). The observed instances of this are many, but Lack's (1953) Robins (*Erithacus rubecula*), fighting a tuft of red feathers, or Tinbergen's (1951) male sticklebacks (*Gasterosteus aculeatus*), reacting aggressively to any red object, have become classic examples. The senior author has found that Wood Thrushes (*Hylocichla mustelina*) will mount and attempt coition with *papier mâché* models of Wood Thrushes (Dilger, 1956), and these same birds will react aggressively or otherwise to small cubes and spheres painted brown above and white with black spots below.

An apparent evolutionary anomaly is the existence of the Wood Duck (*Aix sponsa*) and the Mandarin Duck (*A. galericulata*). The males of both species seem literally covered from head to tail with the most improbable and complicated collection of highly specific releasers that one could imagine, yet these species are not sympatric with any closely related ones or with each other. Like all highly evolved social signals, these are likely to be strongly selected against by predation if they are not even more strongly selected for by the necessity of ready recognition by females of their own species. This would seem to suggest the possible explanation that these species were sympatric with each other or with closely related forms in the near past. However, the only near relative of the Wood Duck which possibly could have been recently sympatric with it is the Muscovy (*Cairina moschata*) of Mexico, and it is a significant fact that hybrids between these two forms are unknown. Likewise, the Mandarin has possibly been sympatric only with the fairly closely related Pigmy Goose (*Nettapus coromandelianus*), a combination for which hybrids are also unknown. If indeed some closely related form had been sympatric with either the Wood Duck or the Mandarin in the past one would think that selection operating through the effects of predation would have caused the males to tend toward a more cryptic plumage since the time of species separation. This is evidently not the case.

Another thought is that ducks of other less closely related genera, and possibly even of other tribes, may be the source of selective pressures if sufficient "mistakes" in mate choices are made that involve these more distant relatives. There is considerable support for this supposition. The Wood Duck is

notorious for forming mixed pairs and has produced hybrids with 26 species of ducks (Johnsgard, MS). Species involved include such unlikely forms as the Common Shelduck (*Tadorna tadorna*), 16 species of *Anas*, and five species of *Aythya*. This would indicate a very high first generation chromosomal compatibility, exceeded only by the Mallard (*Anas platyrhynchos*), which has hybridized with 40 species of Anatidae. It is of significance that the majority of Wood Duck hybrids of known parentage have involved the female Wood Duck, whereas most Mallard hybrids result from the male Mallard copulating with females of other species.

The hybrids produced by Wood Ducks and Mandarins are apparently always sterile, and although they have been reported only from birds in captivity, these facts do demonstrate the Wood Duck's unusual proclivity for mixed pairing. Mandarins, on the other hand, are not known to have hybridized with more than five other species. Paradoxically, the two species of *Aix* will only rarely, if ever, hybridize with each other. The remarkable findings of Yamashina (1952), which indicate that the Mandarin possesses two less chromosomes than the Wood Duck and other anatines, would provide a logical explanation for sterility in alleged Mandarin \times Wood Duck hybrids, and may also explain the former's failure to hybridize with as many species as has the Wood Duck.

Even in view of this extensive mixed pairing it is difficult to explain why the males of *Aix* have evolved such extreme complexities of plumage patterns. The danger of mixed pairs being formed within the genus *Anas*, for example, is equally great, and the male dimorphism exhibited here is extensive—not enormous as it is in *Aix*. Perhaps intertribal pairings are selected against more strongly than are intergeneric ones, but also the elaborate display movements of *Anas* probably substitute in large part for the very elaborate display plumage of *Aix*.

Another, at least partial, explanation may lie in the possible discrepancy between the evolution of the male signal characters and the female RM's. If for some reason, such as a lack of enough genetic variability, the females were not able to evolve a sufficiently refined set of RM's rapidly enough, the greatest part of the burden of selective pressures toward species recognition would fall on the males, resulting in the extreme plumage complex we observe at present.

Perhaps the fact that Wood Ducks, and especially Mandarins, are crepuscular in their habits (Heinroth, 1910*b*, and Savage, 1952) is related to the increased danger of predation from visually operating predators attracted by the showy male plumages. Mandarins are in fact even more crepuscular than Wood Ducks. This may be related to their greater elaboration of contrasting male plumage patterns.

Aix males are also more highly competitive with each other over the attentions of females than are most other ducks. In both species, but particularly the Mandarin, the males congregate around a receptive female and conduct their courtship displays in a highly intense and competitive manner (Lorenz, 1941, and Heinroth, 1910a). This may indicate that there is a comparatively great amount of competition among the males in displaying the optimal stimuli to a female. Although Mandarins appear to be monogamous with long pair bonds (in the wild at least), this initial intraspecific sexual competition and a greatly extended period of display and pair formation must be effective in maintaining the high degree of sexual dimorphism found in this species. This is especially true in the Mandarin, where the choice of a mate lies exclusively with the female (Lorenz, 1941). Selection thus would tend to cause the males to evolve releasers of ever increasing effectiveness. This may perhaps be thought of as an "attempt" to evolve a kind of superoptimal set of stimuli. An additional point of interest is that the males of *Aix* (especially *sponsa*) have displays consisting of numerous primitive and simple actions (Lorenz, 1941) which are largely homologous with the elaborate displays of *Anas*; thus possibly *Anas* males provide a kind of superoptimal stimulation to the RM's of *Aix* females. This may explain the disproportionate frequency of matings with *Anas* males. It has been proven that birds and other animals will often react more strongly to superoptimal stimuli even though these usually do not occur in nature and are manufactured by the experimenter (Koehler and Zagarus, 1937, and Tinbergen, 1951, for example).

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SUMMARY

Several things are pointed out that should be considered by anyone interested in problems of "species recognition." These are:

1. The source of selection controlling development of species-specific signals and releasing mechanisms (RM's) may be *any* of the disadvantageous consequences of mixed pairing (not necessarily hybridization alone).
2. The term "ritualization" should apply equally to the evolution of morphological features and motor patterns which are being selected for toward increasing signal function.
3. It should be remembered that the evolution of RM's proceeds in concert with that of the associated signal characters.
4. Early experience resulting in some form of learning such as "imprinting" may be of considerable consequence in subsequent "species recognition."
5. The reasons why mistakes may be made in "mate choice" should be considered. For example, genetically "normal" animals may respond to suboptimal stimuli because of abnormally lowered thresholds; or genetically "abnormal" animals may respond with unrefined response capabilities.
6. Sympatric, closely related species which are polygamous and which have short term pair bonds are not the only ones upon which strong selective pressures exert their influence toward marked development of signal characters and RM's. Consider closely related, sympatric species with very long pair bonds which are not polyga-

mous such as some of the parrots, etc.

7. Closely related species which are sympatric may not be the only source of selection toward diverse signals and RM's. Any species with somewhat similar signal features and RM's may exert this influence providing that they, of course, are sympatric with the form under investigation.
8. The amount of time taken to form the pair bond as well as its duration is likely to be of importance (*Aix*, for example).
9. It is useful to try to think of these problems from the "bird's point of view." After all, these problems are functions of the animal's *Umwelt*—not ours!

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