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Behavioral Isolating Mechanisms in the Family Anatidae

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The ducks, geese, and swans present a host of species-recognition and isolating-mechanism problems that are equaled by few other groups of birds. As a family, the Anatidae have provided the greatest number of interspecific hybridization records of any avian family (see Gray, 1958, and Johnsgard, 1960*a*) both in captivity and under natural conditions. A surprising number of these hybrids have proved to be fertile, even when obtained between what appear to be well-marked genera. This remarkable capacity for hybridization indicates that isolating mechanisms must be operating effectively if species are to retain their integrity under natural conditions. Since genetic isolation is practically absent in the Anatidae, other isolating mechanisms must, of course, have evolved to take their place. Of these, the most significant appear to be behavioral differences and various morphological (plumage and soft-part) specializations that are usually associated with these behavioral differences. A comparative behavioral study of the Anatidae was undertaken from 1959 to 1961 at The Wildfowl Trust, in England, where I was able to observe in life 125 out of the approximately 140 extant species of Anatidae, including 34 of the 41 genera accepted by the most recent authority on the family (Delacour, 1954–59).

Of the 10 tribes of Anatidae accepted by Delacour (1954–59), all but 1 (Anseranatini), which is monotypic, are characterized by the inclusion of numerous closely related, often sympatric, species. It is, of course, in these groups that behavioral and morphological elaborations associated with pair formation and copulation are most conspicuous, and it is also here where the greatest amount of information regarding the development of isolating mechanisms can be gleaned. The following discussion is subdivided into sections corresponding to the tribes and included genera of Delacour (1954–59), except where results of my studies have suggested certain modifications in his classification (Johnsgard, 1961*a*). As most of the observations given below are my own, I have not resorted to frequent citation to support them. Where terms refer to ritualized displays, the first letter of these terms has been set in capital letters.

SUBFAMILY ANSERANATINAE

Tribe Anseranatini

The Magpie Goose (*Anseranas semipalmata*) stands apart from the rest of the Anatidae in numerous anatomical as well as behavioral respects, and it

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seems unlikely that hybridization with any other species of waterfowl is possible. It is certainly not probable, for in the Magpie Goose copulation occurs on land, which is most unusual in the Anatidae. Furthermore, the associated behavior (see Johnsgard, 1961*b*) is also entirely different from that associated with copulation in the rest of the Anatidae. The Magpie Goose's general behavior is reminiscent less of the true geese and swans (Anserini) than of the screamers (Anhimidae). Copulatory behavior in screamers has not been described, so unfortunately it is impossible to compare them to the Magpie Goose in this respect.

SUBFAMILY ANSERINAE

Tribe Dendrocygnini

The whistling ducks (*Dendrocygna*) are second only to the Anseranatini in their isolation from the rest of the Anatidae, and definite hybrid records have been obtained only for intrageneric combinations among the eight species of *Dendrocygna*. Seven of the species are sympatric with one or more other species, but no natural hybrids have been recorded. In captivity nine hybrid combinations have been obtained, but the fertility of these hybrids is not known. It appears that isolating mechanisms in the whistling ducks include plumage-pattern differences of varying degrees, vocalization differences which are considerable, and relatively less differentiation of visual displays. Each species possesses specific recognition or greeting calls which are distinctive and which, by themselves, could effect species recognition. Although a few species have very similar plumage patterns (e.g. *bicolor* and *arcuata*; *guttata* and *arborea*), such species are allopatric with each other. Visual pair-forming, or "courtship," displays appear to be essentially absent in whistling ducks, and are probably replaced by vocal signals. Unlike the situation in the true geese and swans, there appears to be no behavior functionally related to Triumph Ceremonies.

In their behavior patterns associated with copulation, certain differences are present that might prove effective as isolating mechanisms. Two species (*arborea* and *autumnalis*) copulate on shore or, more often, while standing in shallow water near shore. The others (except possibly *guttata*, which has not been observed in this connection) copulate while swimming. In these former species, precopulatory behavior consists of mutual Drinking movements that do not appear to differ from normal drinking behavior. In the species that tread on water, the precopulatory behavior consists of mutual Head-dipping movements (*bicolor*, *eytoni*, and *arcuata*) or Bill-dipping motions (*javanica*, possibly *viduata*). These precopulatory movements also do not differ markedly from the nonritualized bathing movements of the species.

Postcopulatory displays differ considerably. In the species that perform the precopulatory Head-dipping movements, postcopulatory display is likewise mutual and consists of an energetic Step-dance, during which both birds tread water vigorously and each raises one wing vertically. The Step-dance

is lacking in the two species that copulate on shore. In one of these species (*autumnalis*), there is a slight indication of Wing-raising on the part of the male, but in *D. arborea* this is lacking altogether. Although these two species differ greatly in their adult plumage patterns, they have a strong tendency to form mixed pairs in captivity, which is probably a result of the similarities in their copulatory behavior. Likewise, *D. bicolor* has a tendency to hybridize with the species it most resembles in pre- and postcopulatory behavior.

Tribe Anserini

The true geese and swans comprise 21 species which are divided into 5 genera. Genera that include several closely related species are *Cygnus*, *Anser*, and *Branta*. Hybrids have occurred among 18 of the 21 species, and 5 hybrid combinations have been reported from the wild in *Anser* and *Branta*. Eleven hybrid combinations within these 2 genera, and 5 between them, have proved fertile.

Morphological isolating mechanisms in these genera appear to be primarily based on plumage and soft-part coloration in the head and bill areas, whereas the remainder of the body plumage is more uniform among species of *Anser*, *Branta*, and *Cygnus*. Vocalizations are probably important sources of isolating mechanisms in the true geese and in most of the species of swans. Threat displays and preflight movements are relatively uniform within each genus. The greatest behavioral differences in the tribe occur in the form and vocalizations of the Triumph Ceremonies, which appear to be of primary importance in the formation of pairs among geese and swans (Heinroth, 1911). Such ceremonies are present in all the species of true geese and swans except, apparently, the Coscoroba Swan (*Coscoroba coscoroba*). In some species of swans (*Cygnus olor*, *C. atratus*, *C. melanocoryphus*), they consist of mutual weak calling by both birds while lifting the chin and stretching the neck vertically. In the other swans, the calls are much louder and are accompanied by a waving or flapping of the outstretched wings. In the case of geese, the neck is extended more diagonally or horizontally, and there are often thrusting and horizontal or vertical movements of the neck. These movements during the Triumph Ceremony seem designed to bring into full view the head and bill markings of each bird to its mate or potential mate.

Precopulatory behavior in the Anserini is extremely uniform. It consists, in all but one of the species (*Cereopsis novae-hollandiae*), of Head-dipping movements on the part of both birds. In most of the true geese the tail is also strongly cocked vertically, exhibiting the white undertail coverts. Copulation normally occurs while both birds are swimming. In the Coscoroba Swan it can take place while the birds are standing in shallow water, and in the Nene Goose (*Branta sandvicensis*), a terrestrial species, it normally occurs on land, although the precopulatory behavior nevertheless consists of typical Head-dipping movements.

Postcopulatory behavior in this tribe is more variable than precopulatory behavior, and thus is presumably more effective as an isolating mechanism. In the genus *Cygnus* it is surprisingly variable; the postcopulatory displays of *C. atratus*, *C. olor*, and *C. melanocoryphus* appear to differ markedly from one another and from the other swans. In *C. cygnus* and *C. columbianus* the two birds rise in the water with outspread wings, calling in concert. Heinroth (1911) has described how differences in the postcopulatory behavior of these two groups of swans was partially effective in preventing a mating between *C. olor* and *C. cygnus*. In the Coscoroba Swan both birds stretch their necks and hold their heads high, but do not spread their wings. In the true geese (*Anser* and *Branta*) the postcopulatory displays are almost identical in all species; both sexes call with neck vertical, bill pointed upward, and the folded wings lifted or sometimes partly extended. In the aberrant Cape Barren Goose (*Cereopsis novae-hollandiae*), which seems to be a link between the Anserini and the Tadornini, the birds copulate on land after the male has walked around the female, pecking at her back until she assumes a prone position. The two birds perform what appears to be a Triumph Ceremony as a postcopulatory display, which consists of calling mutually while waving their extended necks vertically and repeatedly lifting their folded wings.

SUBFAMILY ANATINAE

Tribe Tadornini

The shelducks and sheldgeese are a group of 15 species divided into 5 genera as the group is constituted here. Only two of these genera (*Chloephaga* and *Tadorna*) are not monotypic, and hybridization has occurred among the species of these genera fairly frequently in captivity. No wild hybrids, however, are known involving shelducks or sheldgeese, and only a few congeneric species are actually sympatric. As in the preceding groups, pair bonds are often relatively permanent, but in at least some of the shelducks it appears that pair bonds are fairly weak and occasionally may be broken (Heinroth, 1911). Thus, "courtship" displays in males are somewhat more elaborate than in the groups already considered, but generally are not so complex and elaborate as in the following tribes.

Correlated with the fact that pair bonds are less rigid and courtship is more conspicuous in this group are the points that the sexes tend to differ to a greater degree in voice, appearance, and behavior. Males of different species tend to vary in these aspects more than do females, which is to be expected in a mating situation where the female "selects" her mate. Thus, isolating mechanisms tend to be concentrated in the male's plumage, vocalizations, and courtship displays, whereas the females of even rather distantly related species tend to be much more similar in these characteristics. Females of all species of this tribe (and most of the remaining tribes) possess

the major courtship display termed Inciting (Lorenz, 1951–53), which is readily recognizable after it has been thoroughly studied in any one species.

Homologous male behavior patterns are much less easy to distinguish, but in the present tribe the male vocalizations seem to fall into two fairly distinct categories. Displays associated with single-syllabled, but often rapidly repeated, calls appear to have primarily a threat function. In the genera *Cyanochen, Neochen, Chloephaga,* and two species (*tadorna* and *radjah*) of *Tadorna,* these male calls are rapid whistling notes, in *Alopochen* they are huffing noises, and in most of the *Tadorna* species they are throaty honks. The same notes, used in association with a rapid vertical Bowing movement of the head and neck, are used as a sexual display in some species of *Chloephaga.* The major sexual display of the males, however, seems to be a 2-syllabled call which is never a whistle and usually is a throaty or belching note. In *Neochen* and some species of *Chloephaga* (*melanoptera, poliocephala*), this is accompanied by a Puffing of the plumage and a variable raising of the wings as the bird assumes a High-and-erect posture. In *Tadorna* this posture and call are used as a sexual display in most species (all but *radjah* and *tadorna*). This sexual note differs sufficiently in auditory characteristics in each species so that it could serve as a species-recognition signal in itself without the added factors of specificity provided by male plumage patterns and slight differences in posturing.

As in the true geese, precopulatory behavior appears to be uniform throughout most, if not all, species, although several species have still not been observed adequately. In the species where precopulatory behavior has been seen (most *Tadorna* species, *Chloephaga picta*), it consists of Head-dipping movements performed by both birds either while swimming or while standing in shallow water. In *Tadorna tadorna* the Head-dipping often grades into shallow diving, and the male may Preen-behind-the-wing before mounting. Postcopulatory behavior is relatively uniform in the species where it has been observed. The female begins to call as treading is terminated and before the male releases his hold of her nape. The male calls as he releases her, and assumes a High-and-erect posture for a few seconds, usually lifting the wing farthest from the female. This Wing-lifting is strongly pronounced only in a few species (*Tadorna cana, T. tadornoides*), and is barely noticeable in others. There is no Step-dance as occurs in the somewhat similar postcopulatory display of *Dendrocygna.*

It appears, therefore, that isolating mechanisms in the Tadornini may consist largely of vocalizations which may be associated with special male postures. The three species of steamer ducks (*Tachyeres*), included by Delacour (1954–59) in the present tribe, probably should be placed in a separate tribe (Moynihan, 1958). However, so little is known of their behavior that it is not possible to discuss isolating mechanisms in the steamer ducks at the present time.

Tribe Cairinini

The perching duck group consists of 13 species, which are here divided into 10 genera. This collection of almost monotypic genera suggests that the tribe contains few closely related species, and this is corroborated by the scarcity of hybrids recorded among the perching ducks. The only known case of total genetic isolation preventing hybridization between two closely related waterfowl species is found in this tribe, and involves the Wood Duck (*Aix sponsa*) and the Mandarin Duck (*Aix galericulata*) (Yamashina, 1952). Practically all hybrids of perching ducks with one another and with members of other tribes have proved sterile. No natural hybrids are known, and the only case of congeneric sympatry in the tribe occurs between two species of pigmy geese (*Nettapus*).

Sexual dimorphism of voice occurs in all species, and dimorphism of plumage or body size is also found in all species to varying degrees. No species are known to have permanent pair bonds, and pairing either occurs every year or is practically absent altogether. In the genera where pair bonds are weak (*Cairina*, *Sarkidiornis*, and *Plectropterus*), the courtship and copulatory displays are likewise poorly developed. In the other genera (*Pteronetta*, *Aix*, *Callonetta*, *Amazonetta*, and *Chenonetta*), pair bonds are stronger but are probably renewed yearly, and courtship displays tend to be more elaborate. Likewise, male plumages tend to be more complex in pattern and coloration. Although the male courtship displays tend to be numerous, they are mostly derived from simple preening, drinking, shaking, and wing-flapping movements. Male vocalizations are, in most species, various kinds of whistles usually associated with special posturing. Wing patterns in these genera are usually metallic in color and conspicuous, and are exhibited by Preening-behind-the-wing displays. Although these preening displays are performed in essentially the same manner by all species, the unique speculum patterns "flashed" by each species bestow a specificity on the displays that very likely functions as an isolating mechanism.

Precopulatory displays in the perching ducks are, surprisingly, rather variable, which further indicates that the group is not a closely knit assemblage. In at least two species (*Cairina moschata*, *Sarkidiornis melanotos*), it appears that rape of the female is a frequent, if not the usual, situation. Precopulatory Head-dipping occurs in *Amazonetta*; various forms of Bill-dipping or Head-pumping are precopulatory displays in *Cairina scutulata*, *Chenonetta*, *Aix galericulata*, and probably *Pteronetta*; and Bill-dipping occurs in *Callonetta*, *Aix*, *Chenonetta*, and probably *Sarkidiornis*. Perhaps this diversity of precopulatory displays is one reason why hybrids among the perching ducks are so infrequent in captivity. Postcopulatory displays are also very variable. In *Cairina scutulata* the male simply swims rapidly around at random, calling excitedly; in *Aix galericulata* the male swims rapidly away from the female while Turning-the-back-of-the-head; in *Callonetta* the male calls, then turns and Faces the female; and in *Chenonetta* and *Am-*

azonetta the male tends to swim in a circle around the female with the bill held downward and the hindquarters somewhat raised.

It thus appears likely that the visual aspects of male displays and male plumage patterns function in the perching ducks as isolating mechanisms to a greater degree than in the groups previously considered.

Tribe Anatini

This large tribe of approximately 40 species contains 1 major genus (*Anas*) and 4 monotypic genera (*Malacorhynchus*, *Hymenolaimus*, *Merganetta*, and *Marmaronetta*) which appear to have no close relatives. Therefore, the following discussion is entirely devoted to the genus *Anas*, which is an extremely interesting group from the standpoint of isolating mechanisms. Hybridization within this genus is remarkably common, and at least 115 intrageneric hybrid combinations have been recorded among 32 species (Johnsgard, 1960*a*). Of these, at least 39 combinations have produced fertile offspring, and 38 combinations have occurred in the wild. Thus, isolating mechanisms are least well developed in the group, in spite of the fact that courtship displays and male plumages tend to be elaborate and diversified. Since many species in this genus have extremely broad ranges, there tends to be a great deal of sympatry, and nearly all species with breeding ranges that overlap the breeding ranges of numerous other *Anas* species are characterized by having bright male plumages and elaborate courtship displays.

Male courtship displays in *Anas* are exceedingly diversified, although all species do share certain homologous displays. Lorenz (1951–53) was first to study and compare the displays of most *Anas* species, and provided a basis for terminology and comparison of displays in the other species. Displays shared by males of most, if not all, species of *Anas* include Preening-behind-the-wing and Turning-the-back-of-the-head, both of which, by various head-plumage and wing-speculum patterns, very likely function as isolating mechanisms in spite of the uniformity of their performance. Other major male displays include the Grunt-whistle, which occurs in at least 15 species, the Head-up–tail-up, also found in at least 15 species, and the Down–up, found in at least 9 species. A courtship call, or Burp, occurs in most, and probably all, species, but varies greatly in auditory characteristics and associated head movements. It is generally true that closely related species share the greatest number of homologous male courtship displays, but there are several exceptions. Often two sympatric species of *Anas* perform several homologous displays but, by various kinds of differences in display combinations, or "linkages," rather markedly different optical and auditory effects are produced. Secondly, some species normally lack displays that are present in closely related forms, and evidence that such displays have been lost secondarily is provided by (1) the rare occurrence of the display in otherwise normal individuals, and (2) the occurrence of the display in hybrid combinations where

both parental forms lack the display. There are several examples of both these situations in *Anas*. Examples of the first include the Common Mallard (*A. platyrhynchos*), Common Pintail (*A. acuta*), and Bahama Pintail (*A. bahamensis*) when they sometimes perform independent Bridling, the Brown Pintail (*A. georgica spinicauda*) occasionally performing the Head-up–tail-up, and the Falcated Duck (*A. falcata*) rarely performing the Down–up. The Common Pintail and Brown Pintail also often perform a very rudimentary version of Nod-swimming. Lorenz (1958) has cited examples of the occurrence of displays in hybrid combinations, and his student W. van de Wall (pers. comm.) has studied other cases as well.

Cases of incipient secondary loss of displays may be observed in certain island races of *Anas* that lack contact with other congeneric species. Thus, the Laysan Island race of the Common Mallard (*A. platyrhynchos laysanensis*) has practically lost the Down–up display from its repertory. This display occurs in rudimentary form so rarely that it comprises only about 5 percent of the total major displays, whereas in the continental race it usually constitutes from one-third to one-half of the major displays. The other displays are performed in a much less exaggerated fashion than in the continental race. The same is true to lesser degrees in other island races, such as the Hawaiian Mallard (*A. platyrhynchos wyvilliana*), Kerguelen Pintail (*A. acuta eatoni*), and South Georgia Pintail (*A. georgica georgica*). The fact that these races retain any of their male displays is an indication that intraspecific male competition for mates is partially effective in retaining the male secondary sexual characteristics of the species.

The relatively facile genetic control of male courtship displays, indicated above, and their evident importance as isolating mechanisms make it dangerous for the behaviorist to judge evolutionary relationships solely on the basis of male displays. Fortunately, female displays are less subject to these kinds of variation, and so studies of variations, in the form of female Inciting and other kinds of sexual behavior as well as vocalizations, are more useful for judging intrageneric relationships in *Anas*. Females of most, if not all, *Anas* species uniformly have Decrescendo calls, but the auditory quality and number of notes in these calls vary considerably and very likely act as species- or individual-recognition signals.

Precopulatory behavior in *Anas* is remarkably uniform in all the species where it has been observed, and the mutual Head-pumping behavior is one of the best behavioral characterizations of the genus. Postcopulatory behavior is more variable, but in all species studied the male calls one or more times by Burping or Bridling, then often either Faces the female or Turns-the-back-of-the-head toward her. Bridling, followed by Nod-swimming, are the male postcopulatory displays of all the mallard-like ducks.

It thus appears that isolating mechanisms in *Anas* are based primarily on male plumage or soft-part features and the associated courtship displays that exhibit these features. Male vocalizations are almost always associated with

particular courtship postures and, together with morphological features, further enhance the specificity of these courtship displays. The frequency of hybridization in the genus appears to be the combined result of the great amount of natural sympatry, the relatively close relationships of all the species of *Anas*, and the very uniform precopulatory behavior of all the species in this genus.

Tribe Aythyini

The pochards comprise a group of 16 species that are world-wide in distribution. Fifteen of the species might be called "typical" and are included in the two genera *Aythya* and *Netta*. The other is the monotypic and extinct genus *Rhodonessa*, which is neither a typical pochard nor a typical dabbling duck, but rather seems to constitute, with *Marmaronetta*, a link between the two tribes. It is clear from hybrid evidence that the Anatini and Aythyini are very closely related tribes, and some intertribal hybrids have even proved fertile (Johnsgard, 1960*a*). Within the tribe, 14 species have been involved in interspecific hybridization, of which at least 6 combinations have produced fertile offspring. Twelve hybrid combinations have occurred in the wild, indicating that isolating mechanisms are not completely effective in this tribe.

Male plumage patterns in the pochards are somewhat less variable than in the dabbling ducks, with head and bill colors apparently being of greatest importance as morphological species-recognition signals. Male vocalizations tend to be soft, with sharp whistles almost absent, but they nevertheless vary sufficiently among species so that most, if not all, species can be readily recognized by their courtship calls. Unlike the genus *Anas*, males of almost all species studied perform displays that are not only recognizably homologous but also extremely similar in form. Two of these displays, the Head-throw and the Sneak postures (Hochbaum, 1944), are primarily visual displays with which vocalizations are usually associated. Two others, the Kinked-neck Call and Coughing, are primarily vocalizations and are accompanied by less-pronounced body movements (Johnsgard, unpublished MS.). In two species (*Aythya australis* and *A. nyroca*), the Kinked-neck Call is often repeated in fast succession several times. As in the genus *Anas*, males of most and probably all species have Preening-behind-the-wing and Turning-the-back-of-the-head displays that are performed in the same way but exhibit different morphological features. In the Head-throw and Sneak displays, different species vary in the rapidity and the degree of exaggeration of these movements, and these quantitative rather than qualitative differences in display form are possibly of significance in species-recognition systems. A Nodding-swim, similar to Nod-swimming in *Anas*, is performed by males of several but not all species.

As in the genus *Anas*, females of all species are very uniform in their behavior. Inciting behavior is similarly performed by all species and con-

stitutes the major female courtship display. Two male displays, the Head-throw and Kinked-neck Call, are also performed by females of a few species. Females of many species Preen-behind-the-wing as a sexual display.

Precopulatory behavior in the pochards is slightly more variable than in the dabbling ducks. In only one species (*Netta rufina*) does mutual Head-pumping behavior occur; in others only the male performs Head-pumping (*Aythya australis, A. baeri*), and in two (*Netta peposaca* and *N. erythropthalma*) this is performed only by the female. Males of all species perform Bill-dipping and Preening-dorsally movements as precopulatory displays, but only in some species are such movements performed by females as well. Postcopulatory displays are, however, extremely uniform in all the pochard group. In all species of *Netta* and *Aythya* studied (as well as in *Marmaronetta*), the male utters a single courtship call after he releases the female, then swims quickly away in a rigid Bill-down posture.

Behavioral isolating mechanisms in the pochards thus appear to be primarily dependent upon auditory and quantitative visual differences in homologous male courtship displays, and to a smaller extent upon differences in precopulatory displays.

Tribe Mergini

The sea duck tribe, which here includes the eiders (see Johnsgard, 1960*b*), contains 20 species (including 2 extinct species) that are primarily of Northern Hemisphere distribution. Four of the 8 genera are monotypic, but the others contain from 3 to 7 species each. Most species tend to be maritime in distribution, at least during the winter period, and there is considerable sympatry of ranges. Ten species have been involved in intratribal hybridization, and 8 hybrid combinations have been reported among wild birds. These have all involved the polytypic genera *Melanitta, Somateria, Bucephala,* and *Mergus*. Since members of this tribe are rarely bred in captivity, there are very few hybrid records stemming from this source.

This tribe, more than any other tribe in the Anatidae, can be characterized by possessing an extreme degree of sexual dimorphism in plumage, voice (and associated tracheal structures), and displays. Some of the most bizarre male plumage patterns and complex male courtship displays are found among these species, and, as a result, species often appear to be much more distantly related to one another than is probably actually the case. Thus, although practically every species of eider, scoter, and merganser has been placed by some taxonomists in monotypic genera, the bases for such genera have been the male secondary sexual characters that very likely act as isolating mechanisms to prevent hybridization among these closely related forms.

Male courtship displays among the sea ducks are so diverse that it is difficult to point out definite homologies even among such closely related species as the goldeneyes (*Bucephala*) and mergansers (*Mergus*). McKinney

(1961) has even found qualitative differences in the male courtship displays of two races of the Common Eider (*Somateria mollissima*). These elaborate (and relatively effective) behavioral isolating mechanisms led Myres (1959) to conclude that the sea ducks are "ancient and/or polyphyletic," but it seems more likely to me that they are, in fact, monophyletic and that the species are relatively well isolated from one another. Arguments in favor of a monophyletic origin have been presented elsewhere (Johnsgard, 1961*b*).

Behavioral isolating mechanisms are not limited to male courtship displays but may also be found in variations of female behavior patterns. Female Inciting is found in most, if not all, species but varies in form to a somewhat greater extent than is true of the preceding tribes. Except for the Inciting and warning notes, females of all species except eiders tend to be relatively silent. Male courtship calls are very diverse, and nearly every species may be readily recognized by its male courtship note alone.

Only a few unifying behavioral characteristics link all the members of this tribe. The most significant of these is the fact that females assume a Prone posture when soliciting copulation, and may remain in this posture for periods of several minutes. In some genera both sexes normally perform ritualized Drinking before this Prone posture is assumed, whereas in other genera no mutual preceding displays have been observed. Before mounting the female, the males of apparently all species perform various ritualized behavior patterns which may or may not differ markedly from normal comfort movements, and the composition, form, and in some cases the sequence of these movements appear to be of primary importance as isolating mechanisms. These precopulatory male displays are, however, much more conservative than are male courtship displays and provide the best behavioral evidence for judging relationships among genera. These displays include Preening-dorsally or Preening-behind-the-wing, Bill-dipping, and ritualized Drinking, Bathing, and Shaking ("Upwards-stretch" of Myres, 1959). In some species mounting is always immediately preceded by the Upwards-stretch, whereas in others it is always preceded by ritualized Preening-behind-the-wing. Ritualized approaches to the female occur in *Polysticta* and two species of *Bucephala*.

That isolating mechanisms might even operate during treading is suggested by the fact that males of several species of sea ducks vigorously Flick-the-wings (Myres, 1959) varying numbers of times while mounted, producing a drumming noise which very likely has signal value. Postcopulatory displays in the sea ducks are relatively variable. In some species (*Polysticta, Bucephala, Mergus cucullatus*), the male retains hold of the female's nape for several seconds, causing the birds to Rotate (Myres, 1959) about a point, before releasing her. The male may then perform one of its courtship displays (*Melanitta perspicillata, Polysticta, Somateria*) or may Steam away, while often performing lateral Head-turning movements (*Somateria, Polysticta, Bucephala, Mergus cucullatus*).

Tribe Oxyurini

The stiff-tailed ducks are relatively poorly studied from every standpoint, and it is not possible to discuss isolating mechanisms with any degree of assurance because of this fact. Of the 9 included species, 3 are in monotypic genera, and the 6 species of *Oxyura* are so distributed geographically that there is very little sympatry of ranges. Only in South America, where *Oxyura jamaicensis ferruginea* and *O. vittata* are partially sympatric with one another and with *O. dominica*, is there any great likelihood of hybridization, and the only possible record of hybridization within this tribe concerns these two former species.

Male plumage patterns vary less in *Oxyura* than in any other group of Anatinae, and likewise bill coloration is identical in all species. What little is known about male courtship displays, however, suggests that marked differences do occur as isolating mechanisms. Males of some and probably all species of *Oxyura* (as well as *Heteronetta* and *Biziura*) have inflatable tracheal or esophageal structures that function as noise-producing organs, and courtship postures seem to have evolved through the utilization of differing means of producing sound from these structures. Female vocalizations in *Oxyura* are rudimentary and, in *O. jamaicensis* at least, seem to consist of only an aggressive squeaking note. The female of this species also appears to lack anything related to Inciting, and her response to male displays is generally overt aggression.

It seems probable that the precopulatory behavior of *Oxyura* is more uniform than the male courtship displays of the various species. In *O. jamaicensis* this consists of Bill-dipping, followed by a rapid lateral Bill-flicking on the part of the male, to which the female's most frequent response is diving. Similar behavior has been described for several other species of *Oxyura*, but it is uncertain if this occurs in precopulatory situations. In the two species (*O. jamaicensis* and *O. australis*) for which postcopulatory behavior has been described, it differs markedly, so that postcopulatory displays may also be potential isolating mechanisms.

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SUMMARY

The family Anatidae is, for the most part, composed of numerous groups of closely related, often sympatric species which frequently have the capacity to produce fertile hybrids. Isolating mechanisms in these species are a combination of morphological (plumage and soft-part) and behavioral char-

acteristics. The relative importance of morphological and behavioral characteristics as isolating mechanisms varies somewhat in the subgroups (tribes) of the Anatidae. In addition, different aspects of behavior may assume varying degrees of importance as isolating mechanisms in these groups. However, it is generally true that vocalizations and male plumages and soft-part features are probably of greatest importance in preventing hybridization between closely related species, and male courtship displays are only slightly less important in this regard. Pre- and postcopulatory displays and female courtship displays are, on the average, less important as potential isolating mechanisms, and so are of greater taxonomic utility in the determination of evolutionary affinities.

REFERENCES CITED

DELACOUR, J. 1954–59. The waterfowl of the world. Country Life, London. 3 v.

GRAY, A. P. 1958. Bird hybrids. Commonwealth Agricultural Bureaux. Farnham Royal, Bucks, England. 390 p.

HEINROTH, O. 1911. Beitrage zur Biologie, namentlich Ethologie und Psychologie der Anatiden. Proc. V Intern. Ornithol. Congr., Berlin, 1910:598–702.

HOCHBAUM, H. A. 1944. The Canvasback on a prairie marsh. Am. Wildl. Inst., Washington, D.C. 201 p.

JOHNSGARD, P. A. 1960*a*. Hybridization in the Anatidae and its taxonomic implications. Condor 62:25–33.

———. 1960*b*. Classification and evolutionary relationships of the sea ducks. Condor 62:426–433.

———. 1961*a*. The taxonomy of the Anatidae—A behavioral analysis. Ibis 103a:71–85.

———. 1961*b*. The breeding biology of the Magpie Goose. Wildfowl Trust, Twelfth Ann. Rept., p. 93–103.

LORENZ, K. Z. 1951–53. Comparative studies on the behavior of the Anatinae. Avic. Mag. 57:157–182; 58:8–17, 61–72, 86–94, 172–184; 59:24–34, 80–91.

———. 1958. The evolution of behavior. Sci. Am. 199(6):67–78.

MCKINNEY, D. F. 1961. An analysis of the displays of the European Eider *Somateria mollissima* (Linnaeus) and the Pacific Eider *Somateria mollissima v. nigra* Bonaparte. Behaviour, Suppl. 7. 124 p.

MOYNIHAN, M. 1958. Notes on the behavior of the Flying Steamer Duck. Auk 75: 183–202.

MYRES, M. T. 1959. The behavior of the sea ducks and its value in the systematics of the tribes Mergini and Somateriini, of the family Anatidae. Ph.D. thesis, Univ. Brit. Columbia, Vancouver, B.C. 504 p.

YAMASHINA, Y. 1952. Classification of the Anatidae based on the cyto-genetics. Papers from the Coordinating Committee for Research in Genetics 3:1–34 [original not seen].