

SECTION III: CONSERVATION AND RESEARCH AT HOME AND ABROAD

COMPARATIVE BEHAVIOUR OF THE ANATIDAE AND ITS EVOLUTIONARY IMPLICATIONS

Paul A. Johnsgard¹

Summary

AN attempt has been made to summarize, in broad outline, the variations encountered in the behaviour of the Anatidae, and to relate these variations to their probable evolutionary significance. In particular, variations in manner of pair formation and pair bond length, in geographic distribution and ecology, and the related conditions of allopatry or sympatry with other species are discussed and their probable effects on behaviour are suggested. Instances are mentioned where a knowledge of behaviour would be helpful in judging evolutionary relationships that have thus far eluded taxonomists (e.g., *Stictonetta*, *Heteronetta*, *Thalassornis*), and likewise examples are pointed out where behavioural evidence suggests different relationships from those which are currently accepted (e.g., "*Lophonetta*," "*Anas*" *leucophrys*, and the eiders).

Introduction

The critical use of instinctive, or "species-typical," behaviour in systematic studies is a relatively recent, but increasingly important, taxonomic tool. Mayr (1958) has summarized the most important literature in this field, and has shown that behavioural information can often help to solve difficult evolutionary problems. Some of the classical contributions of behaviour to avian systematics, such as those of Heinroth (1911), Lorenz (1941; 1951-1953), and Delacour and Mayr (1945), have concerned waterfowl, and this group is particularly well suited to such a comparative approach.

An understanding of the significance of pair formation, pair bond strength, and the effects of sexual selection is vital to a proper taxonomic evaluation of instinctive, and especially sexual, behaviour, particularly because it varies greatly within the Anatidae. Thus in the subfamilies Anseranatinae and Anserinae (Delacour, 1954) the pair bond is normally lifelong, whereas in most of the Anatinae (except the Tadornini) the pair bond frequently lasts only for a single breeding season. As a result the former groups possess a much smaller capacity for genetic mixing in a large population. This is strengthened in geese and swans (Anserini) by the tendency for a pair's progeny to return to their place of hatching and to mate with closely related individuals, resulting in local inbreeding and thus favouring subspeciation (Mayr, 1942). In migratory ducks of the genus *Anas*, however, males normally mate on the wintering grounds and follow their mates to the females' natal homes, which may be a great distance from the males' birthplaces. This, of course, increases the tendency towards panmixia in duck populations and thus reduces subspeciation. Geese and swans do not become sexually mature until several years after hatching, resulting in a longer life cycle and a correspondingly reduced potential rate of genetic change. Most ducks, however, mature in their first year, and thus evolutionary adaptation is potentially much more rapid. This is also enhanced

¹Visiting scientist at Slimbridge from August, 1959; U.S. National Science Foundation Fellow.

by the larger average clutch size of ducks, which may provide a greater opportunity for selection to act on favourable genotypes. Finally, since in the Anseranatinae, Anserinae and possibly, the Tadornini pair bonds are permanent, mate selection normally takes place only once, and seems to be a very gradual process which allows for the "correction" of incipient mating errors between species. Correlated with this is the fact that in most species of these groups there is but a single moult per year (there is less need for a nuptial plumage after a pair bond is once formed), sexual dimorphism is generally almost lacking (apparently because of reduced sexual selection) and sexual displays are normally simple and are mutually performed by both sexes, since their primary function is probably sexual synchronization. In the rest of the Anatinae sexual selection is enhanced by the fact that mate selection generally occurs yearly, there is much sympatry of closely related species, and females "select" their mates (which are usually in surplus numbers and hence must compete for mates). These factors result in selection for species-recognition signals and male heterosexual stimuli, which generally include elaborate plumage and/or soft part colouration and conspicuous prenuptial displays. These morphological specializations and displays must differ enough among closely related, sympatric species to provide for species recognition and thus prevent hybridization. The evolution of male nuptial plumages, the compression of the winter plumage into the short "eclipse" plumage, the staggered period of pair formation among different species, and the other mechanisms which have been evolved as a result of these selective pressures have been described by Sibley (1957), and will not be further elaborated on here. Sibley has also reviewed the interesting examples of isolated populations (such as *Anas acuta eatoni* and *Anas platyrhynchos wyvilliana*) that have lost their sexual dimorphism as a probable result of the diminished selective pressures for species recognition in areas where no other closely related forms occur.

Summarizing these points, we should expect to find in inbreeding species with a long life cycle and permanent pair bond a relatively slow rate of adaptation, but a fairly strong tendency towards speciation and simple, mutual displays combined with sexual monomorphism and non-elaborate plumages. Conversely, in outbreeding species with a short pair bond and short life cycle we should expect a comparatively rapid rate of evolutionary adaptation but a relatively weak tendency towards continental speciation, and heterosexual, elaborate displays combined with plumage dimorphism. Males of sympatric, closely related species should differ in plumages and/or displays, although one would expect that the most closely related forms would share the greatest number of homologous, if somewhat modified, behavioural patterns. We may now examine the anatin groups, by tribes, to correlate these generalizations with individual cases. Except where recent evidence has suggested modifications, the groupings and scientific nomenclature used is that of Delacour and Mayr (1945) or Delacour (1954-1959).

SUBFAMILY ANSERANATINAE

The monotypic Magpie Goose, *Anseranas semipalmata*, differs from all other members of the Anatidae in numerous anatomical respects and in its general behaviour as well. Males and females are coloured alike, and differ

only slightly in voice and head shape; one would thus expect that any displays would be of a mutual nature. Delacour and Mayr (1945) state that there is no sign of any real display in the species, and the lack of any close relatives probably reduces selective pressures for species-specific behaviour. McKinney (1953) recorded wing-shaking derived from comfort movements as an epigamic display, but no detailed information on sexual behaviour is yet available. It would be of great interest to compare copulatory behaviour in this species with that of the South American screamers (Anhimidae) and the true geese.

SUBFAMILY ANSERINAE

Tribe Anserini

Sexual display in the geese and swans is mutual, and the sexes are generally almost identical in appearance. Sexual recognition and pair formation behaviour seems to have evolved from derivations of the threat displays towards other birds into mutual "triumph ceremonies," described well by Heinroth (1911). Precopulatory behaviour is essentially the same throughout the whole group, involving a rapid head-dipping in and out of the water by both sexes, reminiscent of and probably derived from bathing movements or, possibly, nest-building movements. Post-copulatory behaviour is also mutual and varies considerably among different species. Thus it may serve as an isolating mechanism, since "incorrect" post-copulatory responses can inhibit the formation of a permanent pair bond between two species (Heinroth, 1911).

The swans of the genus *Cygnus* can be divided behaviourally into two major groups. In one group (*olor*, *atratus*, and *melanocoryphus*) vocalizations are reduced, the wings are closed (*melanocoryphus*) or raised while folded (*atratus*, *olor*) during threat display, and the wings remain closed during post-copulatory display. In addition the species wing-flap with the bill pointed upwards (Poulsen, 1949), and in some species at least this wing flapping appears to be modified, or "ritualized" into a threat. The Black-necked Swan (*C. melanocoryphus*) deviates considerably from the other two, but all three species carry their young on the parents' backs, which the other species apparently never do. In the second group (*buccinator*, *cygnus*, *bewickii*, *columbianus* and *jankowskii*) vocalizations are elaborate (and visual plumage signals are correspondingly reduced), the wings are spread during threat display, and are flapped or waved during post-copulatory display and during triumph ceremonies. Species in this group wing-flap with a curved neck (as in geese).

Geese differ mainly from swans in their greater vocal versatility; their behaviour has been described at length by Heinroth (1911). Heinroth felt that the triumph ceremony serves an important role in pair formation, family bond development, sexual synchronization, and other important functions. Blurton Jones and Gillmor (1954) have investigated the components of the triumph displays of *Branta* and *Anser*, and have found that species differ in the number and elaboration of these various components, indicating their probable importance in species recognition. Pre-copulatory display consists of the typical head-dipping found in the swans, and post-copulatory display

is also mutual. The genus *Branta* appears to have fewer vocal signals than does *Anser*, and shows a corresponding increase in plumage pattern differentiation. This is especially true of head patterns, where the cheek and throat patches of *Branta* seem to be associated with flight intention head-tossing. Many species of *Branta* and *Anser* have striations on the neck feathering, which seems associated with the vibrating of the neck feathers in threat situations. All species of *Branta* and *Anser* but one (*A. canagicus*) have white under tail coverts, which is undoubtedly related to the male's courtship behaviour of swimming ahead of the female with the rear part of the body high in the water. Balham's (1954) exhaustive study of the Canada Goose (*Branta canadensis*) provides a basis for specific behavioural comparisons with other species.

The Cape Barren Goose (*Cereopsis novae-hollandiae*) has been placed, because of its general aggressiveness and downy young pattern, in the Tadornini, but numerous skeletal features indicate a closer relationship with the true geese (Verheyen, 1953). A conspicuous triumph ceremony is present in this species, and the similarity of the sexes in voice and display also suggests anserine affinities.

The Coscoroba (*Coscoroba coscoroba*) somewhat resembles the Mute Swan (*Cygnus olor*) in its threat and sexual behaviour, but it apparently forms a true link between the Anserini and the whistling ducks (Dendrocygnini). Pre-copulatory display is of the typical anserine type, although copulation occurs in shallow water (as in the Tadornini). Following copulation there is a mutual display in which both sexes stand together with their necks outstretched and their heads held high, as in the true geese.

Tribe Dendrocygnini

The whistling, or tree, ducks comprise eight species in the single genus *Dendrocygna*. As is true of geese, they are gregarious, highly vocal, and they pair for life. Thus there is little or no sexual dimorphism in plumage or voice, and their visual displays are simple and mutual. All species are very similar in their threat behaviour, which resembles that of true geese, but, as in the geese, these threat displays differ somewhat among different species and may provide clues to intrageneric relationships. No detailed behavioural studies have been done on the group, but evidently pre-copulatory display is the same as in geese and swans. Following copulation, the birds rise up side by side, call, and open one (the far) wing (Finn, 1919, Meanley and Meanley, 1958). Wing colouration in this group is very uniform, usually being black, which may be related to this display, although other body parts vary greatly in plumage and colour pattern. Their specialized downy pattern and tracheal structure indicate that they are more advanced than the Anserini, and are distinctly isolated from them and from the shelduck group.

Stictonetta

There is considerable anatomical evidence that the Freckled Duck (*Stictonetta naevosa*) is more closely related to the geese and swans than to the Anatinae (Verheyen, 1953), as indicated by its large lacrymal, reticulated tarsus, palatine shape, lack of tracheal bulla and the number of cervical

vertebrae. If this is true, it possibly should be accorded a monotypic tribal rank ("Stictonettini"). Its sexual behaviour is still unknown, and a knowledge of it would doubtless aid much in determining the relationships of this extremely aberrant species.

SUBFAMILY ANATINAE

Tribe Tadornini

The sheldgeese and shelducks form a smooth transition between the Anserinae and the Anatinae, indicating the largely artificial distinction between the groups. Like geese and swans, most species pair for life, and in some the sexes are coloured alike. However, in the shelducks at least, there are two molts per year (as in true ducks), and pair bonds are not always permanent (Heinroth, 1911). In most species the pre-copulatory display is of the typical anserine type. However, the sexes differ in their vocalizations, threat, and sexual displays, and in some forms the sexes are coloured very differently. Threat displays usually involve a lifting of the folded wings, the upper and under coverts of which are generally white and very conspicuous. Metallic coloured wing specula (and associated mock preening) are also first encountered in this group, as is the "Inciting" behaviour of females; these characteristics are typical of most of the Anatinae.

The group seems most closely linked with the true geese (and *Cereopsis*) through the Abyssinian Blue-winged Goose (*Cyanochen cyanopterus*), which lacks white wing coverts and, a sharply distinct speculum, both sexes having very similar voices and displays. In the closely related genus *Chloëphaga* there is a remarkable, and as yet unexplained, variation between plumage monomorphism and dimorphism in the two sexes. In all, however, the sexes' voices and displays are very different, the female exhibiting typical inciting behaviour and the male possessing various threat postures. These threat postures reach their highest degree of elaboration in the Andean Goose (*C. melanoptera*). Modifications of the anserine dipping movements are used in pre-copulatory display, which occurs on land or calm water. The closely related genera *Neochen* and *Alopochen* link the typical sheldgeese with the shelducks (*Tadorna*) both in behaviour and morphology. In *Tadorna* the pre-copulatory behaviour may involve mutual bathing, head-dipping, or head-bobbing motions, or the female may assume the receptive posture without previous mutual display (Poulsen, 1957). Pre-copulatory preening occurs in *T. tadorna*; ritualized preening is typical of most of the other Anatinae. Post-copulatory display in *Tadorna* usually consists of the male raising one wing while the female remains crouched, as is also true in *Alopochen* and *Chloëphaga*.

The steamer ducks of South America (*Tachyeres*) are of dubious relationships; Moynihan (1958) found that their threat and pre-copulatory displays are of the typical Tadornini pattern, but that other displays are distinct enough to warrant their placement in a special, separate tribe ("Tachyerini"). Post-copulatory displays involve both sexes swimming apart in an alert posture, with "Head-flagging" and "Grunting."

Tribe Cairinini

The perching ducks were placed by Delacour and Mayr (1945) between the Aythyini and the Mergini, apparently largely because their nesting habits are similar to the latter, but hybridization evidence indicates, rather, that they belong between the Tadornini and the Anatini (Johnsgard, 1960a). The group consists of about a dozen species which possess a strange mixture of very generalized, or "primitive," and highly specialized features. Part of the tribe (*Plectropterus*, *Cairina*, and *Sarkidiornis*) seems, in fact, to represent a group of "relict" species which probably most closely approximate the generalized anatine condition, from which the more specialized groups have radiated. In this more generalized group plumages are generally metallic in both sexes and lack specialized patterns, vocalizations are poorly developed, displays are rudimentary, and pair bonds are weak or absent. No eclipse plumage is present, and even during the breeding season the sexes rarely associate. Copulation in at least two genera (*Cairina* and *Sarkidiornis*) is characterized by the male brutally attacking and raping the female, and the great size dimorphism of the sexes in these species seems to be related to this fact. The African Hartlaub's Duck ("*Cairina*" *hartlaubi*) shows little behavioural similarity to the other species of *Cairina*; likewise both the adult and downy plumages deviate from that genus and suggest affinities with the Anatini. It seems likely that it should be maintained in a separate genus (*Pteronetta*) until its relationships are better understood.

The rest of the Cairinini consists of several genera which show striking similarities to representatives of other tribes (e.g., *Chenonetta* with Tadornini, *Aix* with *Anas*, *Amazonetta* with *Aythya*), thus emphasizing the central position of the Cairinini in the subfamily Anatinae. Unlike the previous group, plumages are usually different in the two sexes, and metallic colouration usually occurs in restricted areas (usually wing and head regions) and in highly specialized patterns. Vocalizations are relatively complex, displays are often elaborate, and pair bonds are stronger. An eclipse plumage occurs in two genera (*Aix* and *Nettapus*), and the sexes associate throughout the year.

There is little known about the behaviour and displays of the pigmy geese (*Nettapus*), but apparently the striking wing patterns are displayed in some species (Delacour and Mayr, 1945). Delacour's (1945) description of the Maned Goose's (*Chenonetta jubata*) displays indicate affinities with *Aix*, and the post-copulatory behaviour consists of an exaggerated and prolonged raising of the male's hindquarters as it swims away from the female, an action only slightly indicated in *Aix* (D. F. McKinney, pers. comm).

The behaviour of the Wood Duck (*Aix sponsa*) has been thoroughly discussed by Heinroth (1910) and Lorenz (1951-1953); these authors have also provided the most complete account of the Mandarin Duck's (*Aix galericulata*) behaviour. The males of these species possess the most elaborate plumage patterns to be found in the Anatidae, and a knowledge of their behaviour contributes to the understanding of this remarkable plumage specialization. Additional comments on the relations between the plumage and behaviour of these species are presented by Dilger and Johnsgard (1959).

The behaviour of the Brazilian Teal (*Amazonetta brasiliensis*) provides a fascinating mixture of components found in species of several different tribes.

The male's wheezy whistle is reminiscent of *Aix*, but the female's inciting is rather like some species of *Anas* or *Aythya*. Female pre-copulatory behaviour is an *Anas*-like head-pumping rather than the soliciting posture of female *Aix*, and following copulation the male swims away in a rigid posture astonishingly like the post-copulatory display of *Netta* and *Aythya* (D. F. McKinney, pers. comm.) and *Anas angustirostris*.

The Ringed Teal ("*Anas*" *leucophrys* of Delacour and Mayr, 1945) seems to belong to the perching duck tribe rather than the Anatini (von Boetticher, 1952), as indicated by its hole-nesting habits, hybridization with *Amazonetta brasiliensis*, and other evidence. Furthermore, the behaviour and voice of the female Ringed Teal is extremely like that of *Aix*, and the copulatory behaviour of the species is also very similar to that of *Aix*, but is totally unlike *Anas*. I therefore believe that the Ringed Teal should be placed in a separate genus *Callonetta* (as originally proposed by Delacour, 1936) and be included in the perching duck tribe adjacent to *Aix*.

Tribe Anatini

This large tribe of typical surface-feeding ducks is comprised of one large genus *Anas* (about 35 species) and several aberrant monotypic genera of dubious relationships. Although males of most species of *Anas* differ greatly in appearance the females tend to be more similar. Display patterns are also similar, and the remarkable degree of interspecific hybrid fertility indicates a closely knit evolutionary group that justifies a broad generic concept. This tribe also typifies the mating situation outlined for ducks earlier, namely a short pair bond, strong sexual selection resulting from male competition for mates, and a high capacity for rapid evolutionary changes by means of a short life cycle and high fecundity.

The displays of two of the monotypic genera, *Hymenolaimus* and *Malacorhynchus*, are so poorly known that they can be omitted here. According to Delacour and Mayr (1945) the major display of the now-extinct Pink-headed Duck (*Rhodonessa caryophyllacea*) was a wheezy neck-stretching, probably corresponding to the "Burp" of male *Anas*, or possibly to the courtship call of male *Aythya*, to which it may be more closely related, as is indicated by its tracheal structure. The highly specialized Torrent Duck (*Merganetta armata*) is also poorly known, but the descriptions of Phillips (1953) and Scott (1954) indicate that the species' behaviour is unique, and shows no distinct similarity to typical *Anas* behaviour.

The behaviour of 14 species in the genus *Anas* (*sensu* Delacour and Mayr) has been carefully investigated by Lorenz (1941; 1951-1953). He has pointed out numerous behavioural homologies among related species, and has thus determined the probable major evolutionary relationships within the group. This important work cannot be adequately summarized here, and should be read in its complete form for details. Most species studied by Lorenz are characterized by numerous display patterns, the number and form of which are usually shared by other species in direct proportion to their degree of evolutionary relationships as suggested by other characters. However, some species (such as *Anas georgica spinicauda*) lack individual displays that are found in closely related species, and it appears probable that this is the result of a secondary loss of such displays, possibly under

the impact of selection for isolating mechanisms under conditions of sympatry. Recent research (Lorenz, 1958) has indicated that the genetic factors governing such displays may be present in a latent condition in these species, and the displays may only appear in hybrid matings. It would be expected that such a secondary loss of an individual display pattern might occur in a region of sympatry with another closely related form in which this pattern forms an important part of its species-recognition system.

Certain behavioural patterns have been found in all the species of *Anas* thus far studied. For example, female inciting has been found in every species observed, and it appears to play a basic role in the pair-formation process of at least some species of *Anas* (Johnsgard, 1959, 1960b). Likewise in the case of males the orientation of the back of the head towards a "courted" female appears to be of primary significance in many species, and special head feather patterns are often exhibited during this display. Pre-copulatory display in all species studied involves a mutual head-bobbing. No special female post-copulatory displays have been recorded, but in males these vary from elaborate displays (as in the mallard group) to those species where such displays are rudimentary or lacking. Major male social displays in *Anas* include (in Lorenz's 1951-1953 terminology) "Burping," the "Grunt-whistle," "Head-up-tail-up," "Down-up," "Bridling," "Chin-lifting," and others. Generalized patterns typical of nearly all species include ritualized preening, drinking, and shaking movements. Correlated with these behavioural patterns, males of many species possess erectile crests or otherwise specialized head plumage, many have elaborate scapular feathering or tail feathers, and nearly all have metallic-coloured specula. Bright bill colouration is also typical of many species.

Behavioural evidence (such as the presence of a "Grunt-whistle") indicates that the Andean Crested Duck ("*Lophonetta*" *specularioides*) should be regarded as a member of the genus *Anas*, probably most closely related to *specularis*, rather than an aberrant shelduck such as Delacour and Mayr (1945) considered it to be.

Tribe Aythyini

The diving duck tribe is much like the preceding one in that the pair bond is short, there are numerous sympatric and closely related species, and there is a one or two year period to maturity. All species exhibit sexual dimorphism, particularly in the head and iris colouration. Metallic-coloured specula are lacking in all species, but white specula are characteristic of most, and mock preening occurs in most if not all species.

Sexual displays in the group show remarkable uniformity, and justify the broad generic concept of Delacour and Mayr (1945). In fact, *Netta rufina* shows such great similarities to some of the Anatini and *Netta erythrophthalma* shows so many characteristics of *Aythya* that any distinct generic separation is difficult. The sexual behaviour is outwardly rather different from that of *Anas*, but the fact that fertile *Anas* x *Aythya* hybrids have been reared on several occasions (Gray, 1958) indicates that the two groups must actually be fairly closely related. In at least one species (*Netta rufina*), pre-copulatory behaviour approaches *Anas*-like head-bobbing, but in most species of *Aythya* thus far studied the female assumes a receptive posture without previous

mutual head-bobbing display. Post-copulatory display in all species of *Netta* and *Aythya* thus far observed is essentially identical, but different from that of *Anas*. The male calls, then swims in a rigid posture with the head pointed downwards and the bill pressed against the breast. Females of most, and probably all, species have inciting displays which contain a strong chin-lifting component (as in the blue-winged ducks and shovelers), alternating with pointing movements.

Almost no comparative behavioural studies on the Aythyini have been published. Lind's (1958) study of the Red-crested Pochard (*Netta rufina*) provides almost the only information on that genus, and Hochbaum's (1944) account of Canvasback (*Aythya vallisneria*) displays is the most complete description of typical *Aythya* behaviour. A courtship call, emitted with a curved neck or head-throw is the major *Aythya* display, and is probably homologous with the "Sneeze" of *Netta rufina* and, possibly, the "Burp" of *Anas*. Neck-stretching occurs in both sexes of many species, and is apparently equivalent to the "Chin-lifting" of *Anas*. The posture Hochbaum termed the "Sneak" is also typical of many species.

Male head-throws have been recorded for all species of *Aythya* except *innotata* (the displays of which are undescribed), as well as for *Netta erythrophthalma* and *N. peposaca*. Group chases over the water surface by several males after a female are typical of this group, and seem to represent a ritualized version of the rape chases that are found in many species of *Anas*.

The Eiders

The four species of eiders were placed by Delacour and Mayr (1945) in the Tribe Mergini, but Delacour later (1956) stated that they belong in a separate tribe, the Somateriini, adjacent to the Anatini. This decision was apparently based on Humphrey's (1958) studies on tracheal anatomy, in which aspect the eiders do resemble the *Anas* group. However apart from this detail of anatomy, and a superficial similarity in female plumages to *Anas* (which is probably the result of selection for concealing colouration in similar nesting habitats), there seems to be little reason to suspect any close relationships between these groups. Myres' recent (1959) comparative behavioural study of the group resulted in his conclusion that the eiders show no behavioural similarity with *Anas*, and also are fairly distinct from the other sea ducks. Females show the inciting behaviour found in the Anatini, Aythyini, and the goldeneyes (*Bucephala*) and mergansers (*Mergus*), and likewise solicit copulation in a prone posture as do the Aythyini and the Mergini. Male displays deviate from those of all other ducks, and thus shed no light on relationships. Male pre and post-copulatory behaviour greatly resembles that of the goldeneyes (*Bucephala*), with many ritualized comfort movements included in the displays (Hoogerheide, 1950).

Tribe Mergini

This tribe of sea ducks differs from the Aythyini mainly in that the species do not achieve sexual maturity until their second or, possibly, third year (in scoters), and they also tend to subsist to a greater degree on a diet

of animal matter. Most forms are Northern Hemisphere in distribution, and there is much sympatry of ranges. Some of the most elaborate displays and male plumage patterns in the entire family Anatidae are found in this tribe. Only two species (the isolated Southern Hemisphere mergansers *Mergus australis* and *M. octosetaceus*) lack sexual dimorphism. Specialized colour patterns tend to occur on the heads, bills, and wings. Erectile crests occur on some species, and sexual dimorphism is frequent in bill, foot, and eye colouration.

Displays in the group are often extremely complex, and it is difficult to generalize on them or to point out homologies. Detailed information is not available for many species, but Myres (1959a) has well summarized the published information and added many additional observations. It may be said that the scoters (*Melanitta*) are the most generalized of the group, and their displays tend to be derived from simple comfort movements. In this group, as in the eiders, bill shape and colouration probably plays an important role in species recognition. McKinney (1959) and Myres (1959b) have described copulatory behaviour of scoters, which is comprised primarily of ritualized comfort movements, such as drinking, preening, stretching and shaking.

The behaviour of the Old-squaw, or Long-tailed Duck (*Clangula hyemalis*) and Harlequin (*Histrionicus histrionicus*) is still inadequately known, but both species appear to have head-throw displays and other displays associated with loud and elaborate calls.

The goldeneyes and Bufflehead of the genus *Bucephala* show striking variations in their behavioural patterns, and Myres feels that the Bufflehead (*B. albeola*) probably deserves generic separation from the goldeneyes on this basis. The displays of the goldeneyes are exceedingly complex, and have been studied by several workers, including Myres (1957), B. Dane *et al* (1959) and others. Myres (1959b) has also described the copulatory behaviour of the Bufflehead, which is essentially like that of the goldeneyes and scoters.

Behaviourally, the goldeneyes seem to be linked to the mergansers through the Smew (*Mergus albellus*) (Lebret, 1958), which exhibits characteristics of both groups and has frequently hybridized in the wild with goldeneyes. The Hooded Merganser (*Mergus cucullatus*) appears to be similar to the Smew in its displays, but the Red-breasted Merganser (*M. serrator*) and Goosander (*M. merganser*) show surprising differences in their male display patterns. However, the mating behaviour of the females of these species is relatively uniform. Nothing is known concerning the displays of the Chinese Mergansers (*M. squamatus*), and very little is known concerning the Southern Hemisphere species. Copulatory behaviour of the mergansers is only very poorly understood. In all species where it has been described the female assumes a receptive posture after mutual drinking display (as in goldeneyes), and the males of at least some species perform ritualized preening and drinking movements, which in the Hooded Mergansers are linked into a sequence almost identical with that found in the goldeneyes.

Subspeciation is very evident in some species of sea-ducks such as the Common and Velvet Scoters (*Melanitta nigra* and *M. fusca*) and the Common Eider (*Somateria mollissima*). This is probably the result of the wide ranges of these forms and the numerous disjunct breeding and wintering areas.

It is interesting that in these cases the American races, which are subjected to the greatest amount of sympatry with other species, have the most elaborate male signal characters of bill form and colouration, whereas the Atlantic races tend to have these characters reduced. It appears likely that in these species the recognition characters have been reinforced in the areas where possibilities for incorrect mate selection are greatest.

Tribe Oxyurini

The stiff-tail group represents a unique section of the Anatidae that has deviated greatly from the remainder of the family in morphology, ecology, and behaviour. The tribe consists of a diverse group of genera which are of uncertain relationships to one another and to the rest of the family. In contrast to nearly all of the other Anatinae, males of all species lack a tracheal bulla, and correlated with this there has been the development of a sound-producing tracheal air sac system. Sexual behaviour has become modified for sound production by this means, and it is a significant fact that in this group, which inhabits weedy, overgrown ponds, auditory rather than visual displays appear to be of prime importance. Although males differ in appearance from females in most species, visual display characters mainly involve bill colour and, in some forms, head colouration. The relatively minor importance of plumage in species-recognition is shown by the fact that in South America two species (*Oxyura vittata* and *O. jamaicensis ferruginea*) occur sympatrically which have almost identical male plumage patterns. However, according to Dr. Martin Moynihan (*in litt.*) these species' displays (and associated vocalizations) are much more different than the degree of difference found in most species of *Anas*. In this group taxonomists must therefore rely on behavioural characteristics and the anatomical basis of display (the oesophagus and tracheal air sac) rather than upon external features. In this respect, the North American Ruddy Duck (*Oxyura j. jamaicensis*) and the Peruvian Ruddy Duck (*O. j. ferruginea*) have essentially identical displays (Moynihan, *in litt.*), but differ greatly from the Argentine Ruddy Duck (*O. vittata*). Correlated with this, the Argentine Ruddy Duck has an inflatable oesophagus and a weakly developed tracheal air sac (Wetmore, 1926), indicating a different means of sound production. By inflating the oesophagus and using jerky head and neck movements to produce sounds, the Argentine Ruddy Duck appears to be similar in its displays to the African Maccoa Duck (*O. maccoa*) and possibly the Australian Blue-billed Duck (*O. australis*). In the North American Ruddy Duck (*O. j. jamaicensis*) the sound produced during display is for the most part a mechanical one, caused by the bill striking the inflated air sac.

No comparative behavioural studies have been done on the tribe as a whole, and to date not even a single species' behaviour has been adequately described. The nearly completed studies of Miss Helen Hays on the North American Ruddy Duck will, however, provide an important contribution to our understanding of the group. Some behavioural information is available for *Oxyura australis* (Brown, 1949; Wheeler, 1953; Scott, 1958) and *Biziura lobata* (Serventy, 1946). In those species where display has been observed, the tail is cocked upwards and some kind of head jerking or bobbing is utilized to produce sound. A backward foot-kicking has also been observed in several

species. Wheeler (1953) has provided the only published account of copulatory behaviour for any species in the group, which in *Oxyura australis* involves an underwater chase, with the female being completely submerged during copulation. According to Miss Helen Hays (pers. comm.), this is entirely different from copulatory behaviour in *O. j. jamaicensis*, in which "Bill-flicking" is the primary male pre-copulatory display, and the usual head-bobbing, or "Bubble," display follows copulation.

Practically no behavioural information is available regarding the Black-headed Duck (*Heteronetta atricapilla*) and the White-backed Duck (*Thalassornis leuconotus*), both of which are only dubiously included in the stiff-tail group. A knowledge of the Black-headed Duck's behaviour would be of great interest, not only because of its uncertain affinities, but also because of its parasitic nesting behaviour, which must certainly have modified sexual behaviour and pair formation.

PROSPECTS FOR FUTURE BEHAVIOURAL RESEARCH

As is all too evident from the above discussion, great gaps still remain in our knowledge of the general behavioural patterns of many species, to which any interested person could contribute much. In no case, even in the commonest species, is any waterfowl species so thoroughly understood that it would not be worthy of additional detailed study. Indeed, careful quantitative study of a single form or a few closely related forms is more likely to greatly increase our knowledge of the function and evolution of behavioural differences than simply pursuing broad-scale qualitative studies. Examples of situations which could be studied especially profitably are (1) geographic variations in the behaviour of well-marked subspecies and (2) variations in the behaviour of closely related, sympatric forms. In the former case, D. F. McKinney's uncompleted studies on the races of the Common Eider (*Somateria mollissima*) will be of great interest, and other promising examples include the races of Common Teal (*Anas crecca*), Velvet Scoter (*Melanitta fusca*) and Canada Goose (*Branta canadensis*), to mention only a few. Examples of studies where the effects of secondary contact in closely related, but rarely hybridizing, forms might be profitably investigated include Grey and Chestnut-breasted Teal (*Anas gibberifrons* and *A. castanea*), Greater and Lesser Scaup (*Aythya marila* and *A. affinis*), and the Goldeneyes (*Bucephala clangula* and *B. islandica*). Cases where secondary contact of incipient species is accompanied by frequent hybridization are especially instructive, as, for example, where the Mallard (*Anas platyrhynchos*) is in contact with the Black Duck (*A. rubripes*) and the Grey Duck (*A. superciliosa*). Finally, the comparison of mainland forms with island races that have lost most of their secondary sexual characteristics of plumage could provide an insight into a similar secondary loss of behavioural characteristics which might have occurred.

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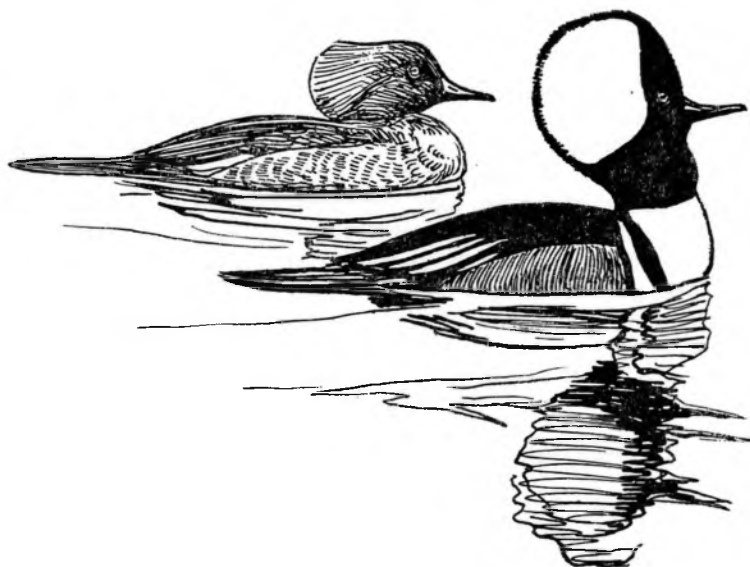
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LITERATURE CITED

- BALHAM, R. W. (1954). The behaviour of the Canada Goose (*Branta canadensis*) in Manitoba. Ph.D. Dissertation, Univ. of Missouri. 244 pp.
- BLURTON JONES, N. G., and R. A. F. GILLMOR. (1954). Triumph display in geese. *Wildfowl Trust Sixth Annual Report*: 82.
- BROWN, G. (1949). Display of Blue-billed Ducks. *Emu*, 48:315.
- DANE, B., C. WALCOTT and W. H. DRURY. (1959). The form and duration of the display actions of the Goldeneye (*Bucephala clangula*). *Behaviour* 14:265-281.
- DELACOUR, J. (1936). Note sur la classification des Anatidés. *Oiseau* 6:366-379.
- DELACOUR, J. (1945). The display of the Maned Goose. *Wilson Bull.*, 57:129.
- DELACOUR, J. (1954, 1956, 1959). *The Waterfowl of the World*. 3 vol. Country Life, London.
- DELACOUR, J. and E. MAYR. (1945). The family Anatidae. *Wilson Bull*, 57:3-55.
- DILGER, W. C. and P. A. JOHNSGARD. (1959). Comments on "species recognition" with special reference to the Wood Duck and the Mandarin Duck. *Wilson Bull.*, 71:46-53.
- FINN, F. (1919). *Bird Behaviour*. London, 363 pp.
- GRAY, A. P. (1958). *Bird Hybrids*. Commonwealth Agricultural Bureau of England. 390 pp.
- HEINROTH, O. (1910). Beobachtungen bei einem Einbürgerungsversuch mit der Brautente (*Lampronessa sponsa* (L.)). *Journ. für Ornith.* 58:101-156.
- HEINROTH, O. (1911). Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. *Verh. V Int. orn. Kongr., Berlin*. 1910. pp. 598-702.
- HOCHBAUM, H. A. (1944). *The Canvasback on a Prairie Marsh*. Amer. Wildl. Inst., Washington. 201 pp.
- HOOGERHEIDE, C. (1950). De Eidereenden. *Somateria mollissima* L., of Vlieland. *Ardea*, 37:139-160.
- HUMPHREY, P. S. (1958). Classification and systematic position of the eiders. *Condor*, 60:129-135.

- JOHNSGARD, P. A. (1959). Evolutionary relationships of the North American mallards. Ph.D. Dissertation, Cornell University. 153 pp.
- JOHNSGARD, P. A. (1960a). Hybridization in the Anatidae and its taxonomic implications. *Condor*, 62:25-33.
- JOHNSGARD, P. A. (1960b). A quantitative behavioural study of the Mallard and the Black Duck. *Wilson Bull.*, (In Press).
- LEBRET, T. (1958). Baltsbewegingen van het Nonnetje, *Mergus albellus* L. *Ardea*, 46:75-79.
- LIND, H. (1958). Eine untersuchung über das Balzverhalten der Kolbenente (*Netta rufina* Pallas). *Zeitschrift für Tierpsychologie*, 15:99-111.
- LORENZ, K. Z. (1941). Vergleichende Bewegungstudien an Anatinen. *Journ. für Ornith.*, 89 (Suppl.): 194-294.
- LORENZ, K. Z. (1951-1953). Comparative studies on the behaviour of the Anatinae. *Avic. Mag.*, 57:157-182; 58:8-17, 61-72, 86-94, 172-184; 59:24-34, 80-91.
- LORENZ, K. Z. (1958). The evolution of behaviour. *Sci. Amer.*, 199(6):67-78.
- MCKINNEY, D. F. (1953). Studies on the behaviour of the Anatidae. Ph.D. Dissertation, University of Bristol. 227 pp.
- MCKINNEY, D. F. (1959). Waterfowl at Cold Bay, Alaska, with notes on the display of the Black Scoter. *Wildfowl Trust Tenth Annual Report*: 133-140.
- MAYR, E. (1942). *Systematics and the Origin of Species*. Columbia Univ. Press New York. 334 pp.
- MAYR, E. (1958). Behaviour and systematics. In: *Behaviour and Evolution*. Yale University Press, New Haven. 557 pp.
- MEANLEY, B. and A. G. MEANLEY. (1958). Post-copulatory display in Fulvous and Black-bellied Tree Ducks. *Auk*, 75:96.
- MOYNIHAN, M. (1958). Notes on the behaviour of the Flying Steamer Duck. *Auk*, 75:183-202.
- MYRES, M. T. (1957). An introduction to the behaviour of the goldeneyes (*Bucephala islandica* and *B. clangula* (Class Aves, Family Anatidae)). M. A. Thesis, University of British Columbia, 254 pp.
- MYRES, M. T. (1959a). The behaviour of the sea-ducks and its value in the systematics of the tribes Mergini and Somateriini, of the family Anatidae. Ph.D. Dissertation, University of British Columbia. 504 pp.
- MYRES, M. T. (1959b). Display behaviour of Bufflehead, scoters and goldeneyes at copulation. *Wilson Bull.*, 71:159-168.
- PHILLIPS, S. (1953). An incident concerning the Peruvian Torrent Duck. *Avic. Mag.*, 59:134.
- POULSEN, H. (1949). Bidrag til Svanerne Ethologi. *Dansk. Ornith. Foren. Tidsskr.*, 42:173-201.
- POULSEN, H. (1957). Notes on the mating behaviour of the Sheld-duck. (*Tadorna tadorna* (L.)). *Dansk. Ornith. Foren. Tidsskr.*, 51:115-118.
- SCOTT, P. (1954). Behaviour of the Bolivian Torrent Duck. In: *Wildfowl Trust Sixth Annual Report*: 69-72.

- SCOTT, P. (1958). Notes on Anatidae seen on world tour. *Wildfowl Trust Ninth Annual Report*: 86-112.
- SERVENTY, V. N. (1946). Display in the Musk Duck. *Emu*, 45:318-321.
- SIBLEY, C. G. (1957). The evolutionary and taxonomic significance of sexual dimorphism and hybridization in birds. *Condor*, 59:166-191.
- VERHEYEN, R. (1953). Contribution à l'Ostéologie at à la Systématique des Ansériformes. *Gerfaut*, 43 (suppl.): 373-497.
- VON BOETTICHER, H. (1952). *Gänse und Entenvögel aus aller Welt*. Die Neue Brehm-Bücherei, Heft 73. 95 pp.
- WETMORE, A. (1926). *Observations on the Birds of Argentina, Paraguay, Uruguay and Chile*. Bull. U.S. Nat. Mus., Washington. 448 pp.
- WHEELER, J. R. (1953). Notes on the Blue-billed Ducks at Lake Wendouree, Ballarat. *Emu*, 53:280-282.



Hooded Merganser *Mergus cucullatus* displaying