Evolutionary trends in the behaviour and morphology of the Anatidae

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Summary

THE major evolutionary trends most clearly evident in the Anatidae are as follows:

1. A trend from monomorphism to dimorphism in plumage, voice (including tracheal structure) and displays, in association with a trend from long pair bonds to temporary pair bonds.
2. A trend from generalized nesting and feeding adaptations to highly specialized ones, with associated specializations in diving adaptations and bill structure.
3. A trend from a single yearly body molt to two molts of the body plumage yearly, usually with an associated separation of nuptial and postnuptial (" eclipse ") plumages in males.
4. A trend towards the development of elaborate, often metallic-coloured, male plumage patterns and wing specula, associated with displays that exhibit these patterns.

Introduction

During the years 1959 to 1961 I was engaged in a comparative study of the family Anatidae, which was primarily behavioural in approach. Parts of this study have been published previously or are yet to be published, but there are certain aspects of the findings which have a bearing on the broader aspects of evolution in birds which will be presented here. These deal with variations in behaviour within the Anatidae that can be traced through many or most taxa of the family and which exhibit changes that can be related to the apparent trends of evolutionary specialization within the group. In the discussion which follows, the taxonomic arrangement is basically that proposed by Delacour and Mayr (1945), as later modified by Delacour (1954-59), but with certain additional modifications indicated by my own studies (Johnsgard. 1961a).

It should be stated at the outset that the impossibility of arranging groups of contemporaneously existing species into sequences of " primitive " to " advanced " species is well recognised (Lorenz, 1951-53). However, it is entirely justifiable to evaluate the number of generalized and presumably primitive features of a species against its specialized features and thus arrange species into series which approximate the trend from generalization to specialization, assuming that no secondary reversion towards generalization has occurred. Such a sequence of intra-familial groups (tribes) of Anatidae, when so arranged, correlates well with the sequence of these groups when arranged according to probable evolutionary relationships, suggesting that in this family the evolutionary trend has been essentially unidirectional, from generalized to more specialized conditions. The sequence of tribes, as used here, will be listed below, together with collective English names for the groups that are used in this paper. The tribal sequence and composition differs only in minor respects from that proposed by Delacour (1954-59):

[1]Studies from the Dept. of Zoology, University of Nebraska, No. 340.

Subfamily Anseranatinae
Tribe Anseranatini—Magpie Goose (1 species)
Subfamily Anserinae
Tribe Dendrocygnini—Whistling (" Tree ") Ducks (8 spp.)
Tribe Anserini—Swans and True Geese (21 spp.)
(Tribe Stictonettini—Freckled Duck)*
Subfamily Anatinae
Tribe Tadornini—Sheldgeese and Shelducks (15 spp.)
(Tribe Tachyerini—Steamer Ducks (3 spp.))*
Tribe Cairinini—Perching Ducks (13 spp.)
Tribe Anatini—Dabbling (or Surface-feeding) Ducks (39 spp.)
Tribe Aythyini—Pochards (16 spp.)
Tribe Mergini—Sea Ducks (including eiders) (20 spp.)
Tribe Oxyurini —Stiff-tailed Ducks (8 spp.)
* Tentative tribe.

General Behaviour

Diving

All waterfowl share certain aspects of general behaviour that are fundamentally important to their survival. Thus apparently all species are able to dive underwater for foraging or to escape from enemies, although I have not personally observed nor read of diving in the Magpie Goose *Anseranas semipalmata*. This species is the least aquatic of all the Anatidae, and its feet are only slightly webbed. Frequent diving for food is found in only some tribes of waterfowl. All species of whistling ducks (*Dendrocygna*) dive when foraging, and keep their wings closed when so doing. However, they perform a coot-like " jump " almost out of the water as they dive vertically downwards. Apparently none of the swans, true geese, sheldgeese and shelducks dive when foraging. Steamer Ducks (*Tachyeres*), which appear to be only remotely related to shelducks, do dive frequently for molluscs and crustaceans. In captivity the Falkland Flightless Steamer Duck *T. brachypterus* uses its wings when submerging, in the same manner as do eiders and other heavy-bodied waterfowl.

Among the perching ducks, none are efficient divers, although it has been reported that in the wild the White-winged Wood Duck *Cairina scutulata* sometimes feeds on small fish and presumably dives when catching them. I have noticed that in captivity this species dives with difficulty and uses its wings when submerging. I have been informed of Mandarin Ducks *Aix galericulata* diving and have rarely observed Wood Ducks *Aix sponsa* diving for food, and the latter also opened the wings when submerging. It is doubtful if any of the anatid species which typically open the wings when diving normally use them for underwater propulsion in the manner of auks (Alcidae) or penguins (Spheniscidae). Rather, the sudden and single flap of the wings during diving seems to function solely for assistance in submerging.

Most if not all species of dabbling ducks dive occasionally in foraging, although the wigeon group appears to be an exception. Most species of *Anas* open their wings when diving, but the Cape Teal *Anas capensis* does not, nor does the small Kerguelen Island race of the Pintail *Anas acuta eatoni*. This suggests that the smaller-bodied ducks, with relatively greater foot area for their body mass, need not use their wings for extra assistance in submergence. Although Torrent Ducks *Merganetta armata* dive frequently when feeding on aquatic larvae, their major food, their manner of diving has not been described in detail to my knowledge. The Blue Duck *Hymenolaimus malacorhynchus*, another stream-dwelling species, dives well in captivity but I have noticed that it too uses its wings when submerging.

The three remaining tribes—Aythyini, Mergini and Oxyurini—are all composed of species which are predominantly diving birds. Of these, the primarily vegetarian forms (the pochards and stiff-tails) and the mollusc and crustacean eaters (eiders and scoters) are rather heavy-bodied, and eiders (*Somateria* and *Polysticta*) and scoters (*Melanitta*) typically open their wings varying amounts when diving. The more streamlined goldeneyes (*Bucephala*) and mergansers (*Mergus*) are superb divers and almost never open their wings. However, during strenuous bathing (" dashing and diving ") or when escaping from an enemy, even these species open their wings and " fly " into the water. Because of the extreme posterior placement of their large feet, the stiff-tails are perhaps the most consummate divers of all the Anatidae, and approach the grebes (Podicipidae) in their skill in submerging. In achieving this, however, they have sacrificed the ability to walk readily and are relatively helpless on land.

Trends in diving therefore, have apparently been from a semi-terrestrial existence where diving is rarely, if ever, performed, to one where adaptations for diving have precluded life on dry land.

Nesting

Nest construction and nest site selection are highly adaptive characters and, as might be expected, vary considerably in the Anatidae. Magpie Geese construct swan-like nests which may be on land or in water, the size of the nest varying with the availability of materials. Like the Anatidae, Magpie Geese lack the innate ability to carry nesting material, and so must rely on what they are able to reach and pass back over their shoulders in the immediate vicinity of the nest.

Whistling ducks are variable in their choice of nest site, which is usually a well-hidden clump of grass or reeds near water or, rarely, a tree cavity. The large heaped nests of swans, built on land, are well known, and true geese build smaller and more concealed nests on land or, sometimes, in water. Sheldgeese build simple nests on land, often with little cover, and shelducks usually nest under rocks, in ground holes and crevices, or (*Tadorna radjah*) in tree holes. Although perching ducks typically nest in tree holes, the Spur-winged Goose (*Plectropterus gambensis*) nests on the ground. On the other hand, most dabbling ducks are ground nesters, with only a few species frequently nesting in trees: two genera (*Merganetta* and *Hymenolaimus*) typically nest in crevices. Pochards are also surface nesters, the site chosen being variable and either on land, by the scaup group, or in reeds over water, by the typical pochards. Sea ducks typically nest on the ground (eiders, scoters, *Clangula*), in crevices (*Histrionicus*), or in tree holes (goldeneyes, most mergansers). The stiff-tails have abandoned ground nesting altogether in favour of aquatic nests in reed beds. Although females of several species of Anatidae sometimes " drop " eggs in the nests of other waterfowl (Weller, 1959), one species of stiff-tail (*Heteronetta atricapilla*) has apparently become an obligate nesting parasite.

It seems that ground nesting is the generalized waterfowl condition, and that nesting in crevices, holes, or over the water are more specialized adaptations that have been adopted independently by various species or groups, with nest parasitism representing a highly specialised condition.

Pre-flight Movements

As gregarious animals, waterfowl have developed numerous social signals. Among the most important of these are the pre-flight, or " flight-intention," movements and calls, which synchronize a pair, family, or flock for take-off. Magpie Geese, which are highly gregarious, call in concert and frequently shake the head laterally as they prepare to take flight. Similar lateral Head-shaking[1] in the pre-flight situation also occurs in species representing all the other tribes of the Anatidae with the possible exception of the Oxyurini.

In the true geese (*Anser* and *Branta*) and in some species of swans (*Cygnus columbianus* and *C. cygnus*) calls are apparently equally or more important than head movements as pre-flight signals, but in most other groups of waterfowl the birds remain silent. Besides lateral Head-shaking, certain waterfowl use other movements in the pre-flight situation. Several perching ducks (*Aix, Cairina*) perform repeated, rather slow, craning movements of the head and bill upwards and forwards. In other perching ducks and the typical dabbling ducks (*Anas*) these are done in a faster and more jerky manner, called " Neck-jerking " by McKinney (1953). Pochards similarly use rapidly repeated upwards movements of the bill, called " Chin-lifting " (McKinney, 1953), but the sea ducks perform only Head-shakes in alert postures, with outstretched necks and bills slightly raised, as they face into the wind ready to take flight. Perhaps because the stiff-tailed ducks are not strong fliers they seem to have lost or never evolved any conspicuously evident pre-flight signals, for in the three genera observed by me (*Oxyura, Heteronetta, Thalassornis*) I have not detected any. Rolling the cheeks on the shoulders has been observed in the pre-flight situation by Miss Helen Hays (pers. comm.), and she considers this " cheeking " to be a probable pre-flight signal in *Oxyura jamaicensis*.

In summary, the trend of evolution in pre-flight signals appears to have been from a combination of lateral Head-shaking and vocal signals to Head-shaking combined with other, usually silent, head movements.

Sexual and Agonistic Behaviour

Precopulatory Behaviour

Of all aspects of waterfowl sexual behaviour, that which is least variable over the greatest number of species is copulatory behaviour, and particularly precopulatory behaviour. The copulatory behaviour of the Magpie Goose has been only very inadequately observed, but appears to consist of the male calling the female to the nest and mounting her as soon as she has climbed on to it. In the cases observed by me the male did not grasp the female's nape during copulation. This is very different from the copulatory behaviour of other Anatidae, nearly all of which copulate on water and apparently always grasp the female's nape during treading.

Whistling ducks have precopulatory displays which range from mutual Drinking or Bill-dipping movements to mutual Head-dipping (" Neck-dipping " of Heinroth, 1911), resembling and apparently derived from feeding or bathing. Mutual Head-dipping (Fig. 1a) movements are utilized by all species of swans and true geese except the Cape Barren Goose (*Cereopsis novae-hollandiae*). Mutual Head-dipping movements are also used by at least one of the four genera of sheldgeese (*Chloephaga*), and by most if not all species of shelducks

[1]movements, postures, or calls which are clearly ritualized into displays and can possibly be homologized among related species are capitalized throughout this paper.

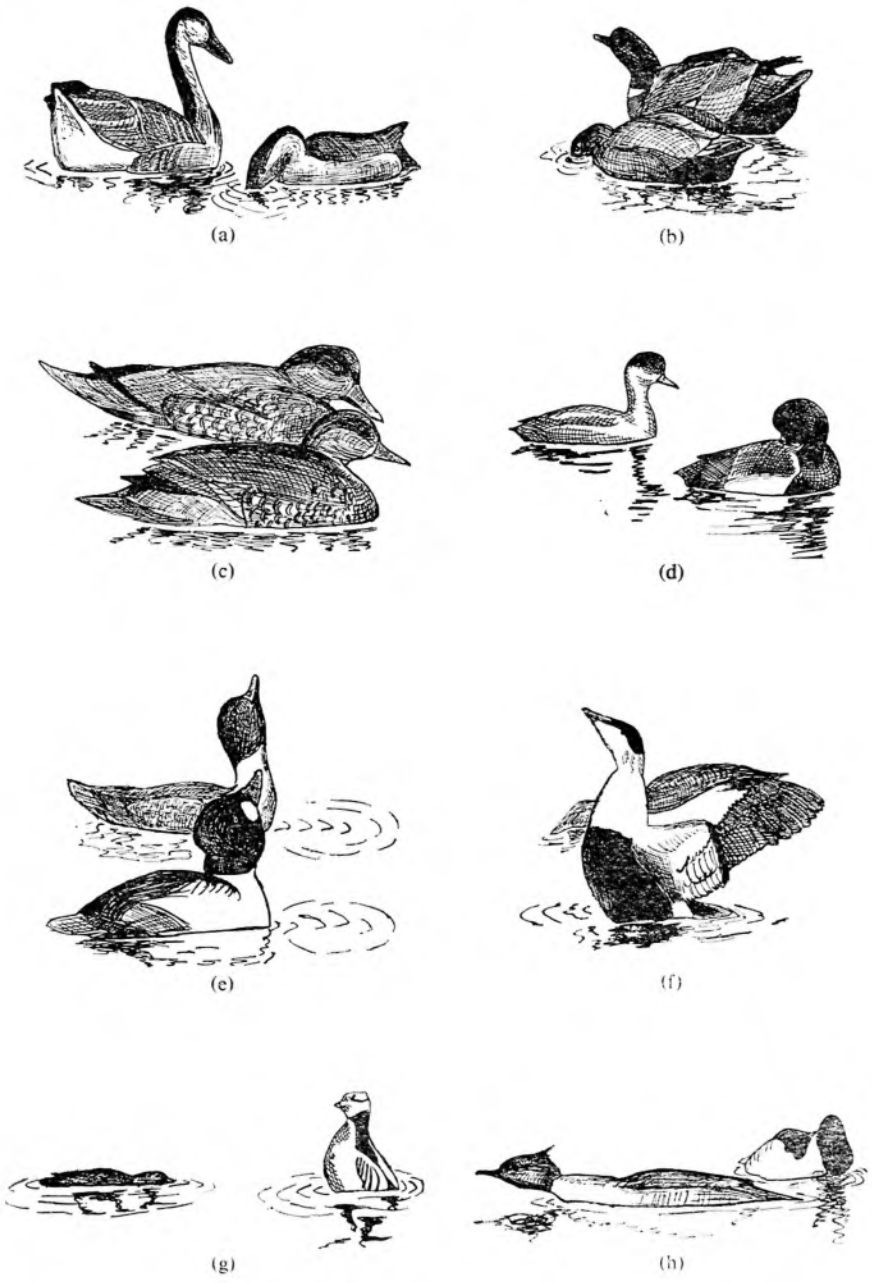

Figure 1. Precopulatory behaviour. Mutual Head-dipping, by a) Swan Geese, and b) Australian Shelducks; c) Head-pumping, by Crested Ducks; d) Head-pumping (female) and Preening-dorsally, by male Red-crested Pochard; e) Drinking, Goldeneyes; f) Wing-flapping by male Common Eider; g) shaking or Upwards-stretch, male Steller's Eider; h) Bill-dipping of male Goosander. *Drawings by P. A. Johnsgard.*

(Fig. 1b). Steamer ducks likewise perform Head-dipping movements, probably mutual, similar to those of sheldgeese and shelducks (Moynihan, 1958).

Among the perching ducks the precopulatory displays are somewhat varied. Mutual Head-dipping has been observed in only the Brazilian Teal (*Amazonetta brasiliensis*). Bill-dipping, performed mutually or by males only, occurs in several genera (*Aix, Callonetta, Nettapus* and possibly *Sarkidiornis*). In the Australian Wood Duck (*Chenonetta jubata*) and the White-winged Wood Duck vertical Head-pumping is performed by the male or by both sexes. It seems probable that Bill-dipping and Head-pumping represent stages in the reduction of the basic Head-dipping movements seen in the preceding tribes. Head-pumping is used (Fig. 1c) by both sexes in at least 32 out of 35 species of *Anas*. Preening, Bill-dipping and Drinking are not used by the typical *Anas* species as precopulatory displays, but both sexes of the Marbled Teal (*Marmaronetta angustirostris*), a " link " species between the dabbling ducks and the pochards (Johnsgard, 1961b), perform Bill-dipping, Drinking and Preening-dorsally in the precopulatory situation. Bill-dipping and Preening-dorsally are also used by all the typical pochards studied to date (13 out of 15 species); these displays are always performed by males (Fig. 1d) and sometimes by females as well. The precopulatory displays of the probably extinct Pink-headed Duck (*Rhodonessa caryophyllacea*), here included in the pochard tribe, are unknown. Mutual Head-pumping occurs in a rudimentary form in one species of pochard (*Netta rufina*), and also is performed by one sex only in at least four other species.

In the sea ducks there is no trace of Head-pumping by either sex, and the only part that the female appears to play in precopulatory display consists of Drinking (Fig. 1e) in some genera (*Mergus, Bucephala*). Otherwise, the female assumes a Prone posture (Fig. 1f to 1h), usually after the male has begun to perform his precopulatory displays. These are extremely varied within the tribe, but usually include Drinking (*Mergus, Bucephala*), Wing-flapping (Fig. 1f), (*Somateria, Mergus cucullatus*), Bathing (*Somateria, Polysticta,* sometimes *Bucephala islandica*), Preening (*Somateria, Polysticta, Melanitta, Bucephala, Mergus*), Shaking or " Upwards-stretch " (Fig. 1g) (*Somateria, Polysticta, Melanitta,* some spp. of *Mergus*), and Bill-dipping (Fig. 1h) (*Polysticta, Melanitta, Bucephala, Mergus*). In some genera (*Polysticta, Melanitta, Bucephala, Mergus cucullatus*) some of these movements are linked into definite sequences, whereas in the others no rigid sequences are apparent. The most complex sequences of precopulatory displays occur in two species of goldeneyes (Myres, 1959) and the Hooded Merganser (*Mergus cucullatus*) (Johnsgard, 1961c). Little is known of the precopulatory behaviour of the stiff-tails, but in at least one species (*Oxyura jamaicensis*) the female takes no part in precopulatory display nor does she usually assume a Prone posture, but rather is suddenly mounted by the male after he has approached her while alternately Bill-dipping and Bill-flicking.

Thus several evolutionary trends in precopulatory behaviour are apparent in the Anatidae. First there is a trend away from land copulation without grasping the female's nape (the Magpie Goose) to treading while standing or swimming in water (nearly all other species) and holding the female in position with the bill. In the species which copulate on water and tend to pair permanently there is usually a mutual precopulatory Head-dipping display involving movements apparently derived from bathing. In some perching

ducks and the dabbling ducks this Head-dipping appears to have been modified into Bill-dipping or Head-pumping movements, performed by one or both sexes. Head-pumping is lacking in most species of pochards, and is replaced by alternate Bill-dipping and Preening-dorsally by one or both birds. In the sea ducks the only mutual precopulatory display is Drinking, and this occurs in only a few species. However, Drinking or Bill-dipping and Preening (dorsally or behind the wing) is a part of the male's precopulatory behaviour in most species and is highly ritualized in a few, the ultimate being reached in two species of goldeneyes and the Hooded Merganser, in which there is a single Preening movement that is a minor part of a complex sequence of displays performed immediately before mounting and at no other time. Not enough is known of the precopulatory behaviour of the stiff-tails to fit them into these trends, but in at least one species mutual displays are lacking. In summary there is a trend away from mutual precopulatory displays apparently derived from bathing towards the evolution of special male displays usually derived from drinking and comfort movements (preening, wing-flapping, shaking, stretching), sometimes linked into special sequences.

Postcopulatory Behaviour

Although the functions of postcopulatory displays in waterfowl are by no means clear, nearly all species which have been studied are known to exhibit some form of stereotyped postcopulatory behaviour. As pairs are apparently formed gradually in swans, geese and at least some ducks, and since copulation sometimes occurs during early stages of pair formation, it seems probable to me that " incorrect " postcopulatory responses could inhibit the formation of firm pairs between distantly related species.

I have not personally seen the postcopulatory display of Magpie Geese, but have been informed that it involves mutual calling and " bowing and scraping " on the part of both birds (Johnsgard, 1961d). In most species of whistling ducks there is a mutual postcopulatory " Step-dance " (Fig. 2a), accompanied by vertical Wing-raising and calling, but in two species which copulate while standing in shallow water or on shore both the Step-dance and marked Wing-raising are lacking. Among the true geese and swans both sexes call as copulation is terminated, and both birds then rise up in the water while extending head and neck vertically, with or without lifting or extending the wings (Fig. 2b & 2c). In the sheldgeese and shelducks which have been observed (seven species), both sexes utter their very different notes as copulation is completed and the male, and to a lesser extent the female, lifts the wing on the opposite side from the partner in a similar manner to the Wing-raising of whistling ducks (Fig. 2d). Steamer ducks swim away from one another following copulation, while simultaneously " Grunting " and " Head-flagging " to each other (Moynihan, 1958).

In the perching ducks, and in the following tribes as well, there is a tendency towards the breakdown of mutual postcopulatory behaviour and the development of special male postcopulatory displays. This is correlated with shorter pair bonds, and the consequent need for efficient signals during pair-bond formation, which must necessarily be less gradual than in the preceding species. In a few of the perching ducks (*Cairina moschata* and perhaps also in *Plectropterus* and *Sarkidiornis*) no distinctive postcopulatory displays have been observed, and in the White-winged Wood Duck the male simply swims

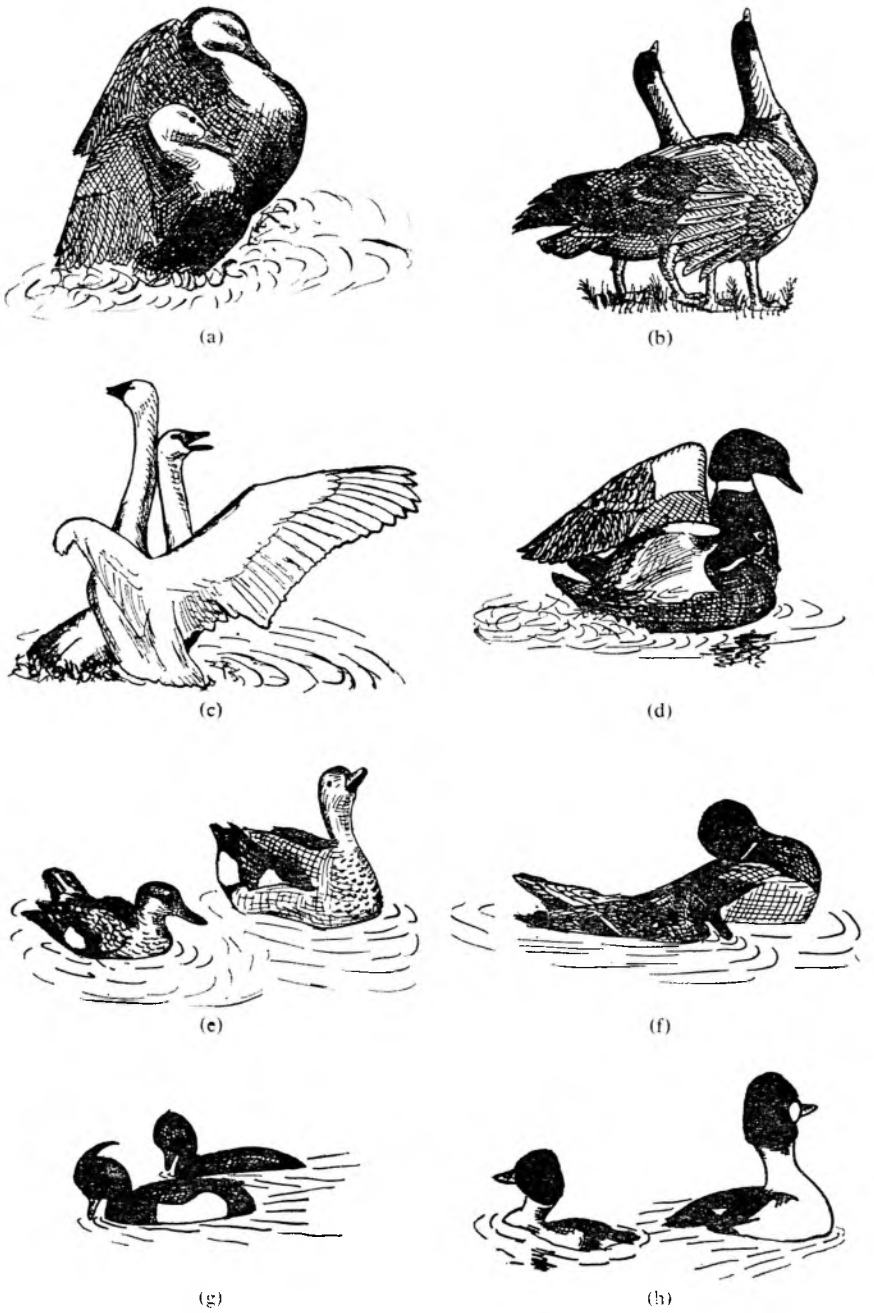

Figure 2. Postcopulatory behaviour. a) " Step-dance " of Whistling Ducks; b) Hawaiian Geese with heads up and wings drooped; c) Trumpeter Swans with heads up and wings extended; d) lifting of far wing by Australian Shelduck; e) male Ringed Teal calling before Facing bathing female; f) male Mallard Bridling; g) " Bill-down " posture by pair of Tufted Ducks; h) male Goldeneye " Steaming " away from female. *Drawings by P. A. Johnsgard.*

about at random, calling excitedly, while the female bathes. In the Ringed Teal (*Callonetta leucophrys*) and the Wood Duck the male calls once (Fig. 2e), then turns and Faces the bathing female, while in the Mandarin Duck and Australian Wood Duck the male tends to swim away from the female for several feet, and sometimes finally turns to face her. In the 20 or so species of *Anas* that have been observed the male calls once with his neck vertically extended in the " Burp " posture or backwards in the " Bridling " posture (Fig. 2f), then faces the female or swims away from her (in some species " Nod-swimming ") and " Turns-the-back-of-the-head " towards her (Lorenz, 1951-53).

In the Marbled Teal and the pochards the postcopulatory behaviour is very uniform. The male calls once as he releases his grasp of the female's nape, then swims away from her in a rigid " Bill-down " posture. Sometimes the female assumes the same posture for a few seconds (Fig. 2g), but often begins to bathe immediately.

The sea ducks exhibit the same bewildering complexity of postcopulatory behaviour that is typical of their other displays. In at least three of the four species of eiders (*Somateria fischeri* unknown), the Surf Scoter *Melanitta perspicillata,* Smew *Mergus albellus* and probably the Red-breasted Merganser *Mergus serrator* the male performs one of its elaborate " courtship " displays immediately after treading is completed. Ritualized " Steaming " away from the female occurs in the goldeneyes (Fig. 2h), eiders, the Hooded Merganser and perhaps other species, and in some (eiders and goldeneyes) is accompanied by lateral Head-turning movements. In all cases the female normally only bathes after copulation. Postcopulatory displays in the stiff-tails are most inadequately known, but in the North American Ruddy Duck *Oxyura j. jamaicensis* the male performs his courtship or " Bubbling " display several times while parallel to or facing the female, who bathes or preens extensively.

Evolutionary trends in postcopulatory displays therefore appear to be away from mutual calling associated with mutual displays that are used only during the postcopulatory situation (species with long pair bonds) to sexually dimorphic postcopulatory behaviour, with the female usually only bathing while the male performs special displays or displays which are also used during courtship (species with short pair bonds).

Pair-forming Behaviour

Pair-forming, or " courtship," displays of waterfowl are extremely diverse and difficult to generalize upon. In most of the groups having long pair bonds (Magpie Geese, whistling ducks, swans, true geese, and perhaps sheldgeese, shelducks and steamer ducks), pair-forming displays are relatively simple. In the true geese, and possibly also in the swans and whistling ducks, the male's major courtship posture appears to consist of swimming ahead of the courted female in a " haughty " attitude (Heinroth, 1911). In the true geese and swans, pairs appear to be formed through the repeated use of the " Triumph Ceremony" (Heinroth, 1911), which is a mutual display typically done after the extrusion of an " enemy " (Fig. 3a), whether real or symbolic. Magpie Geese also appear to exhibit a rudimentary form of Triumph Ceremony (Johnsgard, 1961d), but no obvious courtship displays have been observed.

Pair-forming displays in the sheldgeese and shelducks are much more conspicuous than in the true geese, suggesting that pair bonds are not so rigid as in the latter group. There is independent evidence that this is the case in

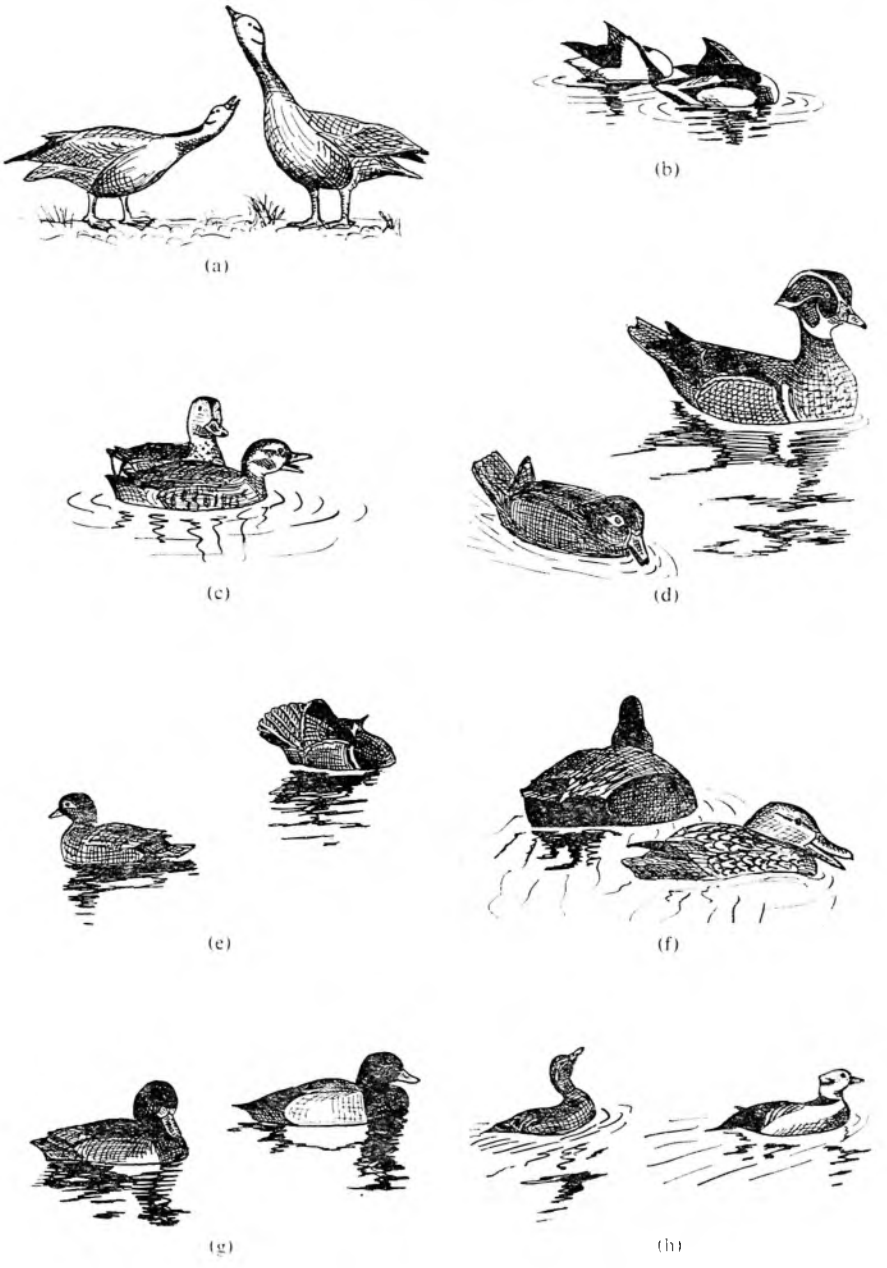

Figure 3. Pair-forming displays. a) " Triumph ceremony " of Bar-headed Geese; b) Common Shelduck Preening-behind-the-wing; c) Inciting and Facing, Ringed Teal; d) Inciting and Burping, Wood Duck; e) Preening-behind-the-wing by male Wood Duck; f) female Gadwall Inciting and made Turning-the-back-of-the-head; g) Inciting and Turning-the-back-of-the-head, Scaup; h) female Steller's Eider Inciting, male Head-turning. *Drawings by P. A. Johnsgard.*

shelducks. Correlated with this weakening of the pair bond there is a double body moult in most and probably all species of *Tadorna*. Shelducks and sheldgeese represent the first group in which the female display termed " Inciting " (Lorenz, 1951-53) or " Hetzen " (Heinroth, 1911) is encountered, and an understanding of this display's significance provides the key to interpreting the pair-forming behaviour of nearly all the species of the subfamily Anatinae. The appearance of this display marks the true beginning of sexual dimorphism in pair-forming behaviour (and in plumage and soft part dimorphism as well). Females typically Incite their actual or potential mates to attack less preferred males or other females, thus " choosing " certain males, probably on the basis of appearance, strength, or reaction to her Inciting, and so providing the basis for sexual selection favouring heterosexual male characteristics of colouration, display, and aggressiveness. Male shelducks and sheldgeese typically overtly threaten or attack the indicated victim, then return to the female and display sexually towards her. In the following tribes the female's Inciting and the male's response both become so highly ritualized that they are sometimes almost unrecognizable, with the trend being that the male's tendency towards overt attack is diminished and his tendency towards responding with elaborate sexual displays or submissive displays towards the female correspondingly increased. In the shelducks and sheldgeese the male's sexual displays usually involve calling (whistled notes in males of the species with large tracheal bullae) in a very erect attitude, sometimes accompanied by spreading or lifting the folded wings and thus displaying the wing speculum patterns (Fig. 4a), which are encountered for the first time in this group. Only one species of shelduck (*Tadorna tadorna*) is known to display its speculum by Preening-behind-the-wing (Fig. 3b), a display which is present in most of the following tribes. Pair-forming displays in the steamer ducks are still only poorly known, but Moynihan (1958) has described several postures and calls of the Flying Steamer Duck (*Tachyeres patachonicus*). One or more of these displays appears to be derived from drinking, and ritualized drinking is typical of most of the remaining tribes. Although Moynihan does not describe Inciting, Delacour (pers. comm.) has informed me that female steamer ducks also possess a true Inciting display.

Among the perching ducks, Inciting has been recorded in most species (Fig. 3c & 3d), although not in the genera *Cairina* or *Sarkidiornis*, and it may also be lacking in *Plectropterus*. In these three genera pair bonds are generally very weak and male courtship displays are rudimentary. Comb Ducks (*Sarkidiornis melanotos*), however, do exhibit in simple form some of the basic male movements of the subfamily Anatinae, namely clearly ritualized Preening-behind-the-wing and possibly ritualized drinking and turning the back of the head toward females. All of these movements are definitely ritualized in the genus *Aix* (Fig. 3e), males of which have also ritualized the general body shake into a sexual display (Lorenz, 1951-53) and which display in social fashion around unmated females. Correlated with the evolution of social courtship displays and definite pair-forming periods is the evolution of distinctly different nuptial and post-nuptial, or " eclipse," male plumages. These are present in *Aix* and one species of *Nettapus*, as well as in all the following tribes.

Pair-forming displays in the dabbling ducks are extremely varied and interesting (Table 1), and in many cases can be related to specializations in plumage or soft part colouration. Lorenz (1951-53) has studied and named the

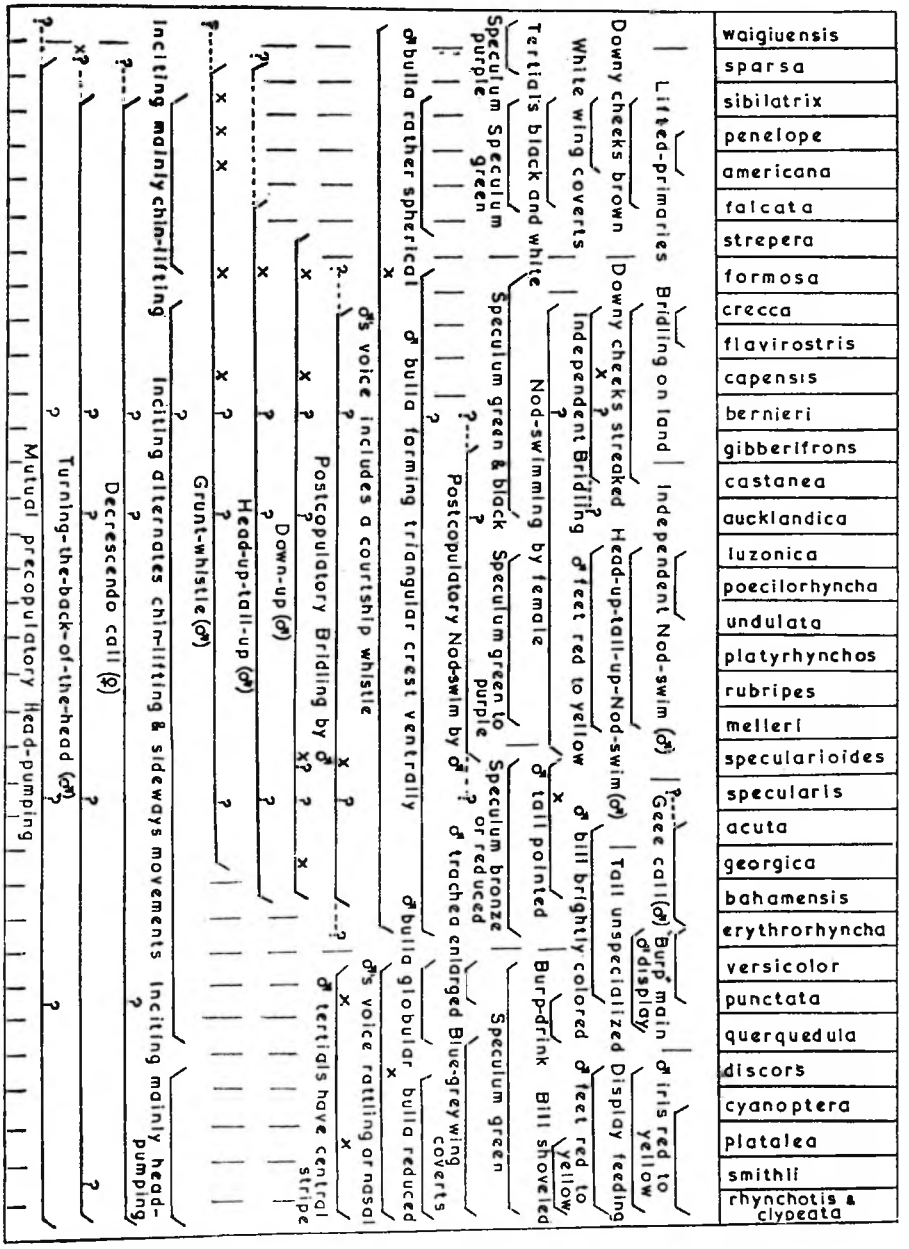

Table 1. Summary of behavioural and morphological features in the dabbling ducks, genus *Anas*. " x " indicates absence of character.

displays of about 14 species of the genus *Anas* (and Table 1 is in part based on his data), and I have been able to observe alive all but two of the 35 species. Females of apparently all species have conspicuous Inciting displays, vocalizations which include a " Decrescendo Call," and females of some species have a special display, " Nod-swimming," which functions in eliciting male displays. Males of nearly all species Turn-the-back-of-the-head and

Preen-behind-the-wing to females, and the combination of female Inciting and Turning-the-back-of-the-head by the male (Fig. 3f) seems to play a basic part in the formation of pairs in this genus as well as several related genera (Johnsgard, 1960b), thus functionally replacing the Triumph Ceremony of the Anserinae. Common male displays of many species of *Anas* include the " Grunt-whistle " (Fig. 4b), " Head-up-tail-up " (Fig. 4b & 4d), " Bridling " (Fig. 4c), " Burp " (Fig. 4e) and " Mock-feeding " (Fig. 4f), all of which have been described by Lorenz (1951-53). The taxonomic distribution of these and other displays and plumage features is of interest (see Table 1). For example, there has evidently been a secondary loss of certain displays in some species, such as the Grunt-whistle and Down-up of the Cape Teal, and the Down-up and postcopulatory Bridling in the Crested Duck (*Anas specularioides*). Secondly, except for certain species which are doubtfully distinct (e.g., *Anas castanea* and *A. gibberifrons, A platyrhynchos* and *A. rubripes*) or allopatric in distribution, there is a remarkable species differentiation of displays and plumage characters, as indicated in Table 1. Thirdly, displays or features shared by the largest number of species (near the bottom of the table) are presumably the most conservative and fundamental to the genus *Anas*, potentially functioning as intergeneric isolating mechanisms, while those found in only a few species are presumably the most adaptive and probably serve as major interspecific isolating mechanisms. Obviously, however, variations in the form or sound of such widespread displays as the Decrescendo Call and Grunt-whistle allow for specificity even within homologous displays.

Pair-forming displays in the pochards are slightly less varied than those of the dabbling ducks, and several behaviour patterns are shared by both of these closely related groups. Preening-behind-the-wing and Turning-the-back-of-the-head (Fig. 3g) by males to Inciting females are of equal importance in both groups. Interestingly, grey or white wing speculum patterns are exhibited by most pochard species when Preening-behind-the-wing, rather than the metallic-coloured specula of dabbling ducks. Pochards perform the " Introductory Shake " (Lorenz, 1951-53) in the same manner as dabbling ducks and some perching ducks, although except in the Red-crested Pochard *Netta rufina* this movement does not function as an " introductory " signal. Although males of nearly all species of pochards share homologous display patterns such as the Kinked-neck (or Courtship) Call (Fig. 4g), the Sneak, Head-throw (Fig. 4h) and Neck-stretching (Hochbaum, 1944), the speed and intensity of these displays differ greatly in various species, as do also the associated vocalizations. Of these displays, the Kinked-neck Call is probably homologous to the Burp of *Anas*, but the more specialized courtship patterns are doubtfully homologous to any of the *Anas* displays. As Lorenz (1951-53) has pointed out, there is no reason to believe that the Head-throw of the Canvasback is homologous to the Laying-the-head-back of the Garganey *Anas querquedula* or the similar postures of the sea ducks. Only the more generalized displays are unquestionably homologous in both tribes and these patterns in the pochards exhibit no evolutionary trends not evident in the dabbling ducks.

Pair-forming displays in the sea ducks culminate the evolutionary trends that have been developed in the preceding tribes. Females of most and perhaps all species have Inciting displays, but these are so highly ritualized and distinct from the basic Inciting movements of female shelducks that at times they are almost impossible to recognize (Fig. 3h). The male displays are so

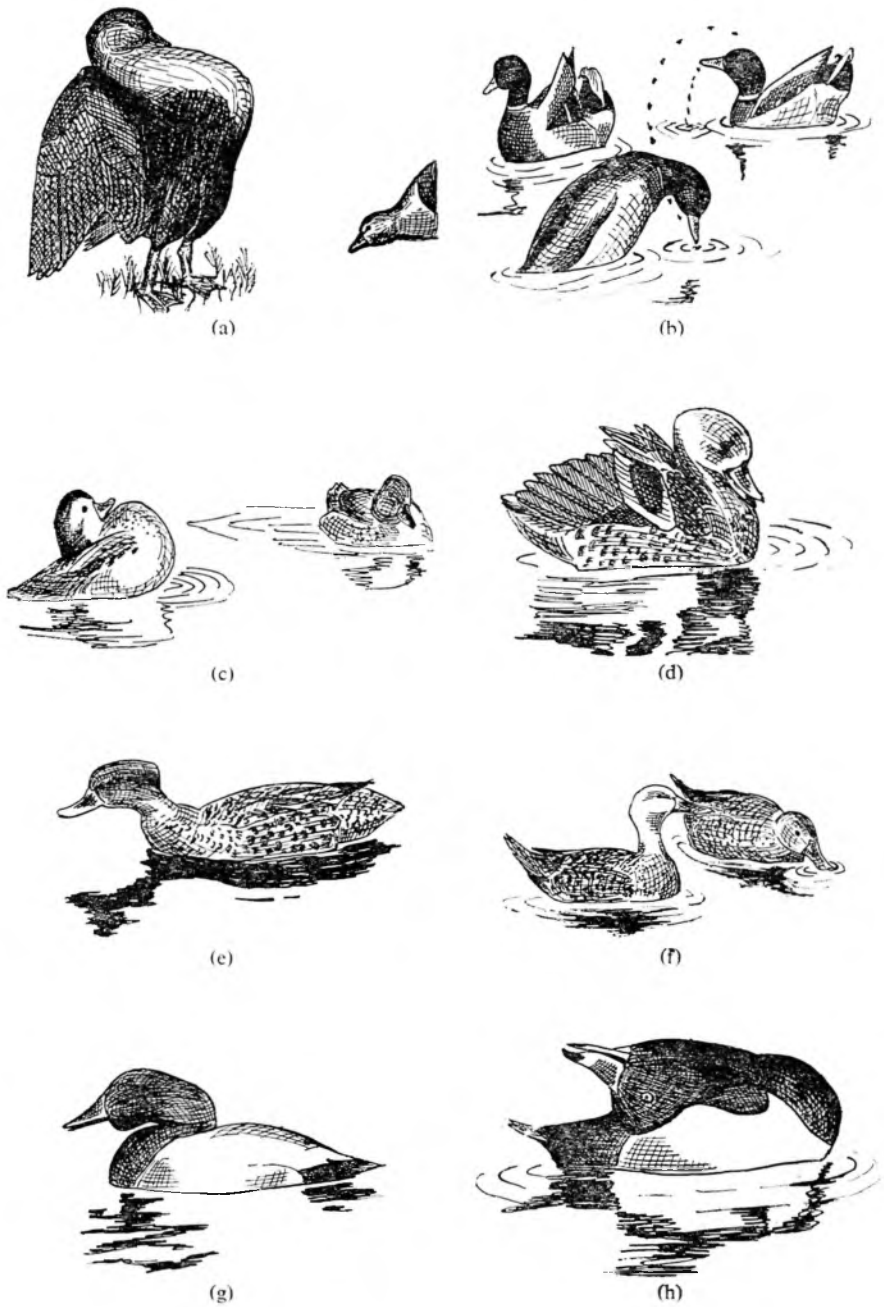

Figure 4. Male pair-forming displays. a) Orinoco Goose lifting folded wing; b) Head-up-tail-up, Grunt-whistle and Down-up of Mallard; c) Bridling of Sharp-winged Teal; d) Head-up-tail-up of Cape Teal; e) Burp of Cape Teal; f) Mock-feeding of Red Shoveler; g) Kinked-neck call of Canvasback; h) Head-throw of Ring-necked Duck. *Drawings by P. A. Johnsgard.*

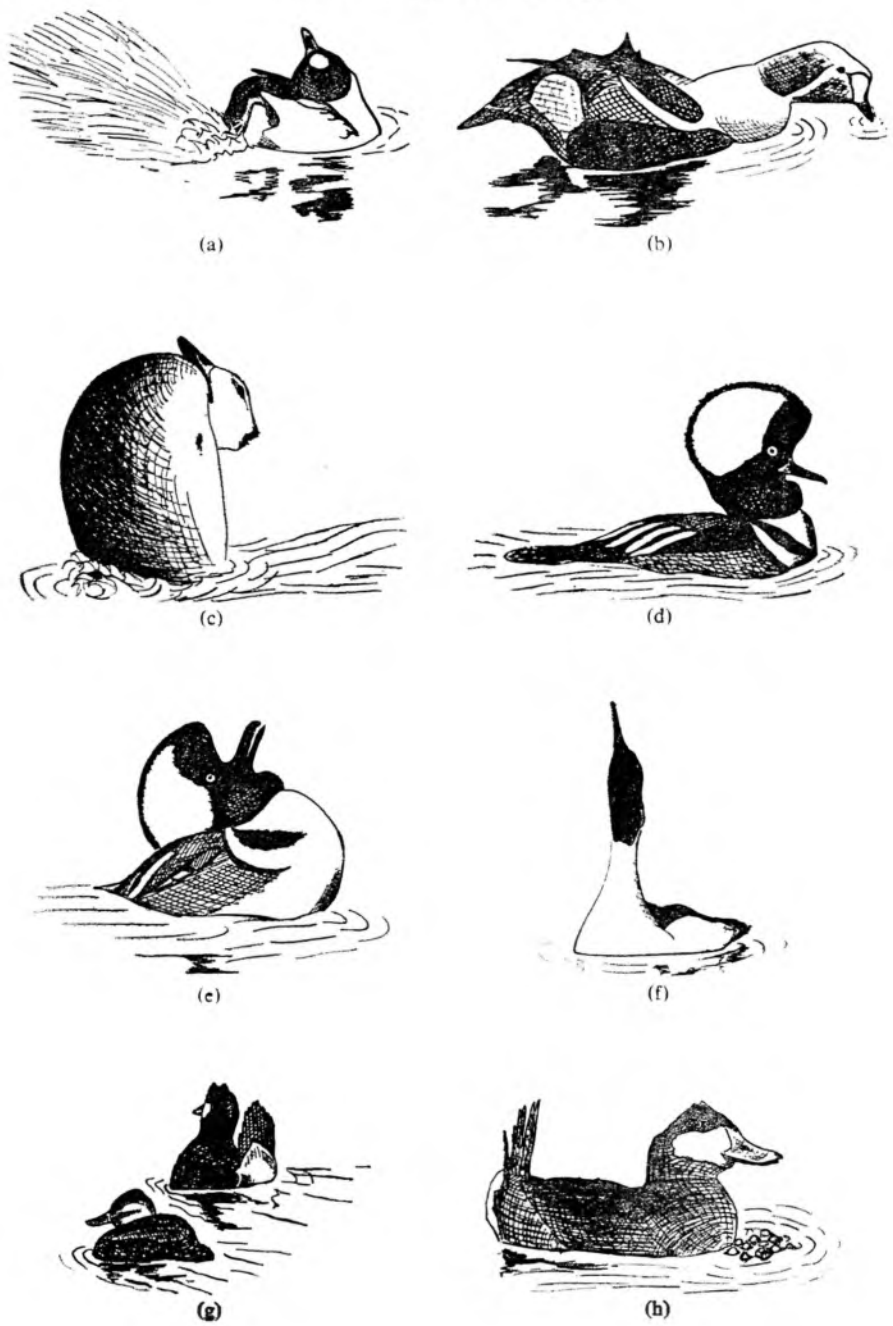

Figure 5. a-f) Pair-forming displays of male sea-ducks: a) Goldeneye Head-throw-kick; b) King Eider Reaching display; c) Steller's Eider Rearing display; d) and e) Hooded Merganser Crest-raising and Head-throw; f) Goosander Salute; g) and h) Ruddy Duck: Male Tail-cocking while swimming ahead of female, and male finishing Bubbling display. *Drawings by P. A. Johnsgard.*

diverse and elaborate (Fig. 5a to 5f) that it is not only difficult to homologize display movements between genera but also within genera, and sometimes different races of one species exhibit qualitively different male displays (e.g., *Somateria mollissima,* McKinney, 1961). Even the more generalized displays are affected by this trend. The general body shake has been ritualized into the Upwards-stretch display (Myres, 1959) in at least some species. Ritualized preening is absent as a courtship display except in scoters, and has been incorporated into the precopulatory displays of several species. Turning-the-back-of-the-head occurs in unmodified form only in some species such as the Long-tailed Duck *Clangula hyemalis* and some mergansers, while in the goldeneyes, eiders, and possibly the Surf Scoter it is functionally replaced by lateral Head-turning. Wing-flapping is highly ritualized in the large eiders (*Somateria*) and is less certainly so in some other species. Short flights to the female are frequent in the Steller's Eider *Polysticta stelleri,* scoters, goldeneyes, and probably other species (McKinney, 1959). The other male pair-forming displays are so diversified that it is impossible to generalize upon them or even, in many cases, to suggest the origins of the movements. Myres (1959) has described many of these displays and has attempted to judge possible homologies among them.

A discussion of the stiff-tails is again hampered by inadequate information regarding most species, although a few generalities are clear enough. In the species studied by me (*Oxyura jamaicensis* adequately, *Heteronetta atricapilla* and *Thalassornis leuconotis* very incompletely) or reported on by others (*Biziura lobata, Oxyura australis*), almost no behaviour patterns have been seen which can be readily homologized with those of other tribes. Male Black-headed Ducks *Heteronetta atricapilla* do Turn-the-back-of-the-head towards courted birds in a typical anatine manner, but Ruddy Ducks tend to hold the head immobile and direct the long axis of the body toward the female, with tail cocked and the under tail coverts exposed to her view (Fig. 5g). Preening-behind-the-wing has not been observed in any species, nor does the general body shake appear to be ritualized. Females of most species are relatively silent, and no behaviour patterns which functionally resemble Inciting have been seen to my knowledge. Male pair-forming displays appear to have been evolved from head and neck movements required for producing sounds from the air sacs or inflatable oesophageal structures that are present in males of most species (Fig. 5h). Ritualized preening of the breast feathers is apparently a major display in two species (*Oxyura australis* and *O. vittata*), although these may be simply sound-producing movements rather than movements derived from preening.

In summary, pair-forming displays in waterfowl species with long pair bonds appear to be mainly Triumph Ceremonies performed by both sexes. In species with less permanent pair bonds the Triumph Ceremony is either replaced by or modified into Inciting on the part of the females and a tendency in males to display sexually towards the female rather than to overtly attack or threaten other individuals. These sexual displays become increasingly more elaborate in the tribes of Anatinae, but are mainly derived from maintenance activities such as drinking, comfort movements such as shaking, preening and wing-flapping, and apparent submissive gestures such as turning the back of the head toward the female. Displays which are associated with vocalizations usually have their origin in the stretching of the neck (and trachea) in order to

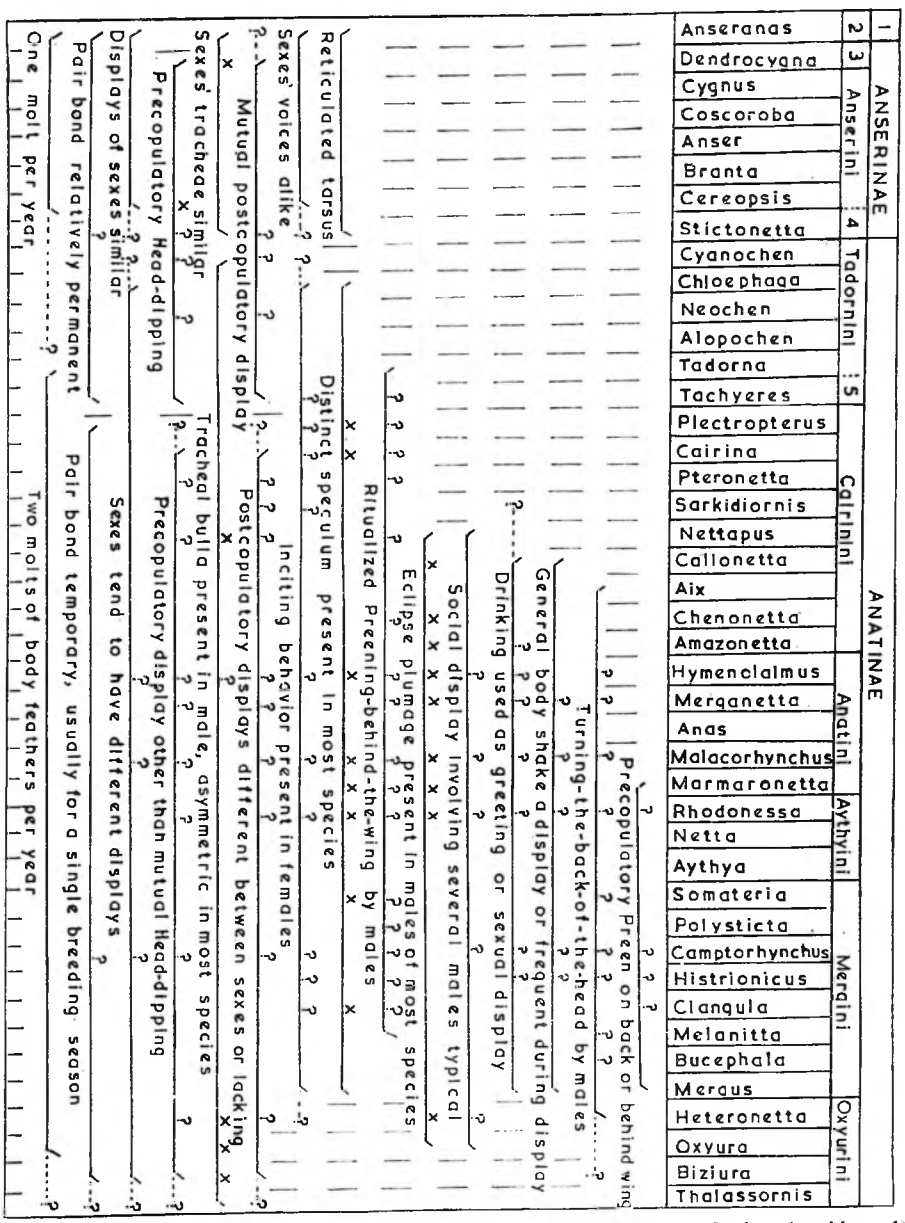

Table 2. Summary of trends in the behaviour and morphology of the Anatidae. 1) Anseranatinae; 2) Anseranatini; 3) Dendrocygnini; 4) Stictonettini; 5) Tachyerini.

produce special sounds. Together with the tendency towards elaborate displays in males, there is also a corresponding tendency towards social display involving several males "courting" one or more unmated females. Wing-preening movements form an important part of the pair-forming displays of the Anatinae, and are usually associated with white or metallic-coloured speculum patterns. The general body shake occurs in essentially unmodified form during courtship display of perching ducks, dabbling ducks, and pochards,

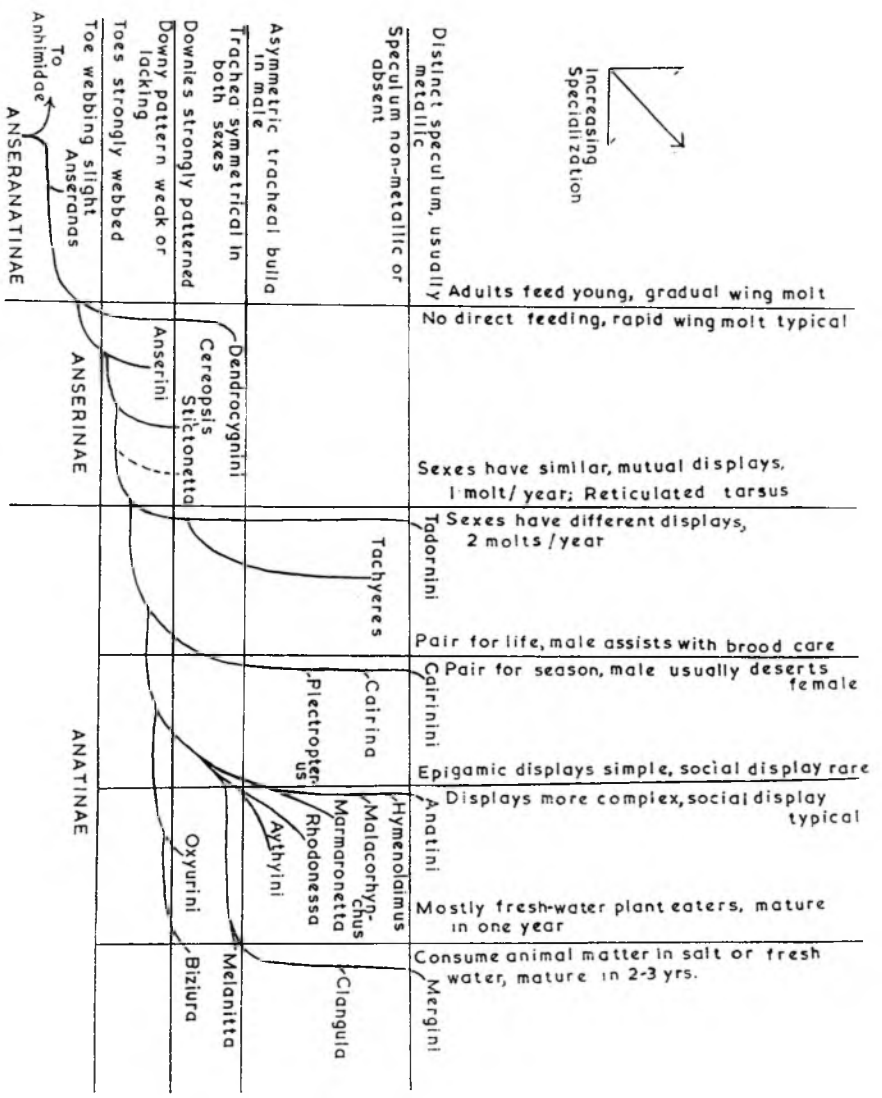

Table 3. Trends in behaviour and morphology of the Anatidae superimposed on a simplified evolutionary tree.

but is ritualized in some of the sea ducks. Drinking, which functions mainly as a greeting, appeasement or courtship display in the perching ducks and dabbling ducks becomes, in pochards and especially in the sea ducks, primarily a precopulatory display. Although Turning-the-back-of-the-head is an important display in many perching ducks, dabbling ducks, and pochards, in some sea ducks it is supplanted by lateral Head-turning and in the typical stiff-tails has been apparently lost.

Discussion

An attempt has been made to summarize in graphic form as many as possible of the trends discussed above, the result of which is shown in Table 2.

As in Table 1, the taxa are arranged vertically across the top of the diagram in what I consider to be the most suitable linear sequence. Behavioural or morphological characters shared by several species or genera are indicated and bracket the appropriate forms, with exceptions or questionable cases noted. Unfortunately, a surprising number of questionable points still remain, some of which can and no doubt will be resolved in the foreseeable future. Nevertheless, the major trends of evolution in the family are clearly evident, and even with additional study it does not seem likely that the concepts presented here will need to be drastically altered.

An alternative means of summarizing the behavioural and morphological trends in the family is presented in Table 3, in the form of a simplified evolutionary tree over which has been superimposed a two-dimensional key of morphological and behavioural characters. This tree is basically the same as was used for illustrating tracheal trends (Johnsgard, 1961e), but both are highly simplified and are not intended to replace the more comprehensive diagram published earlier (Johnsgard, 1961a).

Acknowledgements

This paper was written while the author was being supported by a Public Health Service postdoctoral fellowship. The data were collected at the Wildfowl Trust, Slimbridge, and I would like to state my deep appreciation to these organizations for making the study possible.

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