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Handbook of Waterfowl Behavior: Tribe Cairinini (Perching Ducks)

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dipping movements. After both copulations the birds assumed the Alert posture and swam apart while Grunting and Head-flagging.

TRIBE CAIRININI (PERCHING DUCKS)

Delacour and Mayr (1945) placed the perching duck tribe after the pochards (Aythyini) and adjacent to the sea ducks (Mergini), but hybridization evidence (Johnsgard, 1960a) clearly indicates that the group belongs between the shelducks and the dabbling ducks and closely adjacent to the latter. There is other evidence to support this arrangement. The tracheae of shelducks, perching ducks, and dabbling ducks are all very similar, possessing bullae which in most species are osseous and rounded, and lacking enlargements of the tracheal tube. The downy young of perching ducks and dabbling ducks are very similar, and are usually patterned with dark brown and white or yellow. Woolfenden (1961) has advocated merging the perching ducks and dabbling ducks into a single tribe (Anatini), but although the two groups do tend to overlap in some of their characteristics, I believe that merging them would result in an unduly large and heterogeneous tribe. Such action would, however, resolve the problem of the tribal allocations of such species as the Brazilian teal and ringed teal. Some species of perching ducks mature in two years, although the smaller species mature their first year. Nearly all perching ducks have metallic coloration on the upper-wing surface. With few exceptions they do not dive well or frequently, and apparently all use their wings when submerging. Most of them dabble for their food, and some also graze. Nearly all species are hole-nesters, and have relatively long incubation periods. As here constituted the tribe contains thirteen species; those included in it by Delacour (1959), plus an additional species, the ringed teal (*Anas leucophrys* of Delacour), which is here considered to comprise a separate genus (*Callonetta*).

The members of this tribe present a curious mixture of generalized and highly specialized forms, which do not seem to be particularly closely related to one another and which sometimes show certain affinities with species of other tribes. As I have suggested elsewhere, (1960b) the tribe includes several species which seem to characterize the primitive anatine condition from which the more specialized groups have adaptively radiated. Within the tribe two major subgroups are apparent, one including the several generalized or "primitive" forms (*Plectropterus*, *Cairina* and *Sarkidiornis*) and the other

some highly specialized species. In the first group, the birds tend to be large and to have extensive metallic plumage without specialized patterns; pair bonds are weak or possibly lacking; vocalizations are simple; there is little sexual dimorphism of plumage or displays; and there is much aggressive behavior. In the other group (*Nettapus*, *Callonetta*, *Aix*, *Chenonetta*, *Amazonetta*, and perhaps *Pteronetta*), the birds are smaller and mature in their first year; male plumage patterns are more elaborate and specialized; metallic coloration is more restricted in occurrence; pair bonds, although temporary, are stronger; plumage dimorphism is usually present; displays and vocalizations are more complex; and overt aggressive behavior is less frequent than in the other group. The tribe, although nearly world-wide in distribution, contains many tropical species.

Spur-winged Goose (*Plectropterus gambensis*)

The spur-winged goose is, in its general appearance and behavior, rather similar to the magpie goose. This similarity must be regarded as superficial, but I do believe that the spur-winged goose approximates an extremely generalized anatine condition. Unlike the other species of this tribe, it nests on the ground rather than in holes. The downy young are fairly typical of the tribe, but are not at all like those of the magpie goose as has been suggested. The male has a relatively small and rounded tracheal bulla, which, like that of the white-winged wood duck, is not uniformly ossified. In common also with this species, and with Muscovies as well, spur-winged geese have white wing-coverts which apparently function as threat signals in the same manner as those of shelducks and sheldgeese. On osteological evidence, Woolfenden considers the spur-winged goose to be related to the shelducks and includes the species in that tribe. The sharp wrist spurs of the spur-winged goose are especially effective weapons; they make this species the most dangerous of all waterfowl. The spur-winged goose occurs in Africa and is not sympatric with any near relatives. It has hybridized in captivity with the Muscovy duck and possibly with some other species.

General behavior. Spur-winged geese do not mix with other species in captivity, and they are not very aggressive among themselves. I have not observed any preflight signals, but McKinney (1953) has recorded seeing lateral Head-shaking and Chin-lifting as possible preflight movements.

Agonistic and sexual behavior: female. The female utters a high-pitched *chi-chi-chi* . . . with quick bill-lifting movements when disturbed; whether this is a primitive form of Inciting is not clear. I have noted no other special postures or calls in the female spur-winged goose.

Agonistic and sexual behavior: male. The male has a rather weak, whistling voice similar to that of the female, and a squeaky four-syllable call, *chi-chi'-chi-chi*, which he utters with ruffled scapular feathers and with wing-shaking as he approaches the female (Fig. 27E, F) in what appears to be a courtship display or form of Triumph Ceremony. When threatened, the male also sometimes utters a huffing *chu-chu'*. He appears to have no highly ritualized threat displays, but when disturbed, he often stretches both wings over the back in the usual manner of a stretching bird. This behavior brings into view the wrist spurs and white wing patches, and may possibly function as a simple threat display. When attacking, the male runs rapidly over the ground, often gaping as he spreads or flaps his wings and attempts to strike his opponent (Fig. 27D). After such an attack he usually returns to the female, calling in the manner described above.

Copulatory behavior. I have no information on this. It would be of interest to learn whether copulation occurs in water or on land, as well as to learn what the associated behavior is.

Muscovy Duck (*Cairina moschata*)

The Muscovy duck well typifies that group of perching ducks of more generalized form. The downy young are dark above, with reduced spotting, and yellow below, and they have a clear yellow cheek and a broad dark crown. The juveniles are more brownish than the adults and lack white wing-coverts; this distinctive juvenile plumage also occurs in spur-winged geese, comb duck, and white-winged wood ducks. The adults of both sexes are almost entirely a glossy greenish-black, with pure white wing-coverts. As is also true of spur-winged geese and comb ducks, there is a marked dimorphism in the size of the sexes; the male is roughly twice as heavy as the female. Also as in these species, the bill of the male is adorned by fleshy caruncles. The trachea of the male has a rounded bulla which is rather uniformly ossified throughout and is not in any way unusual. The Muscovy is native to Central and South America, and is not sympatric with any

relatives except the comb duck. It has hybridized in captivity with spur-winged geese and with species of other tribes, but all the resulting birds have proved infertile.

General behavior. Muscovies resemble spur-winged geese and comb ducks in their general behavior. Males and females tend to remain dissociated most of the year, probably because of the aggressive sexual tendencies of the males. Like comb duck males, the males of this species use their powerful and sharp-clawed feet, as well as their wings, when fighting. Before taking flight, Muscovies make repeated Neck-craning movements diagonally upward with the bill; this apparently primitive behavior pattern is shared by several other species of perching ducks.

Agonistic and sexual behavior: female. Heinroth (1911) and, more recently, Steinbacher (1953) have described the behavior of the Muscovy duck. The female apparently has only a simple quack, which she utters when excited or afraid; there appears to be nothing which could be called true Inciting. This may be related to the fact that Muscovies appear to lack almost entirely any kind of pair bond, although Steinbacher (1953) believes that this is perhaps not so true as Heinroth has indicated.

Agonistic and sexual behavior: male. Although the male has a well-developed tracheal bulla, he is practically lacking in voice. His only call is a soft breathing or hissing note, uttered during sexual excitement and hostile situations. While uttering this call he raises his slight crest and shakes his tail laterally, holding his wings slightly away from his body, and moving his head slowly forward and backward (illustrated in Heinroth, 1911). Muscovies apparently have no other sexual or pair-forming displays.

Copulatory behavior. I have not observed copulation, but Heinroth (1911) has described it in some detail. According to him, it normally takes the form of rape, from which the female usually tries to flee but is eventually overtaken and overpowered by the male. During the breeding period, however, the female may assume a receptive posture and actively solicit copulation. Heinroth has described the unbelievable awkwardness and almost sadistic nature of the precopulatory behavior. Before mounting, the male performs his characteristic head movements and pecks at the dorsal body feathers of the female. The female bathes vigorously after treading, but Heinroth did not observe any definite male postcopulatory displays.

White-winged Wood Duck (*Cairina scutulata*)

Although certainly a close relative of the Muscovy, the white-winged wood duck has often been generically separated from it. The downy young have not yet been well described, but apparently they are similar to those of the Muscovy. The juveniles are more brownish than the adults, and two years are probably required for sexual maturity. Adult males and females are very similar in plumage, and do not exhibit quite the dimorphism in size that occurs in the Muscovy. The general plumage color is a glossy greenish black, but there are white feathers on the head and neck, and the slate-colored secondary feathers are different in color from the rest of the wing. Females have more black spotting around the eyes and head than do males. The trachea of the male has a large, dorso-ventrally flattened bulla that is very unevenly ossified (Johnsgard, 1961c). In both sexes the bronchi are ossified, a condition which is apparently unique among the true ducks but which also occurs in the trumpeter swan and its near relatives. The white-winged wood duck occurs in southeastern Asia and the adjacent islands, and is not sympatric with any near relatives. No hybrids are known.

General behavior. White-winged wood ducks appear to be somewhat more gregarious than Muscovies or comb ducks, and the sexes tend to remain together more than in those species. As in the Muscovy, preflight behavior consists of repeated pointing or Neck-craning movements with the bill and head. Although rather awkward in walking, this species seems to be able to dive fairly well, using its wings when so doing, and in the wild it is reported to feed on fish to a considerable degree.

Agonistic and sexual behavior: female. Although Delacour (1959) doubts that calling is well developed in this species, I have heard loud, one-syllable calls in both sexes. The female's call is an unpleasant honking that sounds like a rusty pump in great need of oiling, and the call is accompanied by vigorous head-pumping (Fig. 28A, B). This is usually directed toward males which are performing the same kind of pumping, and it seems to function as a kind of Triumph Ceremony. I have never observed any behavior which could be interpreted as Inciting.

Agonistic and sexual behavior: male. The only display I have seen involved vertical pumping movements like those performed by

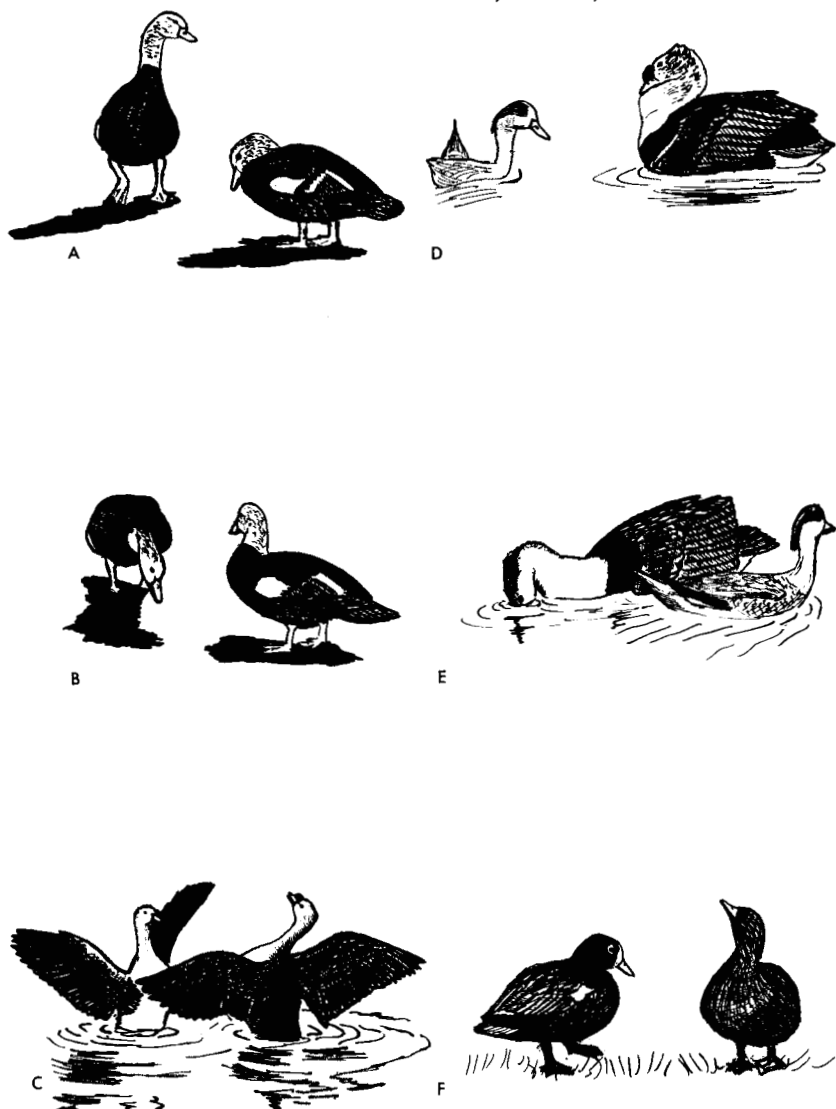


Figure 28. White-winged Wood Duck, Comb Duck, Hartlaub's Duck

A, B. White-winged wood duck pair calling mutually in Triumph Ceremony situation. The male (*left*) is pumping his head vigorously, the female considerably less.

C. Male comb ducks fighting.

D, E. Male South American comb duck displaying to a female crested duck as she Nod-swims around him.

D. Hartlaub's duck pair calling mutually and performing rotary head movements.

the female (Fig. 28A, B). These movements probably correspond to the more horizontal pumping movements of the male Muscovy, but there is no shaking of the tail. As in the Muscovy, the display occurs in both aggressive and Triumph Ceremony situations, with females participating in the latter. In all cases it is accompanied by a loud, trumpeting *ho-ho-ho*, usually of three syllables, rapidly repeated.

Copulatory behavior. Although I have not witnessed treading, I have observed what was no doubt precopulatory behavior, and also postcopulatory behavior. The precopulatory display consisted of very deliberate and silent vertical Head-pumping on the part of both birds, although the movement was more obvious in the male. Later I heard the male suddenly begin to call loudly and repeatedly, and upon seeing the birds I noticed the female bathing and the male swimming rapidly about in random directions.

Hartlaub's Duck (*Pteronetta hartlaubi*)

Although it is certainly related to the two preceding species, Hartlaub's duck shows several features that suggest it is a more specialized form and perhaps should not be retained in the same genus with them. Possibly it should be placed after the following species (the comb duck), but at present too little behavioral information is available to accurately judge its affinities. The downy young resemble the downy young of dabbling ducks more than downy Muscovies, being rather more spotted on the back than Muscovies and having a more *Anas*-like head pattern. Unlike that of the preceding species, the juvenile plumage is identical to that of the adults. The adults are mostly a rich chocolate brown with black heads, and the male has a varying amount of white on the forehead. There is little dimorphism of size, and practically no enlargement of the bill in males. Unlike those of the preceding species, the wing coverts are a light blue and there is no metallic plumage on the wings or body. The male trachea has a rounded osseous bulla of uniform thickness without any distinguishing features; it is similar to those of some *Anas* species. Hartlaub's duck is found in central Africa and is not sympatric with any near relatives. Two subspecies are recognized, and no hybrids are known.

General behavior. I have observed only a single breeding pair and their offspring and obtained little concrete information about them. The breeding pair apparently had a strong pair bond, and they re-

mained closely associated throughout the year. The male appeared to take an interest in caring for the young; he was with them in a closed aviary, however, and thus could not easily avoid them. Preflight movements apparently consisted of vertical Neck-jerking (as in *Anas*) and Chin-lifting (McKinney, 1953).

Agonistic and sexual behavior: female. The voice of the female is a loud quack, similar to that of *Anas*, which is used as a danger signal or is uttered repeatedly during a rotary head-pumping ritual that is clearly a true Inciting (Fig. 28F). During Inciting, the female calls loudly while pointing her bill toward the opponent. A very similar form of calling is used as a Triumph Ceremony between the mated pair. Juvenile birds often join in this display, making similar but silent head movements.

Agonistic and sexual behavior: male. The male's call has been well described as a "quiet high-pitched wheezing noise" (Yealland, 1951). He utters it during the female's Inciting display, and the somewhat rotary movements he makes with his bill are similar to those made by the female. This mutual calling and pumping is no doubt homologous with the similar display of the white-winged wood duck. This is the only display I have seen the male perform, but possibly other courtship postures are performed by unmated males. In its body shape and general appearance, Hartlaub's duck is reminiscent of the African black duck, and the possibility that this species provides a link with the dabbling ducks is not to be discounted.

Copulatory behavior. Unfortunately I have no information on this. I once observed a mutual and silent vertical head-pumping performed by the breeding pair during the egg-laying period, but I do not know whether this was precopulatory behavior or not.

Comb Duck (*Sarkidiornis melanotos*)

Although the comb duck could with some justification be included in the genus *Cairina*, Delacour (1959) has retained it in its traditional genus, and perhaps it does provide a link between the larger, more generalized perching ducks and the more specialized forms such as the pygmy geese. The downy young are very like those of the Muscovy, and the juvenile plumage, also like that of the Muscovy, is distinctive and brownish, and bears a surprising resemblance to the female plumage of the Australian wood duck. The adult plumage is primarily blue-black above and white below, and it is similar in the two sexes.

The male, however, is at least twice as heavy as the female and during the breeding season has a greatly enlarged fatty bill protuberance. In both sexes the head is spotted black and white in a pattern very much like that of the white-winged wood duck. The female is also reminiscent of female pygmy geese, and, as in that group, the underwing lining and upper-wing coverts are blackish. The secondaries have a highly glossy, coppery coloration, forming a kind of simple speculum which is not set off from the rest of the wing. The trachea of the male has an almost rudimentary bulla which is rounded and, at least in some individuals, not wholly ossified. Comb ducks occur in South America, Africa, Madagascar, India, and southeastern Asia, and are divided into two distinctive subspecies. They are sympatric with both species of *Cairina*, but apparently have not hybridized with any species of perching ducks.

General behavior. In its general behavior the comb duck greatly resembles the Muscovy. The sexes do not associate much, since the females generally try to avoid contact with the much larger males. When fighting, the males rear up in the water, striking with their wings and perhaps also with their feet (Fig. 28C). McKinney (1953) has recorded lateral Head-shaking as a preflight movement.

Agonistic and sexual behavior: female. The female of this species is a remarkably quiet bird, uttering at most a very weak quack when disturbed or frightened. As in the genus *Cairina*, I have observed no behavior which could be interpreted as Inciting.

Agonistic and sexual behavior: male. When the male is displaying aggressively, he swims in a very high and erect posture, with his wings slightly spread, and repeatedly and deliberately pumps his head down toward the water, uttering a faint *churrrr* with each pumping motion (Fig. 28D, E). This pumping movement is similar to that of the white-winged wood duck, and when highly excited the comb duck male submerges his head in the water, as also does the Muscovy male. The same head-pumping display is sometimes used toward females, but the major courtship display is quite different. This occurs usually if not always on land, and begins with the male deliberately Wing-flapping two or three times in a very conspicuous manner, then bringing his bill down and Preening-the-breast-feathers in an equally deliberate fashion, and finally turning his head to place the bill behind the wing closest to the female and performing a single, slow Preening-behind-the-wing movement. The whole display seems

to be performed in slow motion, and is interesting in several respects. Except for the common shelduck, which uses Preening-behind-the-wing as a Triumph Ceremony and a precopulatory display, this is the first species discussed which definitely uses Preening-behind-the-wing as a courtship display. This display is typical of most of the remaining species in this and the following tribes. Many of the following species also Preen-the-breast as a sexual display, but in none of them is this movement so conspicuously different from normal preening.

When approaching a female, males often perform a single Drinking movement followed by a turning of the bill slightly away from the female. This appeasement (or courtship) Drinking is also typical of most of the remaining Anatinae, and Turning-the-back-of-the-head is a fundamentally important display in nearly all the remaining species of waterfowl. In its display behavior, therefore, this species exhibits in rudimentary fashion most of the movements basic to the elaborate courtship displays typical of the more specialized waterfowl (Drinking, Preening-behind-the-wing, Turning-the-back-of-the-head), while still retaining such primitive features as simple vocalizations, the lack of female Inciting, and simple posturing.

Copulatory behavior. I have not observed copulation, but Heinroth (1911) states that in the copulation he observed the male approached the female in an erect posture and repeatedly dipped his head and neck, at which point the female fled, only to be overtaken and raped by the male. Heinroth says, however, that this behavior may not have been typical of the female, since she never produced eggs. Whether the head-dipping observed by Heinroth was the same or similar to that described above is also uncertain.

Pygmy Geese (*Nettapus*)

The smallest waterfowl in the entire family Anatidae are the three species of pygmy geese. They are undoubtedly typical perching ducks, having short, high bills somewhat like those of the wood duck group. The downy young are dark gray or black and white, with a spotted back, clear or spotted cheeks, and a distinct eye-stripe. Except in size, they appear to be much like the downy young of ringed teal. The juvenile plumage is like that of the adult female. In the adult there are varying amounts of sexual dimorphism, depending upon the

species, but in all species both sexes have a metallic green on the back and wings. All three species have white markings on the wings, but none have an elaborate speculum. In males of one species (the cotton pygmy goose) there is a true "eclipse," or special post-nuptial plumage, which resembles the female plumage. This is the first species discussed which has such an eclipse plumage in males, and in only one other genus of perching ducks (*Aix*) is such a plumage also present. In at least two of the species, and no doubt in all, the male lacks a real tracheal bulla, but the tracheal rings of the syrinx are fused and slightly enlarged toward the left (see illustration in Johnsgard, 1961c).

As the three species are obviously closely related, and since so little is known about their behavior, they will be dealt with as a group. I was able to observe the African pygmy goose (*N. auritus*) and the cotton pygmy goose, or "cotton teal," (*N. coromandelianus*) at the Wildfowl Trust. The green pygmy goose (*N. pulchellus*) has rarely been kept in captivity. The last two species are sympatric in northern Australia, but no hybrids involving pygmy geese are known.

General behavior. In captivity pygmy geese are very shy and nervous birds, rarely surviving for any length of time. The preflight movements of the two species observed are rapid, repeated vertical Neck-jerking movements such as occur in Hartlaub's duck and most *Anas* species.

Agonistic and sexual behavior: female. The voice of female pygmy geese is generally referred to as a "weak quack" (Delacour, 1959), Scott's (1958) description of the green pygmy goose clearly indicates that the female has a true Inciting display, during which she follows a drake while chin-lifting.

Agonistic and sexual behavior: male. Males of all species of pygmy geese appear to have soft whistling voices. Alder (1963) describes four calls of the African and three of the Indian species. Since they lack tracheal bullae, the males no doubt produce their high-pitched calls by rapidly vibrating the tympaniform membranes of the syrinx rather than by rapidly expelling air past a bulla, or sound chamber, as most ducks do. Of the sexual display of the cotton pygmy goose, Finn (1901) states that the male bends down his bill to arch his neck, and jerks open his wings, thus displaying the white patch. Regarding the African pygmy goose, Delacour (1959) states that the male swims "proudly" while "turning the head slightly to show the beautiful pale

green patches of the sides." Scott (1958) indicates that male green pygmy geese have a short display flight of about six feet.

Copulatory behavior. On two occasions I saw a pair of cotton pygmy geese perform repeated Bill-dipping movements as the male faced the female and pushed her about in circles while attempting to mount her. This Bill-dipping was very similar to the mutual Head-pumping movements typical of *Anas*, except that the bills of the pair touched the water with each downward movement. It is easy to visualize how the typical *Anas* precopulatory Head-pumping could have evolved from Bill-dipping movements. Alder (1963) has recently described some of the calls of pygmy geese and his paper is accompanied by a set of photographs illustrating copulatory behavior in cotton pygmy geese. The male's Bill-dipping is shown well, as is the apparent major postcopulatory posture, in which the male arches his neck, slightly spreads his folded wings, then turns to face the bathing female.

Ringed Teal (*Callonetta leucophrys*)

As stated earlier, the ringed teal is here considered to be a typical perching duck rather than a dabbling duck of the genus *Anas*, as it is regarded by Delacour (1956). There are numerous reasons for believing the species to be a perching duck (Johnsgard, 1960e), of which the following might be mentioned here. The pattern of the downy young is white and blackish and in almost every respect like that of the downy young of pygmy geese. The plumage of the juveniles and adult female is grayish brown and lacks the characteristic barring of *Anas* females, but it is very similar to the female plumage of pygmy geese, the wood duck group, and the Brazilian teal. The underwing linings are black, as in pygmy geese, Brazilian teal, and certain other perching ducks. There is no eclipse plumage in the male. The tracheal bulla of the male is unlike that of any *Anas* species, but in size and shape it falls between the tracheal structure of pygmy geese and that of the wood duck group (see illustration in Johnsgard, 1961c). The ringed teal occurs in central South America, and the only near relative with which it is sympatric is the Brazilian teal. It has hybridized with that species in captivity, but no other hybrids are known.

General behavior. The ringed teal is a capable perching bird, and in common with the other perching ducks it nests in holes, the female has a white nesting down, and there is a relatively long (29

day) incubation period. The species is a surface feeder, and I have never seen ringed teal dive for food. Preflight behavior consists of lateral Head-shaking and repeated Neck-craning movements.

Agonistic and sexual behavior: female. Female ringed teal have a very limited number of vocalizations. They have no calls remotely like the "Decrescendo Call" of *Anas* females (Lorenz, 1951-1953), and their voice is unusual and reminds one of a domestic cat. The only loud call I have heard is a sharp *hou-iii*, rising in pitch toward the end. Before uttering the call the female shakes her head laterally, lifts her bill, then calls as the bill is brought rapidly downward toward the ground or water (Fig. 29B, C). This call is almost identical in sound and head movements to the courtship call, or "Coquette Call," of female *Aix*, except that in those species the introductory head shake is lacking.

Ringed teal perform a true Inciting display, the form of which also indicates a close relationship with the wood duck group. The female makes direct threatening movements in the direction of the opponent while uttering a very soft *tet-tet-tet* . . . ; then she retreats toward her mate. This behavior is almost identical to the Inciting behavior of the female wood duck, and entirely different from that of *Anas* females.

Agonistic and sexual behavior: male. The only male vocalization I have heard is a whistling noise which is probably homologous with the "Burp" (Lorenz, 1951-1953) of *Aix*. The call is a soft, wheezy whistle which, like the female's courtship call, is uttered with a bill-tossing movement and usually after a preliminary head shake. The call might be described as *whhee'-ooo*, and is uttered either on land or in the water. Sometimes the male performs a general body shake, but this does not function as an "Introductory Shake" (Lorenz, 1951-1953) as it does in *Anas*.

Aside from the display whistle, the male's courtship appears to consist merely of swimming beside the female (Fig. 29A) and turning to Face her whenever the opportunity arises. I cannot share Delacour's opinion (1956) that this display behavior is reminiscent of pochards. Rarely, I have observed a very rapid Preening-behind-the-wing display by males, which unlike that of the wood duck and mandarin duck was not linked with Drinking.

Copulatory behavior. In its copulatory behavior the ringed teal also exhibits its affinities with the wood ducks. The male signals his intention to tread by directly approaching the female. He swims

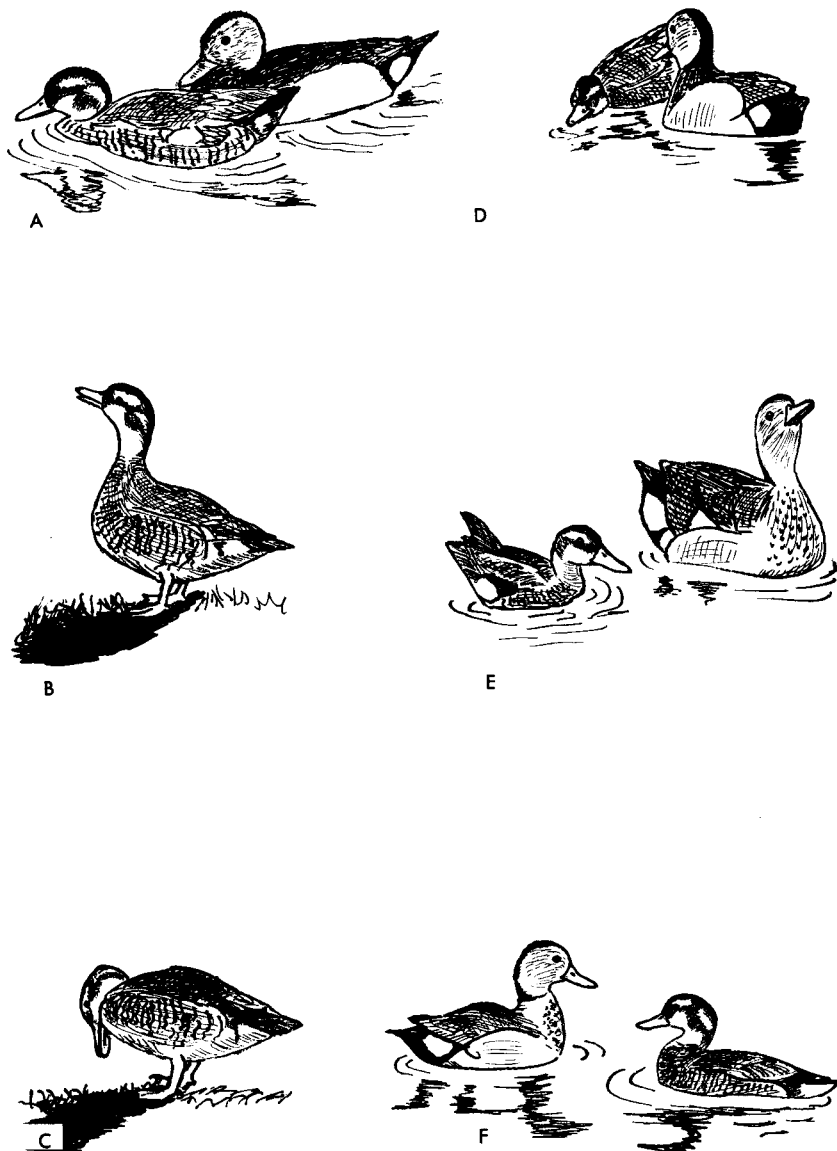


Figure 29. Ringed Teal

- A. Male following female during pair formation, attempting to Face her.
- B, C. Female uttering courtship, or Coquette, call.
- D. Precopulatory behavior, female prone as male approaches.
- E. Postcopulatory call of male after treading. Note lifted tail and exposed wing-speculum pattern.
- F. Male Facing the female after copulation.

toward her with his head held high (Fig. 29D) and may make slight bill-dipping or bobbing movements with his bill. The female usually begins to lie more and more prone, with few or no head movements. The male usually picks at her body feathers a few times, then rapidly mounts. Treading lasts only a few seconds, and as it is completed the male may retain his hold on the female's nape for a few seconds longer, causing the birds to rotate slightly in the water. He then releases her and utters his display whistle with the usual bill-toss, sometimes lifting his tail enough to expose the white under-tail patch momentarily (Fig. 29E); then he turns and, thereafter remaining completely motionless (Fig. 29F), faces the bathing female. In no case in the ten or more copulations I have seen has the male bathed at this point, although that is the normal male postcopulatory behavior of *Anas*.

Wood Duck (*Aix sponsa*)

The American wood duck is certainly a typical perching duck, although it has often been placed near the *Anas* group. The downy young are much like those of pygmy geese and ringed teal, being white below and dark above, and having a rather long tail, an eye stripe, and a dark crown. Juveniles resemble adult females, which are mostly gray and brown, with a gray head and a white throat and eye-stripe. The breeding plumage of the male is highly colored with metallic sheen on the back, head, and wings, and the rest of the body is also brightly colored. There is a distinct eclipse plumage which rather closely resembles the plumage of the female. Males have a rather large, rounded, and osseous tracheal bulla which tends toward a spherical shape (see illustration in Johnsgard, 1961c). The species is not sympatric with any near relatives. In captivity it has hybridized with a remarkable number of species, especially various species of *Anas*. No hybrids have yet proved fertile. It is generally held that there are no authenticated records of hybridization with the mandarin duck, and it is thought that chromosomal differences (Yamashina, 1952) in these species make hybridization impossible.

General behavior. A great deal has been written about the behavior of wood ducks by Heinroth (1910), Lorenz (1951-1953), and others. They do not differ from the other perching ducks in their tree-nesting behavior, surface-feeding tendencies, and perching abilities. They are not very aggressive birds; females often nibble the white

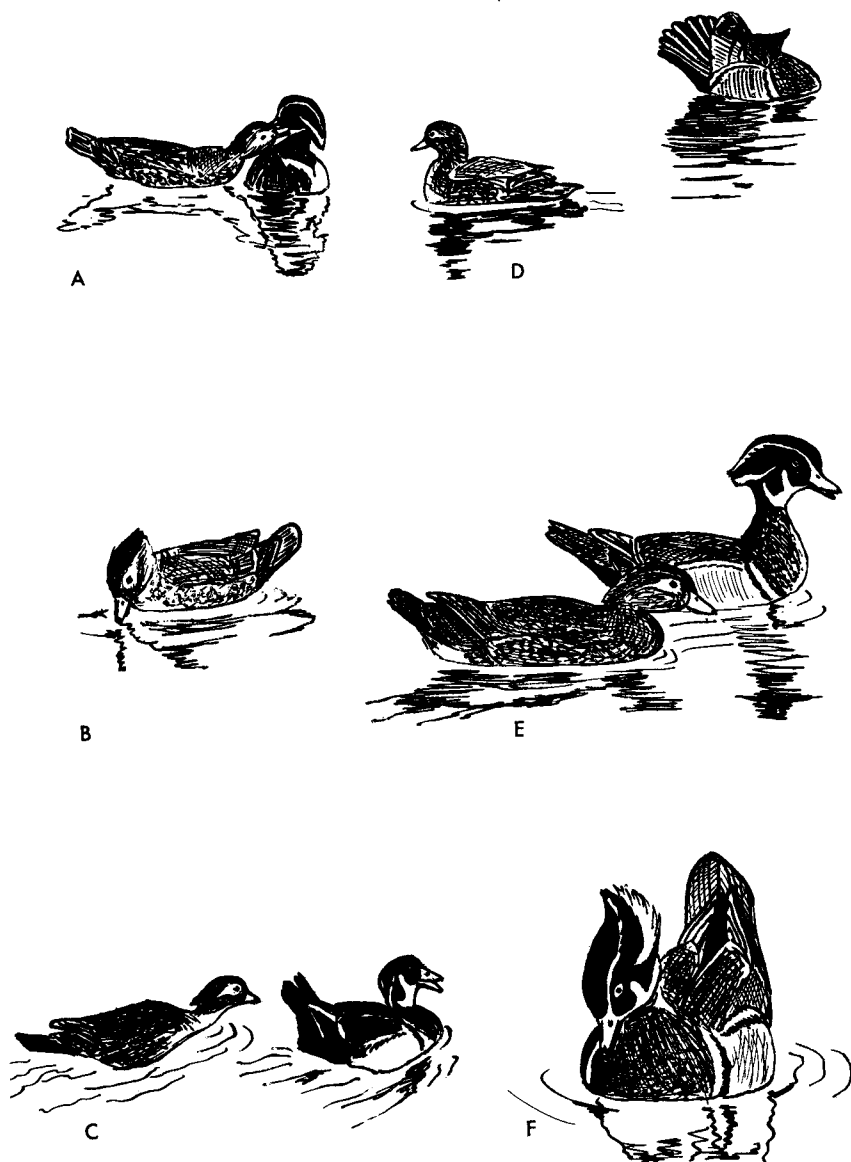


Figure 30. Wood Duck

- A. Female nibbling the throat region of mate.
- B. Female uttering Coquette call.
- C. Female Inciting as male Turns-the-back-of-the-head.
- D. Male Preening-behind-the-wing to female.
- E. Male uttering Burp call.
- F. Male performing Wing-and-tail-flash.

chin region of their mates (Fig. 30A). As Lorenz has pointed out, the preflight behavior consists of Neck-craning motions like those of *Cairina* and most other perching ducks, as well as lateral Head-shaking movements (McKinney, 1953).

Agonistic and sexual behavior: female. Lorenz and Heinroth studied this species thoroughly, and most of the following account is based on their observations. The female wood duck has various call-notes, including a "go-away" call, a general call-note, a danger call, and certain sexually motivated calls. The courtship note, or "Coquette Call," which is uttered as the female suddenly points her bill downward (Fig. 30B), is a one-note call which drops in pitch. It is similar in sound and associated head-movements to the courtship call of the female ringed teal. The flight call is a loud *u-ih*, drawn out and owl-like, and Lorenz feels that this call is homologous with the Decrescendo Call of female *Anas*. Inciting consists of rapid direct pointing movements while calling softly (Fig. 30C), alternated with "caressing" movements toward the preferred drake. A rapid, vertical bill-jerk exactly like that of the male is used as a greeting or threat display.

Agonistic and sexual behavior: male. Aggressive behavior between males consists of chasing and beating one another with the wings, but without seriously hurting each other. The Introductory Shake occurs only rarely in the wood duck, and as in the ringed teal it is not functionally introductory. A highly ritualized Preening-behind-the-wing is a rather frequent and striking display, in which the primaries and secondaries are momentarily spread and flashed toward a female (Fig. 30D). Drinking always precedes this display, but unlike display Drinking in the mandarin duck it also frequently occurs alone, and Preening-behind-the-wing is never performed repeatedly as it is in the mandarin duck. The display call, or Burp, is a whistle accompanied by a vertical stretching of the neck and a raising of the crest (Fig. 30E). Chin-lifting toward the female occurs independently (Fig. 31F) or is fused with Turning-the-back-of-the-head (Fig. 30C) into a single display which is one of the most important and frequent of the male wood duck's courtship patterns. While Turning-the-back-of-the-head toward the female, he swims ahead of her and slightly to one side, with his tail tilted to the side away from the female. The female may or may not be Inciting during this display, but as will be seen later the combination of Inciting and Turning-the-back-of-the-head has a fundamental importance in the pair-formation process of

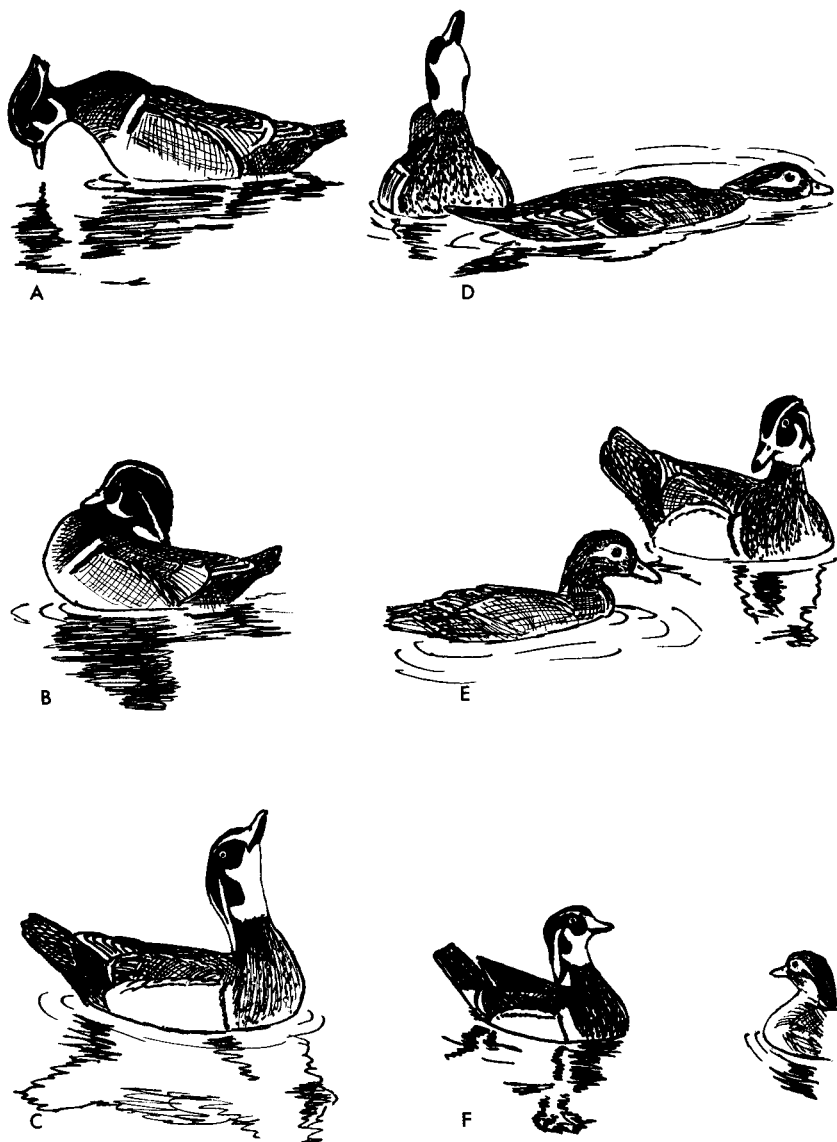


Figure 31. Wood Duck

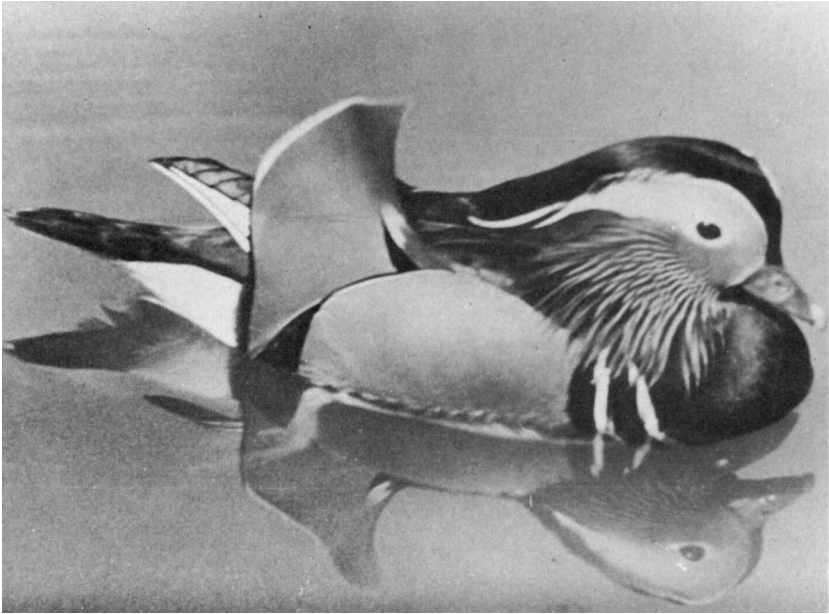
A, B. Two phases of the Display Shake.

C. Male performing Bill-jerking.

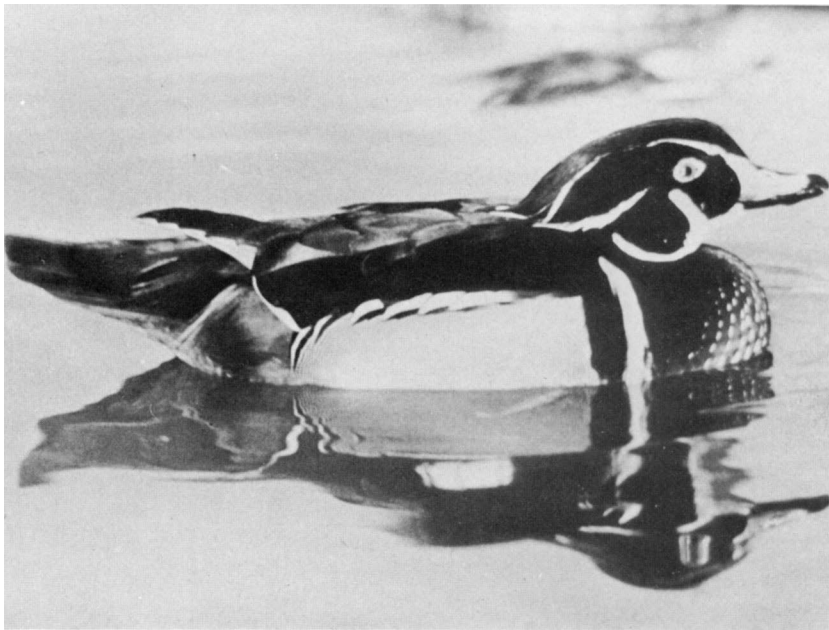
D. Female in copulation position, male performing Bill-jerking movements.
(This is not a typical precopulatory display.)

E. Male Facing the female after copulation.

F. Chin-lifting by male to female. Unlike the Bill-jerking shown above, this posture is held for several seconds.



Mandarin Duck, adult male swimming.



Wood Duck, adult male drinking.



Common Pintail, Grunt-whistle display.
(Courtesy Bird Photographs Inc., Ithaca, N.Y.)



Yellow-billed Pintail, Grunt-whistle display.

most species of Anatinae (Johnsgard, 1960c). The most elaborate courtship movement of the male wood duck is the Display Shake (called the Whistle Shake by Lorenz), which is a highly ritualized general shake combined with a whistling note (Fig. 31A, B). This display and the corresponding ones of the mandarin duck and the Australian wood duck are analogous to the Grunt-whistle of *Anas*, in that they derive from the general shake; these birds do not, however, throw up water in the way that birds performing the Grunt-whistle typically do. A fairly frequent male display (apparently that called the Down-up by Lorenz but certainly not homologous to the Down-up of *Anas*) is a single rapid upward jerk of the bill, flashing the white chin (Fig. 31C, D), which is used as a greeting or sexual display toward females and as a threat display toward males. Wood duck males also sometimes perform a sudden upward jerk of the closed wing and tail (Fig. 30F), which is somewhat reminiscent of the Head-up-tail-up of male *Anas*, but clearly not homologous with that display. I have referred to it as a Wing-and-tail-flash, and I have observed it only in the wood duck and the mandarin duck.

Copulatory behavior. I have observed no mutual displays before the assumption of the prone position by the female, but the male often Faces the female in the same manner as occurs in the ringed teal. While in the prone posture the female holds her head along the water and her tail pointing slightly upward (Fig. 31C, D), as does the female ringed teal. The male swims around her, usually Bill-dipping or Drinking occasionally and pecking at her head, back, and tail. He then mounts and after treading swims rapidly away for several feet while Turning-the-back-of-the-head; then he usually turns around and Faces the female as she bathes (Fig. 31E). The drake did not bathe after treading in the several cases I saw.

Mandarin Duck (*Aix galericulata*)

As Lorenz (1951–1953) has already pointed out, the mandarin is surely a close relative of the wood duck, although the two are perhaps not so closely related as one might judge from the similarities of the females. The downy young of the two species are very similar in pattern, but the mandarin has a yellow rather than a white base color. The juveniles closely resemble adult females. The plumage of the adult male is a fantastic array of metallic and otherwise brightly

colored patterns which show a general similarity to those of the male wood duck. As in the male wood duck there is a distinct eclipse plumage which is very similar to the female's plumage. The wing is much like that of the wood duck except for the remarkably enlarged inner secondary, which is lifted during the Preening-behind-the-wing display. The trachea of the male mandarin has a somewhat larger bulla than that of the male wood duck, but as in that species it is uniformly thin and rather spherical in shape. Mandarin ducks are native to Asia and are not sympatric with any close relatives. Several hybrids involving the mandarin duck have been reported (Gray, 1958), but Prestwich (1960) considers the evidence for these hybrids to be inadequate and claims that chromosomal peculiarities totally prevent hybridization.

General behavior. Besides the book by Savage (1953), the papers of Heinroth (1911) and Lorenz (1951–1953) contain much information on general behavior. Mandarins are gregarious and tend to be most active in the evening or on dark days, presumably because the males are less conspicuous at such times. Females nibble the head region of their mates in the same way as do female wood ducks. Repeated Neck-craning movements are used in the preflight situation.

Agonistic and sexual behavior: female. In nearly every respect the female mandarin resembles the female wood duck. Their Inciting movements and calls are practically identical, and although the Coquette Call of the female mandarin is higher and shorter, the head movements which accompany it are identical in the two species. Unlike female wood ducks, female mandarins sometimes Preen-behind-the-wing to males, but usually they do not Drink before they do so.

Agonistic and sexual behavior: male. Although the male mandarin shares with the wood duck most of its display patterns, the general impression of the display is quite different. While the wood duck male, like the ringed teal drake, courts a single female intensively, the male mandarin tends to be promiscuous, and the behavior of the female is much less important in display (Lorenz, 1951–1953). Only one display, the Drinking–Preening-behind-the-wing sequence, is clearly directed toward a particular female. Lorenz (1951–1953), as well as Dilger and Johnsgard (1959), has commented on the relationships between plumage pattern, mate selection, and sexual dimorphism in this species.

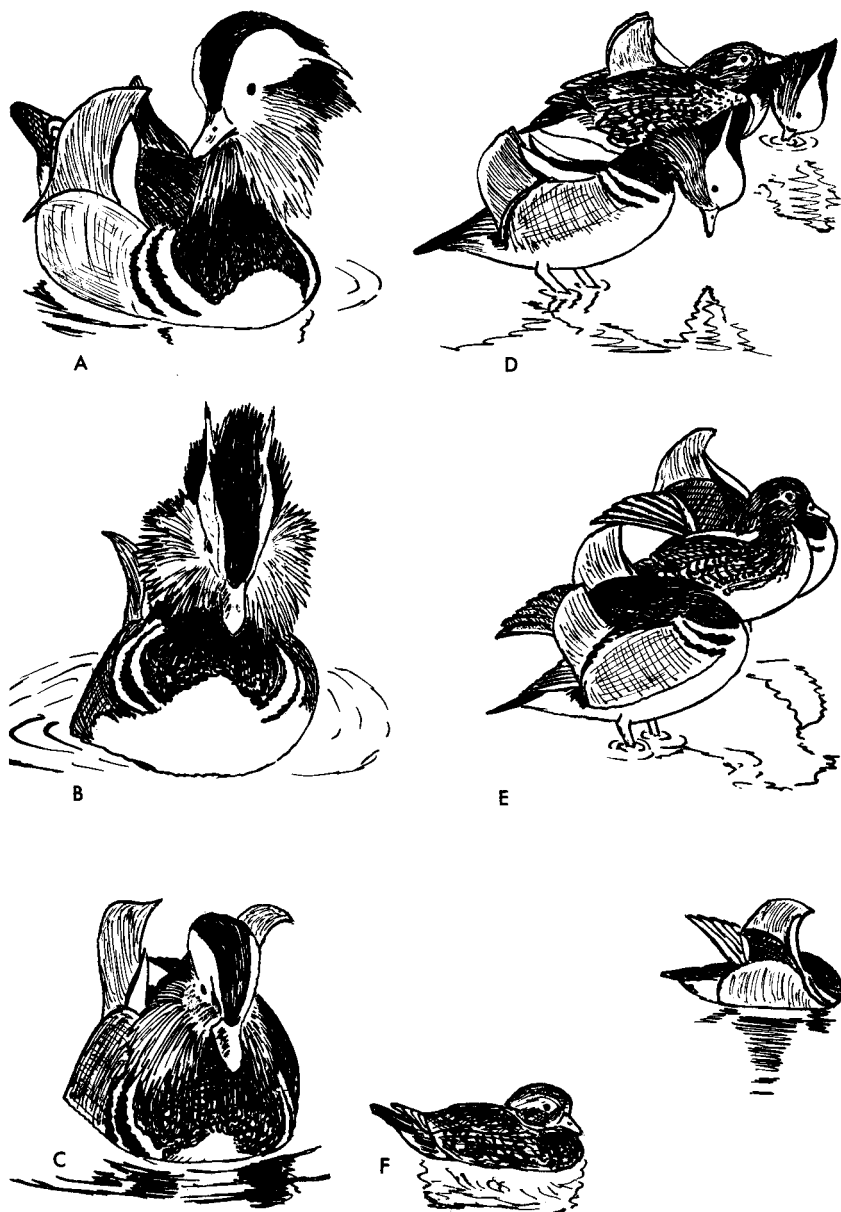


Figure 32. Mandarin Duck

A. Male in Burping posture.

B, C. Two phases of the Display Shake.

D, E. Display Drinking followed by Preening-behind-the-wing.

F. Preening-behind-the-wing to female.

As in the wood duck, the Introductory Shake is of minor importance in courtship display, and the general shake has been ritualized into a more important function. Thus the male mandarin duck has a Display Shake (Fig. 32B, C) which is very similar to the corresponding display of the wood duck. In both species the head is first lowered, then rapidly thrust upward while the head and tail are rapidly shaken and a call is uttered. A second and more complex form of display shaking is the Double Display Shake (called the Double Grunt Whistle by Lorenz). In this display the bill is dipped into the water and a sneeze-like call is uttered as the head is shaken and pulled back to the resting position. This is followed immediately by a second dipping movement, which is very rapidly performed and accompanied by another wheezy call as the head is withdrawn and the tail is vigorously shaken (Fig. 33A-E). As Lorenz has pointed out, this display is somewhat intermediate between the simpler Display Shake and the more complex Grunt-whistle of *Anas*. A very frequent and interesting display is the Drinking-Preening-behind-the-wing sequence (Fig. 32D-F). In this species the male does not spread the whole wing when preening, but lifts only the ornamental "sail" feather on the side toward the female, momentarily exposing the metallic blue outer vane which is normally hidden by the flank feathers. A very rapid bill-flicking to the vertical is performed by the mandarin duck in the same situations as it is by the wood duck. In addition, the mandarin performs the same Wing-and-tail-flashing display as the wood duck. This display is performed in almost the same manner by the two species, but the mandarin performs it much more frequently.

Copulatory behavior. Although generally similar to the wood duck in its copulatory behavior, the mandarin duck does exhibit some interesting differences. The precopulatory display is a form of mutual Head-pumping, performed with repeated forward and upward, rather rotary, movements similar to the preflight pointing movements of perching ducks. The female gradually flattens out prone (Fig. 33F), and the male may perform a few Bill-dipping motions before mounting. After treading, the male immediately dismounts and swims rapidly away for about ten feet while Turning-the-back-of-the-head toward the female with his tail slightly lifted. He does not turn and face her. The female begins to bathe immediately.

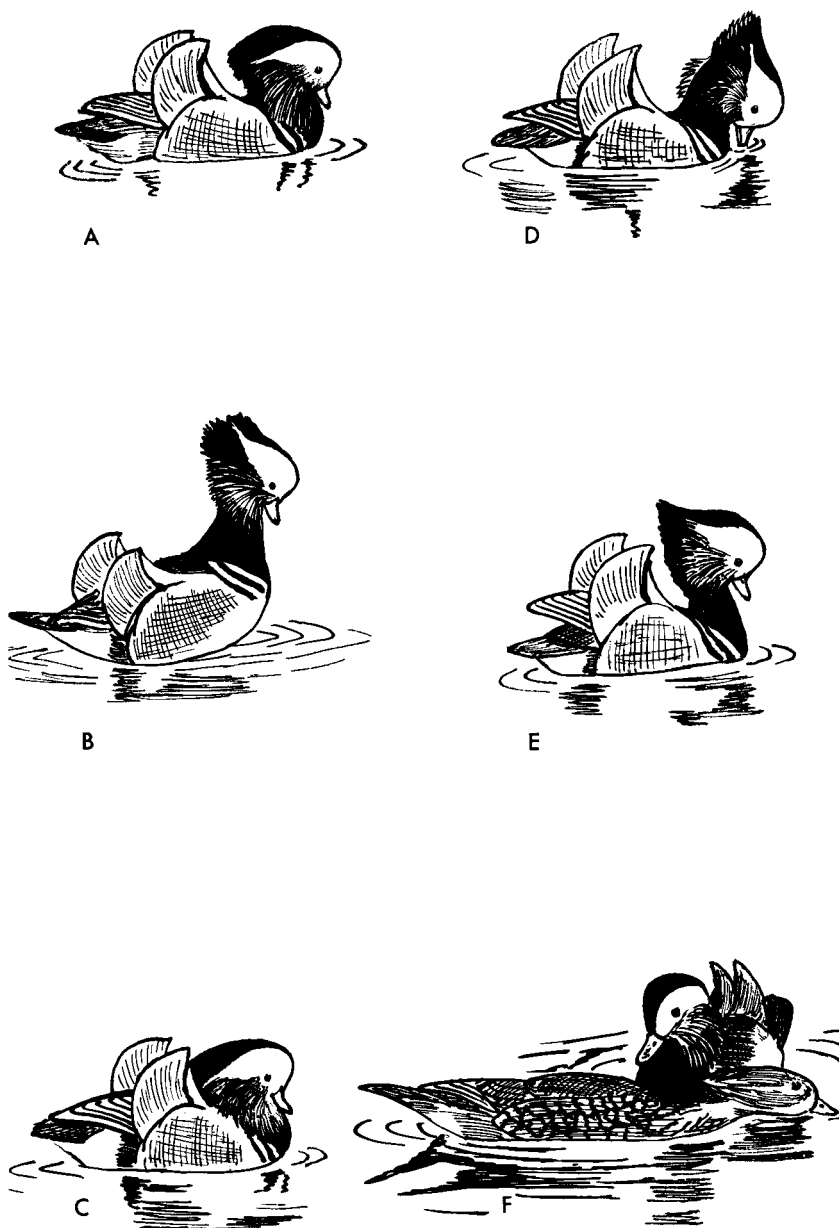


Figure 33. Mandarin Duck

A-E. Sequence illustrating the Double Display Shake. Compare with simple Display Shake (Fig. 32B, C).

F. Female in copulation posture, male about to mount.

Australian Wood Duck (*Chenonetta jubata*)

The Australian wood duck, or maned goose, is undoubtedly a close relative of *Aix*. The downy young are similar in color to downy wood ducks, but have a distinct cheek stripe as well as an eye stripe. Immature males closely resemble adult females. The adult female has a plumage pattern similar to that of females of *Aix*, and differs mainly in having more strongly streaked cheeks. The wings of both sexes are very different from those of the other wood ducks in that metallic coloration is restricted to only part of the secondaries, and there is a white posterior border which widens toward the outer secondaries. The speculum pattern is similar to that of the Brazilian teal, except that in that species the white border narrows toward the outer secondaries. The adult male is mostly covered with finely vermiculated gray feathers, but has a black rump, tail, and under-tail coverts. The head is brown, with a small erectile black crest, or "mane." There is no eclipse plumage. The male tracheal bulla is similar in size and shape to those of *Aix*. The species is not sympatric with any near relatives and apparently has not hybridized with any perching ducks other than the wood duck. Hybrids involving sheldgeese have been alleged, although this seems an unlikely cross.

General behavior. The Australian wood duck is much more terrestrial than its near relatives and does not appear to perch to as great a degree. I have not seen any nibbling of the male by the female. McKinney (1953) and I have both observed rapid Chin-lifting as a preflight movement, and this is quite different from the typical preflight behavior of perching ducks.

Agonistic and sexual behavior: female. The voice of the female is remarkably unlike the usual voices of female ducks. The most frequent call is a loud, hoarse *whroo*, emitted with the neck extended and the bill level. Lorenz (1951-1953) states that there is a descending call intermediate between the flight call of *Aix* and the Decrescendo Call of female *Anas*. I have observed Inciting only a few times. It consists of chin-lifting toward the preferred male, accompanied by repeated nasal *wonk* notes, and alternated with aggressive pointing with the head held low in the direction of the opponent (Fig. 34A, B). This type of Inciting is more like that of the Brazilian teal than that of *Aix* or *Callonetta*.

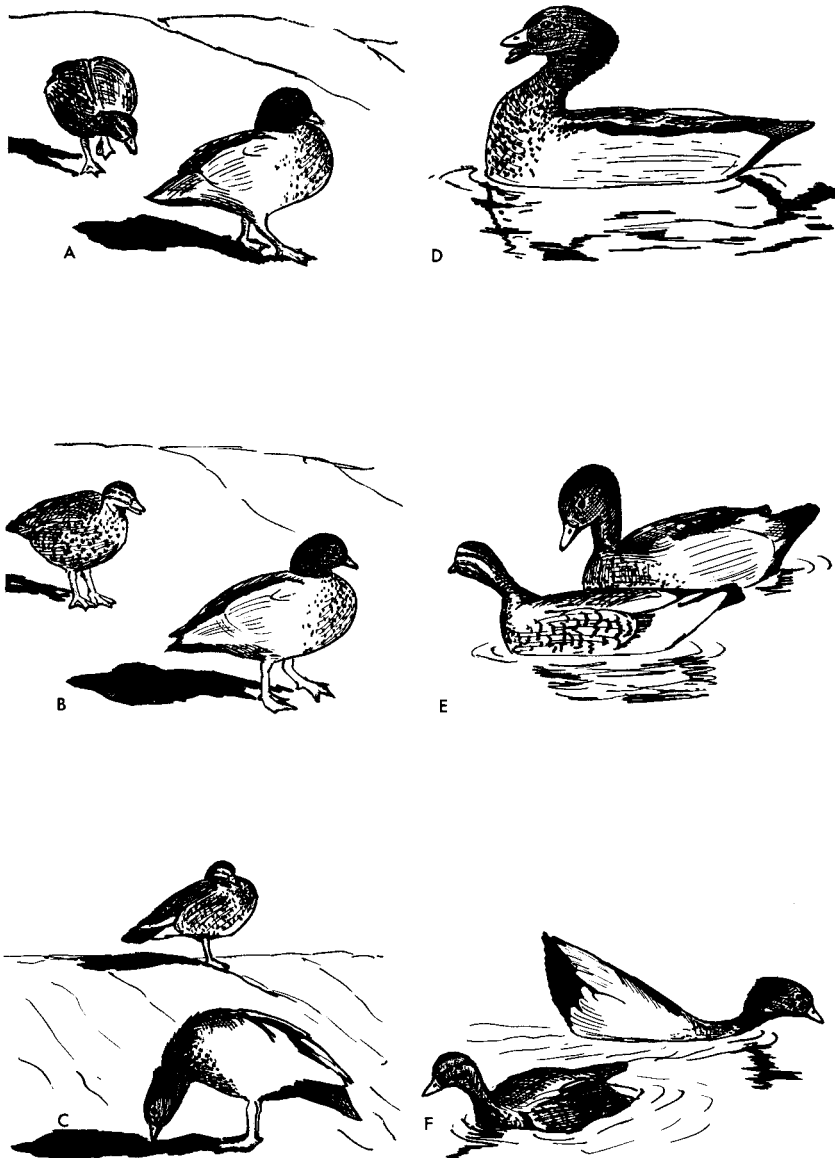


Figure 34. Australian Wood Duck

A, B. Female Inciting.

C. Male Display Shake on land. Compare with Fig. 35B, C.

D. Male uttering Burp call.

E. Precopulatory posture of female. (From photo by D. F. McKinney.)

F. Postcopulatory display of male, female bathing. (From photo by D. F. McKinney.)

Agonistic and sexual behavior: male. Very little has been written on the behavior and displays of this species, apart from a short note by Delacour (1945). The courtship call, or Burp, is uttered with the neck extended, the bill level, and the mane erected (Fig. 34D). The call is a highly distinctive, catlike *wee-ow'*. As in the American wood duck, this call is often uttered when the male is alone and apparently looking for his mate. Preening-behind-the-wing has not been observed, but very likely does occur during display. During Inciting, a male has been observed to swim ahead of the female while Chin-lifting and possibly Turning-the-back-of-the-head, in a posture very much like that frequently assumed by male Brazilian teal. The most elaborate of the male displays is a Display Shake much like those of the wood duck and the mandarin duck, which, like the Display Shake of those species, is no doubt a ritualized general shake (McKinney, 1953). From a preliminary posture of holding the head and neck retracted into the scapulars (Fig. 35A), the bird slowly extends the head down to the ground or water, then rapidly returns it to the resting position in a shaking movement (Figs. 34C; 35B, C). Another probable display begins with the same or a very similar shaking movement, but is immediately followed by a second shake. This display differs from the first in exactly the same way as the mandarin's Double Display Shake differs from its Display Shake.

Copulatory behavior. Precopulatory behavior has been seen a few times, and apparently consists of vertical Head-pumping and Head- or Bill-dipping movements by the male and perhaps also by the female. The variable occurrence of Head-dipping, Bill-dipping, and Head-pumping in this species and in the Brazilian teal suggests that Bill-dipping and Head-pumping represent increasingly more ritualized forms of Head-dipping (which itself appears to be a ritualized form of bathing). Therefore, I do not agree that these precopulatory displays are derived from intention movements to assume the copulation position, bathe, or dive, as various authors have suggested. I have not observed treading, but in a film taken by McKinney the male swam around and away from the female while holding his hind-quarters very high and clearly exhibiting the black under-tail coverts (Fig. 34F).

Brazilian Teal (*Amazonetta brasiliensis*)

A precise taxonomic placement of the Brazilian teal is not yet possible, for the species exhibits characteristics reminiscent of perch-

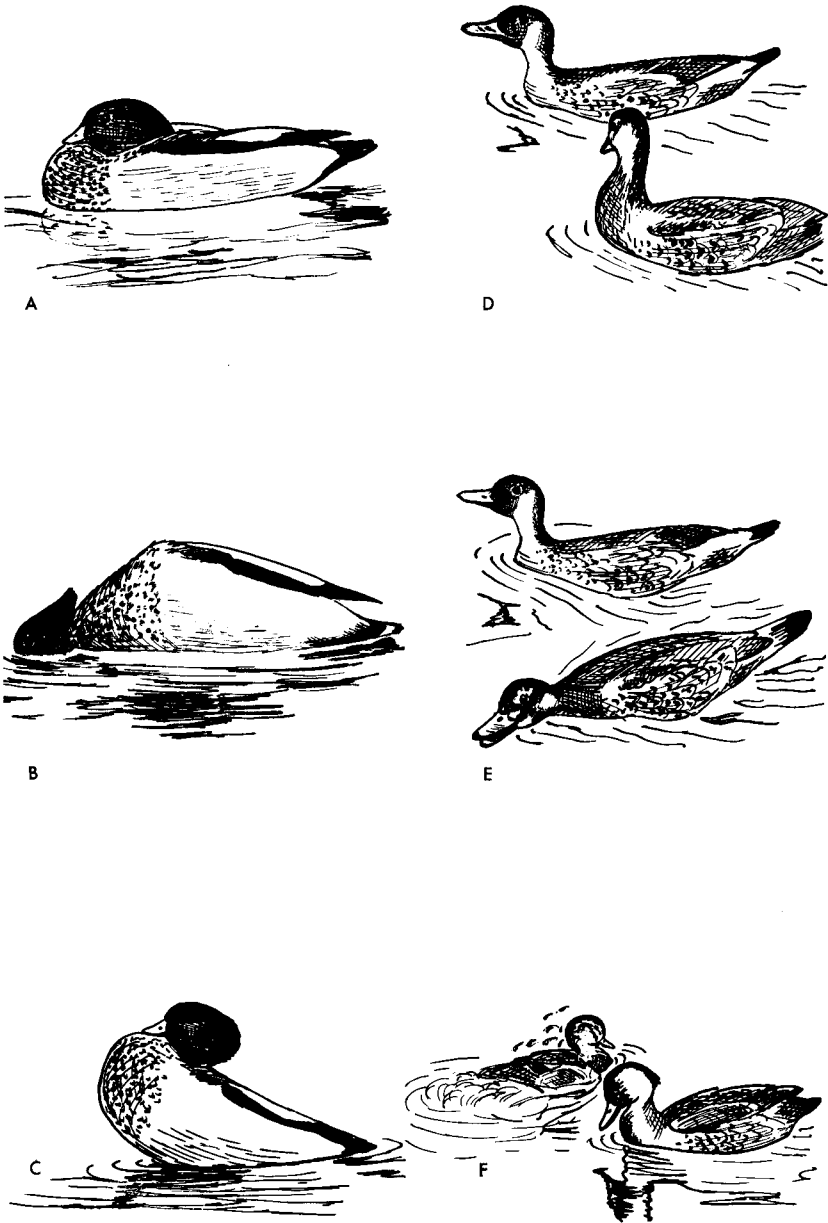


Figure 35. Australian Wood Duck, Brazilian Teal
A-C. Phases of Display Shake in Australian wood duck.
D, E. Brazilian teal, female Inciting, male Burping while Chin-lifting.
F. Brazilian teal postcopulatory display. Female bathing.

ing ducks, dabbling ducks, and even the pochards. I believe it most probable that the species is a perching duck, but one which possibly links the tribe Cairinini with the Anatini. The downy young are much like those of the wood ducks. Juvenile males resemble the adult female. The female is vaguely like the female ringed teal in appearance, although this similarity is for the most part superficial. The male Brazilian teal lacks an eclipse plumage, and has a small black nape crest similar to that of the Australian wood duck. The wing speculum pattern is most striking, and metallic coloration extends to the primaries. The anterior parts of the secondaries are a brilliant green, and the posterior parts have a white border that widens diagonally inward. As in various other perching ducks, the underwing linings are black. The trachea of the male has a bony bulla (Phillips, 1924), but the exact shape and appearance of this bulla is undescribed to my knowledge. The species occurs in South America, and is broadly sympatric with the ringed teal. Infertile hybrids with that species and with two species of *Anas* have been reported.

General behavior. The Brazilian teal is a fairly typical perching duck in its general behavior, although it is a ground-nesting species and, in correlation with this, has a relatively short (25 day) incubation period. According to McKinney (1953) preflight movements consist of lateral Head-shaking; I have also observed an *Anas*-like Neck-jerking.

Agonistic and sexual behavior: female. In her vocalizations the female certainly suggests affinities with the dabbling ducks. She has a call which is probably homologous to the Decrescendo Call of female *Anas*. The notes of the call tend, however, to remain at the same pitch rather than to descend. The Inciting call is a repeated *week* note, uttered each time the female lifts her head toward her mate as she alternates this movement with direct threatening movements toward the opponent (Fig. 35D, E). This Inciting behavior is reminiscent of the Australian wood duck.

Agonistic and sexual behavior: male. Male Brazilian teal appear to have a very simple kind of courtship behavior. The only obvious sexual display consists of repeatedly Burping with erected crest, and simultaneously Chin-lifting (Fig. 35D, E). The call is a strong, piercing whistle, *whew-whew-whew . . .*, almost endlessly repeated. The displaying male swims rapidly ahead of the female, possibly Turning-the-back-of-the-head, but this is not nearly so evident as in

Aix. During extreme excitement the male will often roll his head on his back, or even bathe. I have not observed Preening-behind-the-wing, but W. von de Wall (pers. comm.) has observed a male perform it toward a female. Finally, Wing-flapping appears to be used as a display by males, and it is especially conspicuous because each sequence of it is ended by a rapid stretching of both wings over the back in a posture that makes visible the white axillary feathers, which contrast sharply with the black underwing surface.

Copulatory behavior. Precopulatory behavior consists of the male swimming up to the female, his neck stretched and his crest depressed, and making occasional Bill-dipping movements. He then suddenly begins to perform more vigorous Head-dipping movements, and the female, if receptive, performs similar Bill-dipping or Head-dipping movements. After treading, the male calls as he swims around the bathing female in a circle, his bill pointed almost directly downward (Fig. 35F). A similar postcopulatory display occurs in pochards, but since the precopulatory behavior is different and there is no other reason to suspect that the species are related, the similarities of the postcopulatory displays must be regarded as a chance convergence.

TRIBE ANATINI (SURFACE-FEEDING DUCKS)

The tribe of surface-feeding, or dabbling, ducks is the largest single tribe in the family. There are 40 species in the tribe as it is constituted here. Contrary to the arrangement of Delacour (1956), the ringed teal is included in the Cairinini; and the crested duck, included in the Tadornini by Delacour, is here considered a typical dabbling duck. In addition, the pink-headed duck has been removed from the Anatini and placed in the Aythyini with the pochards, and the freckled duck has been removed from the tribe and is considered a primitive species having anserine relationships. The marbled teal has been removed from the genus *Anas* and placed in a monotypic genus which, I believe, provides an evolutionary link between the dabbling ducks and the pochards (Johnsgard, 1961e).

The Anatini are world-wide in distribution and include the most numerous and widespread species of the family. Most species (and especially those of the shoveler group) forage on the water surface, gathering food from the surface by up-ending or "tipping-up," or, more rarely, by diving. Most species open their wings when diving. A few species, such as the wigeon, graze, and nearly all species are