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Handbook of Waterfowl Behavior: Tribe Anatini (Surface-feeding Ducks)

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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

predominantly vegetarians. Nearly all nest on the ground, but a few species nest in holes or crevices. The downy young are much like those of the perching ducks and are usually strongly marked with brown and white or with yellow. All species mature their first year, and pair bonds are generally renewed yearly. Most species exhibit sexual dimorphism in plumage, and metallic coloration is usually restricted to the head and speculum. The males of most sexually dimorphic species have a distinct eclipse plumage. Nearly all species have metallically colored wing specula. Males of all species studied to date except one have tracheal bullae which are ossified throughout; the marbled teal is the exception, and its bulla has numerous membranaceous fenestrae similar to those found in the pochard group.

The downy young of most and possibly all species have a one-syllable distress whistle (Lorenz, 1951-1953) rather than the two- or multi-syllable note of downy wood ducks and geese. This one-syllable note is used by the adults of at least some species as a warning or aggressive note. In the mallardlike ducks and some other species a two-note call is used by the male as a "conversational" or sexual call.

The tribe's more generalized relatives are clearly the perching ducks, and such species as Hartlaub's duck, the Brazilian teal, and the African black duck are all forms which exhibit features characteristic of both tribes. Woolfenden (1961) has even suggested that the two groups should be merged into a single tribe. On the other hand, the Anatini is also very closely related to the pochards, as evidenced by such transitional forms as the marbled teal and the pink-headed duck. The opinion of Humphrey (1958) and Delacour (1959) that the eiders are closely related to the dabbling ducks has been commented on elsewhere (Johnsgard, 1960f, 1964) and is not accepted here.

Three species which are little studied and of very uncertain affinities are here included in the tribe, following the precedent of Delacour (1956). These are the torrent duck, the blue duck, and the pink-eared duck. All three have become highly specialized for particular environments, and relatively little is known of their behavior.

Blue Duck (*Hymenolaimus malacorhynchus*)

The New Zealand blue, or mountain, duck appears to be specialized for feeding in streams. The downy young, which lack back

spotting, and are dark above and white below, are rather reminiscent of some downy perching ducks. The adult and juvenile plumages are a curious lead-gray color, flecked with brownish spots. There is no speculum, but the secondary feathers are lined with black edges in a pattern similar to that found in Hartlaub's duck. The tail is long and broad. The bill of both sexes has a soft and protruding flap at the tip which provides a tool for scraping algae and animal life off wet rocks. The trachea of the male is still undescribed. The species is restricted to the mountainous districts of New Zealand. An alleged wild hybrid between this species and the New Zealand gray duck has been reported but not authenticated.

General behavior. Blue ducks frequent mountain streams and pick up food from the water or scrape it off the wet rocks. They are poor divers, opening their wings when they submerge, and they probably do not normally feed by diving. If, as reported, they are tame and "stupid" birds, this would account for their now being extremely rare.

Agonistic and sexual behavior: female. Little is known of the female's behavior. One bird at the Wildfowl Trust was heard to utter a low wigeonlike growling note. I have not observed females of this species personally.

Agonistic and sexual behavior: male. Males have been maintained at the Wildfowl Trust for extended periods in excellent condition. One male, lacking a female, became associated with a female common shelduck that was already paired. He followed this bird almost constantly, although he was often chased by the male shelduck. When courting the shelduck, the male blue duck would face her with the forepart of his body low in the water and the tail and hindquarters lifted as he uttered a whistled *zweee* repeatedly, each note rising in pitch toward the end. As he called he lifted his chin and bill strongly and repeatedly (Fig. 36B, C) in a manner resembling the Chin-lifting display of wigeons. He showed no tendency to Turn-the-back-of-the-head toward the female. Males also call from another posture, in which they stretch the head and neck out over the water (Fig. 36A) and utter a strong, wheezy *whee-ooo'*. Both the posture and the call are reminiscent of male Chiloé wigeons. A general shake similar to the Introductory Shake of male *Anas* was observed several times during display. Peter Scott (pers. comm.) once observed the female shelduck assume a copulation posture in front of the blue duck, but the latter paid not the slightest heed to her. Possibly precopulatory

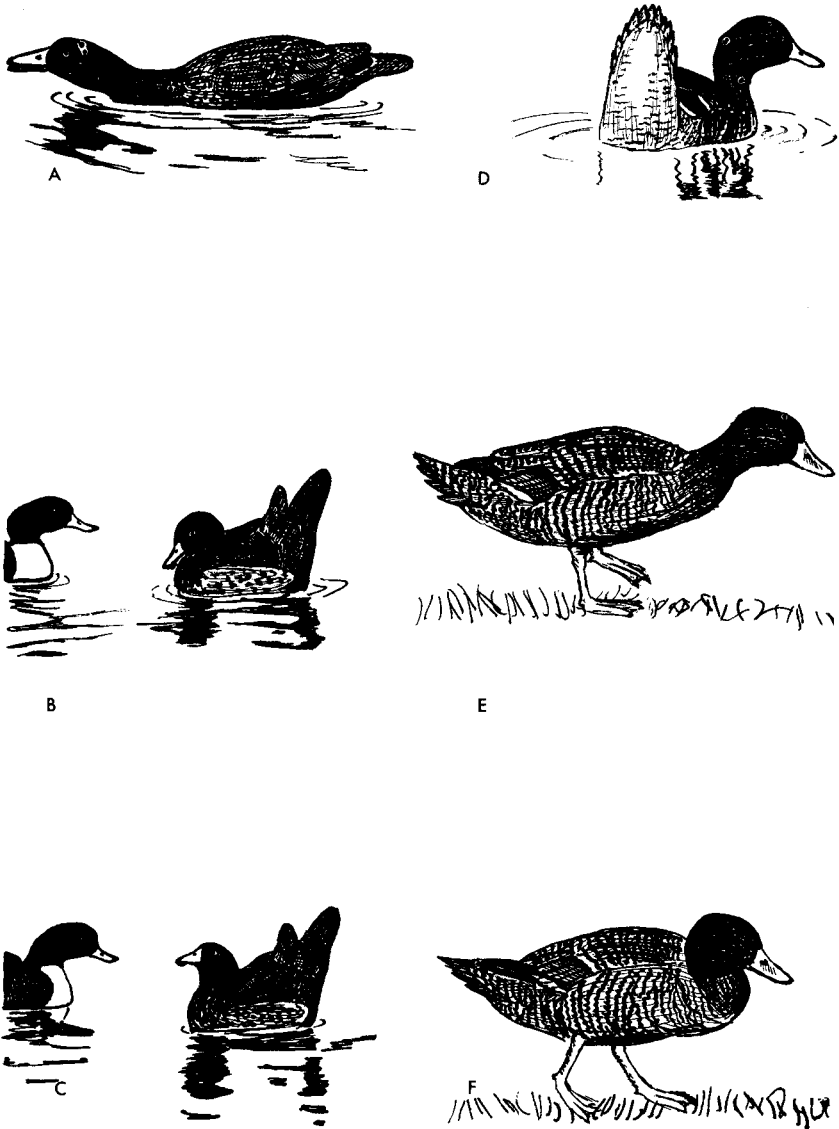


Figure 36. Blue Duck, Salvadori's Duck

A. Male blue duck calling.

B, C. Male blue duck chin-lifting repeatedly while calling and facing courted bird (female common shelduck).

D. Salvadori's duck swimming with tail cocked, an indication of fear rather than a sexual display.

E, F. Method of walking in Salvadori's duck. Note that the distance between the head and the stationary foot remains constant.

behavior in the blue duck consists of some mutual or preliminary behavior which the shelduck did not perform.

Torrent Duck (*Merganetta armata*)

The numerous races of South American torrent ducks appear to be derivatives of an *Anas*-like ancestor that became adapted to living in rushing streams. Although Niethammer (1952) concluded from a comparison of sternal and tracheal anatomy that the torrent duck is not very distantly related to the mallardlike ducks, Woolfenden (1961) advocates the recognition of a distinct tribe for the torrent ducks, as was originally proposed by Delacour and Mayr (1945). The downy young do not differ greatly from those of Salvadori's duck, but have striped rather than spotted backs. Immature birds tend to resemble the adult male rather than the female, but they have barred flanks which remind one of Salvadori's duck. The female plumage differs from that of all other ducks, and is vermiculated gray above and rusty brown below. Adult males have white heads with dark eye- and crown-stripes that extend down the neck and connect at the nape. There is no eclipse plumage. The more northerly races have white under parts and darker mantles, while the southern races tend to have dark under parts and lighter mantles. In the central Andes of Bolivia and Peru there is one very dark-bodied race (*turneri*) and one very light-bodied race (*garleppi*) which occur side by side. This suggests that possibly there has been hybridization between the two forms and a resulting reinforcement of plumage differences, but too few specimens have been collected in the critical regions to test this hypothesis.

General behavior. Extremely little has been written on the behavior of torrent ducks. They nest in holes or crevices, and average only two to five eggs per clutch. The male assists the female in the rearing of the young, which is unusual among the dabbling ducks. Old and young alike are at home in the swiftest torrents, and when standing or walking on slippery rocks the long, stiffened tail is used as a support in woodpecker fashion. The narrow and rather soft bill seems to be used for probing under and between rocks in search of aquatic stonefly larvae, which are a primary source of food.

Agonistic and sexual behavior. Peter Scott (1954) has observed display in the Bolivian torrent duck, and Phillips (1953) has noted some unusual behavior in the Peruvian torrent duck which is of un-

certain significance. Scott's observations indicate that two major male displays are present. The first involves rearing up to a nearly vertical position by treading water, then arching the neck and pointing the bill downward. The second consists of kicking up water and at the same time flicking the hindquarters and opening the wings sufficiently to display the speculum. This latter display is directed to other males as well as to females. When walking or swimming, birds of both sexes "nod" their heads in the manner typical of birds that inhabit fast water, such as Salvadori's ducks and harlequin ducks.

Copulatory behavior. Johnson (1963) has provided the only description of copulation in torrent ducks. Referring to *M. a. armata*, the Chilean race, he states: "Reaching a stretch of relatively calm water, the two birds began to swim round each other, rising in the water and making passes and snapping noises with their bills as if catching flying insects. The tempo of these movements increased, the birds alternately approaching and receding from each other and, as they came close together, practically standing on their tails after the manner of courting grebes. Suddenly the male mounted the female, pushing all but her head under water, and copulation took place. He dismounted very quickly and the two swam upstream, with the female in the lead." This extremely unusual precopulatory behavior has no counterpart in any of the typical dabbling ducks.

TYPICAL DABBING DUCKS

The most successful genus of waterfowl, in terms of numbers of species and individuals, is the genus *Anas*. The probable reasons for their success include their rather generalized feeding and nesting requirements, which have allowed them to exist in a wide variety of environmental conditions. Furthermore, their one-year period to maturity and large clutch size assures a high fecundity rate and the constant selection of the fittest individuals. The tendency for the yearly renewal of pair bonds assures the rapid dissemination of favorable genotypes, but tends to inhibit subspeciation.

Although the group is usually broken up into numerous genera, there are compelling reasons for accepting the broad generic concept of Delacour and Mayr (1945) in this group. Foremost of these is the remarkable interspecific hybrid fertility (Johnsgard, 1960a), and the large number of wild-taken hybrids. Anatomically the group appears to be a close-knit one, and behaviorally it also may be readily defined.

Females of most and probably all species have Decrescendo Calls (Lorenz, 1951–1953), ranging in the number of syllables from one to twenty or more. Females of all species studied have similar Inciting displays. Males of all or nearly all species have several displays in common (Burping, Introductory Shake, and Turning-the-back-of-the-head). Precopulatory behavior in all the species studied to date consists of mutual vertical Head-pumping. Postcopulatory displays vary somewhat, but the male always calls at least once (Burping or Bridling), then turns toward the female or swims away from her (Nod-swimming in the mallardlike ducks). Females of all species simply bathe after copulation.

Salvadori's Duck (*Anas waigiensis*)

The true systematic position of this species is still in much doubt, owing to the meager amount of information regarding it. Until the discovery by Mayr (1931) that Salvadori's duck has a typical mallard-like trachea and sternum, this species was placed in the monotypic genus *Salvadorina*, and was thought possibly to have affinities with the torrent duck. Although this is now considered to be an example of convergence to similar habitats, there is still some reason to believe that the torrent duck and Salvadori's duck might be fairly closely related. The adaptation of both species to rapidly flowing streams no doubt accounts for the long tail feathers and elongated body form that characterize both species. The downy young of the two species are, however, similar, although downy Salvadori's ducks have a spotted rather than a striped back pattern. Immature birds resemble the adults, all of which have strongly barred flanks and backs and are distinct from all species of *Anas*. The wing speculum patterns of the two species are very similar, namely metallic green bordered in front and behind by white. There is no eclipse plumage. The male tracheal bulla is small and similar in shape to that of the torrent duck. The species is found in New Guinea and is probably not sympatric with any near relatives. There is no reason to believe that Salvadori's duck is at all closely related to the Cape teal or silver teal, as Delacour (1959) has unaccountably suggested.

General behavior. Salvadori's ducks have not adapted well to captivity, and the few individuals observed at the Wildfowl Trust have exhibited little tendency to become tame or to display sexually. When walking, Salvadori's ducks nod the head in the manner char-

acteristic of disturbed waterfowl (Fig. 36E, F). As explained earlier, this nodding is an adaptation for more closely observing the environment while walking or swimming. It is performed by keeping the head motionless much of the time when the body is moving constantly.

Agonistic and sexual behavior: female. I have only once observed Inciting in this species, and this was from a considerable distance. The female moved her head in a series of strong, vertically directed pumping movements, with little or no sideways pointing tendency. The call was a harsh *gak-gak*, uttered with each pumping movement. The only other species of *Anas* in which Inciting takes a similar form is the African black duck. No other female calls or displays have been seen.

Agonistic and sexual behavior: male. Although males (and females) frequently assume a tail-cocked attitude (Fig. 36D), this is not a sexual display but only an indication of unease or fear. I have not seen any sexual displays except during Inciting when the male faced the female in a posture resembling Chin-lifting. Scott (1958) has observed what is apparently Burping in this species, and what is probably the most frequent courtship display. He states that the male stretches his neck, moves his head slightly, and utters a whistle. Sketches of this display suggest that it is similar to the Burp posture of such species as the chestnut teal and the pintail-like ducks. A vertical head-pumping has also been observed in the male, which may have been precopulatory Head-pumping.

African Black Duck (*Anas sparsa*)

I am convinced that the African black duck represents the most generalized species of *Anas*, and that it provides a key for the understanding of the behavior of the more specialized species in this genus. The downy young resemble the downies of such *Anas* species as the mallard group, but have a distinctly streaked cheek pattern. Juvenile birds resemble the adults, but unlike the juveniles of any other *Anas* species known to me, they have a white abdomen which contrasts with the darker upper parts. This is lacking in adult birds and presents a most unusual appearance. As adults, the sexes differ only in size and, to a slight degree, in bill color. In their elongated body shape and long tail, adults resemble such perching ducks as Hartlaub's duck. The wing speculum pattern, however, is distinctly mal-

lardlike. The male tracheal bulla is left-sided, rounded, and not very different from those of mallards or Hartlaub's duck. The species is found in central and southern Africa, and although it is sympatric with various *Anas* species, no hybrids are known from the wild or captivity.

General behavior. In their general behavior African black ducks have little in common with the mallardlike ducks. They are not gregarious, and are aggressive toward one another and most other species. Their long tail suggests that they may be perching ducks, but I have observed no perching. According to Delacour (1956) they sometimes nest in tree holes or other holes, but probably they normally nest on the ground. Although they generally feed by up-ending, they can dive well. Preflight movements have not been observed.

Agonistic and sexual behavior: female. Unlike the typical mallards, which often utter Decrescendo Calls, the African black duck has no such call, at least that I have heard. The female's voice is relatively weak, and can hardly be called a quack. I have heard the female call only during Inciting, which takes a remarkably peculiar form in this species. The associated call is a *gak-gak'*, *gak-gak'*, and the Inciting movement (Fig. 37B, C) is a vertical head-pumping with no lateral element at all. This often gives the impression of a Triumph Ceremony, since, as in Hartlaub's duck, the male usually responds by calling with similar head movements.

A second female display of uncertain significance has also been observed several times. During intensive mutual display, the female will sometimes suddenly flatten out almost prone on the water and swim rapidly around the male once or twice. This performance reminds one at once of Nod-swimming (Lorenz, 1951-1953), but it lacks any "nodding" and does not occur in a typical Nod-swimming situation. I believe it must represent a primitive form of Nod-swimming rather than a copulation solicitation display.

Agonistic and sexual behavior: male. Although the male black duck possibly has an Introductory Shake, I have not observed this display. On a few occasions, however, I have observed a true Grunt-whistle (Fig. 37A), which was performed without any preliminary shaking or even any head-flicking. In no case was a female of the species near, and no stimulus for the display could be determined. A high-pitched and weak whistle accompanied the display, and, as in the Grunt-whistle of the typical *Anas* species, an arc of water

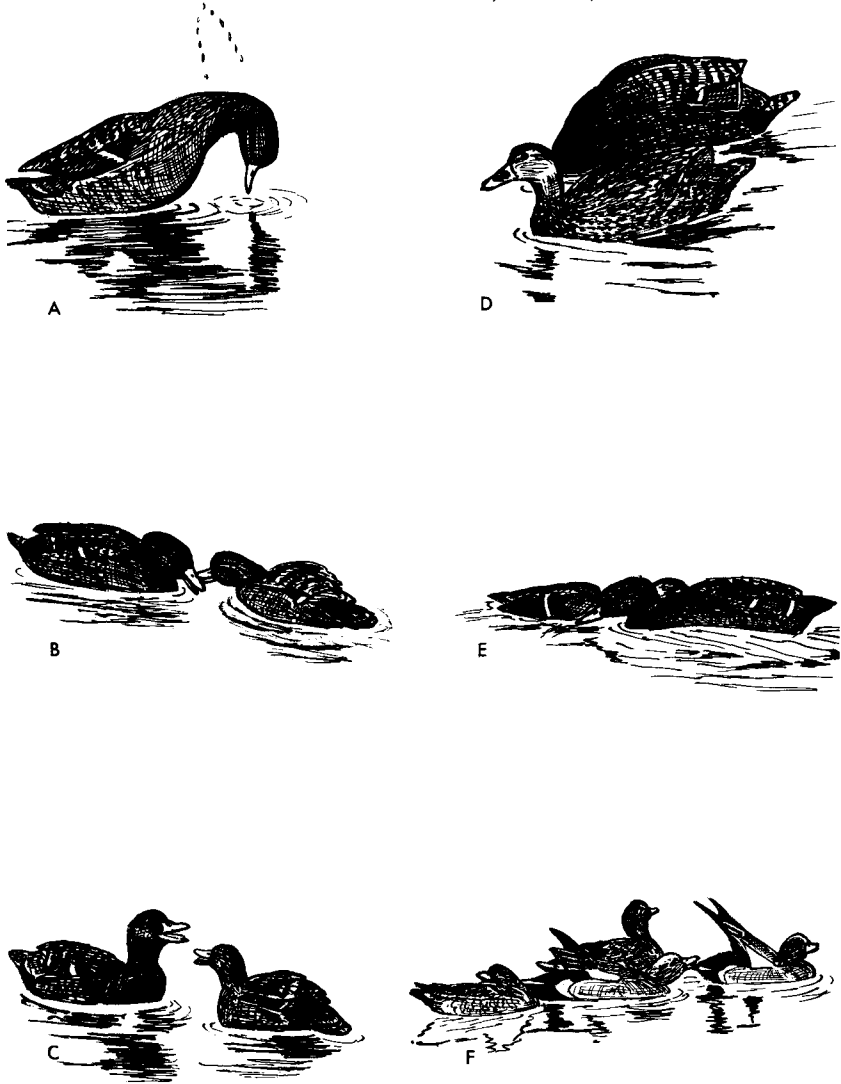


Figure 37. African Black Duck, European Wigeon

- A. Male African black duck performing Grunt-whistle.
- B, C. Mutual calling and Inciting by African black duck pair (*male on left*). Note exposed speculum of male.
- D. Display feeding of male African black duck (displaying to a female mallard). The speculum is exposed in the Wings-raised posture.
- E. Postcopulatory swimming in African black duck. The male is swimming around the female in a Wings-raised posture.
- F. European wigeon courting party, females Inciting and males calling while lifting the folded wings.

droplets was thrown up. A far more common, and probably the major, display is extremely interesting and unique, and occurs during female Inciting. Males respond to Inciting by making head-pumping movements very similar to those of the female (Fig. 37B, C), and at the same time uttering a wheezy whistle and lifting the folded wings sufficiently to expose the blue speculum. This Wing-raising occurs in another situation: when the male swims up to a courted female he lifts his wings and dips his bill in the water in a dabbling or Mock-feeding display, sometimes even up-ending (Fig. 37D). There is no call associated with this display, but it is otherwise very much like the Mock-feeding display of the blue-winged ducks. None of the mallardlike ducks possesses such a display. On one occasion I also observed a display which I immediately took to be a true Head-up-tail-up, such as the mallardlike ducks perform. The lifting of the wings and tail was not, however, nearly so exaggerated as it is in these species, and it very much resembled the Head-up-tail-up of the Laysan duck (see Fig. 48D, E), which occurs in a secondary, simplified form. It is unlikely, however, that the black duck is a degenerate form of mallard, for its other displays are performed intensively and, except for the Grunt-whistle, are wholly distinct from typical mallard behavior. It seems much more likely to me that the black duck is basically a generalized dabbling duck in which the sexual behavior patterns have remained fairly simple.

Copulatory behavior. I have observed only one copulation, which probably was not altogether typical, judging from its unusual form. The female was on land when the male swam toward her, performing his usual head-pumping. The female walked to the water and immediately went prone without any preliminary head-pumping movements. The male swam around her in his Wings-raised display posture for 20 or 30 seconds, pecking at her in the way that a wood duck might. He finally mounted, and treading lasted about ten seconds. As he dismounted I saw no Bridling (the usual post-copulatory display of the mallard group); instead he swam around her in a crouched and Wings-raised position for several seconds (Fig. 37E), in a posture similar to that assumed by Nod-swimming mallards. The female then bathed, the male flapped his wings, and both swam to shore and preened. This combination of rudimentary mallardlike behavior and behavior typical of perching ducks lends additional credence to the possibility that the African black duck provides a link between the

groups. K. M. Davy (pers. comm.) has observed a female black duck copulating with a male common mallard, which suggests that typical precopulatory display in the African black duck might be more mallardlike than is indicated by my single observation; and I once observed a female performing vertical head-pumping movements toward a male, who did not respond to her.

European Wigeon (*Anas penelope*)

All three species of wigeons are certainly closely related, particularly the European and North American species. The downy young of all wigeons are distinctive in their rust-tinted head and reduced eye and cheek markings. Juvenile birds resemble adult females, and, curiously, the pure white wing-coverts of mature males are not fully developed until the second nuptial plumage. Adult females lack the conspicuous flank markings of most *Anas* females. The speculum is green with a black forward border, and the innermost secondary (10th) is white. The "tertials" are black with grayish white borders. Males have a dark brown eclipse plumage. The male tracheal bulla is moderately large, uniformly ossified, and rather spherical in shape. The European wigeon is widely distributed over Europe and Asia, and is sympatric with numerous species of *Anas*. Wild hybrids involving the gadwall, the falcated duck, the Baikal teal, the common teal, the pintail, and the common mallard have been reported. Hybrids with other wigeons are fertile, and so are hybrids with the falcated duck and, at times, the common mallard.

General behavior. As is true of all wigeons, grazing is a common means of foraging. Wigeons also feed on the water surface, but normally do not dive for food. They are gregarious birds, often mixing with other species such as the gadwall. Preflight movements include Neck-jerking and lateral Head-shaking, which are typical of nearly all species of *Anas*.

Agonistic and sexual behavior: female. Lorenz (1951-1953) has already described the behavior of this species in some detail. The female's Decrescendo Call may consist of one, two, or three notes; often it consists of only one. The Inciting call is a continually repeated, growling *errr* note, varying in loudness. This is accompanied by repeated chin-lifting toward the preferred drake (Fig. 37F). Occasionally the female makes threatening movements toward the opponent as well. Another female display which is typical of many *Anas*

species is Preening-behind-the-wing. This is usually done in response to similar Preening-behind-the-wing by a male. It is highly ritualized in all species of *Anas*, and is not a functional form of preening. As stated elsewhere (Johnsgard, 1960c) mutual Preening-behind-the-wing is one of the two mutual displays which probably are important in developing and maintaining the pair bond in dabbling ducks. The second major mutual display, female Inciting and male Turning-the-back-of-the-head, is not well developed in wigeons; male wigeons almost invariably respond to Inciting by performing chin-lifting movements while facing the female.

Agonistic and sexual behavior: male. Lorenz (1951-1953) has mentioned that the male wigeon has only a single call, the "courtship whistle," which also functions as a warning call. In this species it is a moderately loud one-syllable *whew* or two-syllable *wa'-chew*. When a female is Inciting, drake wigeons face them, perhaps Preening-behind-the-wing, then rapidly Chin-lift and call loudly. If other drakes approach too closely, the male threatens them with bill open, neck outstretched, and the folded wings raised high overhead (Fig. 37F). Although a male wigeon will sometimes swim ahead of a female and Turn-the-back-of-the-head toward her, this normally does not occur when she is Inciting. An Introductory Shake is present, but not frequently performed, in this species. Lorenz (pers. comm.) has informed me that he believes he once observed a true Grunt-whistle in this species, a display not normally found in any of the wigeons. Since it is present in the African black duck, however, it may well have been secondarily lost by wigeons and presumably might occur very rarely.

Copulatory behavior. The precopulatory display consists of the usual mutual Head-pumping typical of *Anas*. I have not observed a complete copulation.

American Wigeon (*Anas americana*)

The American wigeon, or baldpate, differs from the European species only very slightly. The downy plumages are almost identical; female and juvenile American wigeons are slightly more grayish or lilac in color. The adult male differs from the European species in having a more grayish and green-tinted head, a white forehead, and more lilac color on the flanks and back. The wing pattern is exactly like that of the European wigeon. There is a distinct eclipse plumage

in males. The male tracheal bulla is smaller than in the European wigeon, and the call is correspondingly weaker. The American wigeon occurs over most of North America and is widely sympatric with many other dabbling ducks. Wild hybrids involving the gadwall, the green-winged teal, the pintail, and the common mallard have been reported. Fertile hybrids with other wigeons are known, and some hybrids involving mallards and blue-winged teal are reported to be fertile.

General behavior. What has been said about the European species applies equally well to the American wigeon.

Agonistic and sexual behavior: female. This is exactly like that of the European species so far as I am able to judge. The Decrescendo Call is reduced in both species to from one to three syllables, and the Inciting call and movements appear to be essentially the same.

Agonistic and sexual behavior: male. The male American wigeon has a markedly weaker and more wheezy call than the European wigeon, and in courtship display the call is usually a three-syllable *whew-whew-whew*, with the middle syllable loudest. The position of the wings during threat is the same in both species. Preening-behind-the-wing, the Introductory Shake, and Turning-the-back-of-the-head also occur in the same manner in the two species.

Copulatory behavior. I have frequently observed mutual pre-copulatory Head-pumping, but only once have I seen a completed copulation in the American wigeon, and that from a great distance. After treading, the male assumed a very erect posture and faced the female for several seconds, just as male gadwall have been observed to do. The distance was too great for me to hear any calls.

Chiloé Wigeon (*Anas sibilatrix*)

The South American, or Chiloé, wigeon differs from the northern species in several ways. The color pattern of the downy young is more strongly contrasting, and the head has a more brownish tint. Juvenile birds are more dull-colored than adult females, which are almost as bright in color as males. In adults the head pattern is somewhat like that of the other wigeons, but the strongly barred black and white breast, the rich orange-brown flanks, and the white tail coverts are unique. The wing pattern is very similar to that of the preceding species, but the tertials are longer and more pointed and are black with white edges, thus resembling those of the falcated

duck. The barred breast also suggests affinities with the falcated duck. Unlike the males of other wigeon species, the male Chiloé wigeon has no eclipse plumage. The species is found in southern South America, and is sympatric with several other species of *Anas*. No wild hybrids are known, but in captivity the Chiloé wigeon has hybridized with the other wigeons and with the falcated duck, the gadwall, the mallard, the Bahama pintail, the common pintail, and the yellow-billed pintail.

General behavior. Although wigeonlike in their grazing and other general behavior, pairs seem to remain together to a greater degree than in the northern species. Males typically assist with the rearing of the young in this species. Preflight movements are the same as in the other wigeons, namely lateral Head-shaking and Neck-jerking.

Agonistic and sexual behavior: female. The female's Decrescendo Call usually consists of one or two notes; rarely, it consists of three. Her Inciting call is lower in pitch than those of the northern species. During Inciting there is a pronounced and rapidly repeated chin-lifting (Fig. 38A, B). Mock Preening-behind-the-wing by the female is also more common in the Chiloé wigeon than in the other species.

Agonistic and sexual behavior: male. More than in any other species of *Anas*, sexual behavior tends to be mutual in the Chiloé wigeon, and I believe that this is the reason for the very similar plumages of the two sexes. Male Preening-behind-the-wing (Fig. 39A) is very frequent and conspicuous in this species. His response to Inciting is to call (Fig. 38C, E) and perform rapidly repeated Chin-lifting (Fig. 37A, B) movements while facing the female. Often these are interspersed with threats or with rubbing the head and cheeks on the back. Unlike the northern species of wigeon, the Chiloé shows little tendency to lift the folded wings over the back when displaying aggressively. As Lorenz (1951-1953) has mentioned, the mutual calling and Chin-lifting in this species takes a form very much like an anserine Triumph Ceremony. Males Turn-the-back-of-the-head to females when swimming in front of them, just as do the other wigeons. Interestingly, the Introductory Shake of this species is highly exaggerated into a major display (Fig. 38E, F) which might easily be mistaken for a Grunt-whistle. In the Introductory Shake, however, the Chiloé neither calls nor strikes the water with his bill; hence the display cannot be called a Grunt-whistle.

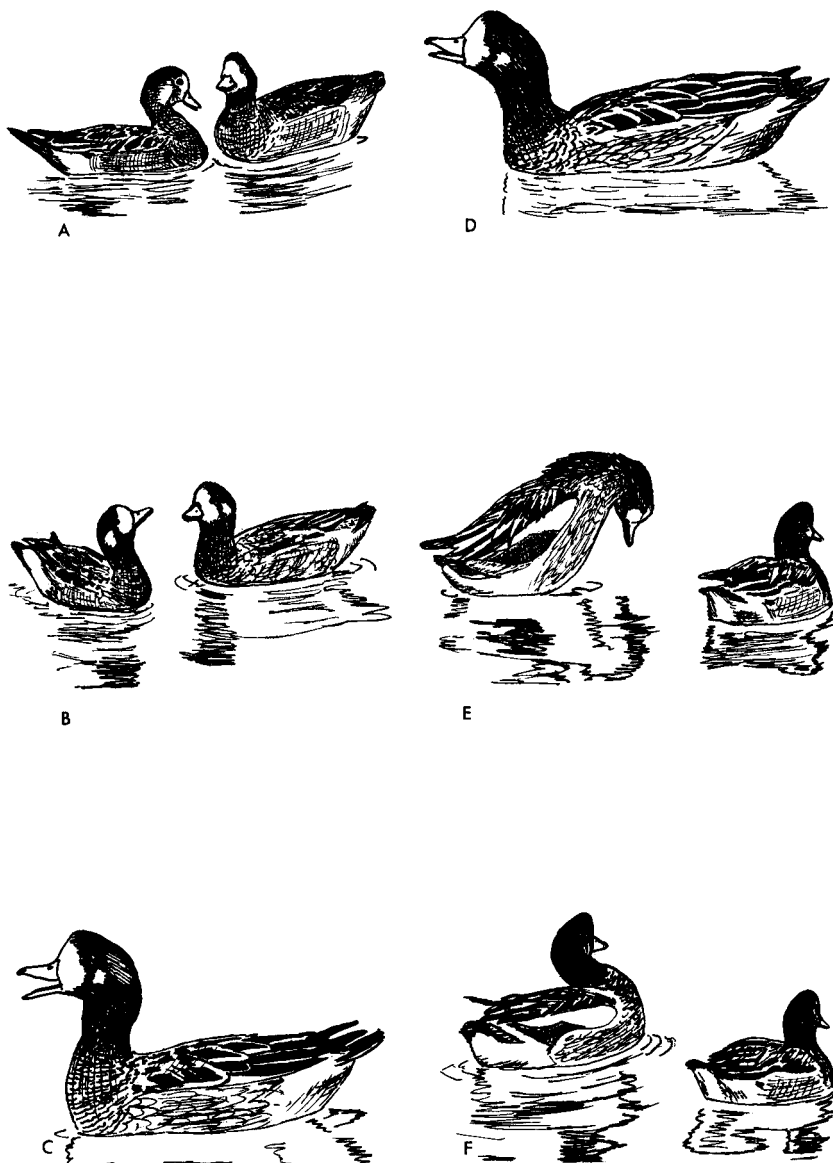


Figure 38. Chiloé Wigeon

A, B. Female (left) Inciting her mate (right), who responds with repeated Chin-lifting.

C, D. Two phases in the call of the male Chiloé wigeon.

E, F. Two phases in the Introductory Shake of male Chiloé wigeon. Note the similarity of this display to the Grunt-whistle of following species.

Copulatory behavior. Although I have often observed precopulatory Head-pumping, I have seen copulation only once. After treading, the male whistled one time with his head fairly erect; then he remained motionless, facing the female in that posture while the female Preened-behind-the-wing several times before she finally began to bathe.

Falcated Duck (*Anas falcata*)

The falcated duck exhibits affinities both with the wigeons and with the gadwall, and is probably rather more closely related to the latter. Its downy young are wigeonlike, with brownish, unmarked cheeks. The juveniles resemble the adult female, which in shape reminds one of a wigeon and in plumage pattern of a female gadwall. The adult male has a very distinctive breeding plumage, but its "scaled" breast pattern is like those of the Chiloé wigeon and the gadwall. The yellow patches in front of the tail are like those on the common teal; the rest of the rump is black as in the gadwall. The wing pattern is of interest. The upper coverts are mostly gray, but tend slightly toward white as in wigeons. The speculum is a wigeonlike dark green. The tertials are much like those of the Chiloé wigeon in color, but they are longer and curve downward in a "falcated" manner. There is a female-like eclipse plumage. In shape the tracheal bulla of the male falls roughly between that of wigeons and that of the gadwall. The species ranges widely in Asia, and wild hybrids have been reported with the European wigeon and the gadwall. It has hybridized with the other wigeons in captivity, and also with various other dabbling ducks.

General behavior. In its general behavior, the falcated duck is very reminiscent of the gadwall. It does not graze like wigeons, but is a surface-feeder. Preflight movements are the usual Neck-jerking and lateral Head-shaking.

Agonistic and sexual behavior: female. I have not recorded a Decrescendo Call in the falcated duck, but Finn (1915) states that it is mallardlike and of about five syllables, while Lorenz and von de Wall (1960) indicate that it is usually from two to four syllables. The Inciting movement is more like that of the gadwall than that of wigeons. The female alternates chin-lifting with lateral pointing and at the same time utters a wigeonlike *rrrr* note. Females often Preen-behind-the-wing to males, and sometimes perform an Introductory

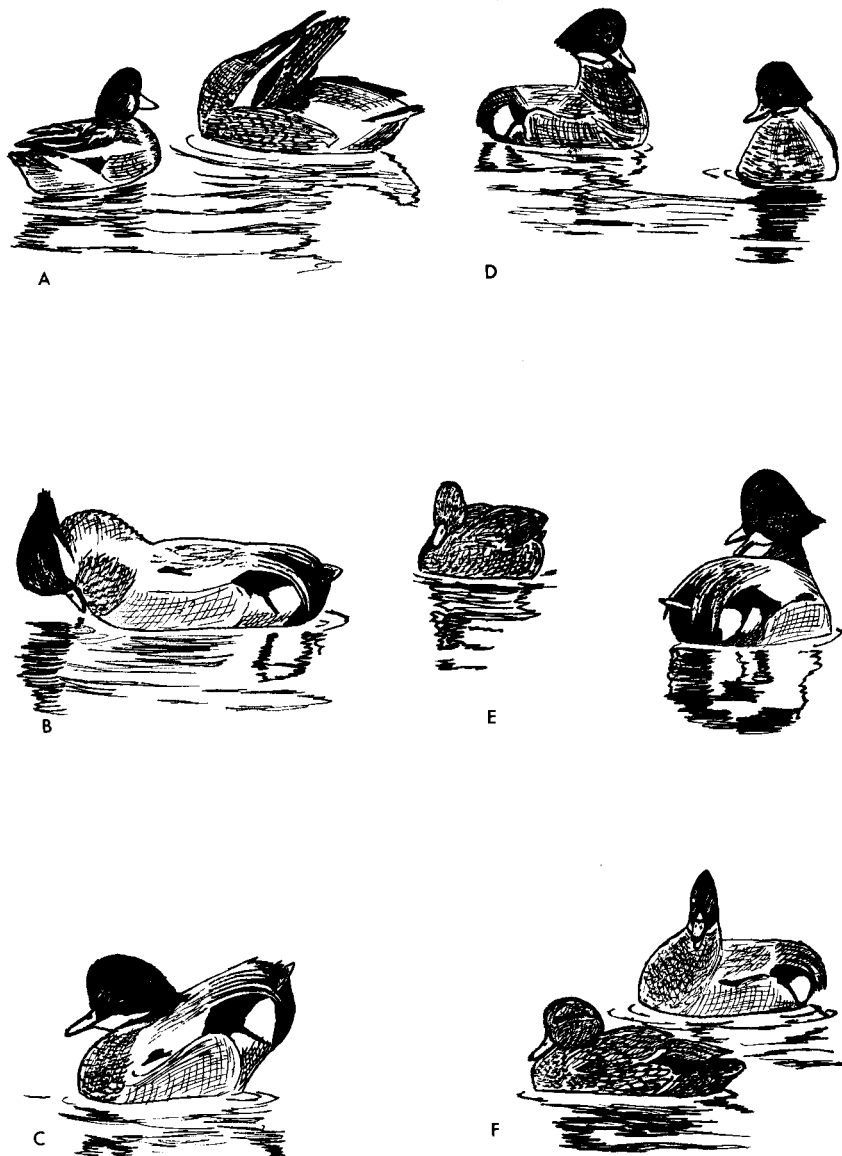


Figure 39. Chiloé Wigeon, Falcated Duck

A. Male Chiloé wigeon Preening-behind-the-wing to female.

B, C. Falcated duck, two phases of the Grunt-whistle. Note conspicuous under-tail covert pattern.

D. Head-up-tail-up display.

E, F. Turning the head toward the female in the second phase of the Head-up-tail-up. Note extreme crest erection.

Shake which is similar in form to that of the male. Finally, females often call at the same time as the male is displaying, so that it sometimes sounds as if the male were uttering a hoarse *gak-gak* as he performs the Head-up-tail-up or the Grunt-whistle.

Agonistic and sexual behavior: male. The falcated duck is the first species discussed here which might be termed a typical *Anas* with regard to its courtship behavior. The Introductory Shake is present and, like that of the Chiloé wigeon, is highly ritualized and marked by a vigorous tail-shaking that makes prominent the yellow tail-patches. There is a Burp call, uttered while stretching the neck, similar to the corresponding display of the gadwall. The call itself is a vibrating *rruh-urr* (Lorenz and von de Wall, 1960). The male utters a high whistle, *lilililili*, when Chin-lifting toward the female. This call is perhaps analogous to the Chin-lifting call of the male wigeon.

Besides the Introductory Shake, which is functionally introductory in this species, the male falcated duck also performs a Grunt-whistle (Fig. 39B, C). This display ends with a strong lifting and shaking of the tail, and is accompanied by a whistle. The Head-up-tail-up (Fig. 39D-F) is a spectacular display, especially in the extreme crest erection and lifting of the body. It is usually performed as the male is almost parallel to the female, and at the peak of the display the male turns his bill toward the courted bird and utters a whistling note. Unlike males of the wigeon group, male falcated ducks swim ahead of Inciting females and Turn-the-back-of-the-head to them in typical *Anas* fashion. Males also frequently Preen-behind-the-wing to females. One major *Anas* display, the Down-up, appears to be lacking in the falcated duck, but von de Wall (pers. comm.) once observed what he believes was that display.

Copulatory behavior. A complete copulation has not yet been seen, although precopulatory mutual Head-pumping has been observed.

Gadwall (*Anas strepera*)

The gadwall provides a convenient connecting link between the preceding wigeon and falcated duck group and the following "green-winged" teal group. It is probably most closely related to the falcated duck. The downy young, however, lack the brownish head color of the preceding species, and approach the pattern of the Baikal teal.

Juveniles resemble adult females. Males have a distinct but subdued nuptial plumage which is more like that of the falcated duck than that of any other species. The wings, however, are unique, having a black and white speculum and being bordered in front with black and chestnut. If the gadwall's white secondaries were metallic green, however, the secondary pattern would be very similar to that of the following group. The tertials are long and pointed, but are gray rather than black and white as in the preceding species. The male has an eclipse plumage which resembles the female's plumage. The tracheal bulla of the male is similar in shape to that of the falcated duck. The gadwall has an extremely broad range throughout most of the Northern Hemisphere and is sympatric with many species of *Anas*. One now-extinct island race, Coues's gadwall, has been described. Wild hybrids have been reported involving the European wigeon, the American wigeon, the falcated duck, the mallard, the common pintail, and the common shoveler.

General behavior. The gadwall is primarily a surface-feeding bird, and rarely resorts to diving to obtain food. Preflight movements are the usual Neck-jerking and lateral Head-shaking.

Agonistic and sexual behavior: female. The Inciting behavior of the female gadwall is almost identical with that of the female falcated duck. It consists of lateral threatening movements (Fig. 41B) alternated with chin-lifting toward the preferred male. The call has the cadence and sound of those of typical dabbling ducks. The Decrescendo Call is infrequent and differs from that of the mallard only in its slightly higher pitch and more rapid sequence of notes. Unlike the female falcated duck, the female gadwall does not perform the Introductory Shake. Preening-behind-the-wing, however, is very frequently performed toward actual or potential mates.

Agonistic and sexual behavior: male. The account of Lorenz (1951-1953) is quite complete; here it needs only to be summarized. Male gadwalls exhibit the full *Anas* display repertoire in fairly typical form. The Introductory Shake is of the usual nonexaggerated type which serves a truly introductory function as a prelude to the major displays. The most common vocalization is the Burp, which is a loud, low grunt uttered with the neck extended (Fig. 40A, B) and usually with the bill pointed toward a female. The Grunt-whistle, which is the most frequent of the major display, is performed much as it is by the falcated duck, except that there is no tail-lifting phase (Fig.

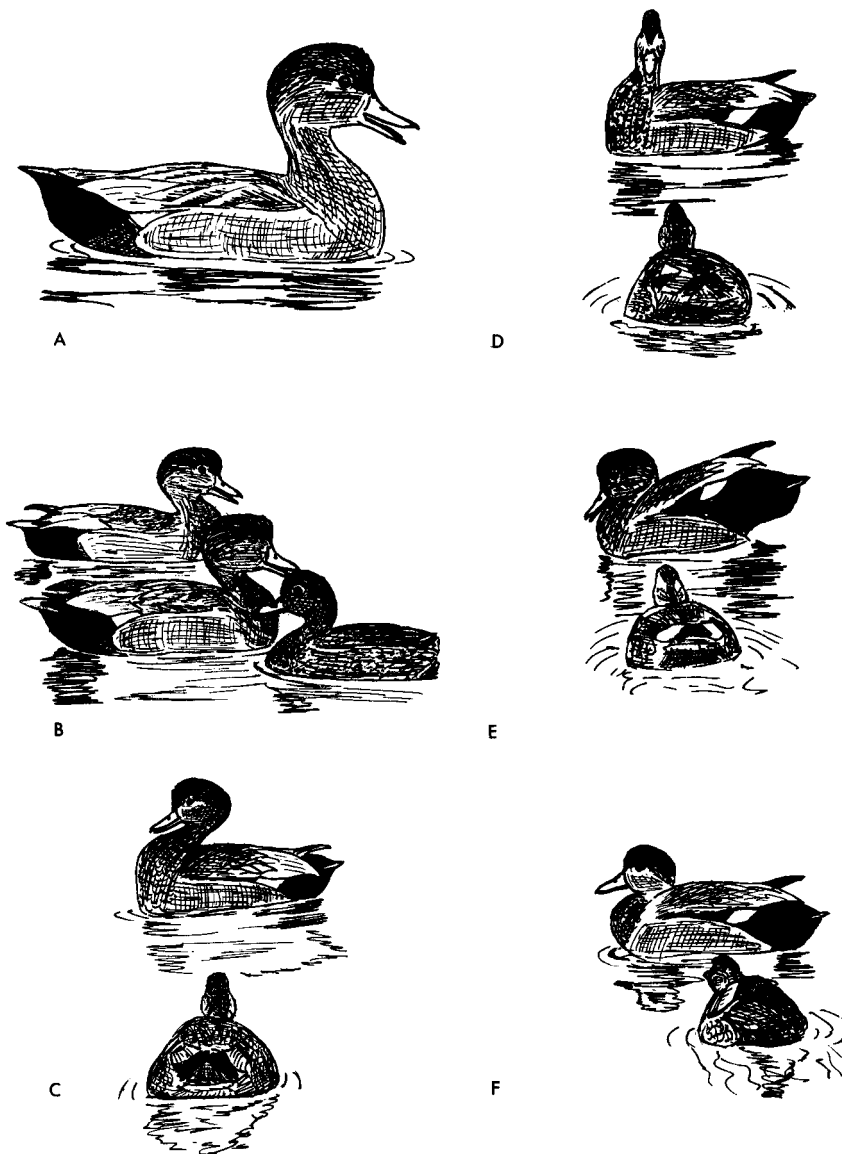


Figure 40. Gadwall

- A, B. Male uttering the Burp call.
- C-F. Head-up-tail-up-Down-up sequence.
- C. Head-up-tail-up.
- D. Turning head toward female.
- E. First phase of Down-up.
- F. Second phase of Down-up.

41A). The call is a loud whistle followed by a low grunt. The Head-up-tail-up is performed much less frequently and is not at all linked to the Grunt-whistle. On the other hand, it is almost always firmly linked to the Down-up, and this results in an interesting sequence of movements and calls. The sequence of movements is: Head-up-tail-up-bill pointed toward female-bill forward-Down-up; and the calls are a distinctive combination of whistles and grunts: *raeb-zee-zee-raeb-raeb* (Fig. 40C-F). The white speculum is visible during these displays. The male gadwall sometimes Chin-lifts to an Inciting female, but much more frequently he swims ahead of her and Turns-the-back-of-the-head (Fig. 41B) in the distinctive way that I have termed Leading (Johnsgard 1960D). Preening-behind-the-wing by males is very frequent and tends to be linked to ritualized drinking.

Copulatory behavior. Precopulatory display consists of the usual mutual Head-pumping. Immediately after treading is completed, the male releases the female, draws his head up into a Burp position and utters a whistle-grunt combination—*zeee-raeb*; then, motionless, he Faces the female as she begins to bathe, and finally he bathes himself. This display is similar to the postcopulatory behavior observed in the Chiloé wigeon, but is unlike the Bridling typical of the following group.

Baikal Teal (*Anas formosa*)

I cannot agree with Delacour (1956) that the Baikal teal is an isolated form with no close relatives. I believe that it is a close relative of the common teal, although the two differ in many respects. The downy young are rather intermediate between those of the gadwall and those of the common teal, and they lack the distinct cheek stripe typical of nearly all the "green-winged" teal. Juveniles resemble adult females, as do also adult males in eclipse plumage. The male nuptial plumage is similar to that of the common teal in the head pattern, the spotted breast, and the vertical bar at the front of the wing. The speculum is also much like that of the following group of species. The inner secondaries are metallic green, the outer ones black, and there is a narrow white posterior border and a broad buffy anterior border. The male trachea has only a rudimentary bulla of the same shape as that of the common teal. The species is restricted to eastern Asia and is sympatric with several species of *Anas*. Wild

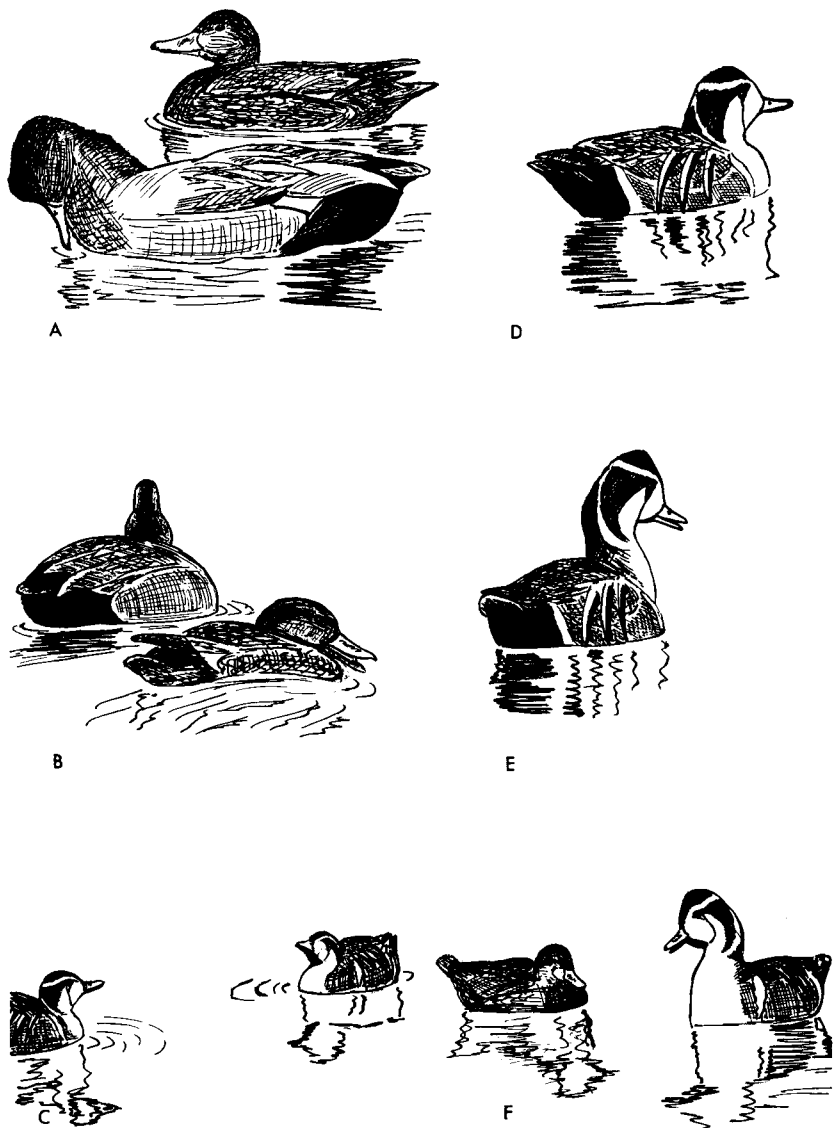


Figure 41. Gadwall, Baikal Teal

A. Gadwall Grunt-whistle.

B. Gadwall male Leading an Inciting female.

C. Baikal teal males performing aggressive Bill-tilting toward each other.
Note black throat pattern exhibited.

D, E. Two phases in the Burp of the Baikal teal. Note crest erection.

F. Male Baikal teal uttering Burp. Note the tilting of the head toward the courted female.

hybrids have been reported with the European wigeon, the common teal, and the common pintail. In captivity fertile hybrids with the common teal have been obtained.

General behavior. Baikal teal tend to be shy in captivity and hence are difficult to observe closely. They are surface-feeding birds, rarely if ever diving. Preflight movements are the usual Neck-jerking and lateral Head-shaking of most dabbling ducks.

Agonistic and sexual behavior: female. Inciting in the female Baikal teal is conspicuous and gadwall-like. It involves threatening movements alternated with strong chin-lifting, and the call is a repeated, fairly soft *geg* followed by a much louder *geg-geg'* as the male displays. In her tendency to call simultaneously with the male displays, the female Baikal teal is much like females of the common teal, the gadwall, and the falcated duck. The Decrescendo Call is infrequent, and it usually consists of one long note followed by about five shorter and descending notes. I have not observed females Preening-behind-the-wing.

Agonistic and sexual behavior: male. Although the male Baikal teal lacks several of the displays found in the gadwall and the common teal (the Grunt-whistle, Down-up, and Head-up-tail-up), he is apparently a typical *Anas*. The most common male display is the Burp, or "clucking" call. The Burp consists of a sudden lifting of the head and an erection of the small crest from a resting position (Fig. 41D-F), and an accompanying *ruk* or *ruk-ruk'* call. The call may be uttered only once or repeated more than forty times as the bird remains in the same position. The call is usually directed toward a female, and the bill and head are tilted slightly in the direction of the courted bird. Males often follow this call with Drinking. As they Lead Inciting females, they perform an exaggerated Turning-of-the-back-of-the-head, which exhibits the complex nape pattern, and also the rear flanks and the black under-tail coverts, since the tail is held high during this display. Males threaten one another with a Bill-tilting posture that brings into view the black throat markings, which are normally obscured from view (Fig. 41C). An Introductory Shake is sometimes performed, and Preening-behind-the-wing is also occasionally performed by males toward females. The Baikal teal is one of the few species in what is here considered the typical *Anas* group (the wigeons and the blue-winged ducks are excluded) which lack such male displays as the Grunt-whistle, Bridling, the Down-up and

the Head-up-tail-up. Whether this indicates that it is a "primitive" species is difficult to judge, since the very elaborate male plumage pattern argues against this interpretation. It seems more probable that the Baikal teal have secondarily lost these displays in favor of more specialized and exaggerated forms of Burping and Turning-the-back-of-the-head, as well as an elaborate male head and body plumage.

Copulatory behavior. The Baikal teal performs the usual mutual precopulatory Head-pumping. I have no other information on its copulatory behavior.

Common Teal (*Anas crecca*)

The common, or green-winged, teal is a typical member of the group here collectively termed "green-winged" teal (common teal, South American teal, Cape teal and Baikal teal), which grade into the "austral" teal (gray teal, chestnut teal and brown teal). The downy young of the common teal have dark eye- and cheek-stripes, sharing this feature with the South American teal. Juvenile birds resemble the adult female, which is similar in pattern to the Baikal teal female. The eclipse plumage of males also closely resembles the female's plumage. The male's nuptial plumage most resembles that of the Baikal teal, but the yellow patches in front of the tail are like those of the falcated teal and presumably have a common genetic origin. They are, however, displayed in an entirely different manner during courtship. The green and black secondary pattern is like that of the other species in the group. The male tracheal bulla of this and the remaining species of green-winged and austral teal exhibits little variation in structure; it is fairly small, rounded toward the left, and forms a rather triangular peak ventrally (see illustration of Cape teal in Johnsgard, 1961c). The species has a very broad range over the Northern Hemisphere, and is sympatric with most Northern Hemisphere *Anas*. Wild hybrids have been reported with the American wigeon, the European wigeon, the Baikal teal, the common mallard, the common pintail, the garganey, and the common shoveler. Those involving the Baikal teal, the mallard, and the pintail have been found to be fertile in captivity, as have also hybrids with the South American teal. Three subspecies are recognized, of which one (*carolinensis*) is often considered a distinct species.

General behavior. The marked shyness of common teal, and their reluctance to breed, prevents easy observation. Preflight movements consist of the usual Neck-jerking and lateral Head-shaking.

Agonistic and sexual behavior: female. I have observed Inciting only from a great distance, but it evidently lacks the strong chin-lifting component typical of the preceding species; it consists, rather, of sideways sweeping movements—similar to feeding movements—over the water surface. Again unlike females of the preceding species, female common teal exhibit a true Nod-swimming as a sexual display. This display, also performed by males, is a jerky forward and back nodding of the head as the female swims among the drakes, and it functions in eliciting displays from the males. Females frequently utter the Decrescendo Call, which is high-pitched and usually of about four syllables. Finally, and most surprisingly, I have also observed one female perform two of the major male displays, the Grunt-whistle and the Head-up-tail-up. These were not performed with the same vigor as by males and possibly represent an abnormal deviation from the female's usual behavior patterns. Females also Preen-behind-the-wing toward males during courtship.

Agonistic and sexual behavior: male. Male displays of the common teal are elaborate and diversified. The most common courtship call, which also functions as a warning signal, is the "Krick" whistle (Lorenz, 1951-1953). This is a two-syllable *krick'-et* note, uttered without markedly raising the head, but it doubtless corresponds to the Burp of other *Anas* species. The Introductory Shake is functionally introductory. The display which frequently follows Introductory Shaking at the start of a sequence of courtship is the Down-up (Fig. 42E, F). In this display there is almost no downward movement of the head, but the tail is strongly lifted and the yellow patches are clearly exhibited as a three-syllable whistle, *zee-zee-zee'*, is uttered. Several males often perform this display in concert. The Grunt-whistle is the most common major display (Fig. 42A, B), but a grunt is either lacking or is very faint, and only a whistle has been heard. As in all true Grunt-whistles, an arc of water is thrown up by the bill on the side toward the courted female. The Grunt-whistle is generally followed after a few seconds by the Head-up-tail-up (Fig. 42C, D), which is characterized in this species by extreme wing- and tail-lifting, exhibiting both the speculum and the tail patterns. As in the gadwall, the male whistles and turns his bill toward the courted female at the

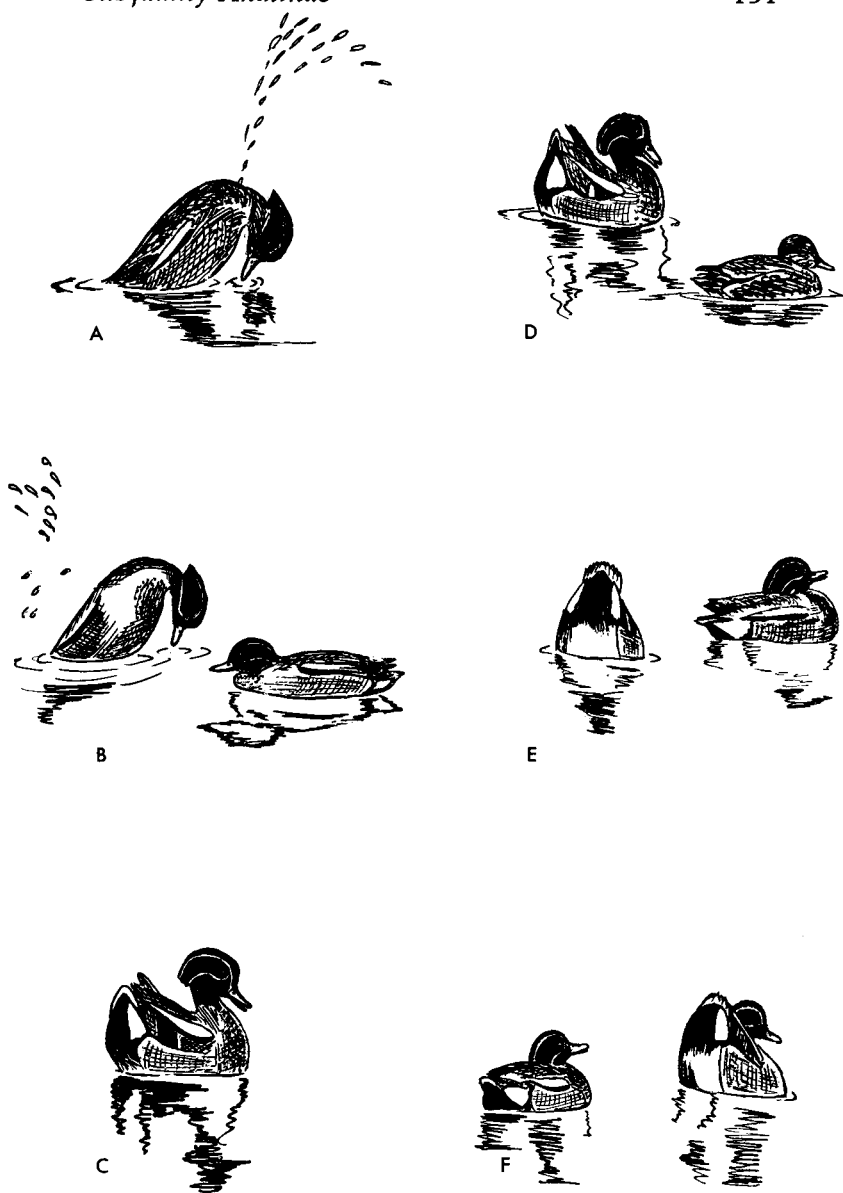


Figure 42. Common Teal

A, B. Grunt-whistle. Note arc of water droplets thrown up by bill.

C, D. Head-up-tail-up. Note how under-tail coverts are exhibited during display.

E, F. Down-up. The male on the left is just completing a Down-up in E, while the male on the right begins a Down-up in F.

peak of the display, but unlike the male gadwall, the male of this species never follows the Head-up-tail-up with a Down-up. The Head-up-tail-up may be held for several seconds as the male Faces the female, or may be followed by a rather jerky Nod-swimming. This is the first species considered in which Bridling (see Fig. 43E, F) occurs as a courtship display. It is infrequently performed, and has been observed only on land. It is also accompanied by a whistled note. Aggressive Bill-tilting toward other drakes occurs as well, but not in so conspicuous a manner as in the Baikal teal. Males Preen-behind-the-wing as a sexual display, and also have a conspicuous Turning-of-the-back-of-the-head, which is usually performed when Leading an Inciting female.

Copulatory behavior. Precopulatory display consists of mutual vigorous Head-pumping. I have observed only one complete copulation, and that from a great distance, but von de Wall informs me (pers. comm.) that Bridling is the male postcopulatory display.

South American Teal (*Anas flavirostris*)

The South American teal is clearly a very close relative of the common teal. There are four fairly distinct races, which differ considerably in the plumages of the adults and the young, and in the soft-part coloration. In all races the downy young have distinct eye and cheek stripes. Juveniles resemble the adults, the sexes of which differ only to a minor degree in plumage. In their breast spotting, their finely barred head pattern, and their scapular and tertial patterns they approach the Cape teal. The wing and speculum pattern is exactly like that of the common teal. Males lack an eclipse plumage, which is to be expected considering the similarity of the sexes. The tracheal structure is practically identical with that of the common teal. The species occurs widely through the highlands of western South America and, in the southern parts of its range, is sympatric with several species of *Anas*. It is of interest that the southern races are more brightly patterned and have bright yellow bills, while the two northern races are darker and have paler bills. In captivity fertile hybrids have been obtained with the common teal, the chestnut teal, and the South American pintail. Hybrids have also been obtained with the Cape teal, the Bahama pintail, the common mallard, the common pintail, and the red-billed pintail.

General behavior. South American teal are totally different from the common teal in their amenability to captivity. The presence of humans does not bother them in the least, and display occurs at almost any time when several males and females congregate. Males often if not usually assist in the rearing of the young, which is unusual among the dabbling ducks, and is otherwise found only in the Chiloé wigeon, the Cape teal, and perhaps a few others. Typical Neck-jerking and lateral Head-shaking movements are performed before flight.

Agonistic and sexual behavior: female. Female Inciting is not very conspicuous, and consists of lateral sweeping movements of the bill along the water and an accompanying *rrrak* call. This behavior is identical with Inciting behavior in the Cape teal and, so far as I have been able to determine, in the common teal. The Decrescendo Call ranges from five to twelve syllables, rapidly uttered and descending in pitch. I have occasionally observed Nod-swimming in females, performed in the same manner as in the common teal, and Preening-behind-the-wing is also used as a courtship display. Von de Wall (pers. comm.) has observed that the Gesture of Greeting that is performed by males is also performed, though rarely, by adult females and by the downy young of both sexes.

Agonistic and sexual behavior: male. Lorenz (1951-1953) has described the behavior of this species in detail. The male's Gesture of Greeting is frequently performed to females (Fig. 43A), and is clearly derived from a threat display. Similar movements, without any accompanying whistle, are performed by male gray and chestnut teal in the same situations. Introductory Shaking occurs as in the other typical dabbling ducks, and the Burp whistle is uttered without marked neck-stretching. As in the common teal, the Krick whistle functions both as a Burp display and a warning note. The most frequent major display is Bridling (Fig. 43E, F). This display may occur either on land or in the water. The head does not move down the median line of the back, but is tilted slightly toward the side of the courted female. The Grunt-whistle (Fig. 43B) is performed exactly as in the common teal, with the body being raised well out of the water. Also as in that species, the display is fairly closely linked to the following Head-up-tail-up and subsequent Facing or turning of the head toward the female (Fig. 43C, D). The Head-up-tail-up is not so exaggerated as in the common teal, and the speculum

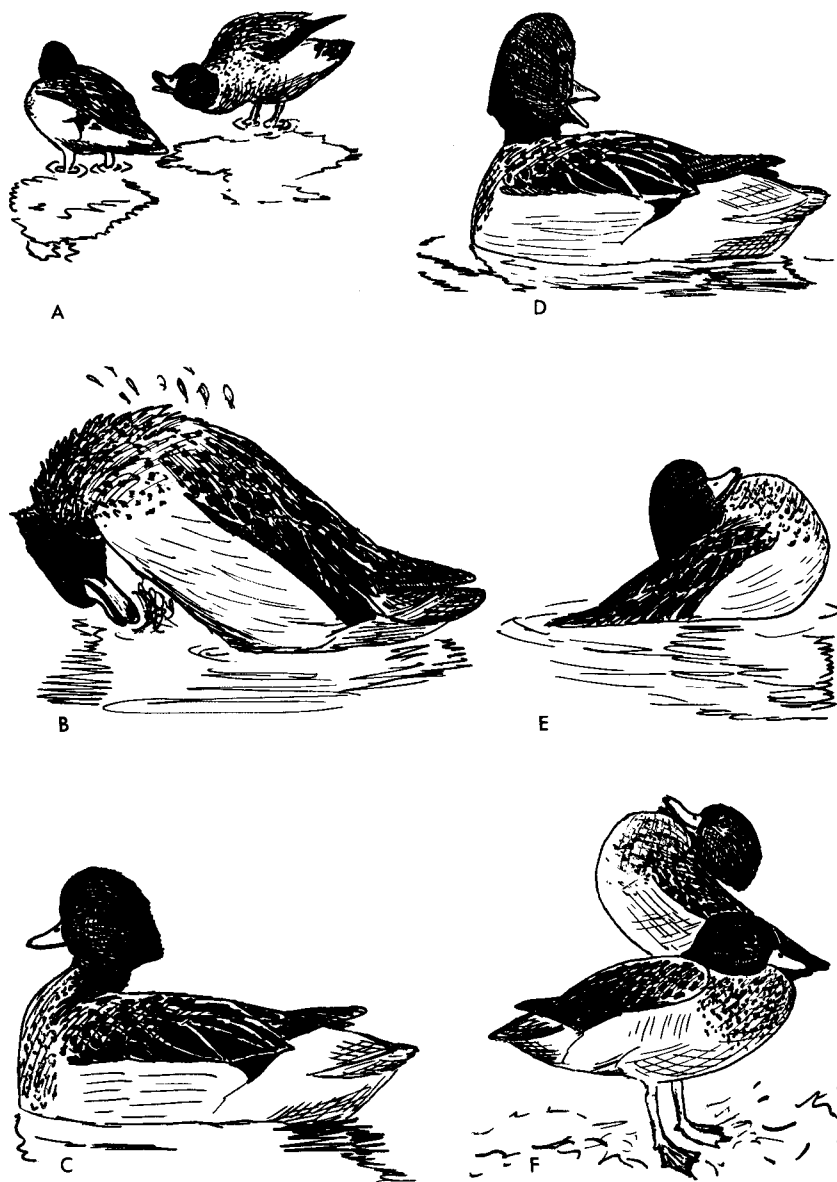


Figure 43. Sharp-winged Teal

A. Gesture of Greeting.

B. Grunt-whistle.

C, D. Head-up-tail-up followed by turning head toward the female.

E. Bridling on water.

F. Bridling on land.

is scarcely if at all visible during the display. The Head-up-tail-up may be held as the male Faces the female for a few seconds, or may be followed by Nod-swimming. Independent Nod-swimming is also performed frequently by males of this species. Males also Turn-the-back-of-the-head toward Inciting females, and McKinney (1953) has recorded Preening-behind-the-wing by males as a sexual display.

Copulatory behavior. Precopulatory display consists of vigorous mutual Head-pumping. After treading, the male performs Bridling and the female bathes.

Cape Teal (*Anas capensis*)

Delacour (1956) considers the Cape teal to be a member of the group of species he calls "spotted" teal, a view to which I cannot subscribe. Although the Cape teal is unique in several respects, I am convinced that it is a member of the green-winged teal group. The appearance of the downy young does not especially support my classification, since they are very light in color (this is perhaps an adaptation to a dry environment) and lack a distinct cheek stripe. Juveniles resemble the adults, the two sexes of which are nearly identical. The adult plumage color is an ashy gray and is also perhaps an environmental adaptation. The speculum is of the typical green and black pattern, but unlike the specula of the other green-winged teal, it has broad white borders in front and behind. The male tracheal bulla is almost identical in shape with those of the common teal and the South American teal, but totally different from that of the "spotted" teal (Johnsgard, 1961c). The Cape teal is sympatric with several African species of *Anas*, but no wild hybrids are known. In captivity it has been hybridized with the South American teal, the chestnut teal, and the yellow-billed pintail.

General behavior. Cape teal resemble the South American teal in their tendency to display on every possible occasion throughout most of the year. As in that species, males often remain with the female and assist in rearing the young. Cape teal are unusual for their excellent diving abilities; they dive with the wings closed, in the manner of the true diving ducks. Although a few other dabbling ducks sometimes dive in this manner, they usually open their wings when submerging. Preflight movements are the usual Neck-jerking and lateral Head-shaking.

Agonistic and sexual behavior: female. Female Inciting in Cape teal is exactly like that in South American teal, both in the lateral sweeping movements of the bill and in the associated calling. Unlike females of the "spotted" teal (the silver and the Hottentot teal), the females of this species do not chin-lift as they Incite. The Decrescendo Call ranges from four to eight syllables. There is little variation in pitch, and the second syllable is usually the loudest. Display Preening-behind-the-wing has been observed in the female only during pre-copulatory display. Females frequently Nod-swim, and this Nod-swimming is, as in males, highly specialized and unique to the Cape teal (Fig. 44D).

Agonistic and sexual behavior: male. The most frequent male display, which is performed throughout most of the year, is the Burp (Fig. 44A). This is a clear whistle, *oo-wheel'-oo*, of three syllables. It is unlike the Burp of the other *Anas* species, in that the neck and head are extended forward rather than upward, and the small crest of the male is raised. That this display is, however, typical Burping, is indicated by the fact that at the Wildfowl Trust a male hybrid between the Cape teal and the yellow-billed pintail calls with a diagonal head movement; thus the posture of the bird strikes a mean between the postures of the parent birds. Introductory Shaking in the Cape teal is infrequent. The major displays are Nod-swimming and the Head-up-tail-up. Nod-swimming (Fig. 44D) is performed without a nodding movement, and is a rapid scudding over the water surface in a semicircle, with the wings slightly lifted so that the speculum is exposed. Both sexes perform the display in exactly the same manner, and many birds often Nod-swim simultaneously. In this species the Head-up-tail-up (Fig. 44B, C) might more correctly be called a "Head-up-wing-up," since the tail is spread rather than lifted, and the folded wings are raised, flashing the speculum pattern, and then lowered as the male points his bill toward the courted female. Afterward there is no Nod-swimming; instead the male remains Facing the female in a motionless "at-attention" posture (von de Wall, 1961). I have rarely observed Preening-behind-the-wing (Fig. 44E) by males during courtship, but Turning-the-back-of-the-head to Inciting females is very frequently performed.

Copulatory behavior. The copulatory behavior is unusual in several respects. First, there is often and perhaps always a mutual Preening-behind-the-wing in the early stages of precopulatory behavior,

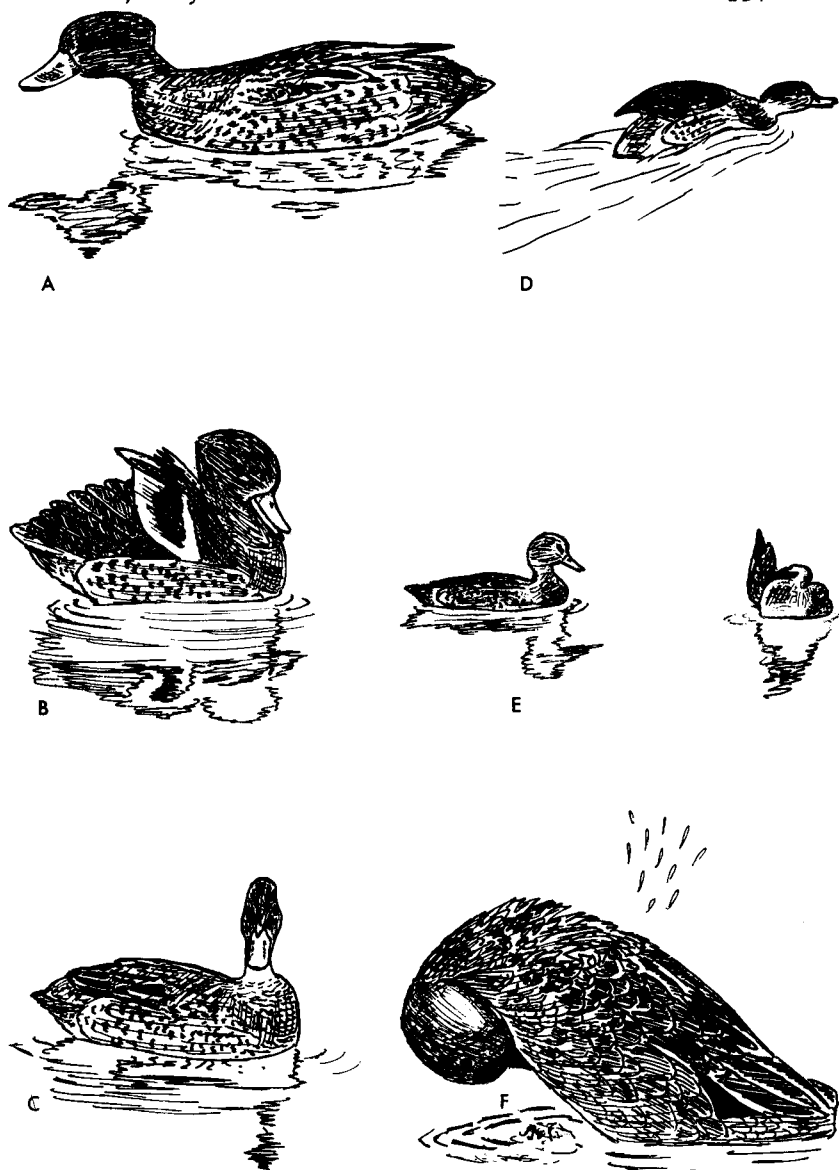


Figure 44. Cape Teal, Gray Teal

A. Cape teal male uttering Burp call.

B, C. Head-up-tail-up followed by turning head toward the female. Note how the speculum is momentarily exposed to the female's view.

D. Nod-swimming by Cape teal.

E. Preening-behind-the-wing as a courtship display by male to female.

F. Grunt-whistle by male gray teal.

which is soon followed by the usual mutual Head-pumping. After treading, the male performs a typical Bridling movement, then immediately follows it with what appears to be a rudimentary Head-up-tail-up, and finally turns and Faces the bathing female. This sequence occurred in all four of the copulations I observed, although von de Wall (1961) observed only Bridling as a postcopulatory posture.

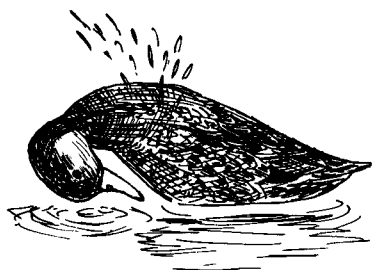
Gray Teal (*Anas gibberifrons*)

The gray teal is the first of the group of species Delacour (1956) calls the austral teal—a group which bridges the evolutionary gap between the green-winged teal on the one hand and the mallard and the pintail-like ducks on the other. All of the austral teal are found in the Australasian region, and they include several island forms of uncertain taxonomic status.

The gray teal, which includes the Andaman, East Indian, and Rennell Island forms, as well as the Australian forms, has a downy plumage almost identical with that of the typical green-winged teal, with distinct eye and cheek stripes. Juveniles closely resemble the adults, in which the sexes are nearly identical. The adults of this species, like those of the chestnut teal and the Cape teal, have crimson eyes. The speculum pattern, like that of the green-winged teal group, is green inwardly and black outwardly and has a white forward border. There is no obvious eclipse plumage. The male tracheal structure is practically identical with that of the chestnut teal and the typical green-winged teal. In Australia the gray teal is partially sympatric with the chestnut teal and several other species of *Anas*, and has produced wild hybrids with the chestnut teal and the Australian black duck. Wild hybrids with the chestnut teal are possibly more common than supposed, and these two forms are probably not “good” species (Ripley, 1942).

General behavior. Gray teal and the other austral teal are rather mallardlike in their general behavior and feeding tendencies. They dive well, using their wings when submerging. Preflight movements are the usual Neck-jerking and lateral Head-shaking. Frith (1959) has shown how the breeding periods of gray teal coincide with rising water levels, a valuable adaptation in a habitat characterized by uncertain and irregular rainy periods.

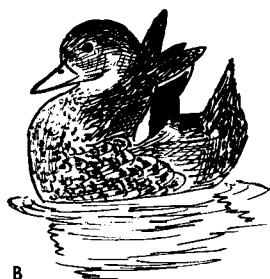
Agonistic and sexual behavior: female. Inciting takes a form more like that of the mallard group than that of the preceding species, in



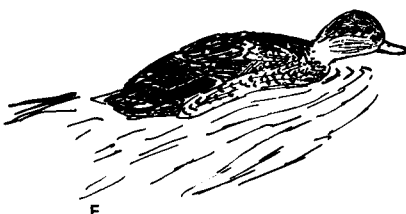
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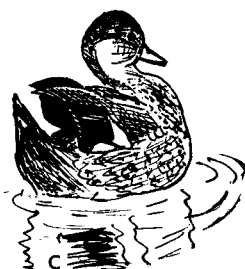
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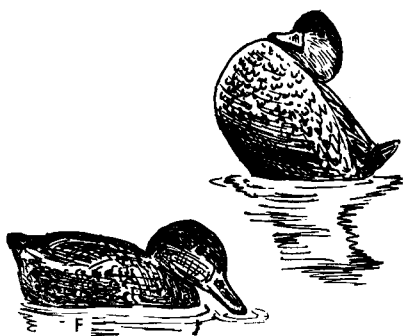
B



E



C



F

Figure 45. Gray Teal

- A. Grunt-whistle.
- B. Head-up-tail-up.
- C. Facing the female after the Head-up-tail-up.
- D. Bridling.
- E. Nod-swimming
- F. Independent Bridling. Compare with D.

that the bill is not held so close to the water surface. The Decrescendo Call is characterized by an extremely large number of syllables, usually 10 to 15, but I have counted as many as 27 in a single sequence. An independent and conspicuous Nod-swimming is also present in females. Preening-behind-the-wing has not been observed.

Agonistic and sexual behavior: male. I have not been able to detect any qualitative or quantitative differences between the sexual behavior of this species and that of the chestnut teal. Both forms possess numerous elaborate displays which indicate affinities both with the preceding group and with the mallardlike ducks. Burping in both species is marked by a vertical neck stretching (Fig. 46D), a tilting of the bill downward and the uttering of a sharp whistled *week*, reminiscent of the bark of a very small dog. An Introductory Shake is present and is functionally introductory to the major displays. Of these, the most common is the Grunt-whistle (Figs. 44F, 45A). This is performed very much as it is in the mallard group, and the call is a sharp whistle followed by a low grunt. Grunt-whistles may occur independently, or may be followed almost immediately by a Head-up-tail-up (Fig. 45B), which in turn is immediately followed by Facing the female (Fig. 45C), Bridling (Fig. 45D), and finally Nod-swimming (Fig. 45E) and Turning-the-back-of-the-head toward the female. Bridling occurs as an independent display fairly often (Fig. 45F), thus showing the gray teal's relationships with the green-winged teal group. Nod-swimming by males rarely if ever occurs independently, and when performed it always has a very exaggerated nodding component. In its linking of Nod-swimming and Turning-the-back-of-the-head the species is mallardlike, and in another display, the Down-up (Fig. 46B, C), relationships with the mallard group are also indicated. The Down-up of this species is not at all like the Down-up of the common teal, but it is almost exactly like that of mallards. The display usually follows aggressive Chin-lifting (Fig. 46A) and clearly functions as an appeasement gesture. Preening-behind-the-wing has been observed as a courtship display by males, who also Lead Inciting females while Turning-the-back-of-the-head in the usual *Anas* fashion.

Copulatory behavior. I have not observed a complete copulation, but copulatory displays are undoubtedly like those of the chestnut teal.

Madagascan Teal (*Anas bernieri*)

The Madagascan teal is very probably only a reddish variant of the gray teal, which it otherwise resembles in every respect except that the speculum has lost its metallic luster and is entirely blackish. It is most doubtful that the Madagascan teal should be considered a full species, but as I have never seen a live specimen I cannot comment on its behavior. Delacour (1956) states that in habits and behavior it appears to be "exactly similar" to the gray teal and the chestnut teal.

Chestnut Teal (*Anas castanea*)

The chestnut, or chestnut-breasted, teal hardly differs from the gray teal except in having a sexually dimorphic plumage. As in the gray teal the downy young have distinct eye and cheek stripes. Juveniles closely resemble adult females, which are more brownish than those of gray teal. The male nuptial plumage is similar to that of the common mallard. The speculum is green inwardly and black outwardly, with white anterior and posterior borders. The male has an indistinct eclipse plumage. The trachea of the male is essentially identical in the bulla shape with those of the green-winged teal and the other austral teal. The chestnut teal is restricted to southern Australia and is sympatric with several species of *Anas*. Wild hybrids with the gray teal have been reported, and numerous hybrid combinations have been reported from captivity.

General behavior. What has been said for the gray teal applies equally well to this form. In Australia, chestnut teal are far less common in the interior than gray teal, but predominate greatly over the gray teal near the coast. Because of the complete similarity of their displays, this geographic or ecological separation must be largely responsible for preventing hybridization between the two forms. The situation may be comparable with that of the North American black duck and the common mallard, in which a sexually dimorphic form and a nondimorphic form have recently come into secondary contact after incompletely speciating. The dimorphic chestnut teal is presumably the older of the two forms, and the gray teal is probably an East Indian derivative which presumably invaded Australia from the north.

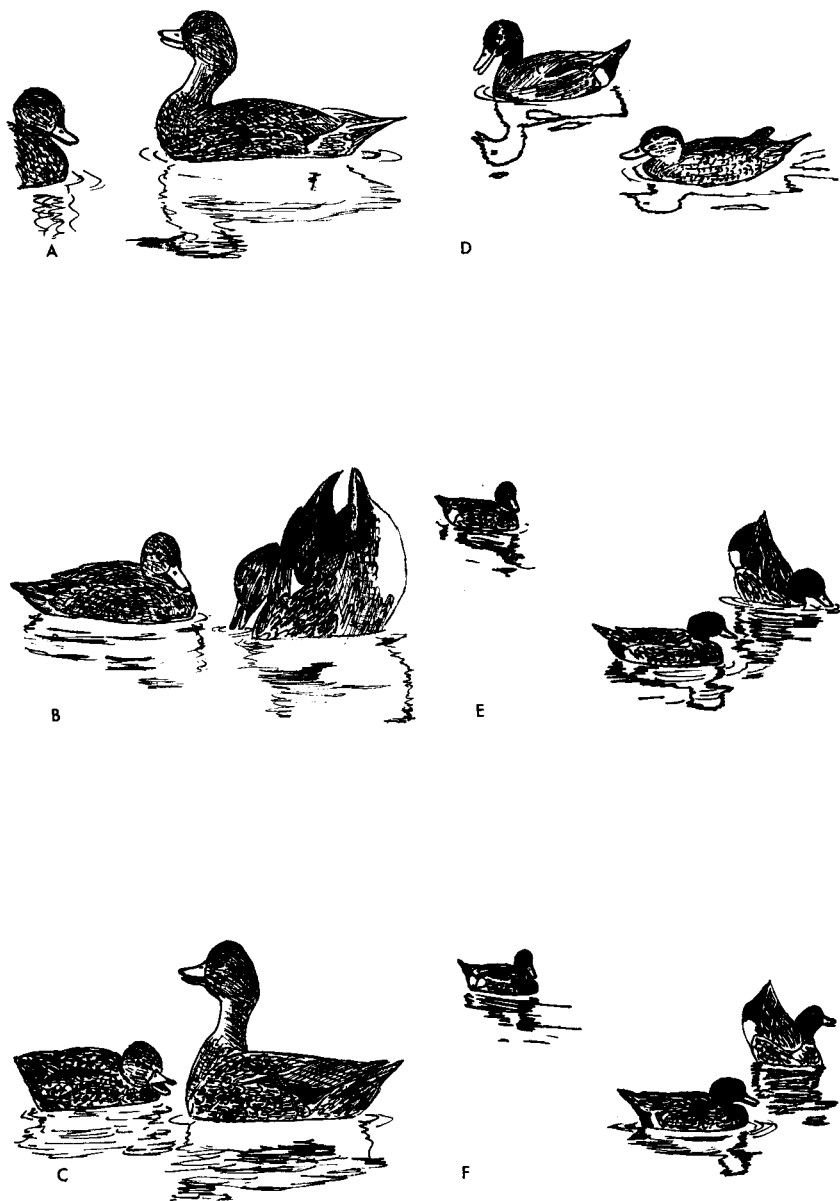


Figure 46. Gray Teal, Chestnut Teal

A. Male gray teal performing Chin-lifting prior to Down-up.

B, C. Two phases of Down-up display in gray teal.

D. Male chestnut teal uttering Burp, female swimming normally.

E, F. Two phases of Down-up in chestnut teal.

Agonistic and sexual behavior: female. Inciting behavior is exactly like that of the gray teal, and the associated calls are also the same. The Decrescendo Call, also like that of the gray teal, is of numerous syllables, often eight to ten, the second note being loudest and highest in pitch. Nod-swimming by females is frequent, and, as in the mallardlike ducks, it obviously serves as a stimulus for eliciting male displays. Preening-behind-the-wing has not been observed in females.

Agonistic and sexual behavior: male. With their green heads and exaggerated display actions, male chestnut teal remind one of miniature mallards in almost every respect. The only display they possess which is not typical of the mallard is independent Bridling. In this display, and in their lack of a *raeb* note, they recall the green-winged teal. As stated above, they apparently do not differ in the slightest from gray teal, and this, considering their diverse and elaborate display repertoire is most surprising and suggests a recent separation of the two forms. Except for the Burp (Fig. 46D) and the Introductory Shake, the Grunt-whistle is the most frequent display. A sizable proportion of Grunt-whistles are followed by the Head-up-tail-up, Facing the courted female, Bridling, Nod-swimming, and Turning-the-back-of-the-head, in that order. Although mallards also have a Head-up-tail-up-Nod-swimming sequence, Bridling is only very rarely intercalated (Johnsgard, 1960d), and the nodding component is often lacking. As in the gray teal, Chin-lifting is frequent and is often followed by the Down-up (Fig. 46E, F). Males frequently Preen-behind-the-wing to females, and they also Lead Inciting females by Turning-the-back-of-the-head. A Gesture of Greeting, similar to that of the South American teal, has been observed a few times.

Copulatory behavior. The usual *Anas* precopulatory mutual Head-pumping is present. After treading, the male performs a single Bridling movement, then tends to Nod-swim and Turn-the-back-of-the-head (Lorenz, 1951-1953). In a few cases, however, I have seen the male omit Nod-swimming after Bridling and simply turn to Face the female, as birds of the green-winged teal group typically do.

Brown Teal (*Anas aucklandica*)

The brown teal of New Zealand and the Campbell and Auckland Islands exhibits a puzzling mixture of mallard-, pintail-, and teal-like features. Although it is probably most closely related to the chestnut

teal, Scott (1958) has pointed out that possibly the brown teal is not simply an island derivative of that species. The downy young are very dark and their head markings are obscured, but their cheeks do have a slightly darker stripe than do those of the downy chestnut teal. Juveniles resemble adult females, which differ from chestnut teal females in having dark brown eyes, a white eye-ring, and more reddish plumage. Males vary somewhat in plumage, but most of them have a greenish head color, which may or may not be confined to the ear region. The males have a white eye-ring, and some of them have a white neck-ring like that of the common mallard. Pintail-like characteristics mentioned by Scott include the blackish patch on the back of the head, the upturned white neck-ring, and the long and rather pointed tail. The flanks are vermiculated as in mallards and the common pintail, and in this respect the species differs from the chestnut teal. The wing speculum is all green with a white rear border (much as in mallards) but with a buffy anterior border (as in pintails). There is an eclipse plumage in at least some individuals. The trachea of the male has a rounded bulla of the same general shape as is typical of the austral teal, mallards, and pintails. Although the brown teal is sympatric with the gray teal in New Zealand, no hybrids are known.

General behavior. Brown teal have an extraordinary tendency to remain hidden quietly in the grass and weeds during the day. They scuttle about like rodents when disturbed, and apparently become active only during periods of relative darkness. This is probably correlated with their shortened wings and reduced flying ability, but as a result practically nothing can be said about their behavior. On one occasion I observed Inciting, which was exactly like Inciting by chestnut teal. A probable Nod-swim, with very conspicuous nodding, was observed in the same female. G. V. T. Matthews informed me (pers. comm.) that when they were first brought to the Wildfowl Trust, the males of this species frequently uttered a pintail-like whistle, and I observed a male respond to female Inciting by uttering a faint, nasal whistle while facing her.

MALLARDLIKE DUCKS

The following group of species includes a number of very closely related forms and an uncertain number of species. There is a strong tendency for the males of this group to lose secondary sexual char-

acteristics wherever populations become isolated from other mallard-like forms. This occurs not only on islands, such as the Philippines, the Hawaiian Islands, and Laysan Island, but also on continents where populations are sedentary or otherwise isolated (Mexico, Florida, the Gulf Coast, etc.). In only two species (the common mallard and the spot-billed duck) are the males very contrastingly colored, and I believe that all the other forms can be thought of as secondarily deriving from one (or both, in the case of the Mariana Island population) of these two sources. Thus I consider the Asian spot-billed duck the parental form of the Philippine duck as well as of the duller southern Pacific races of "black ducks" and "gray ducks." I can see no justification for regarding these latter forms as species separate from the spot-billed duck, and I think that to do so is inconsistent with the current trend toward considering allopatric populations as subspecies. In almost every respect the Chinese spot-bill perfectly bridges the morphological gap between the Indian and Burmese spot-billed ducks and the southern Pacific races. These groups show a continuous decrease in male bill coloration and tertial whiteness and a corresponding increase in general body darkness and facial striping—and these differences are correlated with the degree of natural sympatry with the common mallard. It is also of interest that no wild hybrids between the common mallard and the spot-bill are known from India or Burma, that they are evidently rare in China, and that in Australia and New Zealand, where there is no plumage or soft-part specialization in the gray ducks and black ducks, there has been extensive hybridization with the recently introduced common mallard.

On the other hand the common mallard has given rise to numerous secondary populations. The African yellow-billed duck may be one of these, although possibly it too is a derivative of the spot-billed duck. The Madagascan Meller's duck is certainly an island derivative of the common mallard. The North American black duck is a much more recent derivative that scarcely deserves specific status (Johnsgard, 1961f). The Florida, Gulf Coast, and Mexican populations are certainly only isolated derivatives of the common mallard and have also become nondimorphic in plumage. The Laysan Island population and, to a lesser degree, the Hawaiian Island population represent degenerate and inbred island forms of the common mallard.

It thus appears that there are two superspecies of mallardlike

ducks, and that they are most different where they are sympatric with one another and with other closely related species of *Anas*, and most similar where they are isolated. That, in the mallard group, male plumage characteristics are of greater importance than behavioral differences in species-recognition and the prevention of hybridization between these closely related forms is indicated by the fact that the sexual displays of all forms are qualitatively almost identical, and that differences only occur in minor quantitative details.

Mallard (*Anas platyrhynchos*)

Partly for the sake of convenience, the common mallard and its geographic races will be dealt with first. In all these races the downy young are similar, having spotted backs, an eye stripe, and a small cheek patch. Juveniles closely resemble the adult female. The adult male of the common mallard is too well known to describe, and the males of the other races either differ from females only in their soft-part coloration (as in the Mexican duck, the Florida duck, and the mottled duck), or else are intermediate between the typical male and female plumages (Hawaiian and Laysan ducks), but showing varying amounts of head albinism. The speculum of all forms is metallic green or blue and is bordered in front and behind with white and black bars. In the Florida and mottled ducks the white barring is sometimes obscured. A distinct eclipse plumage is present only in the common mallard. The male trachea has a bulla somewhat larger than those of the preceding group, but it is of the same general conformation. The common mallard is widespread over the Northern Hemisphere and has produced numerous hybrids in the wild and in captivity (see Gray, 1958, and Johnsgard, 1960a).

General behavior. Papers dealing with the general and sexual behavior of the common mallard are numerous. Those of Weidmann (1956) and Lorenz (1951–1953) deal with the nominate race, and my own studies (Johnsgard, 1959, 1961f) have included the other North American forms. Mallards are typical surface-feeding ducks in that although they usually up-end or dabble for food, they can readily dive as well. Preflight movements are the usual Neck-jerking and lateral Head-shaking.

Agonistic and sexual behavior: female. Inciting in female mallards has been well described by Lorenz (1951–1953). There is no marked

chin-lifting, and the call is a characteristic series of *gagg* notes which are irregularly accented. The same call is used in flight when a female is Inciting her mate against a pursuing drake. When a female is being pursued by one or more strange drakes and her mate is not near, however, she performs the Gesture of Repulsion, holding her head back on her shoulders and opening her bill wide as she utters several *gaeck* calls (Lorenz, 1951–1953). (This same behavior occurs in common pintails and is the reaction that Sowls, 1955, describes as “re nesting courtship.”) Besides Inciting, a major female display is Nod-swimming, which in this species involves almost no real nodding and is only a rapid swimming with the head stretched out along the water. This display is the primary means of eliciting sexual displays from males. The Decrescendo Call usually consists of about six notes, with the second note the loudest and highest in pitch. Females also sometimes Preen-behind-the-wing to males.

Agonistic and sexual behavior: male. Behaviorally, male mallards differ from the preceding groups in that the whistled note is replaced by a nasal *raeb* call. The utterance of a single note functions as an alert or warning signal, and the two-note *raeb-raeb'* (Fig. 48B) is a sexual or conversational call. The Burp is a single sharp whistle which is never an independent display but occurs only during the Head-up-tail-up. The Introductory Shake is functionally introductory to the major displays. The Grunt-whistle (Fig. 47A–C) is the most common mallard display. It has exactly the same form as it has in the Florida duck (Fig. 47E), the mottled duck, the Hawaiian duck, and the Laysan duck (Fig. 48C), although in the last-named form the whistled note is replaced by a high-pitched *raeb*. The Head-up-tail-up (Fig. 47A–C) is not linked to the Grunt-whistle as it is in the preceding groups. It also has the same form in the Florida duck (Fig. 47F) and the mottled duck. In the Hawaiian duck it appears to be practically the same as in the mainland forms, but in the Laysan duck (Fig. 48D, E) the posturing is less extreme and, as in the Grunt-whistle, the whistled note is replaced by a *raeb*. In all forms the male points his bill toward the courted female as he utters his call; then he usually Nod-swims for some distance before Turning-the-back-of-the-head toward the female. In the Florida duck, the mottled duck, and the common mallard, Nod-swimming is performed without actual nodding movements of the head, but in the Hawaiian duck and the Laysan duck (Fig. 48F) there is a strong tendency to nod the

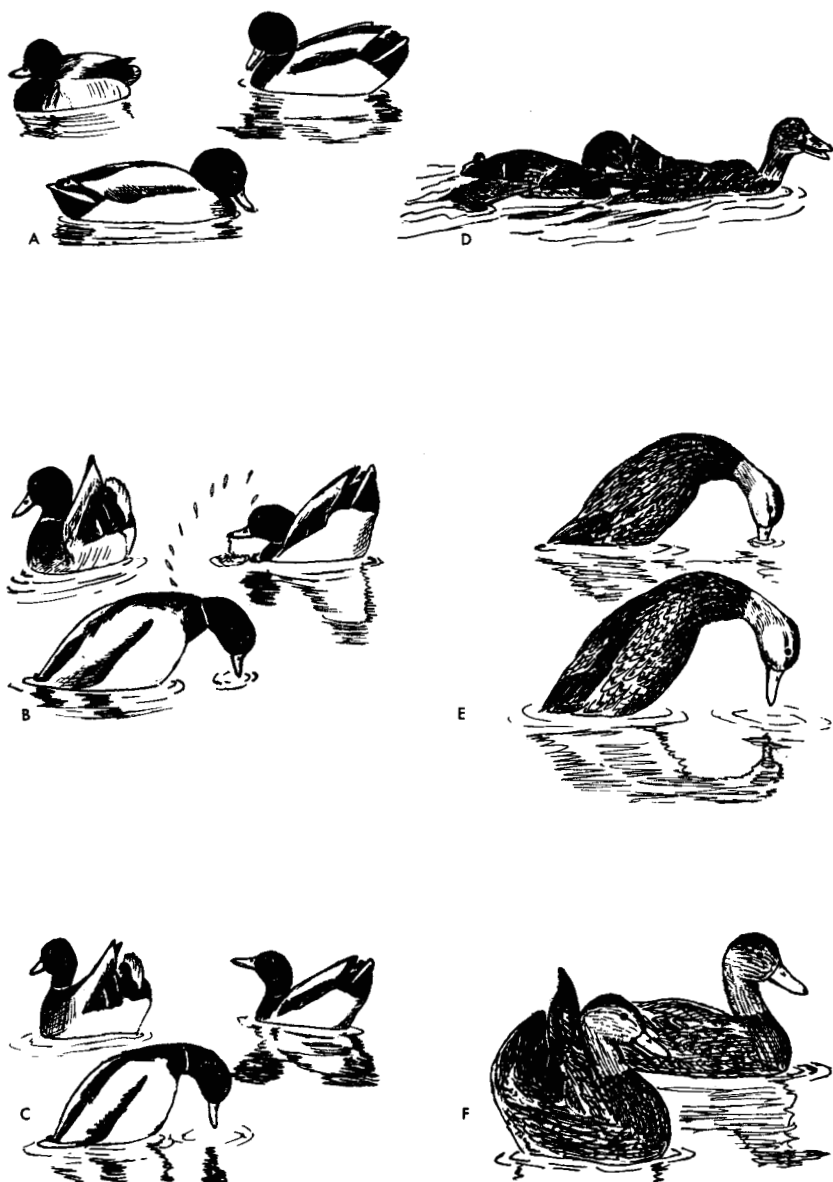


Figure 47. Mallard, Florida Duck

A-C. Stages in the performance of the Grunt-whistle (*foreground*), Head-up-tail-up (*left*) and Down-up (*right*) by mallards.

D. Mallard male attempting to rape a female.

E. Florida duck males performing Grunt-whistle display.

F. Florida duck male performing Head-up-tail-up.

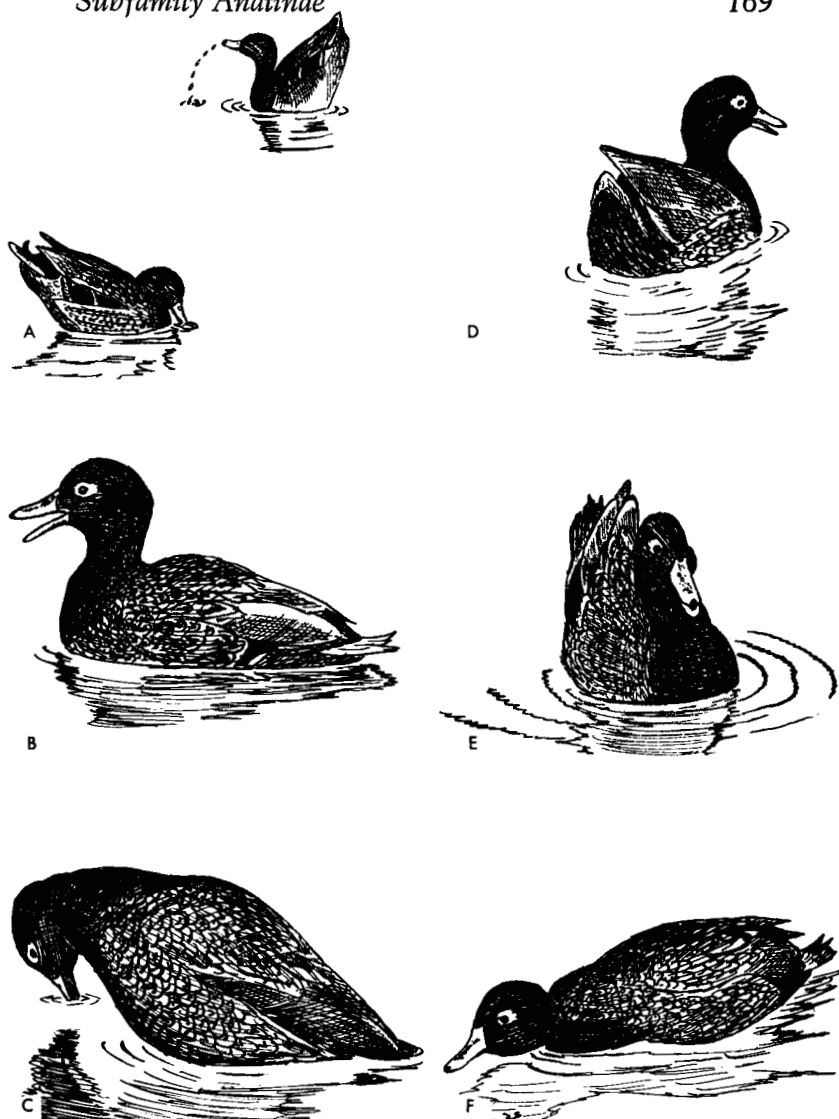


Figure 48. Hawaiian Duck, Laysan Duck

A. Hawaiian duck males performing Down-up.

B. Laysan duck male uttering *raeb-raeb* call. Note slightly curled tail feathers and partial albinism around eye.

C. Grunt-whistle by Laysan duck.

D, E. Head-up-tail-up display by Laysan duck. Both drawings represent the peak of the posturing and are comparable to that shown in Fig. 47B.

F. Nod-swimming after the Head-up-tail-up in Laysan duck.

head. In the latter two forms independent Nod-swimming is also present. The Down-up (Fig. 47A-C) is the least common display, and the call uttered is a sharp whistle followed by a *raeb-raeb'*. The display may be used as a sexual display toward a female or as an appeasement gesture toward another male, and it is often performed simultaneously by many males. The display has the same form and vocalizations in the Florida duck, the mottled duck, and the common mallard. I have seen it only a few times in the Hawaiian duck (Fig. 48A), but it appeared to be of the typical form in this race too. I observed this display only twice in the Laysan duck, although I saw the other two major displays fifty times or more. It was scarcely recognizable as a Down-up, for the bill was not brought down to the water and the tail was not noticeably lifted. Rather it appeared to be simply a drink-intention movement followed by a rapid chin-lifting and the uttering of a faint *raeb-raeb-raeb*. The replacement of a whistled note by a *raeb* indicates that in the Laysan duck the two calls are basically the same, and differ in sound quality by differences in the amount of tension on the trachea. The lower *raeb* note very probably results from the vibration of the membranaceous parts of the syrinx, whereas the whistle results from the rapid passage of air past the bony bulla, which probably functions in the same manner as the sound chamber of a mechanical whistle.

Preening-behind-the-wing is a frequent male display of common mallards, and very likely also occurs in the other subspecies as well. Males also Lead Inciting females by Turning-the-back-of-the-head to them (Johnsgard, 1960d), and this combination of displays apparently plays an important part in pair formation. After pairs are formed, males usually respond to their mate's Inciting by alternately threatening the indicated bird and uttering the *raeb-raeb* call repeatedly toward the female. It is of interest that the Turning-of-the-back-of-the-head to Inciting females during pair formation occurs not only in the common mallard, the Florida duck, and the mottled duck, but also, and in exactly the same way, in the Hawaiian duck and the Laysan duck, indicating the importance of this display in the process of pair formation.

Copulatory behavior. In all forms mutual Head-pumping is the precopulatory display. After treading, the male performs a Bridling movement, then Nod-swims around the bathing female and Turns-the-back-of-the-head to her.

American Black Duck (*Anas rubripes*)

As I have reported elsewhere (Johnsgard, 1959, 1961f), the American black duck is only a forest-dwelling form of the common mallard, and probably should not be considered a full species. The downy young are only very slightly darker than downy common mallards, and juveniles and adults are very similar to the Florida and mottled ducks. In fact there is a continuous gradient in body plumage coloration from predominantly buff to predominantly dark brown in the following sequence of forms: common mallard, Mexican duck, Florida duck, mottled duck, black duck. This gradient is effected by the relative widths of the buff edges and barring on the body feathers. The speculum also exhibits a gradient of increased black border-barring relative to the white, so that in the black duck the white is often almost totally obscured. The dark plumage of the black duck is clearly an adaptation to a forest habitat which, until recently, was free of selective pressures for retaining a dimorphic plumage, since no other near relatives occupied the range of the black duck. Recent forest clearing and introductions of the common mallard into the eastern states have already resulted in hybridization and may eventually result in a genetic swamping of the black duck. The male black duck's plumage differs only very slightly from the female's, and there is a postnuptial male plumage corresponding to the common mallard's eclipse plumage, but it is not easily distinguished from the nuptial plumage. The male tracheal structure is exactly like that of the common mallard. The black duck is now broadly sympatric with the common mallard, and besides the numerous and fully fertile hybrids recorded with it, hybrids with all the other major mallardlike forms have occurred and have proved fertile.

General behavior. Except for slight differences resulting from ecological adaptations, black ducks are exactly like the common mallard in their general behavior.

Agonistic and sexual behavior: female. Female black ducks do not differ in the least from common mallards in their Inciting movements and calls, and the Nod-swimming and Decrescendo Calls are also identical in the two species. Preening-behind-the-wing has also been observed in females.

Agonistic and sexual behavior: male. In a detailed comparison of the sexual behavior of the common mallard and the black duck

(Johnsgard, 1960d), I was unable to find any qualitative differences in the display patterns. Slight quantitative differences are present which suggest that the black duck is more easily stimulated to perform sexual displays and also has a somewhat more specific display response. I have seen no independent Nod-swimming by male black ducks, but since this occurs in several of the races and species of mallards, its presence would not be surprising. Preening-behind-the-wing has been observed, and males Lead Inciting females by Turning-the-back-of-the-head in exactly the same manner as do male common mallards.

Copulatory behavior. This is exactly like that of the common mallard. The postcopulatory Bridling is vigorously performed and the subsequent Nod-swimming and Turning-the-back-of-the-head is performed without any real nodding.

Meller's Duck (*Anas melleri*)

The Madagascan Meller's duck differs only slightly more from the common mallard than does the black duck. The downy, juvenile, and female plumages of Meller's duck are practically identical with those of the common mallard. The adult male has a female-like plumage, but except for its larger size and relatively larger bill, there is scarcely any basis for considering Meller's duck a separate species. It is not sympatric with any other mallards, but in captivity it has hybridized with all of the major mallardlike forms.

General and sexual behavior. I have not observed this species, but Lorenz (1951-1953) states that Meller's duck is like the common mallard in every major respect except that an independent Nod-swimming is performed by males as well as by females. Lorenz also states that the female's voice is thinner in quality and that the male's conversational call tends to have three rather than two syllables. Since independent Nod-swimming also occurs in the Hawaiian and Laysan ducks, this difference is not an important one.

Yellow-billed Duck (*Anas undulata*)

It is uncertain whether the African yellow-billed duck is a derivative of the mallard or of the spot-billed duck groups, since it is fairly distinct from both. The adult plumages are rather more reminiscent of the spot-billed duck, but the dark eye-stripe which is so characteristic of the spot-billed group is lacking, and the nape and

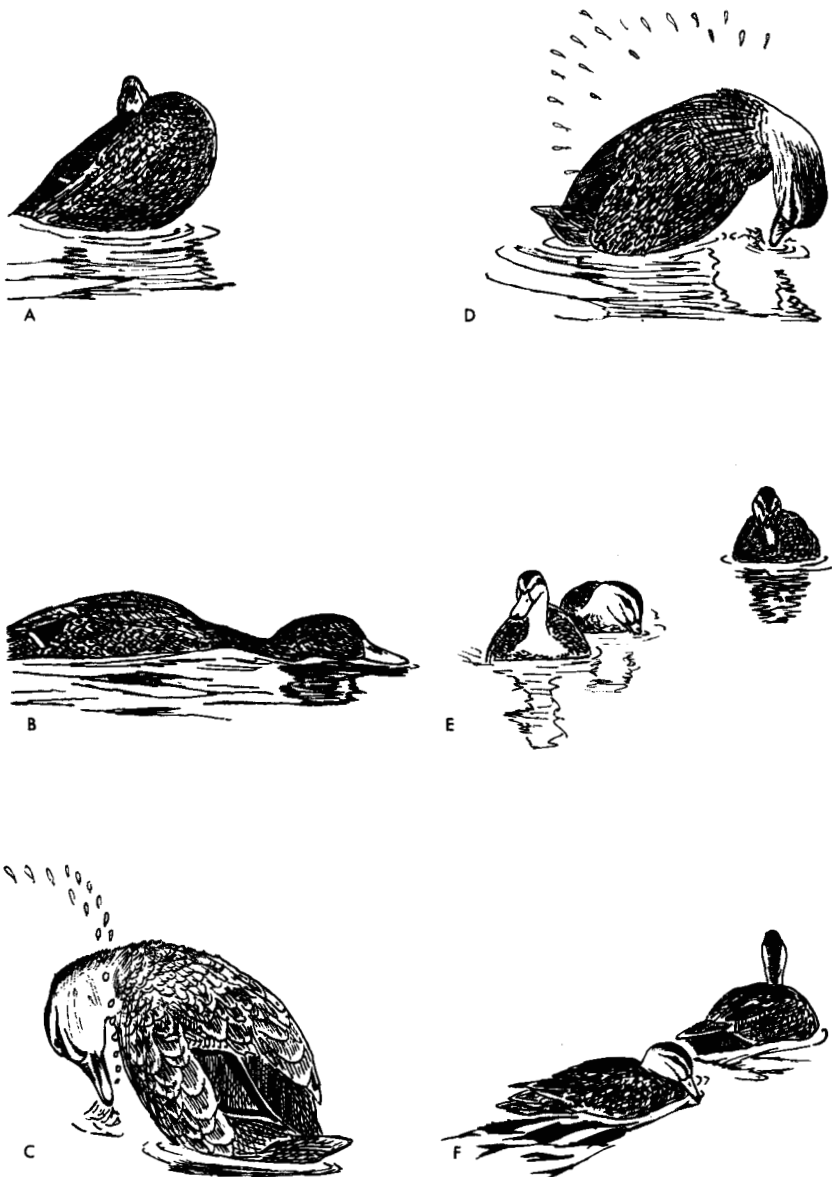


Figure 49. African Yellow-bill, New Zealand Gray Duck

- A. African yellow-billed duck, postcopulatory Bridling by male (female not shown).
- B. Postcopulatory Nod-swimming by male yellow-bill.
- C, D. Grunt-whistle by male gray duck.
- E, F. Male gray duck Leading an Inciting female.

crown are also no darker than the rest of the head. The sexes differ only in the intensity of the bill coloration, the male's bill being a slightly more brilliant yellow than that of the female. I have not seen the tracheal structure, but doubtless it is like that of the other mallards. The species ranges over the southern half of Africa and is not sympatric with any other typical mallards. In captivity it has produced fertile hybrids with various other forms of mallards.

General behavior. This species is a bird of the open country, inhabiting both fresh and alkaline waters, and it probably has little or no contact with the African black duck, which is more of a forest dweller.

Agonistic and sexual behavior: female. Female yellow-billed ducks are very much like common mallards in voice and behavior. The Decrescendo Call is usually of about five syllables and is very much like that of the common mallard. The Inciting is likewise very similar in form and associated sounds. Females frequently Nod-swim, and they do so with the kind of nodding movement typical of spot-billed females. Preening-behind-the-wing has not been observed.

Agonistic and sexual behavior: male. The voice of the male is somewhat higher in pitch and weaker than those of common mallards and spot-bills. In other respects the male is a typical mallard. In addition to the usual displays, an independent Nod-swimming is present in males. The Grunt-whistle, the Head-up-tail-up, and the Down-up are all performed in exactly the same manner as by the common mallard and the spot-billed duck. Males also often Lead Inciting females by Turning-the-back-of-the-head, but Preening-behind-the-wing has not been recorded.

Copulatory behavior. Precopulatory behavior is the usual mutual Head-pumping. After treading, the male performs a single Bridling movement as he whistles loudly (Fig. 49A); then he Nod-swims rapidly away from the female (Fig. 49B). In one case that I observed this Nod-swimming was fairly straight rather than circular, and it lacked any nodding until near the end, when twelve nods were performed. In another case only three or four nodding movements were performed.

Spot-billed Duck (*Anas poecilorhyncha*)

As stated above, there is no justification for not considering the whole series of southeastern Asian and Australasian mallards as a

single species, as was originally proposed by Delacour and Mayr (1945). The downy young of all these forms are essentially identical, and tend to lack the dark ear patch found on the downy young of the common mallard and its near relatives. As adults, the sexes differ only slightly, the males of the northern races having brighter soft-part colors and a slightly more contrasting plumage. The speculum pattern varies from metallic green to metallic blue, and in all cases has the usual black and white anterior and posterior borders. There is no obvious eclipse plumage in any of the races. In shape the tracheal bulla is identical with that of the common mallard. The northern and more brightly colored races are sympatric with the common mallard, but wild hybrids are known only from the Chinese race (*zonorhyncha*). The southern races are not naturally sympatric with the common mallard, but have hybridized with it in Australia and New Zealand, where common mallards have been introduced. There is also apparently a "hybrid swarm" on the Mariana Islands which has resulted from hybridization between the common mallard and the Pacific race of spot-bill (*pelewensis*) (Yamashina, 1948). In captivity various races of this group have produced fertile hybrids with most of the other mallardlike forms.

General behavior. This species is very similar to the common mallard in almost every respect. Presumably there are some ecological differences from the mallard in the zone of major sympatry (India), since the two forms do not appear to mix to any degree in that region. It is clear, however, that unlike the American black duck, the spot-billed duck is not a forest-dwelling form. Preflight movements are the usual Neck-jerking and lateral Head-shaking.

Agonistic and sexual behavior: female. Lorenz (1951-1953) states that the Indian and Chinese races are exactly like the common mallard, and the same can be said for the Australian and New Zealand forms. I have not been able to detect any vocal differences between the females of these forms and common mallard females. Nod-swimming is performed with a conspicuous nodding component, and female hybrids of the two species, which sometimes closely resemble ordinary common mallards, also perform this definite nodding action. Preening-behind-the-wing has not been observed.

Agonistic and sexual behavior: male. Lorenz (1951-1953) states that the only difference he has noted between spot-billed ducks and common mallards is that the "disk-set" of the head feathers during

the Head-up-tail-up is not so pronounced in the spot-bills. In addition, one might mention that Nod-swimming is performed independently of the Head-up-tail-up by male spot-bills, and that it is performed with a definite nodding action. This independent Nod-swimming often follows a series of three or four *raeb* calls, which are uttered with the head erect and the bill opened wide, much as they are during the warning call. Presumably this preliminary calling serves to attract the female's attention. It seems probable that such behavior might have provided the original basis for the Head-up-tail-up, which is clearly a Burp that has become exaggerated through the lifting of the wings and tail. The Grunt-whistle (Fig. 49C, D) and the Down-up are not different from the corresponding displays of the common mallard. Males of most and no doubt all races Preen-behind-the-wing toward females, and in all forms the males Lead Inciting females by Turning-the-back-of-the-head to them (Fig. 49E, F).

Copulatory behavior. This is exactly as it is in the common mallard, with precopulatory Head-pumping and postcopulatory Bridling by the male, followed by Nod-swimming and Turning-the-back-of-the-head. The usual exaggerated nodding is present during Nod-swimming.

Philippine Duck (*Anas luzonica*)

The Philippine duck is apparently a distinct species, but it is obviously a close relative of the spot-billed duck. The downy young of both species lack an ear patch, and the Philippine downy young also have very reduced back spotting. Juveniles resemble adults, both sexes of which have an almost unicolored gray body and a reddish brown head with dark crown and eye stripes. The speculum is metallic green and of the typical mallard pattern. The trachea of the male has a bulla which is not distinguishable from those of the common mallard and the spot-billed duck. The species is not sympatric with any near relatives, but in captivity it has produced hybrids with both the common mallard and the spot-billed duck.

General behavior. This is apparently no different from that of the common mallard and the spot-billed duck. The usual Neck-jerking and lateral Head-shaking are the preflight movements.

Agonistic and sexual behavior: female. Since the female behavior patterns of common mallards and spot-billed ducks are so similar, it

is impossible to state which the Philippine duck most closely resembles. The Decrescendo Call is usually of about seven syllables, and is more squeaky than those of the common mallard and the spot-bill. The Inciting call is also somewhat weaker, although the form of the display is the same. Females perform Nod-swimming with a distinct nodding movement. Preening-behind-the-wing has not been observed.

Agonistic and sexual behavior: male. Male Philippine ducks perform an independent Nod-swimming, and this is one of the most frequent of the male displays. The nodding is more pronounced in this species than in spot-bills, and is almost as exaggerated as it is in gray teal and chestnut teal. Nod-swimming also almost invariably follows the Head-up-tail-up. The Down-up is the least frequent of the major displays, but it is performed with a posturing as extreme as that of the common mallard. The Grunt-whistle is also performed in the same manner in the two species. Preening-behind-the-wing has been observed a few times, and males frequently Lead Inciting females by Turning-the-back-of-the-head while swimming in front of them.

Copulatory behavior. Precopulatory behavior is the usual mutual Head-pumping. After treading, the male performs a single Bridling movement; then he rapidly Nod-swims around the female, nodding his head most vigorously. After one copulation over twenty individual nods were counted during such a Nod-swim, whereas the common mallard seldom nods at all and at most three or four times. The male finally Turns-the-back-of-the-head to the bathing female.

Bronze-winged Duck (*Anas specularis*)

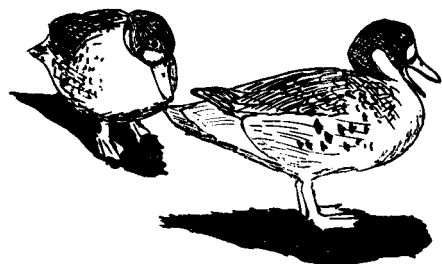
I believe that the bronze-winged duck, together with the crested duck, bridges the evolutionary gap between the typical mallardlike forms and the pintail group. The downy young of the bronze-winged duck are much like those of pintails, having distinct eye and cheek stripes and being whitish below as are downy pintails. Juveniles are much like adults in appearance, and as adults the sexes are identical. The adult body plumage pattern is distinctly like that of the crested duck, but the head color and shape is reminiscent of pintails. The speculum pattern is practically identical with that of the crested duck, being bronze-colored with a posterior black and terminal white border, and lacking any anterior border differentiation. Males do not

have a distinct eclipse plumage. The tracheal bulla is approximately the same shape as that of the crested duck. The bronze-winged duck has a broad range in southern South America and is sympatric with several other species of *Anas*, but no hybrids are known.

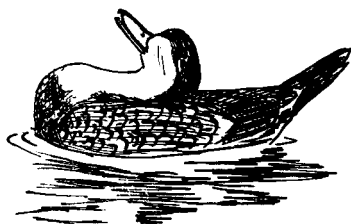
General behavior. Very little has been written about the general behavior of this species, which has rarely been kept in captivity. Pre-flight movements have not been recorded.

Agonistic and sexual behavior: female. Two females of this species were maintained at the Wildfowl Trust for several years, and appear to have been a homosexual pair. I have heard the Decrescendo Call only rarely, and it is very similar to that of the crested duck and the mallards. It is a very loud, five- to six-syllable raucous call which descends only slightly in pitch. Inciting is performed at the slightest provocation, whether of humans or of other birds, and consists of a curious combination of alternate chin-lifting (performed with the bill pointed over the shoulder as the bird utters a *rrrrrrraaaa'*), and lowering the bill as it is brought to the forward position (Fig. 49A, B). Most *Anas* females lift the chin when bringing it to the forward position and lower it when pointing it over the shoulder, but a movement similar to that of the bronze-winged female is used by the crested duck female when she Incites during Nod-swimming. The Inciting call has been described as being similar to the barking of a small dog. I have also observed what is an almost certainly a ritualized Introductory Shake, in which the head is first brought forward and downward, then shaken vigorously as it is rapidly pulled up and back until the neck is past the vertical position and completely extended, and the feathers of the nape are erected to form a slight crest. This movement is certainly homologous to the ritualized shake of the crested duck, although it is less exaggerated.

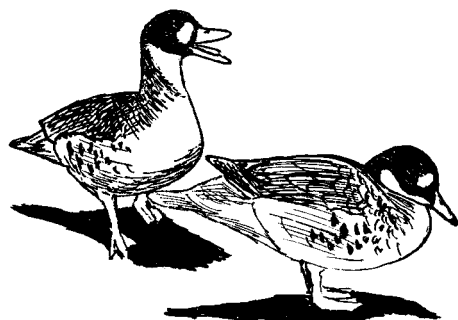
Agonistic and sexual behavior: male. Percy (in Phillips, 1926) reports that the courtship behavior of this species is almost exactly like that of the common pintail. This description must refer to the male's behavior, however, because the female's behavior is not pintail-like. It would be most interesting to learn whether the Grunt-whistle and the Head-up-tail-up are present, as one would predict. Percy speaks of the males uttering a whistle "such as can be reproduced by drawing a cutting whip through the air." This description suggests a pintail-like Burp whistle.



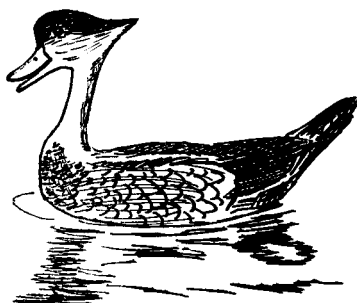
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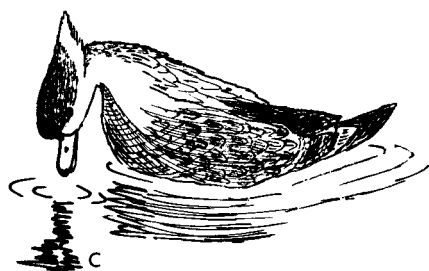
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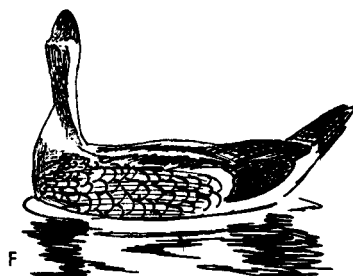
B



E



C



F

Figure 50. Bronze-winged Duck, Crested Duck

A, B. Bronze-winged ducks, two females Inciting.

C. Crested duck, Grunt-whistle. (From photo by D. F. McKinney.)

D-F. Crested duck, Head-up-tail-up sequence. (From photos by D. F. McKinney.)

Copulatory behavior. No information on copulatory behavior is available.

Crested Duck (*Anas specularioides*)

Contrary to Delacour, I consider the South American crested duck to be a typical *Anas* rather than an aberrant genus of the Tadornini ("*Lophonetta*"). Admittedly the downy young are not entirely *Anas*-like, but they are certainly more similar to *Anas* than to *Tadorna*. Juveniles are similar to adults, and in the latter stage the sexes differ only in crest development. The adult plumage is rather distinctive. It is marked by a very elongated tail approaching the pintail type, a pale brownish to grayish body color, and a well-marked crest. There is a superficial similarity between the plumages of this species and those of the marbled teal, but I believe that this represents nothing more than convergence. The wing speculum seems to provide the key to the species' real relationships. The speculum is a green to bronze color, with a black posterior and a white terminal border. The anterior border is not differentiated. Thus the speculum resembles that of the bronze-winged duck and, to a lesser degree, that of the pintail-like ducks. The male tracheal bulla is very similar to that of the bronze-winged duck. The species is found in the mountains of southern South America, and although it is sympatric with several other forms of *Anas*, no hybrids are known from the wild or captivity.

General behavior. Crested ducks occur over a range of habitats from Andean lakes to salt water kelp beds and are very common in some areas. Most observers stress their aggressive disposition, which prompted Delacour (1954) to consider them relatives of the shel-ducks. McKinney (1953) notes that lateral Head-shaking is possibly a preflight movement.

Agonistic and sexual behavior: female. The voice of the female crested duck is very mallardlike, and the Decrescendo Call is so much like that of the common mallard that the two species are easily confused. There are usually five or more syllables in the call, and they descend gradually in pitch. When Inciting, the female utters a regularly repeated *qua-qua-qua-qua . . .*, and shows a tendency to chin-lift. A Nod-swimming is present which is very similar to that of female common mallards, in that the head is held out low over the water, there is no real nodding, and the female tends to swim in cir-

cles around the courted drake. Nod-swimming in this species is unique in that occasional Inciting movements are made with a quick upward flick of the bill and an accompanying *urr-uk'* call. A display analogous to Nod-swimming but performed on land has been observed—a display which is rarely performed by common mallards. Females possess a highly ritualized Introductory Shake in which the neck is first stretched out over the water, then drawn rapidly backward in a shaking movement which ends with the head held high and the crest erect and with the neck fully outstretched vertically. According to Jones (1948), females Preen-behind-the-wing as a sexual display, but I have not observed this.

Agonistic and sexual behavior: male. Male crested ducks evidently lack the *raeb* call of the mallardlike ducks, and have instead only a “windy” whistling note. I have not observed male display, but according to Jones (1948) the courtship note is uttered as the neck is stretched, and the head is shaken as the bill is pointed upward. Jones states that this is repeated several times and is apparently a specialized form of Head-flicking which, like the Introductory Shake of various *Anas* species, serves as an introductory movement. In motion picture sequences taken by Gordon Booth and D. F. McKinney, this introductory Head-flicking is very obvious, and in two cases it is followed by a Head-up-tail-up. The Head-up-tail-up (Fig. 50D–F) is a very specialized one, since the head is first rapidly thrown down to the back and then immediately brought forward as the neck is stretched vertically to the utmost and the call is uttered, and the bill is finally pointed toward the courted bird. The Grunt-whistle is evidently equally specialized, for in a sequence filmed by McKinney it consists of bill-dipping followed by rapidly lifting the bill out of the water and shaking it, and finally by raising the front of the body high in the water as the head is brought back and the tail is shaken (Fig. 50C). Males probably also possess an Introductory Shake similar to that of the female and it is likely that Preening-behind-the-wing is shared by the two sexes.

Copulatory behavior. Precopulatory behavior consists of the usual mutual Head-pumping of the typical dabbling ducks, which is further evidence against shelduck affinities. In the three instances I observed, the male did not perform a Bridling movement after treading, but swam away from the female in a manner suggesting the Nod-swimming of typical mallards. Jones (1948) also mentions the presence of a mallardlike postcopulatory display.

PINTAIL-LIKE DUCKS

The following group of four species might be thought of as constituting the typical pintails. The group may be described as having downy young with distinct eye stripes and cheek markings, and as having elongated tails, long and ornamental scapulars, brightly colored bills, and wing specula that range from bronze to coppery green, with black and buff or white posterior borders (often very broad) and buffy anterior borders. Through the two preceding species the pintails are related to the mallardlike ducks and probably also to the austral teal, of which the brown teal exhibits several pintail-like features. Unlike the mallards, males of these species lack a *raeb* call, but they have a *geeee* call that functionally replaces it. One species (the red-billed pintail) approaches the spotted teal in color pattern, and is considered by Delacour (1956) to belong to that group.

Pintail (*Anas acuta*)

The common pintail is certainly not too distantly related to the mallard and austral teal groups. The downy young differ from mallard downies in having a streaked back, more heavily marked cheeks, and white under parts. Juveniles, and also males in their eclipse plumage, resemble females, which have a plumage pattern of the typical female dabbling duck type. The nuptial plumage of males is distinctive, but the speculum is a bronze-green with a narrow posterior black and white border and a buffy anterior border. It is basically similar to the speculum pattern of the two preceding species. The tracheal bulla is somewhat smaller than that of the common mallard, but is very similar to it in shape. The species has an extremely wide range in the Northern Hemisphere and is sympatric with many species of *Anas*. Wild hybrids are numerous (see Johnsgard, 1960a), and those involving the common teal, the gadwall, and the mallardlike ducks are known to be fertile. Two isolated island populations on the Kerguelen and Crozet Islands are very different from the typical form and have been separated as subspecies.

General behavior. Like mallards, common pintails frequently dive for food, using their wings in submerging. The small Kerguelen Island pintail, however, dives without using its wings, in the manner of true diving ducks. This indicates that the manner of diving is

probably dependent upon the ratio of foot area (and placement) to body size, and thus is not a useful taxonomic criterion. Preflight movements are the usual Neck-jerking and lateral Head-shaking.

Agonistic and sexual behavior: female. Lorenz (1951–1953) has described in detail the behavior of the common pintail. The Inciting of female pintails (Fig. 51D) is accompanied by much less conspicuous bill movements than in that of the mallardlike ducks, and the breast is, curiously enough, lifted slightly during the chin-lifting phase of Inciting, as if the female had a stiff neck. The Inciting call is softer than it is in mallards and is a more continuous series of *rrr-rrr'* notes. The Decrescendo Call is also not so loud as that of female mallards, and is usually of fewer syllables. The Gesture of Repulsion is very similar in both species. There is no Nod-swimming in females of any of the pintail group. Preening-behind-the-wing is a common female display.

Agonistic and sexual behavior: male. Lorenz (1951–1953) has summarized completely the male behavior patterns of this species, and Smith (1963) has made a detailed analysis of its social behavior. Burping, which is an independent display in the pintail group, is the most frequent male courtship display and to a certain extent replaces the Introductory Shake as an introductory activity. The basic Burp call in this species is a *geee* sound rather than a *raeb* as it is in mallards. The call is transformed into a soft, flute-like whistle, *pfüh*, in the same way as the mallard's *raeb* is transformed into a clear whistle by extreme neck-stretching. During Burping the bill is tilted slightly downward and the neck is extended vertically. Males typically crowd around the courted females and Burp repeatedly before performing the first major display, the Grunt-whistle (Fig. 51A). The Grunt-whistle is performed without lifting the front of the body very far out of the water, and the usual whistling note is uttered. The majority of Grunt-whistles are followed in a few seconds by the Head-up-tail-up (Fig. 51B, C); hence the two displays are linked in exactly the same way as they are in the green-winged and austral teal. The Head-up-tail-up is followed immediately by a turning of the bill toward the courted female, and may finally be followed by a rudimentary form of Nod-swimming. Nod-swimming also occurs independently, but it is an inconspicuous display, and one which is probably being secondarily lost, presumably under the pressure of selection for species differences. Males often Turn-the-back-of-the-head

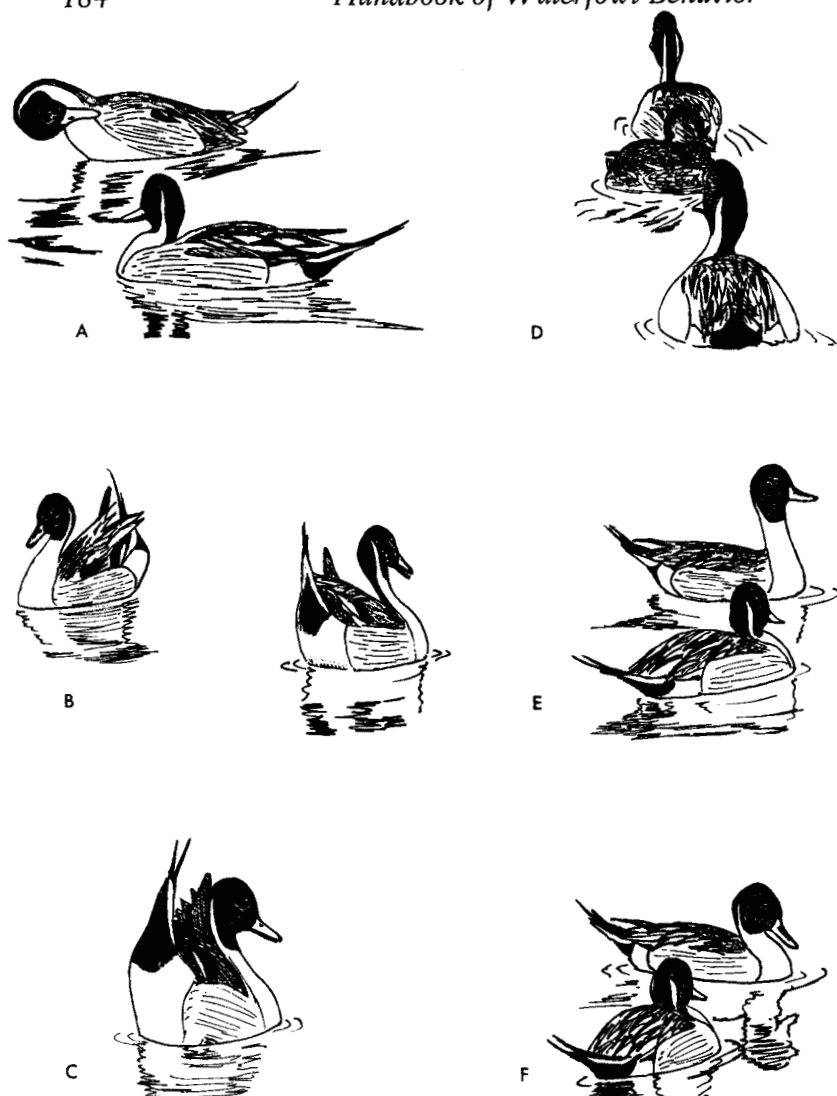


Figure 51. Common Pintail

- A. Grunt-whistle, showing maximum distance that the neck is arched to flick water upward.
- B. Head-up-tail-up. The peak of the posturing, during which both males are calling.
- C. Head-up-tail-up and turning the head toward the courted female.
- D. Female Inciting her potential mate, who is Leading her away from the other drakes. Note the difference in head feather erection between the Leading male and the rear one.
- E, F. Two phases of aggressive Chin-lifting by one male toward another.

after Burping, and they also use this display when Leading an Inciting female (Fig. 51D). At such times the dark nape patch is exhibited and made conspicuous by depressing the head feathers. The Down-up display is completely lacking in the common pintail and also in all the other species of the group except the Bahama pintail. In hostile encounters males often perform a single rapid Chin-lifting movement (Fig. 51E, F). Males often Preen-behind-the-wing as a sexual display.

The Kerguelen pintail has often been observed displaying, and it is of interest that although the typical male plumage pattern has been almost entirely lost in this race, all of the male courtship displays have been observed. Burping and the Grunt-whistle do not appear to have been affected by prolonged isolation, and the Grunt-whistle (Fig. 52A) includes the typical whistle, and the usual arc of water accompanies it. As in the common pintail, the Head-up-tail-up is linked fairly closely to the Grunt-whistle, and in this display there does appear to be a trend toward secondary simplification, since the tail is not normally lifted so strongly as in the larger forms (Fig. 52B-D). Interestingly, males Lead Inciting females by Turning-the-back-of-the-head with a vigor typical of the common pintail, which indicates the probable importance of this display in pair formation.

Copulatory behavior. Precopulatory behavior in common pintails consists of mutual Head-pumping, and after treading the male normally performs a single Bridling movement. There is no indication of Nod-swimming such as occurs in the mallard group after Bridling. In observations of fourteen copulations, Smith (1963) observed Bridling on seven occasions, Turning-the-back-of-the-head six times, and Burping twice, often in various combinations.

Yellow-billed Pintail (*Anas georgica*)

The yellow-billed pintail is clearly a very close relative of the common pintail. The downy young of the two species are almost identical. Juvenile birds resemble adult females, which differ from female common pintails in having yellow bills and a richer brown coloration. Adult males have somewhat brighter yellow bills but otherwise do not differ greatly from females. The speculum is greenish-black but otherwise like that of the common pintail, except that the terminal border is buffy rather than white. The male tracheal bulla is slightly smaller than that of the common pintail. The species

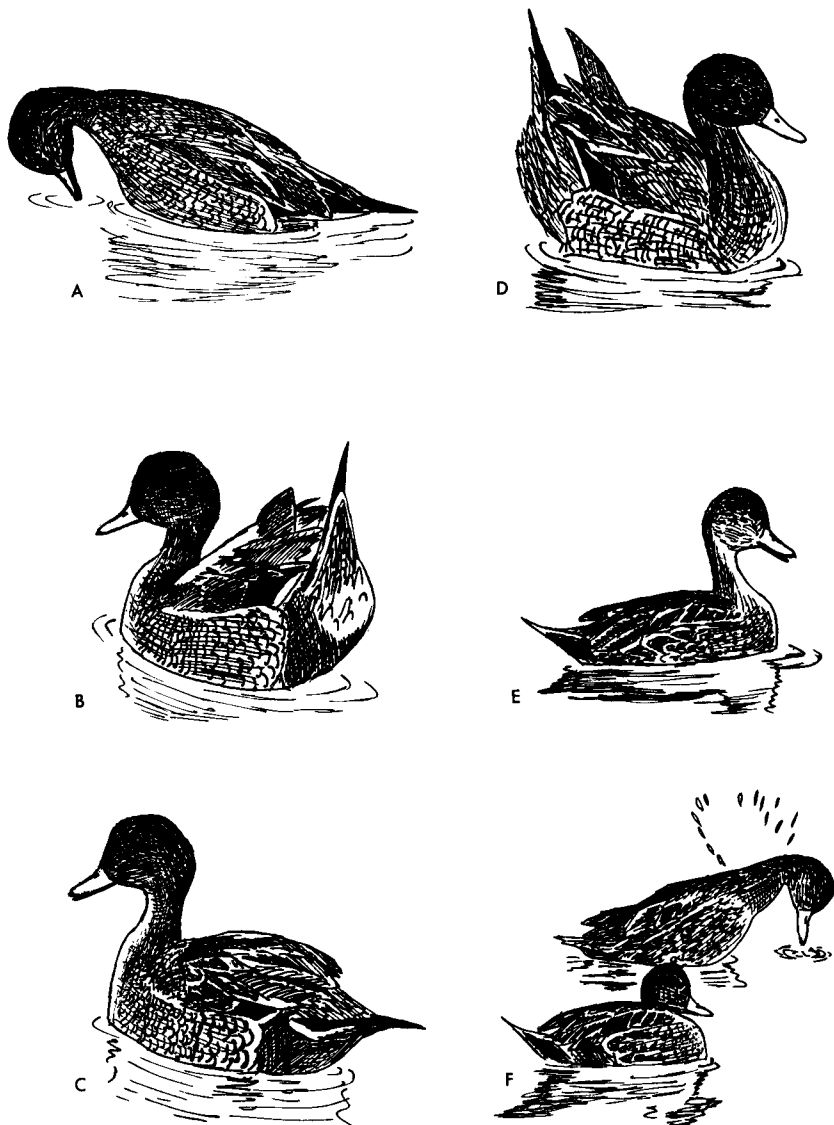


Figure 52. Kerguelen Pintail, Yellow-billed Pintail

A. Grunt-whistle, male Kerguelen pintail.

B, C. Head-up-tail-up, followed by Burp call. Note that the call occurs after the tail is lowered, and compare with Fig. 51B.

D. Head-up-tail-up. In this drawing, as well as in 52B, the peak of the posture is shown. Compare with Fig. 51B, C.

E. Burp call uttered by male yellow-billed pintail.

F. Grunt-whistle of yellow-billed pintail.

ranges widely through southern South America and has been divided into three races, of which one is restricted to South Georgia Island. It is sympatric with the Bahama pintail as well as with several other species of *Anas*. Wild hybrids with the Bahama pintail have been reported, and this cross is known to be fertile from captive hybrids. Fertile hybrids have also been reported with the Chiloe wigeon and the South American teal, and several other hybrid combinations are also known.

General behavior. Yellow-billed pintails appear to be very much like common pintails in their general behavior. Preflight movements consist of the usual Neck-jerking and lateral Head-shaking.

Agonistic and sexual behavior: female. Inciting by females takes exactly the same form as it does in the common pintail. The associated calls are also similar to those of the common pintail and have a "creaking" tone (Lorenz, 1951-1953). The Decrescendo Call is also essentially the same in the two species. Preening-behind-the-wing has not been observed.

Agonistic and sexual behavior: male. As Lorenz has stated, the vocalizations of the male yellow-billed pintail are very much like those of the common pintail, except that the *geeee* call is less conspicuous and the clear whistle is more obvious. The Introductory Shake is even less frequent than it is in the common pintail, and the Burp is correspondingly more frequent (Fig. 52E). Males often Burp repeatedly for ten or fifteen minutes before performing their only major display, the Grunt-whistle (Fig. 52F). This has the same form and vocalization as in the common pintail. Occasionally a male will perform a very rudimentary Nod-swimming in the same manner as described for the common pintail, but, as in that species, the display has apparently been secondarily reduced to the point of being scarcely recognizable. I have never observed a Head-up-tail-up, but von de Wall (pers. comm.) informed me that he has seen this display only a few times in about four years of intensive observation of the species. Thus the Head-up-tail-up has been secondarily lost as an effective signal, and it is of considerable interest that this display is the major display of the closely related and broadly sympatric Bahama pintail, which in turn lacks the Grunt-whistle. Contrary to Delacour (1956), Turning-the-back-of-the-head is present, and males frequently Lead Inciting females in this way, although a special nape pattern is not present in this species. This provides an example of

the principle that instinctive movements are probably evolved before (or concurrently with) the plumage specializations which are exhibited during the display. I have not observed Preening-behind-the-wing, but Lorenz reports that it does occur, though very rarely.

Copulatory behavior. I have not observed copulation, but according to Lorenz (1951–1953) the associated behavior is the same as the corresponding behavior of common pintails.

Bahama Pintail (*Anas bahamensis*)

In practically every respect the Bahama pintail is intermediate between the yellow-billed pintail and the African red-billed pintail. The downy young are more like those of the latter species, being yellowish below and having less conspicuous cheek markings than downy yellow-billed pintails. Juveniles resemble the adult females, which differ from adult males only in having a less sharply defined head pattern and a duller bill coloration. The speculum is a metallic green and resembles that of the yellow-billed pintail except that the posterior buffy border is much broader. The tracheal bulla of the male is almost identical in size and shape to that of the two preceding species. The Bahama pintail extends from the West Indies through most of South America, and it also occurs as a well-differentiated race in the Galapagos Islands. It is believed to have hybridized with the yellow-billed pintail in the wild, and in captivity fertile hybrids have been produced with that species and also with the South American teal and the common mallard. Other hybrid combinations have occurred in captivity (Gray, 1958).

General behavior. Bahama pintails resemble the other species of this group in their foraging and diving behavior. McKinney (1953) recorded only lateral Head-shaking as a preflight movement; I have not noted any preflight movements.

Agonistic and sexual behavior: female. Inciting in Bahama pintails takes the usual form of the pintail-like ducks, with the bill making slight lateral sweeps along the water (Fig. 53E) and the neck held rather stiffly. According to Lorenz (1951–1953) the Inciting call is higher pitched and less creaking than in the two preceding species. The Decrescendo Call and the Gesture of Repulsion are very similar to those of the other pintails. Females often call at the instant that a male displays, in a behavior pattern that Lorenz has called Gasping. Females also Preen-behind-the-wing as a sexual display toward males.

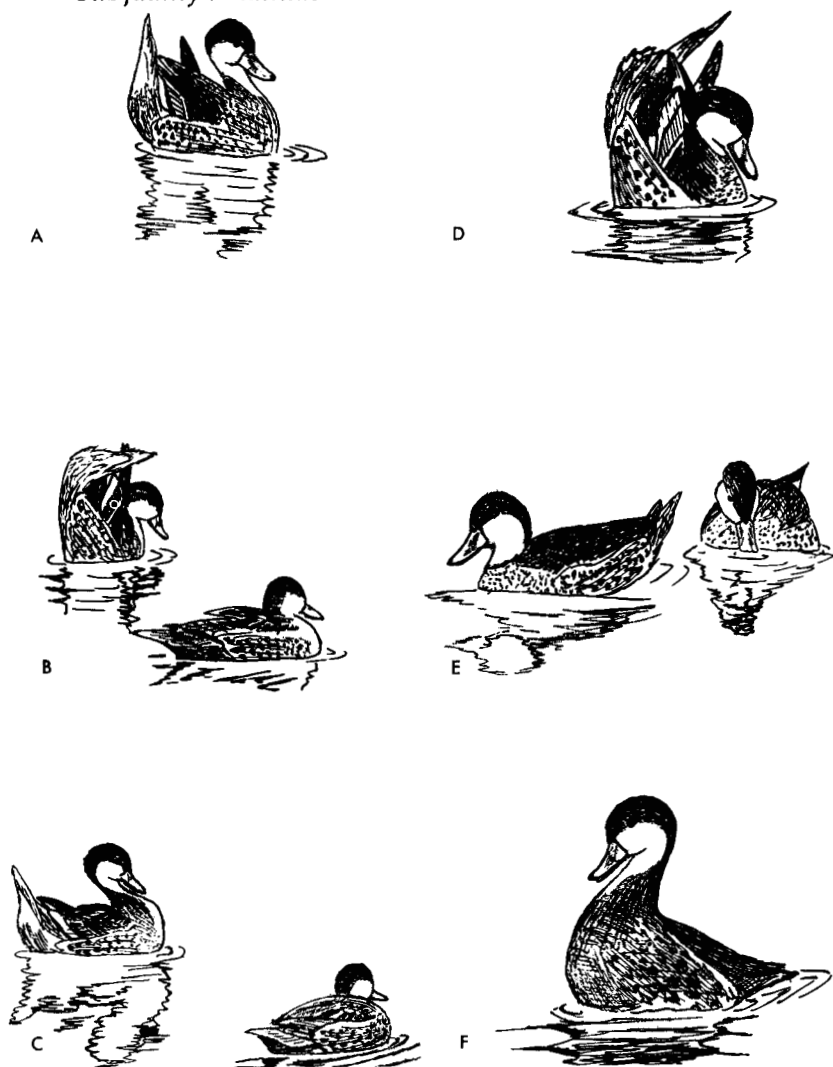


Figure 53. Bahama Pintail

- A. Independent Head-up-tail-up by Bahama pintail.
- B, C. Down-up-Head-up-tail-up sequence.
- B. Down-up phase. Note exposed speculum and tail tilted to one side of folded wings.
- C. Head-up-tail-up phase. Compare with independent Head-up-tail-up above. A turning of the head toward the courted female (right) occurs immediately after the tail is lowered.
- D. Close view of Down-up.
- E. Leading and Inciting.
- F. Postcopulatory Bridling by male Bahama pintail.

Agonistic and sexual behavior: male. The Introductory Shake is somewhat more frequent in the Bahama pintail than in the yellow-billed pintail, and the Burp is correspondingly less frequent. The Burp call is a *geeee* sound, uttered as the neck is stretched and retracted. The major display is one which Lorenz (1951-1953) first believed to be a Head-up-tail-up, but later (1958) identified as a Down-up. I believe that it is in fact a Down-up followed immediately by a Head-up-tail-up and then by a turning of the bill toward the courted female. The call is the usual *geeee*, into which a two-note whistle is inserted. The first part of the display, the Down-up phase (Fig. 53B, D), is highly exaggerated and is held for nearly a second. The second phase is a lowering of the hindquarters and a stretching of the neck with an accompanying Burp as the bill is finally turned toward the female. Evidence that this display is a combination of the Down-up and the Head-up-tail-up is provided by male hybrids of the Bahama pintail and the chestnut teal, in which the two parts of the display are not so firmly linked and are more easily recognized than they are in pure Bahama pintails. Very rarely an independent Head-up-tail-up does occur in the Bahama pintail (Fig. 53A), and equally rarely a Bridling display may be observed, but the Grunt-whistle has never been recorded in this species. The loss of the Grunt-whistle is understandable, considering that the species is sympatric with the yellow-billed pintail and that the fusion of the Down-up and Head-up-tail-up has resulted in a display that sets this species apart from the other sympatric *Anas* which have Head-up-tail-up displays (the South American teal, the crested duck, and possibly the bronze-winged duck). Males Turn-the-back-of-the-head toward females after Burping as well as when Leading Inciting females (Fig. 53E). Preening-behind-the-wing is not a common display.

Copulatory behavior. The precopulatory display is the usual mutual Head-pumping. After treading, the male performs a single Bridling movement (Fig. 53F), and then may utter several Burp calls while the female bathes.

Red-billed Pintail (*Anas erythrorhynchos*)

The African red-billed pintail is surely a member of the pintail group, although Delacour (1955) considers it one of the spotted teal. The downy young are most like those of the Bahama pintail, having distinct eye stripes and cheek markings. Juveniles resemble adults

except that their bills are not so crimson. As adults, the sexes are very difficult to distinguish, and the plumage pattern is much like that of the Bahama pintail except that the facial markings are not so distinct and the tail is not so elongated. In addition, the bill is entirely rather than partially red, and the wing speculum is even more reduced, with the metallic portion being almost entirely obscured by the secondary coverts. The posterior buff border is correspondingly broader, and constitutes almost the entire speculum. The trachea of the male has a relatively larger bulla, but is otherwise of exactly the same shape as in the typical pintails. The species is restricted to southern and eastern Africa, and is sympatric with several other species of *Anas*. The only hybrids known to me are crosses in captivity with South American teal and the yellow-billed duck.

General behavior. Both sexes of red-billed pintails are remarkably quiet and undemonstrative, in which respect they resemble the two following species. Preflight movements are the usual Neck-jerking and lateral Head-shaking.

Agonistic and sexual behavior: female. The Inciting of the red-billed pintail has exactly the same form as it has in the Bahama pintail, and it completely lacks the strong chin-lifting typical of the spotted teal (Fig. 54B, C). The associated call, a very soft *rrrrr* sound, is very much like that of a female Bahama pintail. The Decrescendo Call is very infrequently performed and usually consists of four notes of equal length and of a single pitch, or of five notes with the first (and sometimes also the last) shorter and lower. Preening-behind-the-wing has not been observed.

Agonistic and sexual behavior: male. Lorenz (1951-1953) has described the behavior of the male red-billed pintail. The Introductory Shake is very infrequent in this species, and Burping is correspondingly increased to the point where it is the only social display exhibited! The pintails thus show an extremely interesting trend in displays—a trend which can be summarized as follows: The common pintail has two major displays plus Burping and the Introductory Shake, all of which are used frequently. The Bahama pintail has a single major display (the fused Down-up-Head-up-tail-up) plus Burping and Introductory Shaking. The yellow-billed pintail has a single major display, relatively less Introductory Shaking, and more Burping. Finally, the red-billed pintail lacks elaborate displays altogether, and has replaced them and the Introductory Shake with

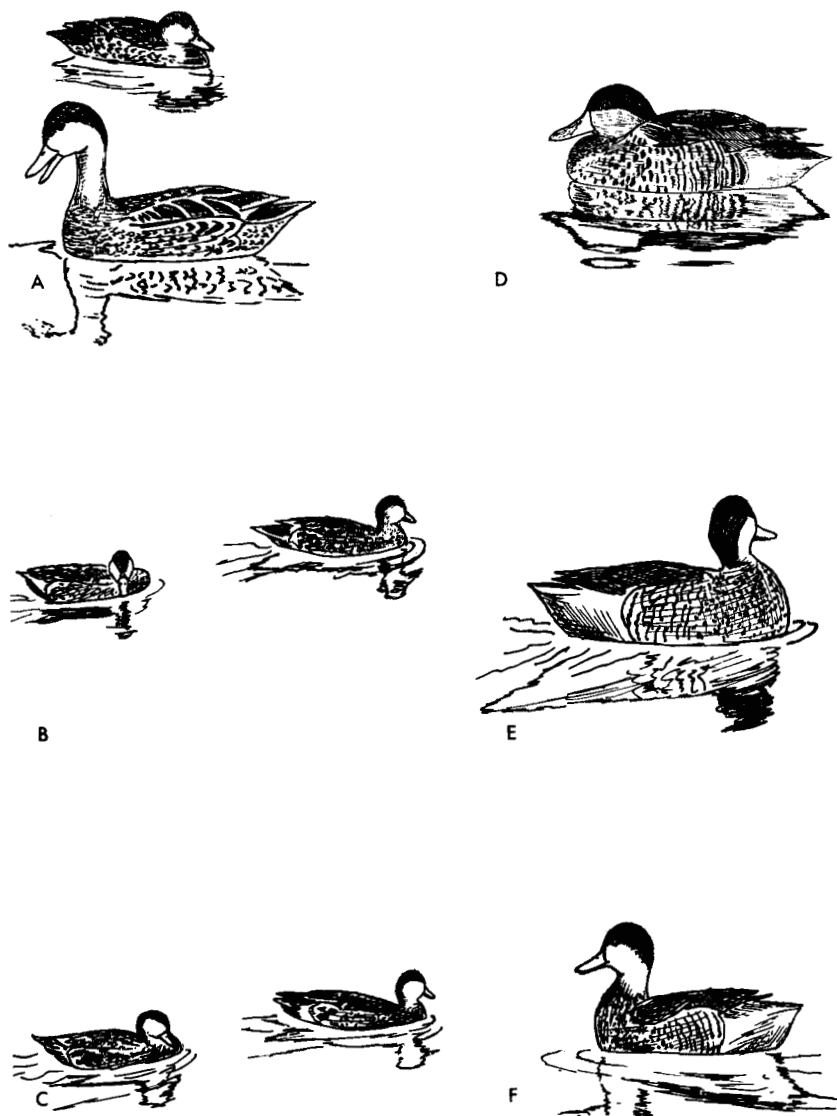


Figure 54. Red-billed Pintail, Silver Teal

- A. Red-billed pintail male (*left*) in Burp position.
- B, C. Red-billed pintail, female (*left*) Inciting a male, who is Leading her by Turning-the-back-of-the-head.
- D. Silver teal male, normal swimming posture. Compare with drawings below.
- E. Silver teal male, Turning-back-of-the-head to female (*not shown*). Compare with B and C.
- F. Silver teal male in Burp posture.

Burping. In this display a *geeeee* call much like that of the Bahama pintail is uttered, but only as the head is moving upward (Fig. 54A). Chin-lifting is also used as a hostile display. Preening-behind-the-wing has been observed on a few occasions, which is of interest because the speculum of this species is almost lacking in metallic coloration. Males also Turn-the-back-of-the-head while Leading Inciting females (Fig. 54B, C), and it is also of interest that, although most of the other major *Anas* displays are lacking, Turning-the-back-of-the-head is present—a fact which suggests the importance of this display in the pair-formation process.

Copulatory behavior. Precopulatory mutual Head-pumping has been observed, but not a completed copulation.

Silver Teal (*Anas versicolor*)

Following Delacour's (1956) grouping, this species and the Hottentot teal might be called spotted teal, although the other species he includes in that group are not here considered a part of it. These two species bridge the evolutionary gap between the pintail-like ducks and the blue-winged ducks, which constitute the remainder of the genus *Anas*. There are two major forms of silver teal, the brighter-colored lowland races and the larger, duller, and more isolated mountain race. Although the two forms are often considered to be distinct species, this is certainly another case of a secondary loss of bright coloration in isolated and allopatric populations. The downy young of silver teal have incomplete eye stripes and a very small cheek patch. Juveniles resemble adults. As adults, the sexes are very similar and resemble the two preceding species in their white cheeks and dark crowns. The scapulars are not so long and pointed as in those species, however, and the flanks tend toward vertical barring. Furthermore, the tail is shorter and not distinctly set off from the tail coverts, which gives the hindquarters of the bird a curious "unfinished" appearance (Fig. 54D). The speculum differs markedly from the pintail type, and is a bright metallic green to blue, bordered behind with a narrow black and terminal white border and in front with a broad white border. Some of the longer tertials have a narrow white central stripe, such as is found in males of the blue-winged ducks. The trachea of the male has a marked expansion near the middle of the tube, a characteristic shared with the Hottentot teal but otherwise unique in the genus *Anas*. The tracheal bulla is fairly intermediate between

the entirely left-sided bulla of the preceding groups and the more rounded and almost symmetrical bulla of the garganey (see Johnsgard, 1961c). The silver teal occurs widely in southern and western South America, and the southern races are sympatric with several other *Anas* species. In captivity hybrids have been reported with Baikal teal and Hottentot teal.

General behavior. Silver teal are remarkably quiet birds and, like the Hottentot teal, usually swim about with the head resting on the shoulders, producing a rather dumpy effect (Fig. 54D). I have not observed them to forage by diving, and this must be done only rarely if at all. No preflight movements have been noted.

Agonistic and sexual behavior: female. Inciting in this species is entirely different from that in the pintail group, in that a strong forward chin-lifting movement is alternated with lateral pointing. The Decrescendo Call seems to vary in the different races. In the southern race (*versicolor*) it consists of one long and high note normally followed by eight or ten (but up to fifteen have been counted) shorter and descending notes. I have heard the mountain race (*puna*) utter four to five weaker and slightly descending notes on various occasions, but I am unsure whether this is typical of the race. Preening-behind-the-wing has not been recorded.

Agonistic and sexual behavior: male. Sexual display in this species is remarkably simple. The Burp is the most frequent display (Fig. 54F). Unlike males of most species of *Anas*, however, the silver teal male does not perform the Burp exclusively as a social display, but seems to perform it almost randomly, regardless of whether a female is present or not. The head is raised slowly in the display, and the tail is also slightly raised, while a very soft call is uttered. This is a faint rattling note on one pitch, reminiscent of the sound produced by the winding of a pocket watch, and it is much weaker than the similar rattling note of the male garganey. The other major display, which is much more rare, is an exaggerated Introductory Shake (Fig. 55A, B) similar to those of the falcated duck and Chiloé wigeon. I have only observed this to occur immediately after a Burp, and I believe that a faint whistle is associated with it. As in the ritualized shakes of the falcated duck and the Chiloé wigeon, the bill does not touch the water, but the display is otherwise much like a true Grunt-whistle. Preening-behind-the-wing is rather frequently performed, usually after drinking. In addition, males Turn-the-back-of-the-head

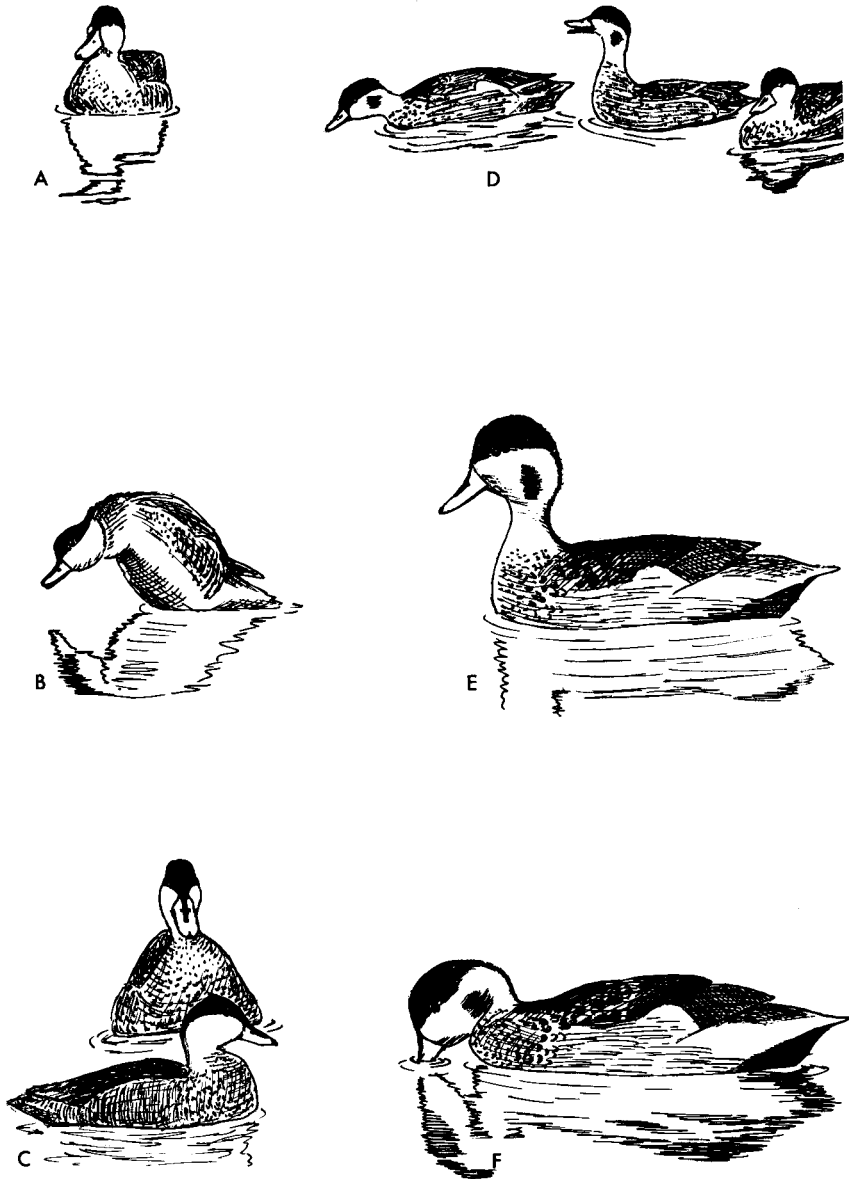


Figure 55. Silver Teal, Hottentot Teal

- A, B. Silver teal male performing Burp, Introductory Shake sequence.
 C. Silver teal postcopulatory display. Male Facing the bathing female.
 D. Hottentot teal. Female (*center*) Inciting preferred male (*left*) against second male.
 E, F. Two phases of Burp-Drink display of male Hottentot teal.

(Fig. 54E) while Leading Inciting females. An exaggerated Chin-lifting is used as an aggressive display toward other birds.

Copulatory behavior. Copulation has been observed in both the northern and puna races of silver teal. In both, the usual mutual precopulatory Head-pumping is present. The postcopulatory display seems to be rather variable. In one case involving the northern silver teal the male appeared to call once in a Burp posture (rather than Bridling, as is typical of the pintail group), then turned and Faced the female in a motionless posture (Fig. 55C) as she began to bathe. In two observations of the puna silver teal the male each time called once in a Burp posture, then simply swam away and flapped his wings.

Hottentot Teal (*Anas punctata*)

The tiny African Hottentot teal is undoubtedly a close relative of the silver teal. The downy young of these two species are very similar in that in both species they exhibit reduced eye stripes and cheek patches. Juvenile birds are less strongly spotted than adults, and adult males have only slightly brighter bills and more distinct markings than females. The adult plumage pattern is much like that of the silver teal, but the vertical flank barring is absent. The bill is blue, as in the silver teal, and the tail and rump have the same "unfinished" appearance in both species. In pattern and color, the speculum is very much like that of the silver teal, but it lacks a white anterior border. In addition the tertials are slightly iridescent in this species. The tracheal tube of the male has an abrupt enlargement near the bulla and a second smaller enlargement near the anterior end, and the bulla is similar in shape to, though it is smaller than, that of the silver teal. The Hottentot teal is fairly widespread in Africa, and is no doubt sympatric with several other species of *Anas*. The only reported hybrid combination involves the silver teal.

General behavior. Hottentot teal are very much like the silver teal in their extremely quiet manner and vocalizations. I have never observed them dive for food, nor have I observed preflight movements.

Agonistic and sexual behavior: female. Intiting in this species (Fig. 55D) has the same strong chin-lifting component typical of the silver teal and, in a modified form, the blue-winged ducks. The associated call must be quite weak, for I have not been able to hear it. I have likewise never heard a Decrescendo Call in this species, but I

do not doubt that one is present. Preening-behind-the-wing has not been recorded.

Agonistic and sexual behavior: male. As in the silver teal, sexual display is not a conspicuous or social affair, and indeed it is easily overlooked. No Introductory Shake has been observed, and the only obvious display consists of a fairly rapid vertical neck-stretching followed immediately by drinking (Fig. 55E, F). Both sexes perform this display, but only in males have I heard any associated vocalization, which consists of a series of about five extremely soft, wooden-sounding *took* notes, all on the same pitch. The same call is also uttered during an independent neck-stretching, with the crown feathers slightly erected and with slight lateral head-turning. In some instances the call certainly functions as a warning signal, but when linked with drinking it is no doubt a true Burp. This linking of the Burp with drinking is also found in the garganey male. Another garganey-like display consists of Wing-flapping followed immediately by drinking and stretching both wings overhead. Preening-behind-the-wing has not been observed, but it is interesting to note that males Turn-the-back-of-the-head to Inciting females in the usual *Anas* manner, although the more elaborate *Anas* displays are lacking.

Copulatory behavior. No information is available regarding this.

BLUE-WINGED DUCKS

The last major group of species in the genus *Anas* can be collectively termed blue-winged ducks, for a grayish or powder blue upper-wing covert coloration is typical of them all. This is present in both sexes, but is more obvious in males. Presumably this light upper-wing covert pattern evolved independently of the similar pattern in the wigeon group, but in both it probably functions as a species-recognition signal through Preening-behind-the-wing. This is a very frequent display in the garganey, but it is less frequent in the other blue-winged ducks. In all the species of this group Inciting assumes an almost uniform pattern and is characterized by marked chin-lifting alternated with bill-lowering, but with very little lateral bill movement. This Inciting is totally different from the Inciting of the wigeons, in which chin-lifting is repeatedly performed and the vertical head movements are replaced by occasional pointing. Inciting in the blue-winged ducks to some degree resembles precopulatory Head-pumping, and this similarity is further strengthened by the tendency of the

male to respond with similar chin-lifting movements. During Inciting and aggressive chin-lifting, however, the bill is tilted slightly upward, whereas in precopulatory Head-pumping it is held level or is tilted downward somewhat. It is of interest that two displays which have such widely differing connotations can be of such similar appearance that they are almost never recognized as distinct in the literature. In all the species except the garganey a second male display occurs which seems functionally to replace the more typical *Anas* displays such as the Grunt-whistle, the Head-up-tail-up, and the Down-up. This is a Mock-feeding display which resembles typical shoveler-type filter feeding except that it is performed only by males and is usually alternated with other displays (Burping, Turning-the-back-of-the-head, etc.) while the female is Inciting. The social feeding method of swimming in circles and foraging in water agitated by the swimming of the bird ahead is not a sexual display, and it occurs at all times of the year among birds of all ages. Blue-winged ducks often follow behind ducks of other species while feeding in this manner, for which their bills are highly adapted. Diving is rare in all species.

Garganey (*Anas querquedula*)

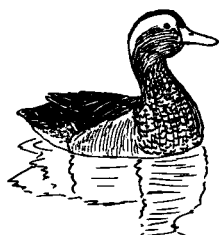
The garganey, as Lorenz (1951–1953) has pointed out, is not an altogether typical blue-winged duck, but, through the spotted teal, it links the pintail group to the more typical blue-winged forms. The downy young have more strongly marked cheeks than do those of the typical blue-winged ducks, but otherwise they have the typical yellow and olive coloration of blue-winged downies. Juveniles and adult females exhibit the cryptic plumage pattern typical of *Anas* females, as do also males in eclipse plumage. In nuptial plumage, males present a mixture of spotted teal and blue-winged duck features. The rump and tail regions are undifferentiated as in the spotted teal. The wing pattern, however, is like that of the blue-winged ducks in that there is a metallic green speculum with a white (but no black) posterior border and a broad white anterior border. The upper-wing coverts are grayish rather than pale blue. The larger scapulars and some of the tertials are greatly elongated and have broad white central stripes that are typical of the blue-winged ducks. As in the spotted teal, the feet are not brightly colored, although colored feet are typical of at least the males of the other blue-winged ducks. The trachea of the male is unique in that it has a large bulla which is very rounded and is

almost symmetrical in development. The garganey occurs over nearly all of Europe and Asia, and is sympatric with numerous species of *Anas*. Wild hybrids have been reported involving the common teal, the common pintail, and the common shoveler, and those with the last-named species are known to be fertile. In captivity the species has also been crossed with the common mallard and with blue-winged and cinnamon teal.

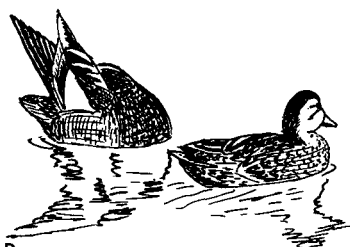
General behavior. I have not observed garganeys to forage socially by feeding at the rear of one another or other ducks, and in structure the bill does not at all resemble the shoveler type. I have also not recorded garganeys diving for food. No preflight movements have been seen by me or McKinney (1953).

Agonistic and sexual behavior: female. Lorenz (1951–1953) has described the behavior of garganeys, and indicated their close affinities with the blue-winged ducks. Inciting has a strongly marked chin-lifting (Fig. 56C) which is alternated with a more distinct lateral pointing movement than occurs in the following species. I have not heard the Decrescendo Call, but Lorenz states that it consists of only two or three notes the last of which are “swallowed.” This type of call, having only a few notes and with the last part sounding as if the bird had suddenly immersed her bill in the water, is apparently typical of the blue-winged ducks. Lorenz also mentions that the females sometimes perform a Laying-the-head-back display similar to that of the males; it thus corresponds to the female Hottentot teal’s Burp-drink movement. Preening-behind-the-wing is frequently performed by females.

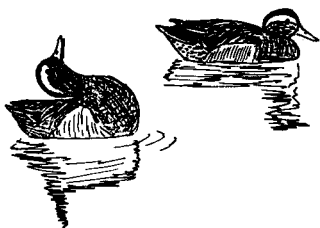
Agonistic and sexual behavior: male. The behavior of the male garganey is generally more like that of the male spotted teal than that of males of the true blue-winged ducks. As in the spotted teal, Burping is the primary display, and in this species it has been elaborated into several forms of varying intensity. In the simplest form it merely consists of uttering the curious wooden rattling call that is unique to this species, with the head only slightly raised, and then following the call with drinking. The next and perhaps more typical form is a rapid upward stretching of the neck with the bill held level as the call is uttered (Fig. 56A); again the display is followed by drinking. This display is practically identical with the Burp-drink display of the Hottentot teal. Finally, the most elaborate form consists of rapidly Laying-the-head-back (Lorenz, 1951–1953), so that the bill assumes



A



D



B



E



C



F

Figure 56. Garganey, Cinnamon Teal

- A. Garganey male, Burp posture.
- B. Laying-the-head-back display of male garganey.
- C. Male garganey (*right*) Leading an Inciting female by Turning-the-back-of-the-head to her.
- D. Male garganey Preening-behind-the-wing to passing female. Note exhibition of speculum pattern.
- E. Cinnamon teal male (*right*) Mock Feeding to female.
- F. Cinnamon teal male (*right*) performing aggressive Chin-lifting to another male.

for a moment a vertical position while the call is uttered, then rapidly bringing the head forward and drinking. As Lorenz has pointed out, this display is clearly an exaggerated form of Burping, and it is certainly not homologous to the head-throw displays of pochards and various sea ducks. Introductory Shaking is neither frequent nor functionally introductory, but Preening-behind-the-wing is perhaps more frequent than in any other dabbling ducks except the wigeons. This is often performed mutually and repeatedly between males and females, and is usually alternated with drinking (Fig. 56D). I have never observed this preening to occur outside the wing, as described by Lorenz. Lorenz has also mentioned that Wing-flapping occurs frequently during social display and is apparently ritualized. This Wing-flapping does not differ markedly from normal wing-flapping, but I agree that in the blue-winged ducks, the Hottentot teal, and perhaps a few other species of *Anas*, wing-flapping is probably ritualized. I have not observed the Turning-the-side-of-the-head described by Lorenz, but certainly Turning-the-back-of-the-head is performed by males in exactly the same way as in the other species of *Anas*, especially when they are Leading Inciting females (Fig. 55C). The white V-mark formed by the eye stripes at the back of the head is especially conspicuous during this display.

Copulatory behavior. I have observed precopulatory mutual Head-pumping. I have no further information on copulatory behavior.

Blue-winged Teal (*Anas discors*)

The least specialized of the true blue-winged ducks is the North American blue-winged teal. As in the remaining species, the downy young have a narrow eye stripe, a small cheek patch, and are yellow to olive in color. Juveniles and adult females have a cryptic brownish body pattern, but their wing coloration is similar to that of the male. Males in nuptial plumage have strongly spotted bodies, slightly iridescent heads, and a blackish rump and tail region which is well differentiated from the rest of the body. The wing pattern is typical, with powder blue upper-wing coverts and a metallic green speculum bordered broadly in front and narrowly behind with white. The larger scapulars are pointed and have buffy central stripes. A distinct eclipse plumage is present. The male has a small, laterally enlarged tracheal bulla. The species is restricted to North America as a breeding bird, but winters as far south as northern and even central South

America. Wild hybrids have been reported with the cinnamon teal and the common shoveler, and both of these crosses have proved fertile in captivity. Other reported hybrids have involved the American wigeon, the chestnut teal, the common mallard, the common pintail, the garganey, and the red shoveler.

General behavior. Blue-winged teal, although they lack shoveler-type bills, are typical blue-winged ducks in every respect. They feed on the surface and up-end for food, although I have not observed the social feeding behavior typical of shovelers. They rarely if ever dive when foraging. Preflight movements include Neck-jerking and lateral Head-shaking (McKinney, 1953).

Agonistic and sexual behavior: female. Inciting is of the typical blue-winged duck type, consisting of chin-lifting while head-pumping, with few if any lateral pointing movements of the bill. The call is a series of one-syllable *rrrr* notes without particular rhythm. The Decrescendo Call is very similar to that of the cinnamon teal. Preening-behind-the-wing has not been recorded.

Agonistic and sexual behavior: male. Male blue-winged teal differ from the other true blue-winged ducks in only one major respect, that of their voice. Instead of the rattling or wooden voices of the other species, the call is an unusually high-pitched and nasal whistle, which can be described as *tseeel*. This call is used, however, in the same context as a Burp, and it is certainly homologous to the Burp of the other blue-winged ducks. Males respond to female Inciting with a similar Chin-lifting movement, which to some extent resembles precopulatory Head-pumping. Such mutual Chin-lifting is very frequent, especially when two mated pairs approach each other. The major sexual display is, however, less conspicuous and differs from that of all the preceding species of *Anas* except the African black duck, in which a similar display is present. This display is the ritualized dabbling that I have called Mock-feeding. It differs from normal feeding in that although the male is treading water fairly vigorously, he tends to remain almost stationary near the female. It is often preceded by calling or Turning-the-back-of-the-head, and may be terminated by up-ending. No special color patterns seem to be exhibited during the display, although the folded wings are sometimes slightly lifted to reveal the speculum. During the up-ending, the black tail coverts and colorful legs of the male are also visible and may play a role in this display; the tail coverts and legs are exhibited

in a similar fashion in all the remaining species of blue-winged ducks. Males also frequently Turn-the-back-of-the-head toward Inciting females, but Preening-behind-the-wing has been recorded only a few times by McKinney (pers. comm.).

Copulatory behavior. Precopulatory behavior consists of the usual mutual Head-pumping, with the bill held level or slightly downward. After treading, the male utters a loud *tseel* and remains motionless for several seconds, parallel to or Facing the female, with his neck extended and his bill tilted slightly downward. After one copulation the male called and then swam away while Turning-the-back-of-the-head toward the bathing female.

Cinnamon Teal (*Anas cyanoptera*)

The cinnamon teal of North and South America is in several ways intermediate between the blue-winged teal and the shovelers. The downy young plumage is almost identical with that of downy blue-winged teal, and the juvenile and female plumages also resemble those of blue-winged teal. The adult male in nuptial plumage, however, has a cinnamon red and sometimes partially spotted coloration that is much like that of the red shoveler. In addition, the bill is, like that of the shovelers, slightly enlarged, and there is a sexual dimorphism in iris coloration—a dimorphism typical of the shovelers but not of the blue-winged teal. The wing pattern is exactly like that of the blue-winged teal, having the same type of elongated and buff-centered scapular feathers. The male has an eclipse plumage which closely resembles the female plumage. The trachea of the male has a larger and slightly differently shaped bulla from that found in the blue-winged teal (Phillips, 1923). The species is sympatric with several close relatives throughout its range, and four subspecies are currently recognized. Wild hybrids have occurred with the blue-winged teal, the common shoveler, and the common mallard, of which those with the first two species are known to be fertile. In captivity the cinnamon teal has also hybridized with the red shoveler, the garganey, the Baikal teal, and the South American teal.

General behavior. What has been said for the blue-winged teal applies to the cinnamon teal, except that in this species social feeding definitely occurs, as we would expect from the rather shovelerlike bill structure. As is also true of the shovelers, only lateral Head-shaking

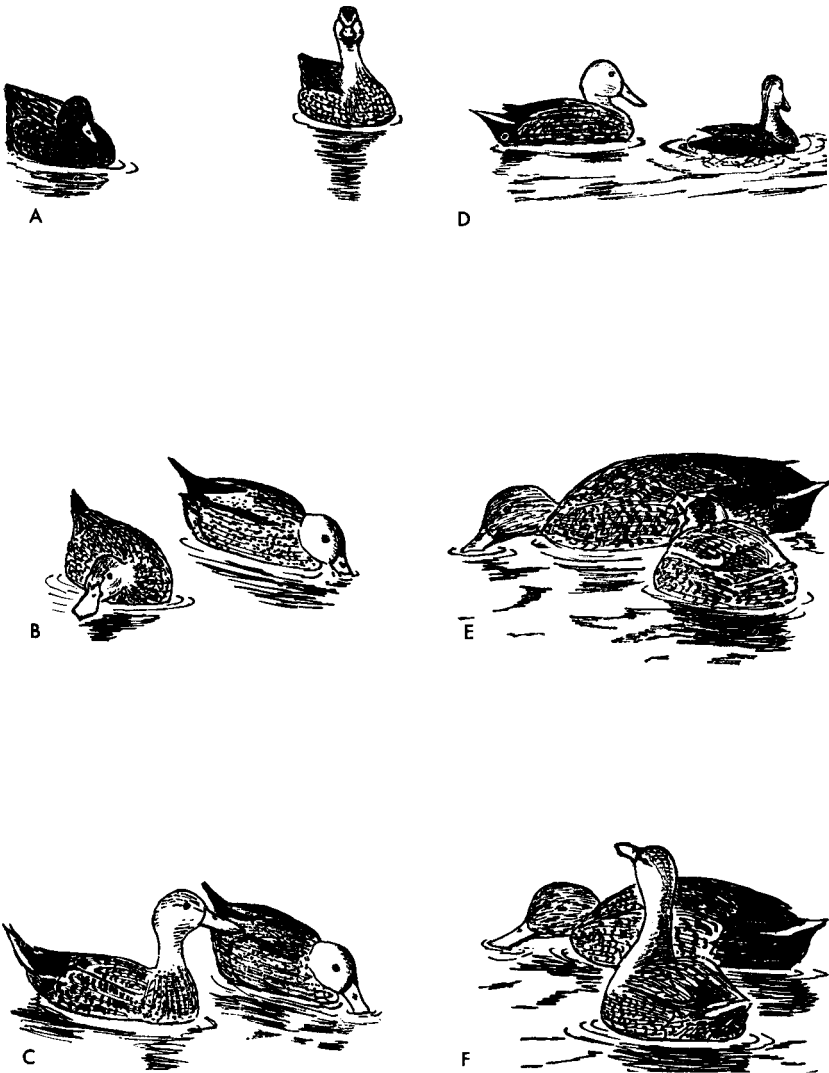


Figure 57. Cinnamon Teal, Red Shoveler, Cape Shoveler

- A. Female cinnamon teal (*right*) Inciting her mate (*left*) against another bird (*off picture to right*). Compare with C below.
- B, C. Inciting by female red shoveler while mate Mock Feeds. Note strong neck-stretching and slight lateral orientation toward object of Inciting (*off picture to left*).
- D. Postcopulatory display in red shoveler. Female watching while male calls (Burping) in motionless posture.
- E, F. Cape shoveler male Mock Feeding while female Incites. Compare with B and C.

has been observed as a preflight movement (McKinney, 1953). The usual Neck-jerking appears to be very reduced in these species.

Agonistic and sexual behavior: female. Inciting is of the typical shoveler type, and consists of alternated chin-lifting and head lowering, with little or no lateral pointing (Fig. 57A). The call is a rattling *rrrrr*, uttered as the bill moves upward. The Decrescendo Call is rarely heard. It consists of three to four notes, and is a weak *gack-gack-ga-ga* much like that of female shovelers, with the last one or two notes often cut off, or "swallowed." Preening-behind-the-wing has not been observed.

Agonistic and sexual behavior: male. The male cinnamon teal is shovelerlike in every way. The Introductory Shake is practically absent, and repeated Chin-lifting (Fig. 56F) is the male response to female Inciting or to any disturbance. This is accompanied by a rattling *chuk-chuk-chuk* reminiscent of male shovelers. When performed near a female, this chin-lifting is often alternated with Mock-feeding, which is performed in the same manner as by shovelers. Like male shovelers, the cinnamon teal male characteristically treads water (Fig. 56E), without really moving much, and often ends the display by up-ending. When courting an Inciting female, males frequently Turn-the-back-of-the-head and swim ahead of the Inciting bird. I have observed neither Preening-behind-the-wing nor the short display flights typical of shovelers, but both of these patterns very probably do occur.

Copulatory behavior. I have observed only mutual precopulatory Head-pumping.

Red Shoveler (*Anas platalea*)

Although a typical shoveler, the South American red shoveler is also not distantly related to the cinnamon teal. The downy young are much like the others of the group, and juveniles and females are somewhat grayish and resemble female Cape shovelers. Males have a distinctly reddish body which is spotted with dark brown. The tails of both sexes are surprisingly elongated and whitish, and in males the tail contrasts with black coverts. The wing and speculum pattern is typical of the group. The scapulars are long and pointed and most of them have a central white stripe. The tracheal bulla of the male is said to be small and faintly bilobed (Phillips, 1923). Like the

Cape shoveler but unlike males of the other blue-winged ducks, the male of this species lacks an eclipse plumage. The species ranges over much of southern South America, and is sympatric with cinnamon teal, as well as with various other species of *Anas*. In captivity it has been hybridized with that species and also with the common shoveler and the Cape shoveler.

General behavior. Like the other shovelers, red shovelers feed primarily by filtering material from the surface or by up-ending. They rarely if ever dive for food. The bill of this species is more shoveler-like in shape than is that of the cinnamon teal, but it is less specialized than the bill of the common shoveler, which indicates that there are many different kinds of shoveler-type bill, and that generic separation on the basis of bill specialization is impossible as well as without justification. Head-shaking is the only preflight movement which has been noted (McKinney, 1953).

Agonistic and sexual behavior: female. Inciting is marked by the usual extreme neck-stretching and chin-lifting of the blue-winged ducks (Fig. 57B, C). The associated call is a *rrrrr* note uttered as the neck is stretched. I have not heard the Decrescendo Call of this species, but it is no doubt much the same as in the other blue-winged ducks. Preening-behind-the-wing has been observed only rarely.

Agonistic and sexual behavior: male. The voice of the male red shoveler is a very characteristic hollow sound, similar to that produced by striking wood with wood, and the most frequent call is a four-note *took-a-took-a-tuk-tuk*. This call is often used as a warning, but more often it serves as an introduction to the Mock-feeding display (Fig. 57B, C). Up-ending is the usual termination of Mock-feeding. Preening-behind-the-wing has been observed a few times, but more frequently the male nibbles behind the wing for several seconds, which may or may not be a real display. Turning-the-back-of-the-head has not been noted, but undoubtedly it is also present. I have not observed males attempt to perform a display flight, but it is probable that this also could be observed with full-winged birds.

Copulatory behavior. Precopulatory behavior consists of the usual mutual Head-pumping, with the bill tilting slightly below the horizontal plane. After treading, the male utters his usual call with a vertically extended neck, then turns and Faces the female as she bathes (Fig. 57D).

Cape Shoveler (*Anas smithi*)

The Cape shoveler falls, both taxonomically and geographically, between the red shoveler and the Australasian shoveler. The downy young have the usual yellow and olive coloration, and juveniles and adult females resemble those of red and Australasian shovelers. Adult males do not have the spotted body markings of red shovelers; they tend, rather, to have the U-shaped flank markings of the Australasian shoveler. The tail is relatively shorter than that of the red shoveler. The wing pattern is like that of the other shovelers, but the scapular feathers lack the light shaft-stripe typical of all the other blue-winged ducks. These feathers and the tertials are, however, of a metallic dark blue coloration. The male tracheal bulla is much like that of the common shoveler, but larger (J. V. Beer, pers. comm.). The species is restricted to southern Africa, where it is sympatric with a few other species of *Anas*. The only hybrid combination reported is with the cinnamon teal.

General behavior. Cape shovelers are like the other species in this group in their foraging and diving behavior. McKinney (1953) records only lateral Head-shaking as a preflight movement.

Agonistic and sexual behavior: female. Inciting takes the usual form in this species and involves the neck-stretching and chin-lifting characteristic of the group (Fig. 57E, F). The Decrescendo Call consists of four to five notes and, as it typically is in the blue-winged ducks, is curiously cut off at the end. Preening-behind-the-wing has not been observed.

Agonistic and sexual behavior: male. The male voice in this species does not have such a wooden quality as that of the red shoveler; it is rather more like a snort or belch. This call is frequently uttered and functions as a warning note as well as a Burp. As in the other shovelers, the neck is somewhat extended during the Burp (Fig. 58A), and the call may be uttered either with the head held motionless or during the repeated Chin-lifting that is so frequent in the shoveler group. Mock-feeding is more conspicuous in this species than in any of the other blue-winged ducks. It is characterized by a marked treading of water and spreading of the flank feathers (Figs. 57E, F; 58B), and it is often accompanied by the belchlike calls. Very often this display is terminated by up-ending, or "tipping-up" (Fig. 58B). When

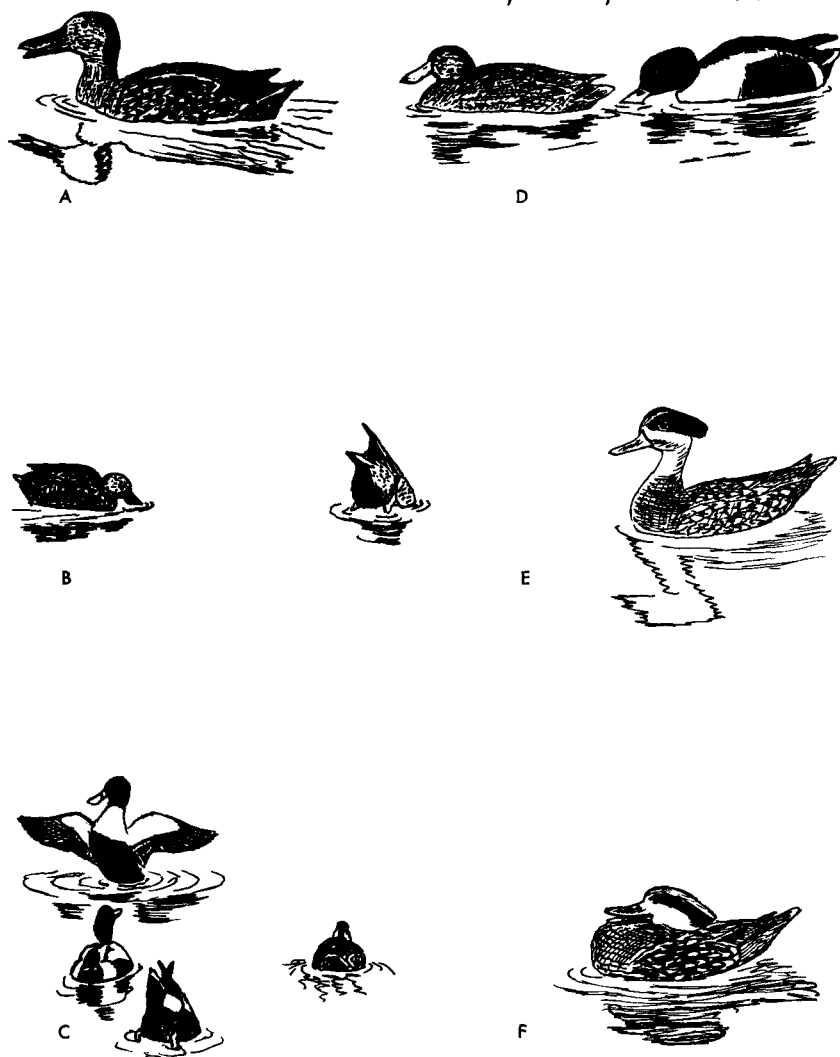


Figure 58. Cape Shoveler, Common Shoveler, Marbled Teal

A. Male cape shoveler in Burp posture.

B. Mock Feeding (left) and Tipping-up (right) by male cape shovellers.

C. Tipping-up (center foreground) and Wing-flapping (rear) by male common shovellers during courtship. Both actions appear to be ritualized in this species.

D. Social feeding by common shovellers. Note position of male relative to female, which is unlike that usually assumed during Mock Feeding (see Fig. 57).

E, F. Male marbled teal performing Neck-stretching, Head-jerking display sequence.

a male happens to fall 20 or 30 feet behind a courting group, or when he notices an unmated female some distance away, he often performs what is clearly a display flight. The head is held level and the neck outstretched as the bird Burps repeatedly; then he takes off and immediately lands near the female, where he begins to Mock-feed or Turns-the-back-of-the-head toward her. Lebreton (1958a) has observed what he calls Jump-flights in numerous species of *Anas*. These display flights appear to have the function of placing the male in a more favorable position relative to the female (usually in front of her, where he can Turn-the-back-of-the-head to her), but only in the shoveler group are these flights conspicuously ritualized, as indicated by the calling beforehand and the noisy rattling of wings during the flight. Preening-behind-the-wing has not been observed in this species, but males frequently Lead Inciting females by Turning-the-back-of-the-head toward them.

Copulatory behavior. Mutual Head-pumping is the precopulatory behavior of this species. In one complete copulation which I observed, the male Burped once, then swam away from the female while Turning-the-back-of-the-head toward her.

Australasian Shoveler (*Anas rhynchos*)

The Australian and New Zealand races of this shoveler are close to the common shoveler in appearance. The downy young, juveniles, and adult females all have plumage very similar to the corresponding plumages of the common shoveler. The male in nuptial plumage differs from the common shoveler only in the brightness and clarity of the patterning, and greatly resembles the male common shoveler in partial eclipse plumage. The white cheek crescent is certainly of no great taxonomic importance, nor does it indicate any affinities with the blue-winged teal; it represents only the reappearance of an ancestral blue-winged duck characteristic which is often found in common shovelers. It is also present in a male hybrid of the common shoveler and the red shoveler at the Wildfowl Trust. The wing pattern is exactly like that of the other shoveler species, and the scapulars and some tertials have white central stripes as in the common shoveler. There is a definite eclipse plumage in males. The male tracheal bulla is more distinctly left-sided than in the other three shovelers (J. V. Beer, pers. comm.). The species ranges over New Zealand and much of Australia, and is sympatric with several other

species of *Anas*. Wild hybrids have been reported with the gray teal and the Australian black duck.

General behavior. The New Zealand shovelers at the Wildfowl Trust are exactly like common shovelers in every respect. Preflight movements have not been recorded.

Agonistic and sexual behavior: female. The Inciting movements and calls of this species do not differ from those of the common shoveler. I have not heard the Decrescendo Call, nor have I seen Preening-behind-the-wing in these birds, which were wild-caught and quite shy.

Agonistic and sexual behavior: male. From the few times I have heard calling in this species, I would judge the voice to be slightly different from that of the common shoveler, and describe the call as *chuck-chuck-chuck*. Delacour (1956) states that it is lower and more whistling than that of the common shoveler. In other respects the behavior of this species appears to be no different from that of the other shovelers, although my observations are still very incomplete.

Copulatory behavior. This has not been described, although I have observed precopulatory Head-pumping.

Common Shoveler (*Anas clypeata*)

The most widespread of all the shovelers is the holarctic common shoveler, and this species also has the most markedly shovel-like bill. The downy, juvenile, and female plumages are all very much like those of the other shovelers. The male in nuptial plumage is the most brightly colored of the shovelers, a characteristic connected with its very broad geographic range. Aside from its slightly more contrasting plumage, it is in almost every respect like the Australasian species. The wing-speculum pattern is as in the other shovelers, but the longer scapulars and tertials are almost entirely white, with only very narrow dark margins. There is a distinct eclipse plumage in males. The male trachea has a very small bulla which is not strongly asymmetrical (see Johnsgard, 1916c). The common shoveler is sympatric with many species of *Anas*, and wild hybrids have been reported with the gadwall, the common teal, the common mallard, the common pintail, the blue-winged teal, the garganey, and the cinnamon teal. Hybrids with the last two species have proved fertile in captivity.

General behavior. Social feeding is extremely common in common shovelers (Fig. 58D) and is often done while following birds of other

species. Up-ending is also common, but diving is very infrequent if done at all. McKinney (1953) observed lateral Head-shaking as a preflight movement, but I have observed only very slight Neck-jerking in this species.

Agonistic and sexual behavior: female. Lorenz (1951–1953) has discussed this species and mentioned that the Inciting movements are like those characteristic of the blue-winged ducks. The Decrescendo Call is slightly descending, and might be written *gack'-gack-gack-ga-ga*, with the last note or two muffled as usual. Preening-behind-the-wing has not been observed.

Agonistic and sexual behavior: male. The call of the male common shoveler consists of repeated *took'a* notes which are not so wooden-sounding as those of the red shoveler. As in the other shovelers, the Introductory Shake is of minor importance, although Wing-flapping (Fig. 58C) has evidently been ritualized into a sexual display. The Burp call is frequently uttered and is often followed by Mock-feeding. Tipping-up, or up-ending, is a frequent termination of Mock-feeding (Fig. 58C), and it also occurs in another situation which indicates its display nature. This is after the male's display flight, in which the bird first calls several times, then takes off with a noisy rattle of wings and flies low and directly toward a female. The male lands near the female and often tips up immediately. The rattling of the wings which is so typical of this species is of uncertain origin, since the primary feathers exhibit no obvious specializations for sound production. Preening-behind-the-wing has rarely been observed (McKinney), but males very often Turn-the-back-of-the-head to females, especially to those that are Inciting.

Copulatory behavior. I have not observed a complete copulation, but Lorenz (1951–1953) states that vigorous Head-pumping precedes treading and that afterward the male utters a single Burp call, then swims restlessly about, and finally Turns-the-back-of-the-head toward the female.

ABERRANT DABBING DUCKS

Pink-eared Duck (*Malacorhynchus hymenolaimus*)

This Australian shovelerlike duck is adapted to feeding on minute aquatic algae, and as a result the bill is much more specialized for filter-feeding than is that of the typical shovelers. Ignoring the bill

structure, the bird is still fairly distinctive and of uncertain relationships to the true dabbling ducks. The downy young are dark above and white below, and have broad "masks" around the eyes. Unlike downy shovelers, which have normal bills, the bill structure is specialized from the time of hatching. Juveniles resemble the adults, but lack the curious pink ear-patch. As adults, the sexes are identical in plumage pattern, which is an unusual barred dark gray and white pattern slightly reminiscent of the marbled teal. There is no metallic speculum on the secondaries, nor is there any metallic coloration elsewhere on the body. The tracheal structure of the male is apparently undescribed, but H. Frith informs me (pers. comm.) that it is *Anas*-like and very similar to that of the gray teal. No hybrids involving this species are known.

General behavior. Pink-eared ducks filter-feed in the same manner as do shovelers, but their bills have longer and more numerous lamellae, and the overhanging flaps of the maxilla are also particularly long, which results in an ability to remove algae and other plankton from the water with great efficiency. There can be little doubt that this type of bill evolved independently of the shoveler type, although the basic structure of the two types is similar. Foraging behavior in the two species likewise demonstrates an interesting example of convergent behavioral evolution. In common with shovelers, pink-eared ducks exhibit communal foraging behavior. Unlike the shovelers, however, who forage by the head-to-tail method, pink-ears tend to forage in pairs, rotating about in tight circles with bodies almost parallel and heads turned in the direction of rotation, so that each bird filter-feeds in the immediate wake of the other. Occasionally a bird will attempt to forage in its own wake in this same manner, and rarely three or more birds will attempt it jointly. Clearly, however, the method is most efficient when performed by only two birds, and thus large flocks will often break up into apparent pairs when foraging in this way. I have observed that before taking flight the birds often perform lateral Head-shaking.

Agonistic and sexual behavior. In spite of the abundance of this species in Australia, relatively little has been written of its behavior, and the notes by Warham (1958) and Frith (in Delacour, 1956) represent much of what is currently available. I observed large numbers of this species in Australia, and the details of these observations are published elsewhere (Johnsgard, 1965a), so that only a short

summary of them will be included here. Owing to the extreme similarity of the sexes, I have not always been able to distinguish males from females, and so the two sexes will be discussed jointly. Both sexes appear to have an aggressive Bill-tilting display, very similar in form to the Chin-lifting of the blue-winged ducks and spotted teal. This is accompanied by neck-stretching and a series of whistle-like rising *we-we-we-we-we-whew'* notes, and is often followed by overt attack. Although no obvious Inciting displays were observed, it is quite possible that Inciting by females takes this form or a very similar one. Two probable male pair-forming displays observed by me included an erect, stiff-neck posture closely resembling the Facing display of various dabbling and perching ducks, and often if not generally oriented toward a female. The same posture was also frequently assumed after a bill-tossing call. In this display the presumed male would toss his bill upward and quickly lower it again while the neck was held vertically, and a curious hoarse and catlike *who-éé-oo* note was uttered. The call and bill movements were often repeated several times in succession, and although it normally appeared to be directed toward a specific bird, at other times it was evidently uttered at random. Three copulations have recently been seen by V. T. and Thomas Lowe (in litt.), all of which lacked distinct precopulatory displays. Postcopulatory behavior consisted of a series of vigorous movements by both birds similar to those made in bathing and foraging.

Marbled Teal (*Marmaronetta angustirostris*)

As I have indicated elsewhere (Johnsgard, 1961c), I believe that the marbled teal is not a typical dabbling duck and that it is perhaps more closely related to the pochard group than to the dabbling ducks, or at least forms a definite link with that group. The downy young are pale in color, and although they possess a dark eye-stripe, they are rather intermediate between the downy young of a typical dabbling duck and those of the red-crested pochard. Juveniles resemble adults, and at all ages the sexes are nearly identical in plumage. Adult males exhibit a slightly longer and darker eye-stripe and crest, and the bill of the male has a light subterminal band which is lacking in the female. The body plumage of both sexes is remarkable in that it consists of buffy spots on a dark background, rather than the usual dark

markings surrounded by lighter edges. There is a superficial resemblance of marbled teal to crested ducks in the body plumage, but the marbled teal does not exhibit the slightest tendency toward a differentiation of the secondary feathers into a speculum. Delacour (1956) includes the marbled teal in the spotted teal group and suggests that it may be closely related to the Cape teal, but in fact these two species could scarcely be more different, as a close comparison of their plumage features will show. The trachea of the male marbled teal is unique (see Johnsgard, 1961e), and the bulla is unlike that of any other dabbling duck in that several membranaceous fenestrae of varying sizes are present. This is typical of the pochard group, as is also the gradually varying diameter of the tracheal tube of the marbled teal. The shape of the bulla is, however, much like that of *Anas*. The marbled teal has an unusual distribution around the Mediterranean and in the Near East. It has not, to my knowledge, hybridized with any species of *Anas*, and the only hybrid known involves a common white-eye. Although other species of dabbling ducks have frequently hybridized with pochards, such species have also hybridized with other dabbling ducks.

General behavior. Marbled teal are very quiet birds, and although they dive well, they open their wings when so doing, in the usual dabbling duck manner. The only preflight movements McKinney (1953) and I have seen are pochardlike Chin-lifting movements which are not, to my knowledge, found in any species of *Anas*.

Agonistic and sexual behavior: female. Female marbled teal deviate from *Anas* females both in voice and behavior. As Jones (1951) has pointed out, they lack a Decrescendo Call completely, and their voice is very weak. Inciting takes a very curious form in this species. It consists of the female making direct threatening rushes toward another bird, then rapidly turning and swimming back to her mate or potential mate in an unusual nodding manner. There appears to be no vocalization associated with Inciting, and if there is one it is very faint. The only call I have heard from females is that uttered when they perform the movement corresponding to the major male display. This involves rapidly drawing the head back to the shoulders and uttering a squeaky note. Females also occasionally stretch the neck and head out low over the water, again in the same manner as males, usually directing the display toward a male. Preening-behind-the-wing has not been observed.

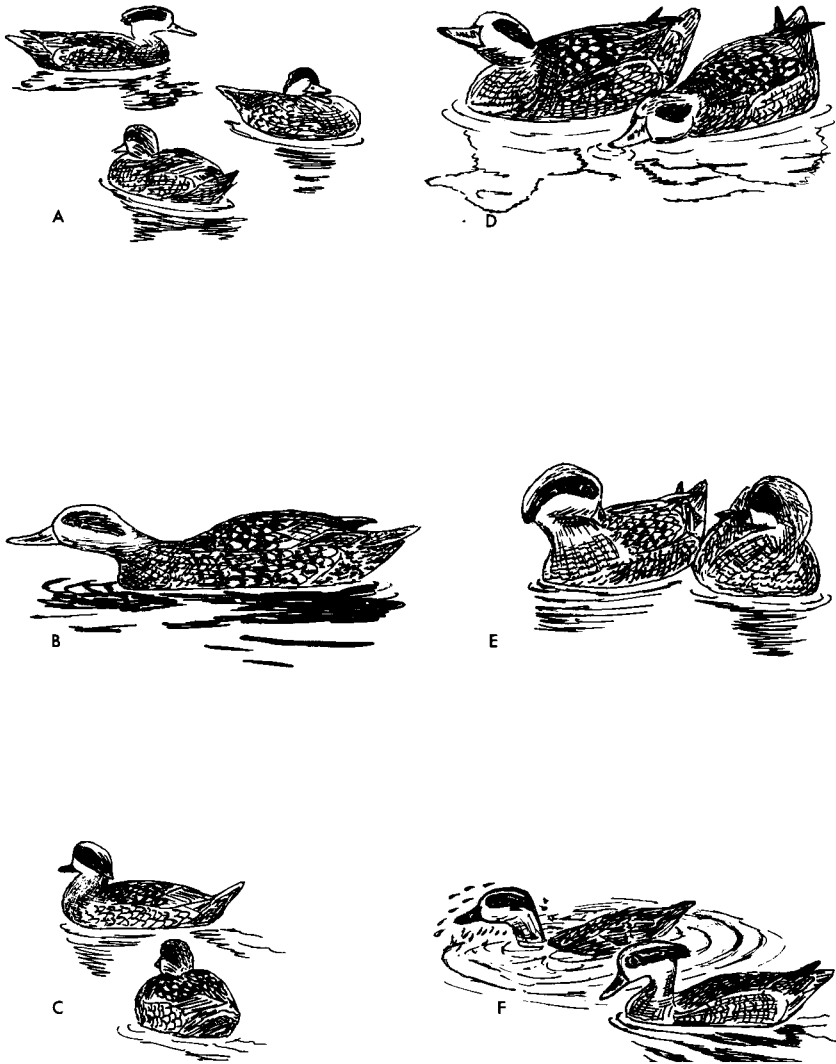


Figure 59. Marbled Teal

- A. Crest-raising (rear) and Head-jerking (right) by male marbled teal (female in center foreground).
- B. Male marbled teal performing display very similar to the Sneak of pochards. Compare Fig. 62B.
- C. Male marbled teal Turning-the-back-of-the-head to female.
- D, E. Precopulatory Drinking and Preening-dorsally by marbled teal (female on right).
- F. Postcopulatory display of marbled teal. Female (right) bathing as male swims in Bill-down posture. Compare with Fig. 60F.

Agonistic and sexual behavior: male. Males differ from *Anas* males in their courtship displays, which are most unusual. Jones (1951) has described the major display, which consists in its complete form of a sudden stretching of the neck (Fig. 58E), a pause, and then an equally sudden jerking of the head back and down to the shoulders (Figs. 58F, 59A). The male's crest is erected during this display, and sometimes the neck-stretching phase is not followed by the jerking back. The call is uttered only if the second phase of the display is performed, and it is a weak, nasal *eeeeep*, emitted as the head touches the back. Strangely, the Introductory Shake sometimes follows this display, but it is never used as an introductory movement. As in many species of *Anas*, males try to assume a position parallel to the courted female when about to display. A second frequent posture is one very similar to the Sneak of the Aythyini (Fig. 59B), which males direct to other males and also to females. This is apparently a silent display. Preening-behind-the-wing has not been observed, but males Turn-the-back-of-the-head to Inciting females in the usual manner of both dabbling ducks and pochards (Fig. 59C).

Copulatory behavior. In its copulatory behavior the marbled teal is totally unlike the typical dabbling ducks and is much closer to the pochards. The precopulatory behavior lacks any indication of Head-pumping, and consists instead of mutual Bill-dipping, Drinking, and Preening-dorsally, usually performed synchronously by both birds (Fig. 59E, F). The female finally assumes a prone posture and is immediately mounted by the male. After treading, the male calls once with his neck extended, then swims away from the female with his bill tilted downward (Fig. 59F) in a posture almost certainly homologous to the Bill-down postcopulatory posture of male pochards.

TRIBE AYTHYINI (POCHARDS)

The dabbling ducks grade almost imperceptibly into the pochard group considered here, and whether *Marmaronetta* and *Rhodonessa* should be included in one tribe or the other may be open to some question. As here constituted, the tribe includes 16 species of almost world-wide distribution which differ from the preceding group in several minor details. The hind toe has a larger lobe than occurs in the dabbling ducks, and it presumably aids in diving. The feet are also correspondingly larger and are set farther apart and more to the rear than in *Anas*. One of the most clear-cut differences is in the