January 1965

Handbook of Waterfowl Behavior

Paul A. Johnsgard
University of Nebraska-Lincoln, pajohnsgard@gmail.com

Handbook of Waterfowl Behavior

Long-tailed Duck, male, Rear-end display. (Courtesy J. V. Beer)

HANDBOOK *of* WATERFOWL BEHAVIOR

By Paul A. Johnsgard

UNIVERSITY OF NEBRASKA

Electronic edition
University of Nebraska–Lincoln Libraries
2008

First published 1965 by Comstock Publishing Associates, a division of

Cornell University Press.

To my parents, who inculcated in me the value and pleasures of studying nature

Acknowledgments

IT would be impossible to acknowledge the assistance of everyone who has helped me in various ways, but I am particularly grateful to the National Science Foundation and the Public Health Service for financing these studies, and to the Wildfowl Trust not only for providing the opportunity to study so many species but also for much kindness and help. Had it not been for the almost singlehanded effort of Mr. Peter Scott in organizing and directing this superb collection of birds, it would have required a lifetime of effort, unlimited funds, and constant traveling to obtain the observations I was able to make in a relatively short time. Furthermore, his experiences and his keen observations on many species not represented in the collection were of special value and help to me. Other persons who have provided observations, or with whom I have discussed various problems, include Hugh Boyd, Sven-Axel Bengtson, K. M. Davy, Jean Delacour, Helen Hays, K. Z. Lorenz, V. T. Lowe, D. F. McKinney, Martin Moynihan, M. T. Myres, R. I. Smith, N. G. Smith, W. von de Wall, and Vincent Weir. For assistance of various kinds I owe my most sincere thanks to Drs. C. G. Sibley, W. C. Dilger, H. A. Hochbaum, J. F. Cassel, J. E. Harris, G. V. T. Matthews, G. A. Swanson, and D. A. West. Mrs. Molly Burns typed the completed manuscript, under a grant I received from the University of Nebraska Research Council. Finally, I must not forget to thank my most tolerant wife, Lois, who has unquestioningly allowed me to wander about the Americas, Europe, and Australia in my constant and, I'm afraid, sometimes blind passion for studying waterfowl.

I should state that the objective of the present report is merely to provide the barest minimum of information on each species that will allow other persons to compare their observations and to develop more detailed and quantitative studies. Many of my conclusions are tentative ones, based on limited observations, and no doubt several of my observations and conclusions may prove erroneous in the light of further studies. No one is more aware of the limitations of this report than its author, and I can only hope that in the end its credits will be found to outweigh its debits. For whatever credits are due I thank the persons mentioned above; the debits are my own responsibility.

PAUL A. JOHNSGARD

Lincoln, Nebraska
April 1965

Contents

Illustrations

PLATES

FIGURES

Handbook of Waterfowl Behavior

Introduction

BACKGROUND AND OBJECTIVES OF THIS STUDY

Of the major avian families, the ducks, geese, and swans of the family Anatidae are among the most intensively studied and perhaps hold the greatest fascination for man. They are of great importance for their esthetic, sporting, and economic value, and the technical literature concerning them is remarkably extensive (see Phillips, 1922–1926, and Kuroda, 1942). Many systematists have given their attention to the Anatidae, using such varied approaches as anatomy, plumage pattern analyses, serology, chromosomal analyses, and general behavior. Perhaps the most successful of these proposed taxonomic systems was that of Delacour and Mayr (1945), who utilized as many sources of evidence as were then available in their now classic revision of the family. Delacour (1954–1964) has since made some additions and corrections to this arrangement, and von Boetticher (1952) has also proposed a classification based largely on the work of Delacour and Mayr. Two osteological studies, those of Verheyen (1955) and Woolfenden (1961), have recently added much to our knowledge of the anatomy of the Anatidae. The latter study has been a particularly valuable contribution.

Following the remarkably thorough and exceedingly significant behavioral studies of Heinroth (1911), whose observations were strengthened by a firm knowledge of evolutionary principles and a lifetime of intimate study of waterfowl in captivity, many behavioral studies on various species were made. Of these, none are more sig-

nificant than those of Lorenz (1941; 1951–1953), who intensively studied a number of surface-feeding ducks and by determining and comparing homologous behavior patterns in these species, was able to establish the probable evolutionary relationships existing within the group. More than anything else, Lorenz's fascinating studies stimulated a widespread interest—manifested by the appearance of many recent papers—in waterfowl behavior. Thus McKinney (1953) investigated the family to determine whether comfort movements had the same taxonomic significance as Lorenz found sexual behavior to have. Although he found that they did not have this significance, his descriptions of comfort movements provide a valuable inventory of the behavioral raw materials utilized in the evolution of actual displays. Except for the present work, McKinney's study represents the only attempt to investigate the entire family from a behavioral standpoint, although numerous studies have been done on various smaller groups. Myres (1959a), for example, studied the so-called sea ducks, which Delacour and Mayr (1945) originally placed in a single tribe Mergini, the homogeneity of which had been questioned on anatomical grounds (Humphrey, 1955). Lorenz's student Wolfgang von de Wall (1963) has expanded Lorenz's studies on the surface-feeding ducks, and has attempted to determine the genetic basis for some of the display patterns.

The present study was undertaken to test and evaluate the various taxonomic arrangements of the family, to discover some of the trends of behavioral evolution, and to provide a basis for future workers to use in naming, describing, and evaluating the behavioral patterns observed in waterfowl. Most of the information presented here was obtained during twenty months at the Wildfowl Trust in Gloucestershire, England, under the sponsorship of National Science Foundation and Public Health Service postdoctoral fellowships. Additional observations were obtained during a NSF research grant (GB 1030) while the author was on the staff of the Department of Zoology and Physiology at the University of Nebraska. The Wildfowl Trust comprises—in terms both of species and of individuals—the largest collection of living waterfowl ever brought together at one place in the world. Since 1959 I have been able to study 133 of the 142 extant species of Anatidae, and 40 of the 43 genera accepted by me. For the relatively few species I have been unable to see, I have attempted to extract pertinent information from the literature and from persons

who have had firsthand experience with them. For the purpose of description and analysis, 16-mm. motion pictures were made of as many of the behavior patterns as possible, and approximately 7,000 feet of film was utilized in writing the following accounts. All drawings are based on direct photographic enlargements of individual 16-mm. frames or, as in a few cases, 35-mm. photographs.

VALUE AND LIMITATIONS OF BEHAVIOR AS A TAXONOMIC TOOL

Before proceeding, some comments on the functions and importance of various kinds of behavior are necessary for an intelligent evaluation of behavior as a taxonomic criterion. To be useful in assessing relationships, a behavioral characteristic must be species-constant and distinctive, and yet recognizably related to the corresponding (homologous) characteristic in other species. Some characteristics, although species-constant, are consistently alike in many or all of the species in the family. Such characteristics as stretching, bathing, preening, and shaking are of almost no value in determining species relationships. Other relatively species-constant characteristics —male plumage patterns, body proportions, feeding behavior, and so forth—are so highly adaptive and subject to change with conditions of environment or with the presence of other species, that it is exceedingly dangerous to use them when trying to determine relationships.

Of all the activities of any species, none is more significant to that species' survival than successful reproduction. Because of the overriding importance of reproduction, natural selection is particularly strong and effective in maintaining the greatest possible reproductive efficiency. As a result, much of the behavior associated with reproduction is "innate," and any individual whose genetic potentialities deviate from the most effective genotype under the existing conditions is less likely to be effective in producing offspring. Along with this selective pressure toward intraspecific stability and constancy in reproductive behavior, there is another pressure toward species distinctiveness. That is, if a species is to be successful it must not only be able to perpetuate itself but must also avoid disadvantageous hybridization with related species. Of course hybridization is most likely to occur if reproductive behavior (and its genetic basis) is nearly identical in two species, and in such situations those individ-

uals having the greatest genetic capacity for obtaining mates of the same species will be favored by natural selection. As a result, divergences in the sexual behavior of different species are to be expected, especially in behavior related to mate selection. Since all available evidence indicates that with most ducks (some shelducks appear to be exceptions) it is the female which "selects" the mate, it is understandable that male "courtship" patterns are more likely to be affected by this pressure toward divergence. On the other hand, there is normally no strong pressure for the divergence of female behavior patterns; thus these patterns are more constant, or "conservative," and may vary little from one species to another. Likewise, sexual behavior patterns which usually occur after mates have been selected, or which are important in forming and maintaining the pair bond (such as copulatory patterns), tend to be more conservative than prepair formation patterns.

We see, therefore, that different aspects of sexual behavior have different degrees of biologic and taxonomic importance, depending on whether they function mainly as species-specific isolating mechanisms (male courtship displays), as pair-maintaining mechanisms (many mutual displays), or are directly related to reproduction per se (behavior associated with copulation). The least conservative patterns, the male courtship displays, are, when proper care and consideration of sympatry are taken into account, useful in determining relationships between very closely related species, but they are practically worthless and may even be misleading at any higher level. Female courtship displays and many mutual displays are generally useful in determining generic relationships within a tribe or subfamily, but are usually of little help in determining affinities within a genus. Copulatory behavior, and especially precopulatory behavior, is in some respects the most conservative of all sexual behavior; hence it is often helpful in assessing tribal relationships. Another very conservative kind of sexual behavior is that related to the actual mechanism of pair formation (as opposed to mate selection). This process is apparently of such fundamental importance that it is relatively immune to selection pressures for divergence; once a potential mate is "chosen," the ensuing patterns which bring about the establishment of a pair bond seem to be relatively uniform throughout the major groups of waterfowl. A few patterns of sexual behavior appear to have little or no taxonomic significance. Among these may be in-

cluded flights associated with the defense of the female or of territory and those involved with the attempted rape of females. Actual aerial courtship possibly occurs in several species, but this has not been adequately investigated and is so often confused with the other kinds of aerial chase mentioned above that speculation on its evolutionary and taxonomic significance would be totally premature. Recent summaries of studies concerning aerial chases are those of Dzubin (1957), Wüst (1960), and Lebret (1961).

A few words should be said about the value and the dangers of using captive and usually pinioned birds when doing comparative studies of the present type. Although there is always the possibility that the behavior patterns seen in captive specimens are not typical of those of birds in the wild, this appears to be a very minor danger and is overwhelmingly countered by the advantages of convenient, extended periods of study at very close quarters, which enable one to observe minor differences of posture, feather position, and faint calls. Such differences might well be completely overlooked when watching wild birds. In addition, since most of the species under observation were in sufficiently good health to breed every year, there is little reason to believe that captivity had in any way caused a deterioration of behavior patterns. Finally, many of the species have been studied in the wild as well as in captivity by this writer and others, and in no case has it been noted that the sexual behavior of wild and captive waterfowl differs significantly. It therefore seems safe to assume that if a particular pattern occurs among captive birds, it may also be observed in wild birds. It is quite possible, however, that some patterns which occur in wild birds might not be observed in captive ones because of their inability to fly, because of insufficient social stimulus resulting from small numbers of a species being present, or because of maladaptation to captive conditions.

BIOLOGICAL CHARACTERISTICS OF THE FAMILY ANATIDAE

As a preface to the species accounts, it seems advisable to give a general account of the over-all aspects of the biology of waterfowl. Such an account will provide us with a theoretical framework into which we may fit, and in terms of which we may interpret, the individual species observations.

Within the Anatidae there are some major differences—in pair

bond length, period to maturity, and pair-formation tendencies—that have resulted in strikingly diverse effects on such matters as geographic variation and subspeciation, and on the capacity for environmental adaptation in various species. In two of the three subfamilies of Anatidae, the Anserinae and Anseranatinae (unless otherwise noted the classification of Delacour, 1954–1964, is followed), including swans, geese, whistling ducks, and magpie geese (see Appendix for a list of scientific names), mates tend to remain paired for life. In addition, geese, swans, and magpie geese require at least two and in many cases three or more years to achieve sexual maturity, whereas the other Anatidae typically mature in their first year. These slow-maturing species with relatively permanent pair bonds therefore have a rather low capacity for numerical increase and a relatively limited ability for genetic exchange in a large population. This is especially true with geese and swans, many of whose breeding populations may remain isolated from one another because of the tendency of familial offspring to return each year to the place of hatching and to inbreed with close relatives (Mayr, 1942). This results, of course, in much local subspeciation and adaptation to local conditions.

In contrast to this, the true ducks (subfamily Anatinae) have less permanent pair bonds (except for sheldgeese and perhaps some shelducks), and often a female may have several different mates during her lifetime. Since most of these species mature in their first year, and clutch sizes tend to be large, there is a fairly rapid mechanism for adaptational changes in gene frequencies and an over-all higher fecundity than occurs with geese and swans. Because of the temporary pair bond situation, the female on her wintering grounds or migration normally must select a new mate every year, during a prolonged period of social courtship in which numerous drakes participate. This yearly shifting of mates has many implications; not only does it tend to inhibit inbreeding, but it also places the male's heterosexual characteristics at a premium. These characteristics are further enhanced by the fact that with ducks there tends to be an excess of males in the adult population, and therefore not all drakes are able to obtain mates. Finally, each male which does obtain a mate follows, rather than leads, the female to her ancestral breeding grounds or place of hatching. This situation tends to foster genetic panmixia and thus inhibits local subspeciation.

To summarize, pair-formation characteristics in most duck species include (1) a high capacity for rapid change in population size and

gene frequencies because of early sexual maturity and a short pair bond; (2) the enhancement of heterosexual characteristics of males because of the annual social courtship, unbalanced sex ratios, and the "choosing" of her mate by the female; and (3) population mixing on wintering grounds and the male's tendency to follow his female to her natal home regardless of his own place of origin, resulting in reduced intracontinental subspeciation. By contrast, with geese and swans there tend to be (1) slower changes in population size and gene frequencies as a result of longer life cycles and an extended period of sexual immaturity; (2) reduction of male heterosexual characteristics because of monogamous, often lifelong pair bonds; and (3) increased intracontinental subspeciation resulting from greater fidelity to the area of hatching in both sexes and from inbreeding of local family groups.

The taxonomic implications of these facts are vital to an understanding of the group. Taxonomists have nearly always placed great emphasis on the heterosexual characteristics of male ducks, often according *generic* rank to features which actually function as *species*-isolating mechanisms. Thus the 38 species placed in the inclusive genus *Anas* by Delacour (1956) have been divided into as many as 27 genera by some authors, despite the fact that the females of the various species are often very similar and most species will produce fertile hybrids with one another (Johnsgard, 1960a).

At first glance it would seem a paradox that the family Anatidae, in which some of the most elaborate avian courtship displays are to be found, actually is responsible for the greatest number and variety of interspecific hybrids of any avian family (Gray, 1958). For example, the mallard has been alleged to hybridize with no less than 45 species of anatids, the wood duck with 26 species, and the pintail with 25 species. Among geese, the species most frequently found to have hybridized are the Canada goose and the graylag goose, which are reported to have hybridized with 16 and 17 species respectively. It must be admitted that many of the waterfowl hybrid combinations have been achieved under the artificial conditions of captivity, and are therefore of decreased significance in the consideration of natural isolating mechanisms. They do, however, point out the importance of such mechanisms for the prevention of gene flow between species. Furthermore, many of the hybrid combinations obtained in captivity have also, when geographically possible (i.e., when between sympatric species), occurred under natural conditions. This anomaly

then—elaborate sexual display and competition among drakes for mates, combined with a surprisingly high incidence of "incorrect" selection on the part of females—must be examined more closely. Have the elaborate displays and signal characteristics of the males been evolved to prevent interspecific hybridization, or have they been evolved as a result of intraspecific sexual selection? In all probability there is truth in both hypotheses, but the first hypothesis seems the sounder of the two. This topic has been discussed in detail by Sibley (1957), and only the following points need to be made here. In areas where many closely related species of ducks are sympatric on their pairing grounds (generally their wintering areas), they tend to be sexually dimorphic and to engage in rather elaborate courtship displays. And although in closely related species these displays often consist of the same or very similar components of behavior, minor differences of plumage, or of the sequence, form, or frequency of the displays, confer distinctiveness upon them, and probably provide the ducks a basis for species recognition and mate selection. Thus those species which have the widest ranges and the greatest amount of sympatry with other closely related species tend to exhibit elaborate displays and complex male plumage patterns.

Substantiating evidence for the first hypothesis is to be found in regions of allopatry, and especially on oceanic islands. Here, where there is no question of interspecific mate-choosing (and hence no question of hybridization), there tends to be a loss of sexual dimorphism, and males acquire a plumage almost identical with that of females. (As will be seen later, sexual *behavior* patterns also tend to be less elaborate in allopatric populations.) Furthermore, this is true not only of permanently allopatric species (those restricted to islands, for example); it is also true of allopatric subspecies of species which, in continental regions (where sympatry is possible), are sexually dimorphic. Thus it appears that selection-pressures against sexual dimorphism (predation is one such pressure) are stronger than is the selection-pressure of intraspecific mate-choosing, which favors sexual dimorphism. Apparently, therefore, a major selection-pressure favoring sexual dimorphism in areas of sympatry is the pressure against *inter*specific mate-choosing—against, that is, hybridization. Otherwise we should expect allopatric populations to exhibit strong tendencies toward sexual dimorphism, since *intra*specific male competition for mates is still present in these populations.

The Subfamily Anseranatinae

TRIBE ANSERANATINI (MAGPIE GOOSE)

The first subfamily and tribe of the Anatidae consists of the single genus and species *Anseranas semipalmata,* or magpie goose. This species deviates in almost every respect from the rest of the Anatidae, and anatomical evidence indicates that it has some affinities with the South American family of screamers, the Anhimidae (Delacour, 1954; Woolfenden, 1961). The screamers are a group of semiterrestrial birds which in turn have some of the characteristics of gallinaceous birds. It appears that the screamers and the magpie goose represent major stages in the evolution of the typical waterfowl from a gallinaceous ancestor. Besides the numerous anatomical similarities between the magpie goose and the screamers, a few other, obvious similarities are of interest. Both kinds of bird have broad wings, long legs, semipalmated feet, and a long hind toe—characteristics which enable them to walk rapidly (Fig. 1*D*) and to perch admirably. Presumably the ancestors of the rest of the Anatidae sacrificed these capabilities when they assumed a more aquatic existence. In addition the magpie goose and the screamers have a gradual wing molt, and thus never completely lack the ability to fly. Apparently a simultaneous wing molt and the resulting temporary inability to fly was a later adaptation to a more aquatic environment, when the ancestral waterfowl were able to utilize their improved swimming and diving abilities as an escape from danger during the molting period. Like screamers (Stonor, 1939) and swans, the magpie goose nests on

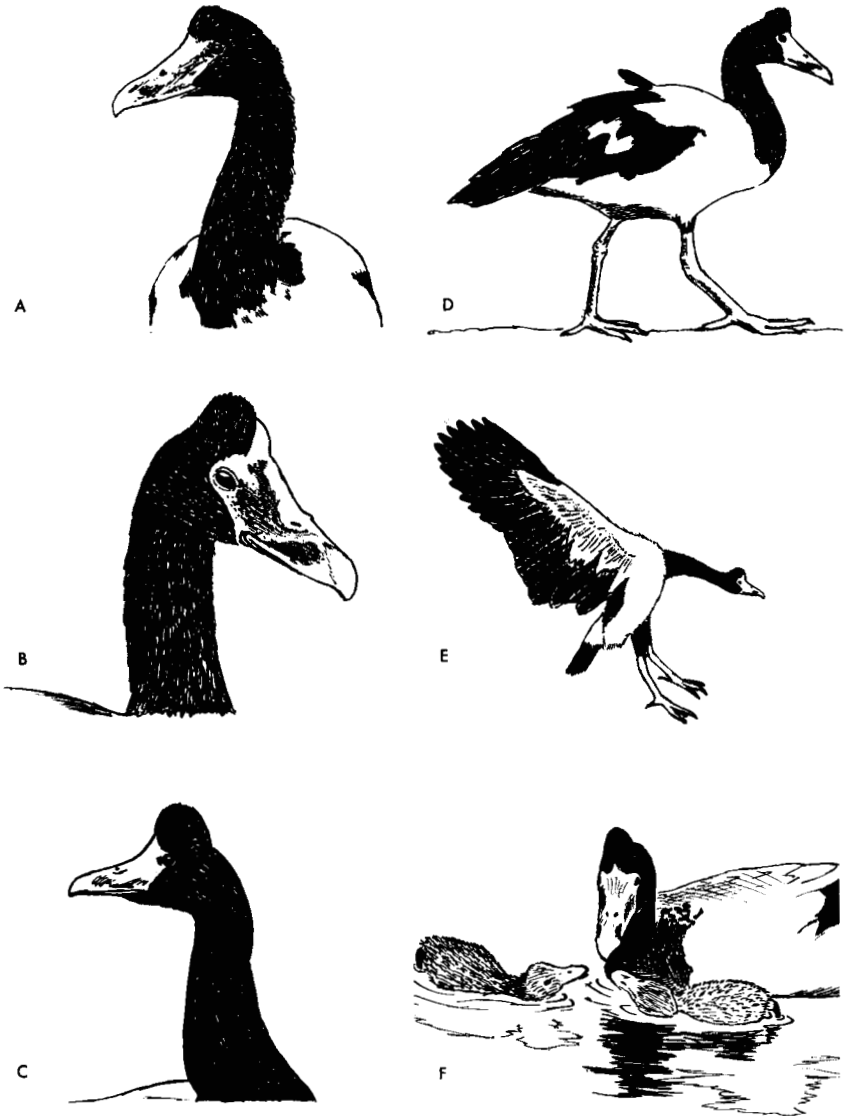


Figure 1. Magpie Goose
A. Immature female.
B. Male aged two and one half years.
C. Adult male.
D. Male walking. Note long toes and semipalmated feet.
E. Male landing. Note broad, rounded wings.
F. Male feeding young. (From photo by J. V. Beer.)

the ground or on mounds of weeds in water (Davies, 1962). The male helps build the nest and incubates part of the time, as do male screamers. In its foraging the magpie goose is mainly vegetarian, but it forages on every imaginable kind of plant, and especially tends to dig for roots in the soil. Although it swims fairly well, it has not been observed to dive.

The downy body-plumage of the magpie goose resembles that of the screamers in being a unicolored gray, shading to white below. The magpie goose has, however, a cinnamon-colored head that makes its downy plumage unique among waterfowl. The adult plumage has the same pattern in both sexes, a strongly contrasting black and white somewhat reminiscent of the horned screamer (*Anhima cornuta*) as well as of the spur-winged goose. Except for a slight difference in size, the sexes differ mainly in their head shape (Fig. 1*A–C*), adult males being marked by a distinct bony crown that increases with age, at least to the third year. The sexes also differ in that the voice of the male is much lower in pitch than that of the female. This is the result of sexual differences in the length of the trachea, which in adult males is a coiled, greatly elongated structure (reaching a length of about 150 cm.) lying between the breast muscle and the skin. The syrinx is small and not differentiated in the two sexes (see Johnsgard, 1961c). The species ranges over much of Australia, Tasmania, and southern New Guinea, and does not exhibit any subspeciation. No hybrids involving the magpie goose are known.

General behavior. Magpie geese are highly social with others of their species, but very seldom associate with other waterfowl. They do not persecute other birds, but captives at least will sometimes not hesitate to attack a human. Their threat behavior consists of approaching the opponent with head held slightly back, then suddenly making a powerful thrust with the open and strong beak, which has a large, sharp nail. Sometimes the birds open and flap their wings, and they have been known to fly at their opponent, striking him with their feet, wings, and beak. The preflight behavior of magpie geese is simple, consisting of short, rapid calls emitted with the neck stretched and, at times, with the lateral Head-shaking* typical of nearly all Anatidae. Vocalizations are fairly simple, adults of both sexes apparently using only a single monotone note. Differences, however,

* Names for behavior patterns which appear to be ritualized (i.e., to have signal function) are capitalized here.

in the loudness, rapidity, and pitch of the call appear to serve different functions. The downy young and juveniles up to about six months of age have a high-pitched whistle and produce chittering notes with a rapid opening and closing of the beak. These notes are emitted during any excitement, and are possibly of importance in keeping the family together during early life. Later, as the trachea lengthens and the adult call is developed, the chittering ceases, but the rapid beak movements continue into adulthood. Mutual nibbling involving similar bill movements has been observed in adults.

Two facts about magpie goose behavior are of special interest and may make this species unique in the Anatidae. The first is that from the time that they leave the nest, the downy young are fed directly by their parents in a bill-to-bill fashion (Fig. 1*F*). The downy young have a loud, sibilant whistle which they utter with their orange bill open, and which seems to function as a food-begging call. They also forage for themselves, but much of their food is obtained by their parents, who bring up aquatic vegetation from under the water and allow the young to take it from their bills. Janet Kear (pers. comm.) has observed possible cases of parental feeding in *Dendrocygna* and *Cygnus*, but these forms apparently exhibit a much more rudimentary form of parental feeding than do the magpie geese. The second fact of special interest is that unlike those of some swan species, the magpie goose family does not return to the original nest at night for brooding; rather, both adults assist in building a "brood nest," which is simply a pile of grass on which the young sleep or rest while being brooded by the mother. This brood nest is used until the young are about two weeks old, by which time they have largely abandoned parental feeding. A more detailed account of the development and the molts of the young has been published elsewhere (Johnsgard, 1961b).

Sexual behavior. Since a detailed account of the breeding behavior of magpie geese has also been presented elsewhere (Johnsgard, 1961b), only the major points will be mentioned here. Magpie geese probably become sexually mature between their second and third years, since males aged two and a half years have a fully elongated trachea and a well-developed crown enlargement (Fig. 1*B*). The pair bonds and family bonds appear to be as strong as they are with other geese and with swans. Unlike all the other waterfowl so far studied except Cape Barren geese and Hawaiian geese, magpie

geese apparently do not copulate while standing in water or while swimming. At least, in the three instances in which copulation has been observed (I have observed it twice), it occurred on or near the nest site. If the cases I saw were typical, there is no elaborate precopulatory display before the female climbs up on the nest and is followed by the male, who immediately mounts. During treading there is no call and little movement, and apparently the male does not grasp the female's nape as does the male of all other waterfowl studied thus far. After a successful treading both birds evidently call while "bowing and scraping" to one another, but in the two instances I observed there was no such calling; hence the treadings were probably not successfully completed. Magpie goose pairs perform a rudimentary sort of "Triumph Ceremony," analogous to those performed by swans and geese, which consists of both birds emitting loud calls and shaking their wings.

The Subfamily Anserinae

This subfamily, by Delacour's classification, contains two tribes, the Dendrocygnini (whistling ducks) and the Anserini (swans and true geese). Both tribes are characterized by the fact that in them the sexes have almost identical plumages and tracheae, and exhibit almost identical behavior. Both tribes are also characterized by a relatively permanent pair bond. Like the magpie goose, they have a characteristic reticulated scale pattern on the surface of the tarsus. Of the two tribes, the whistling ducks appear to be the more specialized, but since they are also more distinctly isolated from the rest of the Anatidae (as indicated by their failure to hybridize with members of any other tribe), and since they exhibit certain anatomical similarities to the magpie goose (Woolfenden, 1961), they will be considered first.

TRIBE DENDROCYGNINI (WHISTLING DUCKS)

The whistling, or "tree," ducks comprise a group of eight species of world-wide, though primarily tropical, distribution. A single genus, *Dendrocygna,* is generally accepted, and indeed the species form such a homogeneous group that it is extremely difficult to establish intrageneric differences upon which to judge probable species relationships. In most respects, whistling ducks are very gooselike, differing from geese mainly in their more specialized tracheal structure, their whistling voices, and their distinctive downy plumage patterns. They possess relatively long legs and large feet (Fig. 2*A*), and they can dive remarkably well. Despite being commonly called "tree ducks,"

they do not perch a great deal and only rarely nest in tree holes. All are vegetarians, usually tipping-up or diving for food, though some grazing is also done. Family bonds are strong, and in at least a few species the male assists with incubation. It is not certain how long it takes them to mature, but since they attain their adult plumage at about six months of age, they probably mature in their first year. In all species, the birds of both sexes have whistling voices; furthermore, the birds of many of the species produce distinctive whistling or whirring noises in flight, by vibrating variously indented inner vanes on the outermost primaries. Most species have light-colored upper-tail coverts, like those found in geese, which are conspicuous in flight and probably serve as flight signals in the same manner as those of geese. Adult plumages are rather variable, and the downy plumages appear to be the best indicators of intrageneric relationships. The following sequence is based on these features as well as on behavioral evidence.

Spotted Whistling Duck (*Dendrocygna guttata*)

In several respects the spotted whistling duck appears to represent one extreme in the genus *Dendrocygna*. The plumage pattern of the downy young—striped back, large cheek patch, ashy-white base color—closely resembles that of the plumed whistling duck. The adult trachea differs in the two sexes, that of the male being symmetrically enlarged while that of the female is not enlarged and has a dorsal membranaceous area near the junction of the bronchi. This arrangement of the female trachea appears to be typical in all species of whistling duck except the Cuban and the red-billed, in which females lack the membranaceous area. Adults have a unique plumage pattern, most of the body feathers having several rounded light spots arranged linearly and connected by narrow bars. Thus the pattern is quite different from the outwardly similar spotted pattern of the Cuban whistling duck. The same type of patterning occurs, however, on some of the upper flank and axillary feathers of the plumed whistling duck. The outermost primary, being deeply indented, produces a whirring noise in flight. The species is restricted to the East Indies and is sympatric with the wandering whistling duck. No hybrids involving the spotted whistling duck are known.

General behavior. This species is a particularly quiet one, both in manner and in voice. The most common vocalizations are a nasal

one-syllable call, *gack,* and a simple whistle, *whee'-ow,* but occasionally I have heard the more complex call *whe-a-whew'-whew.* The only aggressive posture I have seen is the "Head-back" posture. Mutual preening or nibbling is a common form of social behavior.

Sexual behavior. This is the only species of whistling duck on which I have no information about copulatory behavior.

Plumed Whistling Duck (*Dendrocygna eytoni*)

The plumed, or Eyton's, whistling duck appears to bridge the evolutionary gap between the spotted whistling duck and more typical whistling ducks such as the fulvous. The plumage pattern of the plumed downy young is much like that of the spotted downy young, but the former have a smaller cheek patch and are less distinctly striped on the back. The tracheal structure of the plumed whistling duck is very similar to that of the spotted whistling duck. Except that they are uniquely elongated, the flank feathers of the adult plumage are basically the same as those of the fulvous and the wandering whistling duck. The bill of the adult is spotted like that of the spotted whistling duck, but its yellowish iris is unique. The outermost primary is little if at all modified for sound production, but the upper-tail coverts form a conspicuous light buff crescent. The species is restricted to Australia and is sympatric with the wandering whistling duck. Hybrids have been produced in captivity with the fulvous whistling duck.

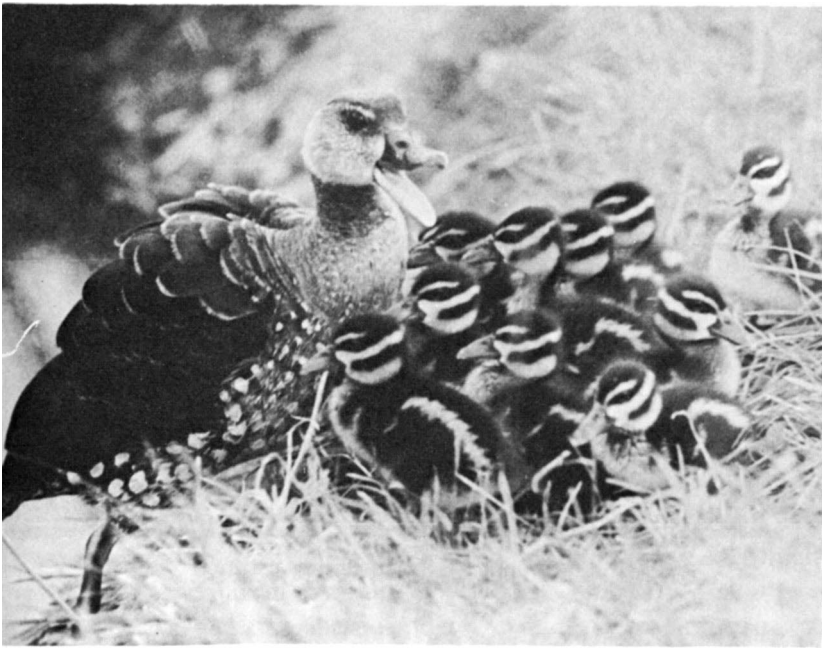
General behavior. The plumed whistling duck strongly resembles the fulvous in its behavior and vocalizations. Its usual call note is a whistled *wa-chew',* although like the other species it also produces softer, "conversational" notes and a rapid, high-pitched, repetitious whistle in aggressive situations. In threat situations I have seen both the Head-back posture and the Head-low-and-forward (see Fig. 3*D*). McKinney (1953) has recorded mutual nibbling in this species.

Sexual behavior. Wolfgang von de Wall informs me (pers. comm.) that in this species copulation is performed exactly as it is by fulvous whistling ducks.

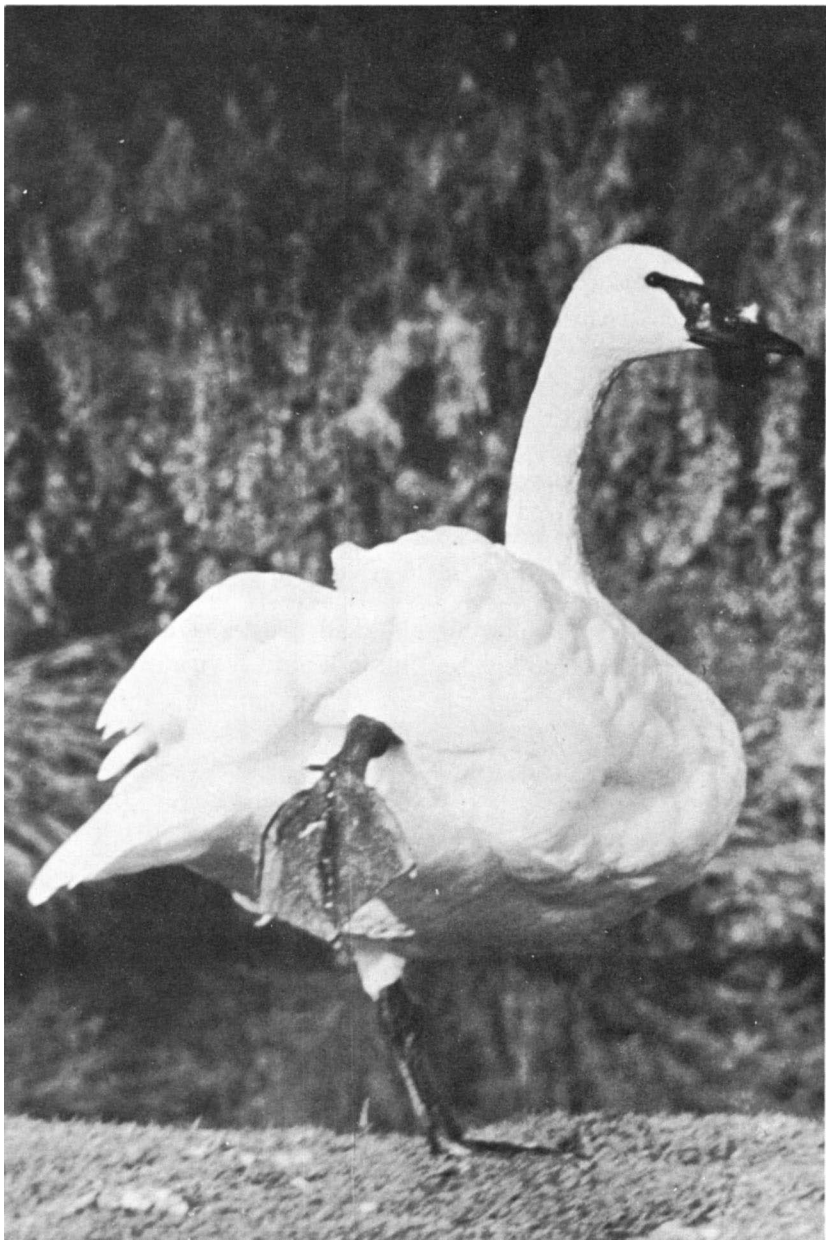
Fulvous Whistling Duck (*Dendrocygna bicolor*)

The fulvous appears to be a typical whistling duck which, with the wandering and the lesser, might be thought of as forming the core of the genus *Dendrocygna.* It is undoubtedly a close relative of

Magpie Geese, adults perching in a tree.



Spotted Whistling Duck, female defending brood.



Adult Trumpeter Swan, resting posture.

these two species, especially of the former, which it resembles in its downy plumage. This plumage consists of a dark, unmarked back, an unmarked light cheek, and an ashy-white base color. The tracheal structure is essentially like that of the plumed whistling duck. The adult plumage closely resembles that of the wandering whistling duck, especially in the flank feathers, chestnut upper-wing coverts, and the striated neck feathers. The fulvous does not, however, produce a loud wing noise in flight, and the upper-tail coverts form a conspicuous light buff crescent. The species occurs over an extraordinarily broad range in North and South America, Africa, Madagascar, and India without obvious subspeciation. It is sympatric with the red-billed, white-faced, and lesser whistling ducks, and in captivity has hybridized with the lesser, wandering, plumed, and white-faced whistling ducks.

General behavior. The fulvous whistling duck is a fairly noisy and aggressive bird. The usual call note of both sexes is a strong, whistled *wa-kew'*, which is often uttered in flight. Like the wandering and lesser whistling ducks, the fulvous uses lateral Head-shaking as a preflight signal. The usual threat posture is the Head-back; the Head-low-and-forward seems to be used relatively seldom (Fig. 3*A*). Neither McKinney (1953) nor I have recorded mutual nibbling in this species, which is not highly social.

Sexual behavior. Although the fulvous whistling duck is perhaps the best-known species of the entire genus, published information on its sexual behavior is extremely scanty. No observer has yet described what might be considered courtship in this or any other species of whistling duck, thus pair-forming behavior in this group is evidently extremely inconspicuous. It seems unlikely that copulation plays an important role in pair formation for, as with swans and geese, it is largely restricted to the period shortly before nesting. At times I have noticed a presumed male swimming ahead of another bird in a posture similar to the "haughty" courting posture of true geese, but I am not certain that this was true courtship behavior.

Copulatory behavior has been described for this species by Finn (1919) and by Meanley and Meanley (1958). I have observed copulation on several occasions, and in every case precopulatory behavior appeared to consist of mutual Head-dipping (Fig. 2*B*), which apparently derives from bathing movements. This lasts for a few seconds, after which the male suddenly mounts. Treading goes on

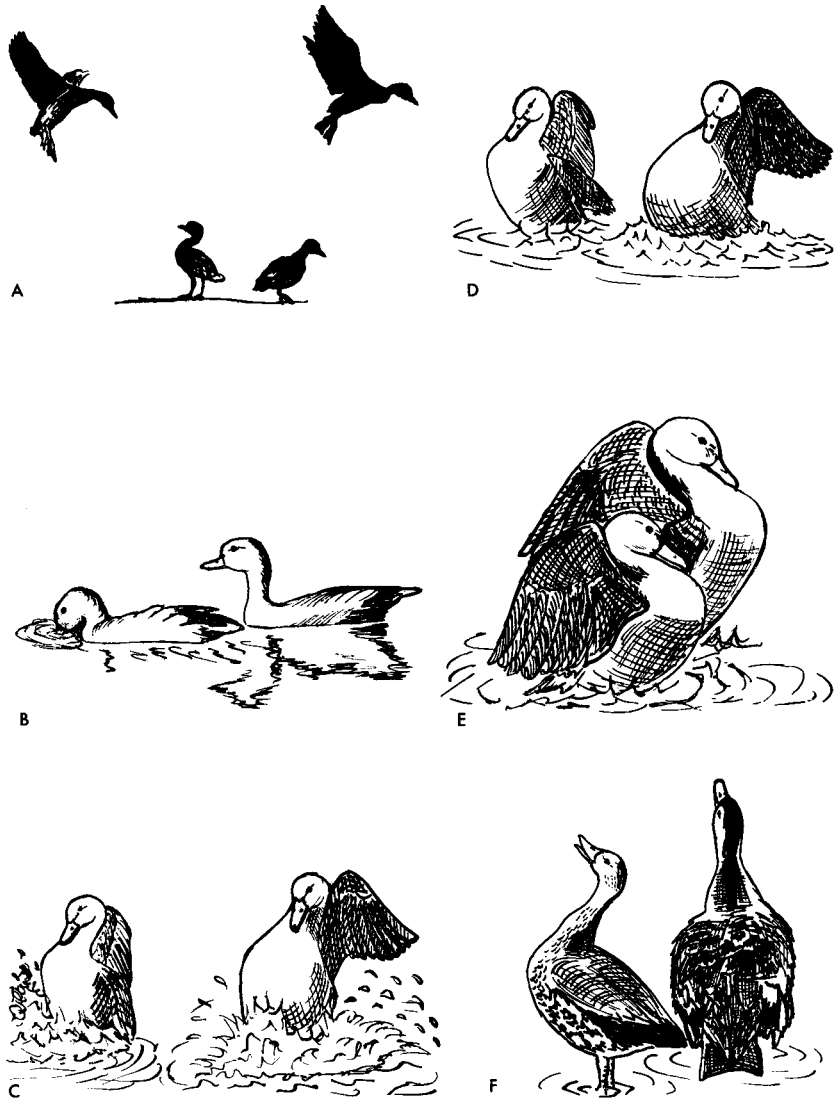


Figure 2. Fulvous and Cuban Whistling Ducks

A. Adult whistling ducks in flight. Note long legs and large feet.

B. Precopulatory behavior, fulvous whistling duck. Male (*left*) Head-dipping, female with neck erect between Head-dipping movements.

C, D. Postcopulatory display, two phases. Note splashing of water caused by vigorous treading of feet.

E. Same as *C* (*female in foreground*).

F. Cuban whistling duck postcopulatory display (*male on left*).

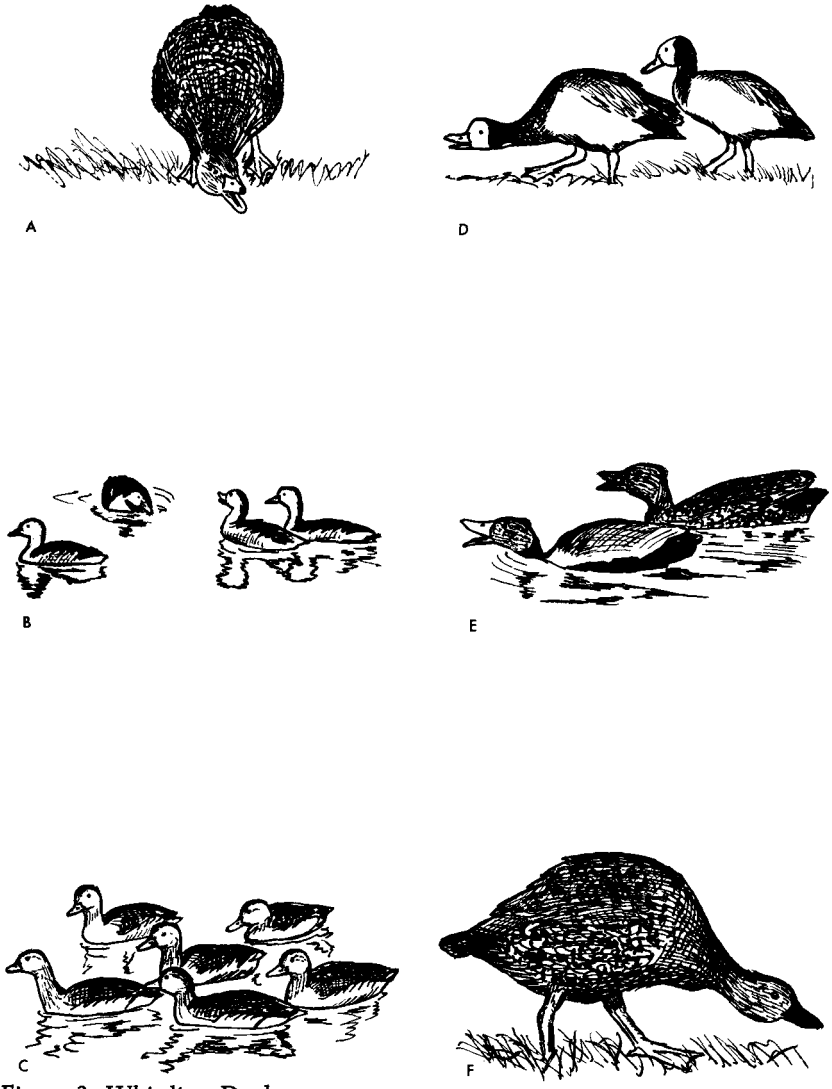


Figure 3. Whistling Ducks

A. Fulvous whistling duck in Head-low-and-forward posture.

B. Wandering whistling ducks in Head-back posture, threatening red-billed whistling duck (*left center*).

C. Lesser whistling ducks in Head-back threat posture.

D. White-faced whistling ducks in Head-low-and-forward (*left*) and Head-back (*right*) postures.

E. Red-billed (*left*) and Cuban (*right*) whistling ducks, in Head-low-and-forward and Head-back postures respectively.

F. Cuban whistling duck in Head-low-and-forward posture.

for only a short time, and immediately after ejaculation, apparently, both birds begin to call loudly and the male slips off to one side; then the birds rise up in the water side by side and facing the same direction (rarely opposite directions), tread water in a "Step-dance," and lift the wing on the side opposite the partner (Fig. 2*C–E*). Slowly the birds assume their normal posture; then they usually swim to shore where they bathe and preen extensively.

Wandering Whistling Duck (*Dendrocygna arcuata*)

In size, shape, and plumage, the wandering whistling duck falls between the fulvous and the lesser whistling duck. It is practically identical to the fulvous in its downy plumage and its tracheal structure. The adult plumage is a richer brown than that of the fulvous, and the head pattern resembles that of the lesser. The neck striations are not so conspicuous as those of the fulvous. The wings make a marked whirring noise in flight and the first primary is distinctly notched. In addition, the upper-tail coverts form a conspicuous crescent in flight. The species ranges widely over the East Indies and Australia, and has been divided into three subspecies. It is sympatric with the spotted, plumed, and lesser whistling ducks, and in captivity it has hybridized with the fulvous.

General behavior. The wandering whistling duck is a less aggressive species than the fulvous, and appears to be somewhat more social. It is not particularly noisy, and its most usual call is a rapid, descending whistle—*wi-wi-wi-wi-wi-wi-whew*—of five to seven notes. I have recorded the Head-back (Fig. 3*B*) and the Head-low-and-forward postures in threat situations. Both McKinney (1953) and I have observed mutual nibbling.

Sexual behavior. In the few copulations I observed, I saw no deviation from behavior typical of the fulvous whistling duck.

Lesser Whistling Duck (*Dendrocygna javanica*)

The lesser whistling duck is the smallest species of the genus. Its downy plumage falls between the two preceding species and the following ones—its back is spotted, it has a small cheek patch, and its base color is an ashy white. Its tracheal anatomy is much like that of the last species. Its adult plumage is similar to those of the fulvous and wandering whistling ducks, but its back is a bluish gray, and it

has a distinctive yellow eye-ring. Furthermore, its upper-tail coverts are a rich chestnut rather than a pale buff. The inner vane of its outermost primary is strongly modified for sound production (see illustration in Heinroth, 1911). The species occurs in India and through much of southern Asia and the East Indies, and is sympatric with the fulvous and wandering whistling ducks. In captivity it has hybridized with the former.

General behavior. This species does not associate with the larger whistling ducks to any great extent, but the birds are gregarious with members of their own species. The call is a high-pitched and soft whistle, and the most frequent call note is a *whi-wheee'*, with the second syllable louder and higher in pitch. Mutual nibbling is frequent among these birds. In agressive situations they assume the Head-back (Fig. 3C) posture, as well as the Head-low-and-forward, and emit a series of rapid whistling notes.

Sexual behavior. If the two copulations I have seen are typical, the sexual behavior of the lesser whistling duck is in some respects different from that of the preceding species. The precopulatory display consisted of the male facing the female and performing "Bill-dipping" movements in the water. The female did not reciprocate, but remained in an erect posture. The male mounted suddenly, and after treading he performed the usual Step-dance of treading water and vertical Wing-lifting while the female responded with only a slight Wing-lifting during the Step-dance. In both cases copulation occurred in water of swimming depth.

White-faced Whistling Duck (*Dendrocygna viduata*)

The white-faced whistling duck possesses a relatively distinctive plumage pattern and appears to be rather isolated from the other forms. Its downy young have a spotted back, a small cheek patch, and a yellow base color—features which indicate affinities with the two species to be discussed next. Like the females of the typical whistling ducks already mentioned, however, the female of this species has a membranaceous area at the dorsal surface of the trachea near the junction of the bronchi. The plumage of the white-faced adult, with its elongated rather than rounded back feathers, its barred flanks, and its strongly patterned black and white head, is distinctive. The head pattern is of special interest, for it is such that when the bird is seen exactly head on, the entire head appears to be white; whereas

when the bird is facing directly away, the head appears to be entirely black. I suspect that the white face accounts for the great tendency of this species to engage in mutual nibbling (which is generally restricted to the front of the head) and may function as a preening stimulus. On the other hand, all whistling ducks have somewhat darker feathers on the back of the head; hence the white-faced whistling duck seems to have evolved a "compromise" plumage pattern. This species does not have a crescent-shaped upper-tail covert pattern; nor are its outer primaries specialized for sound production. Perhaps, however, the over-all contrast of its body plumage functions as an effective flight signal. The species occurs in South America and Africa, and is sympatric with the fulvous and the red-billed whistling duck. In captivity it has hybridized with both of these species.

General behavior. This species is highly social and, as mentioned, engages in mutual nibbling to an extent not found in any other of the whistling ducks. Its most common call notes are distinctive, and might be written *wee-a-whew'*. In aggressive situations it frequently assumes the Head-back and the Head-low-and-forward positions (Fig. 3*D*).

Sexual behavior. I have not observed copulation in this species, but D. F. McKinney (pers. comm.) has observed one instance of it. The birds were swimming about six inches apart and dipping their beaks in the water. One bird (probably the male) rolled its cheeks on its back several times. Copulation lasted only a few seconds. Afterward both birds stood in the water and paddled with their wings open. They then preened. This suggests that mutual Bill-dipping is the precopulatory display and that this species performs the usual postcopulatory Step-dance and Wing-raising.

Cuban Whistling Duck (*Dendrocygna arborea*)

The Cuban, or black-billed, is the largest of the whistling ducks. Its downy plumage consists of a spotted back, a large cheek patch, and a light yellow base color. The female syrinx lacks a membranaceous area on the dorsal surface; thus it conforms in structure to that of the red-billed whistling duck. The adult plumage, although outwardly similar to that of the spotted whistling duck, differs from it in that the flank spots are not rounded and linearly arranged, but are rather more irregular in shape and occurrence. The upper-tail coverts do not form a light-colored crescent, and the wings are not modified

for producing noise, but when the wings are extended their upper surface presents a pattern of ashy gray against a darker background that is conspicuous in flight and corresponds exactly to the white wing-pattern found in the red-billed whistling duck. The Cuban species is, in fact, so much like the red-billed whistling duck in so many respects that it might be considered an island-dwelling, highly modified form which, although deriving from the red-billed whistling duck's ancestors, has obviously achieved the status of a full species. The Cuban whistling duck occurs throughout the West Indies and is not known to be sympatric with any other species, although it possibly has occasional contact with the red-billed whistling duck. These two species have been hybridized at the Wildfowl Trust, but no other hybrid combinations are known.

General behavior. This is certainly one of the quietest of the whistling ducks. Its call is uttered only rarely, and is a multi-syllable *wheet-a-whew'-whe-whew'*. Both McKinney and I have recorded mutual nibbling. Threat behavior in this species consists of the Head-back (Fig. 3*E*) or, much more frequently, the Head-low-and-forward (Fig. 3*F*) posture. When the latter posture is assumed, the scapular feathers are ruffled and the bill is pointed slightly upward.

Sexual behavior. In this species, as in the following one, copulation occurs when the birds are standing on the ground at the edge of the water. Both sexes repeatedly Drink, until the male finally and rather deliberately mounts. As treading is completed, the male drops to the ground, and immediately both birds rear back to a very erect posture, raise their bills high, and call loudly (Fig. 2*F*). The male then rather stiffly "parades" in front of the female as they slowly depress their ruffled feathers and assume normal postures. That the copulatory behavior of the Cuban and the red-billed whistling duck is so similar no doubt explains why birds of the two species tend to form mixed pairs and hybridize in captivity.

Red-billed Whistling Duck (*Dendrocygna autumnalis*)

The red-billed, or black-bellied, whistling duck occupies an extreme position in the genus *Dendrocygna*. The downy plumage is distinctive, and includes a spotted back, a large dark cheek patch, and a bright yellow base color. The tracheal structure is like that described for the Cuban whistling duck. The adult plumage pattern—black abdomen, extensive white on the wings—differs from that of any

other whistling duck. Although there is no crescent of color on the upper-tail coverts and the wings do not produce special sounds in flight, the upper surface of the wing does flash a brilliant white when the bird is flying. The species occurs from the southern tip of the United States through most of South America, and two subspecies are recognized. It is broadly sympatric with the fulvous and the white-faced whistling duck, and possibly also with the Cuban. Hybrids with all these species have been obtained in captivity.

General behavior. The red-billed whistling duck is a highly vocal and noisy bird, and its usual call is more musical than that of any other whistling duck. The call consists of from five to seven notes, and can be written as *whech, wha-chew'-whe-whe-whew* or *whech, wha-chew-whew-whew'*. (The introductory note is sometimes omitted.) It is uttered very frequently when the birds are in flight. Neither McKinney (1953) nor I have observed any mutual nibbling, although the birds are highly social. The usual threat behavior is the Head-low-and-forward posture (Fig. 3*E*) accompanied by the usual whistling notes, which rise and descend in pitch.

Sexual behavior. Meanley and Meanley (1958) have described copulation in this species; my observations are very similar. Treading appears normally to occur on land or while the birds are standing in shallow water. As a precopulatory display the male performs repeated Drinking movements, which the female may also perform. After treading, the male slips off to one side, and the birds stand side by side, calling mutually. The male usually lifts slightly the wing opposite the female, but this is not very noticeable, and unless one looks particularly for it one is not likely to see it.

TRIBE ANSERINI (SWANS AND TRUE GEESE)

The swans and true geese of the present tribe include about 21 species which are primarily temperate and arctic in distribution, with most forms occurring in the Northern Hemisphere. They are generally large grazing or dabbling birds, and all are highly social and have strong family bonds. Plumage patterns are the same in both sexes and tend to be relatively simple, with visual signal characteristics generally restricted to the bill, head, and rump. For the most part the species are very vocal, and in the true geese vocalizations probably reach the highest degree of development in the entire family. In all species the trachea is relatively simple in both sexes and lacks a bulla,

although in some swan species the trachea is very long and convoluted inside the sternum. The voices of the two sexes are alike or very similar. In all species the tarsus has a reticulated surface, and the patterns of the downy young are simple and faint. The group is clearly related to the sheldgeese through the Cape Barren goose, which Delacour (1954) considers a member of the sheldgoose tribe, but which I have included in the present subfamily and tribe. In all species the sexes apparently pair for life (which explains the plumage monomorphism and the single body molt per year), and sexual maturity is probably reached the second, third, or, rarely, fourth year of life. The male assists with the rearing of the young, and in several species males have been seen assisting with incubation. In probably all species, pairs or potential pairs engage in a Triumph Ceremony (Heinroth, 1911), which apparently has great significance in pair bond formation and pair bond and family bond maintenance.

SWANS

Mute Swan (*Cygnus olor*)

The mute swan, together with the black swan and the black-necked swan, differs rather markedly from the other northern swans. In these three swans, which I consider to be more generalized than, and isolated from, the other Anserini, vocalizations are poorly developed and the tracheae are relatively simple and unconvoluted. These swans share other characteristics as well: in all three species the downy young are carried on the backs of parents; the birds frequently swim with one foot while holding the other above the water and over the tail; and flapping the wings constitutes a threat display. As in all species of swan, a ruffling of the neck feathers is an indication of aggression, and a slimming of these feathers is a sign of fear or submission.

The downy young of the mute swan are grayish, very much like those of the black swan. The first-year plumage is brownish. As adults, the sexes differ in the intensity of their bill coloration and in the size of the black frontal knob over the bill. The trachea is simple and is laterally compressed at the large syrinx. The species occurs over much of Europe and Asia, and is sympatric with whooper and Bewick's swans. In captivity the mute swan has hybridized with these two species and also with the black swan.

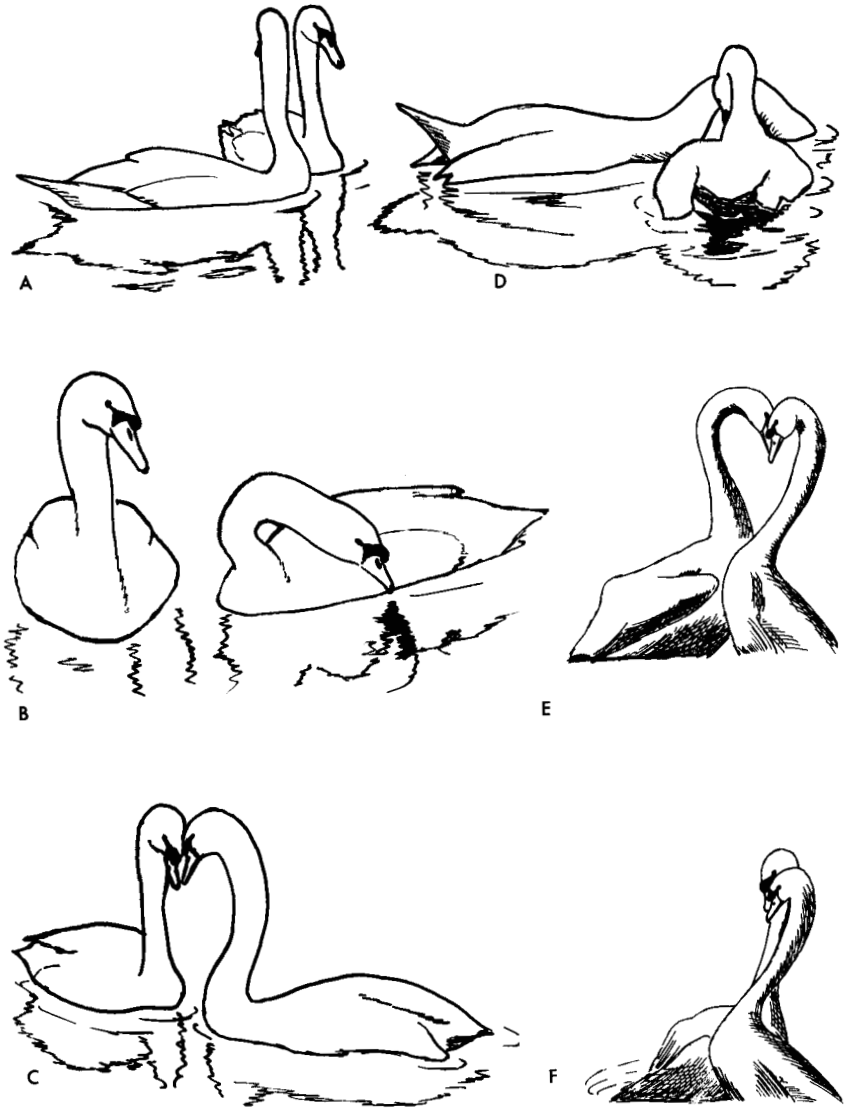


Figure 4. Mute Swan

A. Mutual lateral Head-turning.

B–D. Precopulatory behavior. Note slimmed lower neck and the lowering of the folded wings into the water.

B. Rubbing of flank feathers with bill.

C. Mutual facing toward partner (alternated with Head-dipping).

D. Precopulatory Head-dipping. The head is shaken in a rotary manner as it is lifted out of the water.

E, F. Early and late phases of postcopulatory display.

General behavior. The general behavior of mute swans has been dealt with in detail by Heinroth (1911), Poulsen (1949), and Hilprecht (1956), to mention the major works. Except in family groups, the mute swan is not highly social, and aggressive encounters are frequent. The threat posture of the raised secondaries (Fig. 5*A*) is well known; it is very much like the threat postures of the black swan and the coscoroba swan. As I have already mentioned, Wing-flapping is also used as a threat display. While attacking, the mute swan swims using both feet simultaneously, and hits striking blows with its wings (Heinroth, 1911). I have not observed any definite preflight movements, and in this respect also, the mute swan seems not to differ from black and black-necked swans. Vocalizations are simple and fairly weak. They include a loud "snore," a softer "chir," and other even softer calls (Heinroth, 1911).

Sexual behavior. Heinroth (1911), Huxley (1947), and Boase (1959) have all described various sexual displays. Mutual Head-turning (Fig. 4*A*) occurs frequently and appears to be used as a greeting or courtship display. The Triumph Ceremony of mated birds, which is performed after the repulsion of an "enemy," is similar to the male's threat posture, but is assumed by both birds and is accompanied by mutual calling while Chin-lifting (Fig. 5*A*). Precopulatory behavior (Fig. 4*A–F*) consists of mutual Head-dipping movements alternated with various comfort movements such as preening against the back and flank, head-rubbing movements in the same areas, and even up-ending. As the behavior progresses, the movements of the two birds tend to become synchronized, and between Head-dipping movements the necks are extended vertically and the heads held side by side for a moment. The wings are held very low, often dragging in the water (Fig. 4*D*). The male gradually pushes his neck and body over the female, and after treading the two birds call and rise partially out of the water, breast to breast, with necks extended and bills pointing upward; then, lowering their bills and turning their heads in unison from side to side (Fig. 4*E, F*), they gradually subside into the water (Boase, 1959).

Black Swan (*Cygnus atratus*)

As Heinroth pointed out (1911), the black swan is surely closely related to the mute swan, and the two species are similar in most respects except adult plumage color. The downy young of both

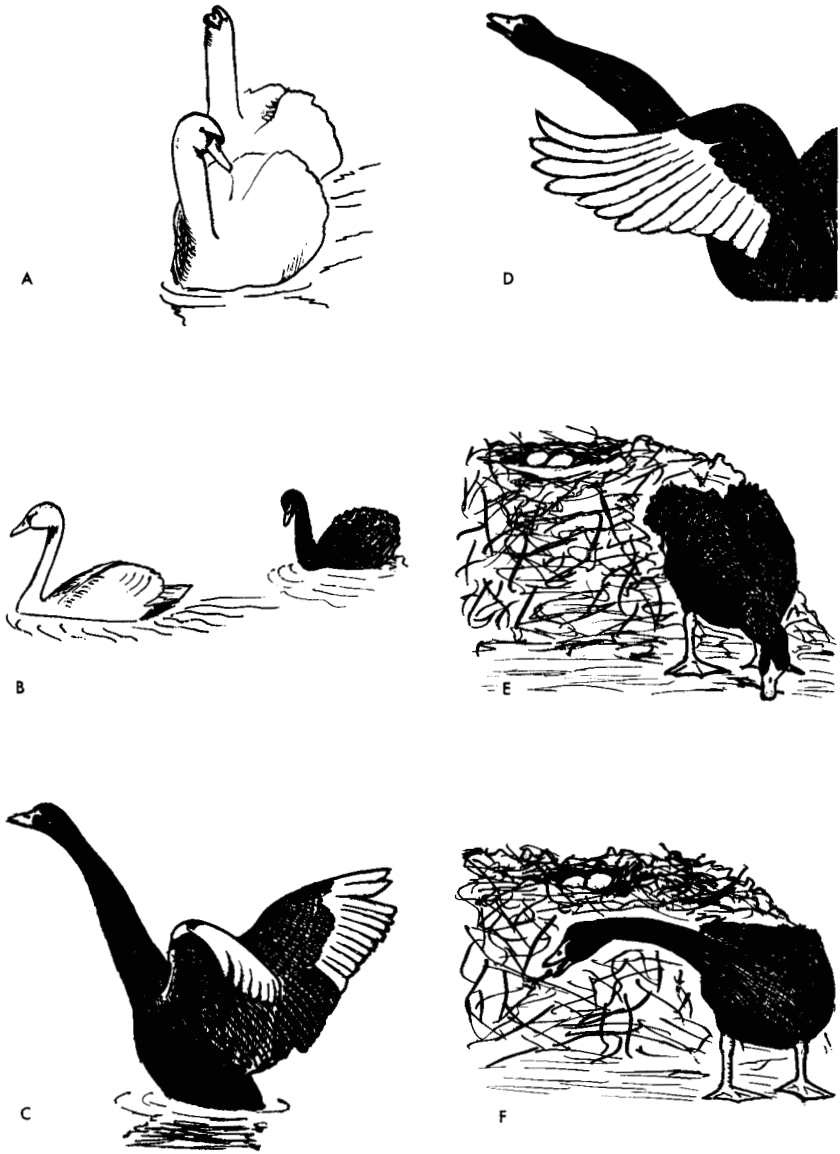


Figure 5. Mute Swan, Black Swan

A. Adult mute swans in threat posture. The bird at the rear is calling while Chin-lifting.

B. Black swan chasing juvenile mute swan. Note black swan's erected neck feathers and raised wings, and compare with *A* above.

C, D. Black swan performing Wing-flapping threat display while calling.

E, F. Nest-building behavior in black swan.

species are gray, and although the adult plumage of the present species is black, the feathers have white bases and the down is whitish. The first-year plumage is brownish like that of the mute swan. The trachea differs from that of the mute swan, in that it is compressed dorso-ventrally rather than laterally at the syrinx, the syrinx is smaller, and the bronchi are much smaller (see Johnsgard, 1961c). The black swan is native to Australia and is not sympatric with any other swans. It has hybridized in captivity with the mute swan and various other swans.

General behavior. Like the mute swan, the black swan has a well-developed threat display, which consists of raising the secondaries. Unlike the mute swan, which lays its head back on its wings during extreme threat, the black swan holds its neck erect, its bill pointed slightly downward and its long neck feathers greatly ruffled (Fig. 5*B*). A vigorous Wing-flapping of two or three strong strokes, acompanied by low *ka-thunggg* notes, is a second threat display (Fig. 5*C, D*). Like those of the mute and black-necked swans, but unlike those of any other swans, the wing feathers make a noise in flight loud enough to be heard for a considerable distance. I have observed no preflight movements in the black swan. The calls of this species are somewhat stronger than those of the mute swan, but they are still relatively weak.

Sexual behavior. The black swan has a Triumph Ceremony, similar to that of the mute swan, in which the male approaches the female with his wings slightly lifted, calling repeatedly while extending his neck and lifting his chin. The female replies in a similar fashion. The precopulatory behavior is also like that of the mute swan, consisting of mutual Head-dipping alternated with erect postures, but it lacks the conspicuous preening and other comfort movements that are characteristic of the mute swan. After treading is completed both birds call with necks stretched and bills pointed upward; then, holding their necks stretched to the utmost at about a 45-degree angle, and with their bills pointed downward at a right angle to the neck, they swim about in a circle (K. M. Davy, pers. comm.).

Black-necked Swan (*Cygnus melanocoryphus*)

Although the black-necked swan resembles the two preceding species in several respects, it is unique in several others and is not very

closely related to them or to the following species. The color of the downy young is white rather than gray. The juvenile plumage is marked with brown, as it is in the two preceding species, but the adult plumage, with its black head and neck, is unique. The trachea is unconvoluted, and the syrinx is small and distinctive in shape. As in the black swan, the bronchi are narrow and ossified. The species is found in southern South America and is not sympatric with any other species of *Cygnus*. It has apparently never hybridized with any other species.

General behavior. In my experience the black-necked swan is the most aggressive (although the weakest) of all swans and is constantly threatening other waterfowl or humans. Unlike the preceding species, this swan keeps its wings close to its body during threat and attack (Fig. 6*B*). As the bird nears its "enemy" it usually stops; and sometimes it lowers its head—which it holds just above the water during the attack—into the water in the manner of the following species (Fig. 6*C*). An alternative threat display involves rearing up in the water, Wing-flapping strongly several times, and then suddenly stopping with the wings fully outstretched, the neck bent, and the bill pointed toward the opponent (Fig. 6*E, F*). While actually fighting, the bird beats its opponent with its wings. After attacking or threatening another animal, the male of this species always returns to the female, calling continuously and making Chin-lifting movements. The female responds in a like manner, and the two birds continue to call with their heads only a few inches apart and their bills almost touching. If young birds are present they also join in the Triumph Ceremony. Although the calling is not loud, it is high-pitched and resembles somewhat the sound of a toy trumpet. Like the male of the mute swan species, and unlike that of the black swan species, the male of this species does not normally help with incubation, but may sit beside the female on the nest. In all three species, however, the young are carried about on the backs of their parents, and this method of transportation is particularly common in the black-necked swan (Fig. 6*F*).

Sexual behavior. I have not observed copulation in this species, but Terry Jones (pers. comm.) has informed me that its copulatory behavior is similar to that of other species of swan, and that no particularly conspicuous postcopulatory display occurs.

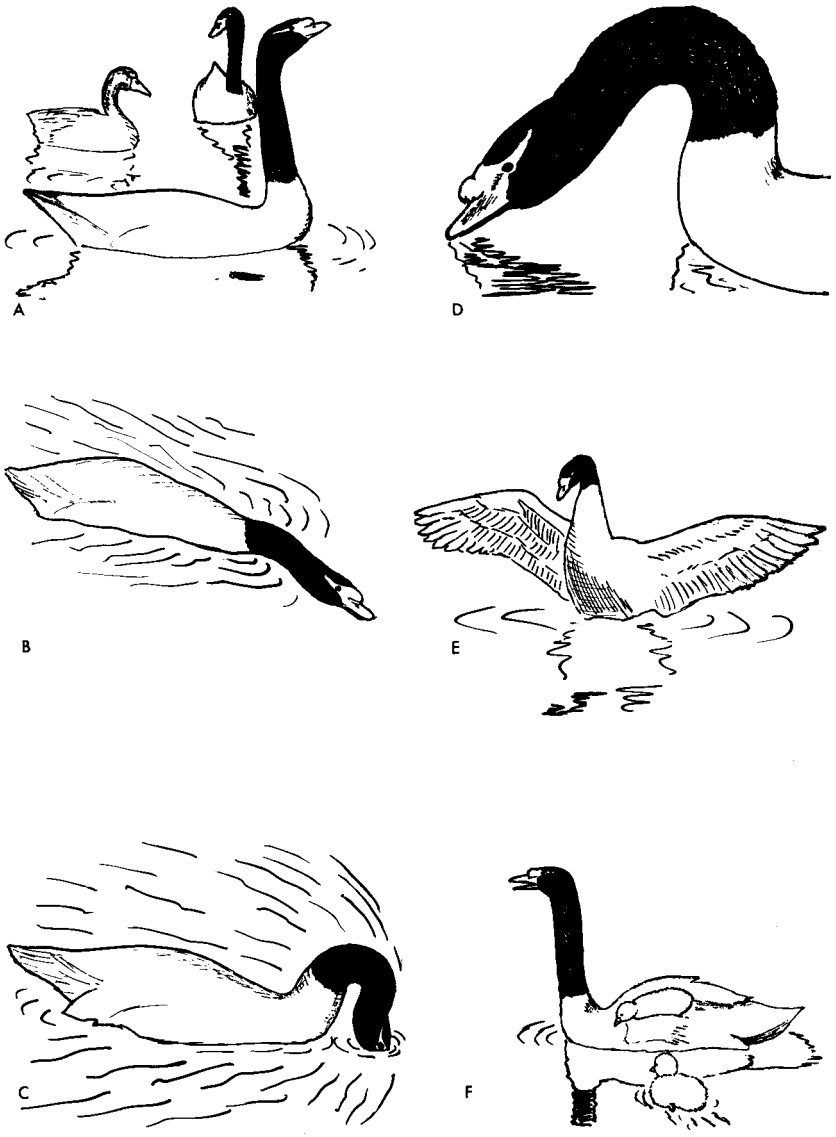


Figure 6. Black-necked Swan

A. Chin-lifting while calling by adult male as threat display. The same posture is used as a Triumph Ceremony by both sexes.

B. Attack by adult male.

C. End of attack. Note partial submergence of the head in the water.

D. Threat by adult male. Note erected neck feathers and bent neck.

E. Threat with outstretched wings after Wing-flapping.

F. Adult female carrying young on back.

Whooper Swan and Trumpeter Swan (*Cygnus cygnus*)

The whooper swan (C. *c. cygnus*) and the trumpeter swan (C. *c. buccinator*) are considered by Delacour (1954) to constitute a single species, and this classification will be followed here, although the two forms differ in certain important respects. In both forms the downy plumage is pure white, as is the adult plumage, and the juvenile plumage is grayish. In both forms the trachea is convoluted inside the sternum, but the degree of convolution (and the associated shape of the sternum) differs somewhat in the two forms, and this difference is considered by some (e.g., Wetmore, 1951) to argue against their conspecificity. The bill of the adult whooper is broadly marked with yellow; that of the trumpeter is not, and the lower mandible of the trumpeter has a conspicuous reddish stripe. Collectively, the forms occur in North America, Europe, and Asia, and are sympatric with the mute swan and the various races of the following species (*Cygnus columbianus*). In captivity one or both forms have hybridized with these species and with the black swan.

General behavior. All of the "northern swans" (whooper, trumpeter, whistling, and Bewick's) are essentially alike in their general behavior. They are highly social and more gooselike than the preceding species, and they often occur in large flocks. They have strong family bonds and numerous vocal signals which tend to keep the family and the flock organized. Unlike the preceding three species, the birds often call loudly in flight. When they flap their wings on land or in the water, their neck is curved and their head held horizontally; otherwise their neck is held straight and erect. The neck feathers are ruffled during aggressive displays, but since the feathers are fairly short, neck-ruffling is not so noticeable as in some of the preceding species. Threat displays may take several forms. One consists of keeping the wings closed or slightly spread, holding the head low and touching the ground with the bill or even submerging the head in the water (Fig. 9*A*), and at times hissing or shaking the wings vigorously (Fig. 7*D*). Before overt attack the wings are usually fully spread (Fig. 9*C*). Wing-flapping does not appear to be used as a threat display; rather the wings are lifted and waved in a partially opened position while the neck is repeatedly bent and extended and calls are uttered. This display is used as a threat (Figs. 7*A*, *B*; 9*B*) and also as a greeting and Triumph Ceremony (Fig. 9*E*), and it occa-

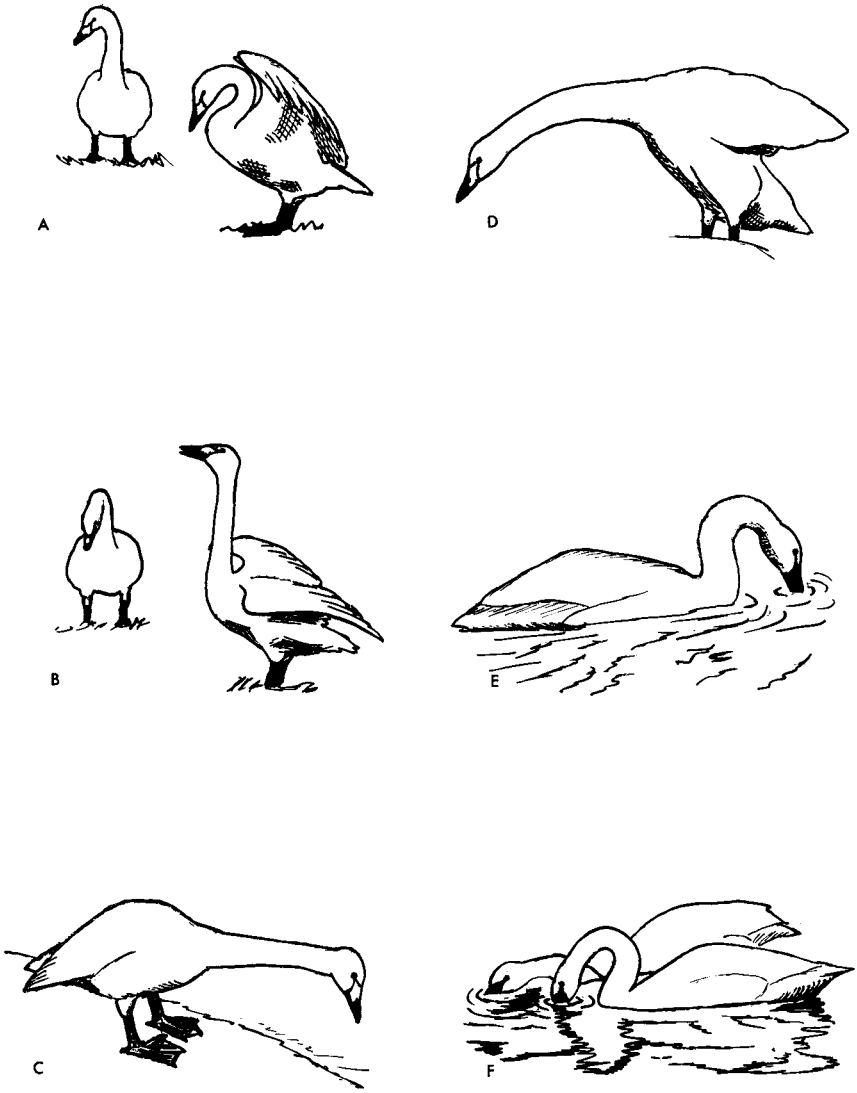


Figure 7. Whooper Swan, Trumpeter Swan

A, B. Whooper swan Triumph Ceremony (*male on right*).

C. Whooper swan male threatening while calling with neck rigidly outstretched.

D. Whooper swan male performing general shake during threat display. This is preceded and followed by a bill-down threat posture as shown in Fig. 9*A*.

E. Male trumpeter swan, precopulatory Head-dipping.

F. Trumpeter swan, mutual precopulatory Head-dipping (*male in foreground*).

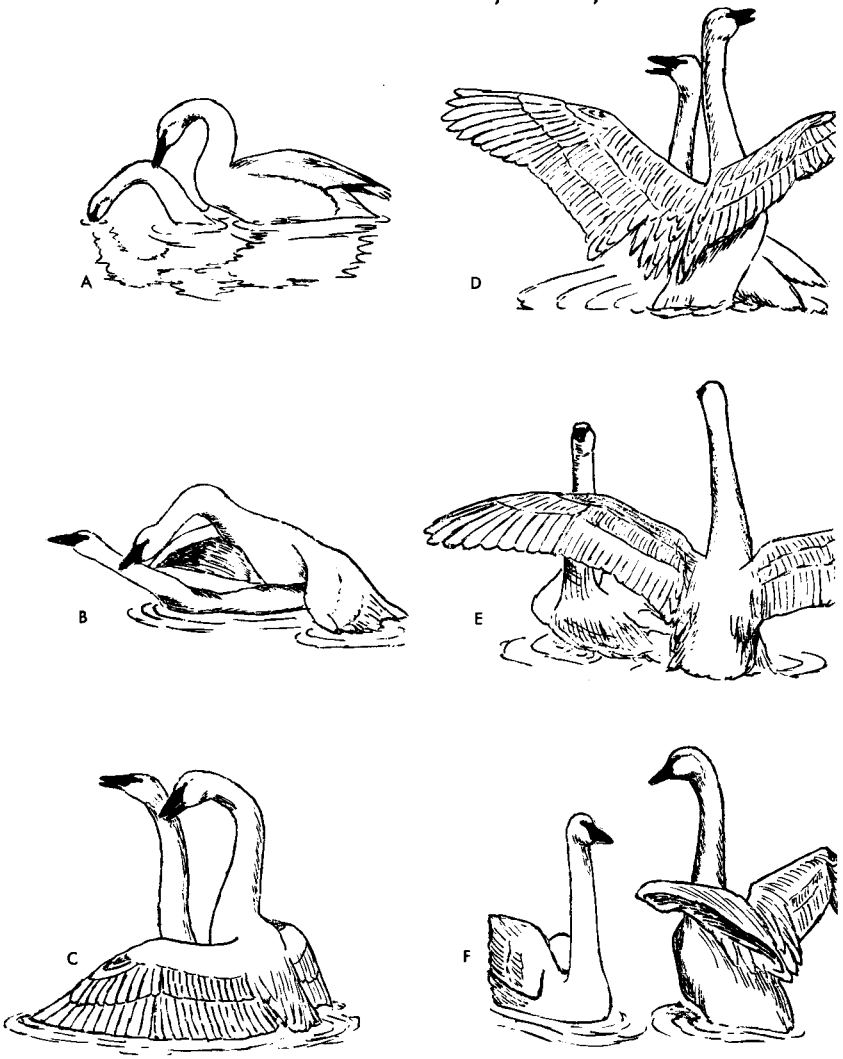


Figure 8. Trumpeter Swan

A–F. Copulation.

A. Treading posture. Note male grasping female's neck.

B. Female starting to call and male extending his wings as treading is completed.

C. Start of postcopulatory display. Both birds rise in the water as the female calls. The male is about to release the female and begin calling too.

D, E. Mutual calling while treading water and rotating in a slight circle.

F. End of postcopulatory display. The male is the last to settle back into the water.

sionally occurs while the birds are in flight. When this happens the waving movements of the wings differ noticeably from those used during normal flight, and the birds gradually lose altitude. All the northern species have conspicuous preflight movements which involve a pronounced pumping of the head and neck while calling (Fig. 9*F*), and, sometimes, a lateral shaking of the head. Males do not typically take part in incubation, although a male Bewick's swan at the Wildfowl Trust has been observed to do so. In none of the forms do the young ride on the backs of their parents. The voices of the two sexes are very similar, with the female possibly having a slightly higher-pitched call. When one bird of a pair is calling, the other usually joins in, often at first calling alternately with its mate, but finally calling in synchrony with it. Whooper swans often terminate this calling with the neck rigidly outstretched (Fig. 7C), but I have not observed this posture in trumpeter swans.

Sexual behavior. I have observed copulatory behavior in trumpeter swans, and no doubt that of the whooper swan is almost identical. The precopulatory display consists entirely of Head-dipping (Fig. 7*E*, *F*) and does not involve the alternate-preening or other displays characteristic of mute and black swans. The Head-dipping movements are clearly derived from bathing and in fact closely resemble the movements of normal bathing, except that in the display the movements are performed synchronously and the birds do not thrash their wings as they are dipping. The precopulatory display normally lasts only a short time (10 or 15 seconds) before the male mounts (Fig. 8*A*). As copulation is completed the male spreads his wings and the female begins to call (Fig. 8*B*), with or without opening her wings. Then both birds rise up in the water, calling in concert and turning in a partial circle (Fig. 8*C–E*) before they settle back in the water (Fig. 8*F*) and begin to bathe.

Whistling Swan and Bewick's Swan (*Cygnus columbianus*)

The whistling swan (*C. c. columbianus*) and the two races of Bewick's swan (*C. c. bewicki* and *C. c. jankowskii*) may be regarded as smaller versions of the whooper and trumpeter swans in almost every respect. Since their tracheae are shorter, their voices are correspondingly higher in pitch, and their actions tend to be slightly faster. The North American whistling swan differs from the European and Asian races in that it has little or no yellow on the bill and exhibits a

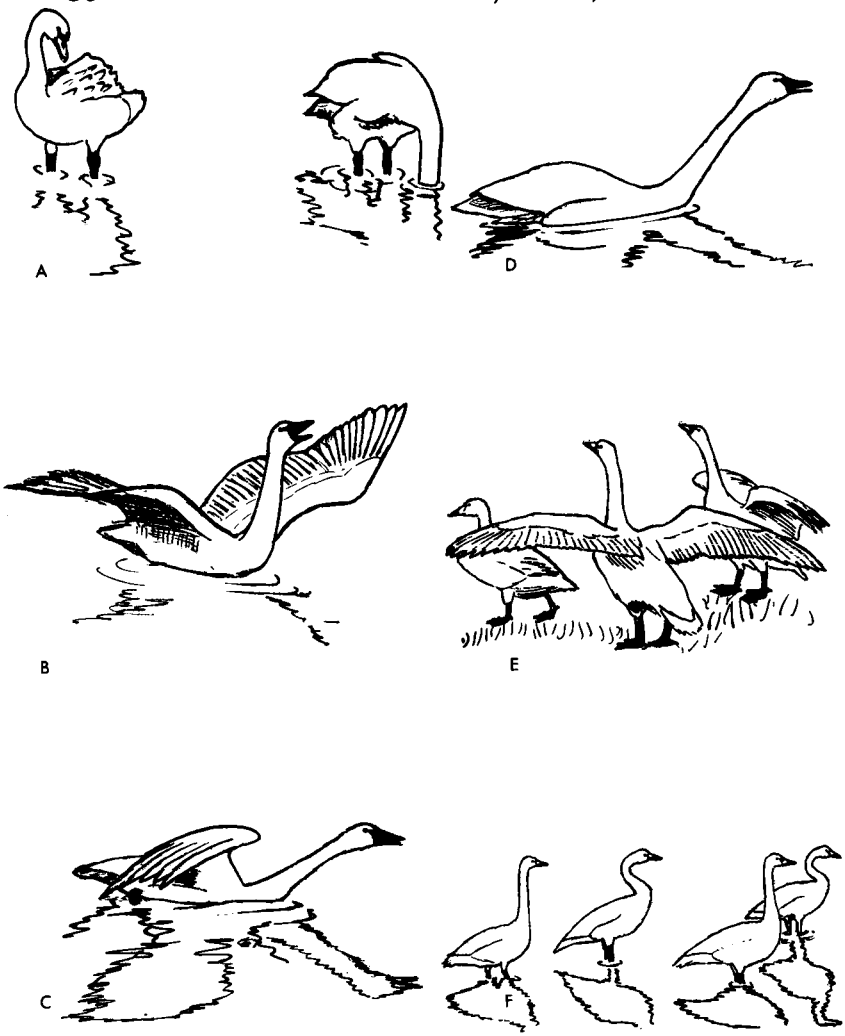


Figure 9. Whistling Swan, Bewick's Swan

A. Whistling swan (*right*) threatening a juvenile mute swan in bill-down, head-submerged posture.

B. Whistling swan threatening while calling with wings extended and waving. The same posture is used as a Triumph Ceremony.

C. Threatening posture of whistling swan. The wings are being held out from the body without waving.

D. Whistling swan calling without extending wings.

E. Bewick's swan pair performing Triumph Ceremony; young bird at left not participating.

F. Preflight calling of Bewick's swan while alternately bending and stretching the neck.

red streak on the mandible; otherwise it is very similar to them. It is most curious that the two American swans, the whistling and the trumpeter, have reddish mandible stripes and little or no yellow on their bills, whereas the old world forms have black mandibles and a great deal of yellow on their bills. One must conclude either that the bill pattern is not a species recognition signal to prevent confusion between sympatric species or, more plausibly, that the evolutionary relationships in this group are not what they are presently considered to be (Timmermann, 1963). No wild hybrids are known, but in captivity whistling and Bewick's swans have hybridized with the two larger swans and also with mute swans and black swans.

General behavior. Whistling swans and Bewick's swans appear to be very similar to trumpeter and whooper swans in their behavior. Although they appear to be rather excitable birds, their aggressive displays (Fig. 9*A–D*) are not markedly different from those of trumpeter and whooper swans.

Sexual behavior. I have observed one copulation in Bewick's swan, and D. F. McKinney has sent me his notes on copulation in the whistling swan. Both my observation and McKinney's notes entirely coincide with my observations on the trumpeter swan and Christoleit's description (1926) of copulation in the whooper swan.

Coscoroba Swan (*Coscoroba coscoroba*)

The coscoroba swan presents a curious mixture of characteristics that prevents any neat taxonomic "pigeon-holing." In its general appearance it is swanlike, being all white except for black wing tips. Unlike the other swans, however, its head is feathered in front of the eyes and thus the bird has a gooselike appearance, which is reinforced by a rather gooselike voice. Its bill is flattened and ducklike, and its very large feet and the pattern of the downy young are somewhat reminiscent of whistling ducks. The trachea, which is unconvoluted and has a syrinx resembling that of the mute swan, shows no affinities with the whistling ducks. Woolfenden (1961) considers this species a swan, but one having some gooselike features. The species occurs in southern South America and is sympatric with the black-necked swan. No hybrids involving the coscoroba swan are known.

General behavior. In its social behavior the coscoroba swan reminds one of the mute swan. Males tend to be aggressive, and their threat display of lifting the folded wings (Fig. 10*A*) is much like that

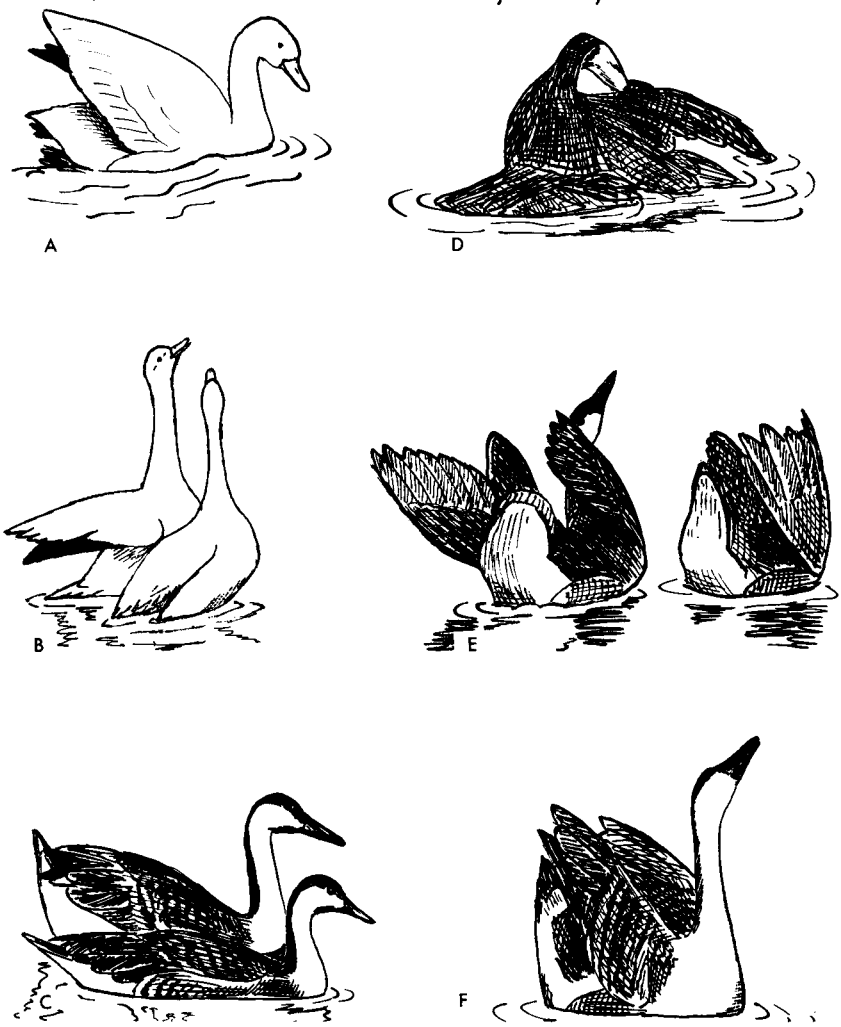


Figure 10. Coscoroba Swan, Swan Goose

A. Coscoroba swan attacking. Note raised wings and compare with Fig. 5*A*, *B*.

B. Coscoroba swan postcopulatory display. (From photo by D. F. McKinney.)

C. Swan goose precopulatory display. The male (*in background*) is in an erect posture that alternates with Head-dipping.

D. Swan goose treading. Male is grasping female's neck; his wings are partly extended.

E. Postcopulatory display, rear view (*male on left*). Note extreme tail-cocking and wing-raising.

F. Postcopulatory display, front view of male.

of the mute swan. When swimming, the birds tend to bring the head as far forward as possible and then to draw it back as their body moves ahead. This results in a "nodding" that is typical of many anatids when they are disturbed. This way of swimming seems to function to keep the head immobile for part of the time while the body moves continuously; thus it no doubt allows for better investigation of the environment (see Fig. 36*E*, *F*). When the birds are calling, the bill is flicked upward, and the commonest call note is a trumpeting *cos-cor-ooo'* or *cos'-cor-oo'-ba*. As in species of true geese, the voice of the male is higher in pitch than that of the female. I have not observed any preflight movements, nor have I observed any Triumph Ceremonies. The apparent lack of a Triumph Ceremony sets the coscoroba swan apart from all other swans and geese, and may indicate affinities with the whistling ducks.

Sexual behavior. D. F. McKinney has observed and filmed copulation, which occurred while the birds were standing in shallow water near the shore. Head-dipping by the male was apparently the only precopulatory display, after which he suddenly flew up on the female's back. The male dropped the female's nape as he finished treading, and the two birds immediately stretched their neck and head vertically as they apparently called in concert and as the male raised his folded wings (Fig. 10*B*). This postcopulatory display is similar to that of certain geese (especially *Branta*), the mute swan, and the Cuban whistling duck.

TRUE GEESE

Although it is clear that—in spite of a difference in chromosome numbers (Yamashina, 1952)—swans and geese are not too distantly related, it is uncertain whether *Branta* or *Anser* provides the closest link. Since *Anser* appears to be somewhat less specialized than *Branta*, the former will be dealt with first; and the swan goose, although it is certainly not a link with the swans, seems to provide one extreme of the genus *Anser*. Geese differ behaviorally from swans in a few small points. The voices of the sexes are very similar, but that of the male is slightly higher pitched than that of the female. Nearly all species have a vertically furrowed arrangement of the neck feathers—an arrangement which is evidently related to the fact that the threat display of geese consists of vibrating these feathers (rather than erecting them as swans do). All of the species are gregarious, highly vocal,

and have strong family bonds and pair bonds. Threat displays usually do not involve the use of the wings, but mainly consist of various neck and head postures with associated calls. Woolfenden (1961) has suggested that the geese and swans be tribally separated.

Swan Goose (*Anser cygnoides*)

The swan goose, the ancestor of the domestic "Chinese" goose, is clearly a member of the genus *Anser,* although it has often been separated generically. It differs externally from the other species only in its longer bill and its neck feathering, which lacks the vertical furrowing. The downy young have the typical brownish and yellow *Anser* pattern. The bill of the adult is all black and the feet are orange; and many birds exhibit white feathers behind the bill, where the white patch occurs on the white-fronted goose. The species occurs widely throughout Asia and is sympatric with bean geese, white-fronted geese, lesser white-fronted geese, and graylag geese. In captivity it has hybridized with all of these except the lesser white-front; no wild hybrids are known. Fertile hybrids have been reared involving the graylag goose and the white-fronted goose.

General behavior. Like the other "gray geese" this species is highly social. I have observed two aggressive displays, the Diagonal Neck (Fig. 11*D*) and the Forward (Fig. 11*E*). The latter is a display which often precedes attack. As in all gray geese, the preflight movement is a repeated lateral Head-shaking, accompanied by a low *ga-ga-ga-ga-ga* . . . call. And as in all geese, the Triumph Ceremony plays an important part in pair formation and in the family life. In this ceremony the male, after threatening or attacking an opponent, runs back to his mate or potential mate and calls loudly; then he emits a low cackle, *gangangangang,* which is repeated by the female. The birds call almost directly into each other's ear, with necks stretched forward and with heads held low over the ground, held upward, or moved about vertically or laterally, depending upon the species (see Figs. 13*A*; 16*A*, *B*). Downy young often join in this display, assuming the same postures as the parents (Heinroth, 1911). According to Heinroth, until two birds participate in a mutual Triumph Ceremony they are not really paired, although copulation may occur between them.

Sexual behavior. Courtship, or pair-formation display, is not easily observed in geese, since they normally undertake it only once, during

the second winter of life (although they may not breed until their third year). In all species of true geese this courtship appears to be essentially the same. Heinroth (1911) has described it for the graylag goose, stating that the male swims ahead of the female in a "haughty" attitude, with his hindquarters lifted higher than usual and displaying the white under-tail coverts (Fig. 12*C*, *E*). Since all the species of *Branta* and *Anser* but one (the emperor goose) have white under-tail coverts, it seems probable that they utilize them in his way during pair formation.

Copulation in swan geese is like that in the other gray geese, and a description for this species will suffice for most. The male swims very high in the water, with his tail cocked almost vertically, and repeatedly performs Head-dipping movements which somewhat more resemble foraging than bathing movements. The head is brought out of the water rapidly (Fig. 10*C*), and this movement is accompanied by a vigorous paddling that moves the body upward rather than forward in the water. The female also performs Head-dipping movements, but these are not nearly so exaggerated as those of the male. The male mounts before the female has assumed a fully prone posture, and treading lasts about five or ten seconds. As it is completed, the male opens his wings slightly (Fig. 10*D*), and the female begins to call; then both birds rise in the water, calling loudly while strongly lifting their folded wings and cocking their tails (Fig. 10*E*, *F*). The head and neck are stretched upward at a vertical angle, and in this species there is an especially pronounced paddling of the feet so as to agitate the water surface. After both birds settle back, the male usually flaps his wings and both birds bathe and preen.

Bean Goose (*Anser fabalis*)

The numerous races of bean geese (here including the pink-footed goose) illustrate the tendency toward intracontinental subspeciation found in geese. All of the races have a typical gray goose plumage pattern, which lacks distinctive marking; and all of them have a black and yellow (or pink) spotted bill, and yellow or pink feet. Some individuals of the various races exhibit white feathers on the forehead, and in all the races the neck feathers have vertical furrows. The downy young are very similar to those of the white-fronted goose. The species has a broad range in Europe and Asia, and is sympatric with swan geese, graylag geese, white-fronted geese, and lesser white-

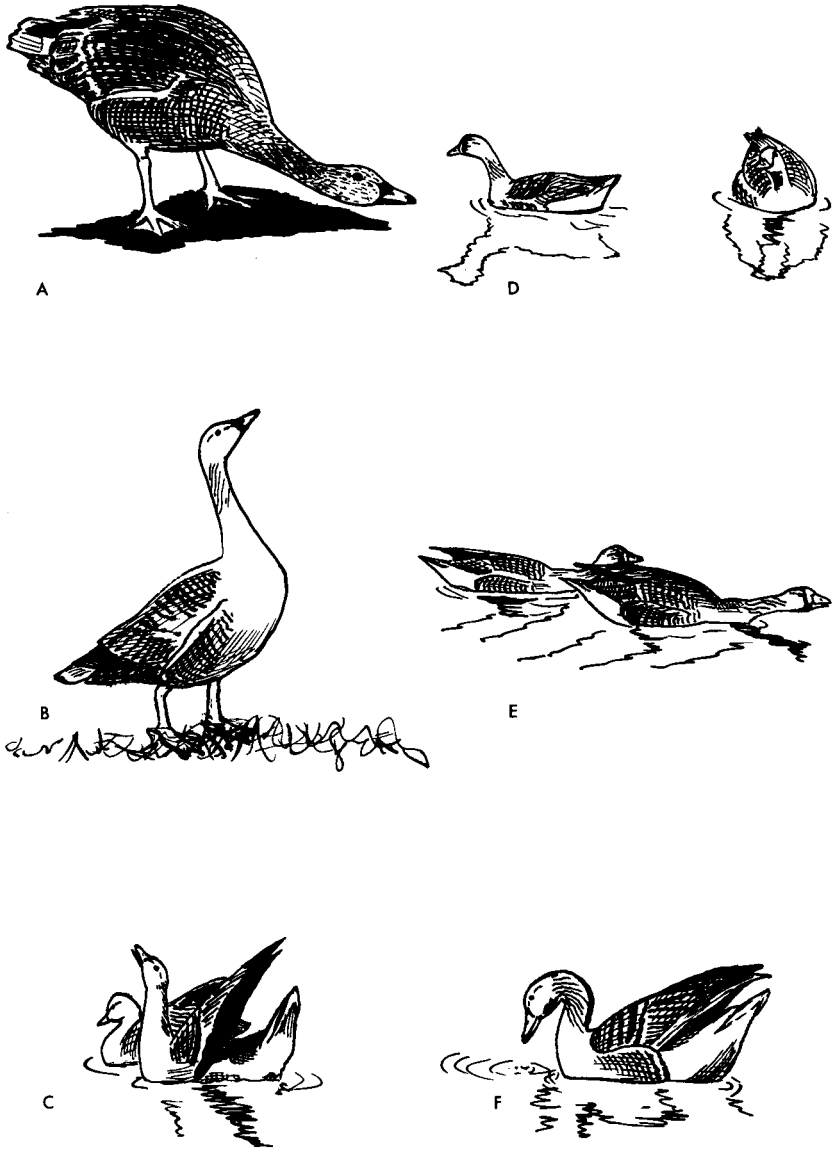


Figure 11. Typical Gray Geese

A. Bean goose, adult male in Forward threat display.
B. Bean goose, adult male in Erect threat display.
C. Bean goose, precopulatory display.
D. White-fronted goose in Diagonal Neck threat posture.
E. White-fronted goose in Forward threat posture.
F. Graylag goose, precopulatory Head-dipping.

fronted geese. Wild hybrids with white-fronted geese have been reported, and in captivity the species has hybridized with graylag and with swan geese.

The various races of bean geese extend from eastern Siberia to eastern Greenland, and may be roughly divided into the forest bean geese, found in the southern and more wooded parts of the range, and the tundra bean geese of the northern and tundra regions (Delacour, 1954). The more northerly races have shorter and higher bills, which may be an adaptation for feeding on the short vegetation of the tundra.

General behavior. Bean geese are typical gray geese in their general behavior. Their aggressive postures include the Erect (Fig. 11*A*), the Diagonal Neck, and the Forward (Fig. 11*B*) displays. After an attack, bean geese often momentarily assume a Bent-neck posture. Except for having a higher-pitched voice, the pink-footed goose does not appear to differ from the other bean geese.

Sexual behavior. The precopulatory and postcopulatory displays of bean geese are like those described for the swan goose, except that postcopulatory wing-raising and paddling are not so conspicuous in this species (Fig. 11*C*).

White-fronted Goose (*Anser albifrons*)

The white-fronted goose has the broadest range of any species of *Anser*, and this species occupies a central position in the genus. The white forehead is evidently an ancient characteristic, for it is present in a reduced form in most of the other species of typical gray geese; and the belly spotting of the adult white-front is also present, to a lesser degree, in the graylag goose. The downy young are very much like those of bean geese, being slightly darker than downy graylags. Unlike that of the bean goose, but like that of the graylag, the bill of the white-front is entirely yellow. The neck feathers are strongly furrowed. Since the species ranges in temperate latitudes throughout most of the Northern Hemisphere, it is sympatric with nearly every other species of *Anser*. Wild hybrids with bean geese have been reported; and in captivity hybrids with swan geese, graylag, lesser white-fronted, snow, and bar-headed geese have been reported. It seems probable that wild hybrids with the graylag occur at times, but such hybrids would be difficult to recognize.

General behavior. Like the other gray geese, the white-fronted goose exhibits such threat displays as the Diagonal Neck (Fig. 11*D*) and the Forward (Fig. 11*E*). It also, like the other species, vibrates its neck feathers as a lateral threat. This threat is visible for only a short distance and probably is most frequently used by grazing birds. The shape of the white forehead and the extent of belly-barring varies greatly among different individuals, and these differences possibly serve as an important basis for individual recognition. The forehead patch is very conspicuous during preflight lateral Head-shaking.

Sexual behavior. Precopulatory and postcopulatory behavior is exactly like that of bean geese and graylag geese, with the posture somewhat less extreme than that described for the swan goose.

Lesser White-fronted Goose (*Anser erythropus*)

The lesser white-fronted goose is one of several miniature forms of geese, which appear to be adapted for breeding in environments unsuitable for the larger species. In this case it is the high-altitude forest tundra of Siberia. Except for its smaller size and a much more conspicuous yellow eye-ring, this species is much like the larger white-fronted goose, and the downy young of the two species are practically identical. Although the lesser white-front is broadly sympatric with the other gray geese of Asia, its smaller size alone probably prevents hybridization. In captivity it is reported to have hybridized with the white-fronted goose and the snow goose.

General behavior. Although it has a higher-pitched voice and more-rapid movements, the species differs in no important way from the other gray geese. I have observed the Diagonal Neck and Forward aggressive displays.

Sexual behavior. The two copulations I observed were in no way different from those of graylag geese or white-fronted geese.

Graylag Goose (*Anser anser*)

The graylag goose, the ancestor of the common domestic goose, is certainly a very close relative of the white-fronted goose. Most individuals have a slightly spotted belly or white feathers on the forehead, and the downy young, although paler, are very similar to those of the white-front. The species ranges throughout Europe and the temperate parts of Asia, and breeds much farther south than the other

typical gray geese. Wild hybrids are not known, but in captivity the graylag has hybridized with most other species of *Anser* and related genera (see Gray, 1958, or Johnsgard, 1960a).

General behavior. Heinroth's excellent discussion (1911) of the behavior of this species cannot be overrated; it should be referred to for a detailed description of vocalizations and general behavior. It may be said here that the behavior of this species is like that of the preceding forms, and that the Diagonal Neck and the Forward postures are the most frequent threat displays. A less conspicuous display, with the head held erect or near the ground while the neck feathers are vibrated, is also frequent. The usual preflight lateral Head-shaking and associated low-calling of this species are typical of *Anser.*

Sexual behavior. The copulatory behavior of the graylag is exactly like that of the white-fronted and the bean goose, and the precopulatory Head-dipping display (Fig. 11*F*) is typical of the genus.

Bar-headed Goose (*Anser indicus*)

Besides the gray geese already discussed, there are four species included by Delacour (1954) in the genus *Anser* which are in some respects rather aberrant and of less certain relationships. Of these, the bar-headed goose is perhaps least aberrant. Its downy young are similar to those of the graylag, but are lighter in color. The adult plumage is very grayish and distinctive. Although the neck feathers are only slightly furrowed, the feathers along the back of the neck are elongated, and these are vigorously vibrated during aggressive encounters. The species has the most southerly distribution of all the forms of *Anser,* breeding in southern Asia and wintering in India and adjacent areas. As a result, the only closely related species with which it has broad contact is the graylag goose. In captivity it has hybridized with this species and also with the swan goose and the white-fronted goose. The hybrids with the last-mentioned species were found to be fertile.

General behavior. Of all the species of *Anser,* the bar-headed goose exhibits the most elaborate visual displays. This is possibly correlated with its reduced vocal diversity; its voice is remarkably nasal and honking, sounding much like an old-fashioned automobile horn. In addition to performing lateral preflight Head-shaking, the bar-headed goose sometimes shakes its head in a rotary fashion, which

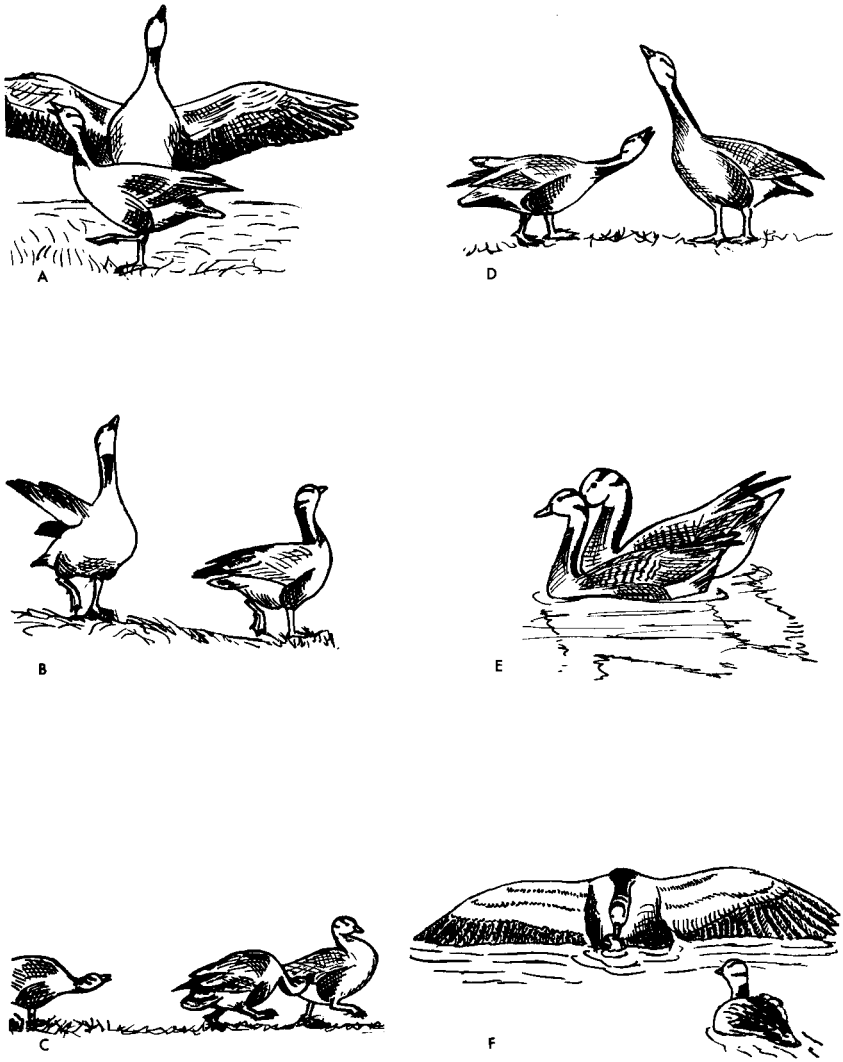


Figure 12. Bar-headed Goose

A. Male in high-intensity Erect threat posture with wings outstretched, facing intruder who is calling in Diagonal Neck posture.

B. Male in Erect posture while Wing-flicking and threatening intruding bird.

C. Male and female in Forward posture and chasing intruding bird.

D. Triumph Ceremony between pair (*male on right*) after the expulsion of intruder.

E. Precopulatory display (*male in background*).

F. Copulation. Male bar-headed geese apparently typically extend their wings fully as they finish treading.

emphasizes its bold head-markings. The Diagonal Neck and Erect postures are very frequently assumed, and they are often alternated rapidly with the Forward Display (Fig. 12*A–C*), which results in graceful and rather sinuous neck movements. During extreme Erect displays, the wings are sometimes extended fully (Fig. 12*A*), producing an impressive threat display. As in most species of geese, the folded wings are often alternately raised and lowered during threat (Fig. 12*B*). During Triumph Ceremonies the birds call with their bills pointed almost vertically upward (Fig. 12*D*).

Sexual behavior. The precopulatory display consists of the usual anserine Head-dipping movements, alternated with an erect and cocked-tail posture (Fig. 12*E*). During treading, the male sometimes spreads his wings to the utmost (Fig. 12*F*), and the postcopulatory display—with the wings and tail lifted to the extreme—is just as impressive as that of the swan goose.

Snow Goose (*Anser caerulescens*)

The second aberrant species of gray goose, the snow (or "blue") goose, is clearly a member of the genus *Anser*. The downy plumage of the white ("snow") phase is very like that of the graylag, although in the "blue" phase it is much darker. The adult plumages of the two phases are distinctive, but the neck feathers are furrowed as in the other gray geese. Cooch (1958, 1961) has discussed the genetic and evolutionary significance of the two color-phases in this species. His work is extremely interesting, and the reader is referred to it for details. Snow geese range through much of North America and extreme eastern Asia. The species is sympatric with Ross's goose, the emperor goose, and the white-fronted goose in North America, and with some additional species in Asia. It has apparently hybridized in the wild with two species of *Branta,* and in captivity with the graylag goose, Ross's goose, and the emperor goose.

General behavior. Behaviorally, the snow goose is not obviously different from the typical *Anser* species. The usual Diagonal Neck and Forward threat postures are present, and the neck feathers are vibrated in aggressive situations. During nest defense the tail is spread, the scapular feathers are ruffled, and the bill is held near the ground (Fig. 13*B*).

Sexual behavior. Snow geese are very similar to the typical gray geese in their sexual behavior, including the courtship posture (Fig.

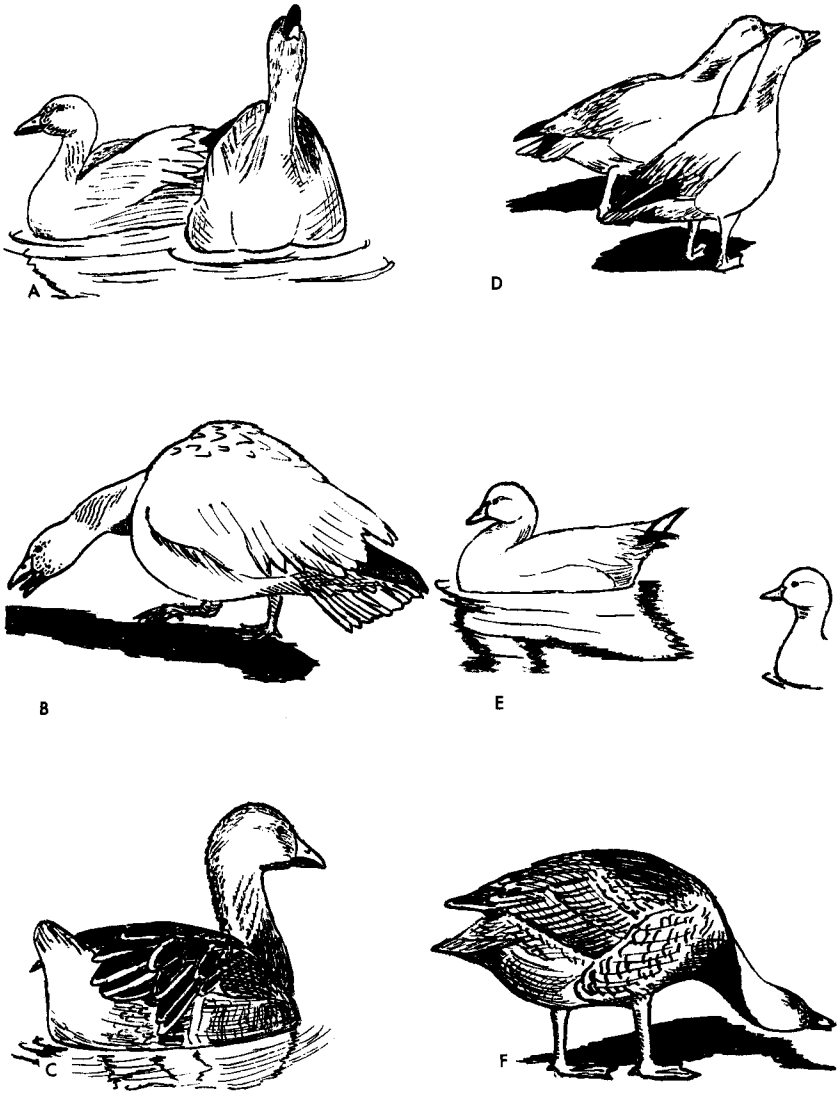


Figure 13. Aberrant Gray Geese

A. Lesser snow goose. Postcopulatory display. The male (*at right*) is calling.

B. Lesser snow goose nest defense by female. Note spread tail and ruffled body feathers.

C. Courtship posture by lesser snow goose (blue phase). Note erect posture and cocked tail.

D. Ross's goose calling in Diagonal Neck threat posture.

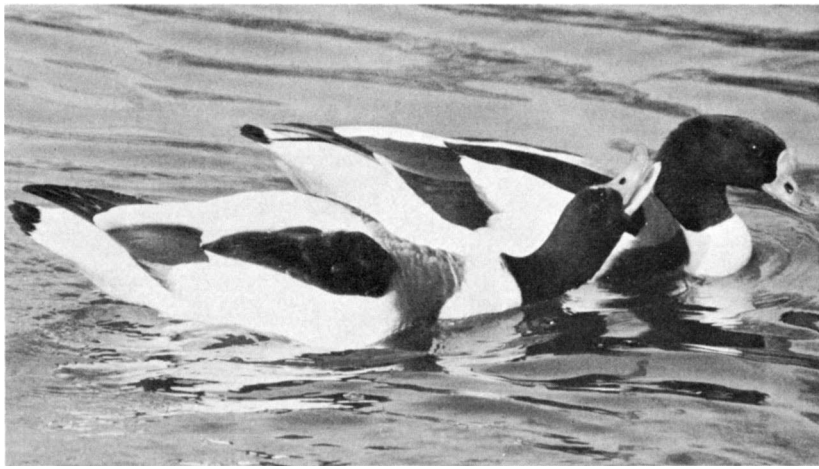
E. Ross's goose male (*left*) courting female. Compare with *C.*

F. Emperor goose in Forward threat posture.

Mute Swan, threat posture of adult male.

Triumph Ceremony of Black-necked Swan.

Threat posture of Red-breasted Goose.



Pair of Common Shelducks, female in Inciting posture.

13C) and the behavior associated with copulation. After treading, the wings are not raised so high and the tail is not so greatly cocked as in the typical gray geese (Fig. 13*A*).

Ross's Goose (*Anser rossi*)

Ross's goose is the second of the miniature forms of geese, and it perhaps has an advantage over the larger snow goose for arctic breeding because of its shorter incubation and fledging period as well as reduced food requirements. In color the downy young exhibit a remarkable polymorphism, but they are generally like the downy young of the white phase of the snow goose. The adult plumage is identical with that of the snow goose. Ross's goose has a very restricted breeding range in arctic Canada and is sympatric with the snow goose. In capitivity hybrids have been obtained with snow geese, graylag geese, and emperor geese.

General behavior. Except during the breeding season, Ross's goose is extremely docile. Threat displays consist of the usual Diagonal Neck and Forward postures, but they are seen only rarely (Fig. 13*D*).

Sexual behavior. The courtship posture of the male Ross's goose (Fig. 13*E*) is like that of typical gray geese. The precopulatory display consists of mutual Head-dipping as in the other gray geese, and postcopulatory posturing is relatively weak.

Emperor Goose (*Anser canagicus*)

The least *Anser*-like species of the aberrant gray geese is the emperor goose. Its downy young are an unusual silvery gray, and the plumages of juveniles and adults are also unique, with a black and white barring on the body feathers that produces a striking "scaled" effect. Unlike those of all other typical geese, the under-tail coverts are not white; rather, they are of a gray color similar to that of the rest of the body. Vertical neck furrowing is absent or nearly so. The bill is multicolored and remarkably short. The species occurs in western Alaska and eastern Siberia, and is sympatric with several species of *Anser*. In captivity hybrids have been reported with white-fronted geese, snow geese, and Ross's geese.

General behavior. The emperor goose is highly social and has few well-defined threat displays. I have seen no vibration of the neck feathers, and the only aggressive display I have noted is a striking Forward posture (Fig. 13*F*), in which the head is held low to the

ground and the white head and nape form a conspicuous pattern against the darker body.

Sexual behavior. I have not observed a complete copulation, and the only probable precopulatory behavior which I have observed lacked marked tail-cocking and rather resembled normal feeding behavior.

BLACK GEESE

Although the black geese (*Branta*) are closely related to *Anser,* they are an easily recognizable group. They differ from the gray geese mainly in having a darker plumage and black bills and feet. Although vertical neck furrowing is conspicuous in only one species, it occurs in all but one of the five species and evidently functions in the same way as it does in *Anser.* Aggressive displays and Triumph Ceremonies are much like those of *Anser,* but the Bent Neck posture (see Collias and Jahn, 1959, and Blurton Jones, 1960) of *Branta* is more conspicuous and tends to replace the Diagonal Neck display of *Anser.* The Forward and Erect postures occur in both genera, and Head-pumping (Collias and Jahn, 1959) is a threat display in at least one species of *Branta.* Copulatory behavior differs only slightly in the two genera.

Hawaiian Goose (*Branta sandvicensis*)

The Hawaiian goose, or nene, is the only true goose which is not of continental distribution. It is almost certainly an ancient derivative of North American Canada goose ancestral stock, although it has deviated from the Canada goose in many respects, primarily in being almost wholly terrestrial. The downy young are silvery gray and very different from those of the Canada goose. The adult plumage differs from that of the Canada goose mainly in its buff-colored cheeks and neck, and in the strongly furrowed neck feathers. The foot webbing is reduced, although the birds are able to swim well and can even dive. It is not sympatric with any other goose and has been hybridized only with the swan goose. Woolfenden (1961) believes that the Hawaiian goose should be placed in the monotypic genus *Nesochen.*

General behavior. Hawaiian geese are by comparison with Canada geese rather quiet birds, and their most frequent call is a low mournful moan; only in great excitement do they utter anything that approaches the honking call of Canada geese. A number of aggressive

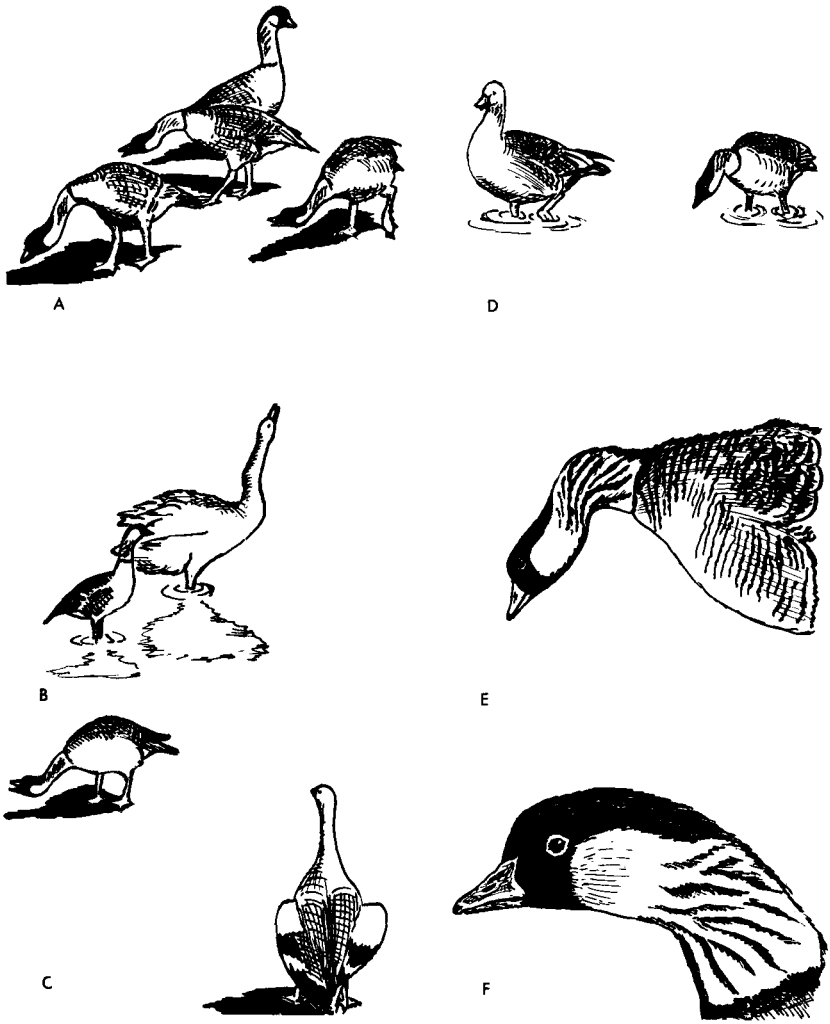


Figure 14. Hawaiian Goose

A. Threat postures. The birds in the rear are in the Erect posture, while the nearer birds are in the Forward posture.

B. Threatening juvenile mute swan in Erect (*left*) and Bent Neck (*right*) postures. The swan is performing a general shake, possibly as a threat display.

C. Threatening a ruddy-headed goose in Forward posture. The ruddy-headed goose is in a typical threat posture as well, standing erect with his wings partly extended.

D. Threatening a graylag goose in the Bent Neck posture.

E. Bent Neck posture as usually seen by opponent.

F. Low-intensity threat display involving the shaking of the striated neck feathers.

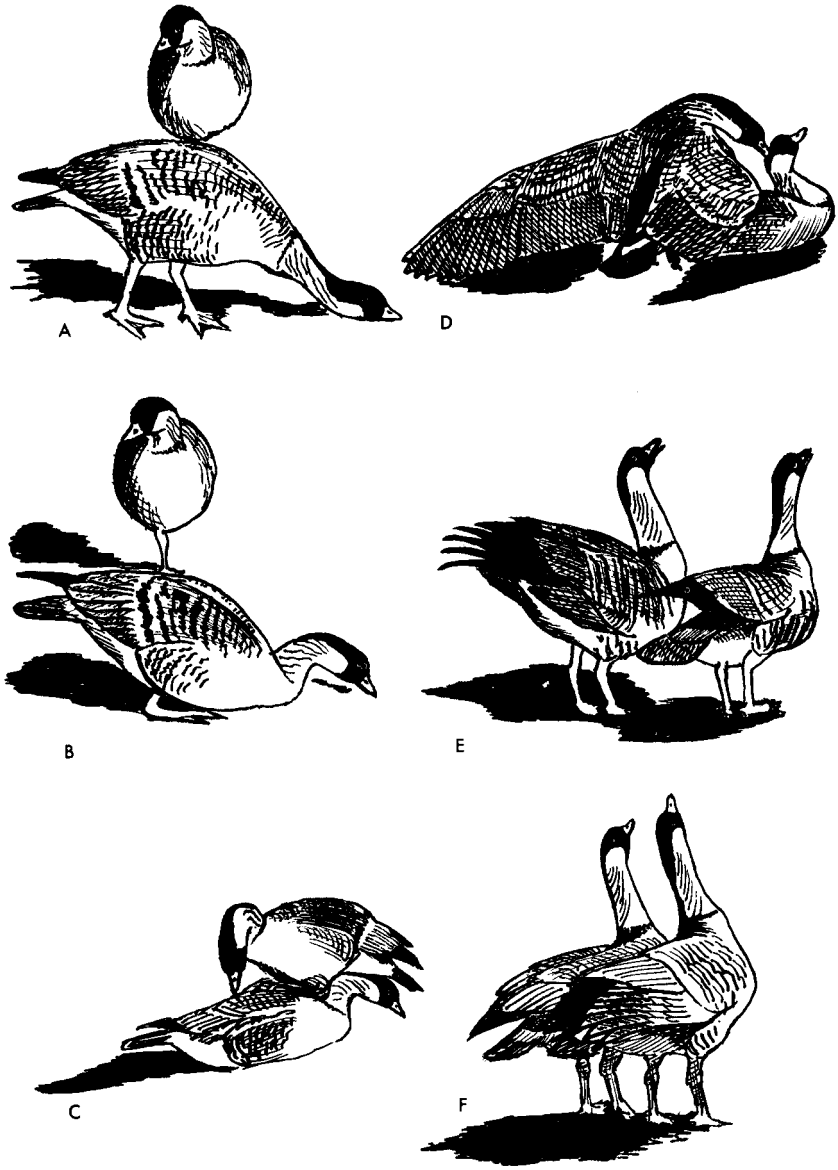


Figure 15. Hawaiian Goose
A–F. Copulatory behavior.
A, B. Precopulatory Head-dipping movements performed by male.
C. Female prone and male mounting.
D. Treading. Note extended wings and pulling of the female's nape.
E, F. Postcopulatory display (two different occasions).

displays are present, the most frequent perhaps being the Bent Neck posture (Fig. 14*D, E*), which is accompanied by vibrations of the neck feathers. The vibrations are especially conspicuous because the neck feathers are not only furrowed but also dark at the base. The vibrations also occur when the head is held in a normal position (Fig. 14*F*) during low-intensity threat. Another threat posture is the Erect (Fig. 14*A, B*), and the Forward posture (Fig. 14*A, C*) is perhaps the most extreme threat. The Triumph Ceremony of this species is much like that of the Canada goose; the pair call mutually with open bills, and they make intermittent sideways and vertical head movements more or less directed toward the opponent.

Sexual behavior. Unlike all other typical geese, Hawaiian geese normally copulate on land or at the shoreline. Young geese usually attempt copulation at the water's edge, and once I observed young birds attempt it while they were swimming. Nevertheless, in all cases the precopulatory display consists of Head-dipping movements which are clearly derived from bathing. Each of the two birds extends its neck and head on the ground (Fig. 15*A*), then rapidly pulls it back, at the same time turning it slightly, just as a bathing bird would (Fig. 15*B*). The two birds tend to synchronize their movements, and the female soon goes prone (Fig. 15*C*). As treading is completed the male opens his wings and pulls back the female's head (Fig. 15*D*); then both birds call and droop their wings, at the same time extending their head and neck almost vertically (Fig. 15*E, F*).

Canada Goose (*Branta canadensis*)

The Canada goose, with its twelve subspecies, provides the best example of the tendency toward intracontinental subspeciation resulting from the mating tendencies and strong family bonds typical of geese. The downy young much resemble those of graylag and other gray geese. The adult plumage is similar to that of Hawaiian and barnacle geese. The Canada goose is found throughout most of North America, and is sympatric with the brant; the latter, however, is a maritime species, and the two species are not normally in close contact. Wild hybrids have been reported with the white-fronted goose, the snow goose, and the brant goose; and many species have hybridized with the Canada goose in captivity (see Gray, 1958).

General behavior. Much has been written on the behavior of Canada geese, the studies of Balham (1954), Collias and Jahn

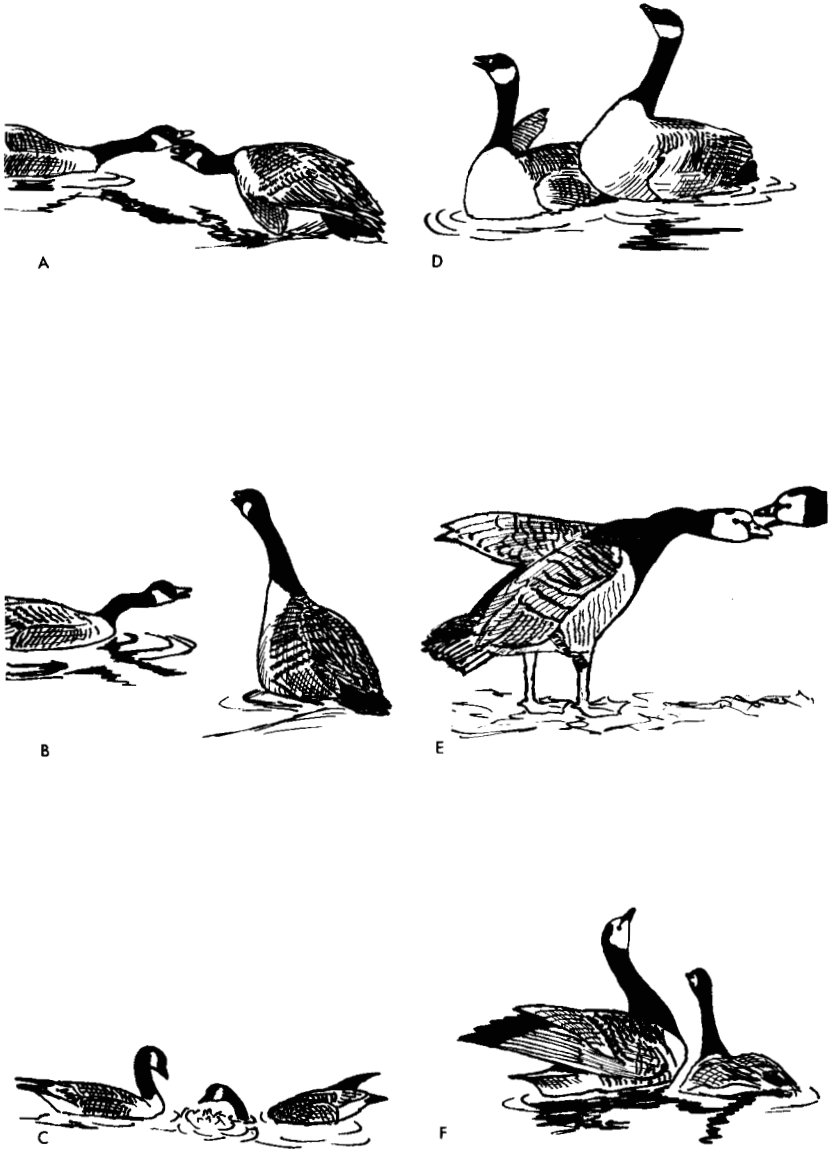


Figure 16. Canada Goose, Barnacle Goose

A, B. Canada goose Triumph Ceremony. Note neck-waving and calling by both birds.

C. Precopulatory Head-dipping by Canada geese (*male on left*).

D. Postcopulatory display by Canada geese (*male on right*).

E. Barnacle goose Triumph Ceremony, with alternate Wing-flicking.

F. Barnacle goose postcopulatory display (*male on left*).

(1959), and Klopman (1962) being only three examples. In behavior, all the races of Canada geese are very similar, and threat displays include the Bent-neck, Forward, Erect, and Head-pumping postures (Blurton Jones, 1960). Canada geese also vibrate their neck feathers during threat, although this action is not conspicuous. They also open their bill and raise their tongue during threat display, and during Triumph Ceremonies they assume a posture similar to the Forward and do much calling and make threatening movements of the head (Fig. 16*A*, *B*). Preflight movements differ from those of any species previously considered, for in addition to making lateral Head-shaking movements, they also lift their chin, exhibiting and flashing their white cheeks and throat most conspicuously. The same type of preflight movement is used by barnacle geese (but not by Hawaiian geese), which have similar cheek and throat markings.

Sexual behavior. The precopulatory display of Canada geese consists of mutual Head-dipping, which is clearly derived from bathing movements (Fig. 16*C*). During postcopulatory display the wings are not noticeably raised, but the neck is stretched and the chin is lifted as both birds call in a mournful wail reminiscent of the Hawaiian goose (Fig. 16*D*).

Barnacle Goose (*Branta leucopsis*)

The barnacle goose is primarily an old world species and a close relative of the Canada goose. Its downy plumage resembles that of the Canada goose, but also has the whitish under-part coloration typical of the downy brant goose. The barnacle goose has produced fertile hybrids with the Canada goose, and the species has hybridized in captivity with the brant goose, with which it is broadly sympatric.

General behavior. Barnacle geese are very like Canada geese in their general behavior, and the two species make almost identical preflight movements. Aggressive postures include the Bent Neck and Forward postures, and the Triumph Ceremony of barnacle geese is very similar to that of Canada geese (Fig. 16*E*).

Sexual behavior. The precopulatory display of barnacle geese consists of mutual Head-dipping very much like that of Canada geese. During the postcopulatory display the male lifts his wings more distinctly than does the male Canada goose, but the posturing is otherwise almost identical (Fig. 16*F*).

Brant Goose (*Branta bernicla*)

The brant goose is a very small, maritime species of *Branta* which, judging from its downy plumage, is probably most closely related to the barnacle goose. The species has the broadest range of any of the *Branta* group, and has speciated into several forms of uncertain taxonomic status. Following Delacour's interpretation, they are here considered a single species. The brant has produced fertile hybrids with the Canada goose, and has also been hybridized in captivity with the barnacle goose and several species of *Anser*.

General behavior. The brant does not seem to be very similar to the preceding species in its general behavior. There is little ritualization of threat postures, and the Forward posture (Fig. 17*A*) usually precedes overt attack. There is also a posture resembling the Diagonal Neck of *Anser*, but I have seen no Bent Neck posture, nor have I observed any preflight movements. The white, crescent-shaped markings on the neck apparently represent a restriction and specialization of the neck-feather furrowing, and at close range it may be seen that these white feathers are indeed vibrated in threat situations. It is also of interest that although this species is the darkest of the black geese, its under-tail coverts (which probably function in courtship display) and its upper-tail coverts (which apparently serve as a flight signal) have remained an immaculate white, clearly indicating the importance of these areas as signals.

Sexual behavior. The precopulatory display of brant geese consists of mutual Head-dipping (Fig. 17*B*), with almost no cocking of the tail. At times the Head-dipping almost takes the form of upending, and it is quite unlike the precopulatory Head-dipping behavior of the red-breasted goose. During the postcopulatory display the wings are not raised at all (Fig. 17*C*).

Red-breasted Goose (*Branta ruficollis*)

The red-breasted goose deviates from the other black geese both in the color of its downy young, which are much darker than the downy young of the other species, and in the plumage pattern of its adults. The rich reddish-brown breast of the adults is unique among geese, and so too is the strikingly contrasting black and white color of the rest of the bird. This is the only species of *Branta* which lacks vertical neck-feather furrowing, but the lengthened "mane" feathers on the back of the neck functionally replace them during threat dis-

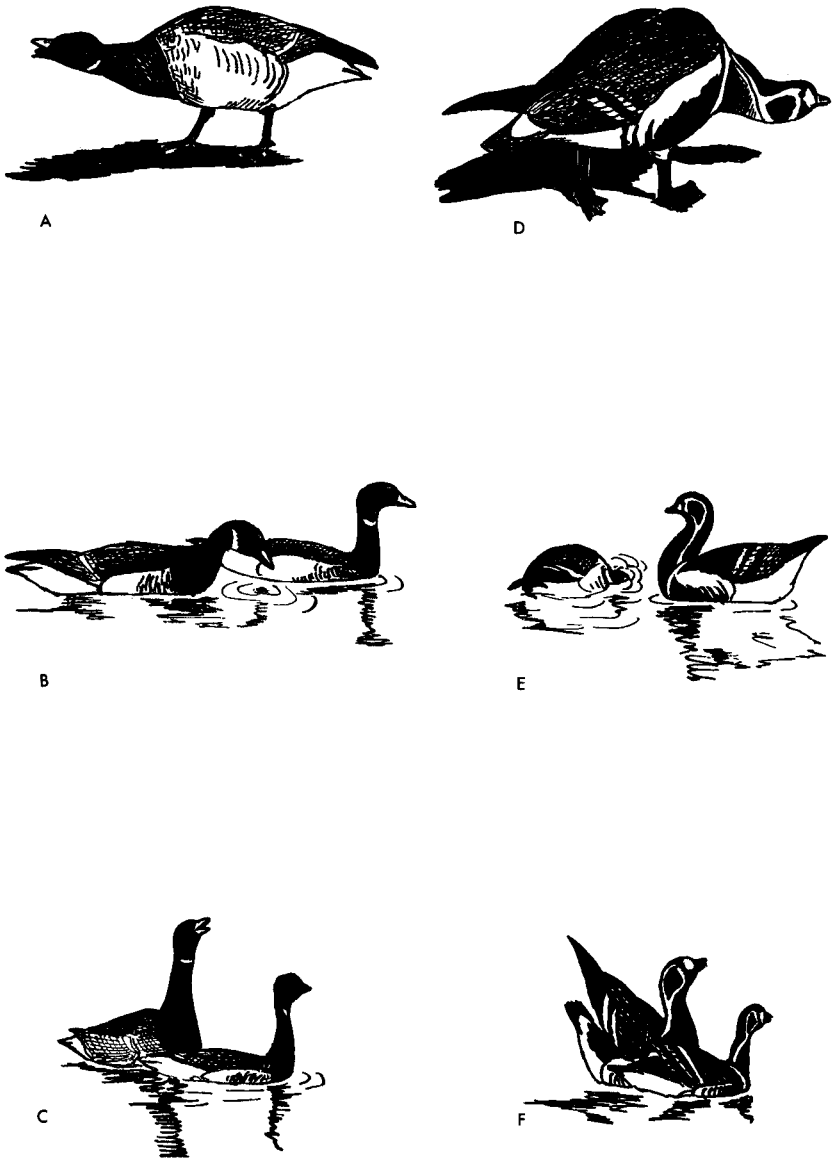


Figure 17. Brant, Red-breasted Goose

A. Atlantic brant in Forward threat display

B. Pacific brant performing precopulatory Head-dipping (*male on left*).

C. Pacific brant postcopulatory display (*male on left*).

D. Red-breasted goose in Forward threat display.

E. Red-breasted goose performing precopulatory Head-dipping.

F. Red-breasted goose postcopulatory display.

play. The species has a restricted range in Europe and western Asia and is sympatric with only the brant goose. In captivity it has produced fertile hybrids with the Canada goose.

General behavior. Red-breasted geese apparently lack the specialized preflight movements typical of Canada and barnacle geese, and use lateral Head-shaking little if at all in this connection. The species exhibits two fairly distinct forms of threat: a lateral threat, in which the head is held erect and the elongated neck feathers are vigorously vibrated; and a more extreme threat involving the Forward display (Fig. 17*D*), in which the head and neck, pointed toward the opponent, are held close to the ground and the head is occasionally shaken in a rotary manner (McKinney, 1953). This Forward display is highly ritualized and often does not lead to an overt attack.

Sexual behavior. The exaggeration of visual display found in the aggressive behavior of the red-breasted goose is also present in its sexual displays. The precopulatory Head-dipping is marked by the same very erect attitude and cocking of the tail that are typical of some gray geese (Fig. 17*E*), and is quite unlike the precopulatory posture of the other black geese. The postcopulatory display is likewise marked by an extreme raising of the wings, cocking of the tail, and stretching of the neck (Fig. 17*F*).

Cape Barren Goose (*Cereopsis novae-hollandiae*)

Although Delacour (1954) placed the Australian Cape Barren goose, or cereopsis, with the sheldgeese in the tribe Tadornini, I feel that in the majority of its characteristics it is closer to the true geese. There is no doubt, however, that it does have affinities with the sheldgeese as well, for the pattern of its downy young clearly indicates that it is related to that group. In its reticulated tarsus, its gooselike trachea (and voice), and in its general anatomy (Verheyen, 1953), however, it more closely resembles the true geese. It is certainly not very closely related to any other species of goose or sheldgoose, and it has never hybridized with any other species. Woolfenden (1961) has designated a monotypic tribe, Cereopsini, within the Anserinae, for this species.

General behavior. The Cape Barren goose, besides being basically a generalized, or "primitive," bird, has become adapted (presumably secondarily) to a highly terrestrial and rather sedentary existence. This is indicated by its semipalmated feet and by the fact that it seldom swims. Although it flies well, I have not observed any preflight

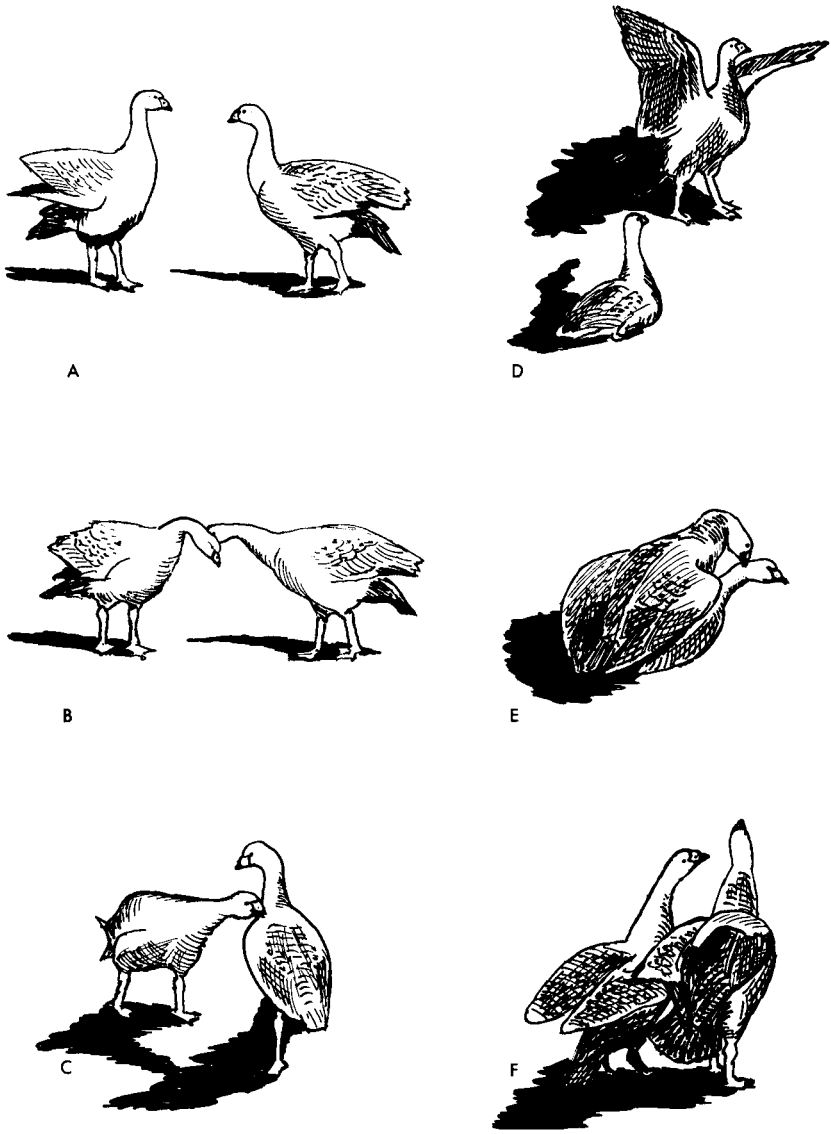


Figure 18. Cape Barren Goose

A, B. Triumph Ceremony (*male on left*).

C–F. Copulatory behavior.

C. Precopulatory circling of the female (*right*) by the male as he pecks at her back and neck.

D. Female prone, male Wing-flapping before mounting.

E. Treading.

F. Postcopulatory display (*male on right*).

movements. The species is very aggressive, and males will run or fly toward an opponent and strike it with their wings. Since these birds, like sheldgeese, have bony knobs at the wrist, their wings make very effective weapons. After making an attack, the male will rush back to the female, and the two birds will perform a typical anserine Triumph Ceremony, calling excitedly and moving the head stiffly up and down with neck extended (Fig. 18*A, B*). As in species of true geese, the voice of the male is higher pitched than that of the female, and both sexes utter piglike grunts of one syllable.

Sexual behavior. Cape Barren geese appear to pair for life and to have strong pair bonds. Copulation apparently always occurs on land, and as evidence that this has been the pattern for a long time, there is no indication of the mutual Head-dipping movements characteristic of all other geese and swans. Rather, the male simply and suddenly begins to walk rapidly around the female, pecking at her back and evidently attempting to push her to the ground (Fig. 18*C*). The female may walk away or, more typically, abruptly settle to the ground with her head and neck still rather erect. The male then walks around her a few times and—I am describing the three cases I observed—flaps his wings before finally mounting (Fig. 18*D*). As soon as the male mounts, the female lowers her head and raises her tail. Treading may last up to about ten seconds, during which the male grasps the female's nape (Fig. 18*E*). Afterward, the male quickly releases the female and dismounts; then the birds call in unison and face one another, shaking their wings and bowing in a manner reminiscent of a Triumph Ceremony (Fig. 18*F*).

TRIBE STICTONETTINI (FRECKLED DUCK)

Freckled Duck (*Stictonetta naevosa*)

At this point I wish to include the Australian freckled duck, as the only member of a proposed tribe Stictonettini, as I originally suggested in 1960 on a tentative basis. Previously the freckled duck had been generally considered an aberrant dabbling duck with several primitive features, such as a reticulated tarsus, simple tracheal structure (illustrated in Johnsgard, 1961c), and absence of metallic plumage coloration or distinct plumage dimorphism. However, Verheyen (1953) found that some of its skeletal features, such as the palatine structure, the shape of the sternal apophysis, and the number of cervical vertebrae, suggest anserine affinities, and he placed

the species near the whistling ducks. Until recently its downy plumage remained undescribed, but Frith (1964) determined that the downy young lack contrasting patterns and are surprisingly similar to those of the black swan. Therefore I believe that my earlier conclusions regarding this species were justified, and that the freckled duck should be accorded the distinction of constituting a monotypic tribe within the subfamily Anserinae. No hybrids have been recorded involving this species, which occurs widely but infrequently over the southern half of Australia.

General and sexual behavior. During rather extended observations which I made on wild individuals of this species, several previously unreported behavioral features were found. These have been reported more extensively elsewhere (Johnsgard, 1965a), and the following short summary may suffice. Freckled ducks are surface-feeders, generally foraging by filter-feeding with only the bill submerged, but occasionally up-ending. No preflight movements have been seen, but during take-off the birds run some distance over the water in the manner of geese, swans, and whistling ducks. In flight and on the water both sexes are relatively quiet and appear to lack alarm calls. During the breeding season the red base of the male's bill readily distinguishes the sexes, and in addition the male seems to have a slightly darker and more crested head. Females appear to lack Inciting displays, and I observed no social courtship during the three weeks that I studied the birds. Indeed, the only clear-cut display I observed was a mutual neck-stretching and calling, similar in form to the Triumph Ceremonies of swans, although not necessarily occurring in the same context. No obvious pairing of birds was detected, and this mutual display appeared to occur between various individuals, often after a gaping on the part of one of the two. The neck-stretching was accompanied by bill movements and probable calling, but I was never close enough to the birds at such times to ascertain this point. According to H. Frith (pers. comm.), freckled ducks have several trumpeting or flute-like calls that are uttered in various situations. The evident absence of well-defined courtship displays, the occurrence of mutual displays, and the apparent lack of Inciting displays by females tends to substantiate the view that this species is anserine rather than anatine in its relationships. Unfortunately its copulatory behavior is still unknown, and when this and additional behavioral evidence is available a more certain appraisal of the freckled duck's affinities will probably be possible.

The Subfamily Anatinae

The last, and by far the largest, subfamily of waterfowl includes the sheldgeese, the shelducks, and the true ducks. The subfamily differs in several respects from the preceding groups. Nearly all the species possess tarsi which have a scutellated rather than reticulated pattern in front, most species have tracheae and syrinxes which differ in the two sexes, and most (possibly all) species undergo two molts of the body feathers annually. These last two features are correlated with the length and strength of the pair bond, as is also the fact that there tends to be a sexual dimorphism in adult plumages. Most and possibly all species mature in their first or second year of life.

TRIBE TADORNINI (SHELDGEESE AND SHELDUCKS)

The first tribe of the Anatinae includes the 16 species of sheldgeese and shelducks ("*Lophonetta*" and *Tachyeres* are here excluded from the tribe) which provide such a smooth transition from the true geese to the true ducks that it is difficult to establish a dividing line between the two groups. I believe that the line is best placed between *Cereopsis* on the anserine side and *Cyanochen* on the anatine side. *Cyanochen* is clearly a sheldgoose, but the plumages and voices of the sexes are practically alike, as are also their displays. *Cyanochen* and the other Tadornini are characterized by a downy plumage that is strongly marked with dark and white, by a tendency to nest in cavities, and by the fact that they forage either by grazing (sheld-

geese) or by grazing and dabbling (shelducks). Metallic plumage coloration is encountered in this group, as are vermiculated feather patterns; both are typical of most of the rest of the Anatinae. Pair bonds appear to be fairly strong in sheldgeese, but less strong in shelducks. Unlike that of the true geese, pair-forming, or courtship, behavior is conspicuous, and in this group may be observed the basic pair-forming mechanism which is to be found, in varying degrees of refinement, in all other tribes of Anatinae. Simply stated, this is the tendency of the female to Incite (Lorenz, 1951–1953) males to attack other males or females, and to "select" her mate on the basis of the male's reaction to this Inciting. Here sexual selection enters the picture, and the complex male plumage patterns and male courtship-behavior patterns can be understood and interpreted only by reference to the principle of sexual selection.

In his highly significant studies on the behavior of the Anatinae, Lorenz (1941; 1951–1953) emphasized this basic principle of pair formation. He states that female Inciting occurs in a homologous manner, although in outwardly different fashions, throughout most of the true ducks. The following quotation clearly states his (and my) views: "I am convinced that it [Inciting] represents a real 'phylogenetic order' for, beyond all doubt, the forms of Inciting as they are found in Casarcinae (= Tadornini) and indeed, to a certain extent in Anserinae, represent the original form of the [Inciting] movement. Until one recognizes this one cannot understand at all the ceremonies of the Anatinae, which, in their significance, are strongly modified." Although Lorenz uses "Anatinae" here in the restricted (Anatini) sense, his statement remains true if the more inclusive, Delacourian usage of the term is accepted. The evolutionary origin of Inciting is obscure and must remain a matter for speculation, but it may have derived from the Triumph Ceremonies typical of the Anserinae.

In the Tadornini, female Inciting is almost completely functional, and the typical male response to Inciting is immediately to threaten, and often to attack, the indicated opponent. In its more primitive form, as found in *Cyanochen* and *Chloëphaga,* Inciting consists primarily of calls, and if visual signals do accompany these calls, they do not have a marked directional orientation. In its more advanced forms (*Alopochen* and *Tadorna*) Inciting clearly has a directional basis, and the form of the Inciting movements is to some degree de-

pendent upon the position of the object of the Inciting. (Later it will be seen that in the more advanced and highly specialized tribes this directional tendency is often secondarily lost, although the "pointing" movements may remain a part of these highly ritualized displays.)

The reaction of the males to Inciting is all-important to their success in obtaining a mate. In motivational terms, they are in conflict between attacking the indicated enemy, escaping from this enemy, and reacting sexually toward the female (Moynihan, 1955). Presumably as a result of these conflicting tendencies, displays have evolved which exhibit varying degrees of compromise among the various tendencies. This aspect of displays will not be considered here, but further discussion on the origin, function, and evolution of displays may be found in the papers of Moynihan (1955) and Hinde (1959), to which the reader is referred.

Abyssinian Blue-winged Goose (*Cyanochen cyanopterus*)

As stated above, I believe that the blue-winged goose is the most generalized species of the present tribe. Indications of this are the absence of plumage dimorphism in the two sexes and the similarity in the behavior and voices of males and females. Both sexes have high-pitched, almost whistling voices, and the female seems to lack the low guttural calls of most anatine females. The male trachea has a fairly small, rounded, and bony bulla. The downy young exhibit the typical contrasting sheldgoose pattern. The adult plumage is mostly grayish, but the secondary feathers have a slight metallic-green sheen. Unlike those of nearly all the other species of the tribe, the upper-wing coverts are not white but pale blue. The lesser coverts, however, and also the underwing linings, are white. The species is restricted to northeastern Africa, and is sympatric with the Egyptian goose, with which it has produced fertile hybrids in captivity. It has also hybridized with the Orinoco goose and two species of *Chloëphaga*.

General behavior. The most characteristic aspect of the general behavior of blue-winged goose is the way in which the bird holds its head back on its shoulders when at rest or while walking undisturbed; a similar posture is sometimes adopted by the Andean goose. The species is a bird of the highlands, and it walks and runs well. McKinney (1953) observed lateral Head-shaking and, possibly, Chin-lifting as preflight movements.

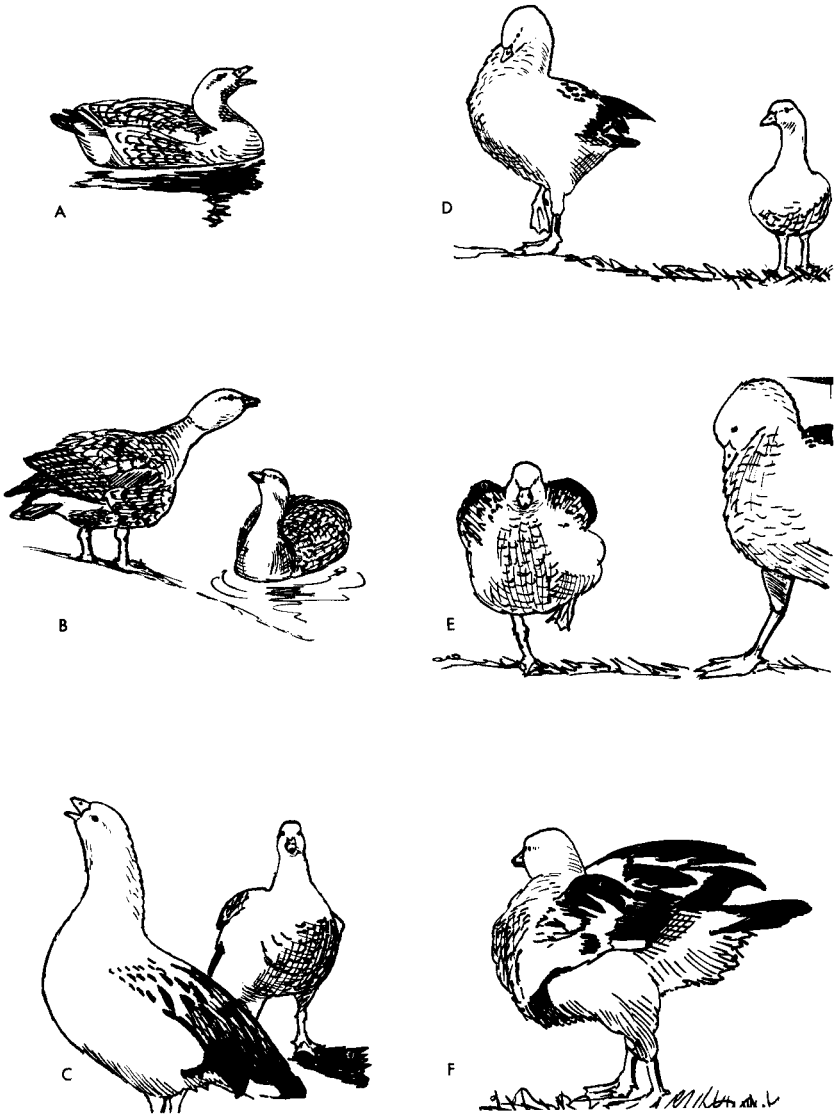


Figure 19. Blue-winged Goose, Andean Goose

A. Blue-winged goose male in threat posture, gaping but not calling.

B. Blue-winged goose pair (*male on left*) calling mutually after an aggressive encounter, apparently a form of Triumph Ceremony.

C. Male Andean goose (*left*) uttering aggressive whistling note.

D. Male Andean goose (*left*) performing Puffing display.

E. Female Andean goose (*left*) Inciting while male performs Puffing display.

F. Female Andean goose Inciting.

Agonistic (attack-escape) behavior. I have observed little aggressive behavior in females, and nothing except repeated calling which I could attribute to Inciting. Males frequently threaten smaller waterfowl, swimming or standing very erect, with neck oustretched and head held high, but with the wings closed and inconspicuous (Fig. 19*A*). After making such a threat, a male runs back to his mate, rapidly whistling *wi-wi-wi-wi-wi-wi*. . . . She responds in the same manner, and the two stand calling with their necks diagonally outstretched, heads close together, and bills almost touching, in what is clearly a kind of Triumph Ceremony (Fig. 19*B*). I have called this posture and call the Wi-wi call, and obvious homologies can be found in the other sheldgeese, but only among males.

Sexual behavior. I have not observed copulatory behavior or been able to learn anything about it.

SOUTH AMERICAN SHELDGEESE

Five species of sheldgeese of the genus *Chloëphaga* form a closely knit group of great evolutionary and behavioral interest. They are all generally very similar and share the common characteristics of having white upper-wing coverts, a metallic-colored speculum formed by the secondary coverts (rather than by the secondaries as in other anatines), and white secondaries. In all species the male voice is a whistle and that of the female a low, ducklike cackle. All have short, high bills adapted for grazing, and all species are semiterrestrial. In three species the sexes differ scarcely if at all in their adult plumage, whereas in the other two species the sexes could hardly be more different. Although the explanation for this is still by no means clear, it does appear that the males of the species which exhibit marked sexual dimorphism in plumage (Magellan and kelp geese) do not perform such elaborate displays as the males of species in which the sexes have similar plumage patterns.

Andean Goose (*Chloëphaga melanoptera*)

On at least two counts the Andean goose appears to be rather closely related to the blue-winged goose. The yellow facial markings and cheek patches of the downy young of both species indicate a close affinity, and the general posture and shape of the adults are also similar in the two species, although this may reflect nothing more than that both species dwell for the most part in the uplands.

The adult plumage pattern of the Andean goose is typical of *Chloëphaga,* and is a contrasting black and white in both sexes. The Andean goose is more northerly ranging and mountain-inhabiting than are the other species of this genus, and it is apparently not sympatric with any of them. Hybrids have been obtained in captivity with the Magellan goose and the Egyptian goose.

General behavior. Although the sexes of the Andean goose are marked exactly alike, there is no difficulty in determining the sex of an adult bird. Besides being larger, the male is almost continually calling and displaying before the female. I have observed mutual nibbling of the cheeks between paired birds (Fig. 20*D*), but I have not recorded any preflight movements.

Agonistic and sexual behavior: female. This is the first species so far dealt with which clearly exhibits a true Inciting behavior. While Inciting, the female calls rapidly and strongly a hoarse *gack-gack-gack* . . . and shakes her tail from side to side and walks with high steps, holding her folded wings and hindquarters in a characteristic high position (Fig. 19*E, F*). There is no directional orientation of the head toward the object of the Inciting; rather, the female tends to walk away from the opponent and around her mate. She holds her head high, never lowering it as the females of some of the following species occasionally do.

Agonistic and sexual behavior: male. It is difficult to distinguish between agonistic and sexual behavior in this and the following species because, as I mentioned earlier, the male displays combine elements of attack, escape, and sexual tendencies. The primarily agonistic displays of the male Andean goose include a number of only slightly modified comfort movements. These are ritualized versions of the general shake (McKinney, 1953), wing-flapping (Fig. 20*A, B*), and head-rolling (Fig. 20*C*). Of these, the last is most striking, being assumed very quickly from a position of outstretched head and neck, and lasting only a fraction of a second. The rolling component is but slightly indicated in the display, and it was obvious only after I had observed unmistakable head-rolling as an apparent displacement activity* in a disturbed male Magellan goose. The other major agonistic display is the Wi-wi call, a rapidly repeated one-syllable whistling

* As used here, "displacement activity" simply means "inappropriate" behavior which has apparently not been evolved (ritualized) into a display (behavior having signal function).

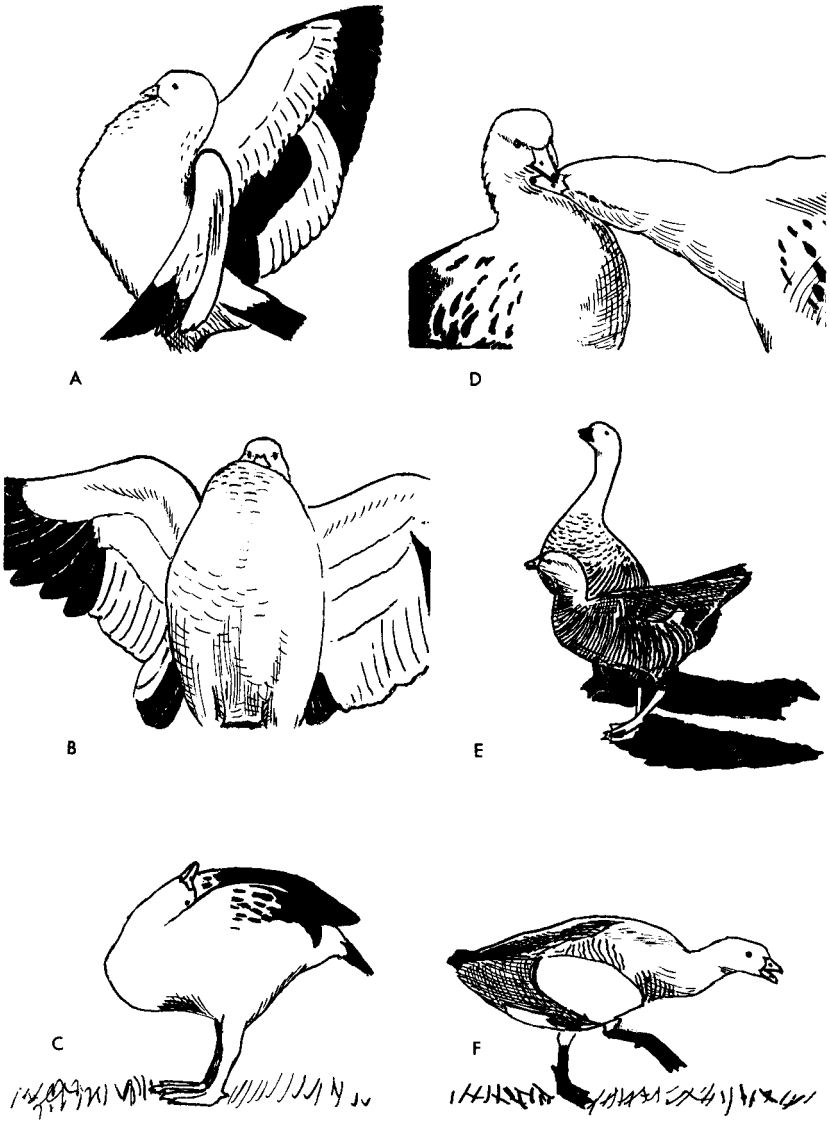


Figure 20. Andean Goose, Magellan Goose

A. Male Andean goose performing Wing-flapping in threat situation.
B. Aggressive Wing-flapping, front view.
C. Male Andean goose performing Head-rolling in threat situation.
D. Male Andean goose nibbling the head region of mate.
E. Magellan goose pair. Female Inciting while male utters whistling notes.
F. Attack by male Magellan goose. Note slightly raised wings with white upper coverts and bony protuberance at wrist.

note uttered with head and neck diagonally outstretched (Fig. 19C), which is performed in much the same way as it is by the blue-winged goose. In this case, however, the display is performed only by the male and appears to function as a threat. Head-rolling often occurs during this display.

I believe that the primary sexually motivated display is one which I have termed Puffing. This display often occurs while the the female is Inciting, or when the male returns to the female after a threat or an attack. The male walks in a very "haughty," rather erect posture, with his body feathers puffed out and his bill resting on his expanded chest (Fig. 19*D, E*). The folded wings are somewhat lifted to reveal the speculum, the tail is shaken frequently, and a loud, rather flatulent *humm-pah* is repeatedly uttered. This display appears to function both in courtship and Triumph Ceremony situations.

Copulatory behavior. I have not observed copulation in this species, but no doubt it is very much like that in other species of sheldgeese and occurs while the birds are standing in shallow water. Mr. Tom Spence (pers. comm.) informs me that the postcopulatory display consists, as it typically does in both sheldgeese and shelducks (see Fig. 24*D*), of Wing-lifting by one or both birds.

Magellan Goose (*Chloëphaga picta*)

Sexual dimorphism in plumage and foot coloration is strongly evident in the Magellan goose, as the male is rather similar in plumage to the Andean goose, and the female approaches the female kelp goose in coloration. The downy young are similar to those of the Andean goose, but lack the yellow tinge on the head feathers. The trachea of the male has a very large syringeal bulla, which is rounded and rather thinly ossified, and which, as with almost all Anatinae, is located on the left side of the syrinx at the junction of the bronchi. The Magellan goose is sympatric with ashy-headed and ruddy-headed geese in southern Argentina and Chile, and with the kelp goose in the Falkland Islands. There are two subspecies, the Falkland Island race being somewhat larger than the mainland form. In captivity the species has hybridized with Andean, ruddy-headed, and Egyptian geese.

General behavior. Like the Andean goose, the Magellan goose is very aggressive; but unlike that species, which displays almost year-around, the Magellan goose engages in intense display only dur-

ing late winter and spring. I have not observed any mutual nibbling, nor have I seen any preflight movements. The birds tend to remain in pairs all year, and presumably the pairs are relatively permanent. Delacour (1954) states that this and the other species of sheldgeese, in common with shelducks, have two molts of body feathers each year, but I have been unable to confirm this statement.

Agonistic and sexual behavior: female. Inciting in this species is similar to that of the Andean goose, but with some interesting differences. The Inciting call is essentially the same, but the tail is not shaken during the display and the walk is not so exaggerated as in that species. The hindquarters, but not the wings, are distinctly raised during Inciting (Fig. 20*E*). The female walks or runs toward her mate with head erect during Inciting, occasionally making rapid and rather rudimentary Bowing movements with the head which resemble intention movements to graze. Much more intensified forms of these movements are found in the ashy-headed and ruddy-headed geese.

Agonistic and sexual behavior: male. Unlike the Andean goose, the Magellan goose does not appear to have ritualized the general shake, wing-flapping, and head-rolling into displays; but these movements occur at times as apparent displacement activities. The primary male response to Inciting is the aggressive Wi-wi call, uttered with body erect, neck outstretched, and with the wings held against the body (Fig. 20*E*). The male faces his opponent during this display, standing more and more erect at higher intensities. One who is familiar with Andean geese constantly expects this display to be replaced by Puffing, but in my experience this has never happened. Occasionally, short and rather inconspicuous Bowing movements may be performed as momentary interruptions to the aggressive calling. The Wi-wi call may be elicited throughout the year even in the absence of an Inciting female. When attacking another bird, the male runs rapidly over the ground with his head low and with his folded wings slightly spread, thus exposing his immaculate white upper-coverts (Fig. 20*F*).

Copulatory behavior. I have observed copulation only once in this species, and it occurred as the pair stood in shallow water. For about ten seconds both birds made repeated and essentially synchronous Head-dipping movements—which very clearly were derived from bathing movements—before the male mounted. As tread-

ing was completed, the female, and probably also the male, called as the male slipped to the ground and slightly raised the wing on the side opposite the female. Mr. Tom Spence (pers. comm.) has also observed postcopulatory Wing-lifting in this species.

Kelp Goose (*Chloëphaga hybrida*)

Judging from my very limited experience with a few Patagonian kelp geese observed at the Philadelphia zoo, this species appears to be somewhat intermediate between the Magellan goose and the two following species. The downy young are essentially all-white, only faintly exhibiting the typical sheldgoose patterning, and the adults present an even greater degree of sexual dimorphism than does the Magellan goose. Aside from the swans, the adult male kelp goose is the only all-white waterfowl—a fact of particular interest because even the secondary coverts are white rather than metallic-colored. Females are very dark, but do exhibit the metallic speculum. Although the kelp goose is generally sympatric with the other non-montane forms of *Chloëphaga,* its special ecological niche among the kelp beds of the rocky coasts probably reduces interspecific contacts. No hybrids involving this species are known. The tracheal bulla of the male closely resembles that of the ashy-headed goose (J. V. Beer, pers. comm.).

Behavior. Cawkell and Hamilton (1961) mention, regarding the Falkland Island race of kelp goose, that during display the male "flung his head back and then forward keeping the beak parallel with the ground whilst the female lowered her head toward the gander and raised her tail." This description fits my few observations fairly well. I observed a definite mutual Bowing display, very similar to those of ashy-headed and ruddy-headed geese (see Fig. 21). During this the male whistled a repeated *wi-wi-wi* . . . while the female uttered a loud cackle as she alternated her erect and lowered-head postures. I did not observe the tail-raising mentioned by Cawkell and Hamilton, which suggests an Inciting similar to that of the Magellan goose. I know of no other information regarding this species.

Ashy-headed Goose (*Chloëphaga poliocephala*)

The ashy-headed goose is smaller than the birds of the preceding species, and only slightly larger than the ruddy-headed goose. As in that species, the sexes are almost identical in appearance. Like both

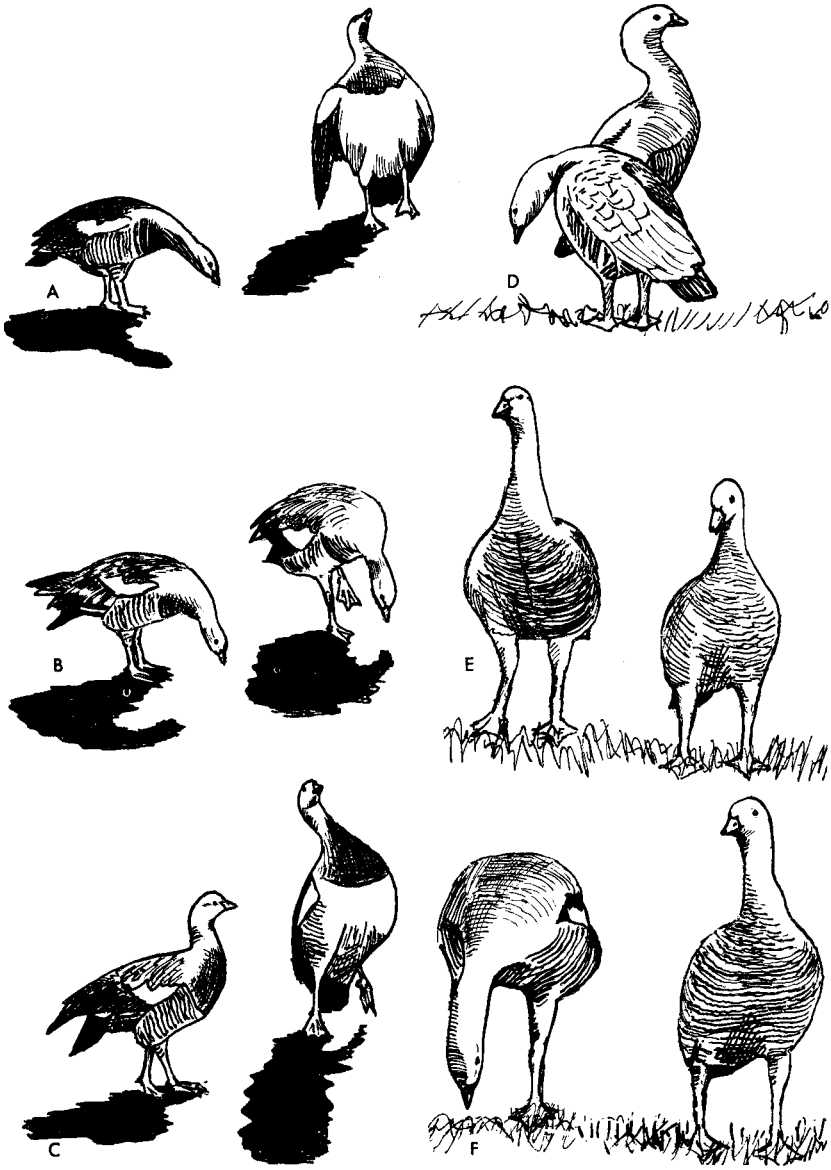


Figure 21. Ashy-headed Goose, Ruddy-headed Goose

A–C. Ashy-headed goose male (*right*) performing Puffing combined with high-intensity Bowing. Female Inciting.

D. Ashy-headed goose pair, both birds Bowing.

E, F. Ruddy-headed goose pair, the male (*left*) Bowing, the female Inciting.

the ruddy-headed and the kelp goose, the ashy-headed goose has a white eye-ring. Although the head is gray and not brown like that of the ruddy-headed goose, at least some individuals of this species exhibit a brownish trace at the back of the head and neck. The downy young also closely resemble those of the ruddy-headed goose. The tracheal bulla of the male is rather smaller than is that of the male Magellan goose (see illustration in Johnsgard, 1961c). The species is sympatric with the Magellan goose and the ruddy-headed goose, and probably also with the kelp goose. In captivity it has hybridized with two species of shelducks.

General behavior. Although small, the ashy-headed goose can be highly aggressive, and it will sometimes attack much larger birds. Like other species of *Chloëphaga,* it tends to remain in pairs throughout the year. I have not observed mutual nibbling or any preflight movements.

Agonistic and sexual behavior: female. The Inciting behavior of the ashy-headed goose appears to be identical with that of the ruddy-headed goose, but distinctly different from that of the preceding species. The tail is not raised or shaken during Inciting (Fig. 21*A–C*), and the female frequently makes rapid Bowing movements toward the ground as she calls in the characteristic manner of Inciting sheldgeese.

Agonistic and sexual behavior: male. The aggressive Wi-wi display of the ashy-headed goose much resembles that of the ruddy-headed goose. Although this display may be elicited at any time, it is most intense during female Inciting. On such occasions the male stands almost perfectly erect, with his wings held far enough away from his body to exhibit his white coverts, and occasionally makes rapid Bowing movements toward the female (Fig. 21*B*). As in the other species, the male attacks by suddenly lowering his head and rushing toward his opponent, beating it with hard blows of the wings. After an attack the male will rapidly return to the female, and sometimes he will perform a display which, both in general appearance and in the associated vocalization, is very similar to, and clearly homologous with, the Puffing display of the Andean goose (Fig. 21*A*). In the ashy-headed species, however, this display occurs very infrequently and always in a Triumph Ceremony situation, whereas in the Andean goose almost any disturbance will elicit it. The apparent absence of Puffing in the Magellan goose and the

ruddy-headed goose is unusual, and perhaps is related to selective pressures for isolating mechanisms in these five fairly closely related species.

Copulatory behavior. I have not seen this and have no information regarding it.

Ruddy-headed Goose (*Chloëphaga rubidiceps*)

The sexes of the ruddy-headed goose are identical in appearance and rather resemble the female of the larger Magellan goose. The ruddy-headed goose has, however, a conspicuous eye-ring and much more delicately barred patterns on the body feathers. The downy young are much like those of the ashy-headed goose. I have not seen the trachea of the male. The species is sympatric with the ashy-headed and Magellan geese, and in captivity has produced fertile hybrids with the latter. It has also hybridized with the Andean goose.

General behavior. Although the smallest of the sheldgeese, the ruddy-headed goose is highly aggressive, and what has been said about the general behavior of the ashy-headed goose applies to this species as well.

Agonistic and sexual behavior: female. Inciting in the ruddy-headed goose is identical with that in the ashy-headed goose; in both species the female frequently performs Bowing movements while Inciting (Fig. 21*E, F*).

Agonistic and sexual behavior: male. As in the ashy-headed goose, the male's response to Inciting is to stand extremely erect, facing his opponent with head held high and wings close to the body, and to utter the aggressive Wi-wi call. Frequently the male, facing the female and moving almost in synchrony with her, performs rapid Bowing movements (Fig. 21*E, F*). When uttering his call, the male usually holds his wings slightly out from the body (see Fig. 14*C*), exhibiting his white wing-coverts and the bony protuberances at his wrists. As in all the Tadornini these protuberances, combined with powerful wings, make effective weapons; and I am convinced that Heinroth (1911) was correct in his belief that the white on the coverts of the Tadornini (and of several species of Cairnini that use their wings in the same manner) is a kind of warning signal. Of the species here included in the Tadornini, only the Orinoco goose has no white at all on the wing coverts, although the coverts of the blue-winged goose are mostly light blue. The "flash effect" of this signal

is most striking in those species which have little or no white on the rest of the body—the ashy-headed, ruddy-headed, and Egyptian geese, and some species of sheldducks. Another plumage feature which these three species of sheldgeese share with most of the sheldducks is their tan to yellowish under-tail coverts. In at least some of these species, and perhaps in all of them, this region is displayed by males as a courtship signal while swimming erect in the water.

Copulatory behavior. I have no information on this.

Orinoco Goose (*Neochen jubatus*)

Although obviously a close relative of *Chloëphaga,* the Orinoco goose does possess some aberrant characteristics and perhaps should be retained in a separate genus. Unlike the other sheldgeese it has black wing coverts and linings. The secondary coverts are metallic green as in *Chloëphaga,* but the secondaries are mostly glossy greenish-black and have a small white circular patch. The downy young, although patterned like typical sheldgeese, have a large dark cheek mark. The male has a rudimentary tracheal bulla, similar in size and shape to those of some sheldducks. The adults are alike in plumage, but the male is larger and has noticeably longer neck feathers. In captivity the Orinoco goose has hybridized with the Egyptian goose and the common shelduck.

General behavior. The Orinoco goose is not highly aggressive and seems to be more social than the other sheldgeese. Males associate freely with one another, at least during the nonbreeding period, and mutual nibbling of the feathers in the head region is particularly characteristic of this species. This occurs not only between paired birds, but also among other birds of the same or opposite sex, and social-preening "triangles" are not uncommon, especially during the postnuptial molt. Orinoco geese perch to a considerable extent in captivity, and we should expect that perching is also frequent in the dense forests which the species inhabits. Preflight movements have not been noted.

Agonistic and sexual behavior: female. During most of the year female Orinoco geese are relatively shy and inconspicuous birds, displaying little aggression toward others of their kind. As the breeding season approaches, however, Inciting may frequently be seen. The Inciting call is much like that of the Magellan or Andean goose, but the Inciting posture (Fig. 22*B*), unlike that of any of the

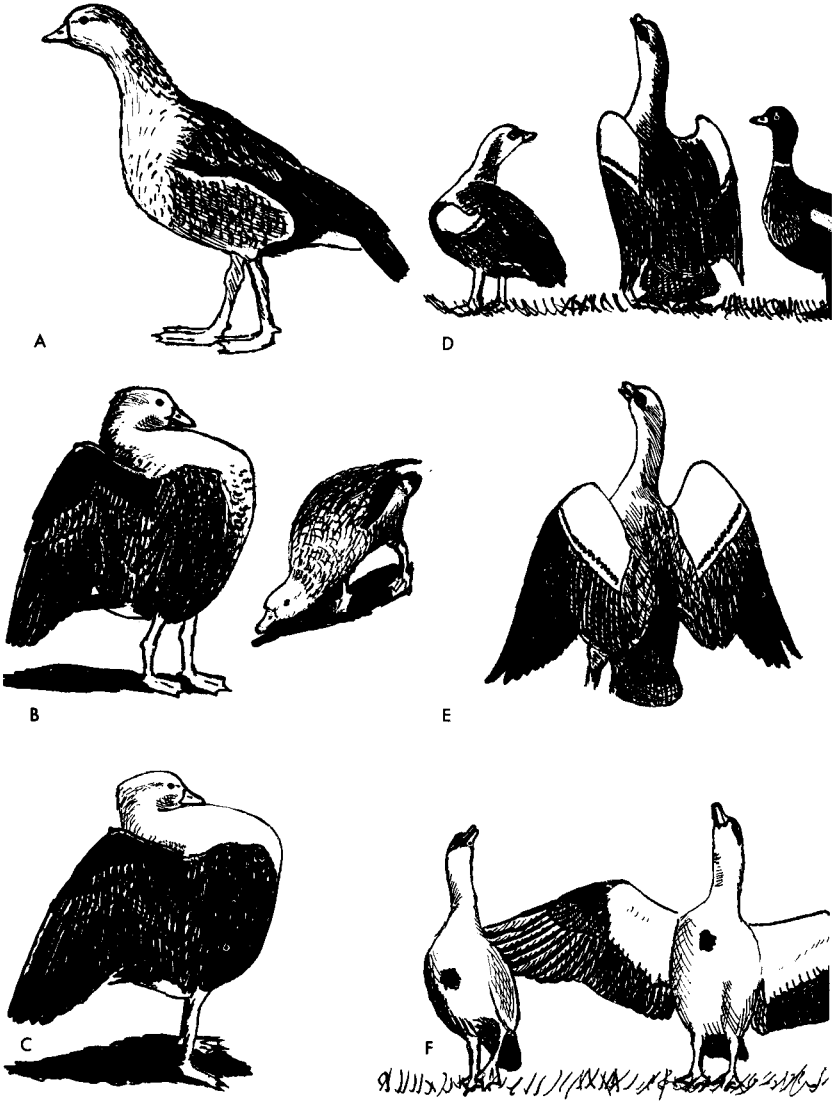


Figure 22. Orinoco Goose, Egyptian Goose

A. Male Orinoco goose uttering whistled threat call.

B. Male Orinoco goose (*left*) performing Puffing display as female Incites.

C. Male Orinoco goose Puffing. Note bony protuberance at wrist.

D. Egyptian goose pair, male (*center*) threatening Australian shelduck as female (*right*) Incites.

E. Egyptian goose, high-intensity threat by male. Note conspicuous wing coverts.

F. High-intensity threat by Egyptian goose.

Chloëphaga species, is characterized by the fact that the neck and head are stretched out along the ground. This Inciting posture is very similar to that of shelducks. Unlike the shelducks, however, Orinoco geese never make lateral pointing movements of the bill and head. As a threat display both males and females erect their elongated neck feathers, which makes them appear to have very thick necks (illustrated in Delacour and Mayr, 1945).

Agonistic and sexual behavior: male. Male Orinoco geese have a whistling threat note and, like male sheldgeese, utter it with a diagonally outstretched neck (Fig. 22*A*). This call can be elicited at any time of the year, but the male's sexual display can only be observed during the period of female Inciting. In this display which is clearly homologous to the Puffing display of certain sheldgeese, the bird holds his body very erect and, with one or both of his wings extended directly backward and his head held back as far as it will go, utters a wheezy *wi-chuff,* which he repeats several times (Fig. 22*B, C*). The male tends to face the female, thus exposing to her view the dark underwing coverts or, at times, the upper-wing surface. The Bowing posture of the typical sheldgeese has not been observed.

Copulatory behavior. No information is available regarding this.

Egyptian Goose (*Alopochen aegyptiacus*)

Except for its larger size, the Egyptian goose might almost be called the Egyptian shelduck, for there is no doubt that the *Alopochen* is a very close relative of *Tadorna.* The downy young have the typical spotted back of the shelducks rather than the striped back of most sheldgeese, and immature birds bear a marked resemblance to immature common shelducks. Males have a left-sided tracheal bulla which is relatively small and completely ossified. The body coloration is generally similar to that of the Orinoco goose, but the wing coverts are white and the speculum is restricted to the secondaries and is of the typical shelduck type. That is, it is metallic green throughout and is bordered on the inner side by chestnut coloration. All the shelducks except one, the radjah, have specula exactly like this. The Egyptian goose and the radjah shelduck are distinctive in that the speculum is bordered in front by a black line on the white wing-coverts. The sexes of the Egyptian goose are very similar in coloration, but the male is larger and has a somewhat more contrasting color pattern. The vermiculations occurring on the body feathers

of both sexes are also typical of shelducks. None of the other sheldgeese exhibit a true vermiculated feather pattern, but one wonders whether evidence of the evolutionary origin of this interesting plumage feature, which is typical of most male Anatinae, is not to be found in the delicately barred pattern characteristic of some species of *Chloëphaga*.

The Egyptian goose is sympatric with the blue-winged goose and in captivity has produced fertile hybrids with it. Hybrids have also been obtained with Andean geese, Magellan geese, Orinoco geese, and three species of shelducks.

General behavior. The Egyptian goose has a particularly aggressive disposition, combining the almost constant fighting of the shelducks with the strength of the sheldgeese. Therefore they are not gregarious to any extent. Like shelducks, they have conspicuous preflight signals which consist primarily of rapid Chin-lifting movements.

Agonistic and sexual behavior: female. As Lorenz (1951–1953) has pointed out, the form of Inciting in the Egyptian goose is partly affected by the position of the object of the Inciting. The female tends to face or stand beside her mate and make threatening movements, or even short attacks, toward the opponent, calling louding and rapidly at the same time (Fig. 22*D*). The pointing movements of the threat are not in any degree ritualized; that is, they are wholly determined by the actual position of the opponent.

Agonistic and sexual behavior: male. Unlike the males of the sheldgeese considered previously, the male Egyptian goose does not have a whistled call. He emits, rather, gusty, strong breathing notes, reminiscent of a steam engine. Such notes appear to constitute the bird's only call, although, depending upon the degree of excitement, the call varies much in intensity and in the rapidity of the notes uttered. When mildly disturbed both birds of a pair stand together making small rotary movements of the head, similar to those made by of *Chloëphaga* in similar circumstances, with one or both birds calling softly. This leads into higher and higher degrees of excitement, until the female is rapidly and continuously Inciting her mate against an opponent; then the male, standing highly erect, suddenly and with a violent release of "steam," flashes open his wings (Fig. 22*D*, *F*). The whole display is so strongly reinforced by a sudden vocal "blast," and the flash effect of the white wing linings and coverts is

so unexpected, that, to humans at least, it is an extremely impressive threat display.

Copulatory behavior. Copulation evidently takes place when the birds are standing in shallow water, and although Heinroth (1911) did not observe this, the precopulatory display probably consists of Head-dipping movements. After copulation the male lifts the wing opposite the female to a considerable angle above his back, and this movement is probably accompanied by calling on the part of both birds (see illustration in Heinroth, 1911).

SHELDUCKS

The seven species of shelducks, of which one is almost certainly extinct, form a rather clear-cut taxonomic group. Four of the species, sometimes placed in a separate genus *Casarca,* appear to be very closely related and are, in structure and behavior, more generalized than the others. The presumably extinct species may also belong to this group. The remaining two species are more specialized in plumage, voice, tracheal structure, and behavior. The more generalized species tend to graze a good deal, whereas the two specialized forms (*T. tadorna* and *T. radjah*) obtain relatively more of their food by dabbling in muddy water.

Ruddy Shelduck (*Tadorna ferruginea*)

The ruddy shelduck may be thought of as a generalized form from which the other "Casarca" species exhibit minor variations. The downy young of all these species, with their dark "capped" heads and spotted backs, are practically identical. As adults, the sexes of the ruddy shelduck are similar, but the female has a white area around the eyes and the male has a black neck-ring and buff-colored rather than white upper-wing coverts. The rusty-tan of the under-tail coverts in this species is essentially the same color as appears on the rest of the body, and I believe that this color is a primitive feature. The trachea of the male has a very small, almost rudimentary, bony bulla at the syrinx (see illustration in Johnsgard, 1961c). The ruddy shelduck occurs over much of Asia and parts of Europe and Africa. It has produced fertile hybrids with the Egyptian goose and with the three other "Casarca" species, and it has also hybridized with common and radjah shelducks.

General behavior. Heinroth (1911) has discussed at length the general behavior of the ruddy shelduck and its near relatives, and has described its aggressive behavior especially well. Chin-lifting, together with lateral Head-shaking, is the preflight movement.

Agonistic and sexual behavior: female. Although Delacour (1954) believes that shelducks mate for life, I doubt that pair bonds are nearly so strong in shelducks as they are in geese or in sheldgeese. Heinroth (1911) has given examples of how a female shelduck will repeatedly attach herself to a new mate (often to one of a different species), her choice being dependent simply upon which male will respond to her Inciting most strongly. An understanding of this aspect of mate selection makes clear the reasons for the tendency toward the sexual dimorphism—in strength, size, and appearance—that occurs in the shelduck group, or at least in the "Casarcas." As Heinroth has explained, it is in this group that females overtly "court" various males to a much greater extent than in any other duck group, and thus there is a tendency toward a reversal of the normal sexual selection process. I am certain that this accounts for the trend toward bright female plumages in these species—a trend which is uniquely culminated in the paradise shelduck, the female of which has distinct breeding (red) and nonbreeding (gray) plumages, whereas the male has the same (gray) plumage all year. Heinroth has also pointed out the correlation between the amount of contrasting white plumage on the heads of the female "Casarcas" and the relative strengths of their tendencies toward Inciting. There is least white on the females of ruddy and Australian shelducks, more on the female of the Cape shelduck, and most on the female of the paradise shelduck—and the last-mentioned is certainly the greatest Inciter.

The Inciting of the female ruddy shelduck is of particular interest, for it illustrates the trend toward the ritualization of the pointing component. During Inciting the female holds her head low over the ground or water with her neck outstretched, calling *gaaa* repeatedly, and frequently making lateral pointing movements with her bill toward the opponent. As Lorenz (1951–1953) has already pointed out, however, this lateral pointing movement is to some degree stereotyped, and may even occur if the opponent is facing directly ahead of the female. This is an important point, for it will be seen that in some of the following tribes the movement has become com-

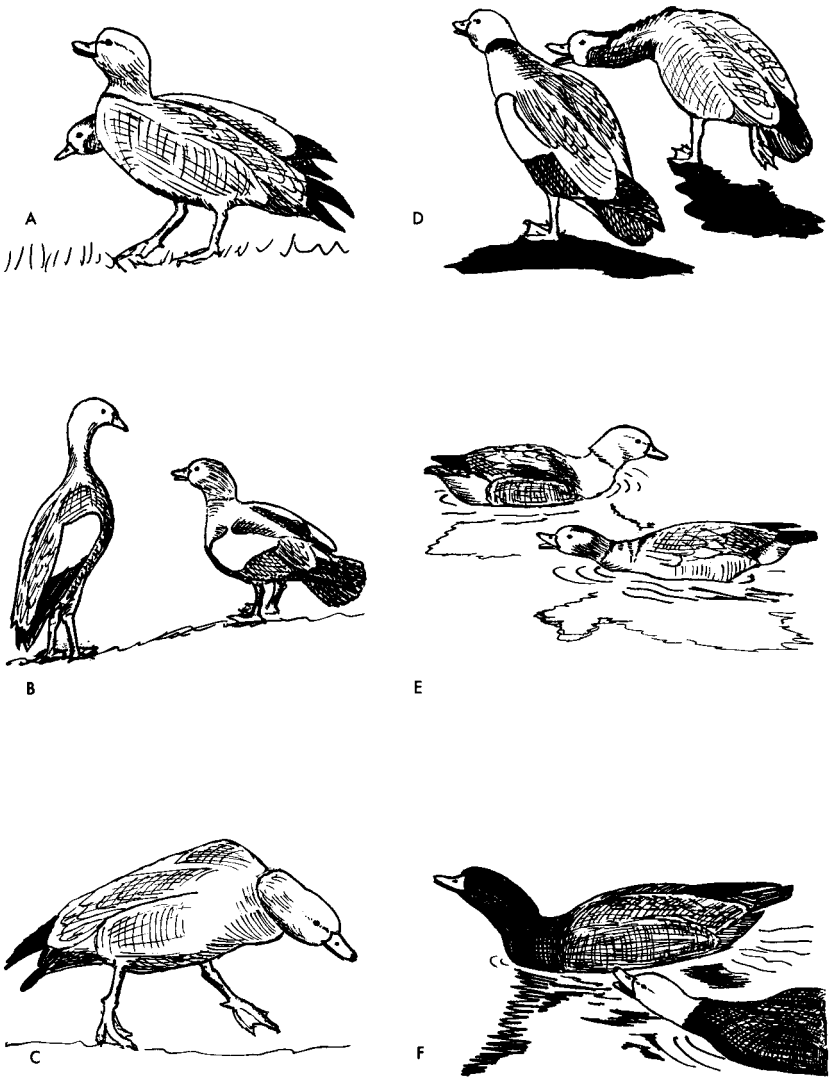


Figure 23. Ruddy Shelduck, Cape Shelduck, New Zealand Shelduck

A. Ruddy shelduck pair. Male (*in foreground*) uttering threat call.

B. Ruddy shelduck female threatening male ruddy-headed goose. Compare the postures of the two species.

C. Female ruddy shelduck in attack posture.

D. Cape shelduck pair, female (*right*) Inciting.

E. Cape shelduck pair, female (*right*) Inciting while male utters his threat call.

F. New Zealand shelduck pair, female (*in foreground*) Inciting while male utters his threat call.

pletely ritualized, and is almost entirely independent of the position of the object of the Inciting. If it were not for such examples of only partially ritualized movements as are afforded us by the female ruddy shelduck, the significance of these completely ritualized movements would be much more difficult to understand.

Agonistic and sexual behavior: male. The male's response to Inciting is usually to utter one of two calls, which appear to be basically different in function. The call of male ruddy (and the other "Casarca") sheldducks is unlike the whistle of the typical sheldgeese; it is a strong honking call described by Heinroth (1911) as *chorr,* with the predominant tone *O* rather than *A* as with females. The one-syllable *chorr* response is indicative of threat, and is analogous to the Wi-wi threat of typical sheldgeese. The other call, however, a two-syllable *cho-hoo',* is, I believe, sexually motivated and thus analogous to the Puffing call of some sheldgeese. In giving this call the male often jerks his head back and sometimes lifts his tail, thus assuming a High-and-erect posture that seems to exhibit the undertail coverts. As the female begins Inciting, the male usually makes his *chorr* call (Fig. 23*A, B*), but this is later often replaced by the two-note sexual call, just as in the Andean goose the Wi-wi call is usually replaced by Puffing at higher degrees of excitement.

Copulatory behavior. Ruddy sheldducks copulate in water deep enough for the birds to swim in. The precopulatory display consists of mutual Head-dipping movements, with the male frequently uttering his two-note call. As treading is completed, the female begins to call before the male does. After the male begins to call, he remains mounted a few seconds, still holding the female's nape; then he slightly lifts the wing opposite the female and slides off to one side in a High-and-erect posture. Both birds then begin to bathe.

Cape Shelduck (*Tadorna cana*)

The Cape, or South African, shelduck is certainly very closely related to the ruddy shelduck, and the two forms might best be thought of as a superspecies. The downy plumage is slightly lighter in color than is that of the downy ruddy shelduck; and adults of the two species differ mainly in that both sexes of the Cape shelduck have ashy-gray rather than buff-colored heads, and the white area on the head of the Cape shelduck female is larger than that on ruddy shelduck females. In addition, the flank and back feathers are strongly

vermiculated, a feature which is even more pronounced in the three following species. The male trachea is almost identical with that of the ruddy shelduck. The species is not sympatric with any other shelducks, but in captivity it has produced fertile hybrids with the ruddy shelduck and has also hybridized with the paradise and common shelducks.

General behavior. Except for having a somewhat more aggressive disposition, the Cape shelduck is in almost every way very similar to the ruddy shelduck. In the fights I have seen between the ruddy shelduck and the Cape shelduck, the latter has always been the victor. Chin-lifting and, to a smaller extent, lateral Head-shaking are the preflight movements.

Agonistic and sexual behavior: female. The Inciting call and posture of the Cape shelduck are exactly like those of the ruddy shelduck (Fig. 23*D, E*). As is true of that species, Inciting can be elicited throughout the year, but is most frequent during spring.

Agonistic and sexual behavior: male. The male's response to Inciting is like that of the ruddy shelduck. The one-syllable threat note might be written as *korrr,* and the two-note sexual call as *ka-thoo'*. At the same time as the latter note is uttered the head is jerked up and back, and the characteristic High-and-erect posture is assumed. This differs from the threat call posture, in which the head is held forward and the neck is outstretched (Fig. 23*D, E*).

Copulatory behavior. Treading occurs in water of swimming depth, and pronounced Head-dipping movements resembling bathing are performed by the male and less often by the female. Treading is like that of the ruddy shelduck, with the female beginning to call several seconds before the male calls and dismounts. In this species the male lifts the wing on the side opposite the female to a directly vertical position, holding it in that position for several seconds while in a High-and-erect posture. Both birds then begin normal bathing.

Paradise Shelduck (*Tadorna variegata*)

The paradise, or New Zealand, shelduck should perhaps be placed between the Cape and the Australian shelduck, although geographical distributions suggest that the Australian species should be placed between the other two. The downy plumage of the paradise shelduck is very dark above and is much like that of the ruddy shelduck. The breeding plumage of the adult female (all shelducks

apparently have two body molts per year, but this double molt is conspicuous only in the paradise shelduck) is a rich reddish chestnut, with vermiculations on the back and flanks. In nonbreeding plumage the female has a grayish body similar to that of the male. In both plumages the female's head is pure white. The male has at all times a dark gray body and a glossy greenish-black head, but his under-tail coverts and his wings are of the typical shelduck color and pattern. There is a greater sexual dimorphism of size and color in this species than in any of the other shelducks. The male tracheal bulla is slightly larger than those of the two preceding species and, in size and shape, approaches the bulla found in the Australian shelduck (J. V. Beer, pers. comm.). The paradise shelduck is not sympatric with any near relatives, but in captivity it has formed fertile hybrids with the ruddy shelduck and has also hybridized with common and Cape shelducks.

General behavior. As we would expect from the distinct breeding and nonbreeding plumages of the female, this species tends to be more seasonal in its social behavior than are the other species of the group. When the female is in her gray plumage, it is in my experience impossible to elicit Inciting; but when she is in her breeding plumage, it is almost impossible to *avoid* eliciting it. As in the other shelduck species, preflight signals consist primarily of Chin-lifting, with some lateral Head-shaking.

Agonistic and sexual behavior: female. Inciting in this species is of the typical shelduck type already described (Fig. 23*F*), differing only in its frequency and intensity. The lateral bill and head movements made during Inciting are especially conspicuous as a result of this bird's striking white head-plumage. Heinroth (1911) has described how a female paradise shelduck paired with an ashy-headed goose rather than with a male of her own species, illustrating well the tendency of females to court the largest and strongest potential mates.

Agonistic and sexual behavior: male. The calls and reactions of the male paradise shelduck are very much like those of males of the preceding species. The threat and the sexual calls are somewhat lower in pitch than are those of the other forms, and they may be written as *horr* and *ha-hoo'* respectively. The sexual call is usually uttered in the High-and-erect posture.

Copulatory behavior. Although the copulatory behavior of this species is no doubt similar to that of the other "Casarcas," I have no information on it.

Australian Shelduck (*Tadorna tadornoides*)

The Australian shelduck is certainly a close relative of the paradise shelduck, but its downy young are also very similar to those of the Cape shelduck. Its adult plumage, however, is to some degree reminiscent of the common shelduck, and there are a few elements of behavior which are indicative of this affinity as well. I have not seen the male trachea, but to judge from the voice, it cannot be very different from those of the other "Casarcas." Unlike those of the other typical shelducks, the under-tail coverts are greenish black rather than brownish. The plumage of the female is much like that of the male, and the white area on the head is restricted to the region around the eyes. The only near relative with which it may be sympatric is the radjah shelduck. In captivity it has hybridized with the common shelduck and produced fertile hybrids with the ruddy shelduck. The tracheal bulla of the male is larger and more strongly ossified than those of the three preceding species (J. V. Beer, pers. comm.).

General behavior. In general behavior the Australian shelduck appears to be a typical "Casarca." The birds are not gregarious, and remain rather aggressive throughout the year. As in the other species, Chin-lifting and lateral Head-shaking movements constitute preflight signals.

Agonistic and sexual behavior: female. Inciting is essentially the same as it is in the other shelducks (Fig. 24*A*). There is much lateral pointing, and the greenish-black head contrasts vividly with the brownish breast.

Agonistic and sexual behavior: male. The male Australian shelduck responds to Inciting with either the one-syllable threat call *ho* or the two-syllable call *ha'-poo* (Fig. 24*A*). In this species the emphasis of the latter call tends to be on the first syllable, rather than on the second as it is in the paradise shelduck. The two-note call is uttered in the High-and-erect posture typical of the group (Fig. 24*B, C*). During a state of general excitement, both sexes, and especially the male, sometimes perform a body shake, but there does not appear to be any call associated with this shake, nor is it especially different from the normal general shake. The fact that the common shelduck male has a highly ritualized Whistle Shake (Lorenz, 1951–1953; Fig. 26*A*) which derives from the general shake makes this behavior of particular interest.

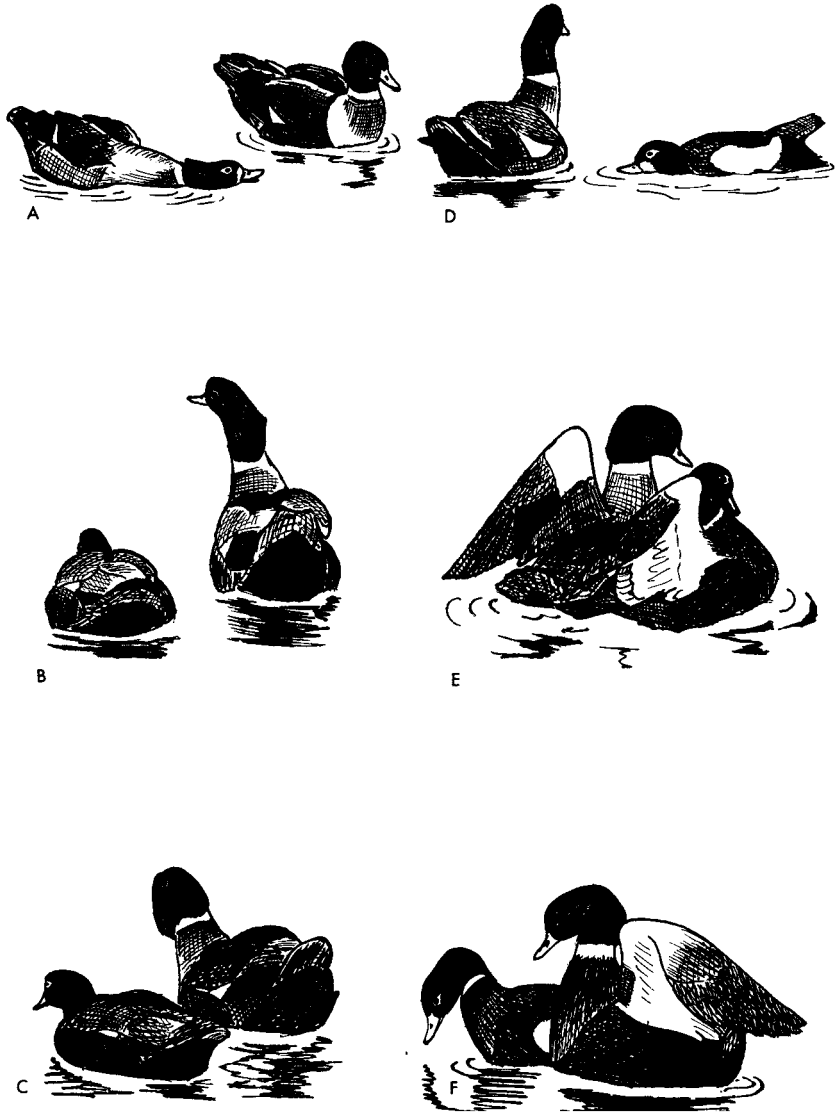


Figure 24. Australian Shelduck

A. Female (*left*) Inciting as male utters threatening notes.

B, C. Male calling in High-and-erect posture during precopulatory display. Note cocked tail and sleeking of the male's head feathers (except in nape region).

D. Precopulatory display, male in High-and-erect posture while female is in prone position.

E, F. Early and late phases of postcopulatory display. In the late phase the female is about to begin bathing.

Copulatory behavior. Head-dipping by the male, alternated with calling in the High-and-erect posture, appears to be the typical precopulatory behavior of Australian shelducks (Fig. 24*B, C*). The female may also perform Head-dipping before she goes into a receptive position (Fig. 24*D*). The postcopulatory display is a most elaborate one, with the female calling loudly as copulation is completed, and with both birds lifting the wing opposite the partner as they swim about in High-and-erect attitudes (Fig. 24*E*). The female does not assume quite so extreme a posture as the male, and after a few seconds she begins to bathe (Fig. 24*F*).

Crested Shelduck (*Tadorna cristata*)

This almost certainly extinct and practically unknown species is included at this point simply on the basis of its general appearance. There can be no doubt that the few specimens known represent a true species rather than a hybrid, for both the wing pattern and the under-tail coloration are perfectly typical of *Tadorna.* The male is more grayish than the female, and has a black chest similar to that of the paradise shelduck. Since the female has a relatively white head, vermiculated flanks, and under-tail coverts of a yellowish brown, it seems probable that this species is a member of the "Casarca" group.

Common Shelduck (*Tadorna tadorna*)

The common shelduck and the radjah shelduck represent, I believe, two rather specialized offshoots of the shelduck group. Although the males of both species have whistling voices, and although both sexes of the two species exhibit a great deal of white in their plumages, and feed to a greater extent on animal material than do the preceding shelducks, the species are perhaps not very closely related. The downy common shelduck has a striped back and large black "cap," and is rather distinct from the downy radjah shelduck. Unlike those of the other shelducks, the juveniles of this species have a plumage which is different from the plumage of either parent and resembles in some respects the juvenile plumage of the Egyptian goose. The adults of the two sexes are very similar; the female is slightly smaller than the male, has a less brilliantly green head, and lacks the bill enlargement typical of the male. The trachea of the male is unique, for the bulla is inflated on both the right and left sides to roughly the same degree. The common shelduck occurs over most of Europe and Asia, and is broadly sympatric with the ruddy

shelduck. In captivity it has hybridized with this species and also with the radjah, Cape, and Australian shelducks.

General behavior. This species is a relatively gregarious one, at least during the nonbreeding season. The postbreeding flocking and migration to restricted molting areas is well known. As in the other shelducks, preflight movements include lateral Head-shaking and, probably, Chin-lifting.

Agonistic and sexual behavior: female. Inciting behavior is of the same form, and has generally the same vocal characteristics, as that of the preceding species. As in them, the lateral pointing movements are distinctly ritualized (Fig. 25*A*, *B*). Besides the Inciting display, the female has a second courtship display of interest. This is Preening-behind-the-wing (Fig. 25C), which exposes the female's metallic speculum to her mate. This usually occurs after the male returns from an attack on his opponent and Preens-behind-the-wing on the side toward the female. She almost invariably responds to this display by also Preening-behind-the-wing, on the side toward the male. The preening movement appears to be almost functional, in contrast to the highly ritualized preening movements typical of most perching ducks and dabbling ducks. Except for certain swan species (mute, black, and probably black-necked), in which preening in various areas occurs in precopulatory or Triumph Ceremony situations, this is the only species discussed so far which definitely utilizes ritualized preening as a sexual display. Thus it is clear that the metallic-colored speculum of the other shelducks and sheldgeese did not evolve in association with this display; but perhaps it evolved in connection with the postcopulatory display of lifting the wings, or with the slight lifting of them during various courtship displays such as Puffing. In the common shelduck the speculum has perhaps secondarily been modified into a special courtship signal by the ritualization of the movements involved in preening behind the wing.

Agonistic and sexual behavior: male. The voice of the male common shelduck is totally unlike that of males of the "Casarca" group. It is a soft, melodious, and high-pitched whistle not very different from that of some cardueline finches. It may be uttered while the bird is holding his neck erect and his head motionless, while he is performing rotary pumping movements of the head and neck (Fig. 25*A*, *B*) in hostile situations, or while he is flicking his head to the vertical position (Fig. 26*B*, *C*). The significance of these different postures in calling is not at all clear. The first-mentioned posture

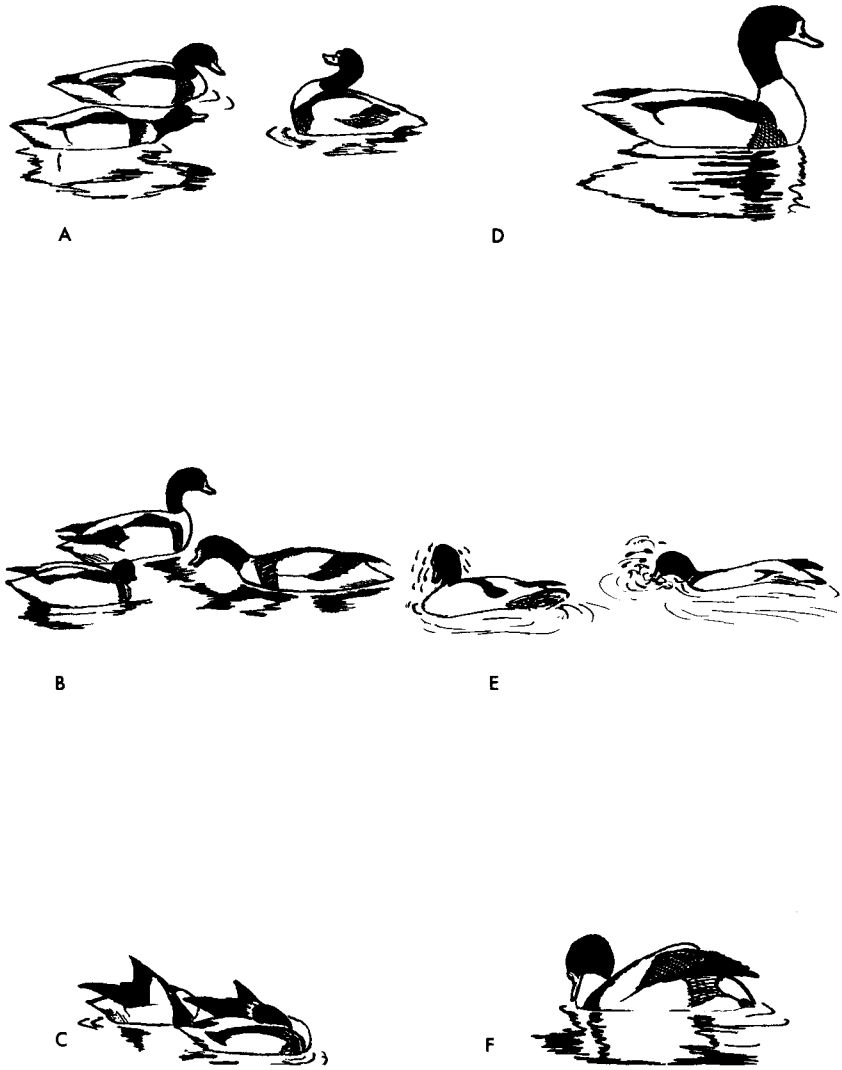


Figure 25. Common Shelduck

A, B. Female (*left foreground*) Inciting her mate (*right*) to attack other male (*rear center*). Both males are performing rotary pumping movements of head.

C. Mutual Preening-behind-the-wing by a pair after the male (*in foreground*) has returned from an attack.

D. Male calling in High-and-erect posture.

E. Precopulatory Head-dipping by a pair (*male on left*).

F. Postcopulatory High-and-erect posture. The male has just released the female (*hidden behind him*) and is raising the nearer wing slightly.

seems to correspond to the High-and-erect courtship posture of the shelducks already described (Fig. 25*D*). The vertical head-flicking may simply be an exaggerated preflight movement. The rotary pumping movement is the usual male response to Inciting, and may have sexual as well as hostile implications. It is clearly a threat display toward other birds, and is often followed by an overt attack in which the bird flies over the water surface, striking with its outstretched wings. As the male returns to his mate he Preens-behind-the-wing in the manner already described (Fig. 25*C*). A second major display of uncertain significance is the Whistle Shake (Fig. 26*A*), which is an exaggerated general shake accompanied by a whirring whistle. This behavior occurs throughout the year, and completely replaces the ordinary, or autochthonous, general shake. It occurs frequently when the birds have been disturbed by a person coming into view, and may function as a kind of alarm signal, but it also occurs at times during an aggressive display. Females shake in a less exaggerated manner than males, and they lack the whistling call.

Copulatory behavior. The precopulatory display consists of a very vigorous Head-dipping by both birds while they are swimming rapidly; hence the movements sometimes appear to be shallow dives (Fig. 25*E*). Often a female appears to be fleeing from the male, but sometimes she assumes a prone and motionless posture in the water. When this happens the male normally Preens-behind-the-wing before he mounts, in exactly the same manner as he does after an aggressive encounter. Treading is like that of the preceding species, and as the female begins to call the male grasps her nape even harder than he has before and pulls her head back, causing the birds to rotate slightly in the water; at the same time the male assumes a High-and-erect posture, with the wing opposite the female slightly raised (Fig. 25*F*). When he finally releases the female, she begins to bathe immediately.

Radjah Shelduck (*Tadorna radjah*)

The radjah shelduck occupies an extreme position, representing a highly specialized species, in the genus *Tadorna*. The downy young have brown "caps" and reduced back spotting, and are quite distinct from other downy shelducks. The trachea of the male has a bulla which is different from those of the "Casarcas" as well as from that of the common shelduck, and which is quite similar to the bullae of the typical dabbling ducks (see illustration in Johnsgard, 1961c). The

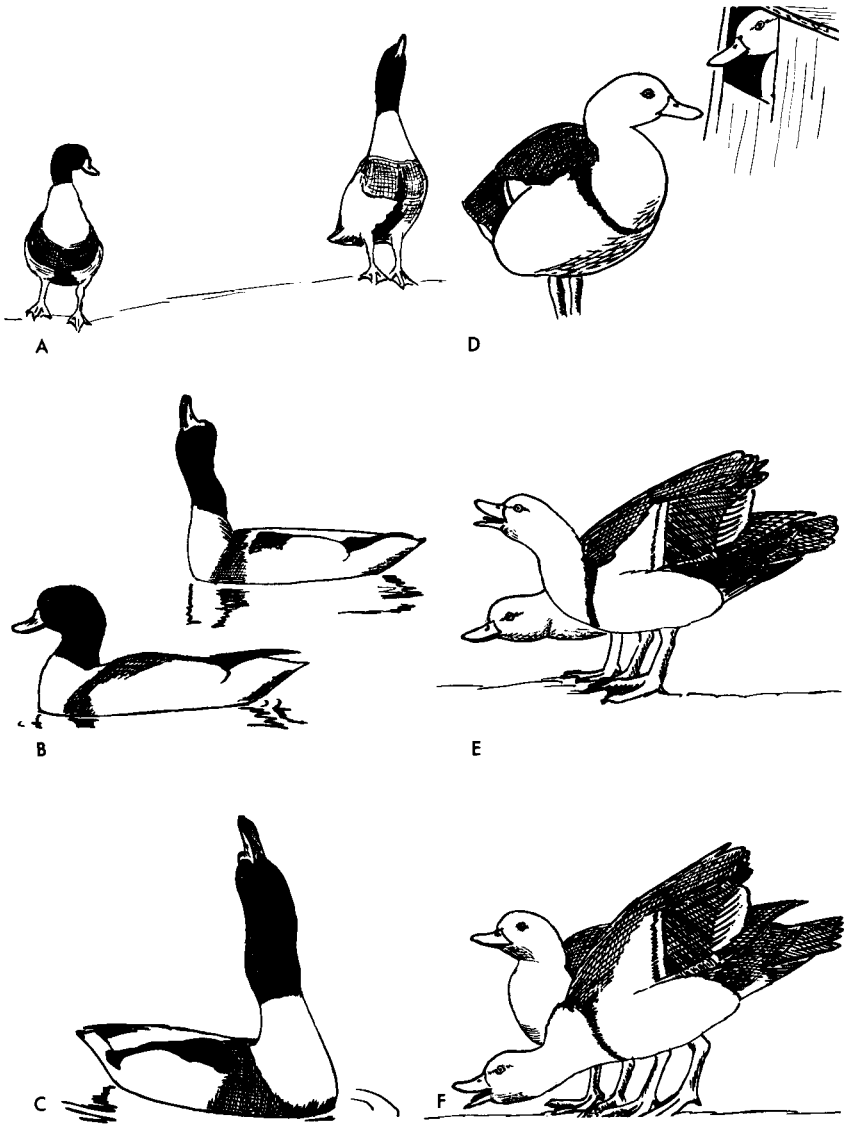


Figure 26. Common Shelduck, Radjah Shelduck

A. Male common shelduck (*right*) performing Whistle Shake.

B, C. Male common shelduck calling with bill held vertically.

D. Radjah shelduck pair. Female investigating nesting box as male waits outside.

E, F. Threat display in radjah sheldducks. Both birds are calling and performing diagonal movements of the head toward the opponents.

adult plumages of the sexes are identical, and unless one hears the birds call, it is extremely difficult to distinguish one sex from the other. The white plumage pattern is rather like that of the common shelduck, but this may be only a superficial similarity. The wing pattern of the radjah is more specialized than that of the other species of *Tadorna* in that the metallic speculum is bordered in front by a black line (as it is in the Egyptian goose) and in the rear by a broad white border. The under-tail coverts are gray to white, and thus also are not typical of *Tadorna*. The species, which has been divided into two races, occurs from northern Australia to New Guinea and the surrounding islands, and is probably not sympatric with any near relatives. In captivity it has hybridized with ruddy and common shelducks.

General behavior. Although not an especially powerful bird, the radjah shelduck often, throughout most of the year, engages in aggressive displays, but it restricts its attacks to birds of its own size or smaller. Pair bonds appear to be fairly strong in the species. I have not observed any preflight movements. Although all species of shelduck are cavity nesters, the radjah is apparently the only one which typically nests in tree holes, and it may also select nesting boxes for its site (Fig. 26*D*).

Agonistic and sexual behavior: Female. The voice of the female is rather less ducklike than that of the females of the other shelduck species, and is a wheezy, low-pitched note that could scarcely be termed a quack. Inciting takes a specialized and aberrant form in this species; the female makes diagonal pumping movements forward and downward in the direction of the opponent, and there are no lateral bill movements at all (Fig. 26*E, F*). The folded wings are raised during this Inciting, revealing the speculum. I have not, however, observed Preening-behind-the-wing by either sex.

Agonistic and sexual behavior: male. The whistling voice of the male is somewhat like that of the male common shelduck, but it is stronger, more wheezy, and less variable in pitch. Like the male common shelduck, the male radjah may call when he is holding his head stationary, as when, for example, he appears to be curious. But he calls loudest when he is responding to Inciting, at which time he stands beside or slightly facing the female and makes rapid and repeated diagonal pumping movements similar to those of the female. The male's movements are more energetic, however, and he usually raises the folded wings higher above his back (Fig. 26*E, F*). This

mutual display may constitute either a threat toward other birds or a Triumph Ceremony after an aggressive encounter.

Copulatory behavior. On various occasions I have seen what was clearly precopulatory behavior, with the male performing repeated Head-dipping movements in front of the female, to which she did not overtly respond. On one occasion I saw the female lying prone while the male attempted to mount. After several unsuccessful attempts, copulation was apparently completed. As the male released the female he raised the wing opposite her almost vertically for a moment, then lowered it. The female did not raise her wing at all, and neither bird assumed the expected High-and-erect postcopulatory posture. Thus either this single observation was not typical, or radjah shelducks have a postcopulatory display quite different from that of the other shelducks. I was unable to determine whether either bird called after the copulation.

TRIBE TACHYERINI (STEAMER DUCKS)

Following the arrangement of von Boetticher (1952) and the suggestion of Moynihan (1958), I shall here consider the three species of steamer ducks of the genus *Tachyeres* to constitute a separate tribe. These authorities agree that although steamer ducks are perhaps most closely related to the true shelducks, the steamers are sufficiently different to warrant removing them from the shelduck tribe. Their downy young lack the strongly contrasting coloration typical of shelducks, and the adult plumage pattern is distinct both from that of the shelducks and from that of the other anatine groups. There is a slight sexual dimorphism in bill color, head color, and possibly in the degree of tail-feather curling. Pair bonds appear to be strong, and Murphy (1936) was of the opinion that steamer ducks pair for life. At least two years are required for the birds to reach maturity. There are apparently three similar-appearing species, of which two are virtually flightless. The voices of the sexes are very different, and the males have tracheae with rounded, osseous bullae which are similar to those of *Anas* (see illustration in Johnsgard, 1961c). There is no metallic coloration in either sex; the wings have white secondaries and secondary coverts. All species dive extremely well, and the birds feed to a great extent on marine animal life off coastal South America and the Falkland Islands. I have observed two species, the Falkland flightless steamer duck (*T. brachypterus*) and the Magellanic flightless

steamer duck (*T. pteneres*). The following summary of behavior is based on these observations as well as on Moynihan's (1958) observations of the flying steamer duck (*T. patachonicus*). Woolfenden (1961) has recently proposed that the steamer ducks be included in the Anatini as aberrant dabbling ducks, but there is still not enough behavioral evidence to warrant the adoption of this proposal. Woolfenden also includes the perching ducks in the tribe Anatini; therefore I feel that leaving *Tachyeres* in its place between the Tadornini and Cairinini is, for the present, justified.

General behavior. All species of steamer ducks tend to be aggressive, and most of their displays appear to be motivated by hostility. Juveniles and yearlings flock together in large numbers, but adults are not very gregarious. I have noticed that captive flightless steamer ducks use their wings when diving. No preflight movements have been observed.

Agonistic and sexual behavior: female. Moynihan's observations (1958) on the flying steamer duck indicate the following behavior patterns, which are apparently purely hostile in motivation. Females perform "False Drinking" and a "Stretch," which differs from False Drinking in that it is faster, has an associated call, and is not preceeded by bill-dipping movements. The Stretch appears to be more highly ritualized than False Drinking, but both displays may serve appeasement functions. The female's call has been described by Moynihan as a "grunt," and it is deeper in pitch than the male's call and may consist of a single note or of numerous notes. In the Magellanic and Falkland flightless steamer ducks the bill is opened wide before the note is uttered and held open for some time afterward. The Grunting call and the call uttered during the Stretch are low groans, reminiscent of a creaking floor or of tree branches rubbing together. Females also utter a barking note with the bill almost closed. Moynihan states that he did not hear any vocalizations during the Stretch of the flying steamer duck. The short, barking notes uttered by female steamer ducks possibly represent Inciting calls, as they are common during disputes, but pointing movements of the bill similar to those of shelducks have not been observed to my knowledge.

Agonistic and sexual behavior: male. Males of the flying steamer duck perform False Drinking in the same manner as females, but in my experience with the Magellanic flightless steamer ducks, I observed that the preliminary bill-dipping was often omitted, and thus a chin-lifting form of display resulted. This was often performed in

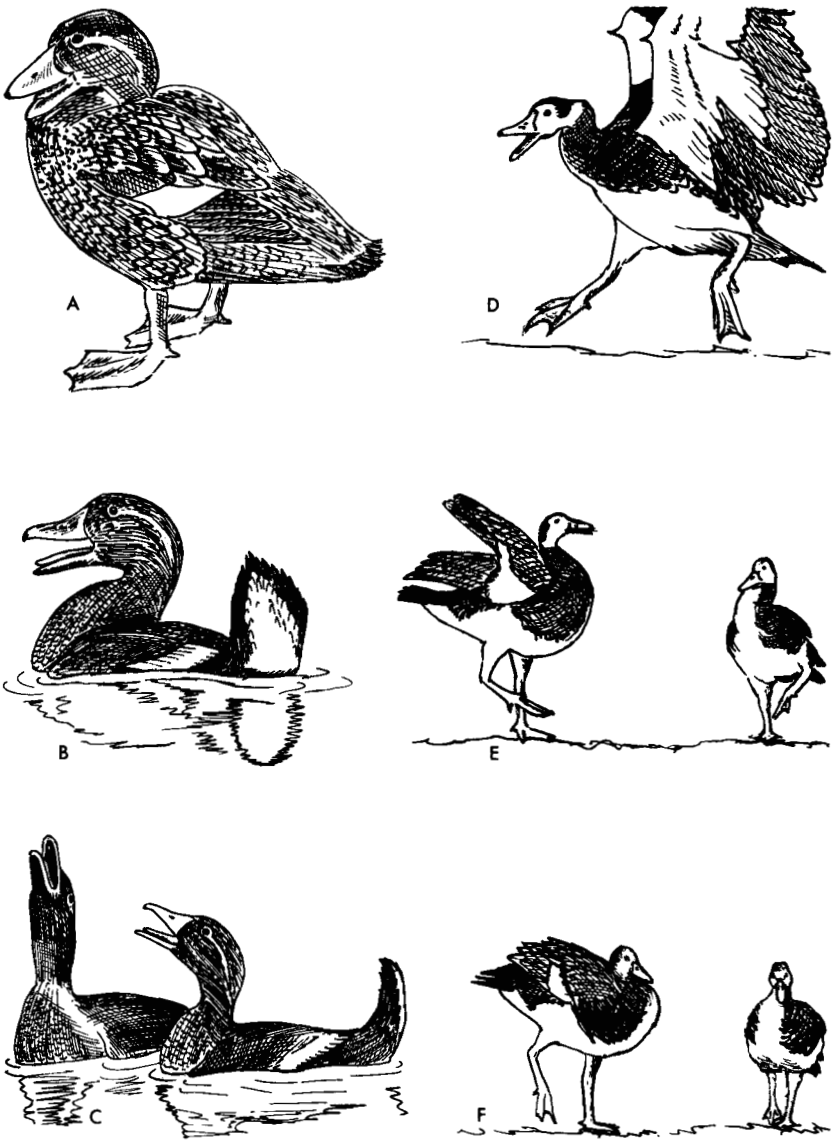


Figure 27. Flightless Steamer Ducks, Spur-winged Goose

A. Female Falkland steamer duck uttering Grunting call.

B. Male Magellanic flightless steamer duck in Short-high-and-broad posture.

C. Pair of Magellanic flightless steamer ducks, female (*left*) calling in Stretch posture as male chin-lifts toward her.

D. Spur-winged goose attacking.

E, F. Male spur-winged goose returning to mate after attack and calling while flicking his wings alternately.

response to the Stretching display of the female, apparently as an appeasement gesture. Moynihan separated the vocal displays of the flying steamer duck into three types, "Rasping Grunts," "Ticking Grunts," and "Sibilant Grunts." The Rasping Grunt is intermediate between the female's Grunt and a pure whistle, the Ticking Grunt is a rapid series of mechanical ticking noises, and the Sibilant Grunt is almost a pure whistle. The Magellanic flightless species utters a liquid, gurgling *ge-ee-ow,* which probably corresponds to the Sibilant Grunt. These calls usually occur on water, but they may also be uttered on land or in the air. Moynihan suggests that the Rasping Grunt is highly aggressive, that the Ticking Grunt is less so, and that the Sibilant Grunt is the least aggressive of the three. Head-flagging (Turning-the-back-of-the-head) is associated with the Sibilant Grunt. The most conspicuous visual display of the flying steamer ducks is the "Short-high-and-broad" (Fig. 27*B*) posture, which varies in intensity but in its extreme form is always associated with Rasping Grunts. In the Magellanic flightless species I noted that this posture was always assumed by males after threats or attacks, as they swam back to their mates, calling repeatedly. As he reached the female, she usually performed the Stretching display and the male usually chin-lifted in a kind of Triumph Ceremony (Fig. 27*C*). During the Short-high-and-broad display the under-tail coverts are exposed by a cocking of the tail, and the wing specula are exhibited by spreading and dragging the wings on the water. The posture is very similar to the High-and-erect posture of shelduck males. A second visual display is the "Submerged Sneak," which is a form of attack. This posture, which is also assumed by females (at least in the two flightless species), consists of swimming with only the head, bill, and top of the back out of the water. Sometimes the bird disappears under the water, but neither Moynihan nor I have observed a completed underwater attack.

Copulatory behavior. Moynihan observed two complete copulations in the flying steamer duck. Precopulatory display consisted in one case of mutual Bill-dipping, which graded into Head-dipping alternated with an erect "Alert" posture. Ritualized Drinking was also observed in both cases, but it may not have been associated with the precopulatory situation. The female flattened out more and more, until the male suddenly swam toward her and she went prone and was mounted. In the other copulation only the male performed Head-

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

TRIBE CAIRININI (PERCHING DUCKS)

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

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

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

Spur-winged Goose (*Plectropterus gambensis*)

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

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

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

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

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

Muscovy Duck (*Cairina moschata*)

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

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

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

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

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

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

White-winged Wood Duck (*Cairina scutulata*)

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

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

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

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

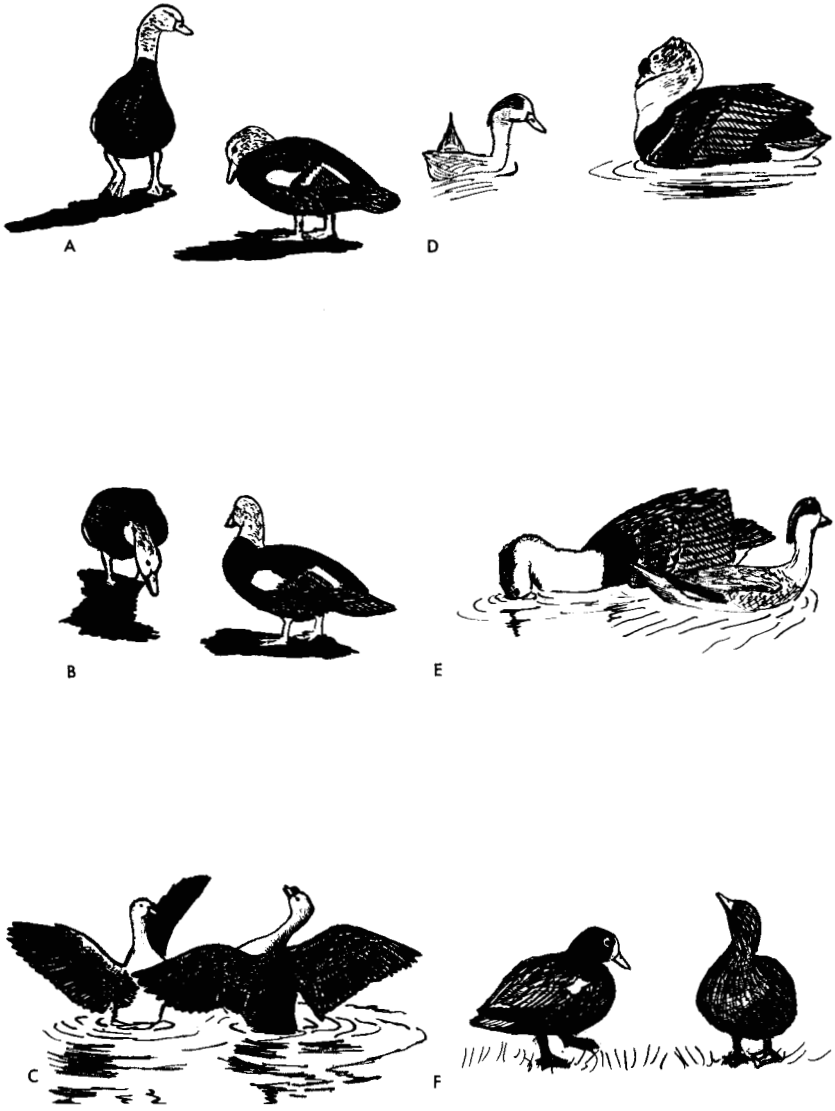


Figure 28. White-winged Wood Duck, Comb Duck, Hartlaub's Duck

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

C. Male comb ducks fighting.

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

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

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

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

Hartlaub's Duck (*Pteronetta hartlaubi*)

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

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

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

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

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

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

Comb Duck (*Sarkidiornis melanotos*)

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

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

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

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

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

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

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

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

Pygmy Geese (*Nettapus*)

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

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

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

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

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

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

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

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

Ringed Teal (*Callonetta leucophrys*)

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

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

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

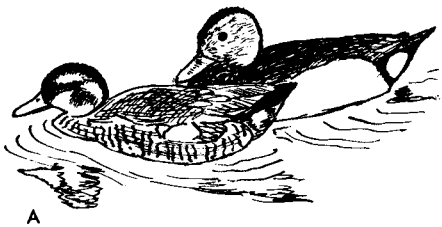
Agonistic and sexual behavior: female. Female ringed teal have a very limited number of vocalizations. They have no calls remotely like the "Decrescendo Call" of *Anas* females (Lorenz, 1951–1953), and their voice is unusual and reminds one of a domestic cat. The only loud call I have heard is a sharp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

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

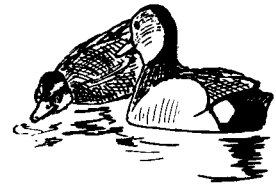
Agonistic and sexual behavior: male. The only male vocalization I have heard is a whistling noise which is probably homologous with the "Burp" (Lorenz, 1951–1953) of *Aix.* The call is a soft, wheezy whistle which, like the female's courtship call, is uttered with a bill-tossing movement and usually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

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

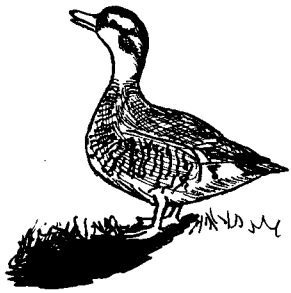
Copulatory behavior. In its copulatory behavior the ringed teal also exhibits its affinities with the wood ducks. The male signals his intention to tread by directly approaching the female. He swims



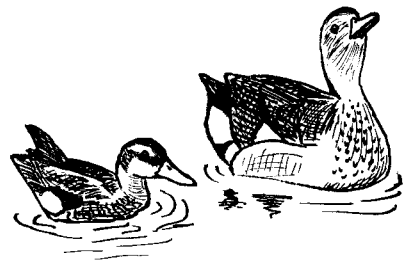
A



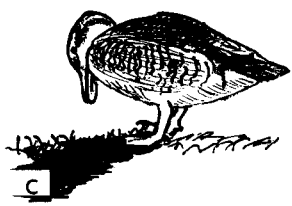
D



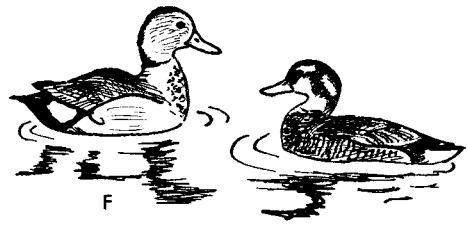
B



E



C



F

Figure 29. Ringed Teal

A. Male following female during pair formation, attempting to Face her.

B, *C*. Female uttering courtship, or Coquette, call.

D. Precopulatory behavior, female prone as male approaches.

E. Postcopulatory call of male after treading. Note lifted tail and exposed wing-speculum pattern.

F. Male Facing the female after copulation.

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

Wood Duck (*Aix sponsa*)

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

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

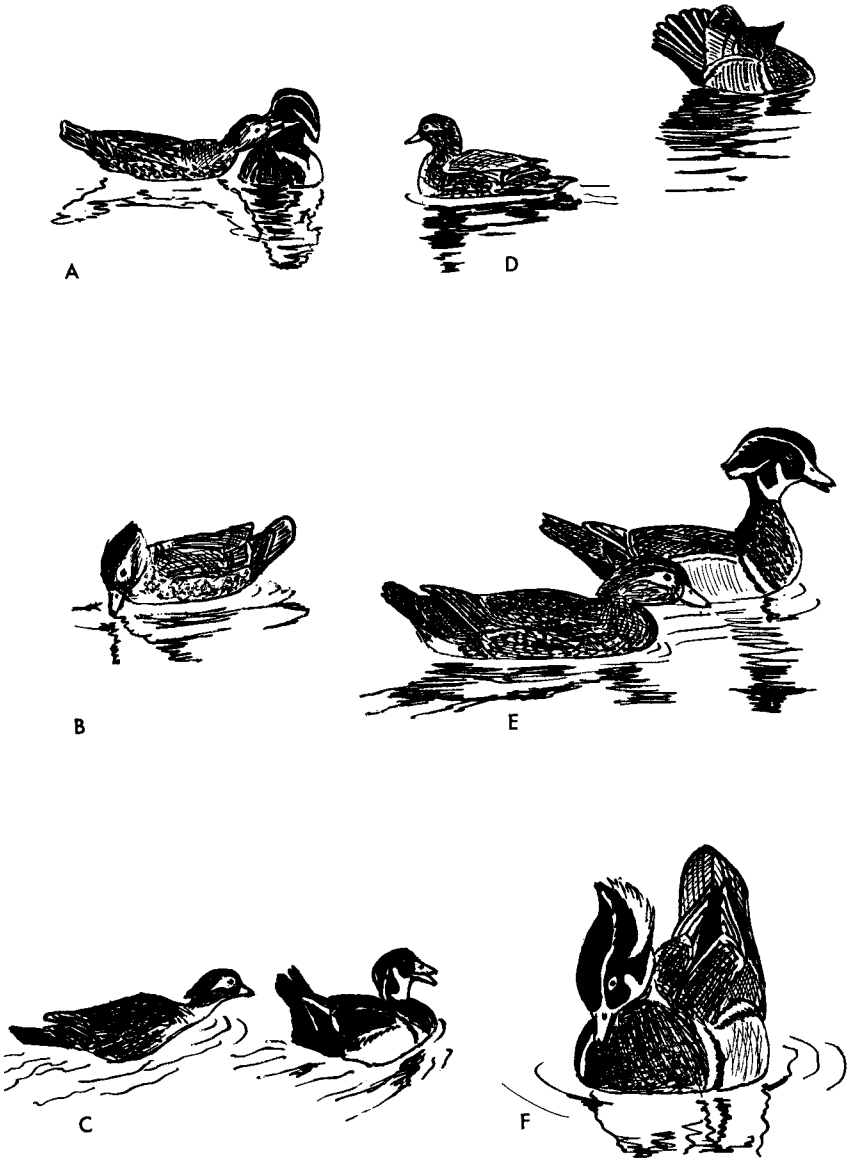


Figure 30. Wood Duck
A. Female nibbling the throat region of mate.
B. Female uttering Coquette call.
C. Female Inciting as male Turns-the-back-of-the-head.
D. Male Preening-behind-the-wing to female.
E. Male uttering Burp call.
F. Male performing Wing-and-tail-flash.

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

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

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

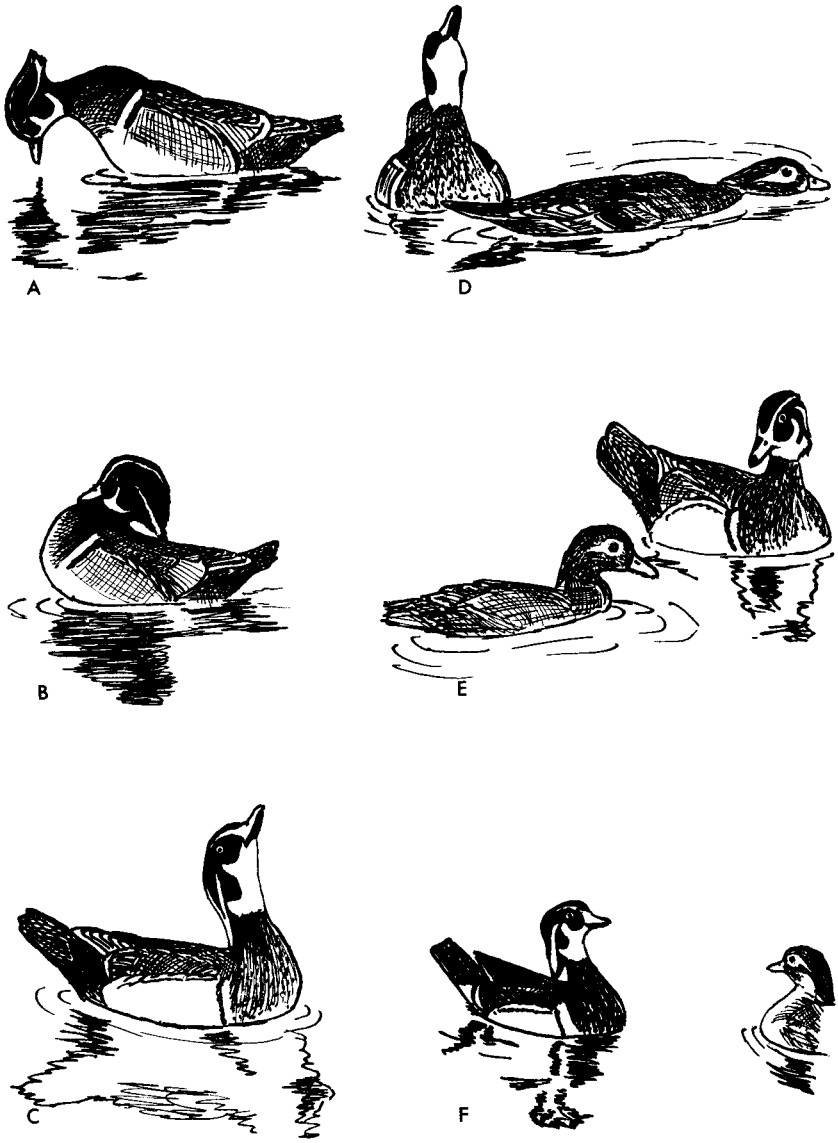


Figure 31. Wood Duck

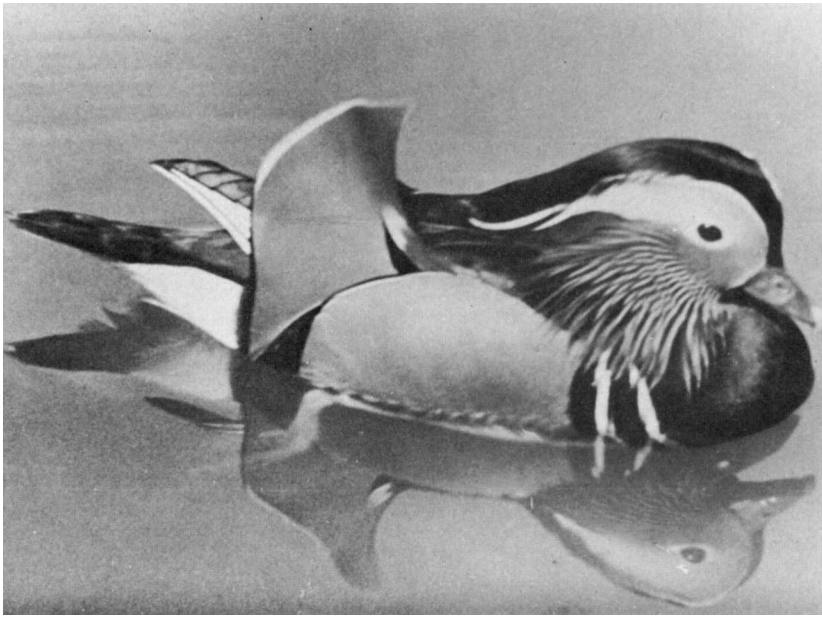
A, B. Two phases of the Display Shake.

C. Male performing Bill-jerking.

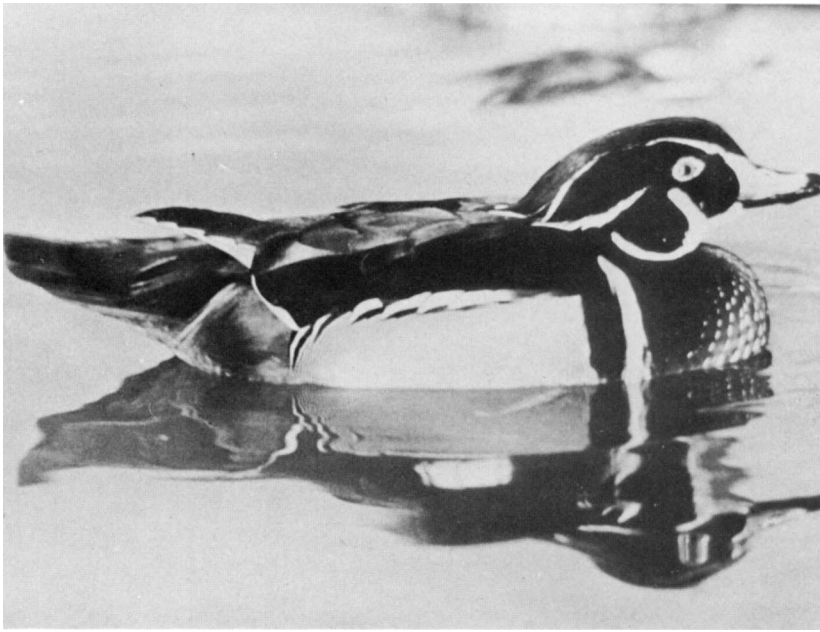
D. Female in copulation position, male performing Bill-jerking movements. (This is not a typical precopulatory display.)

E. Male Facing the female after copulation.

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



Mandarin Duck, adult male swimming.



Wood Duck, adult male drinking.

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

Yellow-billed Pintail, Grunt-whistle display.

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

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

Mandarin Duck (*Aix galericulata*)

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

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

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

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

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

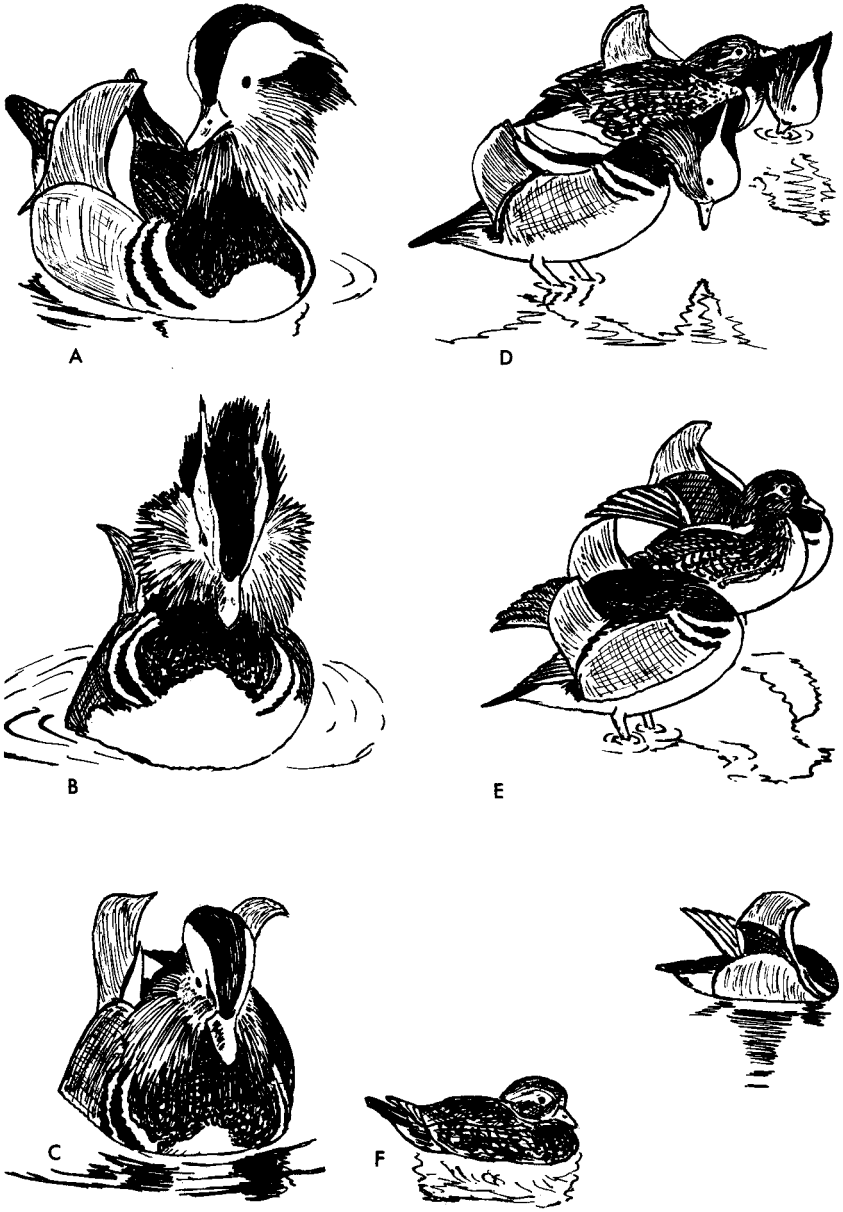


Figure 32. Mandarin Duck
A. Male in Burping posture.
B, C. Two phases of the Display Shake.
D, E. Display Drinking followed by Preening-behind-the-wing.
F. Preening-behind-the-wing to female.

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

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

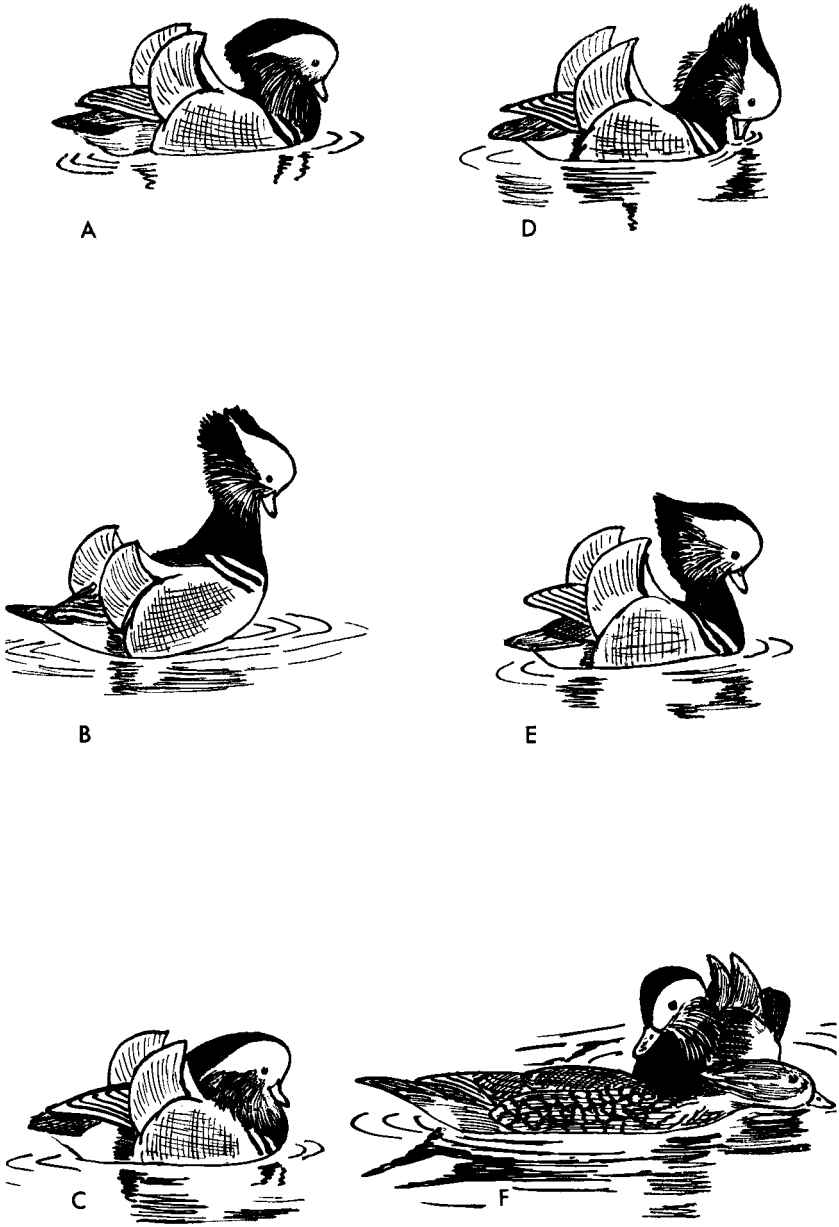


Figure 33. Mandarin Duck

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

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

Australian Wood Duck (*Chenonetta jubata*)

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

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

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

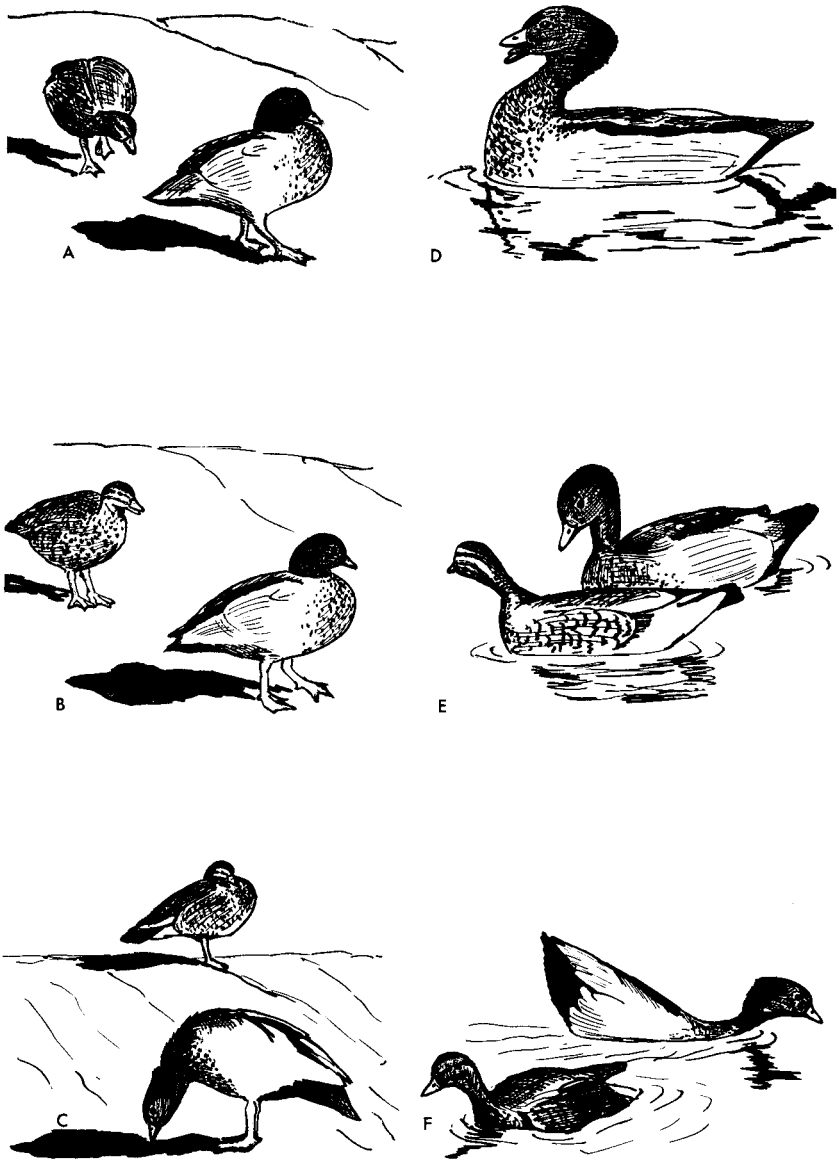


Figure 34. Australian Wood Duck
A, B. Female Inciting.
C. Male Display Shake on land. Compare with Fig. 35*B, C.*
D. Male uttering Burp call.
E. Precopulatory posture of female. (From photo by D. F. McKinney.)
F. Postcopulatory display of male, female bathing. (From photo by D. F. McKinney.)

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

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

Brazilian Teal (*Amazonetta brasiliensis*)

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

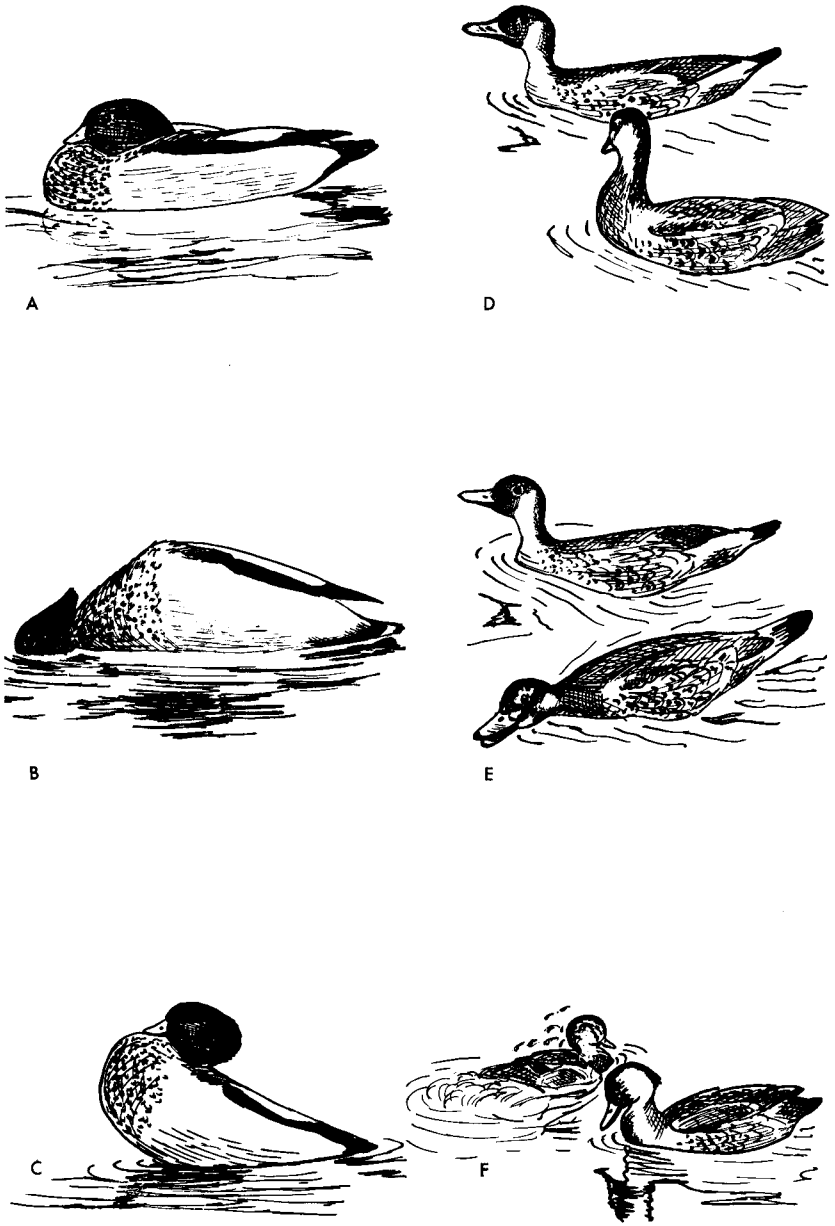


Figure 35. Australian Wood Duck, Brazilian Teal
A–C. Phases of Display Shake in Australian wood duck.
D, E. Brazilian teal, female Inciting, male Burping while Chin-lifting.
F. Brazilian teal postcopulatory display. Female bathing.

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

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

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

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

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

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

TRIBE ANATINI (SURFACE-FEEDING DUCKS)

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

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

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. 36*B*, 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. 36*A*) 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

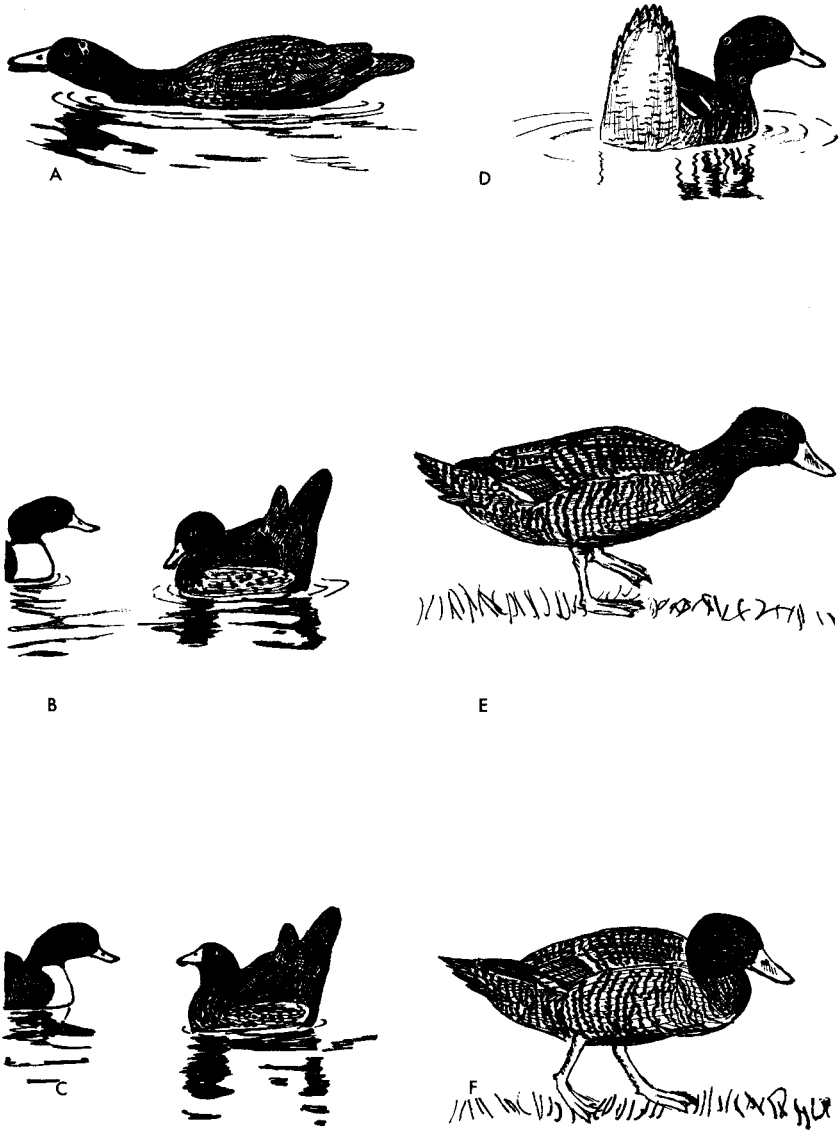


Figure 36. Blue Duck, Salvadori's Duck

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 DABBLING 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 waigiuensis*)

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. 36*E, 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. 36*D*), 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. 37*B, 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. 37*A*), 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

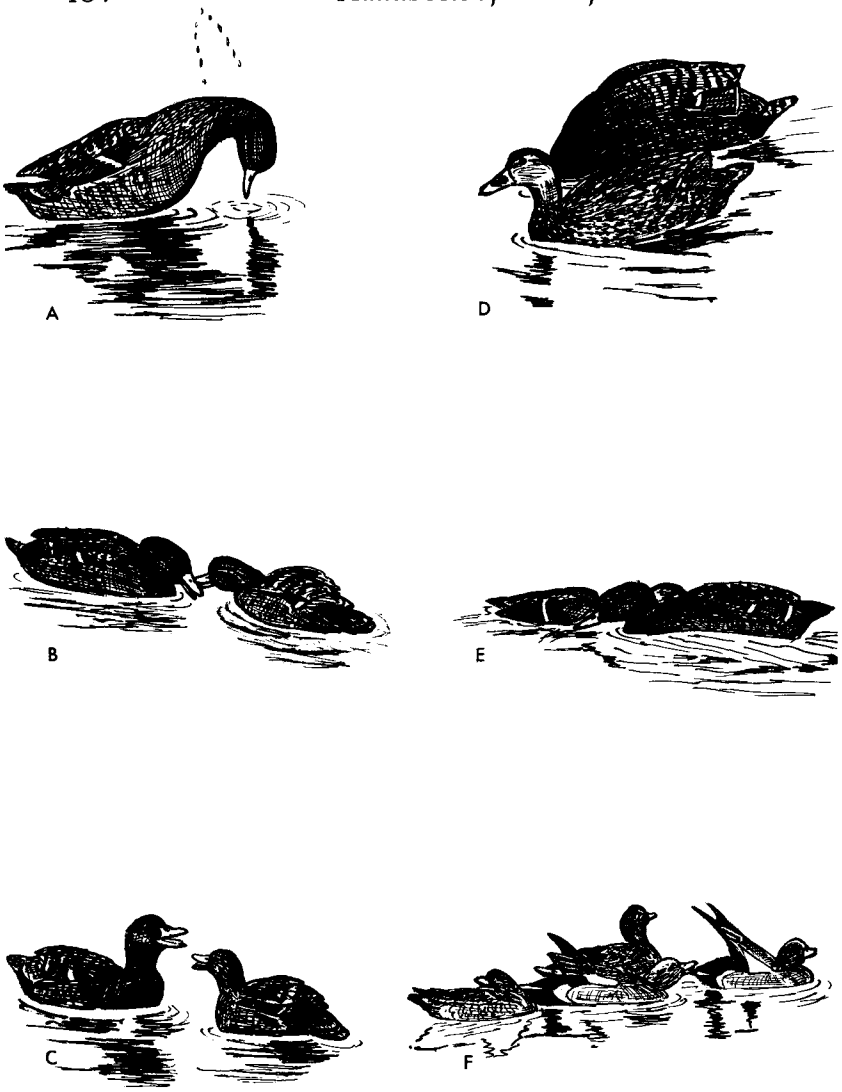


Figure 37. African Black Duck, European Wigeon

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. 37*B, 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. 37*D*). 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. 48*D, 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. 37*E*), 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. 37*F*). 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. 38*A*, *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. 39*A*) is very frequent and conspicuous in this species. His response to Inciting is to call (Fig. 38*C*, *E*) and perform rapidly repeated Chin-lifting (Fig. 37*A*, *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. 38*E*, *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.

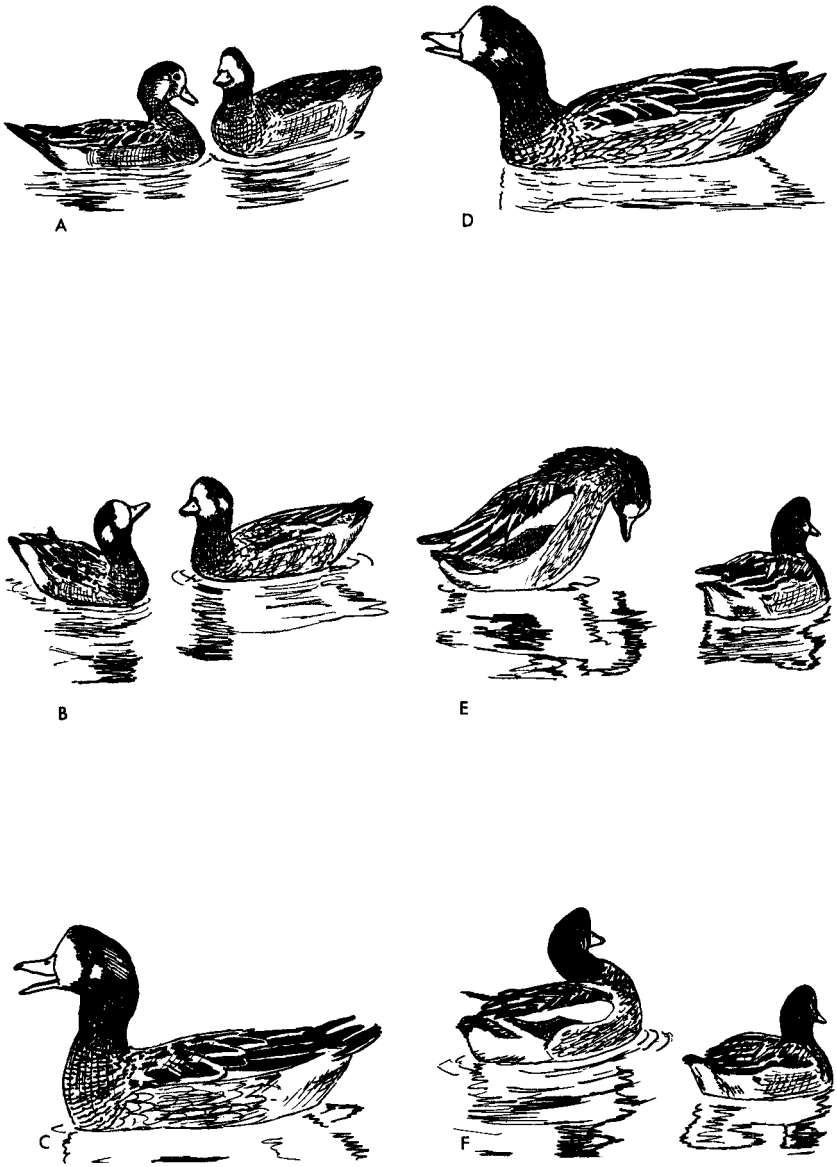


Figure 38. Chiloé Wigeon

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.

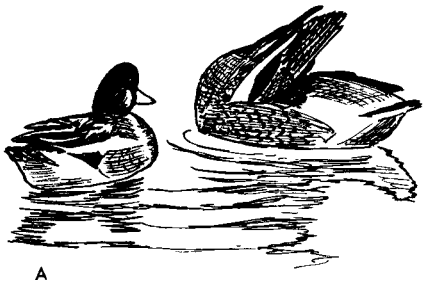
Copulatory behavior. Although I have often observed precopulatory Head-pumping, I have seen copulation only once. After treading, the male whistled one time with his head fairly erect; then he remained motionless, facing the female in that posture while the female Preened-behind-the-wing several times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

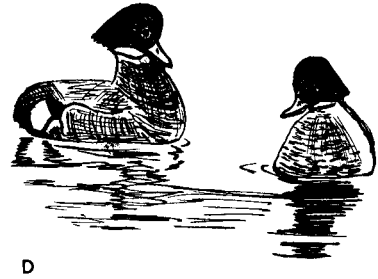
Falcated Duck (*Anas falcata*)

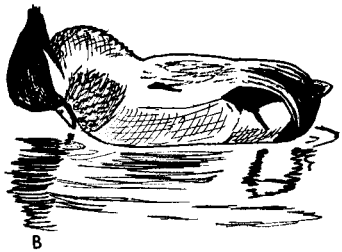
The falcated duck exhibits affinities both with the wigeons and with the gadwall, and is probably rather more closely related to the latter. Its downy young are wigeonlike, with brownish, unmarked cheeks. The juveniles resemble the adult female, which in shape reminds one of a wigeon and in plumage pattern 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 wigeon-like 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.

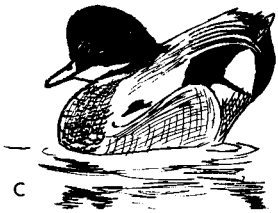
General behavior. In its general behavior, the falcated duck is very reminiscent of the gadwall. It does not graze like wigeons, but is a surface-feeder. Preflight movements are the usual Neck-jerking and lateral Head-shaking.

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









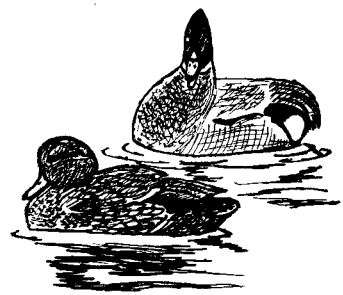


Figure 39. Chiloé Wigeon, Falcated Duck

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, *lililili,* 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. 39*B, 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. 39*D–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. 41*B*) 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. 40*A*, *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.

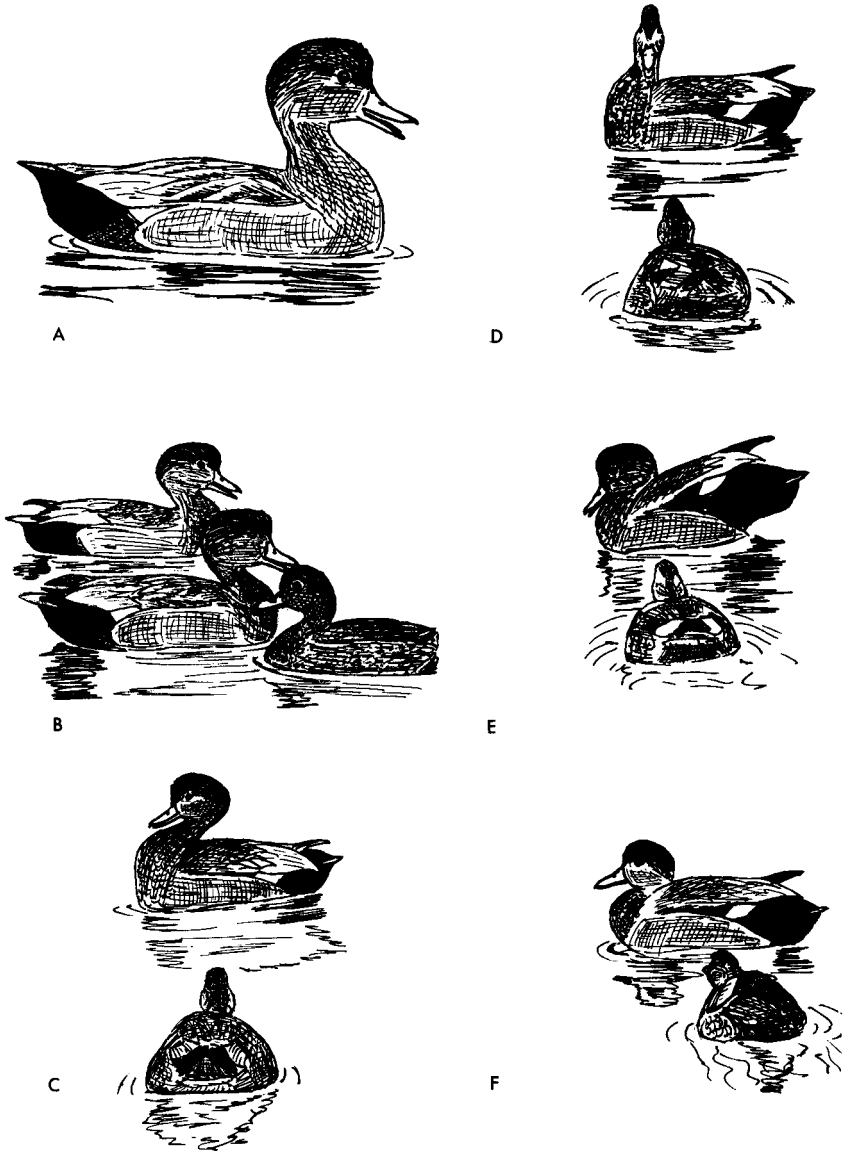


Figure 40. Gadwall
A, B. Male uttering the Burp call.
C–F. Head-up-tail-up–Down-up sequence.
C. Head-up-tail-up.
D. Turning head toward female.
E. First phase of Down-up.
F. Second phase of Down-up.

41*A*). 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. 41*B*) 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

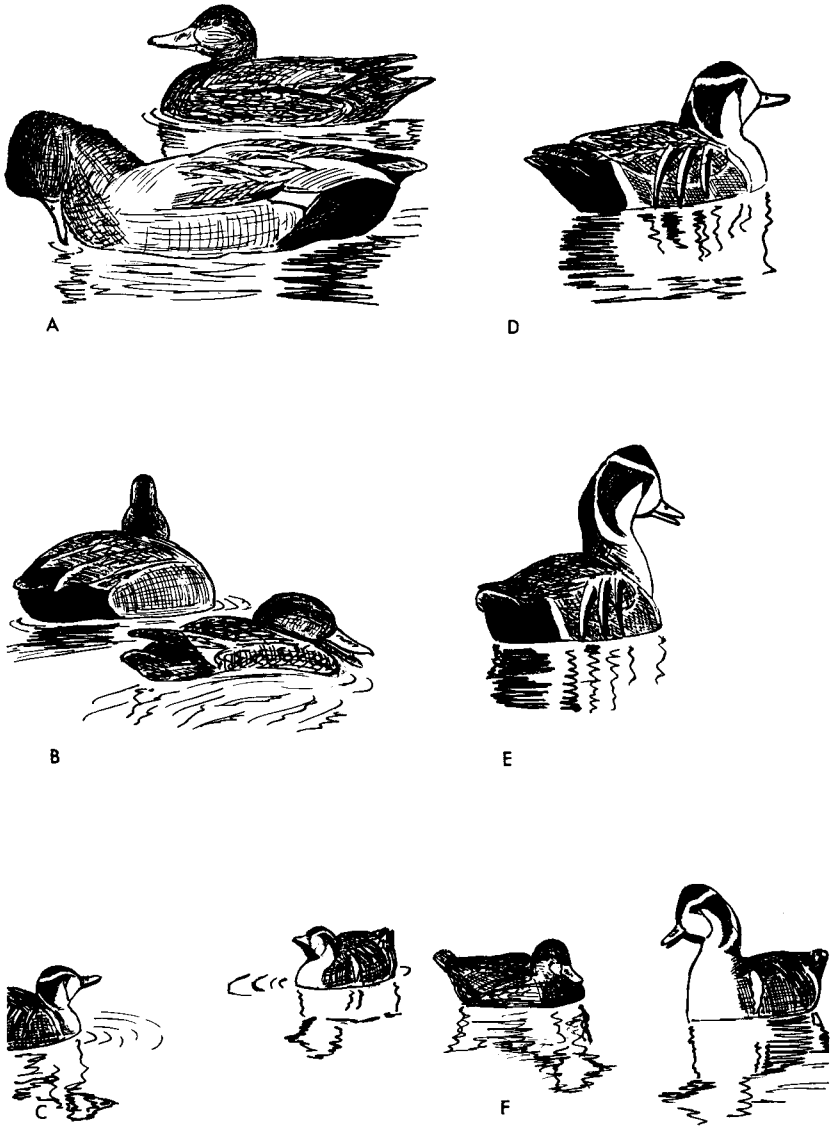


Figure 41. Gadwall, Baikal Teal

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 conists of a sudden lifting of the head and an erection of the small crest from a resting position (Fig. 41*D–F*), and an acompanying *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. 42*E, 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-zeet'*, is uttered. Several males often perform this display in concert. The Grunt-whistle is the most common major display (Fig. 42*A, 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. 42*C, 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

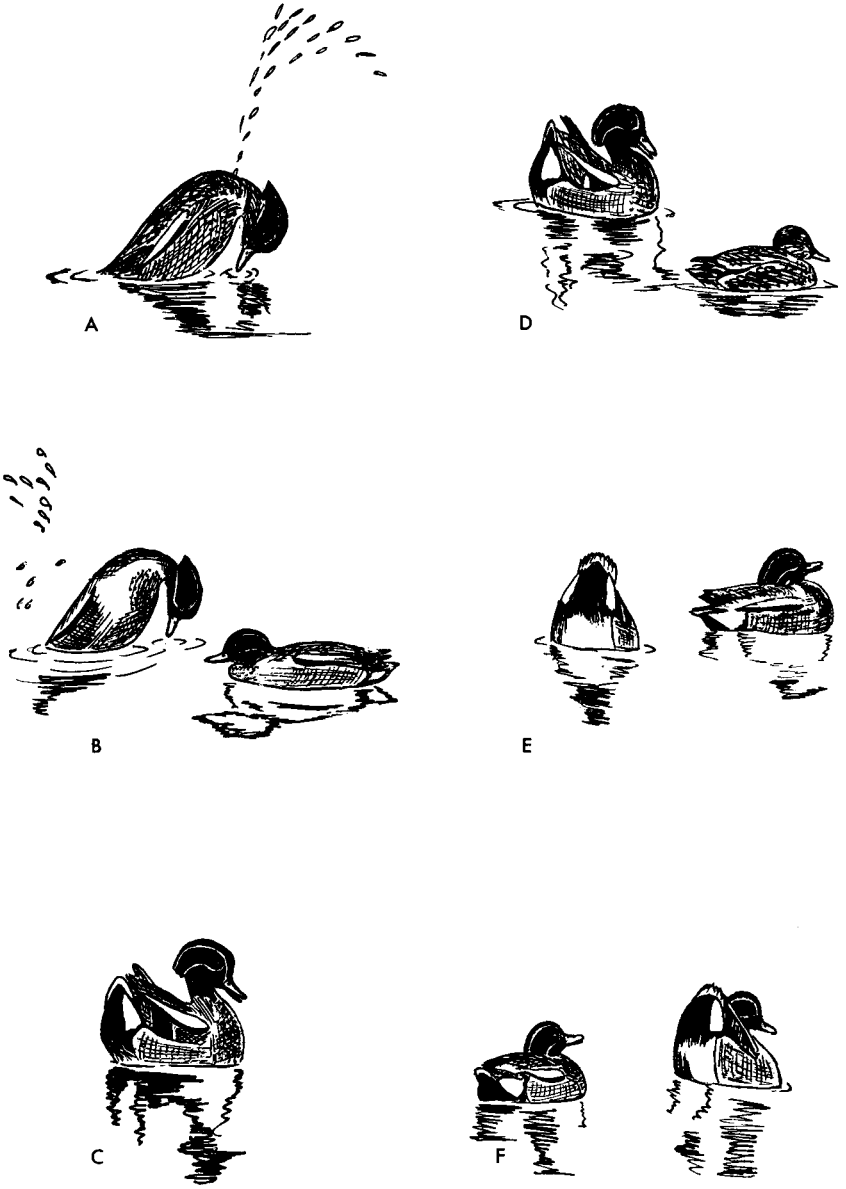


Figure 42. Common Teal

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. 43*E*, *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. 43*A*), 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. 43*E, 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. 43*B*) 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. 43*C, D*). The Head-up-tail-up is not so exaggerated as in the common teal, and the speculum

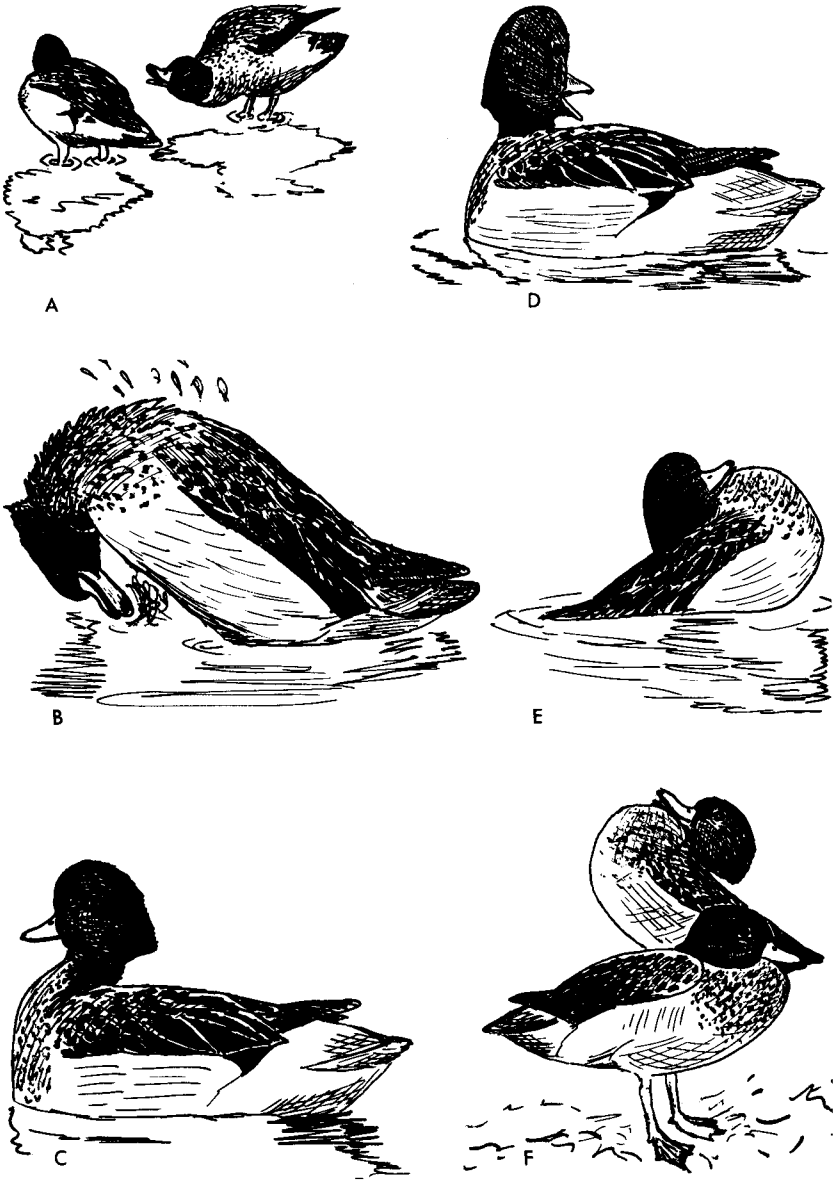


Figure 43. Sharp-winged Teal
A. Gesture of Greeting.
B. Grunt-whistle.
C, D. Head-up-tail-up followed by turning head toward the female.
E. Bridling on water.
F. Bridling on land.

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 precopulatory display. Females frequently Nod-swim, and this Nod-swimming is, as in males, highly specialized and unique to the Cape teal (Fig. 44*D*).

Agonistic and sexual behavior: male. The most frequent male display, which is performed throughout most of the year, is the Burp (Fig. 44*A*). This is a clear whistle, *oo-whee'-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. 44*D*) 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. 44*B, 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. 44*E*) 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,

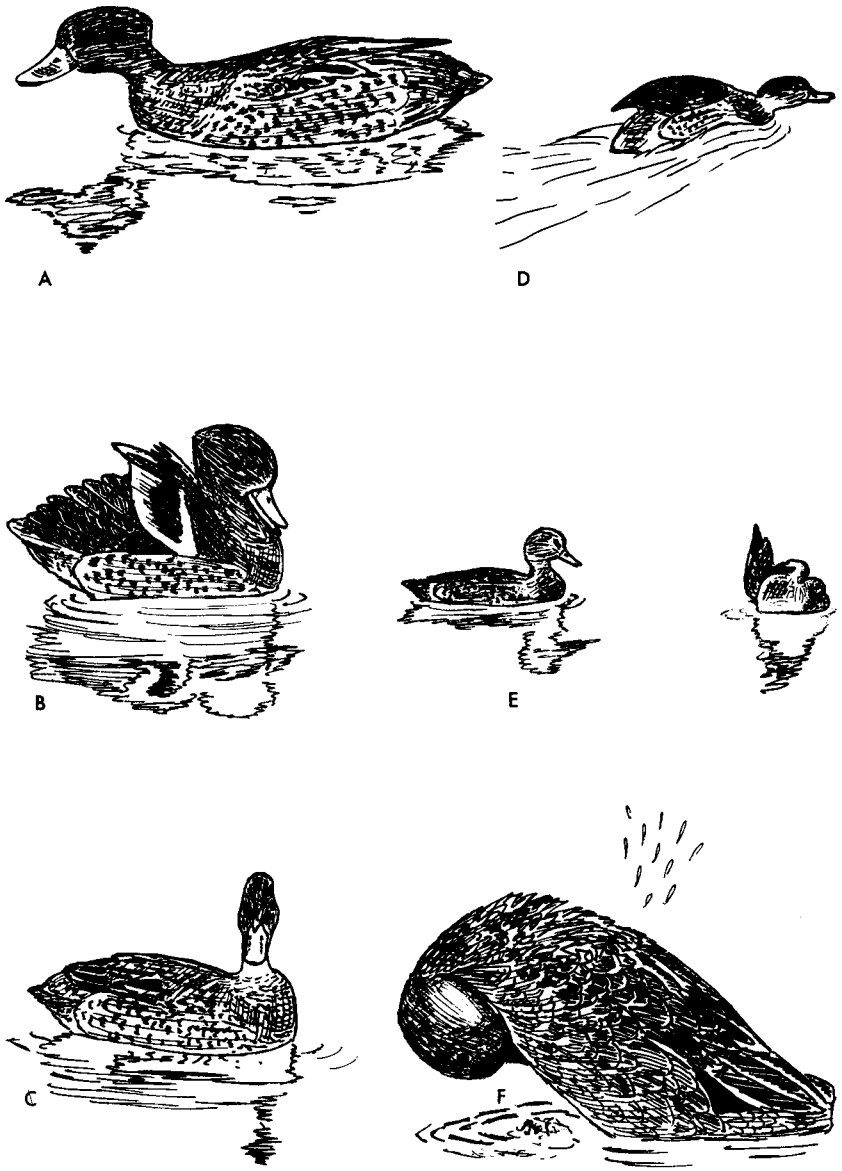


Figure 44. Cape Teal, Gray Teal

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

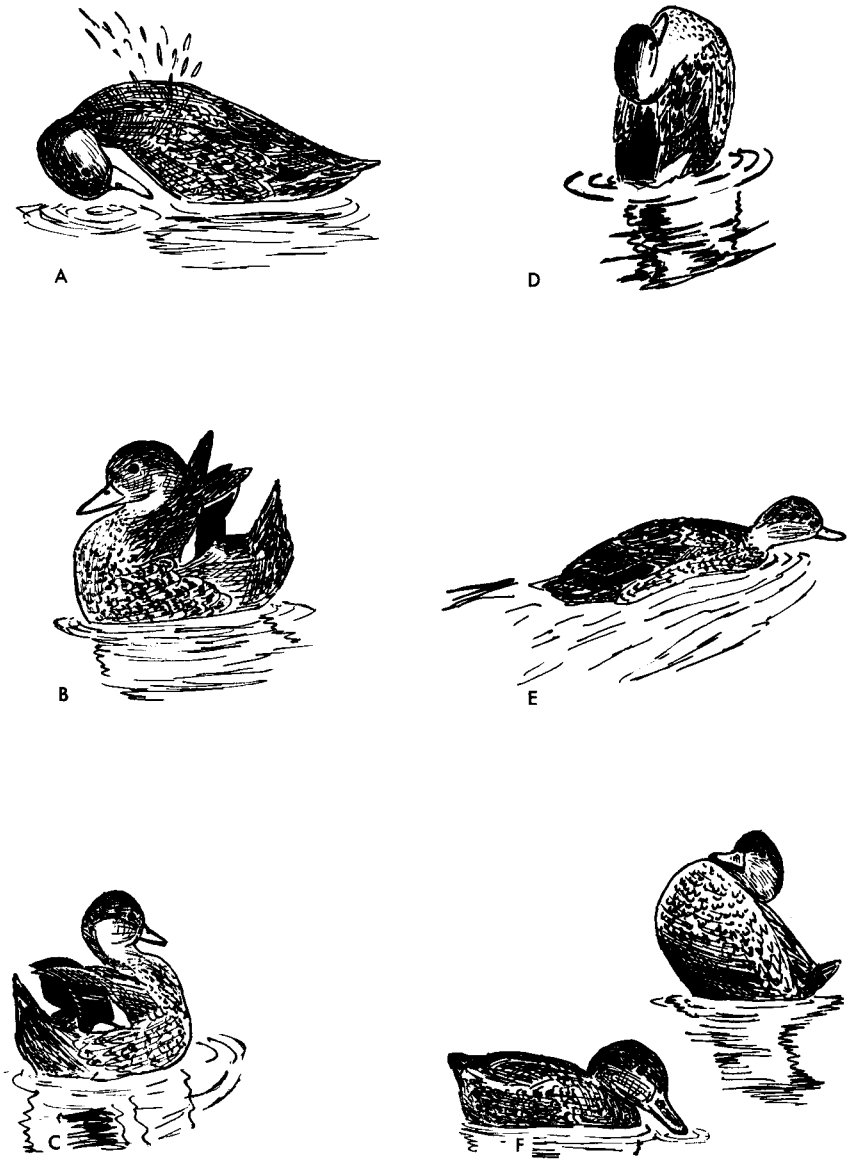


Figure 45. Gray Teal
A. Grunt-whistle.
B. Head-up-tail-up.
C. Facing the female after the Head-up-tail-up.
D. Bridling.
E. Nod-swimming
F. Independent Bridling. Compare with *D.*

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. 46*D*), 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. 44*F*, 45*A*) 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. 45*B*), which in turn is immediately followed by Facing the female (Fig. 45*C*), Bridling (Fig. 45*D*), and finally Nod-swimming (Fig. 45*E*) and Turning-the-back-of-the-head toward the female. Bridling occurs as an independent display fairly often (Fig. 45*F*), 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. 46*B, 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. 46*A*) 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 chesntut 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.

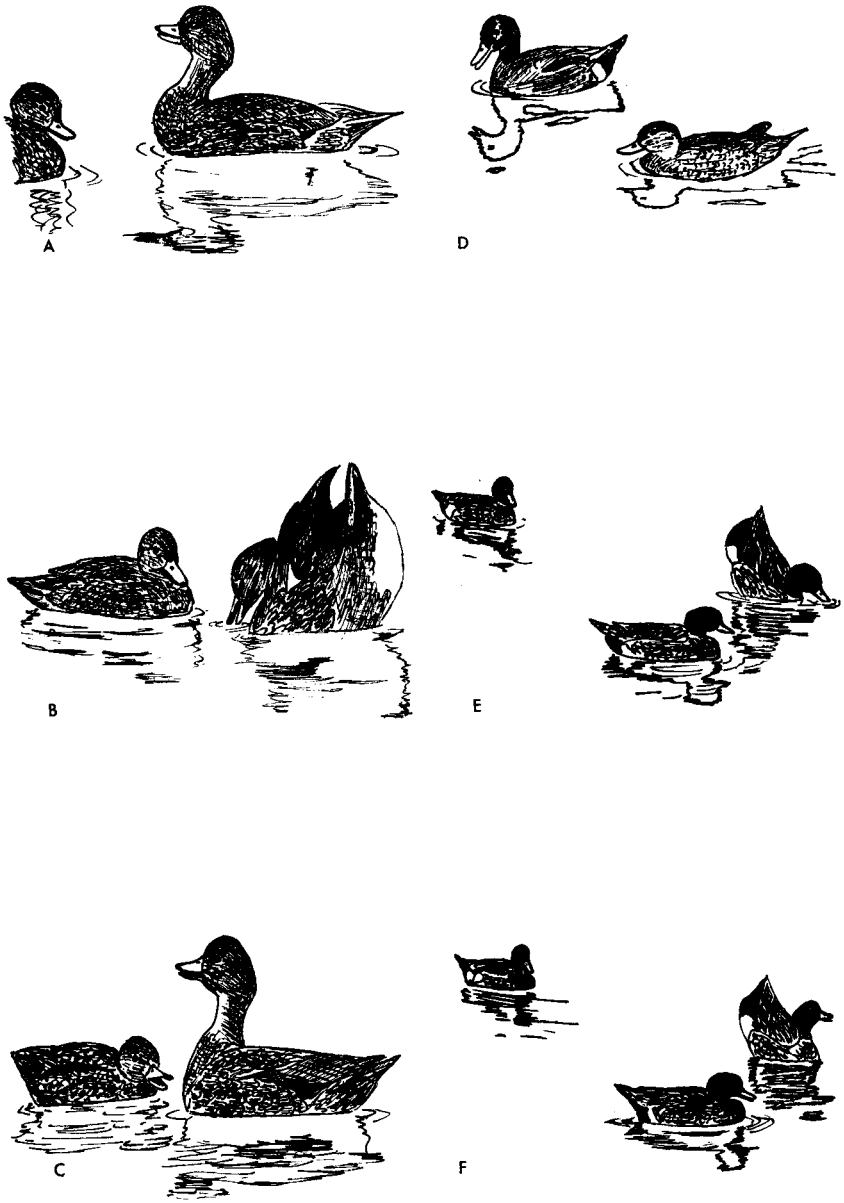


Figure 46. Gray Teal, Chestnut Teal
A. Male gray teal performing Chin-lifting prior to Down-up.
B, C. Two phases of Down-up display in gray teal.
D. Male chestnut teal uttering Burp, female swimming normally.
E, F. Two phases of Down-up in chestnut teal.

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. 46*D*) 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. 46*E, 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 "renesting 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. 48*B*) 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. 47*A–C*) is the most common mallard display. It has exactly the same form as it has in the Florida duck (Fig. 47*E*), the mottled duck, the Hawaiian duck, and the Laysan duck (Fig. 48*C*), although in the last-named form the whistled note is replaced by a high-pitched *raeb*. The Head-up-tail-up (Fig. 47*A–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. 47*F*) 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. 48*D, 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. 48*F*) there is a strong tendency to nod the

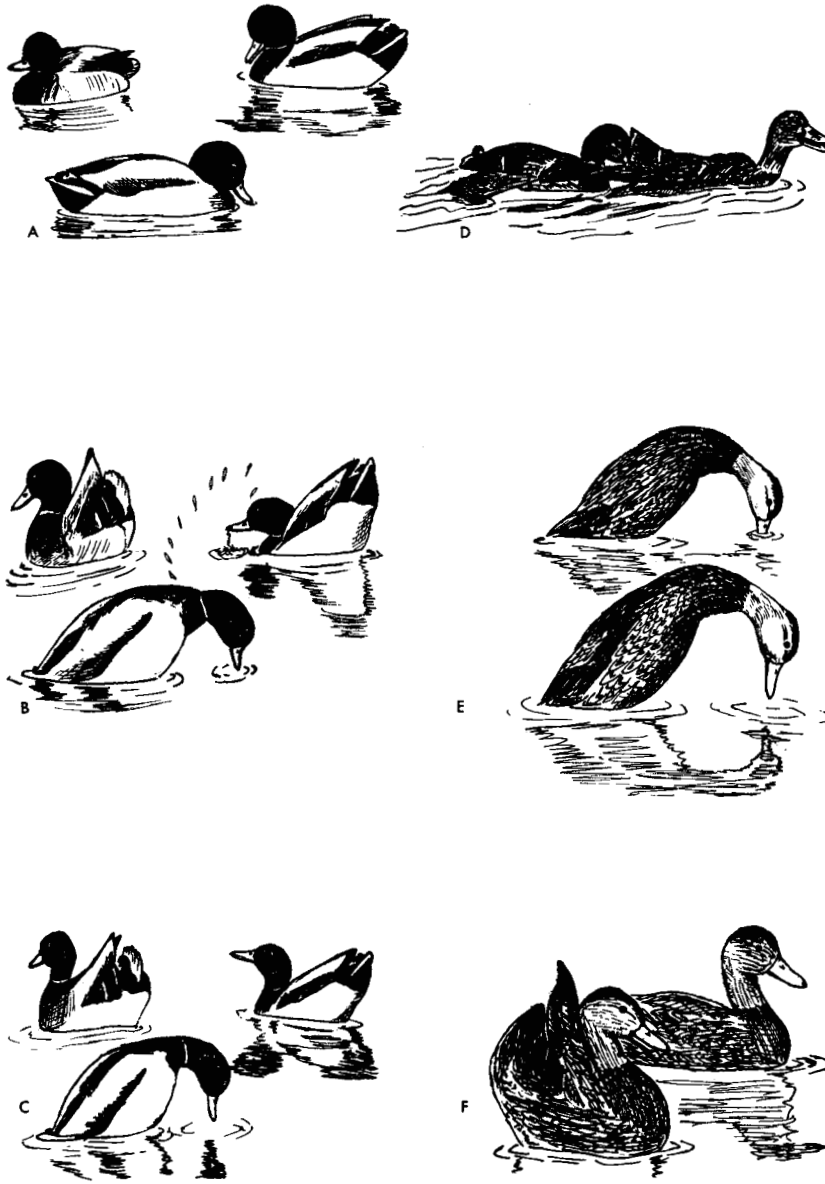


Figure 47. Mallard, Florida Duck

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.

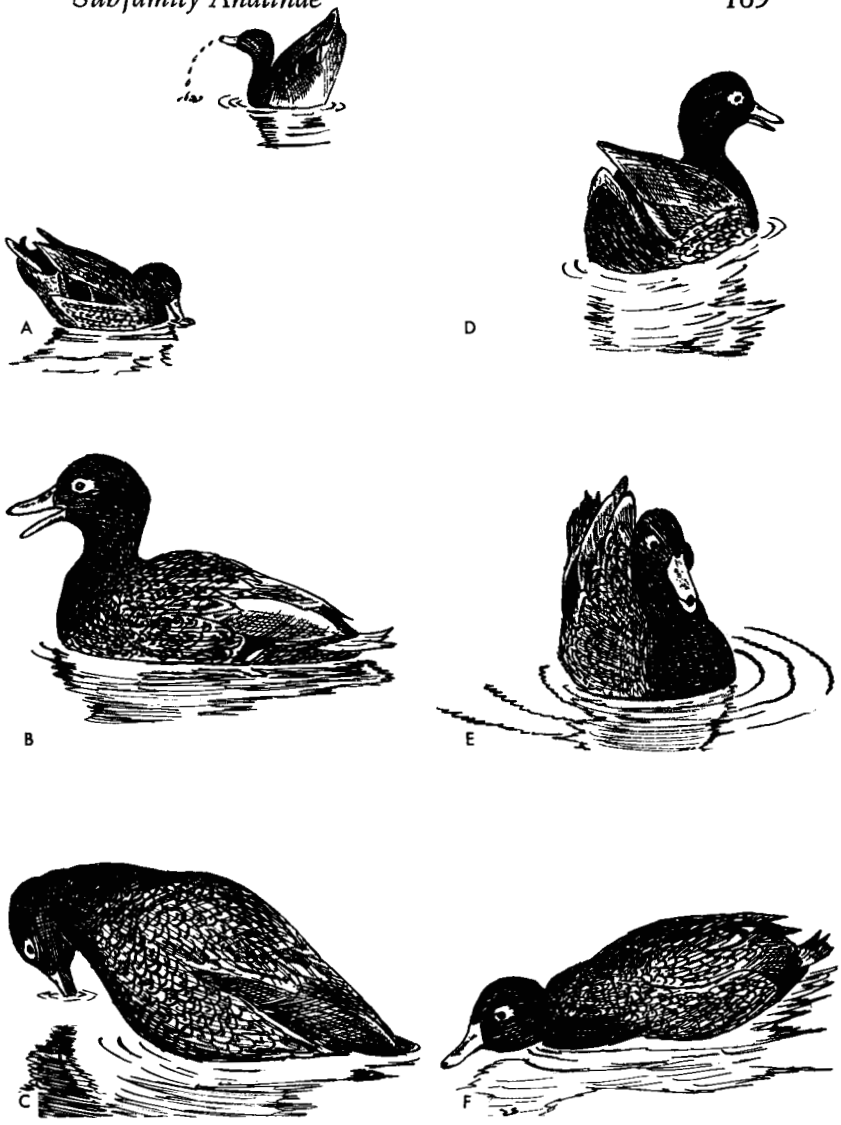


Figure 48. Hawaiian Duck, Laysan Duck

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. 47*B*.

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. 47*A–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. 48*A*), 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

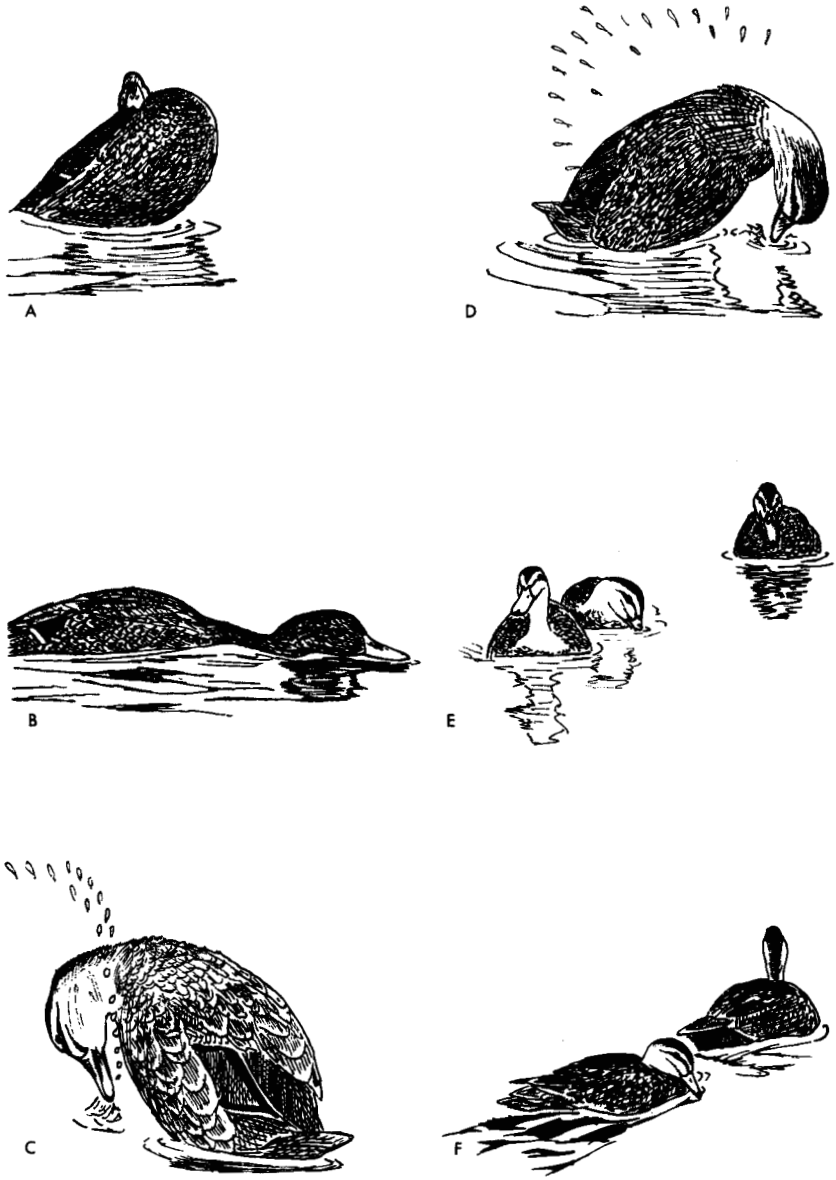


Figure 49. African Yellow-bill, New Zealand Gray Duck

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. 49*A*); then he Nod-swims rapidly away from the female (Fig. 49*B*). 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. 49*C*, *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. 49*E*, *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. Preflight 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. 49*A, 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.

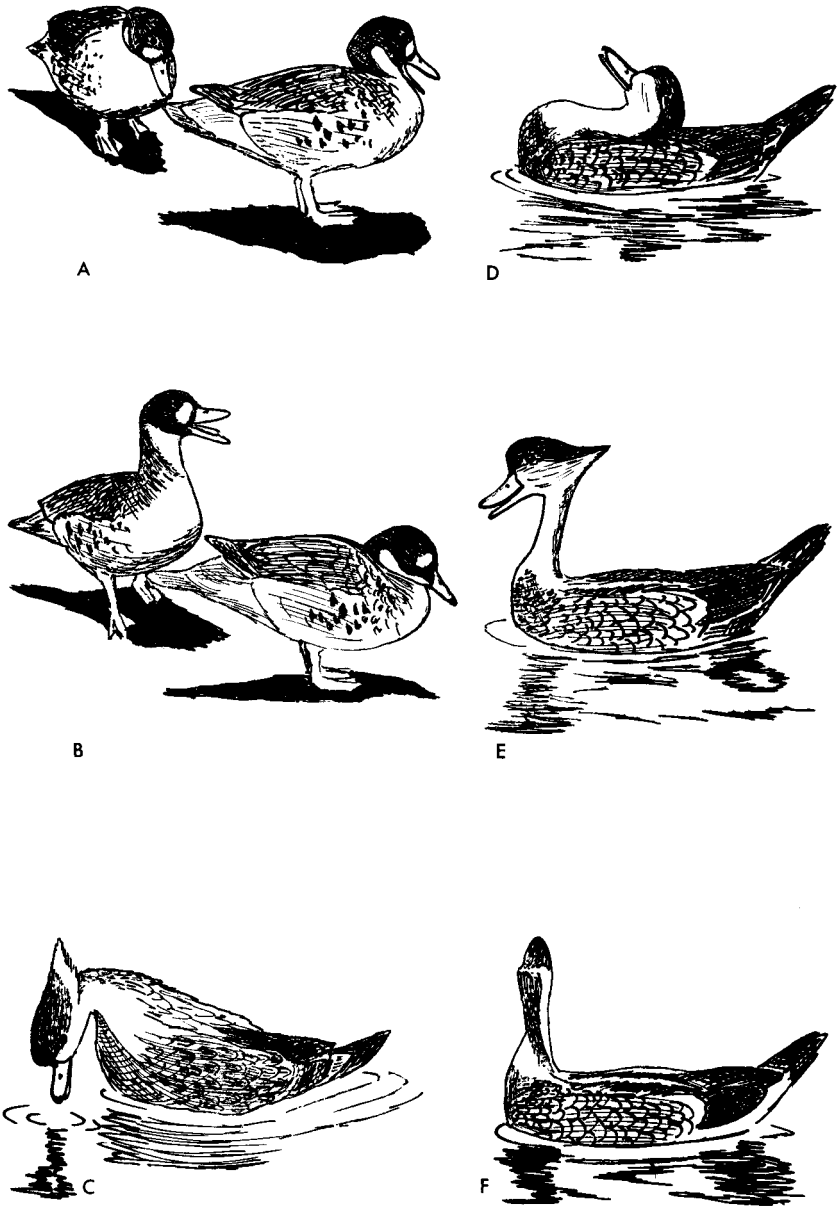


Figure 50. Bronze-winged Duck, Crested Duck
A, B. Bronze-winged ducks, two females Inciting.
C. Crested duck, Grunt-whistle. (From photo by D. F. McKinney.)
D–F. Crested duck, Head-up-tail-up sequence. (From photos by D. F. McKinney.)

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 shelducks. 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. 50*D–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. 51*D*) 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-rrt'* 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. 51*A*). 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. 51*B, 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

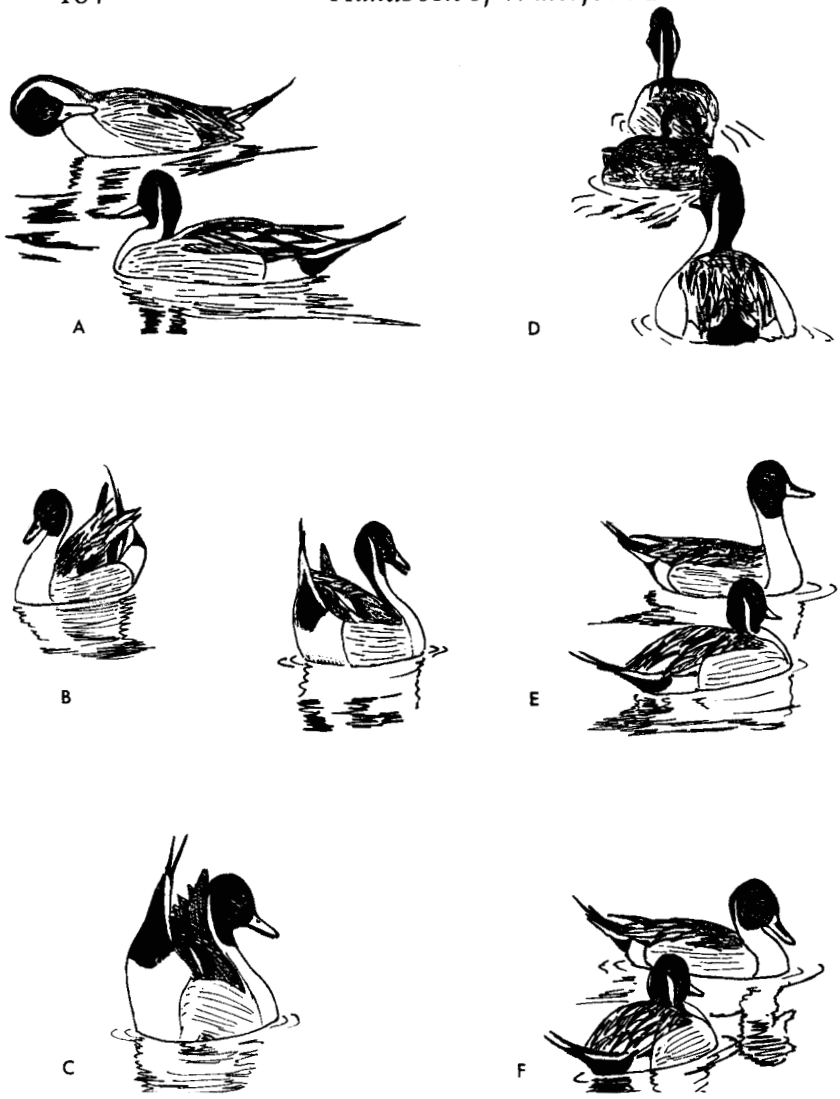


Figure 51. Common Pintail

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. 51*D*). 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. 51*E, 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. 52*A*) 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. 52*B–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

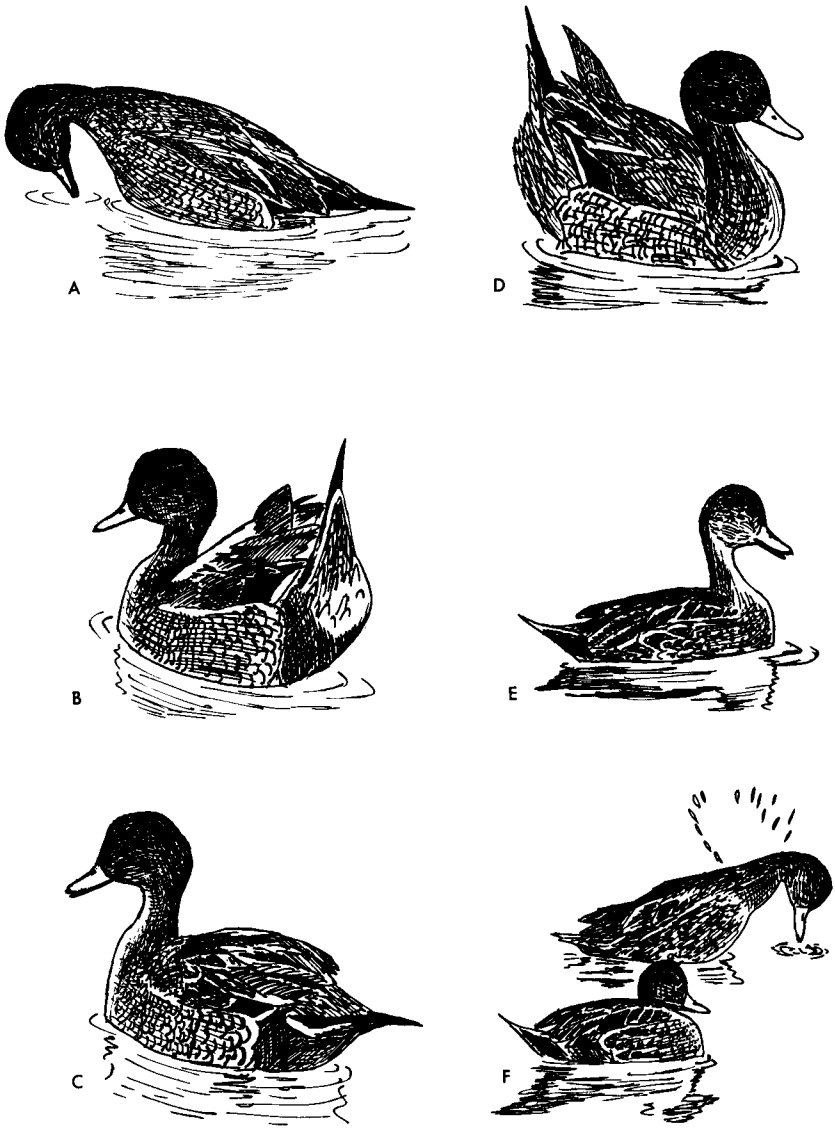


Figure 52. Kerguelen Pintail, Yellow-billed Pintail

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. 51*B*.

D. Head-up-tail-up. In this drawing, as well as in 52*B*, the peak of the posture is shown. Compare with Fig. 51*B, 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 Chiloé 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. 52*E*). Males often Burp repeatedly for ten or fifteen minutes before performing their only major display, the Grunt-whistle (Fig. 52*F*). 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. 53*E*) 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.

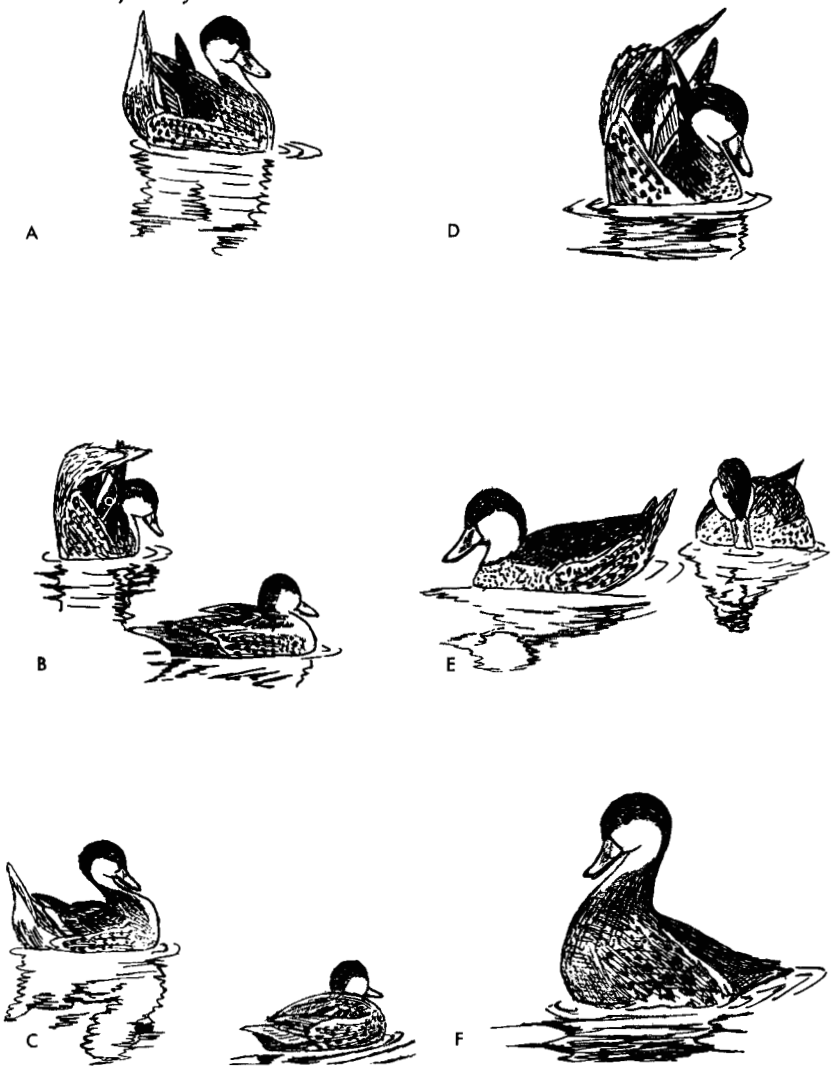


Figure 53. Bahama Pintail

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. 53*B, 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. 53*A*), 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. 53*E*). 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. 53*F*), and then may utter several Burp calls while the female bathes.

Red-billed Pintail (*Anas erythrorhyncha*)

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. 54*B*, *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

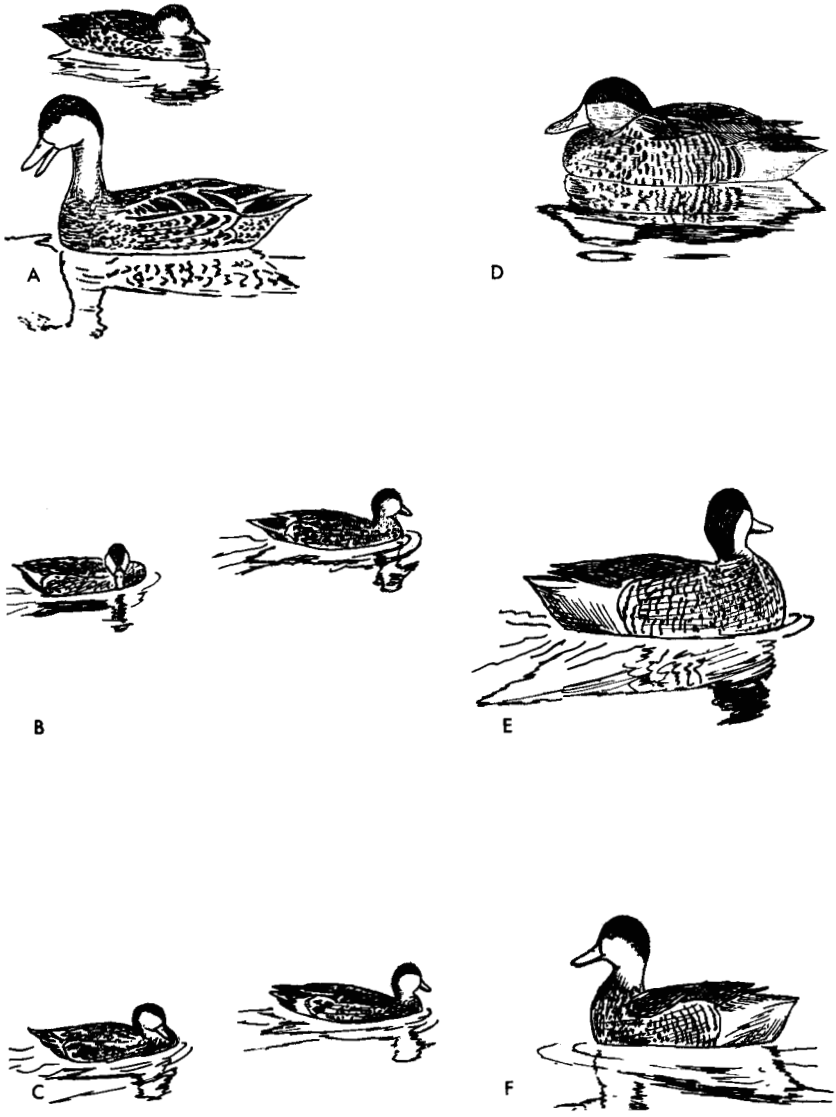


Figure 54. Red-billed Pintail, Silver Teal

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. 54*A*). 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. 54*B, 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. 54*D*). 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. 54*D*). 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. 54*F*). 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. 55*A, 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

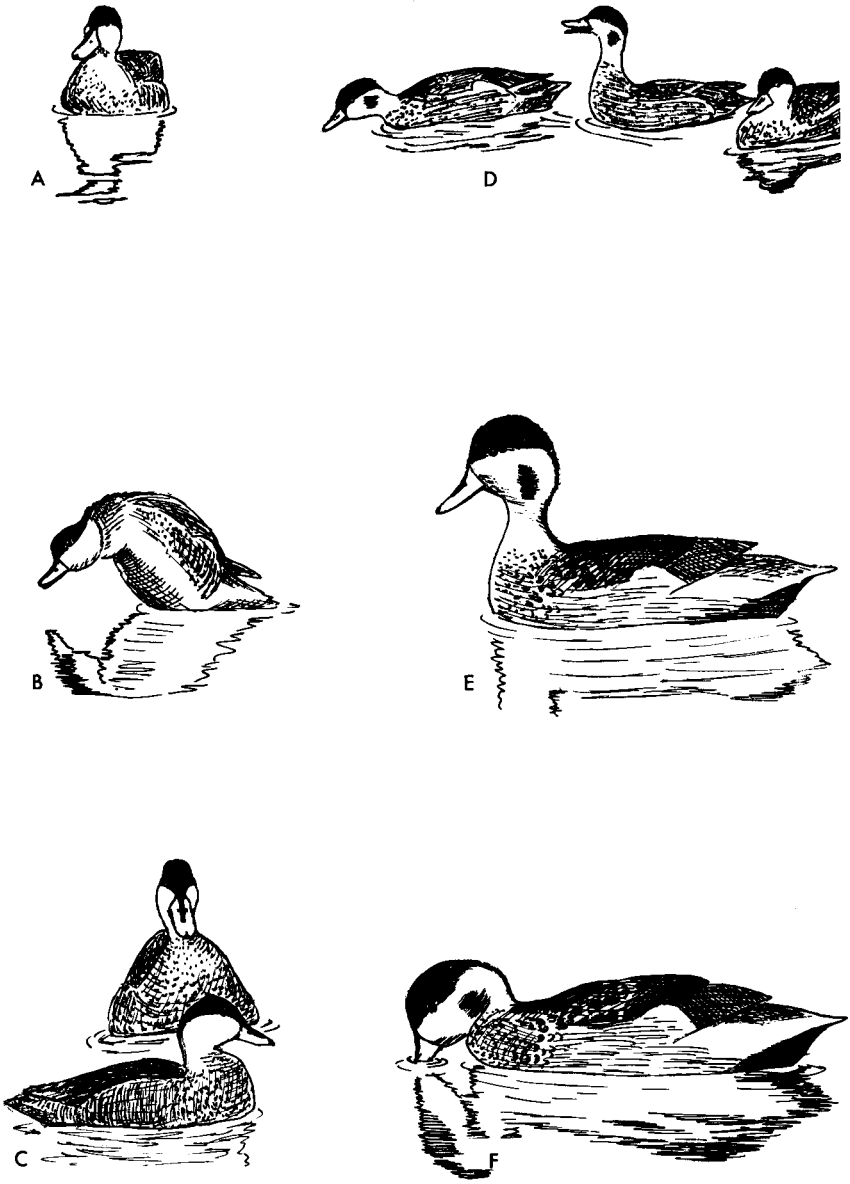


Figure 55. Silver Teal, Hottentot Teal

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. Inciting 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. 55*E, 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. 56*A*); 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

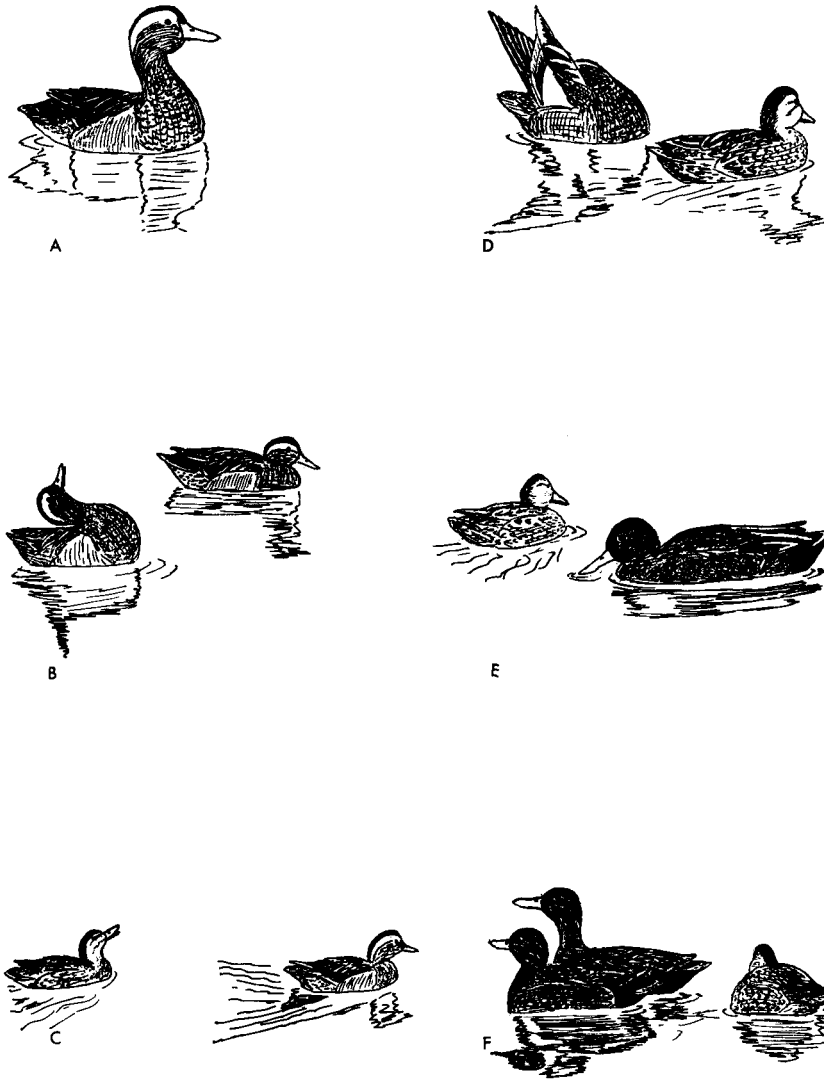


Figure 56. Garganey, Cinnamon Teal

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. 56*D*). 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-piched 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 *tseeel* 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

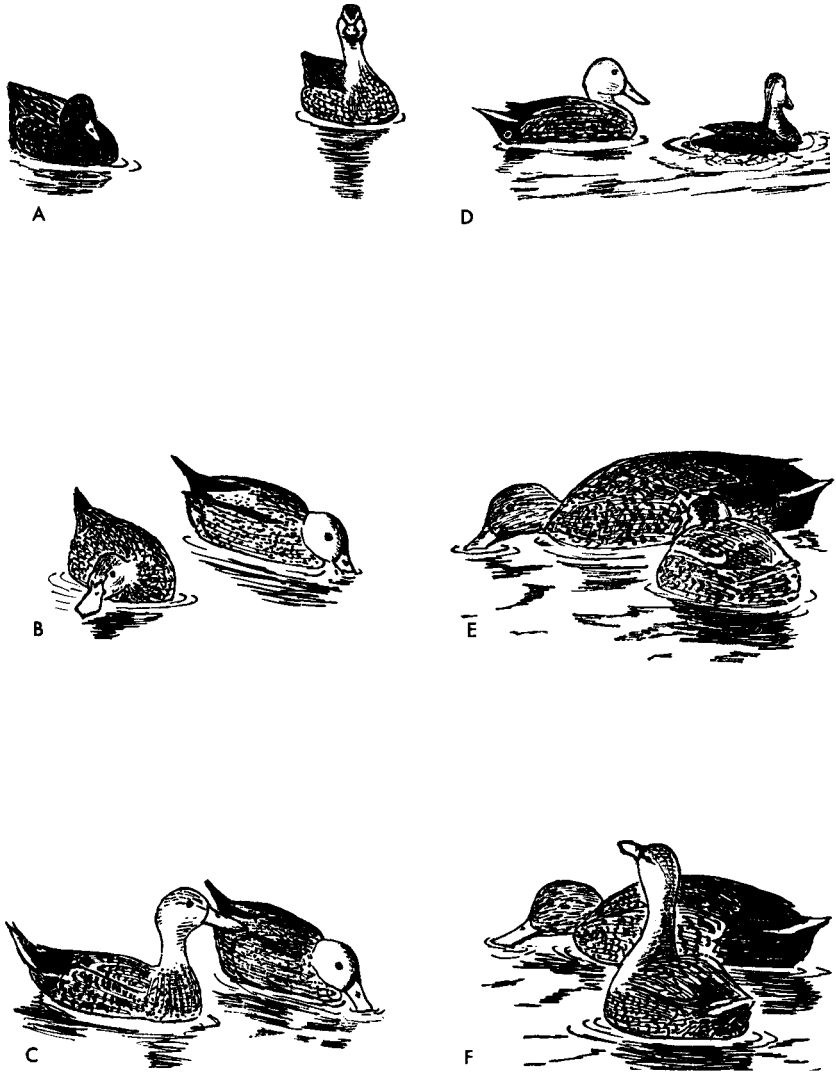


Figure 57. Cinnamon Teal, Red Shoveler, Cape Shoveler

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. 57*A*). 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. 56*F*) 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. 56*E*), 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. 57*B*, *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 *tooka-tooka-tuk-tuk*. This call is often used as a warning, but more often it serves as an introduction to the Mock-feeding display (Fig. 57*B*, *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. 57*D*).

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. 57*E, 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. 58*A*), 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. 57*E, F*; 58*B*), and it is often accompanied by the belchlike calls. Very often this display is terminated by up-ending, or "tipping-up" (Fig. 58*B*). When

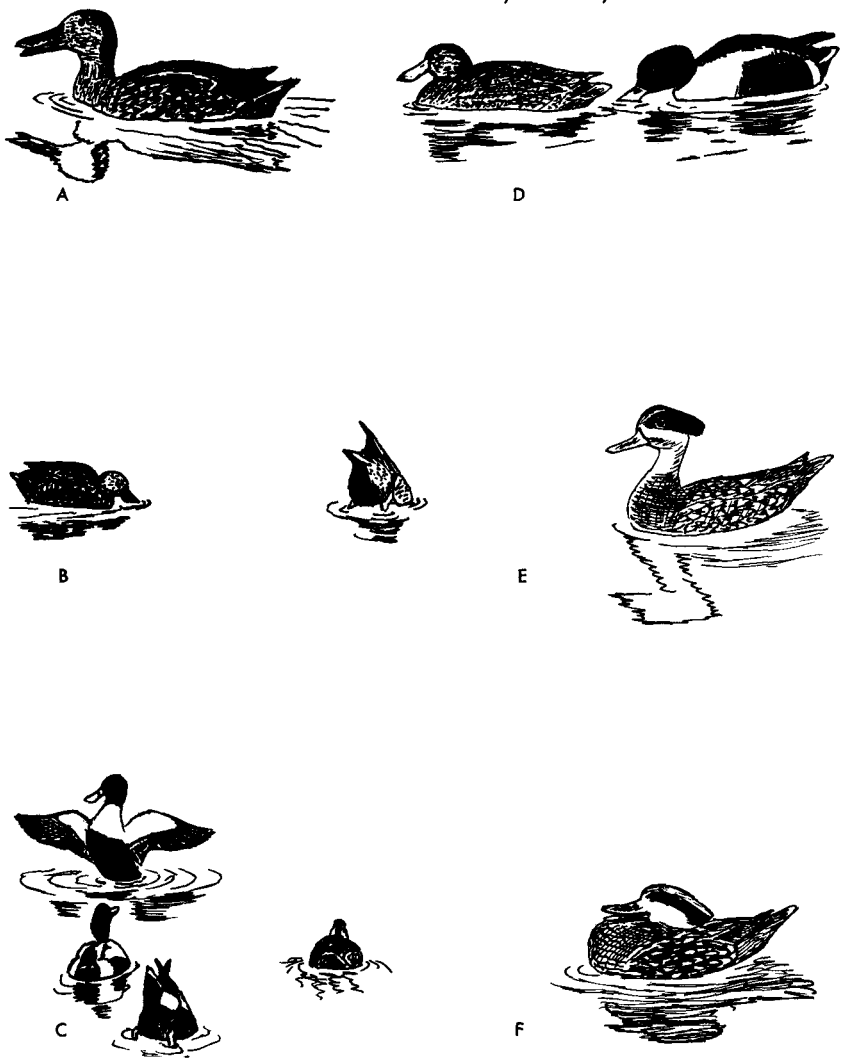


Figure 58. Cape Shoveler, Common Shoveler, Marbled Teal

A. Male cape shoveler in Burp posture.

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

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

D. Social feeding by common shovelers. 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. Lebret (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 rhynchotis*)

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. 58*D*) 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 DABBLING 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-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-eé-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 membranceous 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.

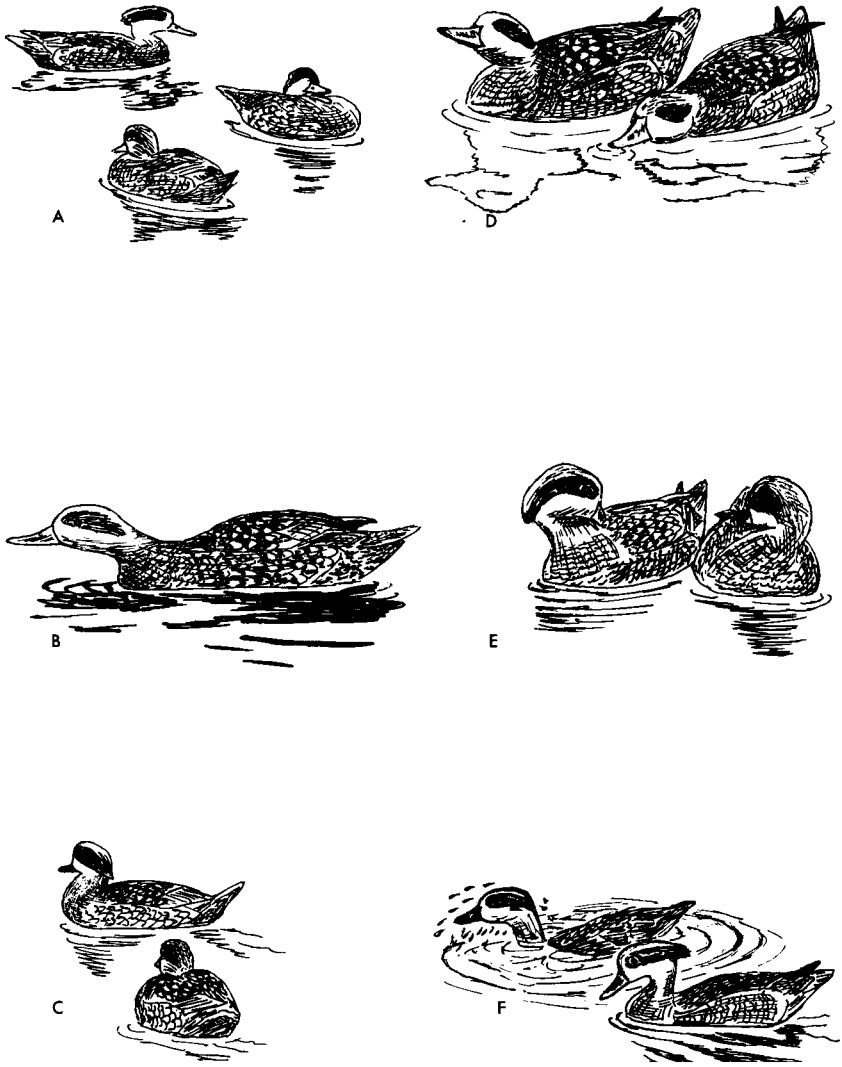


Figure 59. Marbled Teal

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. 62*B*.

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. 60*F*.

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. 58*E*), a pause, and then an equally sudden jerking of the head back and down to the shoulders (Figs. 58*F*, 59*A*). 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. 59*B*), 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. 59*C*).

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. 59*E*, *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. 59*F*) 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

tracheal structure of the male. Instead of a rounded and entirely osseous tracheal bulla such as occurs in *Anas,* the bulla is larger, rather angular, and contains several membranceous fenestrae of varying sizes. Although the bulla structure of *Netta* and *Aythya* is strikingly different from that of the *Anas,* the genera *Marmaronetta* and *Rhodonessa* provide such perfect intermediate stages that the evolutionary development of this structure is very clear (Johnsgard, 1961c). In addition, the tracheal tube of males of nearly all species (*Aythya novae-seelandiae* and *A. collaris* are apparently exceptions) varies in diameter and is enlarged toward the middle. Unlike the typical dabbling ducks, none of these species have metallic-colored specula, and metallic coloration is restricted to the head plumage of the males of some species. Although some species (especially *Rhodonessa* and *Netta*) frequently feed on the surface, all species dive well and typically do not open their wings when submerging. Most species are predominantly vegetarian, but the scauplike ducks tend to consume a high proportion of animal material. Nests may be built on land, usually near water, or on reed beds over the water surface, and females lack the disruptively marked plumage pattern typical of female dabbling ducks. Downy young tend to lack eye stripes and cheek marks, and also generally have reduced back spotting. Most if not all species become sexually mature during the first year; the scauplike ducks may take slightly longer. All species exhibit sexual dimorphism in plumage and/or soft-part coloration, and nearly all species have distinct eclipse plumages. Although metallic-colored specula are absent, the secondaries have a contrasting white pattern in many species.

Diving ducks are less vocal than dabbling ducks, and males are generally silent except during courtship. Probably only one species, and at most two, exhibits female calls which might correspond to the Decrescendo Call of *Anas,* but all species have Inciting calls, and some of them have other courtship calls as well. Sexual behavior patterns of the males are very uniform, and it is relatively easy to recognize homologous movements. Either these species are a much more homogeneous group than *Anas,* or quantitative difference in displays are more important than qualitative ones for species recognition among pochards. Precopulatory and postcopulatory displays are also remarkably constant in the group. The former consists of Drinking (or Bill-dipping) and Preening-dorsally by males, and sometimes by

females as well, and a rudimentary form of Head-pumping occurs in a few species. In all species studied the postcopulatory behavior consists of the male's calling once and then swimming away in a rigid Bill-down posture. The female may assume the same posture for a few seconds, but usually she begins to bathe immediately.

Pink-headed Duck (*Rhodonessa caryophyllacea*)

The now apparently extinct pink-headed duck is considered by Delacour (1956) to be an aberrant member of the Anatini, presumably because of its slightly lobed hallux and its surface-feeding tendencies. The tracheal anatomy of the male, however, leaves little doubt that the species is a close relative of the pochards (Johnsgard, 1961c); Woolfenden (1961) and Humphrey and Ripley (1962) have found additional evidence favoring this hypothesis. In addition, the body plumage, including the black abdomen, nonmetallic wing pattern, and brownish body, is certainly more similar to that of *Netta* than to any species of *Anas*. The downy young have never been described. It seems probable that the pink-headed duck is not too distantly related to the red-crested pochard. The two species are easily confused, and this accounts for the repeated reports of pink-headed ducks being seen or shot in India during recent years.

General behavior. Most of what is known about the pink-headed duck has been summarized by Salim Ali (1960). Delacour, who kept pink-headed ducks for some years, states (1956) that the female has a low quacking voice and the male has a whizzing whistle and behaves in a mallardlike fashion. The males display socially, puffing out the short head feathers with the neck shortened and resting on the back, then stretching the neck upward as they utter their call. This may seem to be a reversed version of the marbled teal's display, but actually the behavior is nothing like that of the typical mallard. Nothing has been written concerning the copulatory behavior of this species, which would have been of much greater value in judging relationships than an incomplete account of the male courtship displays.

NARROW-BILLED POCHARDS

Delacour (1959) has grouped three species of pochards into a genus which he considers less well adapted to diving than the rest of the group. Of these, one species (the red-crested pochard) is pre-

dominantly a surface-feeder and is the least *Aythya*-like of the group. A second species (the southern pochard) outwardly resembles the typical pochards but deviates from them somewhat in its displays, and the third species (the rosy-bill), although rather specialized, appears to provide the closest link with the genus *Aythya*.

Red-crested Pochard (*Netta rufina*)

The red-crested pochard exhibits affinities both with the pochards and with the dabbling ducks, but it is predominantly pochardlike. This is one of the few species of pochards in which the downy young exhibit a distinct, although faint, eye stripe such as is typical of *Anas* downies. Juvenile birds resemble adult females, which have a two-tone head pattern quite unlike that of the other female pochards. The male in nuptial plumage bears a general similarity to some of the other pochards, but is unique in its "shaving brush" crest. The secondaries and inner primaries are a pale whitish color that contrasts with the darker parts of the wing and provides a simple speculum. There is a distinct eclipse plumage which closely resembles the plumage of the female. The trachea of the male varies gradually in diameter, with two enlargements, and the bulla has the trihedral shape and fenestrated structure typical of all the pochards (see Johnsgard, 1961c). The species occurs over much of Europe and Asia, and is sympatric with no other *Netta* species but with several species of *Aythya*. Wild hybrids have been reported involving the common pochard, and fertile hybrids have been obtained in captivity with the common pochard and the rosy-bill. Hybrids with five other species of *Aythya* have also been reported.

General behavior. Although red-crested pochards frequently feed by up-ending, they can dive very well in the usual pochard manner of using only the feet. They often associate with other pochards, and they are more adept at walking on land than are these birds. This species differs from species of *Anas* in using repeated Chin-lifting instead of Neck-jerking as the primary preflight movement.

Agonistic and sexual behavior: female. Female Inciting is a slightly ritualized combination of direct threatening movements alternated with neck-stretching toward the preferred male (see illustration in Lind, 1958). The associated call is a soft *rarr-rarr*. Steinbacher (1960) states that in this and the other pochards there are two distinct female calls, *kurr* and *gock*, and that the former is especially

indicative of anxiety and the latter occurs during vigorous threat. I have not heard any calls which resemble the Decrescendo Call of *Anas,* but von de Wall (pers. comm.) informs me that he has heard a possibly equivalent call. Females often Preen-behind-the-wing toward mates or potential mates, and in general female Preening-behind-the-wing is more frequent in the pochard group than in the dabbling ducks. Females also perform an *Anas*-like Gesture of Repulsion when they are being chased by males attempting to rape them.

Agonistic and sexual behavior: male. Lind (1958, 1962) and Steinbacher (1960) have both discussed the behavior of this species in some detail. As in the dabbling ducks, general display movements include the Introductory Shake and Preening-behind-the-wing. Rapid head-shaking often precedes or alternates with other displays. Wing-flapping is fairly frequent in this and other species, and is probably ritualized. Ritualized Drinking is primarily a precopulatory display. The male's head feathers are erected into a bushy crest during courtship, and the black patch on the nape is consequently conspicuous. This patch is often exhibited to an Inciting female as the male swims in front of her in a display equivalent to Leading in the dabbling ducks. While displaying, males frequently perform Neck-stretching, during which they often utter a *geng* call with the crest raised. Often the male will lower his crest and stretch his neck out over the water as he points his bill toward a female and utters a nasal call. This movement, which has been called Sneaking (Hochbaum, 1944), closely resembles an aggressive posture. The typical courtship call, the "Sneeze," is usually uttered with the crest erect, the neck withdrawn, and the crest "thrown" toward the female with a sideways movement of the head (see Fig. 60*E*). At times this same call and movement is directed toward other males, but at such times the crest is usually depressed and the movement is forward rather than sideways. That this Sneeze call is probably homologous to the Burp of *Anas* and the Kinked-neck call of the more typical pochards is indicated by the fact that hybrids of this species and the yellow-billed pintail perform a pintail-like Burp with a sideways head movement, and hybrids with the redheaded duck perform the Sneeze with a distinct kink in the neck. Lind (1962), however, believes the Sneeze to be homologous with the pochard's Sneak posture. Lind (1958) describes the Sneeze call as *chrriib,* but in general it is reminiscent

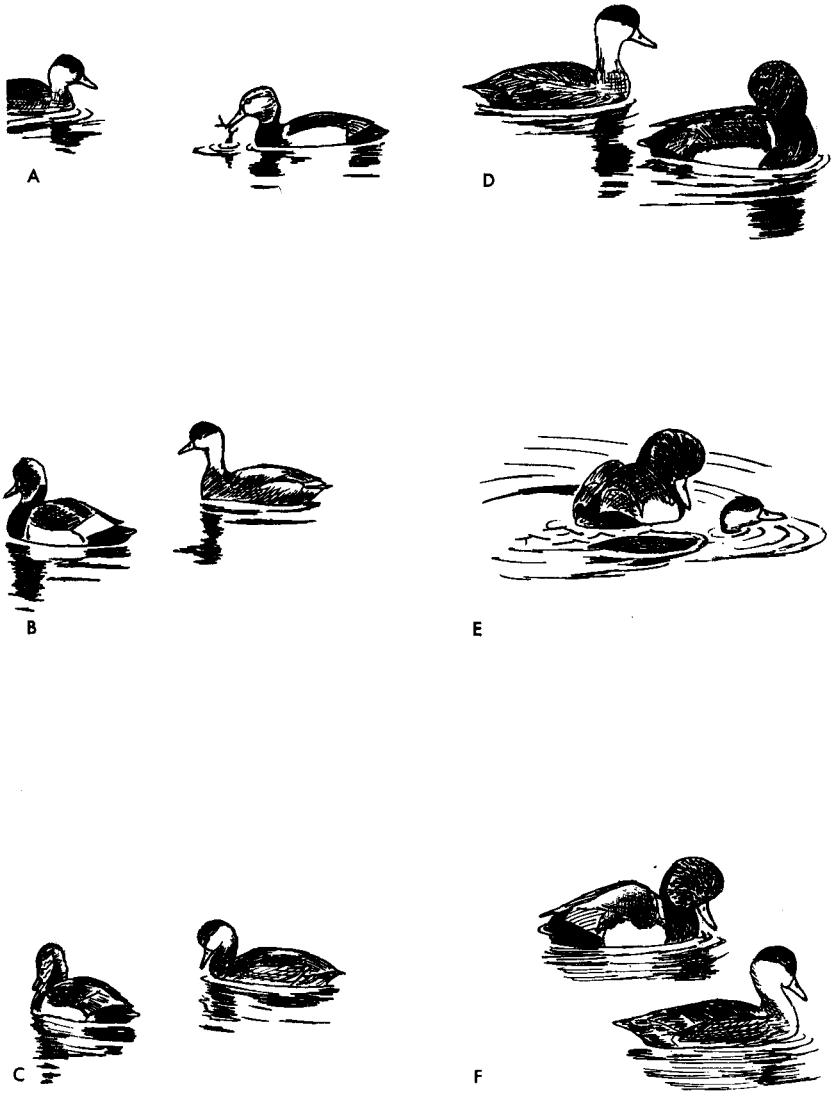


Figure 60. Red-crested Pochard

A. Courtship feeding. The male has just surfaced with some vegetation which he is about to take to the female.

B, C. Precopulatory Head-pumping by red-crested pochards.

D. Precopulatory Preening-dorsally by male. Note that the head is turned toward the side facing the female.

E. Postcopulatory Sneeze uttered by male immediately after treading is completed.

F. Postcopulatory Bill-down posture of male. Female is about to start bathing.

of a half-repressed sneeze. The red-crested pochard is the only species of Anatidae which to my knowledge exhibits anything like a true "courtship feeding." Males will dive to the bottom of a pond and bring up anything from aquatic vegetation to submerged sticks (Fig. 60*A*), which the female then takes from the male's bill and attempts to eat. This behavior appears to be confined to well-formed pairs; thus it is probably a pair-maintenance activity rather than true courtship. Attempted rape by males is more evident in this species than in the other pochards.

Copulatory behavior. The copulatory behavior of red-crested pochards presents an interesting mixture of pochard and dabbling duck components. Males initiate precopulatory display by Bill-dipping and Preening-dorsally, interspersing these movements with Preening-behind-the-wing, preening in other areas, lateral head-shaking, and a rudimentary form of Head-pumping (Fig. 60*B–D*). The female responds with what is definitely a Head-pumping movement, although it is not quite so marked as it is in the dabbling ducks (Fig. 60*B, C*); then she gradually assumes a receptive posture (illustrated in Steinbacher, 1960), in which the tail and body are held low in the water and the neck is stretched out diagonally. As the male completes treading, he performs a single Sneeze toward the female (Fig. 60*E*), then swims away with his bill pointed downward in the usual pochard Bill-down posture (Fig. 60*F*). The female begins to bathe immediately.

Southern Pochard (*Netta erythropthalma*)

The southern pochard is outwardly similar to the scauplike ducks, but Delacour (1959) has pointed out that the similarity is only superficial. The downy young closely resemble those of the rosy-bill, being bright lemon-yellow below, dark above, and lacking any eye stripes. Juveniles and females are an almost uniform brown except for lighter head markings and a white speculum. The adult male is somewhat similar to the rosy-bill male, but differs in having dark brown flanks, a dark brown abdomen, and dark under-tail coverts. The white speculum on the secondaries contrasts sharply with the otherwise dark plumage. There is no eclipse plumage. The tracheal tube of the male has only a single enlargement, and the bulla is similar in shape to that of the red-crested pochard. The species consists of two races, one South American and one African. The South American race

does not appear to be sympatric with the rosy-bill. A captive-bred hybrid of the southern pochard and the common pochard has been reported.

General behavior. This species appears to dive to a somewhat greater extent than do the other two species of *Netta*. Preflight movements consist of the usual Chin-lifting.

Agonistic and sexual behavior: female. Inciting in the southern pochard is somewhat more ritualized than in the red-crested pochard, and consists of lateral bill movements alternated with forward neck-stretching toward the preferred male (Fig. 61*A, B*). The call is a harsh *rrrrr-rrrr*. I have not heard any sound approaching the Decrescendo Call of dabbling ducks. Preening-behind-the-wing is frequently performed by females.

Agonistic and sexual behavior: male. The male courtship call is uttered in a manner that differs both from the Sneeze of the red-crested pochard and the Kinked-neck call of the following species. The bill is held level and directly forward with the neck somewhat extended, and the call is uttered as the head is drawn into the shoulders with the bill remaining level. The call, a soft, rather mechanical *eerooow,* sounds like a rapidly unwinding spring. There appears to be no second courtship call which would correspond to the "Coughing" call of the following species. The Sneak is rarely performed and is very inconspicuous, consisting of only a slight extension of the neck and head toward the female as a three- or four-note call similar to the courtship call is uttered. Unlike the red-crested pochard, this species performs a true Head-throw display (Fig. 61*C*). This is performed fairly rapidly (in about ¼ second) after a few preliminary head-shakes, and the bill is thrown back vertically over an arc of about 135 degrees. The call appears to be exactly like the usual courtship call. The display is symmetrical in that the head and bill follow the median axis of the body. The male responds to female Inciting by swimming ahead of her with his head feathers depressed as he Turns-the-back-of-the-head to her (Fig. 61*A, B*). Males frequently Preen-behind-the-wing to females, and pairs often do this as a mutual display, alternating it with mutual Drinking.

Copulatory behavior. Copulation is initiated by the male, who performs Bill-dipping movements together with Preening-dorsally. He also preens in other places, such as the flanks, the breast, or behind the wing. The female performs a few slight Head-pumping move-

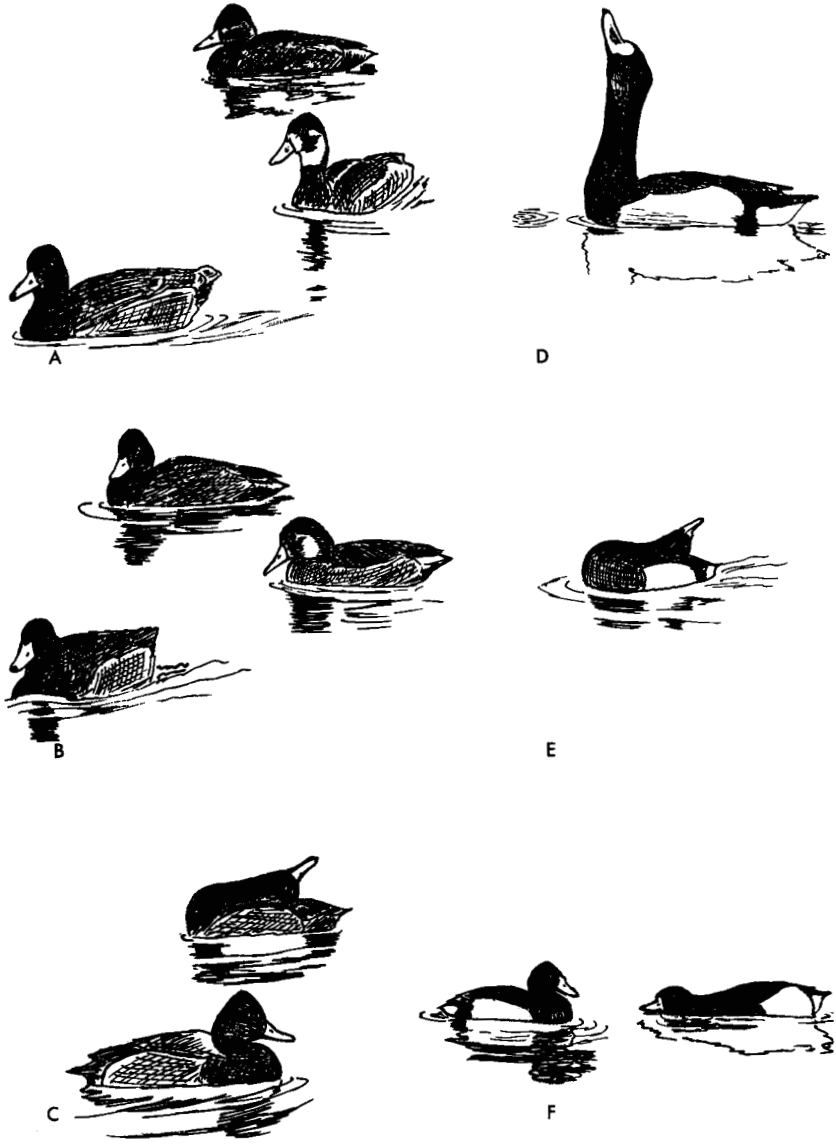


Figure 61. Southern Pochard, Rosy-bill

A, B. Southern pochard male Leading an Inciting female by Turning-the-back-of-the-head toward her. Note lowered crest of male as compared with that of other male behind.

C. Head-throw display by male southern pochard.

D. Ritualized Drinking by male rosy-bill.

E. Head-throw by male rosy-bill.

F. Male rosy-bill (*right*) performing Sneak display toward another male.

ments, but in the instances I observed she did no Bill-dipping or Preening-dorsally. She soon assumes a receptive posture, and the male mounts. As the male completes treading he utters a single courtship call, then swims away in the typical Bill-down posture. The female then bathes.

Rosy-bill (*Netta peposaca*)

Although this species has the least external similarity to the pochards of the genus *Aythya,* behaviorally it is the species most similar to that group. The downy young are much like those of the three following species, and juveniles and females also have plumages which fairly closely resemble the corresponding plumages of the canvasback, the redhead, and the common pochard. The adult male's crimson and basally enlarged bill sets it apart from the other pochards, but in other respects the head and body are typically pochardlike. Unlike those of the other species of *Netta,* the undertail coverts are white, and the white speculum extends to the inner primaries as in some of the scaups. There is no eclipse plumage. The male trachea has a very abrupt central enlargement rather than the gradual enlargement typical of other species of pochards. The bulla differs from those of the two preceding species in that the right chamber is somewhat inflated in a manner characteristic of the scaup group. The rosy-bill ranges over southern South America, but is probably not sympatric with the southern pochard. It has been hybridized in captivity with numerous species of *Aythya* as well as with the red-crested pochard. The latter cross has proved fertile.

General behavior. The rosy-bill, although an excellent diver, feeds to a considerable degree from the surface. Preflight movements are the usual Chin-lifting of pochards, which in males is very conspicuous because of the brightly colored bill.

Agonistic and sexual behavior: female. Rosy-bills are of interest in several respects. For example, I once heard a decrescendo-like call of three or four syllables on one occasion, although like other pochards the female tends to be relatively quiet. Inciting takes the usual, only slightly ritualized, form of threatening movements alternated with neck stretching. A harsh *krrrr* is uttered with each movement. Steinbacher (1960) describes this call as *errrr,* and the other common female call as *kack.* Females perform a conspicuous Preening-behind-the-wing and in addition perform the same form of highly

ritualized Drinking as males. The Sneak posture is also performed by females, and in exactly the same manner as by males.

Agonistic and sexual behavior: male. Although somewhat specialized in its form and postures, the rosy-bill shows very clear affinities with *Aythya.* The two most conspicuous displays are highly ritualized. The first is a type of Drinking (Fig. 61*D*) which in this species entirely replaces normal drinking. It occurs whenever two birds meet, regardless of their sex. The second display is a highly exaggerated Sneak (Fig. 61*F*), in which the male stretches his head and neck out along the water surface toward another bird and utters a low, gutteral *krrrrr*. A third major display is the Head-throw, which is performed relatively infrequently (Fig. 61*E*). There are no preceding head shakes, and the display is a fairly slow one (taking approximately ½ second) in which the bill travels an arc of approximately 135 degrees. The associated call is a faint *wheee-ow*. The same call is uttered during what is clearly homologous with the Kinked-neck call of *Aythya.* This call may be uttered while the neck is partly extended or when the head is resting on the shoulders. A final call is one which appears to be homologous to the Coughing call of *Aythya.* It is emitted without any neck movement, though there is a distinct compression of the body plumage, and consists of a soft whirring sound which closely resembles the courtship call of the southern pochard. In addition, wing-flapping occurs frequently during display and is possibly ritualized, and Preening-behind-the-wing is also very frequently performed. Males swim ahead of Inciting females while Turning-the-back-of-the-head to them and holding the head feathers very depressed (the "gedrucktes Schwimmen" of Steinbacher, 1960).

Copulatory behavior. I have not observed a complete copulation, but I have seen precopulatory behavior on a few occasions. This consists of the male Bill-dipping and Preening-dorsally, while the female performs rudimentary Head-pumping movements similar to those of the southern pochard. Lind (1962) reports rudimentary Head-pumping in the male. McKinney informs me (pers. comm.) that the male assumes the typical Bill-down postcopulatory posture.

TYPICAL POCHARDS

The typical pochards of the genus *Aythya* consist of 12 species, which can be divided into several subgroups. All the species have, however, several characteristics in common. Females lack any calls

similar to the Decrescendo Call of dabbling ducks. Their common vocalizations consist of Inciting and aggressive calls, and the females of some species have calls homologous to male display calls. Males are relatively quiet except during courtship display. Male courtship calls are of two major types. The first is uttered during obvious neck-stretching (in the Kinked-neck and Head-throw), and the second is uttered without special neck-stretching (Coughing). Males of all species studied (11 out of 12) exhibit the Kinked-neck call, the Head-throw, the Sneak posture, Coughing, and Turning-the-back-of-the-head. Preening-behind-the-wing is probably present in all species as well. Precopulatory displays consist of Bill-dipping and Preening-dorsally by males, and sometimes also by females. Rudimentary Head-pumping occurs in males of a few species, but not in females. After treading, the male always utters a single Kinked-neck call and swims away in the Bill-down posture.

There are three fairly distinct subgroups of *Aythya*. These include the true pochards (the canvasback, the redhead, the European pochard, and the ring-necked duck), the white-eyes (the common white-eye, the Australian white-eye, Baer's white-eye, and the Madagascan white-eye) and the scauplike ducks (the tufted duck, the New Zealand scaup, the greater scaup, and the lesser scaup). I do not accept Delacour's grouping (1959) of the ring-necked duck with the scaup group, for as Hollister (1919) pointed out, it is clearly a member of the true pochard group.

Canvasback (*Aythya vallisneria*)

It is difficult to judge which of the *Aythya* species is closest to *Netta*, but the true pochards appear to be the most generalized in their plumages and behavior, and they will be considered first. Downy canvasbacks are very similar to downy rosy-bills, and juveniles and adult females also have a similar uniformly brownish coloration. Females of all the true pochards have light eye-rings and narrow eye-stripes, and also exhibit sexual dimorphism in iris coloration. The male in nuptial plumage is very similar to the European pochard, and the differences in head and bill shape between the canvasback and the redhead can probably be attributed to selection pressures for species recognition. Males have an eclipse plumage which approaches the female pattern. The trachea of the male has a partially membranaceous bulla which is very similar to that of the European

pochard, and the tracheal tube varies gradually in diameter. The canvasback ranges over most of North America and is widely sympatric with the redhead. I am not aware of any wild hybrids involving these two species, but such hybrids would be very difficult to recognize. In captivity fertile hybrids of these two species have been obtained, and hybrid combinations involving the ring-necked duck, the greater scaup, and the lesser scaup have also been reported.

General behavior. Hochbaum's (1944) classic study of the canvasback is the standard reference on the general biology of this species, and also the primary reference for pochard courtship displays. Preflight movements consist of repeated Chin-lifting.

Agonistic and sexual behavior: female. Inciting consists of overt threatening movements alternated with neck-stretching toward the preferred male, and the uttering of a soft *krrr-krrr* note. Neck-stretching also occurs independently of Inciting, often being elicited in response to a male's Neck-stretching. Hochbaum (1944) reports observing a single captive female perform the Head-throw display; I have rarely seen this and agree with him that it is not typical of normal birds (see the redhead account).

Agonistic and sexual behavior: male. The canvasback exhibits all of the *Aythya* displays, and Hochbaum's terminology is largely used here. Hochbaum's "Courtship call," however, is here called the Kinked-neck call (Fig. 62*D–F*), since there is more than one type of courtship call. In addition, the "Threat" posture appears to me to be an unritualized pre-attack posture and not to function as a sexual display. The Head-throw (Fig. 62*A*) has been well described by Hochbaum. In this species there is no preliminary head-shake, and the display is relatively slow (lasting about ⅔ second). It tends to be asymmetrical, with the bill diverging from the vertical plane toward the courted female. The associated cooing note has been described by Hochbaum. The second courtship call, Coughing, is infrequent and inconspicuous in the canvasback. There is no neck or throat movement, but the wings and tail are slightly flicked, and a soft *hfff* is uttered. The Sneak (Fig. 62*B*) display is highly developed in the canvasback, but it apparently differs from the Sneak of the rosy-bill in that there is no associated call. Neck-stretching (Fig. 62*C*) is also very frequent, serving both as a hostile display toward other males and an apparent sexual display toward females. Males respond to Inciting by swimming ahead and Turning-the-back-of-the-head (Fig.

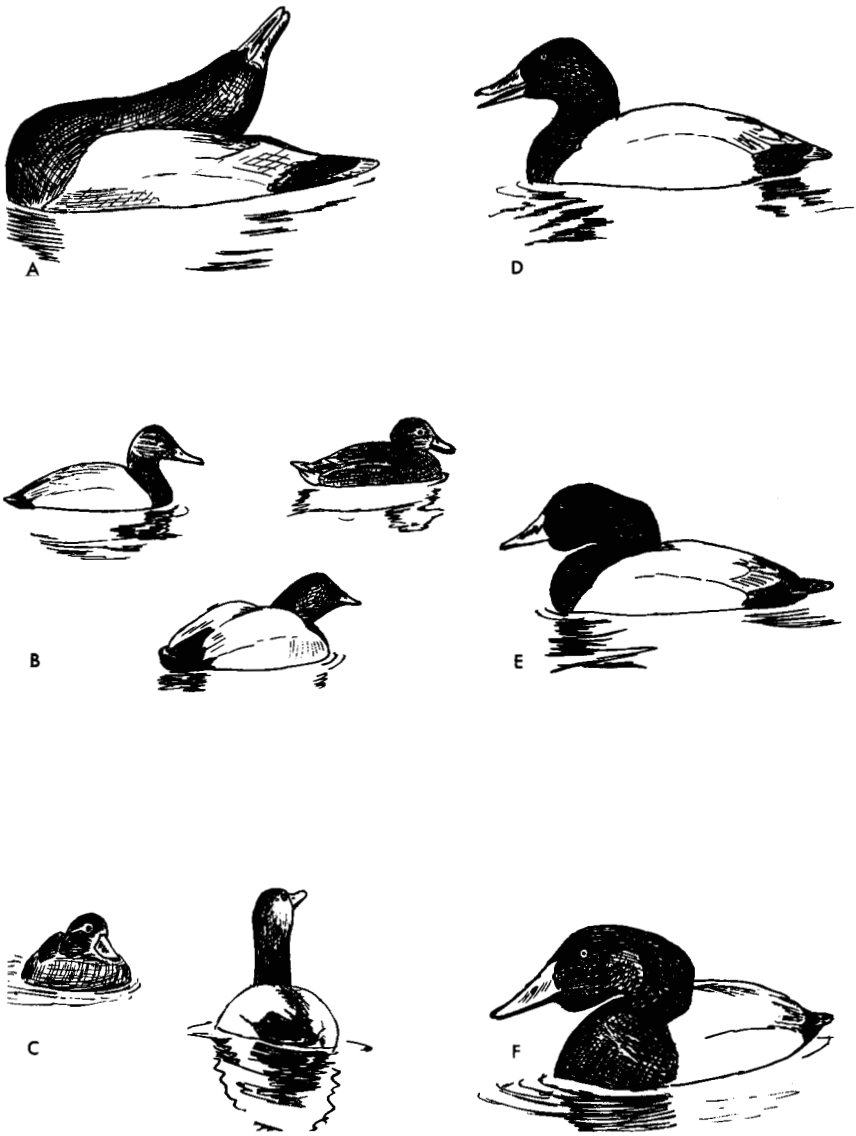


Figure 62. Canvasback

A. Head-throw by male canvasback.

B. Sneak posture performed by male canvasback (*foreground*) to female redhead (*right background*).

C. Neck-stretching by male canvasback to female redhead.

D, E. Two phases of the Kinked-neck cell in male canvasback. Note bulge in throat, probably produced by lowering the tongue.

F. Close view of the Kinked-neck call.

63*A*). Preening-behind-the-wing has not been recorded in either sex of canvasback. The aerial chases so well described by Hochbaum, (1944) in which the male attempts to catch the female by the tail, may be examples of attempted rape, since I have observed similar behavior in mallard rape chases.

Copulatory behavior. The male initiates copulation by alternately Bill-dipping and Preening-dorsally. The female may respond with similar Bill-dipping and Preening-dorsally, but there is no Head-pumping as in the three preceding species. The female soon assumes the receptive posture, and the male then mounts. After treading, the male utters a single Kinked-neck call (Fig. 62*B*), then swims away in the Bill-down posture (Fig. 62*C*). The female may also assume this posture for a short time before bathing.

European Pochard (*Aythya ferina*)

In appearance, the European pochard falls between the canvasback and the redhead, but it is probably more like the former. Presumably it approximates the ancestral condition from which the two American species diverged. Downy, juvenile, and adult plumages are all very much like those of the canvasback and the redhead, and the tracheal structure is also very similar to that of those species.

General behavior. Like the canvasback and the redhead, the European pochard is a vegetarian, diving frequently while foraging. Preflight consists of repeated Chin-lifting movements.

Agonistic and sexual behavior: female. I have observed relatively little display in this species, but the movements of both sexes are very much like those of the canvasback. Steinbacher (1960) describes the two major female calls as *pack* or *back,* and *brerr* or *errr*. The latter call is typically used in Inciting. The Inciting movements are much like those of the canvasback, as lateral threatening movements are alternated with neck-stretching. Preening-behind-the-wing has not been observed.

Agonistic and sexual behavior: male. According to Steinbacher (1960), two courtship calls are present, a soft breathing *wiwierrr* and a loud *kilkilkil,* which varies in the number of syllables. The former note is used in the Head-throw (Fig. 63*D*) and Sneak (Fig. 63*F*) postures, as well as in the Kinked-neck call. The louder call probably corresponds to the Coughing call, but I have not observed display sufficiently to be certain of this. Neck-stretching (Fig. 63*E*) occurs

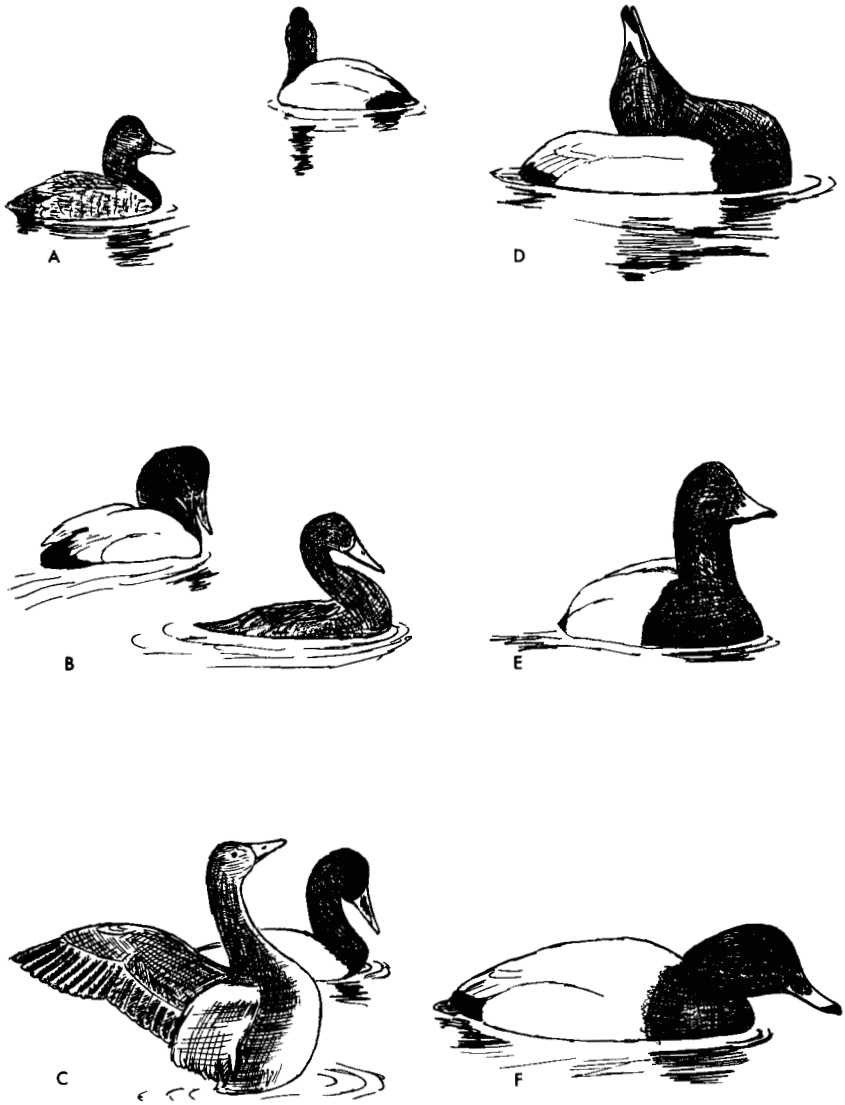


Figure 63. Canvasback, European Pochard

A. Male canvasback Turning-the-back-of-the-head toward female.

B. Postcopulatory display by canvasbacks. Male utters the Kinked-neck call as female bathes.

C. Male canvasback in postcopulatory Bill-down posture as female flaps wings after bathing.

D. Male European pochard performing Head-throw.

E. Neck-stretching by male European pochard.

F. Sneak posture by male European pochard.

frequently during display, and thus the species strongly resembles the canvasback. As in the canvasback, the Head-throw is a fairly slow display (lasting approximately ½ second), and the bill does not travel back much beyond the vertical. I have not observed Turning-the-back-of-the-head and Preening-behind-the-wing, but very likely they occur.

Copulatory behavior. I have not observed copulation, but no doubt it is very much like that in the canvasback and the redhead.

Redhead (*Aythya americana*)

The redhead of North America is very similar to the European pochard in most aspects of its plumage, although it has a higher forehead, darker back and flanks, and, in males, a yellow rather than reddish iris. The downy young are somewhat lighter than those of either the canvasback or the European pochard. Juveniles and females have the uniformly brownish coloration typical of all true pochards. Males have an eclipse plumage which closely resembles the plumage of the females. The male trachea is enlarged for most of its length, and in shape the bulla is very much like that of the European pochard, with the right chamber scarcely enlarged. The species ranges over much of North America, and is sympatric with the canvasback and the ring-necked duck, as well as with several other species of *Aythya*. Wild hybrids have been reported with the ring-necked duck, the lesser scaup, and the greater scaup.

General behavior. Redheads inhabit much the same kinds of marshes and lakes as canvasbacks, and one must presume that they exhibit certain differences in feeding behavior to avoid interspecific competition. The two species sometimes associate, but courting flocks tend to remain separated. Preflight movements are the usual Chin-lifting with the neck slightly stretched.

Agonistic and sexual behavior: female. Inciting in this species (Fig. 64*E*) lacks such extreme neck-stretching as occurs in the canvasback, but the Inciting calls and movements are very similar in the two species. A soft *errrr* note accompanies Inciting in the redhead. Independent Neck-stretching is not nearly so conspicuous in the redhead as in the canvasback. I have observed the Head-throw a few times in an old female that had assumed a partial male plumage, but I have never seen other females perform it, and I judge that it is not

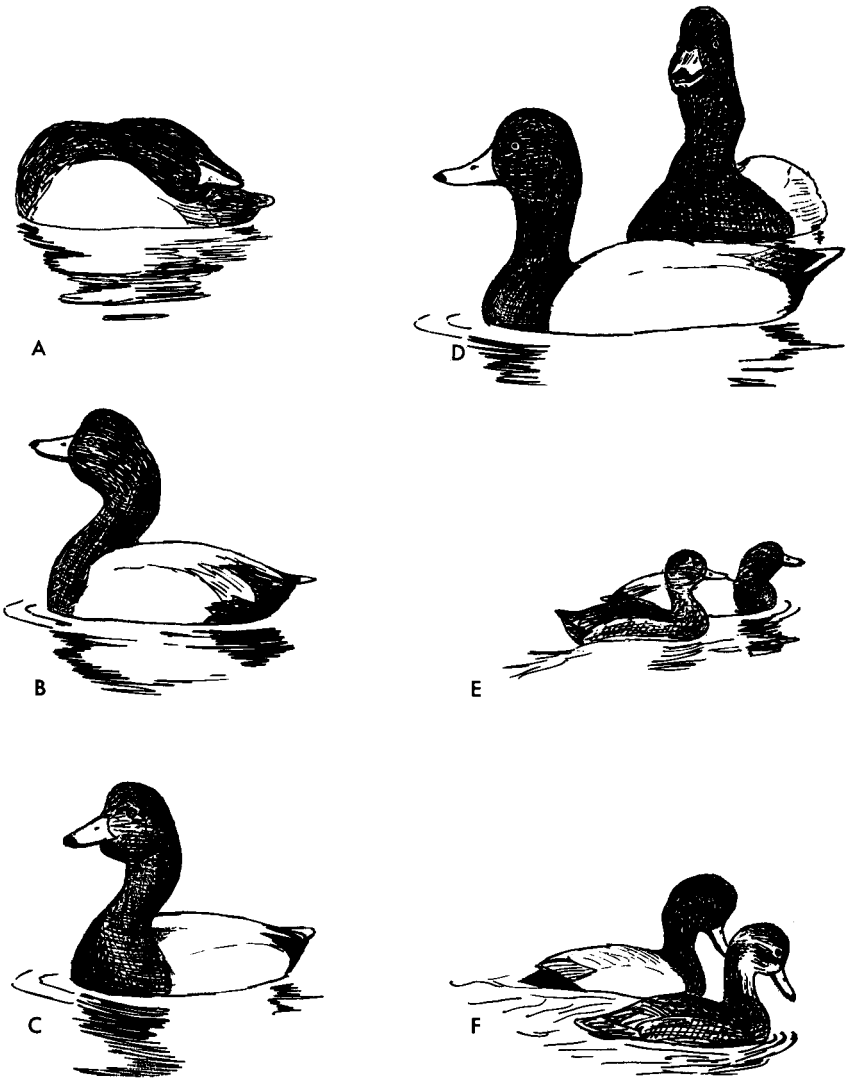


Figure 64. Redhead

A, B. Stages in the performance of the Head-throw. The call is uttered during the second stage of the display.

C. Kinked-neck call as uttered without accompanying Head-throw. Compare with B above.

D. Front view of Kinked-neck call. Compare with Fig. 62*F*.

E. Male redhead Leading an Inciting female. Note lowered head feathers of male and compare with other drawings on this page.

F. Postcopulatory Bill-down display in redheads. Both birds are in this posture.

normally used by females during courting. Preening-behind-the-wing is rather infrequent in female redheads.

Agonistic and sexual behavior: male. Although the male redhead performs the same displays as the canvasback, there are considerable differences in the form and vocalizations of these displays. One is therefore inclined to attribute these differences to selection for species-specific signals that will avoid hybridization. Thus the Kinked-neck call of the canvasback is a cooing sound, usually uttered with the head held near the shoulders, whereas in the redhead the call is a distinct *wheee-oww,* uttered with the neck almost fully extended (Fig. 64*B–D*). The Sneak posture, which is so conspicuous in the canvasback, is reduced to little more than an intention movement in the redhead. The Head-throw, however, is a highly exaggerated and spectacular toss of the head back 180 degrees to the base of the tail (Fig. 64*A*). There is no preliminary head-shake, and the display is relatively long (taking approximately one second). As in the canvasback, the bill is tilted in the direction of the courted female. The Coughing call is infrequent and inconspicuous. Neck-stretching is also relatively less frequent and conspicuous than in the canvasback. Males also Preen-behind-the-wing to females fairly frequently, a display which I have not observed in the canvasback. Males will Turn-the-back-of-the-head to Inciting females, depressing their head feathers in the usual manner of most if not all pochards (Fig. 64*E*).

Copulatory behavior. Unlike the courtship pattern, the copulation patterns of the redhead differ little from those of the canvasback. The male initiates copulation by alternately Bill-dipping and Preening-dorsally to the female, preening his back on the side toward her in the usual fashion. Females sometimes respond with similar Bill-dipping and Preening-dorsally, but often they assume the copulation posture without mutual display. After treading, the male utters a single Kinked-neck call, then swims away in a Bill-down posture (Fig. 64*F*). The female often swims for a short distance in this same posture before beginning to bathe.

Ring-necked Duck (*Aythya collaris*)

Although Delacour (1959) considers this species to be closely related to the tufted duck, the similarity of the adult males of these two species is almost certainly a case of convergence. The downy young of the ring-necked duck do not in the least resemble those of

the tufted duck or the scaup, and are practically identical to those of the true pochards and white-eyes. Juveniles resemble adult females, which have the uniform brown coloration and light eye-stripe and eye-ring of the pochard group. Adult males in nuptial plumage outwardly resemble tufted ducks, but they lack the white speculum pattern typical of the scauplike ducks, exhibit sexual dimorphism in iris coloration, and, unlike the scaups, have a narrow bill with a light subterminal band such as occurs in redheads, European pochards, and Australian white-eyes. The trachea of the male, to judge from the one specimen I have seen, apparently lacks the conspicuous enlargements found in most other pochards, but the bulla is of the usual pochard type. The right chamber of the bulla is slightly inflated in this species as it typically is in the white-eye and scaup groups, suggesting that the ring-necked duck may be a linking form between the pochards and the white-eyes. The species is restricted to North America and is sympatric with numerous *Aythya* species. Wild hybrids have been reported with the redhead and the lesser scaup, and captive-bred hybrids have been reported with these two species and also with the canvasback, the tufted duck, and the red-crested pochard.

General behavior. Mendall (1958) provides an excellent account of the ecology and general behavior of this species. The ring-necked duck is more of a forest bird than any of the other pochards, but—like the true pochards and unlike the scaups—it is primarily a vegetarian. Chin-lifting is the only preflight movement noted.

Agonistic and sexual behavior: female. I have seen very little display in this species, but the Inciting movements of the female appear to be like those of the other pochards, and a soft *rrrrrr* call is uttered. Head-throws have not been observed in females, but Preening-behind-the-wing has been noted as a female display.

Agonistic and sexual behavior: male. I have observed display only a few times in captive birds, and also only a few times in wild birds (Johnsgard, 1955). The Kinked-neck call is uttered without noticeable bending of the neck and is emitted during Neck-stretching. The call is a soft breathing note, similar to but weaker than that of the redhead. The Coughing call is fairly frequent and is conspicuous because of its loud, clear note and also because of the slight wing-flick visible as the call is uttered. The Head-throw is almost exactly like that of the redhead, in that there is no preliminary head-flick

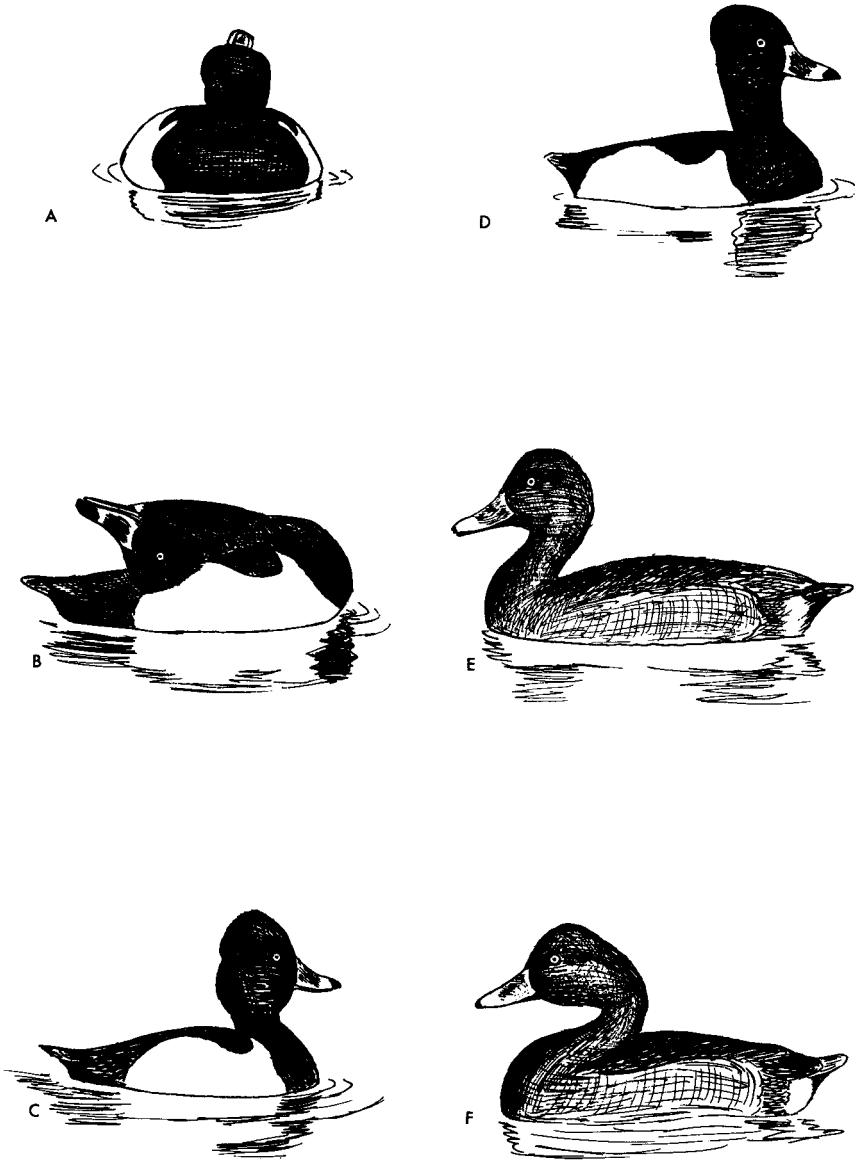


Figure 65. Ring-necked Duck, Australian White-eye

A. Ring-necked duck Head-throw, front view.

B, C. Two phases of Head-throw performed by male ring-necked duck. Note the slight tilting of the bill toward the right.

D. Triangular-crest posture of male ring-necked duck. Compare with normal head shape as shown in *C.*

E, F. Two phases of Kinked-neck call by male Australian white-eye.

and the bill traverses an arc of 180 degrees as the head is brought back almost to the tail (Fig. 65*A–C*). As in the redhead the display is slightly asymmetrical, depending upon the position of the female, and it is a moderately slow display (lasting approximately ½ second). Unlike the males of the previous species, but like the male white-eye, the ring-necked male performs a Nod-swim in which, as he swims rapidly about nodding his head, he erects his crest feathers to a distinctive angle, producing a triangular crest (Fig. 65*D*). Neck-stretching may be associated with this display. Males also Turn-the-back-of-the-head toward Inciting females, and at such times the crest is strongly depressed. I have not observed what was without doubt the Sneak posture, but Westfall (in Mendall, 1958) illustrates it, and the drawing suggests that it is similar to that of the canvasback. Ripley (1963) describes an apparently similar posture as a threat. Preening-behind-the-wing has been observed by McKinney (1953). Ripley (1963) has reported an unusual lateral threat display in this species as well as in southern pochards.

Copulatory behavior. I have not observed a complete copulation, although I have seen the male Bill-dipping and Preening-dorsally, to which the female responded by Bill-dipping. According to McKinney (pers. comm.) the postcopulatory display is the same as in the other pochards.

Australasian White-eye (*Aythya australis*)

The Australian and Banks Island races constitute the first of the white-eye group. They are characterized by sexually dimorphic iris coloration (brown in females, white in males) but reduced sexual dimorphism in plumage. In this group both sexes are predominantly brownish, but have white under-tail coverts, white wing specula, and whitish under parts. Juveniles and females lack the light eye-rings typical of the preceding group, and males of all species have brownish breasts and flanks. Both sexes of the Australasian white-eye have a broad white subterminal bar on the bill which approaches the bill-barring of the preceding group. There is no distinct eclipse plumage, which is understandable considering the similarity of the sexes. The tracheal tube of the male is enlarged toward the middle and the bulla is almost identical in shape to that of the ring-necked duck. The species is sympatric with only the New Zealand scaup, and no hybrids are known.

General behavior. The preflight movements of this species are the usual Chin-lifting of pochards.

Agonistic and sexual behavior: female. Inciting in this species is only slightly ritualized, and consists of overt threatening movements to the side (Fig. 66*A*), followed by rapid retreats toward the preferred drake in a neck-stretched posture (Fig. 66*B*). The Inciting call is a harsh and rather loud rattling noise similar to that produced by drawing a stick along a lathe fence. Preening-behind-the-wing has not been recorded, but almost certainly is present. Females also exhibit an additional display, the Head-throw. This occurs only rarely, and apparently abnormally, in all the preceding species of pochards but in the Australian white-eye it is a frequent and conspicuous part of courtship display. The call is a hoarse *gaaack,* and the form of the Head-throw is essentially the same as in males. I have also observed females utter the Kinked-neck call, but this is less frequent than in the ferruginous white-eye, the females of which frequently perform both the Head-throw and the Kinked-neck call.

Agonistic and sexual behavior: male. The Australian white-eye differs most markedly from the preceding species in that the Kinked-neck call of the male is strongly exaggerated and is often uttered several times in rapid succession (Fig. 65*E, F*). There is a very conspicuous bending of the neck each time the call is emitted, although the tongue is not so strongly depressed as in the canvasback or redhead. In addition, the Kinked-neck call occurs in association with the Sneak posture. The male stretches his neck toward the courted female (or another male) with his head low over the water, then as he withdraws it he utters the Kinked-neck call (Fig. 66*E, F*). A very similar display occurs in Baer's pochard. The Coughing call occurs only infrequently in this species and is a very soft whistling note. The Head-throw is a conspicuous display in this species (Fig. 66*C, D*). The display is a relatively slow one (lasting approximately ⅔ second), and is distinctly asymmetrical, with the bill being sharply tilted toward the courted female as it is brought back from a point well past the vertical. The Head-throw and Kinked-neck call is a soft *whirrrr.* Males perform the Nod-Swim only infrequently and not very conspicuously. Preening-behind-the-wing has been noted several times, as would be expected because of the conspicuous white speculum pattern. In common with the other pochards, males Turn-the-back-of-the-head to Inciting females in the usual manner. The

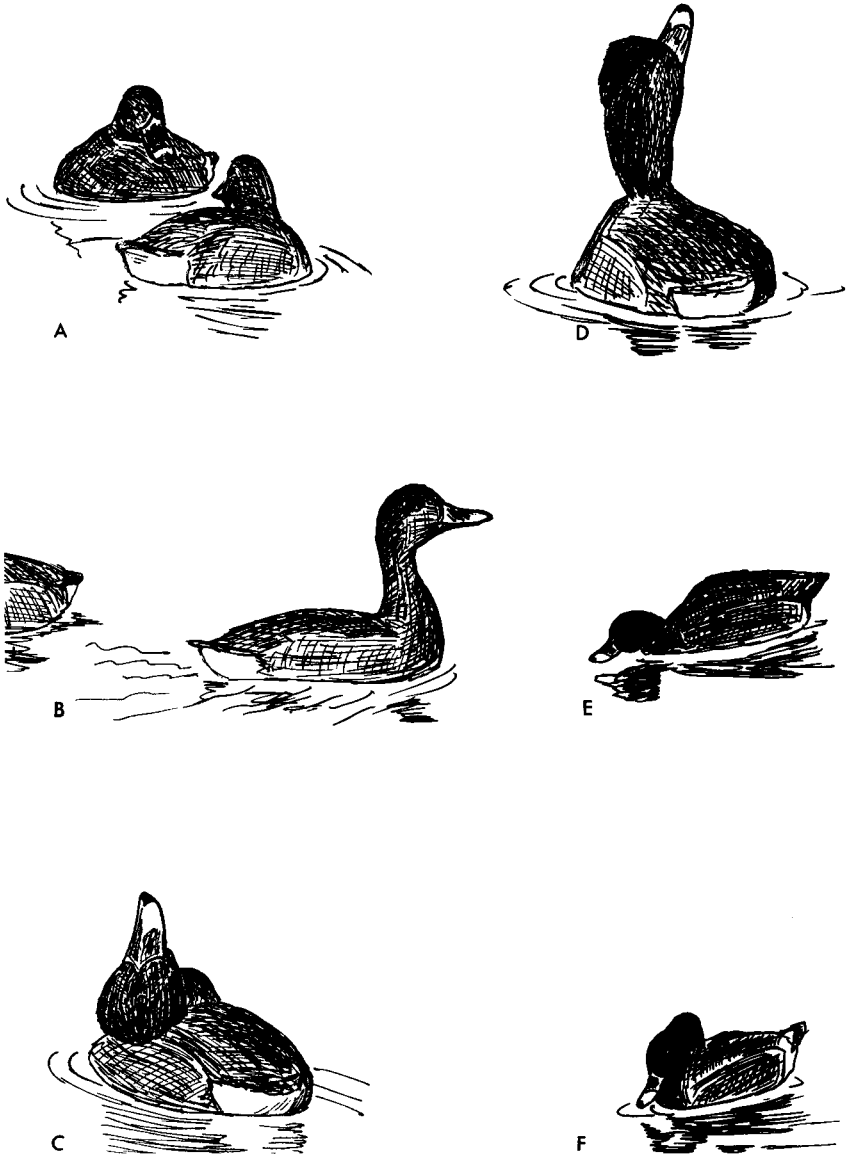


Figure 66. Australian White-eye

A, B. Inciting by female Australian white-eye. Note direct threats alternated with extreme neck-stretching.

C, D. Two phases of Head-throw by male. Note marked asymmetry of head movement. (*Female off picture to right.*)

E, F. Two phases of Sneak–Kinked-neck call display. Compare with corresponding displays in Figs. 67, 68.

white under-tail coverts do not appear to be displayed in any obvious fashion, and although the white iris of males is doubtless a signal characteristic, it is uncertain whether the size of the pupil can be altered during display.

Copulatory behavior. The Australian and Baer's white-eyes are the only species of *Aythya* I have observed in which the males perform slight Head-pumping movements which are alternated with Bill-dipping and Preening-dorsally. There is no obvious response of the female to these movements, but eventually she assumes the typical pochard copulation posture. After treading, the male utters a single Kinked-neck call and swims away in the usual Bill-down posture, and the female begins to bathe.

Baer's White-eye (*Aythya baeri*)

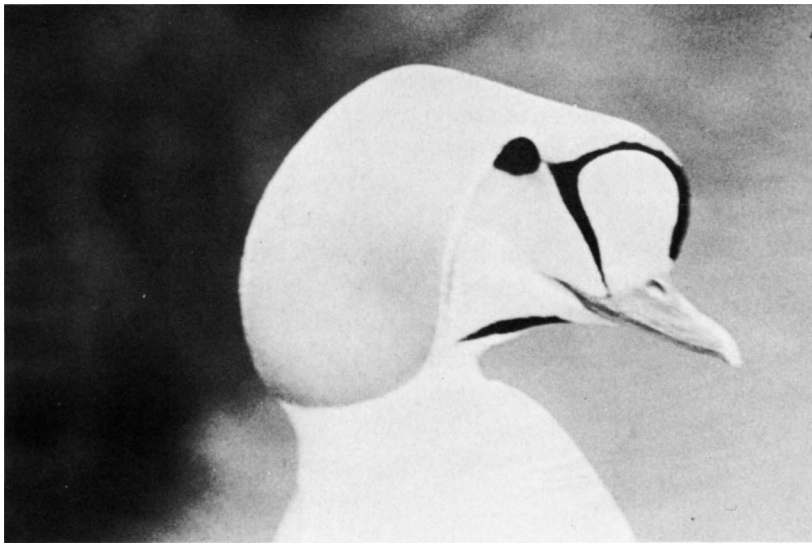
Baer's white-eye, or "Baer's pochard," is certainly a typical member of the white-eye group. Little is known about the species, and it has often been thought possibly to represent an eastern race of the common white-eye. This hypothesis is not, however, supported by the behavior of the species. The downy young are undescribed, and it would be of interest to learn if they have the grayish and white coloration found in the Australian white-eye or the blackish and yellow color of the common white-eye. The juveniles and females are very similar to those of the common white-eye, although both females and adult males have a slightly metallic-green head color that is absent in the other white-eyes. The trachea has a gradual enlargement toward the middle and the bulla is very similar in shape to that of the Australian white-eye. Baer's white-eye is not sympatric with any other species of the white-eye group. A possible hybrid between this species and the redhead has been reported from captivity.

General behavior. The few individuals of this species that I have seen could not be distinguished easily from the other white-eyes. In general appearance they are reminiscent of the common white-eye, but their behavior suggests that they are closer to the Australian species. The preflight signal is the usual Chin-lifting, which is rather exaggerated and jerky in this species.

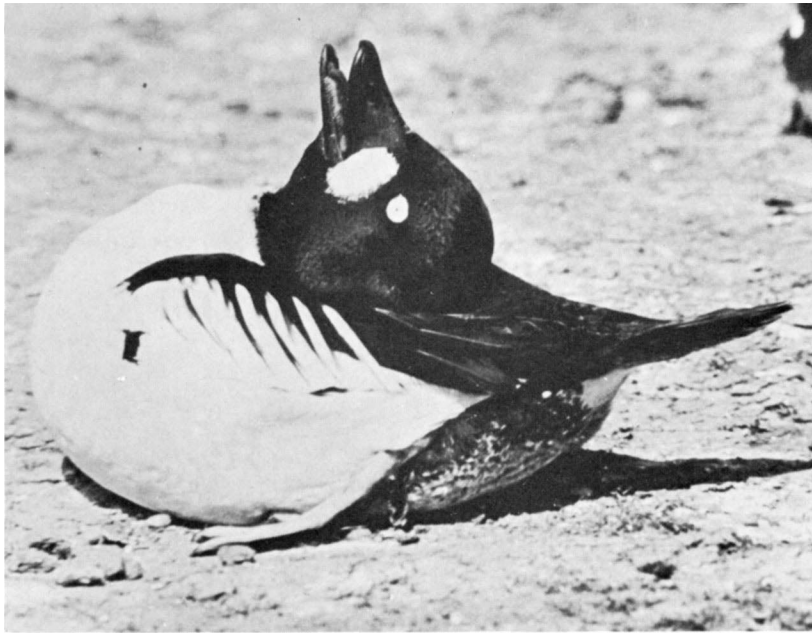
Agonistic and sexual behavior: female. Female Inciting is of the usual slightly ritualized pattern, and the call is a fairly loud and coarse *gaaaa* similar to that of the other white-eyes. Females also possess a Head-throw display, in which a similar *gaaak* note is

Canvasback, Sneak display by male.

Common White-eye, Head-throw by male.



King Eider, Neck-stretching by male.



Common Goldeneye, Head-throw by male on land.

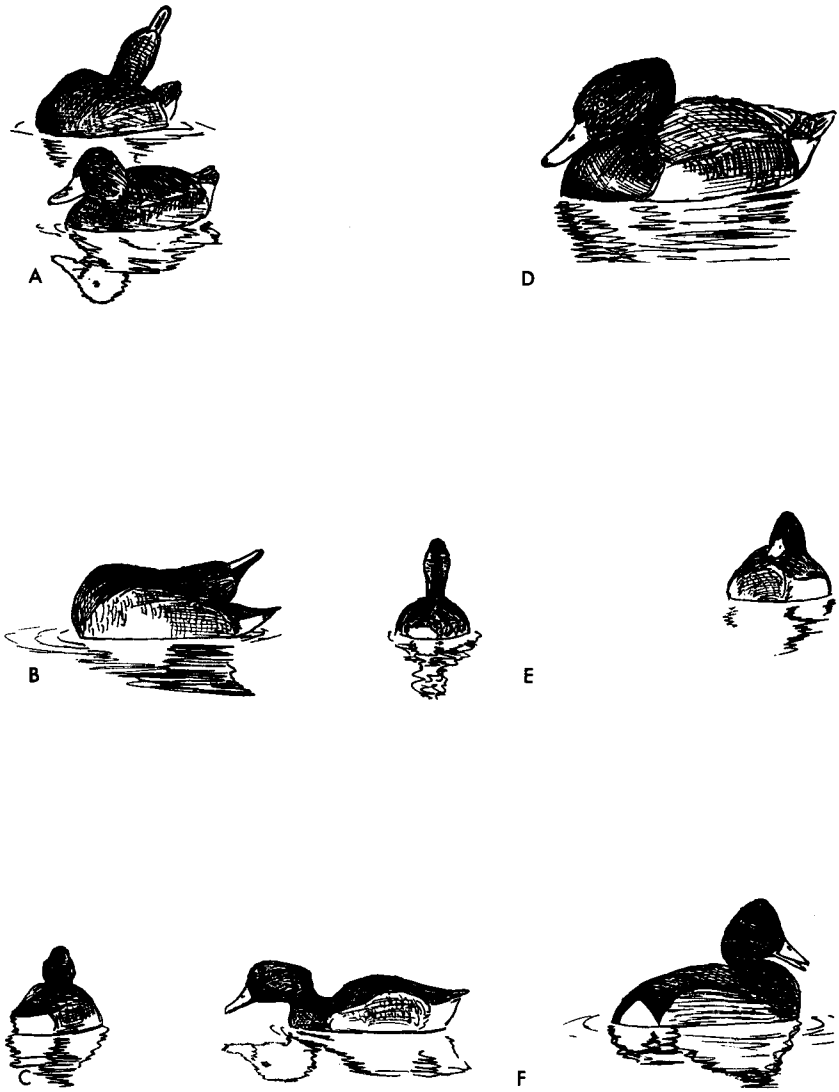


Figure 67. Baer's Pochard, Common White-eye.

A. Head-throw by male Baer's pochard. Note tilting of bill to side nearest female.

B. Another view of Baer's pochard male performing Head-throw.

C. Sneak posture of Baer's pochard.

D. Kinked-neck call by male Baer's pochard.

E. Precopulatory Preening-dorsally by male Baer's pochard. Note that preening is on side toward female.

F. Kinked-neck call by common white-eye male. Note that tail is tilted downward to form white triangular patch.

uttered, and during which the head is thrown back slightly beyond the vertical. I have not observed females perform the Kinked-neck call such as occurs in the Australian and common white-eyes. Females do, however, frequently Preen-behind-the-wing to males.

Agonistic and sexual behavior: male. Male displays in this species are very much like those of the Australian white-eye. The Kinked-neck call (Fig. 67*D*) is sometimes performed repeatedly, but this is not done as frequently as in the Australian white-eye. The call associated with this display and the Head-throw is extremely unusual, and is a harsh female-like *krraaaa* that has a distinctly ventriloquistic effect. As in the Australian white-eye, the Sneak (Fig. 67*C*) is linked to the Kinked-neck call and is always directed toward another bird. The Head-throw (Fig. 67*A, B*) is sometimes preceded by one or more head-shakes, but this is not typical. It is a moderately slow display, (lasting approximately ½ second), and the bill is brought back almost 180 degrees. The display is distinctly asymmetrical, toward the side of the courted female. The Coughing call and the Nod-swim are inconspicuous and infrequent. Preening-behind-the-wing is frequently performed as a mutual display with females, and males also often Turn-the-back-of-the-head to Inciting females.

Copulatory behavior. As in the Australian white-eye, males initiate copulation by performing slight Head-pumping movements, which are alternated with Bill-dipping and Preening-dorsally (Fig. 67*F*). The female sometimes Preens-dorsally and Bill-dips in response before assuming the receptive posture. After treading, the male utters a single Kinked-neck call and swims away in the usual Bill-down posture.

Common White-eye (*Aythya nyroca*)

The common, or ferruginous, white-eye differs somewhat from the two preceding species, and possibly represents a connecting form between the white-eyes and the scauplike ducks. The downy young are darker than those of the Australian white-eye, but lack any facial markings. Juveniles and females resemble adult males except for their duller plumage and different iris coloration. The male in nuptial plumage has a rich brownish-red head and breast and, like the two preceding species, has white under-tail coverts and a white speculum. A female-like eclipse plumage is present. The male tracheal tube is enlarged over most of its length, and the bulla is al-

most identical in shape to that of the Australian white-eye. The common white-eye has a broad range in Europe and eastern Asia, and is sympatric with several species of *Aythya*. Wild hybrids have been reported with the European pochard, the tufted duck, and the greater scaup. Hybrids with the first two species have proved fertile in captivity. Captive-bred hybrids have also been reported with the red-crested pochard, the rosy-bill, the lesser scaup, and the New Zealand scaup.

General behavior. On the water, common white-eyes are, in general appearance and shape, rather more reminiscent of tufted ducks and scaups than of the two preceding species. The rapid Chin-lifting movements typical of the whole pochard group constitute the preflight signal.

Agonistic and sexual behavior: female. Inciting by the female is characterized by frequent overt attacks, after which the female swims back to the preferred male, neck-stretching and repeatedly calling *gak-gak-gak*. Females rarely perform Preening-behind-the-wing, but, surprisingly, frequently perform Head-throws (Fig. 68*D*). The Head-throw call is also a *gaaak*, and the bill is scarcely tossed back past the vertical. As in the Australian white-eye, females also perform a Kinked-neck call similar to the male's. Steinbacher (1960) has also recorded this and noted that the associated call is an *errr*.

Agonistic and sexual behavior: male. The courtship postures of this species are rather different from those of the preceding forms. The usual male posture is one in which the tail is depressed into the water, producing a triangular white pattern with the under-tail coverts (Fig. 67*F*). In this posture the male frequently moves with jerky forward and backward head movements in a Nod-swim. The Kinked-neck call (Fig. 67*F*) is frequently uttered and may be repeated several times as in the two preceding species, although the neck movements are not so exaggerated. I have written this call as *wheeoooo*, but Steinbacher (1960) describes it as *wückwück*. Sneaking is very frequent, during which a similar call is uttered, and from the Sneak posture the male always goes directly into the Neck-stretching display (Fig. 68*A*, *B*). The Head-throw (Fig. 68*C*) is always preceded by one or more head-shakes, and the display is relatively rapid (lasting approximately ⅓ second). The bill travels through an arc of about 135 degrees, and scarcely if at all leaves the vertical plane. The call is the same as that uttered during the Kinked-

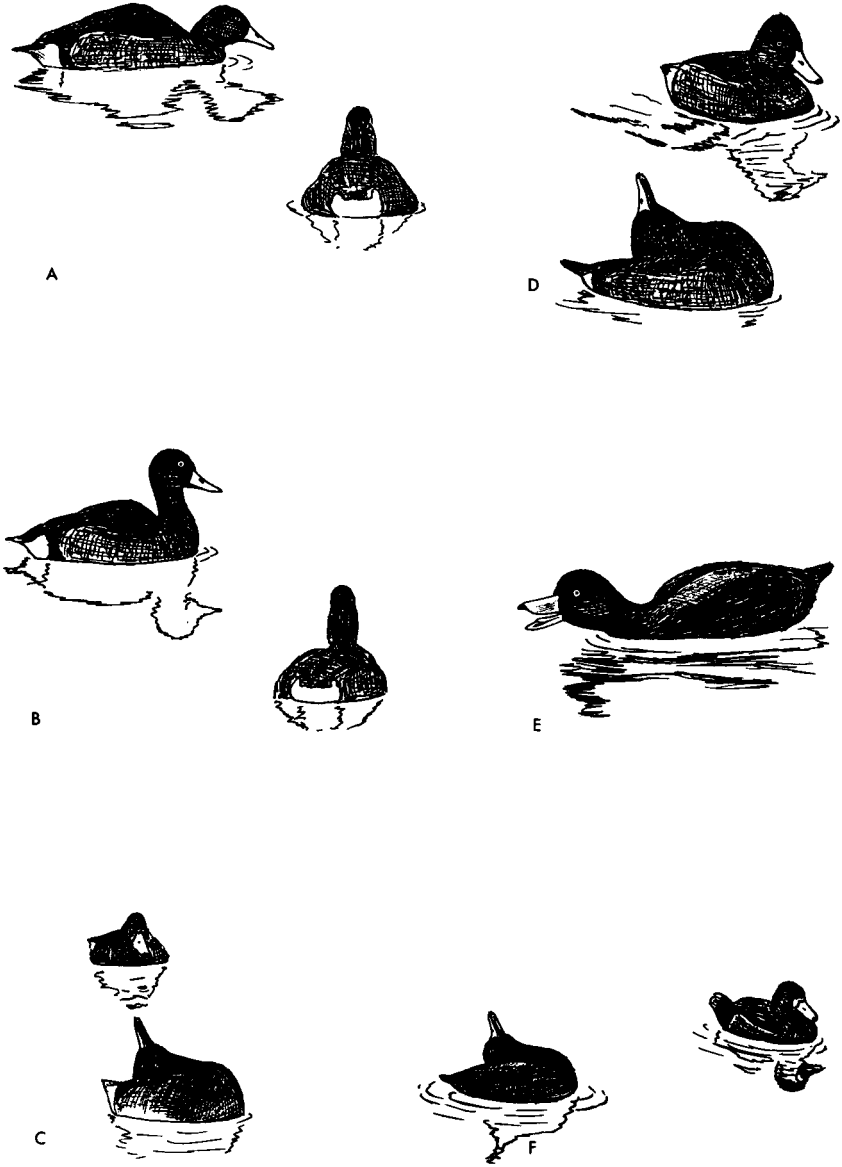


Figure 68. Common White-eye, New Zealand Scaup

A, B. Two phases of Sneak–Neck-stretching display of male common white-eye.

C. Head-throw by male common white-eye.

D. Head-throw by female common white-eye.

E. Male New Zealand scaup in Sneak posture.

F. Head-throw by male New Zealand scaup.

neck call. Coughing is fairly frequent and conspicuous in this species. It consists of rather high-pitched *wee'whew* and a noticeable rapid flick of the wing tips as the call is emitted. Males respond to female Inciting by swimming ahead and Turning-the-back-of-the-head. Preening-behind-the-wing is also occasionally performed by males.

Copulatory behavior. Thus far I have not observed a complete copulation, but I have seen obvious precopulatory behavior. This consisted of the male performing repeated Bill-dipping and Preening-dorsally, and the Head-pumping observed in the two preceding species was not evident. The female made no obvious response to the male's displays. According to Mr. Vincent Weir (pers. comm.) the postcopulatory display is like that of the other pochards.

Madagascan White-eye (*Aythya innotata*)

The Madagascan white-eye is a little-known species which is almost certainly an island derivative of the common white-eye. Its downy young are almost identical with those of that species, and the female plumage is likewise very similar in both forms. The adult male is rather darker throughout, and although it is said to have a more rounded head shape than the male of the common white-eye, this is questionable. The tracheal structure is, to my knowledge, undescribed. In captivity this species has produced fertile hybrids with the common white-eye.

General and sexual behavior. Delacour (1959) states that this species resembles the redhead in its general appearance and voice. I have not observed living specimens, but I doubt that the species differs markedly in behavior from the common white-eye.

New Zealand Scaup (*Aythya novae-seelandiae*)

The New Zealand scaup is a typical member of the last subgroup of *Aythya,* the scauplike ducks. Species in this group are typified by sexually nondimorphic iris coloration, downy young that are very dark in color, males with metallic head coloration and black breasts and under-tail coverts, and females which are generally brownish except for a white patch behind the bill. The bill is broad and bluish in both sexes. Downies of this species lack the dark cheek and eye marks typical of the remaining species, and also have some dorsal spotting, which is absent on the others. In addition, the males

are unusual inasmuch as they are almost entirely blackish, although, as in the other species, there is a conspicuous white speculum. The male tracheal tube is only slightly enlarged and the bulla is exactly like that of the tufted duck. The species was sympatric with the Australian white-eye, but the latter is no longer found in New Zealand. In captivity hybrids have been reported with the common white-eye.

General behavior. As in the other scaups, the preflight movements consist of very rapid Chin-lifting, which might be better described as upward bill-flicking.

Agonistic and sexual behavior: female. Inciting is similar to that of other scaups, in that it lacks overt threats and consists mostly of neck-stretching with occasional lateral and downward pointing movements of the bill (see Fig. 70*A, B*). The call is a high-pitched and repeated *errrrr*. As in the other scaups, Preening-behind-the-wing is frequently used as a display, but I have never observed a female Head-throw.

Agonistic and sexual behavior: male. The most frequent and conspicuous male courtship display is Coughing. This is a clear, high-pitched whistle that is audible for fifty yards or more. It is usually a three- or four-note call, *whe-whe-whe-whew,* with all the notes on the same pitch and the last note prolonged, reminding one of a Morse Code signal—dot-dot-dot-dash. Males also often perform a conspicuous Nod-swim similar to that of tufted ducks and white-eyes. The Kinked-neck call is frequent, but the neck is not strongly kinked, and the call is a double-note *whe-whe*. The Head-throw is less frequent, and is always preceded by one or more head-shakes. It is a rapid display (lasting approximately ¼ second), and the bill travels back only slightly past the vertical (Fig. 68*F*). The display is symmetrical, with the bill following the median plane of the body. This species differs from the other scaups in that Sneaking is a conspicuous and frequent display (Fig. 68*E*). A soft note accompanies this display, which is directed to males as well as females. Although females frequently Preen-behind-the-wing, I have not recorded this display in males. Males do Turn-the-back-of-the-head to Inciting females while swimming rapidly in front of them, and, as in the other scaups, the head feathers are strongly depressed during this display.

Copulatory behavior. The precopulatory behavior consists of the male Bill-dipping and Preening-dorsally, to which the female may or

may not respond in the same fashion. After treading, the male calls once, then swims away in the Bill-down posture.

Tufted Duck (*Aythya fuligula*)

The tufted duck is without doubt a very close relative of the true scaups, and could appropriately be called the tufted scaup. The downy young are practically identical with those of scaups, being very dark above without back spotting, and with dusky faces crossed with cheek and eye stripes. Juveniles resemble adult females, which have the typical scaup pattern of a brownish body and white face-markings. The male in nuptial plumage differs from scaups mainly in its occipital crest, which together with the dark back probably functions as a species-recognition signal that reduces confusion with the greater scaup. Unlike the ring-necked duck, this species has an iris which is the same color in both sexes, a white wing-speculum, and a broad, short bill. Males possess a distinct eclipse plumage. The male tracheal tube is only slightly enlarged and the bulla is of the usual scauplike type in that the right chamber is somewhat inflated. The species occurs over nearly all of Europe and Asia, and is broadly sympatric with several other species of *Aythya*. Wild hybrids have been reported with the greater scaup, the common white-eye, and the European pochard. Those involving the last two species have proved fertile in captivity. Captive-bred hybrids have also been obtained with several other pochards.

General behavior. Unlike the ring-necked duck, the tufted duck is a bird of large lakes and reservoirs. It is unusual in that nesting frequently occurs near or among gull colonies. Preflight signals consist of very rapid and repeated Chin-lifting movements like those of scaups.

Agonistic and sexual behavior: female. Inciting in this species consists of scauplike neck-stretching alternated with slight threatening movements, and a soft *kärrr*. Steinbacher (1960) has also heard a *quack* or *gack* sound uttered by female tufted ducks. Unlike other scaup females, the female of this species sometimes performs the Head-throw, and also Preens-behind-the-wing fairly frequently.

Agonistic and sexual behavior: male. In practically every respect the behavior of the male tufted duck is like that of male scaups. The Kinked-neck call is performed frequently, but, as in the scaups, the neck is not strongly bent during the call. The note uttered during this

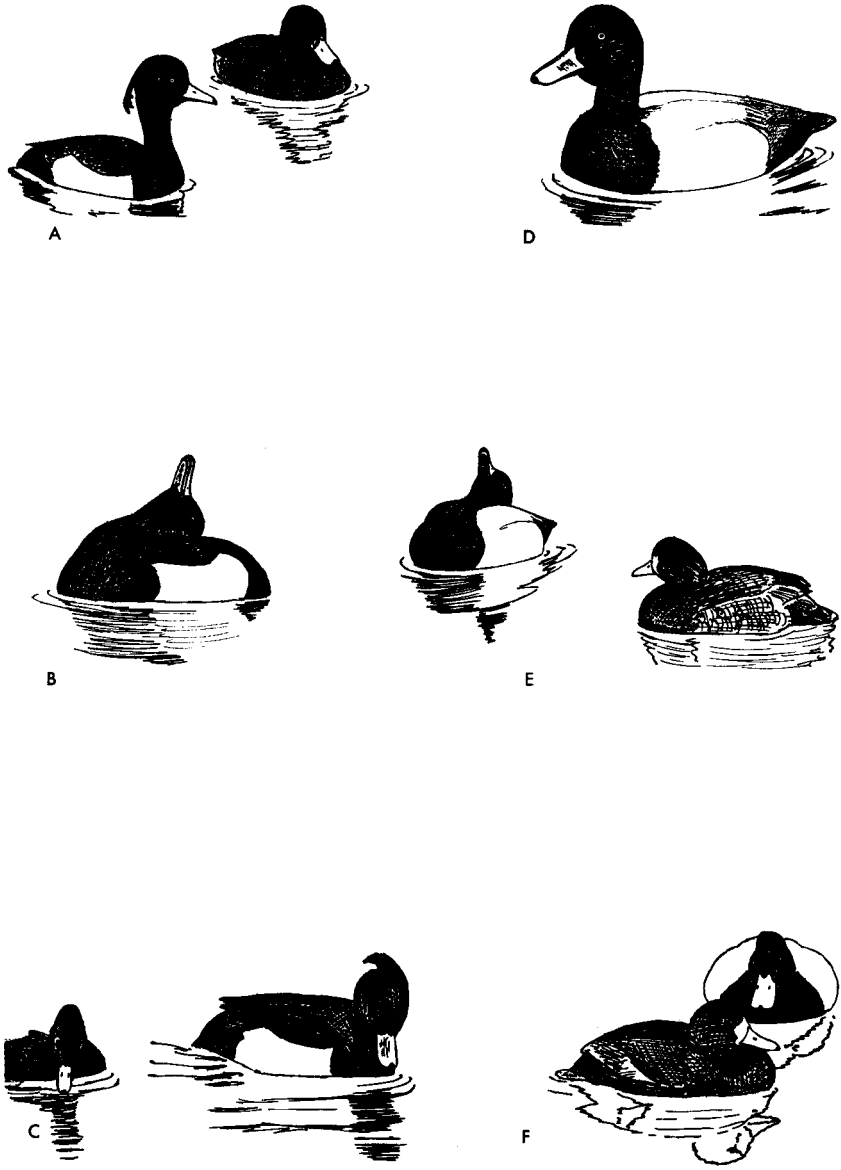


Figure 69. Tufted Duck, Greater Scaup

A. Coughing posture of male tufted duck (*left foreground*).
B. Head-throw by male tufted duck.
C. Postcopulatory Bill-down display by male tufted duck, female bathing.
D. Kink-necked call by male greater scaup. Note bulge in throat.
E. Head-throw by male greater scaup.
F. Sneak posture by male greater scaup.

display, and also during the Head-throw, is a mellow *whee'oo*. The Head-throw (Fig. 69*B*) is a relatively fast display (lasting approximately ¼ second), in which the bill is brought rapidly back to a point just beyond the vertical without being removed from the median plane. The Cough is very frequently performed, and as in the scaups, it is conspicuous for the distinct wing- and tail-flick that accompanies the call (Fig. 69*A*). This is a three-note whistle, much like that of the New Zealand scaup—a rapid and windy *wha'-wa-whew* with the first note highest and loudest, and the last most prolonged. I have not observed Sneaking in this species, but Hans Lind (pers. comm.) has noted it, and I suspect that it is as inconspicuous as it is in the greater and lesser scaups. Preening-behind-the-wing has been seen often, although it is perhaps not so common as in greater and lesser scaups. Males respond to female Inciting in the usual manner, by Turning-the-back-of-the-head while strongly depressing the head feathers. Males also at times perform a Nod-swim, a display which is typical of New Zealand scaup but not the greater and lesser scaups.

Copulatory behavior. Copulation is initiated by the male. Occasionally he Bill-dips, but mainly he Preens-dorsally and at times also Preens-behind-the-wing. The female may respond with some of these same movements; sometimes she suddenly assumes the receptive posture. As treading is completed, the male utters the usual Kinked-neck call and swims away in the Bill-down posture (Fig. 69*C*).

Greater Scaup (*Aythya marila*)

The greater scaup has the widest range of all the *Aythya* species, and is found throughout the Northern Hemisphere. The downy young are very dark all over and have slight facial striping as in the tufted duck and the lesser scaup. Females have the usual blue bills, white face-marks, and white specula of the group. The adult male has a rounded and green-tinted head plumage, but he is otherwise very similar to the male lesser scaup. There is a distinct eclipse plumage. The male trachea is enlarged throughout most of its length, and the bulla is large and has a markedly expanded right chamber. Although sympatric with numerous other species, the greater scaup is rather maritime in its distribution and contact with other species is thus probably reduced. Wild hybrids involving the redhead, the common white-eye, and the tufted duck have been reported, and several other combinations have been obtained in captivity.

General behavior. Because of the greater scaup's tendency to remain on salt water or on the largest and deepest lakes, there does not appear to be much contact between it, and the lesser scaup. Because of the great similarity of the two forms, it is not surprising that no wild hybrids involving them have been reported. Preflight movements are the usual rapid Chin-lifting of the scauplike ducks.

Agonistic and sexual behavior: female. Female Inciting consists mainly of neck-stretching, with occasional lateral movements of the bill (Fig. 70*A*, *B*). The associated call is a low *arrrr*. I have never observed a female Head-throw, but Preening-behind-the-wing is very frequently directed toward males.

Agonistic and sexual behavior: male. As in the other scaups, the Cough is the most frequent and noticeable courtship display. This has the usual flick of the wings and tail, and the call is a soft and very fast whistle—*week-week-whew*. A rapid and very soft *wa'hoooo* (described as *kucku* by Steinbacher, 1960) is used in both the Head-throw and the Kinked-neck call. The Kinked-neck call is uttered with the neck slightly stretched, and the only obvious movement is the enlarging of the throat caused by the lowering of the tongue as the note is uttered (Fig. 69*D*). The Head-throw is always preceded by one or more head-shakes and is a very fast movement (lasting approximately ⅙ second) in which the bill is brought back approximately to the vertical without leaving the median plane. In this species, as in the lesser scaup, Sneaking is reduced to little more than an intention movement (Fig. 69*F*), and is apparently performed without an associated call or with only a very faint one. One of the most common and conspicuous male displays is Turning-the-back-of-the-head while swimming in front of an Inciting female. This display is characterized by an extreme depression of the head feathers, which produces a very flat head profile (Fig. 70*A*, *B*). Males often Preen-behind-the-wing to females (Fig. 70*C*), and mated birds frequently direct this display mutually toward one another. The greater scaup apparently differs from the two preceding species in not having a Nod-swimming display.

Copulatory behavior. Copulation is initiated by the male as he Bill-dips, Preens-dorsally, and Preens-behind-the-wing. The female usually responds with these same displays and then assumes the receptive posture. After treading, the male utters the Kinked-neck call, then swims in the usual Bill-down posture (Fig. 70*D*). The female often swims a few feet in the same posture before bathing.

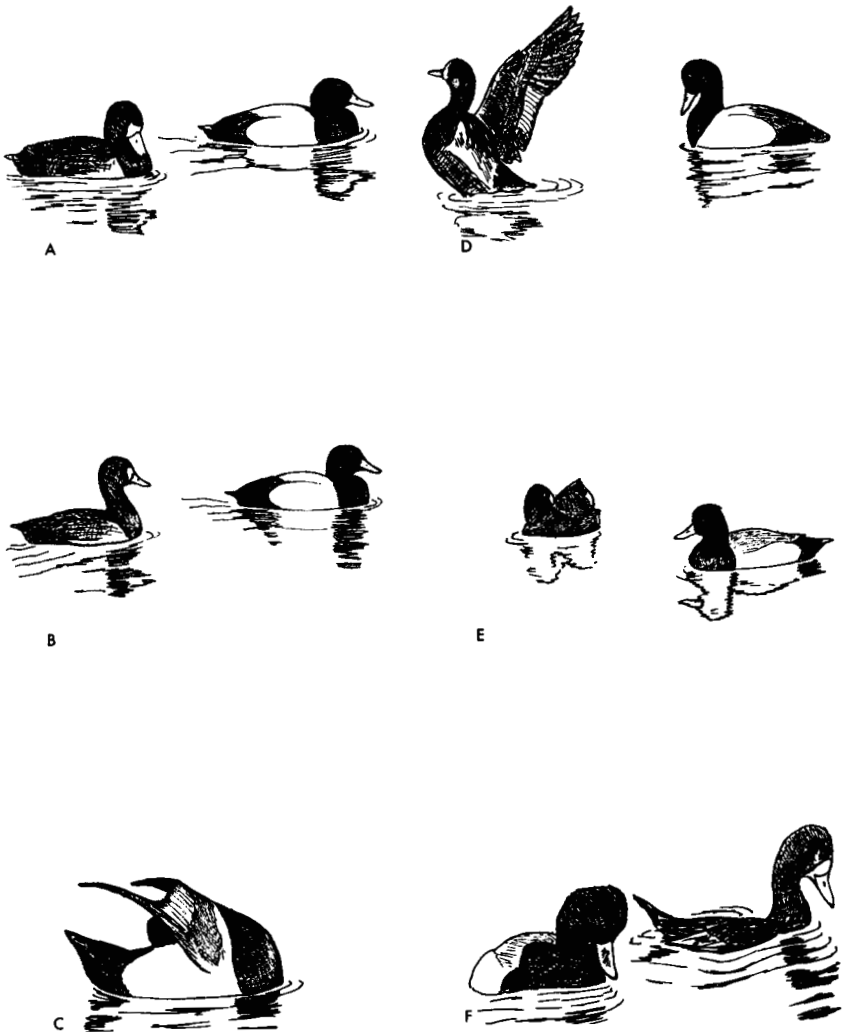


Figure 70. Greater Scaup, Lesser Scaup

A, B. Male greater scaup Leading an Inciting female by Turning-the-back-of-the-head toward her. Compare male's profile with Fig. 69*D*.

C. Male greater scaup Preening-behind-wing. Note speculum pattern exhibited.

D. Postcopulatory Bill-down posture by male greater scaup; female wing-flapping after bathing.

E. Female lesser scaup Preening-behind-the-wing to male in precopulatory situation.

F. Postcopulatory display by lesser scaup. Both birds are in the Bill-down posture.

Lesser Scaup (*Aythya affinis*)

The lesser scaup of North America, like the tufted duck of Europe and Asia, is clearly a derivative of the greater scaup stock. Downy, juvenile, and female plumages of greater and lesser scaup are almost identical, and males in nuptial plumage differ mainly in that those of the lesser scaup have a more grayish back and a more crested and purplish-tinted head. There are also slight differences in the extent of the white wing-speculum. I have not observed the trachea of the lesser scaup male, but no doubt it too is very much like that of the greater scaup male. The species is restricted to North America and is sympatric with several other pochards. Wild hybrids have been reported with the canvasback, the redhead, and the ring-necked duck. As indicated earlier, hybrids with the greater scaup would be almost impossible to recognize with certainty.

General behavior. The pre-flight signal is Chin-lifting, which is performed even more rapidly in this species than in the greater scaup. The tendency of this species to feed on small lakes and marshes distinguishes it from the greater scaup, although both species consume a high proportion of animal material in their diets.

Agonistic and sexual behavior: female. Inciting takes a form practically identical with that of the greater scaup, although the Inciting call is even weaker than in that species. I have never observed a female perform the Head-throw, although Preening-behind-the-wing is a very frequent display.

Agonistic and sexual behavior: male. Displays of the lesser scaup are very similar to those of the greater scaup, differing mainly in the speed of performance and the associated vocalizations. The Coughing Call is frequently uttered, and, as in the greater scaup, the wings and tail are distinctly flicked. The call is a one-note whistle, *whew*. The Kinked-neck call and Head-throw call is a faint *whee-ooo*. As in the greater scaup, the Kinked-neck call is emitted with very little neck movement. The Head-throw is an extremely fast display (lasting approximately $1/20$–$1/30$ second) which is rarely seen unless one watches for the special head-shakes that always precede it. It is probably significant that all the species with fast Head-throws have preliminary head-shakes which apparently serve to draw attention to the male, whereas those with extended Head-throws tend to lack such preliminary head-shakes. In this species the head movement is the

fastest of any in the pochard species; it is only a blur to the human eye. At times the bill appears to be thrown back to the vertical, but slow motion sequences (64 frames per second) suggest that the usual arc is less than 45 degrees. As in the other scaups, the bill is not tilted away from the vertical plane. In the lesser scaup Sneaking is exactly like that in the greater scaup and is easily overlooked. Males also Turn-the-back-of-the-head toward Inciting females in exactly the same manner as greater scaup males, with their head feathers similarly depressed to produce a remarkably low profile. Preening-behind-the-wing is frequently performed by males, and often this display is performed mutually with females.

Copulatory behavior. The male precopulatory display consists of Bill-dipping, Preening-dorsally, and Preening-behind-the-wing. As in the other scaups, the female may or may not respond with the same displays before assuming the receptive posture (Fig. 70*E*). After treading, the male, and usually also the female, swims in the Bill-down posture (Fig. 70*F*). No doubt the male utters his Kinked-neck call as well, but I have never been close enough to hear this.

TRIBE MERGINI (SEA DUCKS)

As constituted here, the tribe Mergini includes all the species which Delacour and Mayr (1945) originally placed in the group. Delacour later (1959) removed the four species of eiders and placed them in a separate tribe, Somateriini, between the dabbling ducks and pochards. This was done apparently as a result of Humphrey's anatomical studies (1955, 1958), which suggested that the eiders might be more closely related to *Anas* than to the other "sea ducks." I have discussed this problem elsewhere (Johnsgard, 1960f, 1964) and concluded that the original inclusion of the eiders in the Mergini seems to fit the facts more adequately. Woolfenden (1961) has reached the same conclusion using anatomical evidence.

The tribe includes 20 species of which two are extinct. Except for two Southern Hemisphere species, the group is of northern and arctic distribution. All species consume a high proportion of animal material, although they are by no means all "sea" ducks. All dive extremely well, although the manner of diving varies in that some species usually open their wings when diving and others never do. All the species except the isolated Southern Hemisphere forms exhibit considerable sexual dimorphism in plumage, voice, and behavior, and

there is much sympatry of ranges. Some genera (*Somateria, Polysticta, Clangula, Melanitta*) normally nest on the ground, and those species which usually nest in the open (the eiders) tend to have cryptic and disruptively patterned female plumages. The other species tend to nest in crevices or holes in the ground (the harlequin), or in trees, and females of these species lack such cryptic coloration. Metallic coloration is restricted to male head plumage in most species, but there is a metallic-colored speculum in two genera (*Polysticta* and *Histrionicus*). The other species either have white wing-specula or lack any wing patterning. In most species the male trachea varies in diameter, and the structure of the bulla is exceedingly variable (see Johnsgard, 1961c), ranging from a simple, almost rudimentary form (*Melanitta*), through an *Anas*-like left-sided and bony bulla (the eiders and the harlequin), to partially membranaceous bullae of very diverse shapes (the goldeneyes and mergansers).

All species of sea ducks apparently require at least two years to attain reproductive maturity. Pair bonds are renewed each year and courtship displays tend to be elaborate and very diverse. Partly because of the great morphological and behavioral diversity exhibited by the sea ducks, relationships within the group and to other groups are sometimes difficult to determine. Although Delacour (1959) believes that the tribe's closest affinities are with the perching ducks, evidence from hybridization, downy patterns, and behavior argue against this and suggest that the group probably was derived from pre-dabbling duck and pochard stock before these two groups diverged. Although the group is therefore of fairly ancient origin, it contains some of the most highly specialized species in the Anatidae.

Behaviorally, male courtship patterns are so diverse and elaborate as to be almost useless for taxonomic purposes, although a few rather general patterns are typical of most species. These include a display Shake (the "Upward-stretch" of Myres, 1959) and perhaps also a ritualized Wing-flapping. Females of most species studied exhibit an Inciting display, but this varies so much in form from one species to another and is so highly ritualized in some species as to be almost unrecognizable. The most valuable behavioral evidence for the homogeneity of the group is to be found in the precopulatory behavior. In all species studied the female assumes a Prone posture, soliciting copulation, often after mutual Drinking between the pair. Before the male mounts he performs a varying number of movements and pos-

tures which usually include Drinking, Bill-dipping, Bathing, Preening-dorsally or Preening-behind-the-wing, and the Upward-stretch or Shake. These movements are firmly linked into definite sequences in some species, while in others they appear to occur in random order. Postcopulatory displays in several species include a ritualized retreat from the female ("Steaming") while Turning-the-back-of-the-head or lateral Head-turning.

EIDERS

Behaviorally the eiders have very little in common with the dabbling ducks, which the females resemble superficially. The Inciting of female eiders is not so highly ritualized as in typical dabbling ducks, but rather alternates overt threats with chin-lifting and neck-stretching, as in some pochards. Male courtship displays have nothing in common with those of dabbling ducks, but the Shake or Upward-stretch of eiders is much like that of scoters. The lateral Head-turning movements of eiders are also much like those of goldeneyes and are used in similar situations. Precopulatory displays are distinctly similar to those of *Melanitta* and *Bucephala*, and postcopulatory behavior is also much like that of *Bucephala*. Female eiders nest on the ground, often in very exposed places, and at times in colonial fashion. Strong sexual dimorphism is present in all species, but metallic coloration is restricted to the wing speculum of one species. Males of all species have a remarkable green pigmentation on the head, as well as dark abdomens and white coloration on the wings or elsewhere.

Common Eider (*Somateria mollissima*)

The common eider and the two following species differ in several ways from Steller's eider, which probably belongs in a separate genus. The females of these species have a more distinctively disruptive plumage, the downy young lack dorsal spotting, and the males have a unique blackish eclipse plumage which is entirely unlike the plumage of females. Juveniles and females of the common eider have a vertically barred brownish plumage very similar to that of the spectacled eider. The males in nuptial plumage have a distinctive head pattern, but in their body and wing coloration they are more like the king eider than like the spectacled eider. The eclipse plumage of adult males is almost entirely black, except for the white wing-coverts and tertials, which are usually almost hidden from view.

Immature males in eclipse are more female-like, with distinct breast barring, and the juvenile plumage of eiders is also distinctly female-like. Downy common eiders are an almost uniform grayish brown, with tan eye-stripes and throats.

The tracheal anatomy of this and the other species of *Somateria* is of interest because of its distinctly *Anas*-like features, namely the uniform-diameter tracheal tube and the rounded, left-sided, and osseous tracheal bulla, which is mallardlike in shape. This similarity was a major point in Humphrey's argument (1958) that the eiders should be placed near the dabbling ducks. Countering this argument, however, is the fact that the harlequin has an equally *Anas*-like tracheal bulla, as apparently also had the Labrador duck. Furthermore, unlike the bronchi of the dabbling ducks, those of this and the other species of *Somateria* are enlarged, as are those of many of the sea ducks (see Johnsgard, 1961c). Finally, the cooing sounds uttered by male eiders are unlike those uttered by any of the dabbling ducks, perhaps because the notes are apparently produced (as are some goose calls) by inspiration rather than expiration.

General behavior. Eiders are strictly maritime birds, often feeding in shallow water for mollusks, which they crush with their strong bills or swallow whole. They are heavy-bodied birds, distinctive in flight for their rapid wing beats and almost perfectly straight course, and lacking the agility of the smaller Steller's eider. Lateral Head-shaking is the only preflight movement which has been observed.

Agonistic and sexual behavior: female. D. F. McKinney has studied several races of common eiders, and his observations on the European and Pacific races have recently (1961) been published. The Inciting behavior is only slightly ritualized, and consists of overt threatening movements with neck outstretched over the water alternated with chin-lifting and neck-stretching toward the preferred male. Repeated one-syllable notes accompany the display (Fig. 72*A*, *B*). This has little in common with the Inciting of dabbling ducks; it is more like that of some pochards. Females also have a *gog-gog* call, and they perform rudimentary versions of such major male displays as Neck-stretching and the various "Cooing Movements."

Agonistic and sexual behavior: male. Male displays of the European eider are numerous, but three movements with associated vocalizations constitute the primary sexual displays. The first is a tossing of the bill almost to the vertical (Fig. 71*C*, *D*). This display, also

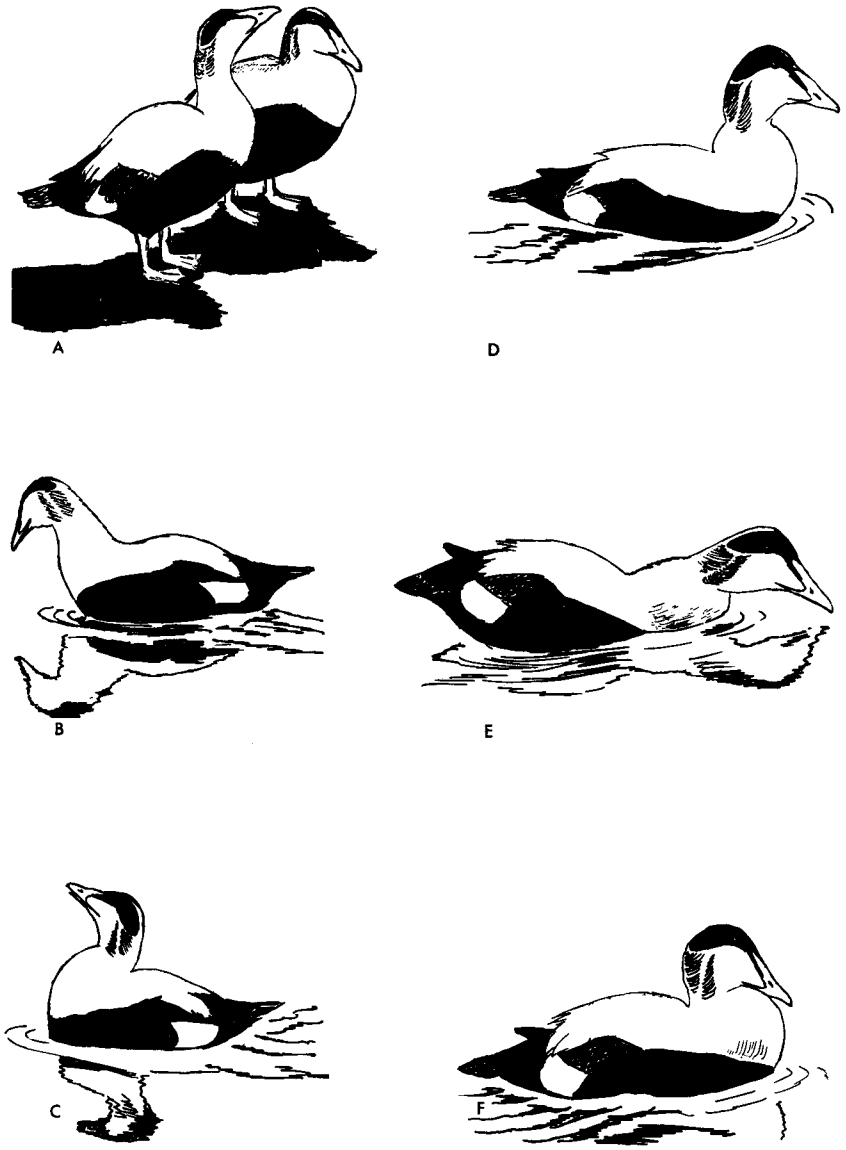


Figure 71. European Eider

A. Chin-lifting by male eider. Compare with Fig. 72*A*.

B, C. "Double Cooing Movement" by male eider. The Neck-jerking display (Cooing Movement 2) in *B* is followed immediately by the Bill-toss (Cooing Movement 1).

D–F. Male eider performing Reaching display (Cooing Movement 3) consisting of Neck-stretching (*D*), reaching forward (*E*), and rapidly returning the head to a resting position (*F*).

called "Cooing Movement 1" (Hoogerheide, 1950; McKinney, 1961), has an *ah-hoo'* call associated with it. "Cooing Movement 2" is a jerking of the head diagonally upward and forward, as if the bird were hitting a ball with his head as a soccer player might (Fig. 71*B*). This display is clearly homologous to the Neck-jerking display of spectacled eiders. When the display is performed alone, the call is a *hoo,* or *ah-hoo',* similar to that of the preceding display, but the Bill-toss and Pushing movements are often linked into a "Double Cooing Movement," and sometimes Pushing both precedes and follows the Bill-toss, producing a "Triple Cooing Movement" and a *hoo—ah-hoo'—hoo"* call. "Cooing Movement 3," which is homologous with the "Reaching" of the king eider (Myres, 1959a), consists of a neck-stretching followed by a reaching forward of the bill until it almost touches the water; then the head is brought back rapidly as the call, *hoo-hooo',* is uttered (Fig. 71*D–F*). Occasionally Neck-stretching occurs without being followed by a Reaching movement, and a silent and repeated Chin-lifting is used as a hostile display (Fig. 71*A*). Males sometimes also utter soft cooing notes without head movements, and this behavior has been termed "Roo calling." Males usually precede the Head-toss with lateral Head-turning, a display homologous to but not so highly ritualized as lateral Head-turning in king eiders. Three clearly ritualized comfort movements occur during display—Bathing, Wing-flapping, and the "Upward-stretch" (Myres, 1959a). The Bathing is similar to a normal though very vigorous bathing, but it is usually followed by ritualized Wing-flapping. When Wing-flapping the male rises very erect in the water, with his bill pointed almost vertically, and flaps his wings strongly two or three times before settling in the water. The Upward-stretch is a ritualized form of the general shake, possibly differing from it in that the body rises higher out of the water and there is little if any shaking of the tail (which is a conspicuous feature of the Introductory Shake of dabbling ducks and pochards). Additional comfort movements such as head-rolling, head-shaking, and bill-dipping are frequent during courtship and are probably also ritualized. D. F. McKinney (1961) has studied the Pacific race of the common eider and found some qualitative and quantitative differences in its displays from those of the European race. In particular, Cooing Movement 2 (Neck-jerking) is absent in the Pacific race, as are the Compound Cooing Movements of which this display is a part. I have noted, however, that the Ameri-

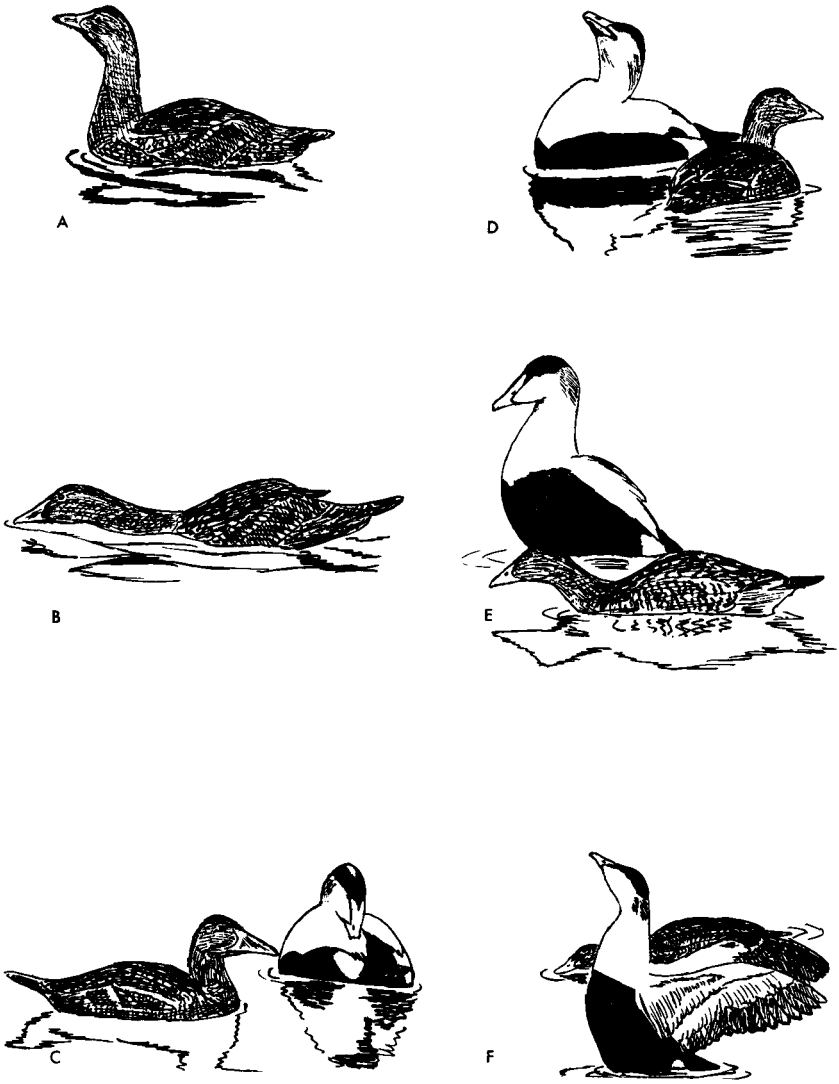


Figure 72. European Eider

A, B. Inciting by female eider. Chin-lifting (*A*) is followed and alternated with direct threatening movement. Compare with Inciting in Steller's eider (Fig. 76) and other sea ducks.

C–F. Precopulatory behavior.

C. Preening-dorsally by male.

D. Bill-toss (Cooing Movement 1) by male; female starting to go Prone.

E. Male Upward-stretch; female nearly Prone.

F. Male Wing-flapping; female completely Prone.

can eider, found on the Atlantic coast, does possess these displays and thus is closer to the European race in its behavior patterns.

The precopulatory displays of the common eider are very interesting, and provide additional evidence that the eiders belong in the tribe Mergini. Females assume the receptive, or "Prone," posture gradually, usually after Inciting. There is no obvious mutual precopulatory behavior, and the male's behavior changes only slightly after the female has assumed the receptive posture. He continues to perform all his usual courtship displays, but in particular he tends to perform Neck-stretching, Bathing, Preening-dorsally, and the Upward-stretch, but in no set sequence (Fig. 72*D–F*) (McKinney, 1961). Preening-dorsally (Fig. 72*C*) by the male is similar to the corresponding display of pochards and, as in that group, possibly serves to initiate copulatory sequences. The male common eider differs from males of some of the following genera in having no single display which he always performs immediately before mounting. He performs no Wing-flicks or other displays during treading. As soon as he releases the female he performs a single Reaching display and swims directly away from her while performing lateral Head-turning movements. The female then normally begins to bathe.

King Eider (*Somateria spectabilis*)

To judge from hybrid records and behavior, the king eider is probably more closely related to the common eider than to the spectacled eider. The downy young of all three species are very similar except for the facial patterning. The juvenile and female plumages differ somewhat from those of the other *Somateria* species, in that the body feathers tend to have U-shaped dark brown markings rather than vertical barring, producing a rather mallardlike effect. The nuptial plumage of the male is distinctive in that the upper-wing coverts are more extensively black and the head has bluish in addition to greenish pigmentation, and the fatty base of the bill is much enlarged. The blackish eclipse plumage unique to the larger eiders is also present in this species. The tracheal structure is very similar to that of the common eider, and the bulla is only slightly smaller than in that species. King eiders are sympatric with common and spectacled eiders, and wild hybrids have been reported with the former.

General behavior. King eiders range slightly farther north than do common eiders, although the breeding ranges of the two species

overlap. Both species dive well and consume great quantities of mollusks. No preflight movements have been observed.

Agonistic and sexual behavior: female. Female king eiders are very similar to common eiders in their displays. Inciting takes the same form as in that species, and consists of a little-ritualized alternation of threatening movements and chin-lifting. The *gog-gog-gog* . . . calling of this species sounds like a hammer hitting a hollow wooden wall. As in the common eider, females sometimes perform incomplete versions of several male displays, such as Reaching, Pushing, Bathing, the Upward-stretch, and Wing-flapping.

Agonistic and sexual behavior: male. The king eider surpasses even the common eider in ritualizing comfort movements into displays. When Wing-flapping, for example, males often face the female as they rise almost vertically in the water and twice flap their wings strongly (Figs. 73*F*, 74*A*). Head-rolling (rubbing the cheeks and crown on the shoulders) is very frequent in king eiders and is certainly ritualized; it or Wing-flapping frequently follows Bathing. Like the spectacled eider, the king eider has a conspicuous Pushing display which is, however, usually repeated several times (Fig. 74*B–D*). A tremulous *hooo* note is uttered with each Pushing movement. The second major male display is Reaching, first named by Myres (1959a), which is performed in a manner very similar to Cooing Movement 3 of the common eider (Fig. 73*A–E*). The call, however, is very different—a tremulous and fading *hoo-oo-oo-oo* . . . The king eider usually follows this display with lateral Head-turning, which is typically a preliminary movement in the common eiders. Lateral Head-turning in the king eider (Fig. 74*E, F*) is even more highly exaggerated than in the common eider; the head swings ponderously through a 180 degree arc. Lateral Head-turning is usually accompanied by Neck-stretching, but Neck-stretching is also occasionally performed independently. Male king eiders also sometimes perform slight Chin-lifting movements, as do male common eiders. Although such displays as Preening-dorsally and Bathing are occasionally seen in courting parties, these are probably more properly regarded as precopulatory displays.

Copulatory behavior. The precopulatory behavior is much like that of the common eider, with the female gradually assuming a Prone posture, often interrupting it to make slight Inciting movements. Before mounting, the male performs an extended series of

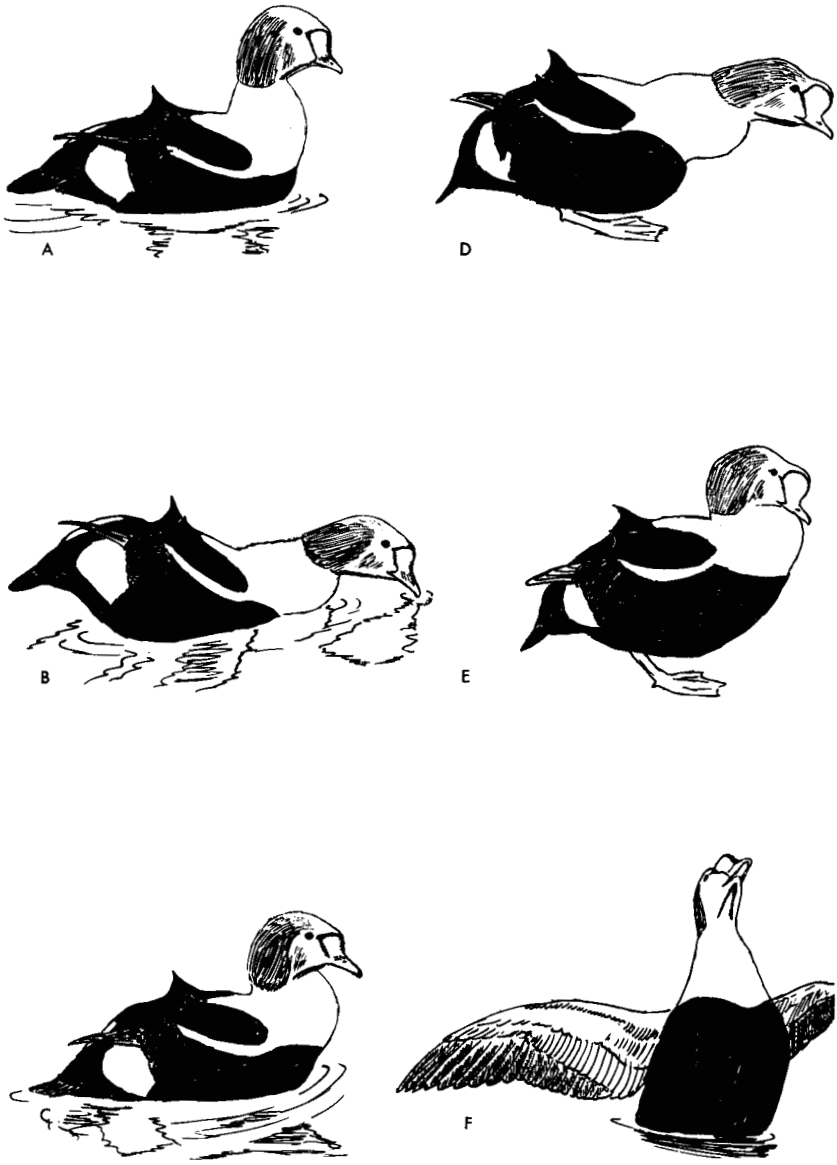


Figure 73. King Eider

A–C. Male king eider performing Reaching display. Neck-stretching (*A*) is followed by reaching forward (*B*), and finally bringing the head rapidly back. Compare with European eider (Fig. 71).

D, E. Reaching on land. Note bulge in neck region.

F. Display Wing-flapping. Note extremely upright body posture and exhibition of V-mark on throat.

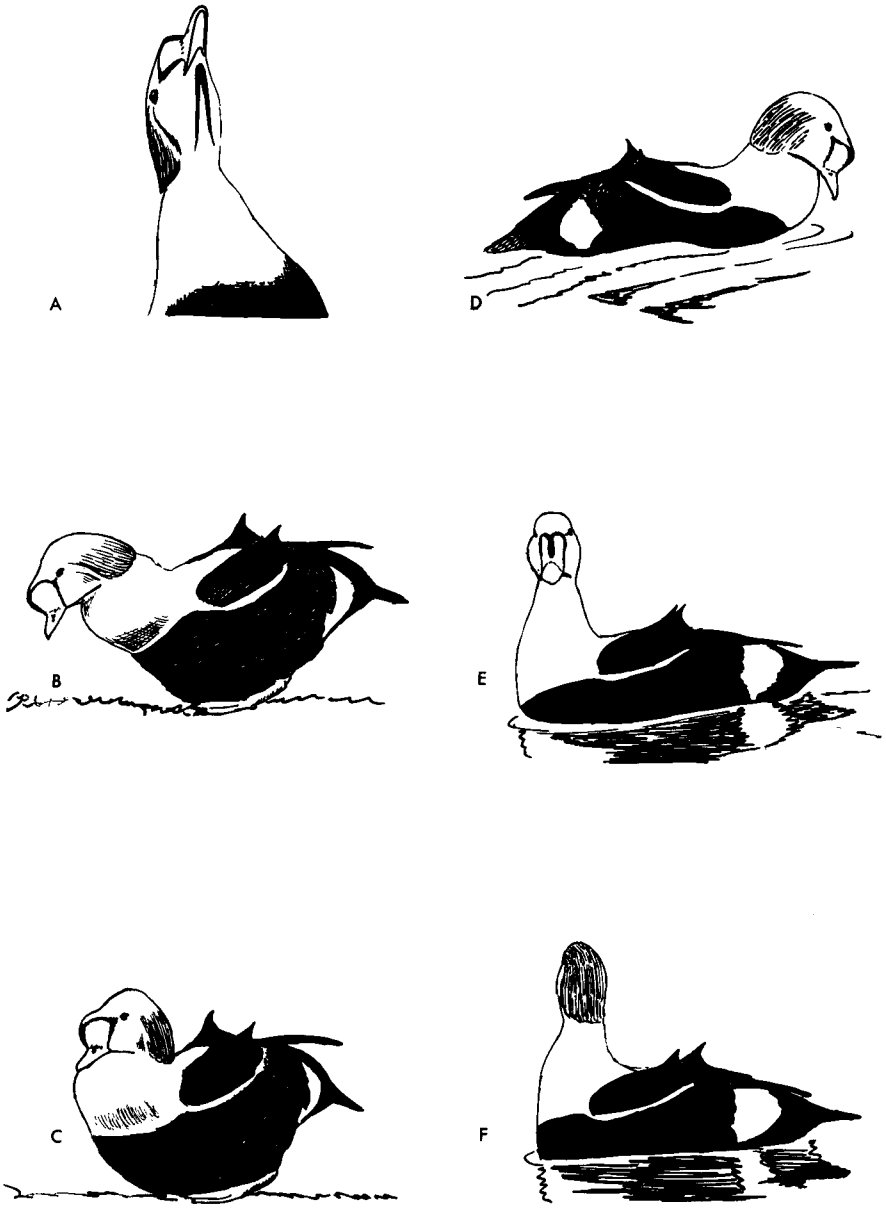


Figure 74. King Eider

A. Display Wing-flapping by male king eider, showing throat markings.
B, C. Male performing Pushing display on land. Compare with Fig. 71*B*.
D. Male performing Pushing on water.
E, F. Male performing lateral Head-turning.

display movements, including both Pushing and Reaching, and in addition such displays as Bathing, Head-rolling, Wing-flapping, and the Upward-stretch. Mounting apparently is frequently preceded by Wing-flapping. After treading, the male appears to retain his hold on the female's nape for a second or two, although no true Rotations are produced. As the male releases the female, he performs a single Reaching display, then swims away fairly rapidly while Head-turning. The female then bathes.

Spectacled Eider (*Somateria fischeri*)

The spectacled eider would appear from its plumage to be a close relative of the common eider, and doubtless it belongs in the genus *Somateria,* but in a few behavioral respects it also resembles Steller's eider (Johnsgard, 1964). The downy young has a slightly lighter face pattern than does the common eider duckling, but the two are otherwise similar. Juvenile birds and females are also similar to female common eiders, possessing the same type of vertical barring on the flanks. Males in nuptial plumage have a wing pattern and body plumage much like those of the common eider, although the head pattern is distinctive. As in the other large eiders, there is a blackish eclipse plumage quite unlike the female plumage. The tracheal structure is also similar to that of the common eider (Humphrey, 1958). Although the species is sympatric with both other species of *Somateria,* no hybrids are known.

General behavior. Judging from my experience with this species at Igiak Bay, Alaska, it is much like the other large eiders in its general behavior. I observed that it commonly foraged by diving under the water, opening its wings as it submerged, and it has also been observed to feed by tipping-up. Before taking flight both sexes frequently shake the head laterally, and they sometimes also perform the general shake in this situation.

Agonistic and sexual behavior: female. I observed that females perform the same type of Inciting behavior which is found in the other two species of *Somateria,* and which is quite distinct from that of *Polysticta.* I heard what was doubtlessly the call corresponding to the *gog-gog-gog* . . . calls of king and common eiders, but distances were too great for me to judge similarities with these other species. I observed no other female displays.

Agonistic and sexual behavior: male. Virtually the only information available on the behavior of this species is based on my observations—often made from rather great distances—of wild birds at Igiak Bay. The spectacled eider differs from the two preceding species in that the Upward-stretch is important in pair formation; in addition, the form of this display is much as it is in Steller's eider, with the bill directed down toward the water as it is shaken. Wing-flapping is not so highly ritualized as in the king and common eiders (Fig. 75*A*); there is no distinct pause before flapping and no orientation toward the female. The primary male courtship display is one I have called Rearing, since it is clearly homologous to the Rearing of Steller's eider. This is usually performed a few seconds after the Upward-stretch, and consists of a rapid jerk upward and backward of the head and neck, bringing the black chest into prominence (Fig. 75C). Although this independent Rearing occurs frequently, it also occurs as the final phase of a display I have termed the Head-forward—Rearing posture, which closely corresponds to Reaching in the king eider and to Cooing Movement 3 in the common eider. In this sequence the neck is first stretched vertically (Fig. 75*D*); then the head is swung forward (Fig. 75*E*) and quickly retracted (Fig. 75*F*), producing a Rearing of the body that is not nearly so marked as during independent Rearing. A very weak *ah-hoo'* hardly audible beyond a few yards, accompanies this display. There are at least two other major male displays, which I have called the Bill-toss and Neck-jerking. The Bill-toss corresponds to, and is certainly homologous to, Cooing Movement 1 of the common eider, while the Neck-jerk is obviously equivalent to Cooing Movement 2 of the common eider (Fig. 75*B*). These two displays are frequently linked into a combination I have called the Bill-toss–Neck-jerk, and although I have observed independent Neck-jerking, I have not recorded Bill-tossing without Neck-jerking associated with it. Lateral Head-turning is infrequent and inconspicuous in this species.

Copulatory behavior. On the basis of limited observations, I would judge that the precopulatory behavior of this species is much like that of the king and common eiders, with the male performing such displays as Bathing, Preening-behind-the-wing, Preening-dorsally, Pushing, and Wing-flapping. In the instances I observed, however, the male, like the male Steller's eider, performed the Upward-stretch only once, immediately before mounting. After treading, the male re-

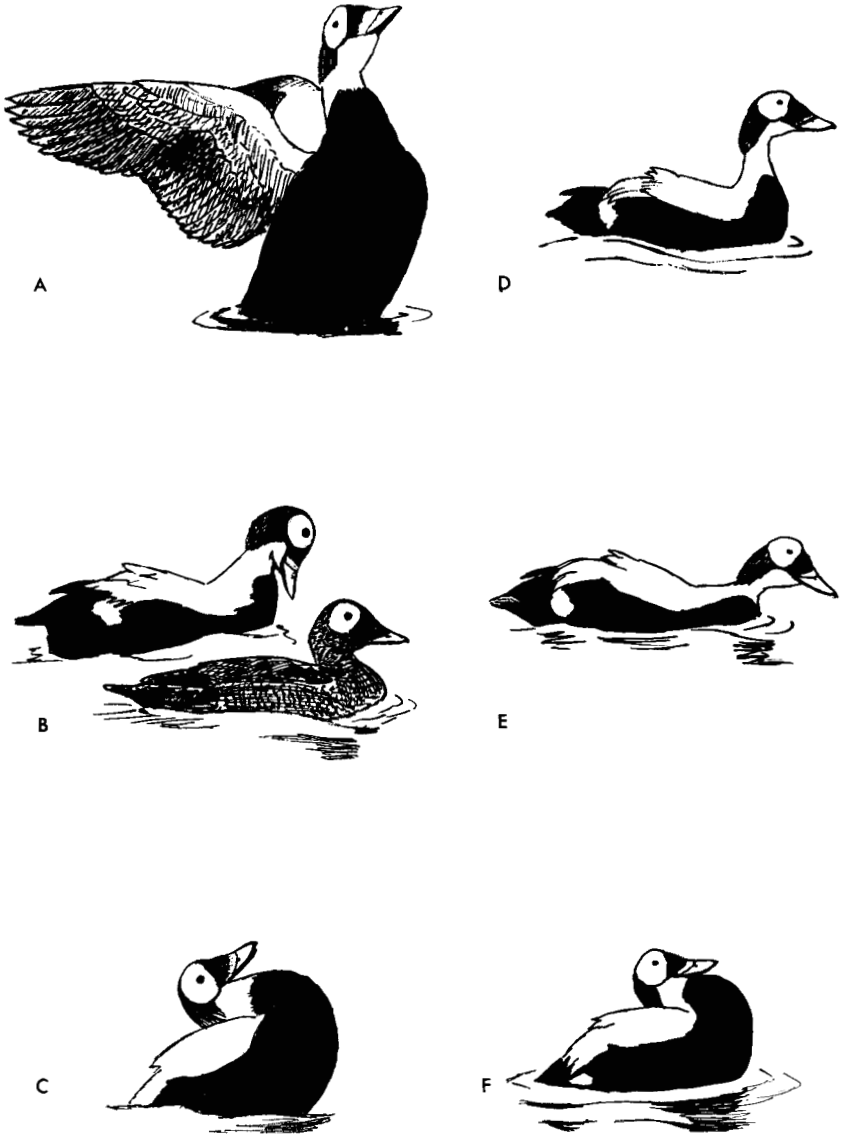


Figure 75. Spectacled Eider

A. Display Wing-flapping by male spectacled eider.
B. Neck-jerking by male spectacled eider.
C. Independent Rearing by male spectacled eider. Compare with Fig. 76*C*.
D–F. Head-forward–Rearing sequence.
D. Preliminary neck-stretching. Compare with Fig. 73*A*.
E. Head-forward phase. Compare with Fig. 73*B*.
F. Rearing phase. Compare with Fig. 73*C*.

leased the female's nape, performed a single Head-forward–Rearing display, and finally made about four lateral Head-turning movements. The female bathed after copulation.

Steller's Eider (*Polysticta stelleri*)

Steller's eider is a somewhat more specialized form than the larger eiders, and has a soft-edged bill that approaches that of the extinct Labrador duck. The downy young are dark brown above, grayish brown below and, unlike the larger eiders, have light dorsal spots. Juveniles resemble females, which have a completely dark-brown barred body plumage except for a white eye-ring and a metallic-blue wing speculum. Adult males in nuptial plumage approach the larger eiders in their dark abdomen, curved and elongated tertials, and green head patches, but they are unique in their white head, cinnamon under parts, and ornate, elongated scapulars. The wing has a metallic-blue speculum much like that of the harlequin duck. There is an eclipse plumage which, unlike that of the larger eiders, is almost identical to the female plumage. The trachea of the male is slightly variable in diameter, and the syrinx has a small left-sided osseous bulla. No hybrids are known, and the species has a very restricted distribution along the Bering Sea.

General behavior. Steller's eiders are not so ungainly as the larger eiders when on land or in flight, but they do usually open their wings when diving. They feed to an even greater degree than the larger eiders on animal materials, and during the breeding season nearly ninety percent of their food is from this source (Kortright, 1943). Except during courtship the birds are very quiet, and even then only the female is especially vocal. Lateral Head-shaking in an alert posture is the only preflight signal.

Agonistic and sexual behavior: female. The Inciting of Steller's eiders is more ritualized than that of the larger species, and consists of a slight lateral threatening movement followed by a rapid and exaggerated chin-lifting and an associated loud *qua-haaa'* that can be heard for a considerable distance. Females lack any call equivalent to the *gog-gog* call of the larger eiders, but they do often perform Bathing and Upward-stretch movements which are similar to the corresponding movements of the males. McKinney (MS) has heard a "rapid, rippling, gutteral call" uttered "constantly" by wild females,

but the captive birds I observed did not perform this call to my knowledge.

Agonisic and sexual behavior: male. Male Steller's eiders are remarkably different from the larger eiders in their displays, and only the lateral Head-turning and Bathing movements suggest close affinities. Lateral Head-turning is performed in a much faster manner than in the larger eiders, which is not surprising considering the difference in body size. The Upward-stretch of Steller's eiders is like that of the preceding species in that the body is not raised high out of the water and the head is shaken with a vigorous downward movement, so that it nearly touches the water (Fig. 75*C*). This type of Upward-stretch is also very similar to that of the black scoter. The major sexual display is a very rapid rearing up of the head and foreparts of the body well out of the water, bringing into momentary view the brown and blackish under parts (Fig. 75*E*). This display, which I have called Rearing, is performed silently, and the only note I have heard male Steller's eiders utter at all is a soft growling threat note. The courtship displays are frequently linked into a definite sequence. The male begins by assuming an "Alert" posture, with his neck stretched and his tail cocked diagonally. He then suddenly performs the Upward-stretch, and immediately begins Steaming rapidly toward the courted female while performing lateral Head-turning (Fig. 75*A*). As he approaches the female he quickly performs a single Rearing display (Fig. 75*C*), then veers and Steams rapidly away from her while still performing lateral Head-turning. A rapid and silent Chin-lifting is used as an aggressive display between males, a movement which brings into sudden view the black chin markings (Fig. 76*D*). Males also swim rapidly ahead of Inciting females and perform lateral Head-turning or Turn-the-back-of-the-head to them (Fig. 76*B*). The latter display does not occur in this context in *Somateria,* but it resembles the combination of Inciting and Turning-the-back-of-the-head found in many other ducks.

Copulatory behavior. The behavior associated with copulation in Steller's eiders is most interesting, and provides clear evidence of their relationships with the following genera such as *Melanitta.* The female assumes a Prone posture directly rather than gradually, although this posture is often preceded by Bill-dipping and Preening-dorsally on the part of the male and, sometimes, also the female. As soon as the female goes Prone, the male begins to perform vigorous Bill-dipping

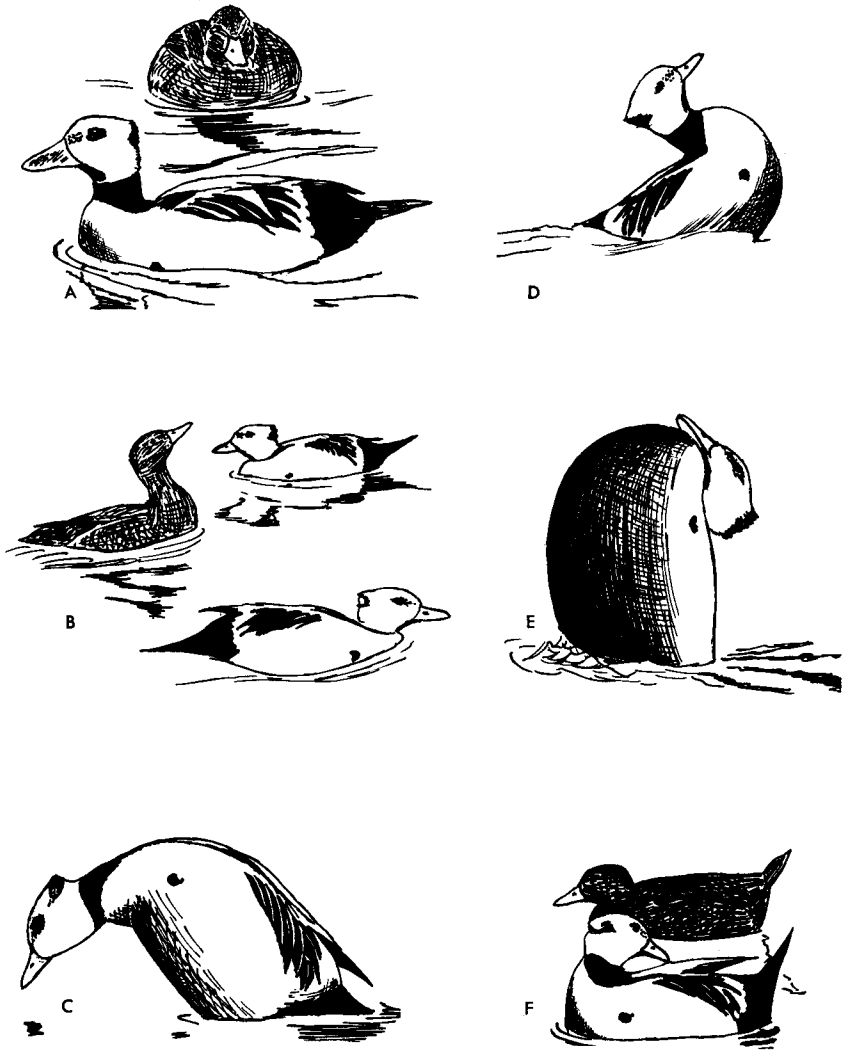


Figure 76. Steller's Eider

A. Lateral Head-turning by male Steller's eider.

B. Female Steller's eider Inciting preferred male (*right foreground*) against second male. The preferred male is performing Head-turning.

C. Male performing Upward-stretch.

D. Aggressive Chin-lifting by male Steller's eider. This appears to be a modification or a low-intensity version of the Rearing display.

E. Rearing by male Steller's eider.

F. Precopulatory behavior. Preening-dorsally in the region of the ornamental scapulars on the side toward the female.

or Bathing movements, which are alternated regularly with Preening-dorsally behind the ornamental tertials (Fig. 76F). This combination of Bathing and Preening-dorsally may be continued for a minute or more, but eventually the male follows Bathing with a single, sudden Upward-stretch, after which he "surfboards" to the female with astonishing speed, with his chest well out of the water, and mounts her immediately. As in the typical eiders, there is no Flick-of-the-wings during treading. Before the male releases the female, the two birds Rotate almost a complete circle in the water. The male then immediately performs a single Rearing display, and finally Steams away, performing lateral Head-turning, and the female bathes. Several features of this copulatory behavior, such as the female's Prone posture, the male's combination of Bathing and Preening-dorsally, and his ritualized Steaming to and from the female, all indicate affinities with the scoter-goldeneye group and show no evidence of relationships with the dabbling ducks.

Labrador Duck (*Camptorhynchus labradorius*)

The extinct Labrador duck is so little known that it is only tentatively placed here and presumed to have been related to the scoters and perhaps also to Steller's eider. The downy plumage is unknown, but the female plumage was gray. Though weakly patterned, it was rather scoterlike. As in the white-winged scoter, there was a large speculum formed by the secondaries and their coverts in both sexes. The male in breeding plumage was strongly marked with black and white in an eiderlike pattern, but the wings were entirely white except for the primaries. It is uncertain whether an eclipse plumage was present. The trachea of the male was described by Wilson (1829). As in the scoters, there was an expansion of the tracheal tube at the anterior end and two enlargements (rather than one as in scoters) near the middle of the tube. The bulla is described as having been large, "bony and round, puffing out from the left side." This asymmetrical and osseous bulla is unlike that of the scoters, and the only other sea ducks with such bullae are the eiders and the harlequin duck. This suggests that the Labrador duck might provide an evolutionary link between the eiders and such other sea ducks as the harlequin and the scoters. Woolfenden (1961) has commented on the intermediate form of the Labrador duck's pectoral girdle between

those of Steller's eider and the harlequin. Humphrey and Butz (1958) have reviewed the anatomical features of the Labrador duck and concluded that it was probably related to the scoter group.

Very little is known about the general or sexual behavior of the Labrador duck, although it is known to have foraged at least partially on shellfish. Possibly the soft-edged bill of this species was related to specialized feeding requirements which were perhaps a factor in its extinction.

Harlequin Duck (*Histrionicus histrionicus*)

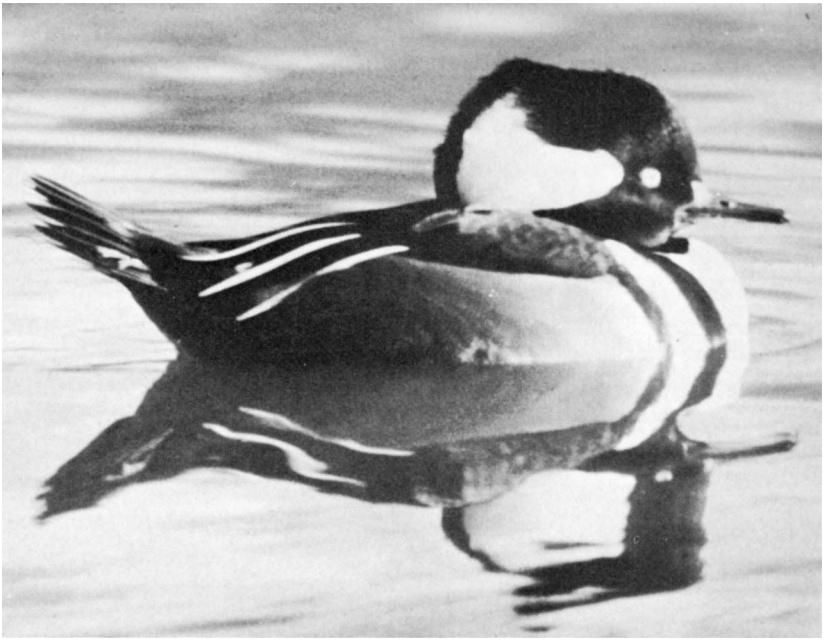
The genus *Histrionicus* does not really "fit" into any sequence of the sea ducks which might be devised. This may be in part due to the fact that it is a highly specialized bird which is adapted to mountain streams. The young are most like those of the scoters and the long-tailed duck, having a dark back and crown and light cheeks and under parts. Juvenile males resemble females and have a plumage pattern much like that of scoters. The wing pattern is brown and lacks the metallic-colored speculum of the male. Adult males in nuptial plumage have a body coloration and pattern which is completely unique in the Anatidae. Unlike the other sea ducks except Steller's eider, the wings exhibit a metallic-blue speculum. There is a distinct eclipse plumage which closely resembles the female plumage. The trachea is of variable diameter, and unlike that of the scoters, has a completely osseous and left-sided bulla much like those of the eiders (see illustration in Johnsgard, 1961c). The harlequin has a wide range in the Northern Hemisphere, and is sympatric with many other sea ducks. No hybrids are known.

General behavior. The harlequin, more than any of the other sea ducks, is a bird of mountain streams. It is highly adapted to living in such habitats and, like the torrent duck and Salvadori's duck, swims with constant head-pumping motions. Like the eiders, scoters, and the long-tailed duck, it usually uses its wings when diving. Preflight movements have not been recorded.

Agonistic and sexual behavior: female. Myres (1959a) has observed this species, and states that Head-nodding is the only female display he has seen, and that it is exactly like the Head-nodding of males. It is a somewhat elliptical movement, with the long axis of the ellipse parallel to the water, and with the bill held horizontally.

Several high-pitched notes have been attributed to the female, and Sven-Axel Bengtson (pers. comm.) has recently observed a form of Inciting similar to that of goldeneyes.

Agonistic and sexual behavior: male. Myres (1959a) believes that the Head-nodding described above is the only male display. It is accompanied by a high-pitched note, single or trilled, reminiscent of "a group of fighting mice." Bretherton (1896) has described a much more complex display, in which "the head is thrown far back with the bill pointed directly upward and widely open; then with a jerk the head is thrown forward and downward as the cry is uttered, and at the same time the wings are slightly expanded and drooped." This display has not been observed by any others to my knowledge. Little has been recorded concerning the behavior of Harlequins, but Neal G. Smith (pers. comm.) and Sven-Axel Bengtson (unpublished MS) have made recent observations of interest. Bengtson believes that Head-nodding is the primary male display, used in situations of courtship, slight disturbance, and early stages of threat display, varying somewhat in the vigor with which it is performed. Threat postures and aggressive rushes toward the opponent were also frequently observed. Bengtson mentions seeing a male shake his bill laterally in the water, a movement probably corresponding to the Water-twitch (Myres, 1959a) of scoters. Both Bengtson and Smith have observed wing-flapping by males as a possible display; Smith informed me that this movement was the most conspicuous male activity aside from Head-nodding. As in eiders, the wings were flapped only about two complete beats. In one case Smith observed that one of the males called, then the other ran across the water (without using his wings) for about four feet, stopped, and wing-flapped. Smith did not observe the Upward-stretch without wing-flapping, and Bengtson mentions this posture only in respect to copulatory behavior. Both observers have observed repeated series of wing-flapping; in one case Smith observed a series of five wing-flaps. Females frequently called as the males wing-flapped, and in three cases females were observed to perform "bill-wetting" in response to this display. Smith described that call as very high-pitched, staccato, and not a whistle, but rather like the call of a least tern (*Sterna albifrons*). Males also called without special posturing, and followed such calls with lateral head-shakes (as do black scoters). Smith and Bengtson frequently observed male-to-male threats and attacks over the surface, but no underwater attacks.



Hooded Merganser, male with crest down.

Hooded Merganser, male with crest raised.

North American Ruddy Duck, Bubbling display.

North American Ruddy Duck pair, Tail-cocking by male.

Copulatory behavior. Myres (1959a) has summarized the few published observations regarding copulation in this species, which appears to lack elaborate or stereotyped copulatory behavior. Neal G. Smith has observed several attempted copulations, all of which were disrupted by other birds. In the first observed instance the male was about ten feet from the female, who was not prone. He dipped his bill in the water, called with bill erect, then "skidded" rapidly over the water to the female, who escaped by diving. Later, four attempted copulations were seen. In these cases the female assumed a Prone posture which she sustained except during those times when the copulation attempts were interrupted. In each case the male mounted her by suddenly "taxiing" over the water very rapidly. Smith's description of this approach clearly indicates that it is much like the rapid "surfboarding" approach of Steller's eider. Each time the male mounted, however, another bird broke up the attempted copulation. No particular displays were observed immediately before the "taxi" to the female, but these could have been easily overlooked. Bengtson has observed 17 attempted and five completed copulations, and noted that copulations are initiated by mutual Head-nodding, which is usually followed by mutual "Bill-dipping" with lateral movements. The male is more likely to perform these latter movements, which consist of three to five dips in rapid succession. Bengtson states that the rush toward the female is identical to those occurring during courtship and agonistic behavior; the male skids toward the female with his bill wide open and uttering a mouselike squeaking sound. Mounting may be preceded by from five to 20 rushes before treading is achieved. In one precopulatory sequence a male preceded the rush with five "body-ups" (Upward-stretches). In two instances Bengtson observed the female assume a Prone posture from ten to 20 seconds before treading. During copulation there are apparently no wing-flicking movements, and there is little or no indication of postcopulatory Rotations. No distinctive postcopulatory postures or calls have been noted.

Long-tailed Duck (*Clangula hyemalis*)

The long-tailed duck, or old squaw, is probably a rather isolated species with no very close relatives. The downy young are much like those of the harlequin duck and the scoters, having unspotted brownish backs and crowns, and white under parts and cheeks. Juveniles

resemble adult females, which, unlike those of other sea ducks, have distinct summer and winter plumages. The summer plumage is generally similar to the plumage of the female harlequin and is rather dark (including the down). The winter plumage is much lighter on the flanks, breast, and head, and the winter down is also whitish. The males have an extraordinarily complex sequence and pattern of plumages, about which there has been much discussion and argument (Stresemann, 1948; Salomonsen, 1949). In nuptial plumage the male is predominantly white, with a black breast and back, a black ear patch, and a grayish color between the ear patch and bill. The tail is greatly elongated, and the dark central feathers may reach a length of almost ten inches. Most sexual display is done in this plumage, which is retained until about April, when the white feathers of the head and neck are replaced with black ones, the gray flank feathers with white ones, and the long white scapular feathers with shorter tan feathers having dark central stripes. This plumage is assumed before the breeding period, but it is a duller plumage which appears to be a functional eclipse. Some of the white feathers behind the eye and the gray cheek feathers are retained, producing a white eye-ring of varying size in different birds. This plumage is held until July, when there is a further loss and/or fading of the longer scapulars and a molt of the tail. The loss of the wing feathers also occurs at this time. By September the tail and flight feathers are again fully grown, and the brownish scapulars, and also the black head and neck feathers, are replaced with white ones. At this time the grayish cheek feathers, holdovers from the preceding winter's plumage, are also molted and replaced with white ones. These white cheeks are retained, however, for only a month or two before being replaced with the gray cheeks of the winter plumage.

The trachea of the male is of somewhat variable diameter, and although the bulla is partially membranaceous it is distinct in shape from those of the other sea ducks (see illustration in Johnsgard, 1961c). The species occurs throughout the arctic zone and is sympatric with most if not all the other northern sea ducks. Although wild hybrids have never been reported, a captive hybrid involving the chestnut teal has been alleged.

General behavior. The long-tail is an open-water bird and is perhaps more northerly in its breeding distribution than any other

duck. It is also a highly vocal bird, and the male's calls carry long distances. Long-tails usually open their wings when diving, although in captivity at least this is sometimes not done. Lateral Head-shaking is the only preflight movement which has been noted.

Agonistic and sexual behavior: female. Myres (1959a) states that Chin-lifting is the major female display, but it is rare compared with this display in female scoters. It is a rapid movement, involving only the bill, and the head remains on the shoulders. Presumably it is functionally equivalent to Inciting, but I have not personally observed female display. Drury (1961) states that when tossing the head (presumably Chin-lifting) the female utters an *urk; urk, urk, ang, ang, ang, goo* or *gut-gut-goo'ah-góo'ah.*

Agonistic and sexual behavior: male. Male long-tailed ducks have several conspicuous displays, of which two are associated with calls. The most frequent call is the "Ah-har-lik" call (Myres, 1959a), which may be uttered without any head movement or with a rapid Bill-toss (Fig. 77*A, B*). The Ah-har-lik call is preceded by two preliminary notes, and the last syllable is loudest, thus: *ugh, ugh, ah-oo-gah'*. The second call is distinctly different and is associated with the "Rear-end display" (Myres, 1959a). This call can be written as *a-oo, a-oo, a-oo'-gah,* with the penultimate syllable the loudest. The male begins this call with his head erect and his neck vertical; then he rapidly swings his head down over the water, with neck still extended, as he erects his tail to the vertical and kicks both feet slightly out of the water (Fig. 77*C, E*). Displays not mentioned by Myres include Neck-stretching (Fig. 77*D*) and Turning-the-back-of-the-head (Fig. 77*C, D*). Neck-stretching is often followed by or combined with Turning-the-back-of-the-head, and it resembles the erect, or "Sentinel," posture of scoters. Drury (1961) has also observed Short Flights by males. Unlike the scoters, these birds apparently do not engage in underwater attacks on one another. Except during display, the male's head feathers are not raised, and the forehead profile is low and sloping (Fig. 77*F*).

Copulatory behavior. Myres (1959a) has observed copulation in this species, and reports that the female remained in a Prone posture for periods ranging from only momentarily up to 15 seconds or more before the male mounted. No specific precopulatory displays were observed, and during treading no Flick-of-the-wings was seen. There

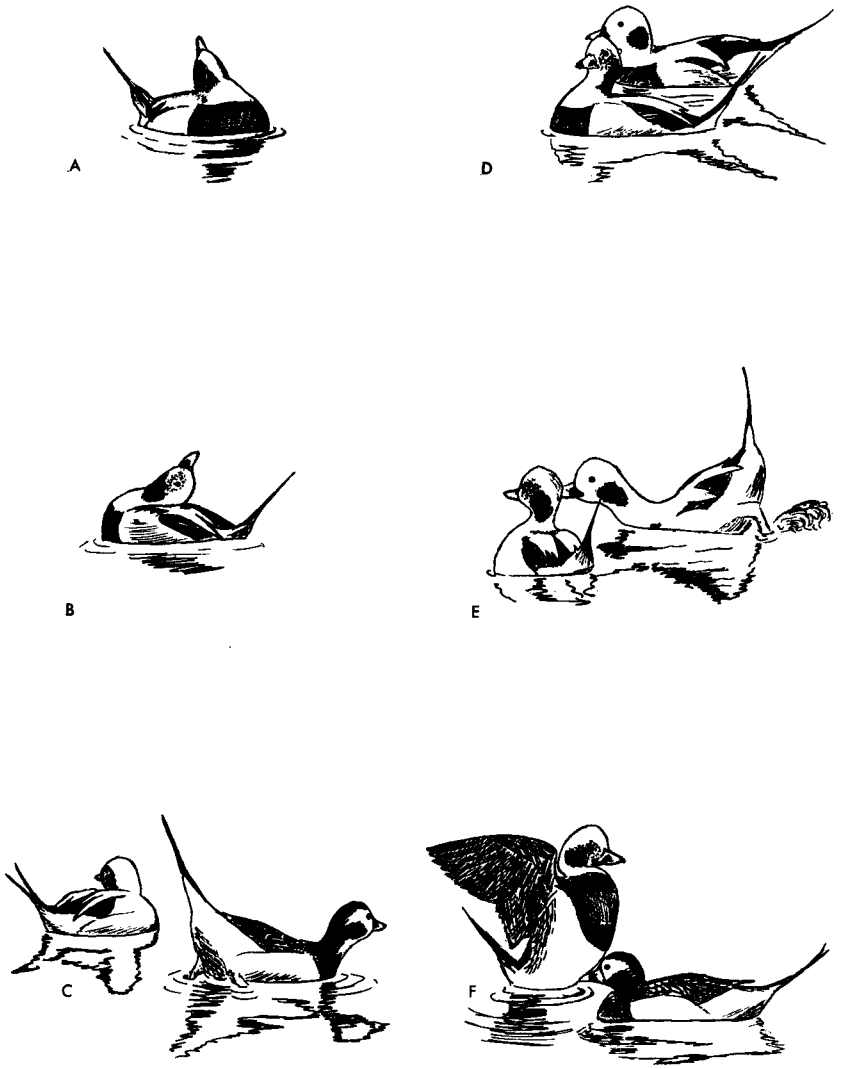


Figure 77. Long-tailed Duck

A, B. Two views of Bill-toss by male long-tailed duck while uttering the Ah-har-lik call.

C. Turning-the-back-of-the-head by one male (*left*) as the other performs the Rear-end display.

D. Turning-the-back-of-the-head by one male to another (apparently a homosexual pair), combined with Neck-stretching.

E. Rear-end display by male just assuming winter plumage. Note white cheeks.

F. Wing-flapping (possibly a display) by male in full winter plumage. The male on the right is just molting out of its summer plumage.

were no postcopulatory Rotations, and no other special postcopulatory behavior was observed.

Black Scoter (*Melanitta nigra*)

The black scoter diverges from the other two species of *Melanitta* in several respects. The downy young are rather eiderlike in that they are predominantly dark brown with no dorsal spotting and with only an indistinct cheek patch. Juvenile males resemble females, which have a two-tone head plumage unlike the other scoters but otherwise are uniformly brownish in color. Adult males are almost entirely black except for a variably enlarged yellow bill protuberance. The wing is unpatterned and has a very narrow outer primary that produces a whistling noise when the wings are flapped. There is no obvious eclipse plumage. The tracheal structure of the male is extremely simple, with a tracheal tube of uniform diameter and a small, symmetrical syrinx. The bronchi, however, are much enlarged (illustrated in Johnsgard, 1961c). The species has a broad range in the holarctic region and is sympatric with both of the other species of scoters. No hybrids have been reported involving this species.

General behavior. Like the other scoters, black scoters are essentially salt-water birds, coming inland only during the breeding season. They dive well, normally opening their wings when so doing, but this appears to be rather variable, at least in captivity. Like most other sea ducks, the black scoter indicates its intention to fly by swimming in an alert, neck-stretched attitude and occasionally performing lateral Head-shakes.

Agonistic and sexual behavior: female. Neither I nor others have observed any calls or movements which obviously function as Inciting, although Myres (1959a) has observed a slight chin-lifting which may be such a display. At times the female calls in unison with the male when he utters the courtship whistle, and the female's call is a similar, frequently repeated, whistling note that is grating rather than mellow, and reminds one of the swinging of a door with rusty hinges. It is uttered from an erect posture like the calling posture of males. One obvious female display consists of Preening-behind-the-wing (Fig. 79*B, E*) toward a male as he utters the courtship whistle, and this preen appears to be a frequent stimulus for the male to perform the Low Rush. Myres (1959a) mentions the Tail Snap and Low Rush as being performed by females. I have not seen these displays, but

lateral Head-shaking, the Upward-stretch, Wing-flapping, and various preening movements are all frequent and may have signal function.

Agonistic and sexual behavior: male. Male courtship displays have been described by Gunn (1927), Humphrey (1957), McKinney (1959), and Myres (1959a). My observations on the European race compare very closely with those of McKinney on the American race. It is extremely difficult to separate true display from ordinary comfort movements in this species, for most displays are only slightly modified versions of such movements. Thus the Upward-stretch (the "Shake" of McKinney), Wing-flapping, lateral Head-shaking, and preening in various places all occur frequently during display and appear to have signal function. McKinney (1959) has named the major displays, which include the Low Rush (Fig. 79*C, F*), the Tail-snap (Fig. 79*A, D*), the Short Flight, and Steaming toward the female. The Tail-snap is almost always followed by the Low Rush, but the latter display is sometimes performed independently. In its complete form the male display sequence involves a complex series of movements. In the order of their usual performance, these are as follows: Courtship whistle in Erect posture (Fig. 78*A*), Tail-snap, Low Rush, Water-flick (Fig. 78*C*), Breast-preen (Fig. 78*D*), Forward-stretch (Fig. 78*E*), Upward-stretch (Fig. 78*F*), and lateral Head-shake (Fig. 78*B*). The Tail-snap and the Low Rush are fairly often omitted from the sequence, and in its simplest form the display consists of the courtship whistle followed by lateral Head-shaking (Fig. 78*A, B*). I have not observed the display that Humphrey (1957) termed "Bowing," but Myres (1959a) considered it to be the courtship call posture ("Neck-stretching").

Copulatory behavior. My observations on copulation agree with those of McKinney (1959) and Myres (1959a). Unlike most other sea ducks, the female does not remain in the Prone or soliciting posture for long, but assumes it just before the male mounts, after both sexes have Preened in various places. The male performs an Upward-stretch when the female goes Prone, then mounts immediately (compare Steller's eider). The male does not Flick-the-wings while mounted, and he releases the female as soon as copulation is completed, then swims away from her while calling in the usual Neck-stretching posture. The female begins to bathe immediately. Myres (1959a) observed the Tail-snap, Low Rush, and Upward-stretch sequence after one copulation.

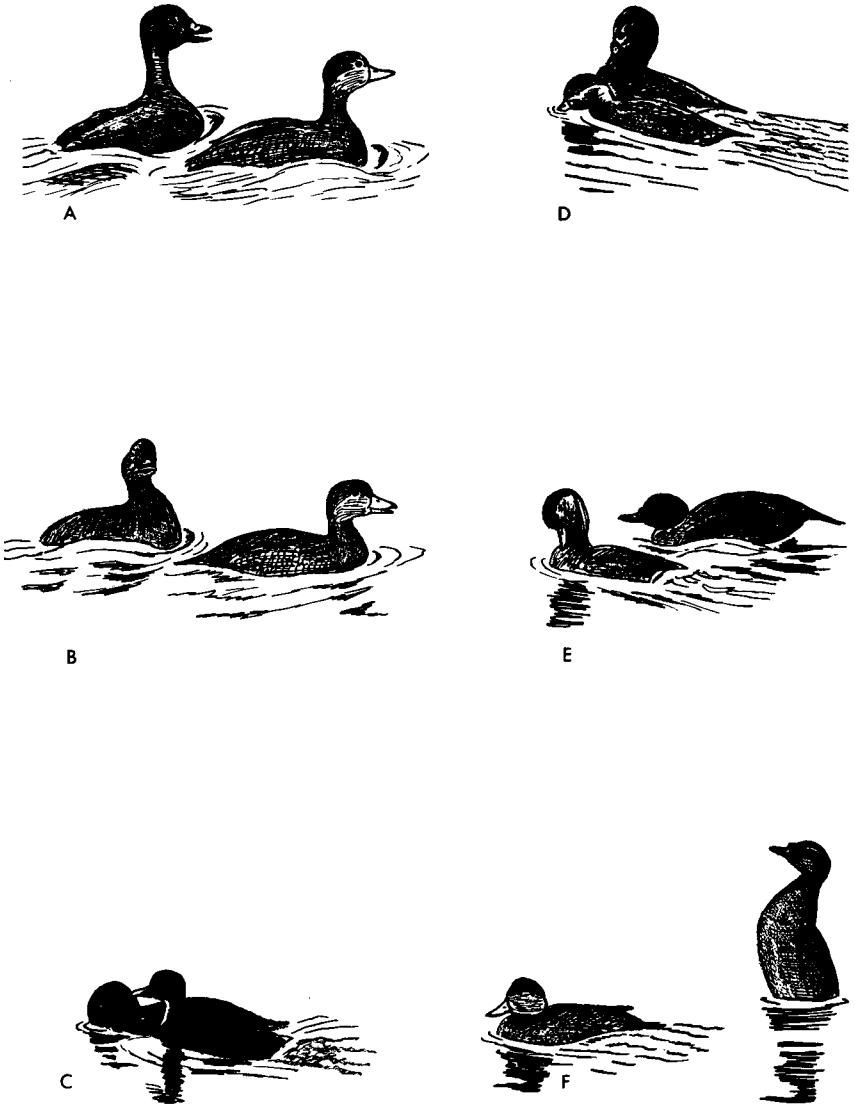


Figure 78. European Black Scoter

A. Male scoter (*left*) uttering courtship whistle in Neck-stretching posture.

B. Lateral Head-shake performed by male scoter after courtship whistle; female calling.

C–F. Water-flick–Breast-preen–Forward-stretch–Upward-stretch sequence.

C. Water-flick.

D. Breast-preen.

E. Forward-stretch (female preening breast).

F. Upward-stretch.

Figure 79. European Black Scoter

A. Tail-snap by male scoter following courtship whistle.
B. Female scoter (*right*) Preening-behind-the-wing to male.
C. Low-rush by male.
D–F. Another Tail-snap–Low-rush sequence.
D. Tail-snap
E. Female Preening-behind-the-wing as male lowers tail.
F. Low-rush by male.

Surf Scoter (*Melanitta perspicillata*)

Although probably more closely related to the white-winged scoter than to the black scoter, the surf scoter exhibits a few similarities to other species, including Steller's eider. The downy young closely resemble those of the black scoter, but they have a more contrasting pattern which approaches the black and white pattern of the white-winged scoter. First year males and females have a brown-and-white-spotted head pattern which closely resembles that of the white-winged scoter. Adult males resemble the black scoter in their lack of a white wing-speculum, but in their sexually dimorphic white iris coloration they are like the white-winged scoter. In their orange leg and foot coloration they also approach the white-winged scoter. Bill and head coloration in this species is the most elaborate of all the scoters and, as in the other species, there is no distinct eclipse plumage. The trachea of the male has a swelling near the anterior end of the tube and a mid-tracheal swelling which apparently varies in size in different individuals. The species is restricted to North America and is sympatric with both of the other scoters. Hybridization with the white-winged scoter has been reported.

General behavior. The surf scoter seems slightly heavier-bodied and less agile than the black scoter and lacks the markedly elongated tail of that species. Males also lack the extreme narrowing of the outer primary of that species, but their wings do nevertheless whistle slightly when flapped. Preflight movements have not been observed.

Agonistic and sexual behavior: female. I have not observed display in this species, but Myres (1959a) has presented a full account. Chin-lifting, accompanied by a "crow-like" call, is directed toward a specific male, and presumably it is very similar to the marked chin-lifting and harsh calling during Inciting by Steller's eiders. Females also perform several of the male courtship displays, according to Myres.

Agonistic and sexual behavior: male. The "Threat" and "Crouched" aggressive postures of this species are much like those of the white-winged scoter, according to Myres, and, as in that species and the goldeneyes, underwater chases are frequent. The "Sentinel" posture described by Myres is apparently equivalent to "Neck-stretching" in the black scoter and the "Neck-erect-forwards" of the white-winged scoter. In this posture "Breast Scooping" occurs, which

is apparently a combination of lateral Head-shaking and breast preening movements, and is accompanied by a "liquid gurgling call" (Myres, 1959a). A display not found in the other scoters is "Chest-lifting," which is a rapid throwing back of the head and raising of the front of the body out of the water in a manner very similar to the Rearing display of male Steller's eiders (Myres, pers. comm.). There is a "Fly-away" display similar to the Short Flights of black scoters, Steller's eiders, and *Bucephala,* and as the bird lands the wings are momentarily raised into the "Upward-wings-raised" posture as in *Bucephala* (Myres, 1959a). There is also a "Tail-raised and Head-Turning" display which is perhaps homologous to the Tail-snap of black scoters and the lateral Head-turning of eiders and goldeneyes.

Copulatory behavior. Myres (1959a, 1959b) has provided the only account of copulation in this species. The female remains in a Prone posture for a longer period (up to two minutes) than in the other scoters. No preceding mutual behavior was noted. While the female was Prone, the male performed the Water-twitch (dipping the bill while shaking the head laterally) and Preening-behind-the-wing. Ritualized Drinking was observed in four out of eight pre-copulatory sequences. The male mounted slowly, and in most cases Flicked-the-wings once during treading. In seven out of the eight cases the male performed a Chest-lifting movement as he dismounted, but no other displays were seen. The female usually flapped her wings after copulation.

White-winged Scoter (*Melanitta fusca*)

The white-winged, or velvet, scoter appears to be the most specialized species of scoter, and approaches in several respects the genus *Bucephala.* The downy young are strongly patterned with black and white, and are very similar to goldeneye downies. First-year males and females have a brown plumage and a spotted head-pattern like that of the surf scoter. Adult males have white irises as in the surf scoter, which are emphasized by a white eye-stripe. The body is otherwise dark except for a large white patch on the secondaries and their coverts. There is no eclipse plumage. The trachea of the male has two distinct enlargements in the tracheal tube and an almost bilaterally symmetrical bulla (see illustration in Johnsgard, 1961c). The species ranges widely across the arctic and is sympatric with both of the other species of scoters. Hybrids with the surf scoter have

been reported, and hybrids with the common goldeneye have also been alleged.

General behavior. White-winged scoters usually open their wings when diving, and keep them open when under water, and it has been alleged that the wings are used for steering when the birds are submerged. Like the other scoters, this species is primarily a saltwater bird, although during the breeding season it moves great distances from any ocean, into the central part of North America.

Agonistic and sexual behavior: female. To judge from Myres' account (1959a), Chin-lifting appears to be the primary female display. It is similar in form to the preflight Chin-lifting of the lesser scaup and is accompanied by a "very thin whistle." It is directed to a favored male or occurs in a Triumph Ceremony situation; thus it is clearly equivalent to true Inciting. Ritualized Drinking is also performed by females.

Agonistic and sexual behavior: male. Besides Myres' account (1959a), Koskimies and Routamo (1953) have described the displays of this species in detail. Threat display is much like that of the surf scoter and the goldeneyes, and underwater attacks often occur. The "Neck-erect-forward" (Myres, 1959a) is assumed during rapid swimming. Males also frequently perform ritualized Drinking in an exaggerated fashion much like that of the common goldeneye. Although Drinking is frequent during courtship, it, Water-twitching, and ritualized Preening are probably primarily precopulatory displays. Males also utter a whistling note during display, but it is not certain whether this occurs during special posturing. As in the other scoters, the Upward-stretch and Wing-flapping are frequent during display and are almost certainly ritualized. Myres (1959a) mentions a posture observed in a male during apparent pair formation, when he held his bill downward, with a very "swollen" head and neck.

Copulatory behavior. Myres (1959a, 1959b) has observed copulation on several occasions. As in the black scoter, the female assumes the Prone posture only shortly before the male mounts. Before this the pair usually performs mutual Drinking, and the male performs Water-twitching and Preening-behind-the-wing. This latter display can occur independently, but when Water-twitching is performed it is usually followed immediately by Preening-behind-the-wing. Preening is not restricted to the wing (where it exposes the white speculum), but also occurs dorsally and on the sides and shoulder. Ap-

parently no particular display occurs just before mounting. When mounted, the male sometimes (once or twice out of five times) performs a double Flick-of-the-wings, and upon dismounting he sometimes momentarily retains his hold of the female's nape, producing a slight rotary movement by the two birds. The male then releases the female and swims slowly away, rearranging his wings. The female does the same and may also flap her wings (Myres, 1959a, 1959b).

Bufflehead (*Bucephala albeola*)

Of the three species in the genus *Bucephala,* the bufflehead appears to be the least specialized. Myres (1959a) suggested that the goldeneyes might be related to the scoter group through the bufflehead, and that possibly the latter should be placed in a monotypic genus. Although I agree that the bufflehead is a probable link between *Melanitta* and *Bucephala,* I do not believe that generic separation is warranted. The downy pattern of the bufflehead is exactly like that of the goldeneyes, and juvenile males and females are very similar to those of goldeneyes except for the white head-markings and dark-colored eyes. Males in nuptial plumage differ from the goldeneyes only in having a dark iris, pink rather than yellow feet, and slightly different head patterning. There is a complete eclipse plumage which closely resembles the female plumage. The trachea of the male lacks any swellings, and the bulla is fairly small and simple in form, approaching the simple scoter type of bulla. Buffleheads are restricted to North America and are sympatric with both species of goldeneyes. No hybrids have been reported.

General behavior. As is true of the other species of *Bucephala,* buffleheads differ from scoters in that they are primarily fresh-water birds and cavity-nesters rather than ground-nesters. In correlation with this the females are grayish rather than brown, and possess white rather than dark gray nesting-down. Unlike the preceding sea ducks, all species of *Bucephala* dive with their wings closed. Preflight movements have not been noted.

Agonistic and sexual behavior: female. As in the goldeneyes, there is a great deal of aggressive behavior in both sexes, and postures derived from or related to threat displays are conspicuous features of display. The female apparently has two major displays. The first of these is the "Head Display" (Myres, 1959a), which is similar to the

Crest-erection of males and apparently stimulates males to display sexually. The second is "Following," in which the female follows a male (presumably a preferred individual), calling and alternately stretching and withdrawing her neck (Myres, 1959a). This display is at least functionally equivalent to Inciting, although it is entirely different from the lateral Inciting of goldeneyes or the chin-lifting form of Inciting in scoters and eiders. It resembles somewhat the Inciting of female smews.

Agonistic and sexual behavior: male. Male displays are largely derived from attack and escape behavior. They include the aggressive "Head-forward" posture (Myres, 1959a), which is exactly like the Crouch posture of scoters and the Laying-the-neck-on-the-water posture of goldeneyes. A similar posture, but with the bill held well out of the water, is assumed during the commonest male display. Myres (1959a) calls this posture Head-bobbing, but I believe it is homologous to the Bowsprit-pumping and Rotary Pumping of the common goldeneye and Barrow's goldeneye, though it is performed in a much more rapid and jerky fashion (Fig. 80*A*). This posture, which might be called Oblique-pumping, is sometimes momentarily interrupted by a sudden lifting of the folded wings, retraction of the head, and down-tilting of the tail (Fig. 80*B*), after which the male usually resumes his Oblique-pumping. I have not heard any male vocalizations. Lateral Head-turning movements are sometimes also performed, and are similar to but more rapid than those of goldeneyes. Other sexual displays of males include Crest-erection and "Leading" (Myres, 1959a) a particular female (who Follows him), with or without Head-turning. This Leading and Following combination is no doubt functionally equivalent to the Turning-the-back-of-the-head and Inciting combination of dabbling ducks, pochards, and some other sea ducks. Frequently the male will make rapid Bill-pointing movements back toward the female behind him (Fig. 80*C*). Ritualized "Short Flights" are frequent, during which a male takes off, flies toward a female, and lands near her, immediately after which he Wing-flaps, ending with a resounding slap of the wings and sometimes raising the folded wings high over the body. On one occasion I observed what I believe was a display corresponding to the Bowsprit of the common goldeneye. It was performed in almost exactly the same manner as the Bowsprit is performed in that species. I have also observed a vertical head-pumping of uncertain significance.

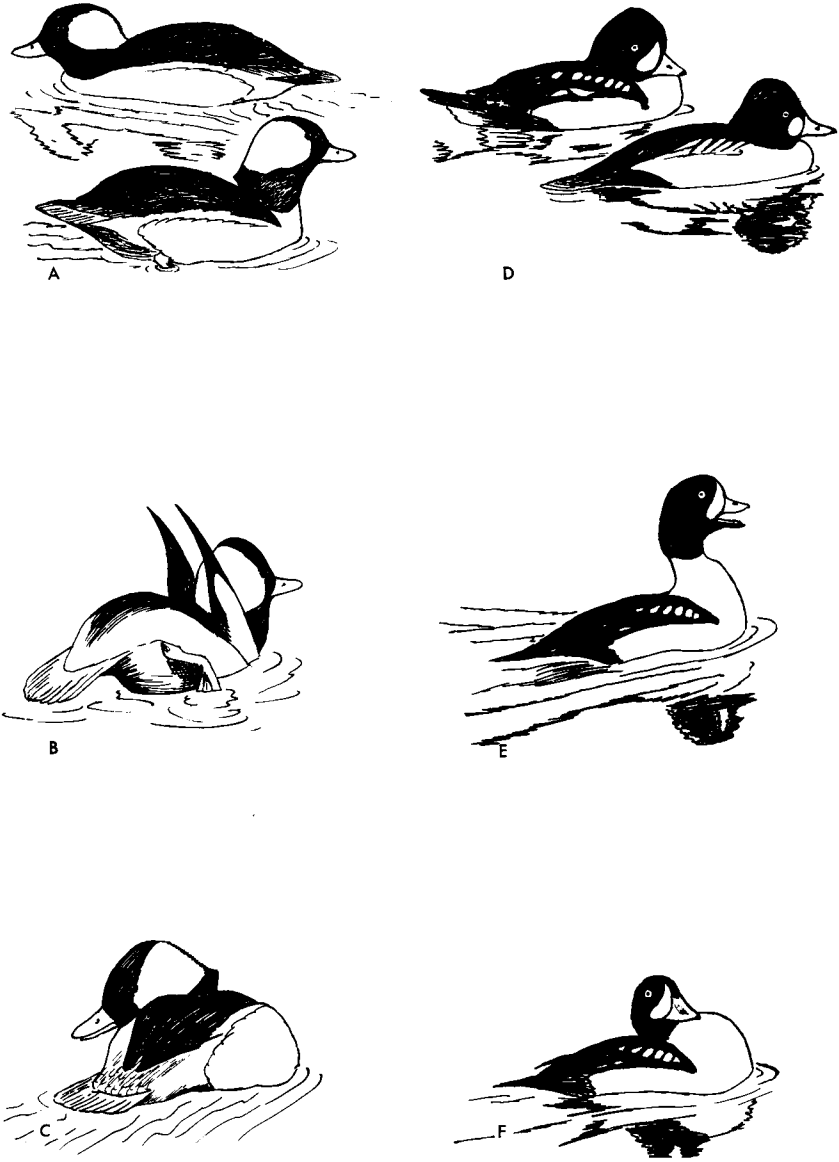


Figure 80. Bufflehead, Barrow's Goldeneye

A. Two phases of Oblique-pumping by male buffleheads.

B. Folded-wings-lifted posture of male bufflehead.

C. Male bufflehead performing Bill-pointing to female behind him.

D. Comparison of male plumages of Barrow's goldeneye (*left*) and common goldeneye (*right*).

E, F. Neck-withdrawing by male Barrow's goldeneye.

Copulatory behavior. Myres (1959a, 1959b) has described in detail the copulatory behavior, which differs from that of goldeneyes in several important respects. The female is in a Prone posture for a variable period, but never for more than a few minutes. The male repeatedly performs two movements—the Water-twitch (lateral bill-shaking in the water, as in scoters and goldeneyes) and, less commonly, Preening-dorsally, which sometimes follows the Water-twitch. Ritualized Drinking was apparently not observed by Myres, nor was the Wing-and-leg-stretch, although these are the two most common goldeneye precopulatory displays. The male suddenly mounts the female without any special preceding movements, and a Flick-of-the-wings was seen by Myres on three out of eight occasions. The male retains hold of the female's nape after completing copulation, and the two birds "Rotate" (Myres, 1959a) from one to several full turns. The male then releases her and either immediately "Plunges" under the water or begins to "Splash-bathe." The female bathes and then flaps her wings. In one copulation I observed, the male swam rapidly away from the female while performing Head-turning movements after he emerged from his dive.

Barrow's Goldeneye (*Bucephala islandica*)

In nearly every respect Barrow's goldeneye is almost identical with the common goldeneye. It is virtually impossible to distinguish the downy young of the two species, and the juvenile males and females of the two species differ only slightly in bill shape and head shape. Females from the western United States apparently have all-yellow bills during the breeding season, while those from the eastern population have little or no yellow on their bills. This may be related to the fact that the western breeding population is sympatric with the common goldeneye, whereas the eastern population apparently is not. Males in nuptial plumage differ from those of the common goldeneye in their head shape and plumage, and in the pattern of the wings and scapulars. There is an eclipse plumage which is essentially identical to the female plumage. The male trachea has a bulla almost exactly like that of the common goldeneye, although the tracheal tube has a gradual rather than abrupt enlargement near the middle. The species occurs in western and eastern North America, Greenland, and Iceland, and is sympatric with both species of *Bucephala*

and several mergansers. Hybrids have been reported only with the common goldeneye.

General behavior. Goldeneyes are found both on salt and fresh water, often in fairly large flocks. They are excellent divers, and feed primarily on animal materials. Preflight movements consist of lateral Head-shaking while holding the head erect and facing into the wind.

Agonistic and sexual behavior: female. Although similar in appearance to the female common goldeneye, the female Barrow's presents some interesting behavioral differences. The head-pumping movements take a rotary form ("Rotary Pumping" of Myres, 1959a) rather than an elliptical one as in the common goldeneye. The "Head-up" posture (Myres, 1959a) is like that of the common goldeneye, but Inciting (the "Jiving" of Myres, 1959a), which is much more frequent in this species (Fig. 81*D*), consists of alternate side-to-side pointing movements, silently performed. On the other hand, the "Neck-dip" of the female common goldeneye is either lacking altogether or performed very rarely. Ritualized Drinking is frequent in both species, and is the usual prelude to copulation. In addition, females of both species assume the aggressive postures of the males, and sometimes will attack other birds from under water.

Agonistic and sexual behavior: male. In his aggressive displays, the male Barrow's goldeneye is exactly like the male common goldeneye, and the Laying-the-neck-on-the-water posture (Fig. 81*A*) usually precedes underwater attack. Rotary Pumping is the most frequent display and consists of rotary movements of the bill and head. It is no doubt homologous to the Bowsprit Pumping of the common goldeneye, but differs from it in that the bill is held almost level. It is directed to males, females, and even to downy young. The "Crouch" posture (Myres, 1959a) (Fig. 81*B*) is frequent during sexual display and there is an associated clicking sound uttered with the bill open. The Crouch does not occur in the common goldeneye, but in this species it is a frequent prelude to the Head-throw-kick display (Fig. 81*C*), which is a rapid toss back of the head and a simultaneous kick with both feet. The bill is turned slightly to the side nearest the female, and a weak, grunting *ka-kaá* call is uttered at the same time. Similar, but softer, grunting sounds are also uttered during Rotary Pumping. The usual male response to female Inciting is to swim ahead of her with neck erect while lateral Head-turning (Fig. 81*D*), or to stretch the neck vertically while opening and closing the bill

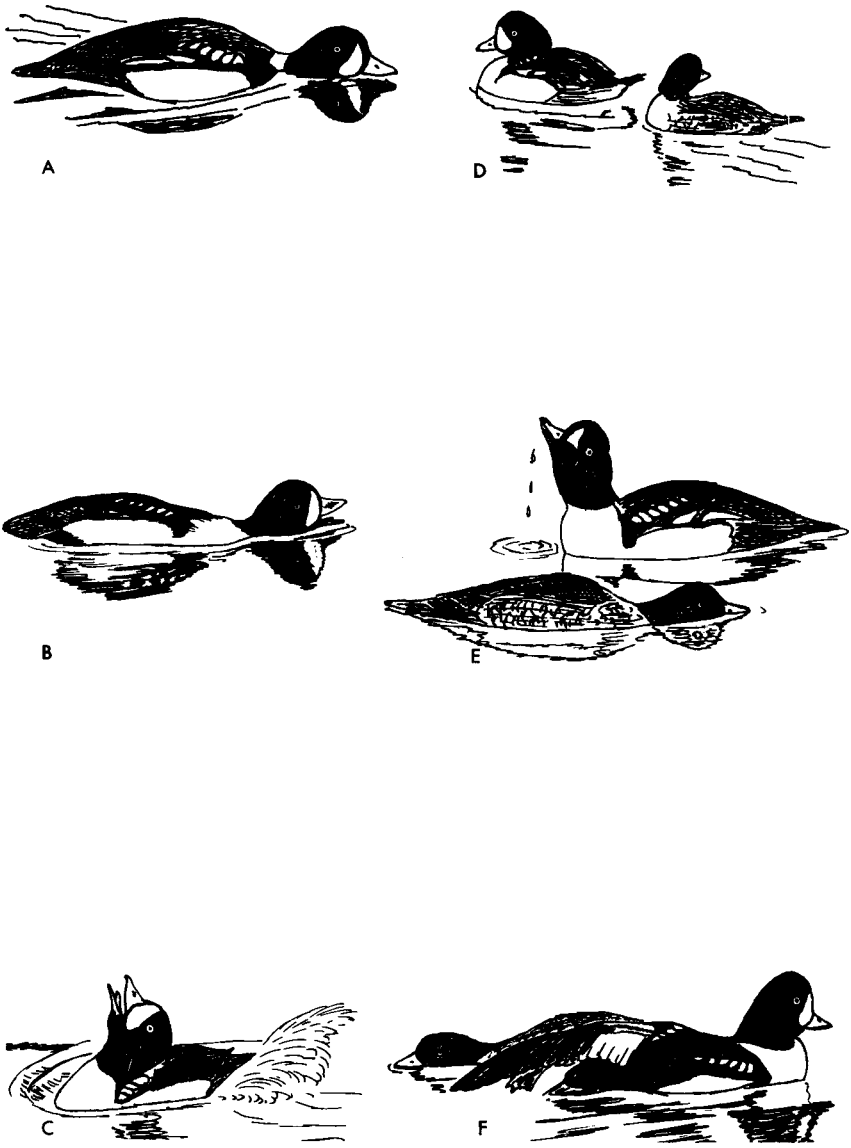


Figure 81. Barrow's Goldeneye

A. Male Barrow's goldeneye in Laying-the-neck-on-the-water aggressive posture.

B. Crouched posture of male Barrow's goldeneye. Compare with *A.*

C. Head-throw-kick display of male Barrow's goldeneye.

D. Inciting by female Barrow's goldeneye and lateral Head-turning by male.

E. Female Prone, male performing display Drinking.

F. Precopulatory Wing-and-leg-stretching by male Barrow's goldeneye.

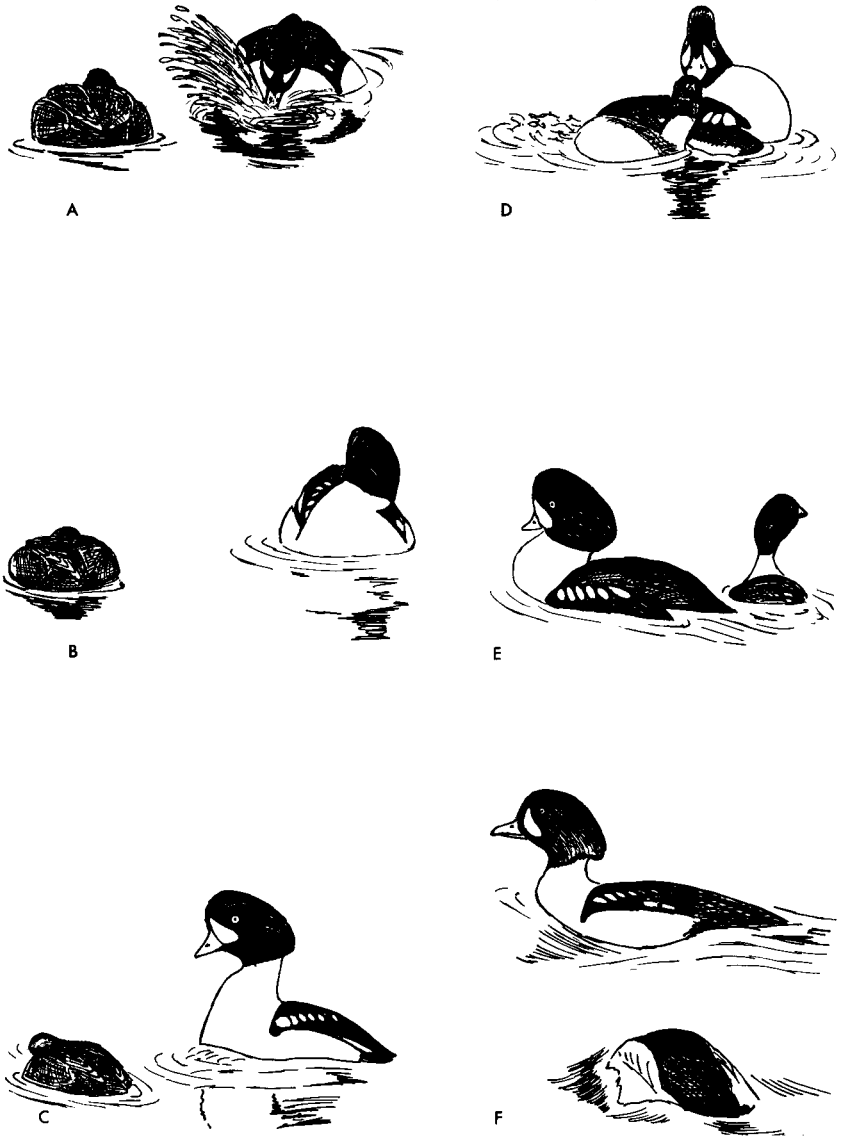


Figure 82. Barrow's Goldeneye, Common Goldeneye
A–E. Copulatory behavior, Barrow's goldeneye.
A. Jabbing by male Barrow's goldeneye.
B. Preening-behind-the-wing.
C. Precopulatory Steaming to female.
D. Rotations terminating copulation.
E. Postcopulatory Steaming.
F. Male common goldeneye attacking male Barrow's goldeneye underwater.

with a clicking sound, and periodically drawing the head down and back on the shoulders in a display that Myres (1959a) calls "Neck-withdrawing" (Fig. 80*E*, *F*). Short Flights toward the female are common, as also are the Upward-stretch and Wing-flapping, all of which are apparently ritualized. There are no displays which correspond to the common goldeneye's Masthead, Bowsprit, or simple Head-throw.

Copulatory behavior. The usual precopulatory behavior is mutual Drinking (Fig. 81*E*), which in this species is not so exaggerated as in the common goldeneye, and is interspersed with Wing-and-leg-stretching (Fig. 81*F*). Water-twitching is infrequent, however, and is often replaced with Bathing movements (which suggests that Water-twitching is a low-intensity form of Bathing). Rarely, both wings are stretched over the back. Vigorous Water-twitching, or "Jabbing," (Fig. 82*A*) occurs only during the stage just prior to mounting, which is very much like that of the common goldeneye. As in that species this stage consists of a series of rapid sideways shakes that splash the water high in the air. These shakes are suddenly terminated as the male Preens-dorsally once on the side toward the female (Fig. 82*B*), then rapidly Steams at her with his bill pointed down toward her. Then he immediately mounts the female, who has assumed the Prone position (Fig. 82*C*), and he always performs one or more Flick-of-the-wings while treading. When treading is completed the male retains hold of the female's nape for several seconds as the birds Rotate in the water (Fig. 82*D*). He then releases her and Steams rapidly away with head erect (Fig. 82*E*), performing lateral Head-turning and uttering repeated grunting sounds. This post-copulatory behavior is identical to that of the common goldeneye.

Common Goldeneye (*Bucephala clangula*)

The common goldeneye has a much broader range than Barrow's goldeneye, extending over most of the temperate, wooded portions of the Northern Hemisphere. The downy young of the two species are identical except, possibly, for a slight difference in foot coloration, and juvenile males and females differ from those of Barrow's goldeneye mainly in having a more pointed head. Adult males in nuptial plumage have a high, pointed, greenish head set off with a rounded white mark in front of the eye, and the scapulars are primarily white, with black border stripes running diagonally parallel

above the wings. The upper wing-surface is also more extensively white than in Barrow's goldeneye. The male trachea has a bulla shaped almost identically like that of Barrow's goldeneye, but the tracheal tube has an enlargement that tapers abruptly posteriorly and gradually anteriorly. This allows for a "telescoping" of the tube that is probably functionally related to the extreme head-throw displays (Johnsgard, 1961c). The common goldeneye is sympatric with the other two species of *Bucephala* and with five species of mergansers. Wild hybrids have been reported involving Barrow's goldeneye, the smew, the hooded merganser, the goosander, and the white-winged scoter.

General behavior. While Barrow's goldeneyes are mainly birds of the mountains and coniferous woodlands, the common goldeneye occurs more broadly over the hardwood forests and prairies. In winter they occur both on salt water and far inland. Preflight movements consist of the usual lateral Head-shaking while facing into the wind and holding the head erect in an alert posture.

Agonistic and sexual behavior: female. Much has been written on the behavior of goldeneyes, the most recent contributions being those of Myres (1957, 1959a), Dane *et al.* (1959), and Lind (1959). Since Myres has also studied the bufflehead and Barrow's goldeneye, his terminology is the most useful for naming the numerous and elaborate displays. The most common female display is Head-pumping (also called Nodding and the Oblique display), which is a silent, diagonal pumping movement (Fig. 85*B*, *C*). The "Head-up" is a posture indicating general excitement, and it occurs frequently during display. It is a silent display, in which the neck is extended and the head feathers usually depressed. Dane *et al.* (1959) have observed the Bowsprit display in females, but I have not seen this. Perhaps the most purely sexual display of females is Neck-dipping (Fig. 83*A*) (called the Dip by Dane *et al.*, and considered part of Inciting by Lind). In this the head is brought forward as the neck is submerged and the tail cocked downward, a weak screeching cry is uttered, and the head is lifted out of the water. This display resembles rather strongly the Curtsy of the male red-breasted merganser, and is usually directed toward a particular (the favored) male. A weak kick may accompany the display. The last major female display, and a very important one, is Inciting (the "Jiving" of Myres, 1957; the "Head-forward" of Dane *et al.*). In this display two males

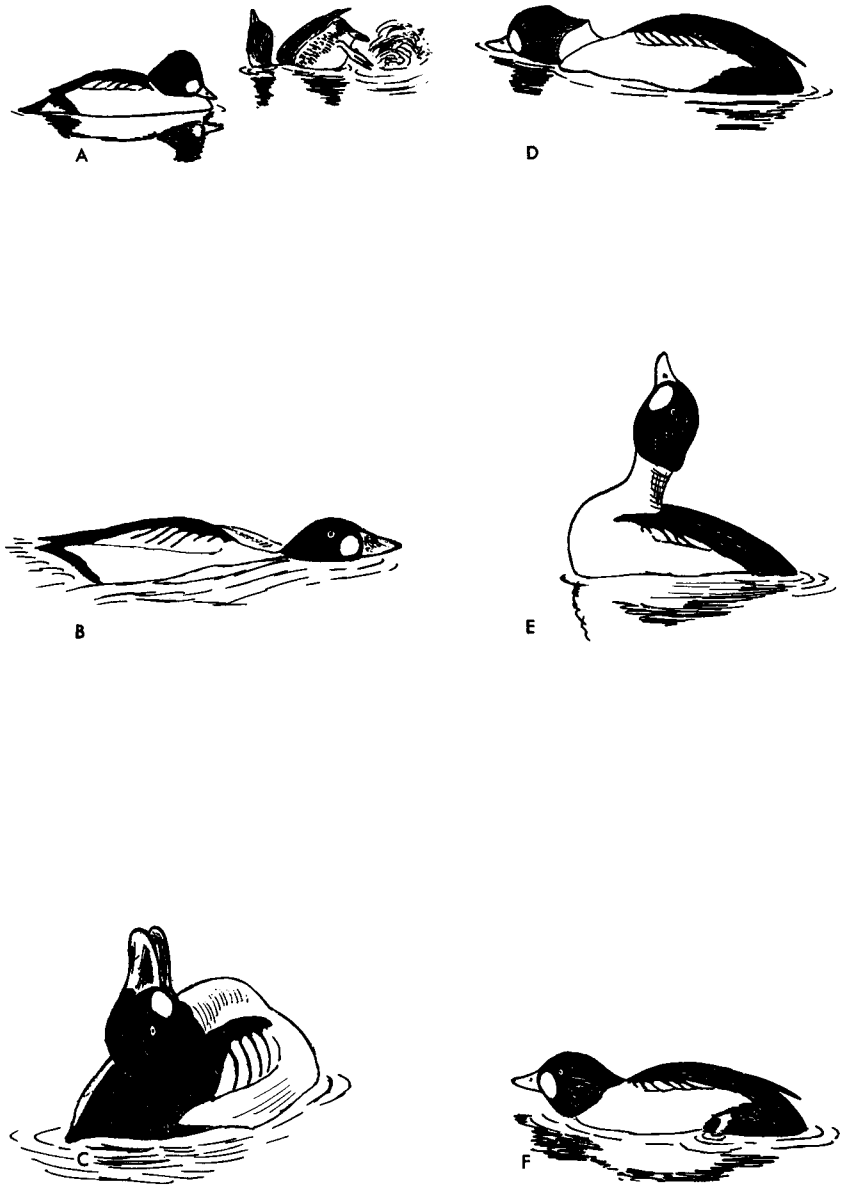


Figure 83. Common Goldeneye

A. Neck-dipping by female common goldeneye.

B. Aggressive Laying-the-neck-on-the-water posture of common goldeneye.

C. Common goldeneye male performing the Head-throw.

D–F. Stages in the performance of the Masthead display. Note depressed head feathers and downward tilting of the tail.

are typically involved, the favored male and an intruder. The female silently swims behind the favored male, turning her head first over one shoulder and then the other toward the second male behind. Sometimes Neck-dipping occurs during Inciting, and this produces intermediate behavior patterns.

Agonistic and sexual behavior: male. The bewildering number of male goldeneye displays warrant a much more detailed discussion than can here be given, and the reader is referred to the papers of Myres, Lind, and Dane *et al.* mentioned above. Perhaps the most frequent male display is Bowsprit-pumping, which corresponds to and is often done during female Head-pumping. This display (called Nodding by Dane *et al.*) is a silent movement with the neck being repeatedly extended diagonally and then withdrawn to the normal position. Often several males perform the display together, and it gives the impression of being primarily a hostile display. This same diagonal neck posture is assumed during the Bowsprit display (Fig. 85*B*, *C*) (called the Oblique posture by Lind), in which the neck and head are first extended along the water, then rapidly and rigidly brought up to the diagonal position as a soft *rrrrrrt* is uttered. Lind has clearly shown that this display has hostile motivation. The preliminary part of this display, Laying-the-neck-on-the-water (Fig. 83*B*), is a highly aggressive posture that is often assumed by rival males. It may precede direct attack, which often occurs under-water (Fig. 82*F*). A final and very frequent male display that probably has important significance is lateral Head-turning (called Ticking by Dane *et al.*). In this display, which is often performed by a favored male as he swims ahead of an Inciting female, the neck is extended upward, the bill is held horizontally, and the head is mechanically turned from side to side as the head feathers are puffed out. As in Barrow's goldeneye, Neck-withdrawing movements sometimes occur during this display, but these are not nearly so conspicuous as in that species.

The most common of the "head-throw" displays is the simple Head-throw (Fig. 83*C*), in which the head is tossed rapidly back to the rump and held there while a rattling *rrrrt* is uttered. Two kinds of head-throws, which differ in the rapidity of performance, are associated with kicks. The Fast Head-throw-kick (Lind's Kick-throw I) lasts about one second, and is the more frequent of the two (Figs. 84*E*, *F*; 85*A*). The head is thrown back rapidly, both feet are kicked,

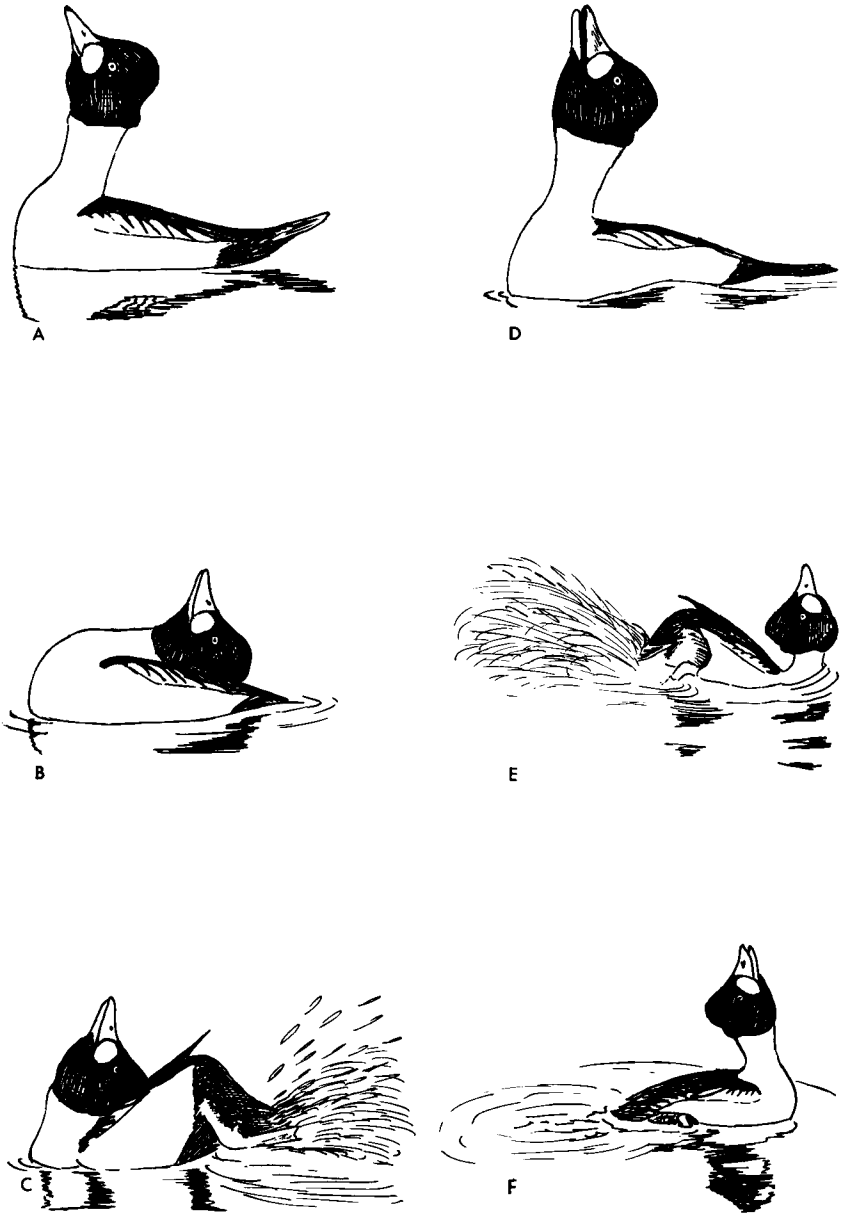


Figure 84. Common Goldeneye

A–D. Stages in the performance of the Slow Head-throw-kick of the male common goldeneye.

E, F. Stages in the performance of the Fast Head-throw-kick of the male common goldeneye.

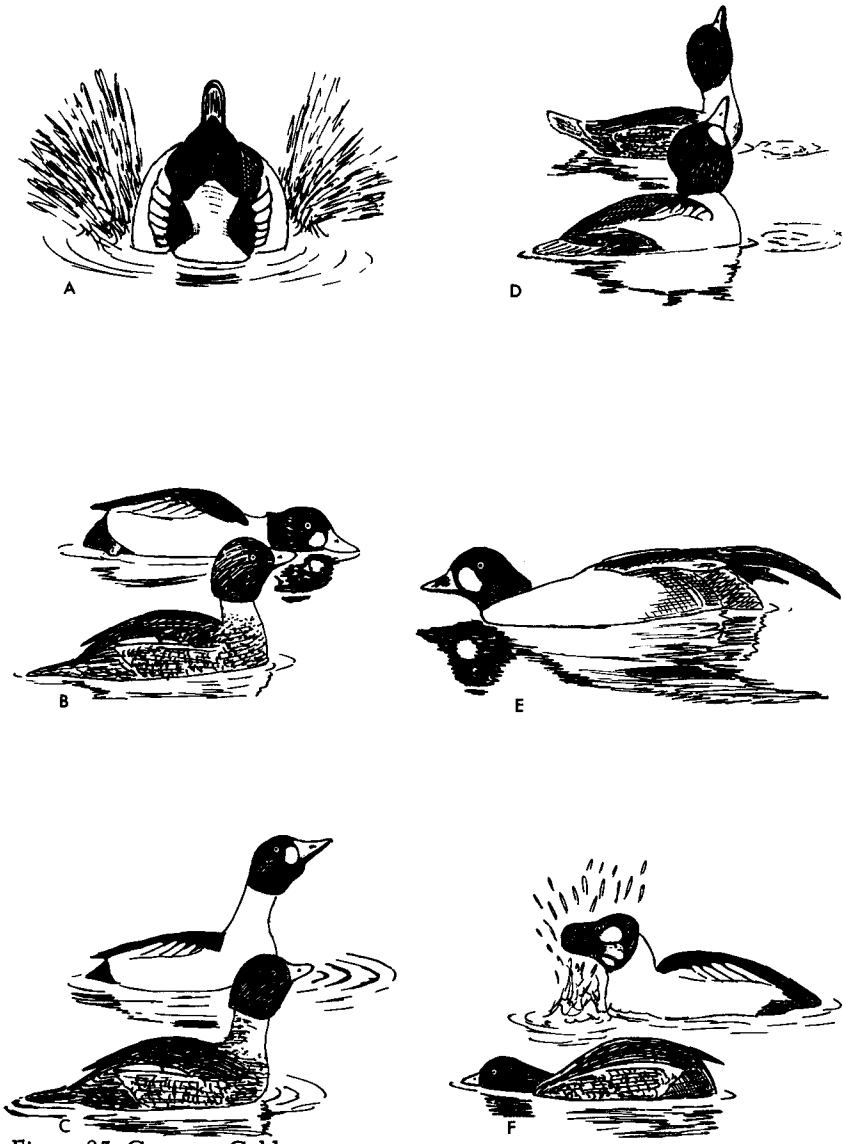


Figure 85. Common Goldeneye

A. Front view of the Fast Head-throw-kick display of the common goldeneye.

B, C. Stages in the performance of the Bowsprit display of male common goldeneye. The female is performing Head-pumping.

D–F. Precopulatory behavior.

D. Mutual display Drinking.

E. Wing-and-leg-stretching.

F. Jabbing by male, female Prone.

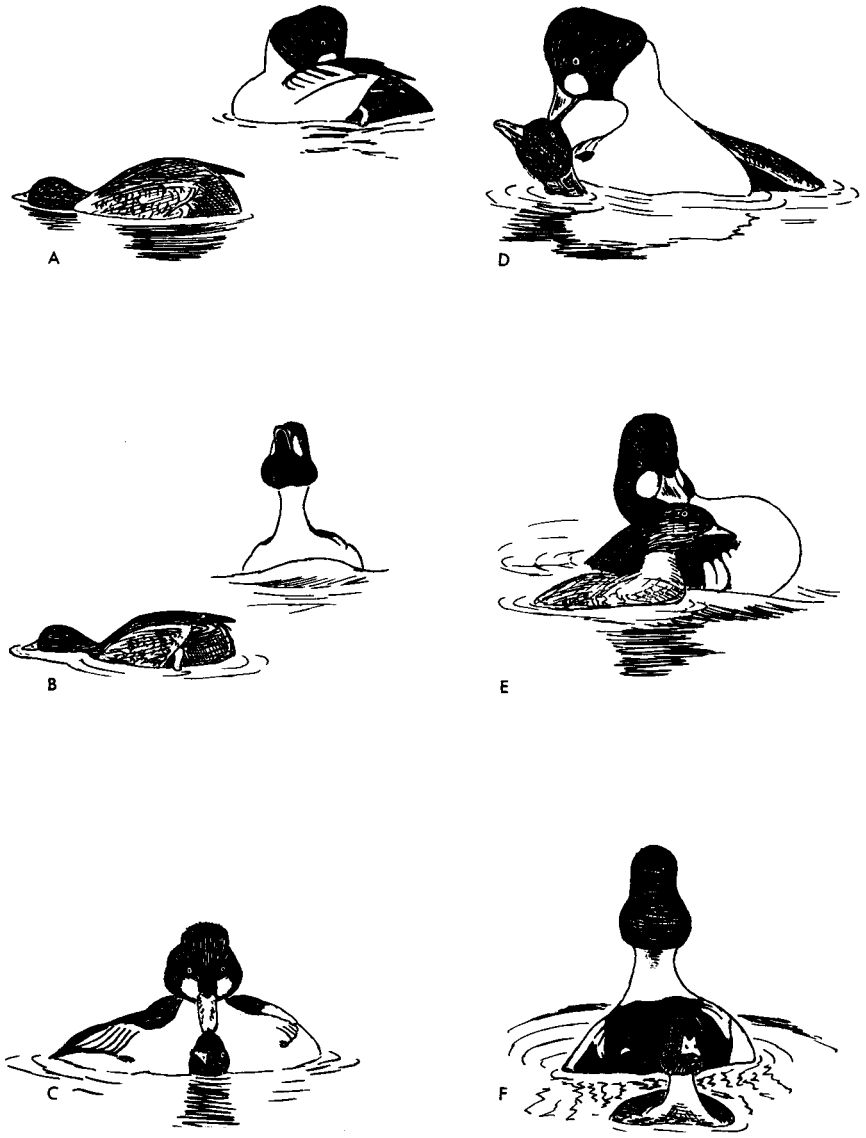


Figure 86. Common Goldeneye
A–F. Copulatory behavior.
A. Preening-behind-the-wing following Jabbing.
B. Precopulatory Steaming to the female.
C. Copulation.
D, E. Rotations terminating copulation.
F. Postcopulatory Steaming. Note extreme feather erection of the male's head.

and a loud *zeee-zeee'* is uttered. In the Slow Head-throw-kick (Lind's Kick-throw II) the head is thrown back much more slowly after a rapid start which brings the bill to the vertical, the back is strongly arched, and the same type of call is uttered (Fig. 84*A–D*). Finally, the last major display is the Masthead (also called the Crouched-up-down). This display starts in the same manner as the Bowsprit, with the head and neck low over the water. The bird brings his head rapidly to a vertical position and immediately returns it to the starting position, without bending his extended neck (Fig. 83*D–F*). The call is a soft *rrrrt* as in the Bowsprit, and both displays appear to be aggressive. Males also frequently perform Short Flights toward females, and, as in Barrow's goldeneye, the Upward-stretch and Wing-flapping occur frequently but are not obviously ritualized.

Copulatory behavior. Copulatory behavior is initiated by either sex, through ritualized Drinking toward the other bird (Fig. 85*D*). The female then fairly rapidly assumes the Prone posture and remains in it, although she may perform rudimentary Drinking movements in response to male Drinking while in this posture. The male then performs two major precopulatory displays, ritualized Drinking (also called the Water-flip) and the Wing-and-leg-stretch (also called the Wing Display) (Fig. 85*E*). The male also, but less frequently, performs Bathing, Water-twitching, and rolling the cheeks on the shoulders. Water-twitching is at first interspersed with other displays, but eventually, in exaggerated form (Jabbing), it alone is performed (Fig. 85*F*). After a series of rapid Jabs the male suddenly reaches back and Preens-dorsally on the side toward the female (Fig. 86*A*), then rapidly Steams toward her, bill tilted upward, uttering a faint *bzzzzt* call (Fig. 86*B*). He immediately mounts, and while treading always Flicks-the-wing one or more times. After treading is completed, the male retains his hold on the female with his bill and one foot, as the two birds Rotate in circles (Fig. 86*D, E*). The male then releases her and Steams rapidly away while performing lateral Head-turning and emitting low grunts (*uig-uig-uig* . . .). Finally, both birds bathe and flap their wings.

MERGANSERS

Although the mergansers have traditionally been placed in a distinct subfamily on the basis of their bill structure, the fallacy of this division has been repeatedly pointed out by several authors, and is

entirely analogous to the unjustified separation of the shovelerlike ducks from the other species of *Anas*. The goldeneyes grade into the mergansers in the same way as the typical *Anas* species grade into the shovelers, and there is even some evidence that the merganser with the least specialized bill shape (the smew) is not as closely related to *Bucephala* as is one species with a typical *Mergus* bill (the hooded merganser). In no anatomical or behavioral respect do the mergansers deserve more than a generic separation from the goldeneyes.

Hooded Merganser (*Mergus cucullatus*)

The hooded merganser provides an almost perfect link between *Bucephala* and *Mergus*. The downy young are similar to those of goldeneyes except that they have a brownish tone on the upper parts which suffuses the white cheeks. There is no cheek stripe as is typical of most other mergansers. Juvenile males and females generally resemble female goldeneyes except for their different head and bill shape. As in the goldeneyes and the other mergansers, the wings have a black and white speculum pattern on the secondaries. The male in nuptial plumage has a unique erectable white crest and vermiculated brown flanks, but is otherwise not very different in patterning from male goldeneyes. There is an eclipse plumage which is very female-like. The tracheal tube of the male is slightly enlarged near the posterior end, and the bulla is relatively larger, with membranaceous fenestrae, and very similar in shape to those of goldeneyes (see the illustration in Johnsgard, 1961c). The species is restricted to North America, and is sympatric with the three species of *Bucephala* and with the red-breasted merganser and the goosander. Wild hybrids have been reported with the common goldeneye.

General behavior. The hooded merganser is primarily a freshwater bird, and tends especially to frequent woodland ponds and swamps. Although it has a typical merganser-type bill, it consumes fairly large quantities of animal material other than fish. Preflight movements have not been noted.

Agonistic and sexual behavior: female. The female hooded merganser does not take a very active part in sexual display, and seems to lack special calls or movements for eliciting male displays. The only definite sexual display I have observed is a form of Inciting. This differs from the lateral pointing type of goldeneye Inciting, and

is more like the "Bobbing" of female smews. It consists of a rapid lateral pointing movement toward another female or unfavored male, immediately followed by a jerky upward and forward movement of the head, with crest depressed, at the same time as a hoarse *gak* is uttered (Fig. 87*A*). Except for the preliminary lateral pointing movement (which is sometimes lacking), it is almost exactly like the Bobbing type of smew Inciting. Ritualized Drinking is primarily a precopulatory display in the female. Females also perform a Pumping movement exactly like that of the male.

Agonistic and sexual display: male. Male hooded mergansers have numerous displays, which are described more fully elsewhere (Johnsgard, 1961d). The major displays include a Crest-raising (Fig. 87*C*), which is very frequent. After raising the crest, the male performs several Head-shaking movements (Fig. 87*D*), raising the front of the body slightly each time, and after three or four such movements a Head-throw usually follows (Fig. 87*E*). This display, performed without such extreme neck-stretching as the Head-throws of the common goldeneye, is accompanied by a rolling, froglike *crrrroooo* note as the head is brought forward. As the head is returned to its normal position, the male Turns-the-back-of-the-head toward the courted female. Sometimes, after several Head-shakes, the male simply opens his bill and utters a hollow *pop*. At other times he performs a silent Pumping movement (Fig. 87*B*). A diagonal Tail-cocking is also frequent, and is usually associated with swimming ahead of the female and Turning-the-back-of-the-head with crest depressed (Fig. 87*A*). The ornamental tertials are also sometimes repeatedly lifted and lowered, although this may not constitute a true display. The Upward-stretch and Wing-flapping are also commonly performed during courtship, usually with the crest erected.

Copulatory behavior. In its copulatory behavior the hooded merganser exhibits clear affinities with the goldeneye group. Copulation is initiated by mutual Drinking (Fig. 87*F*), and soon the female assumes a Prone posture with her head and tail both near the water surface. The male immediately begins to swim about with his crest erect, performing rather jerky head movements that are similar to the "Pouting" movements of male smews. The male performs the Upward-stretch and also Drinks, but I have not seen the Wing-and-leg-stretch (typical of goldeneyes) or independent Preening-dorsally (typical of the other mergansers). The male soon replaces the ritual-

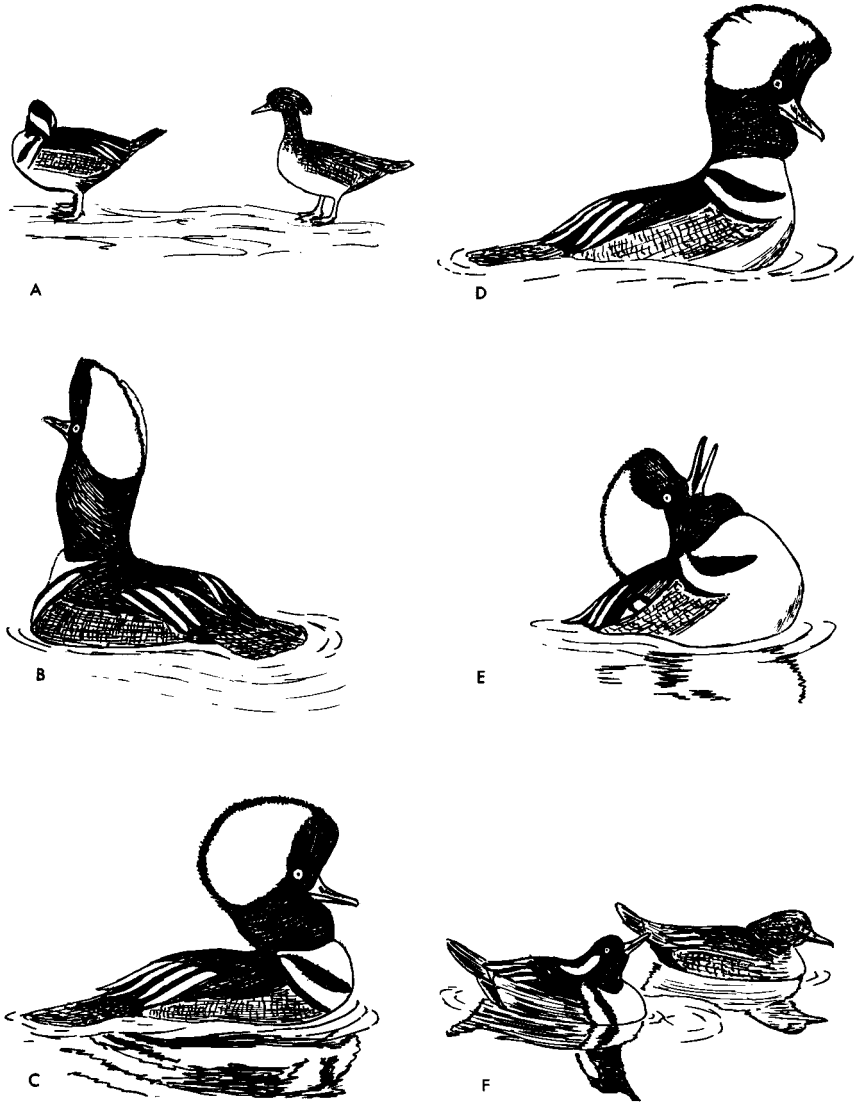


Figure 87. Hooded Merganser

A. Male Turning-the-back-of-the-head to female, who is performing low-intensity Inciting movements.

B. Pumping posture of male hooded merganser. Note how the neck appears to be swollen.

C. Crest-raising.

D. Head-shaking preceding the Head-throw.

E. Head-throw.

F. Precopulatory Drinking display.

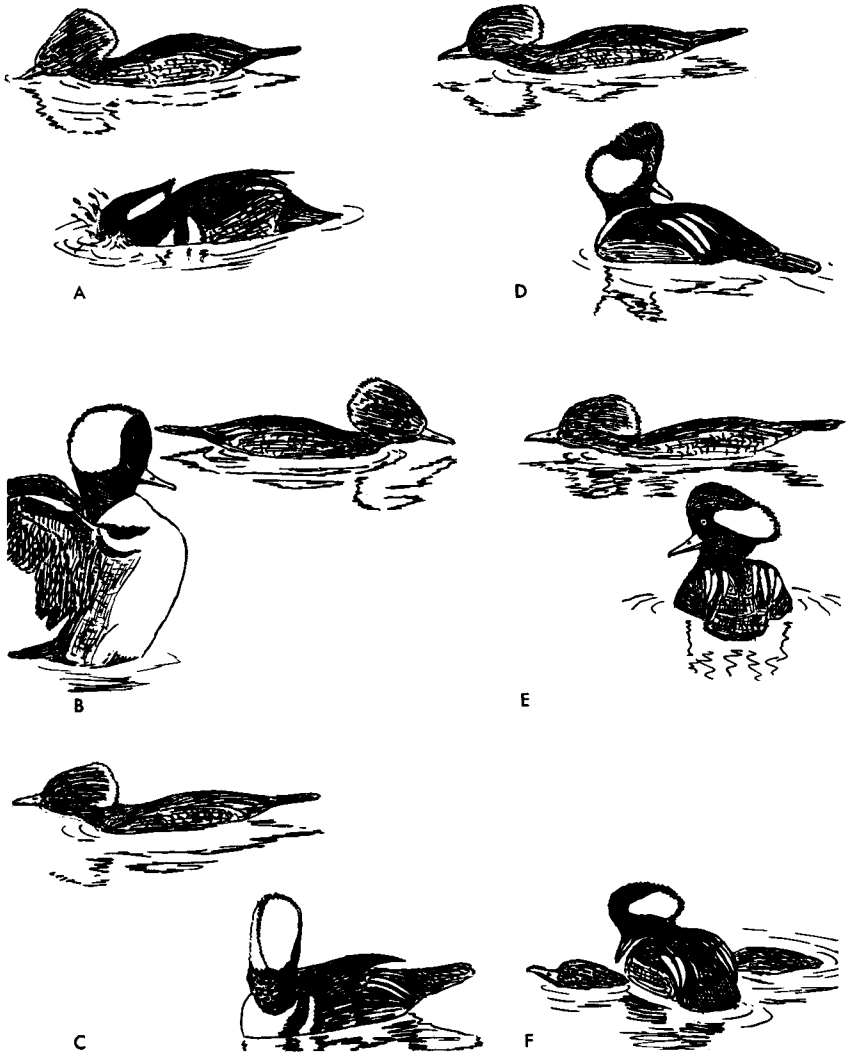


Figure 88. Hooded Merganser

A–F. Copulatory Behavior.

A. Precopulatory Water-twitching (or Jabbing) by male, female in Prone posture. Compare with Fig. 85*F*.

B. Wing-flapping. Note fully expanded crest and lateral orientation to female.

C. Preening-behind-the-wing (or behind the slightly raised wing). Compare Fig. 86*C*.

D, E. Tacking toward the female. Note turning of alternate sides of crest to female's view.

F. Mounting.

ized Drinking with energetic Water-twitching (or Jabbing) movements (Fig. 88*A*), such as are performed by goldeneyes. After several such Jabs, the male stops, performs an Upward-stretch or a Wing-flap (Fig. 88*B*), then settles back in the water and makes a rapid Preening movement (probably dorsally or behind the slightly raised wing) on the side toward the female (Fig. 88*C*). Precopulatory Steaming in this species differs from that of the goldeneyes in that the male approaches the female in a "Tacking" route (Fig. 88*D, E*), still performing the head-jerking movements and alternately presenting the two sides of his crest to her view. The male mounts the female as soon as he reaches her; then he raises his crest fully and Flicks-the-wing while treading. After treading he retains hold of the female's nape and the two birds Rotate nearly a complete circle. The male then releases the female and Steams away from her in a Crest-raised posture. In one of the two cases seen, the male Steamed away for about 25 feet before beginning to bathe, and in the other case he Plunged under the surface after swimming about five feet. The post-copulatory Steaming was like that of goldeneyes except that no lateral Head-turning could be definitely seen, although the distances from the birds were considerable.

Smew (*Mergus albellus*)

The smew is certainly, with the hooded merganser, a link between *Bucephala* and *Mergus,* and the pattern of the downy young is clearly more like that of *Bucephala* than like that of the typical *Mergus* downies. Juvenile males and females are distinct both from the other mergansers and from the goldeneyes, although an extension of the brown head over the white cheeks and throat would produce a very goldeneye-like effect. The male nuptial plumage, which is mostly black and white, is also *Bucephala*-like. The male eclipse plumage is like the female plumage. The tracheal tube of the male is of only slightly varying diameter, and the bulla is more similar in shape to that of the goosander and red-breasted merganser than to that of the hooded merganser and the goldeneyes. Smews range widely over Europe and Asia, and are sympatric with the common goldeneye, the goosander, the red-breasted merganser, and the Chinese merganser. Hybrids with the common goldeneye have been reported.

General behavior. Smews feed on fish to a relatively small degree; they tend, rather, to consume aquatic insects and larvae, as do golden-

eyes. This no doubt explains why the two species often associate in the wild. Like the goldeneyes and most of the other mergansers, smews are tree-nesters.

Agonistic and sexual behavior: female. The female smew takes an active part in courtship, and smew display is a very energetic affair. The female Inciting call is a harsh, rattling *krrrrr, krrrrrr,* emitted at low intensities without special head movements, but this is usually followed by a louder version, associated with violent upward and forward body lunges, the bill being pointed sharply downward with each movement forward (Fig. 89*A, B*). Hollom (1937) termed this display, which is clearly a form of Inciting, Bobbing, but this does not express well the energetic nature of the movements. There is little if any lateral pointing involved in this display, and it is certainly a very highly ritualized type of Inciting.

Agonistic and sexual behavior: male. The descriptions of Hollom (1937) and Lebret (1958b) are fairly complete, and Hollom's terminology is followed here. The most frequent male display, except perhaps for the Upward-stretch or Wing-flapping, is "Pouting." This is a smooth Bridling-like movement of the head back along the back, with the bill remaining level (Fig. 87*F*). This may be performed while the bird is standing on land, but more often it is done while he is swimming. The associated call is a soft mechanical rattle which Lebret described as the noise made by the winding of a wristwatch. During Pouting the feathers of the forehead are erected to form a shaggy crest, but the black V-pattern of the nape is never erected in any way. During display the males often assume a Neck-stretching posture, which is accompanied by the same rattling call as during Pouting (Fig. 89*C*). The most elaborate male display is the Head-fling (Fig. 90*A, B*). This occurs unexpectedly during Pouting, and perhaps is an exaggerated version of it, except that the head is suddenly flung back over the back, raising the body axis about 45 degrees. The head does not touch the back, but stops short of it, and is just as rapidly brought back in a manner very much like the Bobbing movement of females, with the bill pointed sharply downward, so that the black V-pattern of the nape is visible to a person in front of the displaying bird. There is no obvious kick associated with this display, although Lebret (1958b) reported seeing water splashed up behind. The call is like that uttered during Pouting, but somewhat louder. Males Turn-the-back-of-the-head to females very often, especially

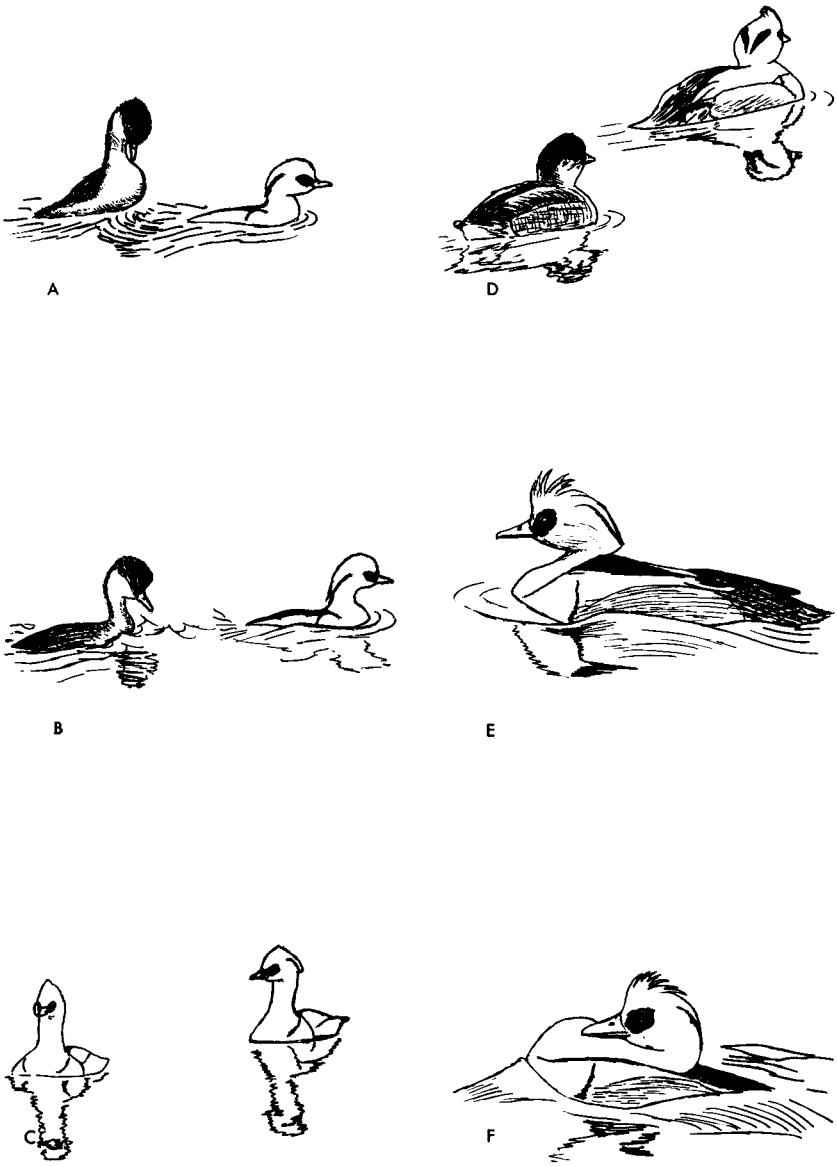


Figure 89. Smew

A, B. Inciting (Bobbing) by female smew, as the male Turns-the-back-of-the-head.

C. Neck-stretching in male smews.

D. Turning-the-back-of-the-head by male smew.

E. Crest-raising by male smew.

F. Pouting by male smew; alternated with posture in *E.*

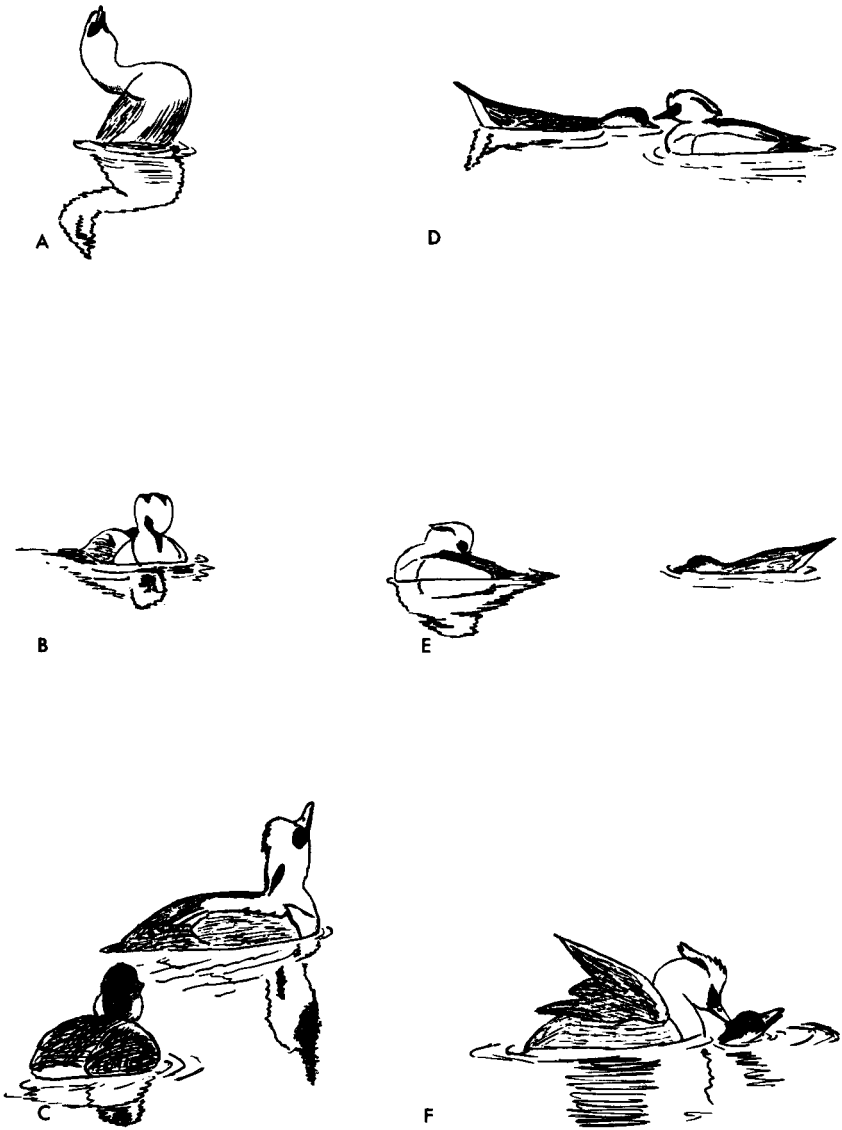


Figure 90. Smew

A, B. Stages in the Head-fling display of male smew. Note asymmetrical position of the head.

C–F. Copulatory behavior.

C. Precopulatory Drinking by male smew.

D. Prone posture of female. Note tilted tail, which is shaken frequently.

E. Preening-dorsally by male.

F. Flick-of-the-wing during treading.

when they are being followed by an Inciting (Bobbing) female. Ritualized Drinking is sometimes seen during courtship, but probably should be considered as an invitation to copulation. Mr. Vincent Weir (pers. comm.) has observed males attack one another under water, but this is not done so frequently as by goldeneyes.

Copulatory behavior. Both sexes typically perform ritualized Drinking (Fig. 90*C*) before the female goes Prone, or the female may assume the Prone posture after Bobbing a few times toward the preferred male. The Prone posture in this species differs from that of other mergansers in that the head is held near the water and the tail is held up at about a 30-degree angle and quivered frequently (Fig. 90*D*). The male makes repeated Drinking movements, together with Upward-stretches, Preening-dorsally (Fig. 90*E*) and, possibly, Preening-behind-the-wing. He repeatedly approaches and retreats from the female, who often suddenly erects herself, Bobs a few times, then goes Prone again. I have not observed any Water-twitching, and the single instance of Preening-behind-the-wing observed appeared to be normal preening. When the male finally succeeds in mounting the female he Flicks-the-wings from two to five times (Fig. 90*F*). After treading is completed the male releases the female immediately and performs a Head-fling; then he swims rapidly away from the female while Turning-the-back-of-the-head toward her. Whether this postcopulatory swim should be considered Steaming is doubtful, for it lacks the stereotyped appearance of such Steaming in the goldeneyes, eiders, and the hooded merganser. The female either bathes or follows closely behind the male, Bobbing in the usual fashion.

Brazilian Merganser (*Mergus octosetaceus*)

The Brazilian merganser apparently does not represent an isolated derivative of one of the northern mergansers, but rather must have had an earlier origin and has developed several unusual features. The downy young have the incomplete breast band and streaked cheeks found in the large, northern mergansers, but they lack the brownish head coloration typical of all merganser downies except those of the smew. As adults, the sexes are colored alike, and both have metallic-green heads with long, narrow crests. The rest of the body is rather uniformly gray and brown, and the wings have the usual type of white speculum on the secondaries. The male

trachea has been described by Humphrey (1955) as being very similar to that of the red-breasted merganser, and also as having some affinities with that of the hooded merganser. The species is restricted to southeastern South America and is not sympatric with any near relatives.

General behavior. According to Partridge (1956) this species is rare and very shy, and is a river and stream dweller. Partridge has given a good account of feeding and nesting behavior. Like the goosander, this species is a tree-hole nester.

Agonistic and sexual behavior: male and female. Partridge (1956) has observed what he believes was courtship display. His observations, and those of Giai (1950), suggest that circular swimming, while paddling with the wings, is one of the courtship displays. This behavior is altogether unlike the displays of any of the other mergansers known to me, and it is probable that other displays are present which are still undescribed.

Copulatory behavior. Partridge (1956) observed one copulation. The female assumed the Prone posture after bathing. She was Prone for only a few seconds before the male mounted, and both birds were then totally submerged. After treading, the female "uttered a long cry," and both birds then bathed. This is also quite different from copulatory behavior in the other species of mergansers which have been studied.

Red-breasted Merganser (*Mergus serrator*)

The red-breasted merganser is probably a close relative of the Chinese merganser. Red-breasted downy young are somewhat darker than Chinese downies; the downy young of the two species are otherwise almost identical. Red-breasted juveniles and adult females have a darker and less contrasting body plumage than do those of the Chinese species, but males of both species are similar in head pattern and wing-speculum patterns. Red-breasted males are unique in their reddish-brown breast and their shoulder patterns. The trachea of the male has one gradual enlargement and a very large bulla that is approximately equally inflated on the left and right sides (see illustration in Johnsgard, 1961c). The red-breasted merganser is widely distributed throughout the Northern Hemisphere, and is sympatric with all the northern species of *Mergus* as well as *Bucephala.* No definite hybrids are known, but mixed pairs of red-breasted mergansers and

goosanders have frequently occurred at the Wildfowl Trust, and some young have hatched and lived several weeks which were thought to represent this cross.

General behavior. In its distribution and ecology the red-breasted merganser is similar to the goosander, but whereas the goosander is a hole-nester, the red-breasted merganser usually nests on the ground and has dark-colored down. Preflight movements consist of swimming with neck outstretched and bill tilted slightly upward, with frequent lateral Head-shaking.

Agonistic and sexual behavior: female. Females tend to be rather aggressive toward males, and they do not take a very active part in courtship displays. Curth (1954) and Ringleben (1951) have mentioned head-nodding displays, but I have not observed any such movements. The female has a harsh *krrrr-krrrr* call, which can be uttered without special head movements, and the same call is emitted during a type of Inciting similar to the Bobbing movement of female smews. From a normal swimming position the female suddenly lurches forward and upward with her head, but with the bill pointed downward. This may be repeated once or twice; but unlike the smew's Bobbing, it is apparently never continued in a longer sequence. I have only observed this Inciting a few times, but it is probably not so rare as these few observations suggest. No obvious sideways pointing movements were seen, although such movements may possibly be a typical part of the display, as it is often lacking in the Inciting of female hooded mergansers.

Agonistic and sexual behavior: male. Male threat display consists of a Crouched posture, somewhat like that of goldeneyes. I have observed one underwater attack, and Armstrong (1947) also reports such behavior. Males often rush over the water surface in a closed-wing "Sprint" (Fig. 92*E*) that sometimes serves as an overt attack, but more often brings the male close to the female or simply attracts the female's attention. Besides the Sprint, the major male sexual display is an extremely complex and variable sequence collectively termed the "Knicks" (German for "bending"). This consists basically of two postures, the Salute and the following Curtsy. The simplest form of this occurs in early winter, when from a normal swimming position the male suddenly jerks his head out diagonally, so that the bill, head, and neck form a straight line (the Salute) and a second jerk pulls the neck slightly downward as a soft and catlike

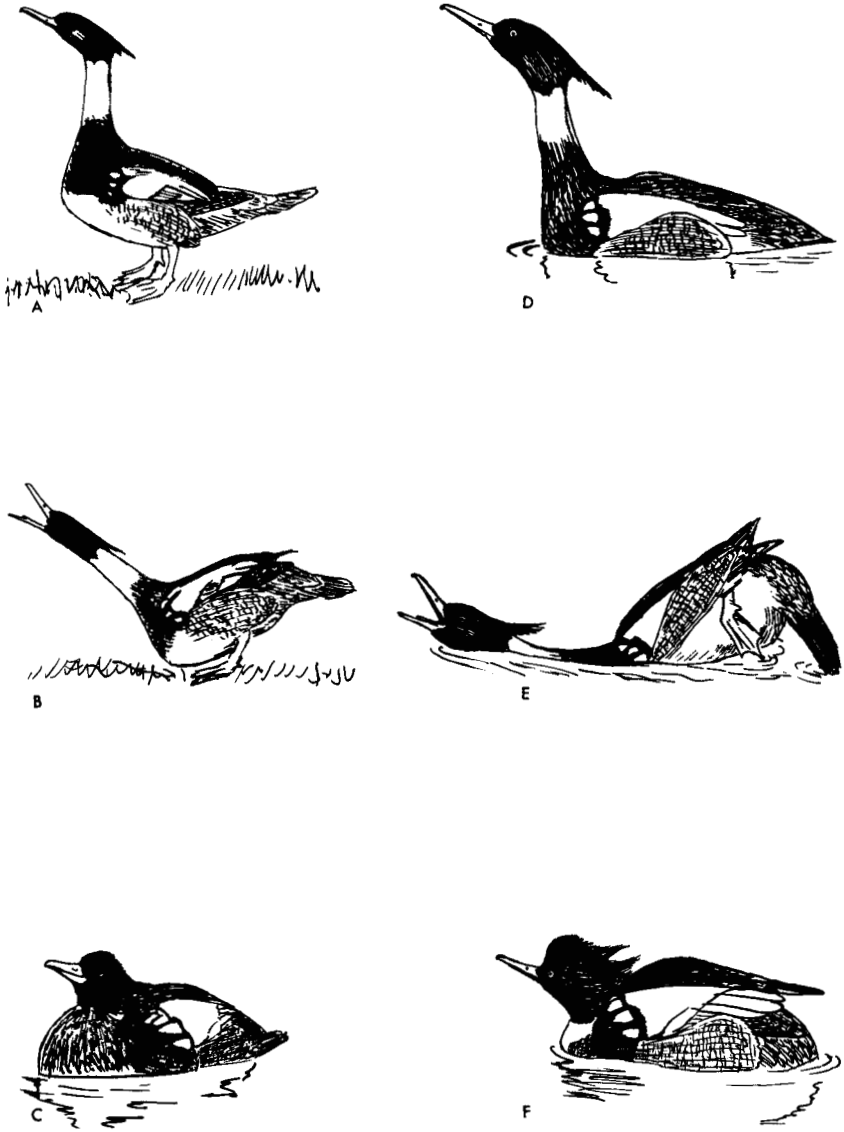


Figure 91. Red-breasted Merganser

A, B. Male performing Salute (*A*) followed by Curtsy (*B*) on land.

C–F. Knicks sequence, side view.

C. Starting posture. Note lowered crest.

D. Salute posture.

E. Curtsy.

F. Finishing position, with neck withdrawn, tail bent down, and crest raised.

yeow is uttered (Fig. 91*A*, *B*). Later, when the males begin to swim in a characteristic "ready" posture, the complete display may be seen. In this posture (Figs. 91*C*, 92*A*) the head is withdrawn into the shoulders, the crest is erected, and the bill is tilted slightly upward. As the display begins, the crest is suddenly depressed, and within about a second the neck is suddenly extended diagonally upward and forward. The head is momentarily "left behind," but it quickly swings up into line with the neck to form the Salute, which is generally performed at "profile view" to a female (Figs. 91*D*, 92*B*). This phase, marked by a *yeow* call, is held for an instant, then the neck, as if weighted at the base, is brought down into the water, and simultaneously the tail is pointed downward. As the head is brought down into the Curtsy phase the crest is raised, the bill is opened and pointed toward the courted female (or another male), and the second of two faint *yeow* notes is uttered (Figs. 91*E*, 92*C*). The display can end in a partially extended neck posture (Fig. 92*D*), or the head may be strongly withdrawn into the shoulders while the tail is still pointed downward and the feet back-paddle slightly (Fig. 91*F*). Very often males Turn-the-back-of-the-head to the courted female as a finale to this display sequence. This display is one of the most bizarre of all waterfowl displays and is completely different from the sexual displays of the other *Mergus* species studied to date. Males often perform the display in synchrony or near-synchrony. Males swim ahead of Inciting females, probably Turning-the-back-of-the-head to them, although this is not certain. Males also sometimes swim with their tails slightly cocked, which possibly represents a display, and the Upward-stretch and Wing-flapping are frequent during courtship and are very likely ritualized.

Copulatory behavior. Copulatory behavior has been only inadequately observed, but the general form of display is evident. As in the other mergansers, both sexes perform ritualized Drinking, and the female soon assumes a Prone posture like that of the goosander, with both the head and tail flat on the water. The male then repeatedly Drinks, Preens-dorsally, Wing-flaps, and does the Upward-stretch, though in no particular sequence. In addition, the male frequently does a rudimentary form of the Knicks, and apparently always mounts the female immediately after the Knicks, approaching her in a manner similar to the Tacking of the hooded merganser. It is not known whether there is a Flick-of-the-wings during treading,

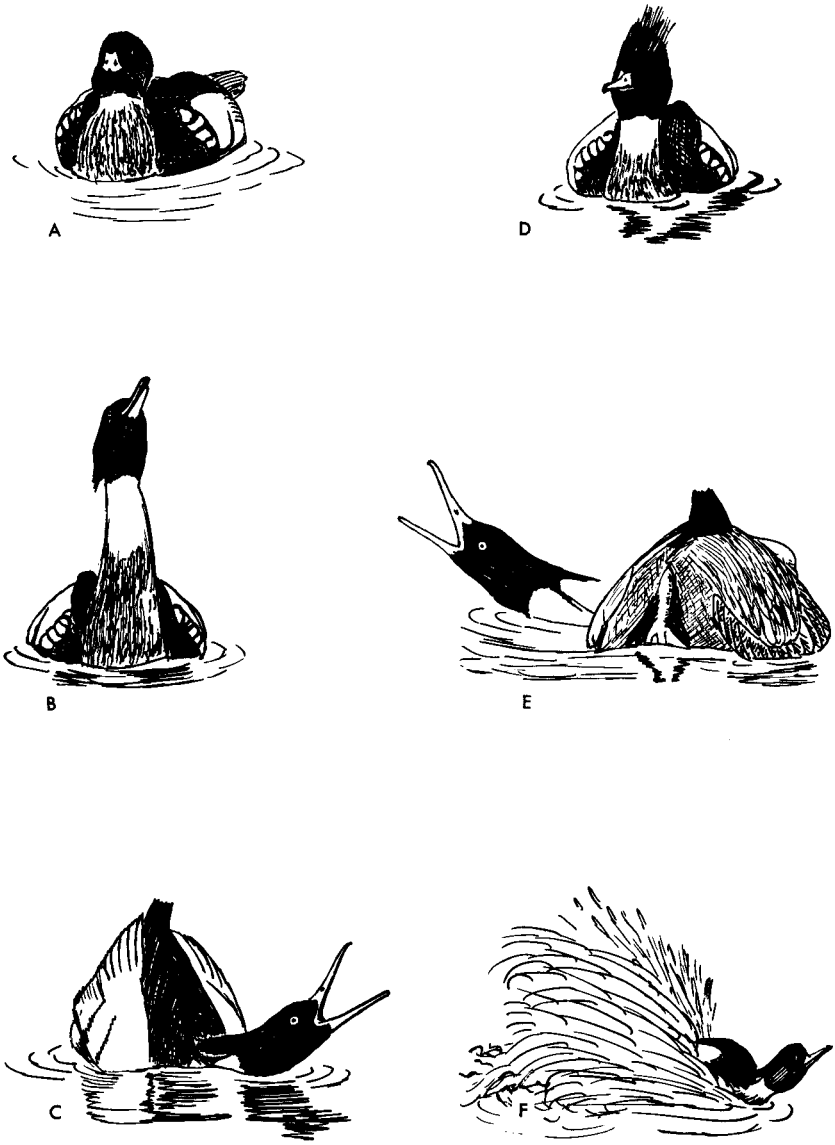


Figure 92. Red-breasted Merganser
A–D. Knicks sequence, front view.
A. Starting posture.
B. Salute.
C. Curtsy.
D. Finishing position.
E. Curtsy, rear view. Note raised hindquarters, bent tail.
F. Sprint, male red-breasted merganser.

or whether postcopulatory Rotations are present. After treading, however, the male evidently performs a variation of the Knicks, then bathes or Sprints some distance over the water and finally Plunges under the surface (Adams, 1947).

Chinese Merganser (*Mergus squamatus*)

Very little is known of the Chinese merganser, but it appears to occupy a position roughly between the goosander and the red-breasted merganser. The downy young seem to be somewhat more like those of the red-breasted merganser, but juveniles and adult females have plumages closely resembling the corresponding plumages of the goosander. The male in nuptial plumage has a crested head much like that of the red-breasted merganser, but the body plumage is rather more similar to that of the goosander. The wing coverts are gray rather than white as in these two species, although the speculum pattern is almost the same in all three. The male has a female-like eclipse plumage, and the male trachea is very similar to that of the goosander (Humphrey, 1955). The species has a restricted range in China and is no doubt sympatric with both the red-breasted merganser and the goosander. No hybrids have been reported.

General and sexual behavior. Aside from the fact that it is a hole-nester like the goosander, virtually nothing is known of the behavior of the Chinese merganser. In view of the great differences in the sexual behavior of the goosander and the red-breasted merganser, it would be of special interest to obtain information on the courtship and copulatory behavior of this species.

Goosander (*Mergus merganser*)

The goosander is the largest and perhaps the most specialized of the mergansers. The downy young are very similar to those of the two preceding species, having incomplete breast bands, streaked cheeks, and brownish heads. Juvenile males and females are very similar to those of the Chinese merganser. Males in nuptial plumage have an entirely green head and a predominantly white body. The breast and flanks of breeding males have a salmon-tinted "bloom" such as occurs in the Chinese merganser. There is a female-like eclipse plumage. The male trachea has a major anterior enlargement followed by a smaller one, and the bulla is extremely large and rather triangular in shape, with large membranceous fenestrae (illustrated

in Johnsgard, 1961c). The goosander is widespread over the Northern Hemisphere and is sympatric with all the Northern Hemisphere species of *Bucephala* and *Mergus*. Hybrids have been reported with the common goldeneye and hybridization with the hooded merganser has also been alleged. Three races are currently recognized.

General behavior. The goosander is found on both salt and fresh water, and frequents large deep-water areas. Unlike the red-breasted merganser, the goosander tends to nest in holes or crevices, and its down is white. Preflight movements are lateral Head-shakes, performed in an alert posture with head feathers depressed and neck extended.

Agonistic and sexual behavior: female. Females are highly aggressive toward courting males, and often jab at them with their bills. Their call is a loud, harsh *karrr, karrr,* which serves as a warning note as well as for Inciting. Inciting in this species is not highly ritualized, and consists of a quick sideways pointing movement toward an unfavored bird followed immediately by a spurt forward and upward as the call is uttered, but without a marked down-tilting of the bill. This is not usually repeated more than once or twice and, as is also true of the other mergansers, preferred males always respond to it by swimming rapidly ahead of the Inciting bird, usually Turning-the-back-of-the-head toward her (Fig. 93*B*).

Agonistic and sexual behavior: male. Courtship among male goosanders is marked by a great deal of activity and frequent overt attacks, which usually occur above water as the males race toward one another. Such surface chasing is apparently not equivalent to the Sprinting of red-breasted mergansers, although it is similar in form. Underwater attacks apparently occur (Peter Scott, pers. comm.), but I have not observed them. The most frequent male display involves extending the neck, erecting the head feathers, and repeatedly uttering a rather faint *uig-a* note reminiscent of the twanging of a guitar string (Fig. 93*A*). The throat enlarges slightly with each call. The only elaborate display I have seen is the Salute, which is probably, but not definitely, homologous to the Salute of the red-breasted merganser. From either a normal resting posture or the courtship call position the head is suddenly lifted vertically upward until the neck is stretched to the utmost. The posture is held for a fraction of a second with the bill pointed toward the zenith as a faint, high-pitched, bell-like note is uttered (Fig. 93C); then the head is

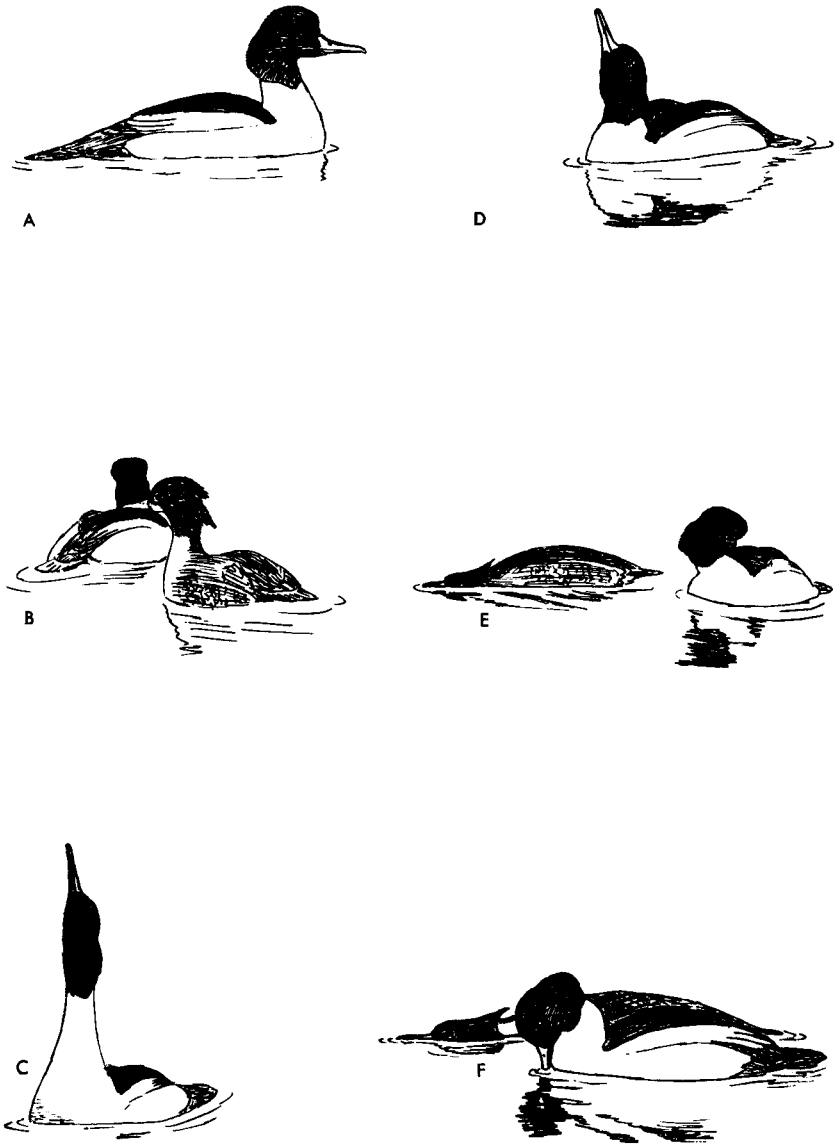


Figure 93. Goosander

A. Courtship call of male. Note bulge in throat.

B. Turning-the-back-of-the-head by male to female. Note shape of male's head formed by feather erection.

C. Salute posture of male. Compare with display Drinking below.

D. Precopulatory Drinking.

E. Male Preening-dorsally, female in Prone posture.

F. Male Water-twitching.

rapidly returned to the starting position. The display is reminiscent of the common goldeneye's Masthead display and, like it, is probably rather aggressive in motivation. Males Turn-the-back-of-the-head to females, especially Inciting females, and also perform a diagonal Tail-cocking. The Upward-stretch and Wing-flapping occur frequently during display and are no doubt ritualized. I have not observed a Kick display in this species, but it has been frequently reported in the literature, and Vincent Weir (pers. comm.) has observed it. He informs me that there is no associated head movement or call, and that the jet of water is thrown back much farther than in the common goldeneye's Head-throw-kick.

Copulatory behavior. Copulatory behavior is initiated by either sex through ritualized Drinking. The pair Drink mutually several times (Fig. 93*D*), and each time the female lifts her bill as she pumps her head forward, outward, and finally downward, with her crest depressed. Soon she assumes a Prone posture, stretched out completely on the water (Fig. 93*E*). If the male does not respond she may become erect, Drink, and again go Prone. At times I have observed a Prone female hunch her head into the shoulders, then back-paddle, in a movement reminiscent of the Neck-dip of common goldeneyes. The male repeatedly Drinks with head feathers depressed, interspersing this with Preening-dorsally (Fig. 93*E*), and sometimes also with Preening-behind-the-wing. He also performs the Upward-stretch frequently, and I have observed Bill-dipping and probable sideways shaking movements of the bill in the water, as in the Water-twitch of the hooded merganser and the goldeneyes (Fig. 93*F*). The male apparently lacks a ritualized approach to the female, and there is no Flick-of-the-wings during copulation. There are also no postcopulatory Rotations, and after releasing the female the male swims rapidly away from her, Turning-the-back-of-the-head toward her and repeatedly uttering his courtship call with erected head feathers. The female immediately bathes.

Auckland Island Merganser (*Mergus australis*)

Practically nothing is known about this species, which is now almost certainly extinct. Unlike the Brazilian merganser, it does seem to represent an island population derived from one of the northern mergansers which has secondarily lost its sexual dimorphism and bright male plumage. The downy young are of the typical *Mergus*

type, juveniles resemble adults, and the sexes of adults do not differ in plumage. The adult plumage pattern is similar to that of the female red-breasted merganser, and the speculum pattern is of the typical *Mergus* type, but there is little white on the upper-wing coverts. Humphrey (1955) has described the male trachea, which is very similar to those of the goosander and the Chinese merganser. The species, if it survives, is restricted to the Auckland Islands and is not sympatric with any near relatives.

TRIBE OXYURINI (STIFF-TAILED DUCKS)

The stiff-tailed ducks constitute a unique section of the Anatidae that is possibly the most isolated of all the tribes with the exception of the Anseranatini. There are eight species which almost certainly belong in the group, plus one more that is only very tentatively included. The tribe is of worldwide occurrence. Seven of the species have long, narrow, and stiffened tail feathers that function as rudders in underwater swimming, at which all species are very adept. These species also have a dense and shiny body plumage much like that of grebes, but lack metallic coloration altogether. The typical species have short, thick necks with loose-fitting skin that can be expanded through the inflation of the esophagus or special air sacs. All species have large feet and their legs are placed well toward the rear, which results in a poor walking ability. All species but the most aberrant one (the white-backed duck) exhibit sexual dimorphism. Vocalizations are extremely variable, and male calls are often produced by extra-tracheal structures. Sexual maturity is probably reached in the first year in all but one of the species (the musk duck), and pairs are probably renewed yearly in most and quite possibly all species. Male displays are generally elaborate and tend to produce sound. Nests are generally built over the water surface and the eggs are generally chalky white and relatively large, the young being very precocial at hatching.

Affinities with other tribes are uncertain. No definite intertribal hybrids are known, although an alleged hybrid of the greater scaup and the North American ruddy duck has been mentioned (Sibley 1938). One species, the black-headed duck, appears to be the least specialized of the group and in its downy plumage, female plumage, and tail structure resembles the dabbling duck group. It also has an unlobed hallux and a bill which rather resembles that of a typical

dabbling duck, and it tips-up a good deal. Thus I consider that the Anatini are the Oxyurini's closest relatives, although the two groups are no doubt well isolated.

Black-headed Duck (*Heteronetta atricapilla*)

The South American black-headed duck has often been included with the species that now constitute the Anatini, but Wetmore (1926) first pointed out its similarities with the stiff-tails. Unlike the downy young of the stiff-tails, however, downy black-headed ducks have a yellow-and-brown-spotted pattern and a dark eye-stripe much like downy dabbling ducks. Juveniles resemble adult females, which have a general similarity to female cinnamon teal. The male has a uniformly black head. Although the body feathers of the male have the characteristic sheen of those of the stiff-tails, they lack the ruddy coloration typical of the stiff-tailed ducks. There is no eclipse plumage. The tracheal structure indicates probable affinities with the stiff-tails, since there is a large throat sac which in the region of the lower jaw is projected forward into two sacs that connect with the mouth, and it is no doubt inflatable. The trachea is of simple structure, lacking a large bulla, and there is an enlargement near the middle of the tube (Wetmore, 1926). The anterior end of the esophagus is enlarged and is possibly also inflatable. The species is sympatric with two species of *Oxyura,* but no hybrids are known. Woolfenden (1961) has concluded that the black-headed duck is the least specialized of the stiff-tailed ducks and a possible evolutionary link with the dabbling ducks.

General behavior. Black-headed ducks are common birds in their restricted range, and they mingle both with dabbling ducks and with stiff-tails. Although they often feed by up-ending, they can dive very well. Apparently they have the unique characteristic of being obligate nest-parasites, since no nests have ever been found which could be positively identified as belonging to black-headed ducks. Females lay their eggs, which are large, roundish, and rough-textured, in other birds' nests, with little regard for the species they are parasitizing.

Agonistic and sexual behavior: female. I have not observed females of this species, and the only account of their behavior comes from Wetmore (1926), who states that they behaved "like other ducks" during courtship display, swimming about with the head

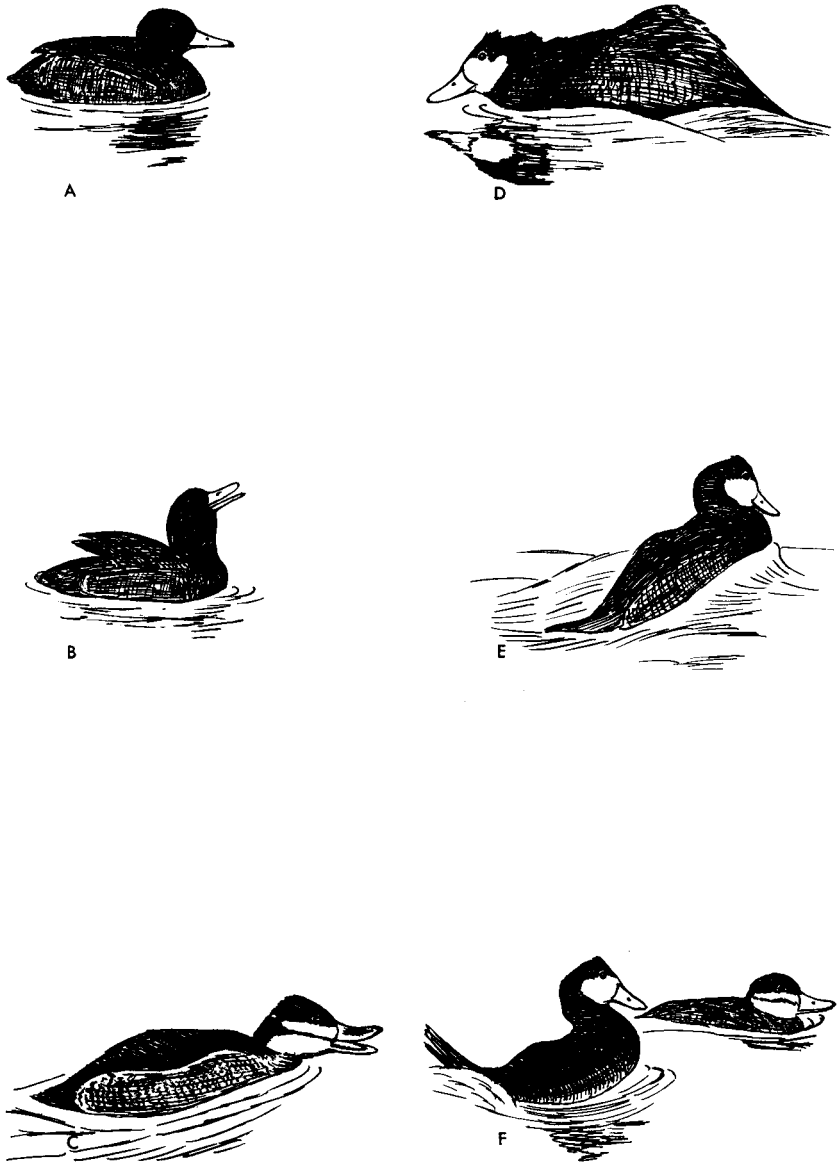


Figure 94. Black-headed Duck, North American Ruddy Duck

A. Black-headed duck male, normal swimming posture.

B. Black-headed duck male, performing Gulping display. Note partly raised wings, expanded throat.

C. Female ruddy duck performing aggressive gaping.

D. Aggressive Hunched Rush by male ruddy duck.

E, F. Stages in the Rush to the female.

erect. It would be of interest to learn if an Inciting display is present, as it is apparently lacking in at least some of the typical stiff-tails.

Agonistic and sexual display: male. A single male (Fig. 94*A*) has been in the Wildfowl Trust collection for some years and has been observed to display on a few occasions. When this bird is preparing to display, he expands his neck considerably and then swims near the courted bird and Turns-the-back-of-the-head toward her, in exactly the manner of a dabbling duck. In the same situation a typical stiff-tail would direct his tail, rather than the back of his head, toward the courted bird. There is no preliminary shake equivalent to the Introductory Shake of dabbling ducks; rather, the major display is preceded immediately by a single lateral head-shake. The bird then cocks his stubby tail vertically, lifts his folded wings a few inches (as a male ruddy duck does during the latter part of his Bubbling display), and suddenly performs about three rapid "Gulping" movements with his bill and head as if he were attempting to catch and then swallow flying insects (Fig. 94*B*). Finally the tail is lowered and shaken to terminate the display. The associated call is weak and hard to hear, but seems to be a three-note *pic-pic-pic,* with the first note loudest, the last weakest, and each associated with a "Gulping" movement. I have never heard any other calls, although Wetmore (1926) states that males puff out their throats and utter low *quah-quah* notes, and members of the Wildfowl Trust staff have mentioned hearing soft whistles and clucking notes. One of the ground staff informed me that he had observed the male "imitating" the head-pumping movements of a Chiloé wigeon (presumably precopulatory Head-pumping), and it would be of great interest if the precopulatory display of the black-headed duck actually is a mutual Head-pumping. It appears, however, that although the black-headed duck shares behavioral characteristics with both the dabbling ducks and the stiff-tails, it is closer to the latter group.

TYPICAL STIFF-TAILS

The following six species, the "blue-billed" or "ruddy" ducks, may be considered the most typical representatives of the stiff-tail tribe. Males of all these species have brilliant cobalt-blue bills and rich ruddy brown body plumages during the breeding season. The head patterns of males are various combinations of black, white, and brown. The tails are long and stiff, and the wings are short. Females

of all species are rather uniform in appearance, being primarily a barred brownish color, with distinct eye and cheek stripes in most species. The downy young are miniature editions of their mothers, with dark crowns and cheek markings. One species, the masked duck, differs from the rest in its less-specialized bill structure and plumage pattern, and in its well-marked white wing-speculum. The other five species seem to fall into two major species groups, a southern, lowland group (the maccoa duck, the blue-billed duck, and the Argentine ruddy duck) and a northern, or montane, group (the white-headed duck and the North American, Colombian, and Peruvian ruddy ducks). In the former group the downy young tend to be more whitish below and on the cheeks, and the males have all-black heads and relatively narrow bills. In the latter group the males tend to have white on the cheeks and throat and somewhat wider bills. A second possible, but not yet definite, difference may be that in the latter group the males have inflatable tracheal air sacs which are used as "sounding boards" during display, whereas at least the Argentine ruddy duck inflates its esophagus and uses jerky neck and head movements to expel the air and produce sound. The blue-billed duck is similar to the Argentine ruddy duck in this respect, but the maccoa duck is less certainly so.

Masked Duck (*Oxyura dominica*)

The masked duck differs from the other species of *Oxyura* in several respects and is apparently somewhat less specialized than they. Woolfenden (1961) supports this view and advocates the generic separation of this species. The downy young have a spotted back and a head pattern approaching that of *Heteronetta,* although there is also the typical *Oxyura* cheek stripe. Juveniles resemble females, which have strongly contrasting eye and cheek stripes as well as a white speculum. Adult males have an interesting plumage pattern with a distinct back and flank spotting which is not found in the other *Oxyura* species. The ruddy body color extends over the back of the head, producing a restricted black "mask," and white is restricted to the chin. As in the females there is a large white speculum formed by the secondaries and their coverts. It is uncertain whether there is an eclipse plumage, although it is unlikely that there is. The trachea of the male lacks a bulla, but the tracheal tube is enlarged anteriorly. Dr. A. Wetmore informs me (pers. comm.) that the male tracheal

tube has an attached air sac similar to that of the ruddy duck; apparently there is a syrinx-produced call-note. Masked ducks are sympatric with two other species of *Oxyura* in Central and South America, but no hybrids are known.

General and sexual behavior. The masked duck has been little studied, and practically nothing can be said of its behavior. The male is said to have a loud, distinct call, described as a *kuri-kirro,* and the female is said to have a lower, hissing voice. Unlike the other species of *Oxyura,* masked ducks can take flight by "leaping" out of the water in the manner of dabbling ducks. Diving, however, is done with the same consummate skill as characterizes the other stiff-tails.

Ruddy Duck (*Oxyura jamaicensis*)

It is reasonably certain that the South American forms *andina* and *ferruginea* should be considered as southern montane populations of the North American ruddy duck which have progressively lost their white cheek markings and have become larger. The downy young are all blackish, with a dusky cheek and an indistinct cheek stripe. Juveniles resemble females, which in the northern race have strong cheek stripes but in the South American and West Indian populations have duskier cheeks. Adult males of the North American population have clear white cheeks and exhibit distinct nuptial and eclipse plumages, whereas the southern populations have cheeks with a varying amount of black (the further south the population, the more black on the cheeks) and lack an eclipse plumage. In at least the North American race the males possess a large tracheal air sac which is inflatable during display. The South American populations very probably also possess such structures. There is no tracheal bulla, and the syrinx is extremely simple in both sexes. The southern populations of this species are sympatric with the masked duck and Argentine ruddy duck, but no definite hybrids are known.

General behavior. Miss Helen Hays has completed a detailed study, as yet unpublished, on the ecology and behavior of the North American ruddy duck, and when published it will no doubt be the standard reference on the species. So far as possible I have followed the terminology of Miss Hays. Ruddy ducks apparently lack preflight movements and, except during migration, rarely take flight at all. Miss Hays (pers. comm.) has observed head-rolling ("cheeking") movements which she believes to be preflight signals. Ruddy ducks do

not walk well on land, and they usually sleep in the water with the bill tucked into the scapulars. North American ruddy ducks make large nests over the water, which are usually ramped. Females often drop their eggs in other birds' nests, and the young are extremely precocial at hatching. I have not studied the South American races, and the following comments refer to the North American ruddy duck.

Agonistic and sexual behavior: female. Female ruddy ducks are highly aggressive toward males and often gape at them with outstretched neck and ruffled scapulars (Fig. 94C). The only vocalization I have heard is a high-pitched, almost rodentlike squeak, which is uttered infrequently when the female is threatening or fleeing from other birds. Females seem entirely to lack any behavior which is functionally related to Inciting; for the most part they apparently ignore the frantically displaying males as they rush about trying to attract attention. Rarely, females (and also the downy young) will perform the same "Bubbling" display as the males, but this is of uncertain significance.

Agonistic and sexual behavior: male. The male displays of ruddy ducks are several and varied. Throughout most of the courtship situation the male keeps his long tail cocked vertically, although usually not spread. This Tail-cocking (Fig. 95*A*) brings into full view the white under-tail coverts, which the male trys to exhibit to the female by swimming directly in front of her in what Miss Hays calls the Tail-flash display. Unlike male dabbling ducks, the male of this species does not try to keep the back of his head toward the female; rather, he keeps his head stationary and maneuvers his whole body as he jockeys for position. The Tail-flash is a purely sexual display and is never directed toward other males. The major sexual display, however, is also used as a threat toward other males. This display, called the Bubbling display, is an elaborate and complex one. The male begins by erecting his "horns," inflating his neck, and cocking his tail (Fig. 95*A*, *D*). He then suddenly begins to beat his bill against his inflated neck, forcing air out from under the feathers and causing bubbles to appear at the surface of the water, and at the same time producing a hollow tapping sound (Fig. 95*B*, *E*). The tapping speeds up toward the end of the display, and at the same time the tail is cocked even farther toward the head and the folded wings are slightly lifted for a moment just before the display terminates with a partial

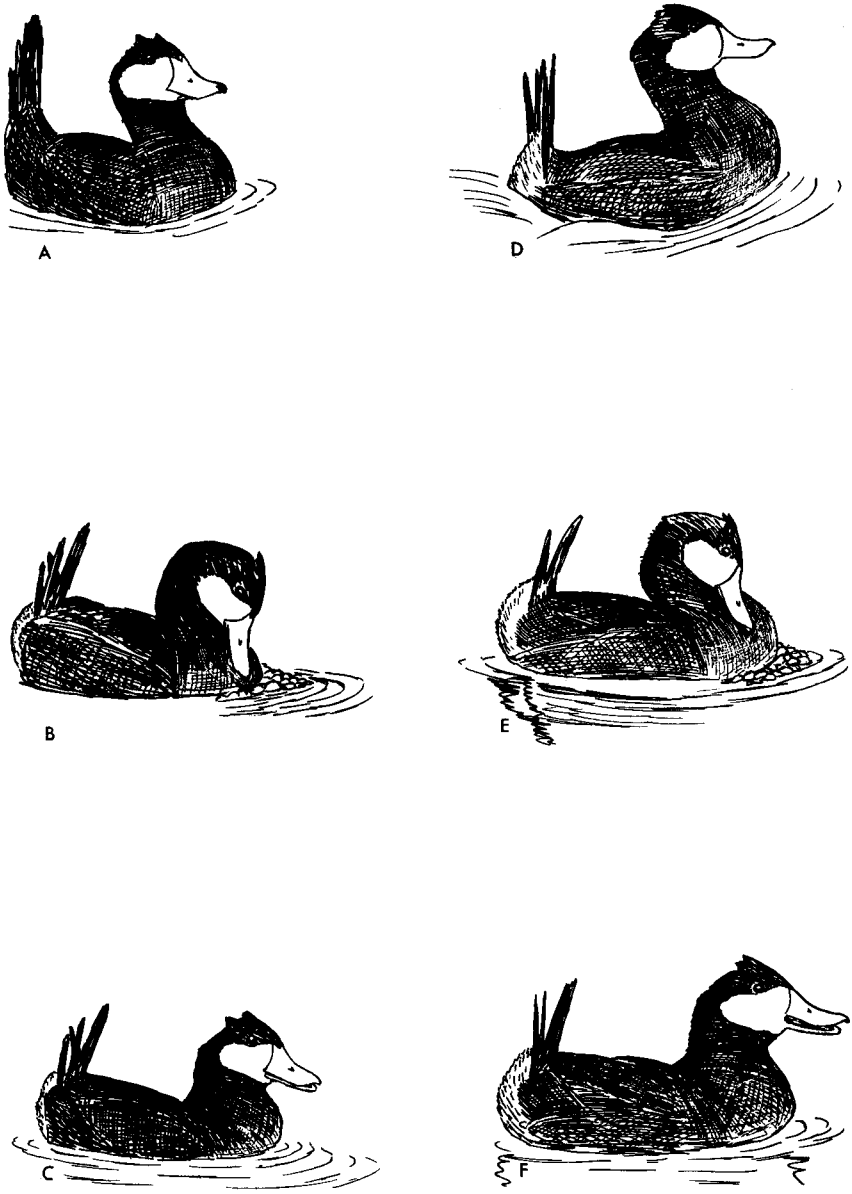


Figure 95. North American Ruddy Duck
A–C. Stages in the Bubbling display.
A. Starting posture.
B. Bill-drumming on breast. Note bubbles produced.
C. Termination of display by calling.
D–F. Same as *A–C.*

deflation of the air sac, accompanied by a forward movement of the head as the bill is opened and a low belching sound is uttered (Fig. 95*C, F*). When the courted female is approached too closely by a second drake, the possessive drake rushes after him with bill gaping, head near the water, and back feathers ruffled, in a threat posture that has been called the Hunched Rush (Fig. 94*D*). The attacking bird then rapidly turns about and Rushes back to the female in a totally different posture. In this the hind parts of the body are submerged, the partially cocked but submerged tail is almost level with the water surface, and the breast is raised out of the water and the bill is held against the breast (Fig. 94*E, F*). In this posture the male "surfboards" back to the female, sending up a wake of water behind him. As soon as he reaches her, he does an "about face" and once again turns the cocked tail toward her. Males also perform short display flights, or "Ringing Rushes," toward females (Fig. 96*A, B*). From an alert and stretched-neck posture, the head stationary and the tail cocked, the partially spread tail is suddenly lowered to the water and the bird "skitters," with a ringing sound produced by the wings, over the surface to within a few feet of the female, whereupon he stops and usually immediately turns around to perform the Bubbling display. The only vocalization I have heard is a soft noise produced at the end of the Bubbling display. Miss Hays has observed a high-intensity threat posture which I have never seen, in which two males face each other motionless, nearly bill-to-bill, for ten seconds or more before they begin actually to fight.

Copulatory behavior. Precopulatory behavior is entirely different from that of any previously discussed species. The male cautiously approaches the female while slightly nodding his head in the manner of ducks that are swimming while very alert, and he frequently dips his bill in the water (Bill-dipping) and immediately withdraws it and shakes it sideways, flicking water to both sides. Although this display (Fig. 96*C, D*) is similar to the Water-twitching display of sea ducks, the bill is not left in the water, and Bill-flicking is perhaps the best name for the movement. The female does not return this display; rather, she usually dives, and she may even threaten the male. Sometimes, however, the male is able to approach close enough so that he can suddenly and without warning mount her. Sometimes the female will assume a partially submerged receptive posture. Treading lasts only a few seconds, during which the female is almost entirely sub-

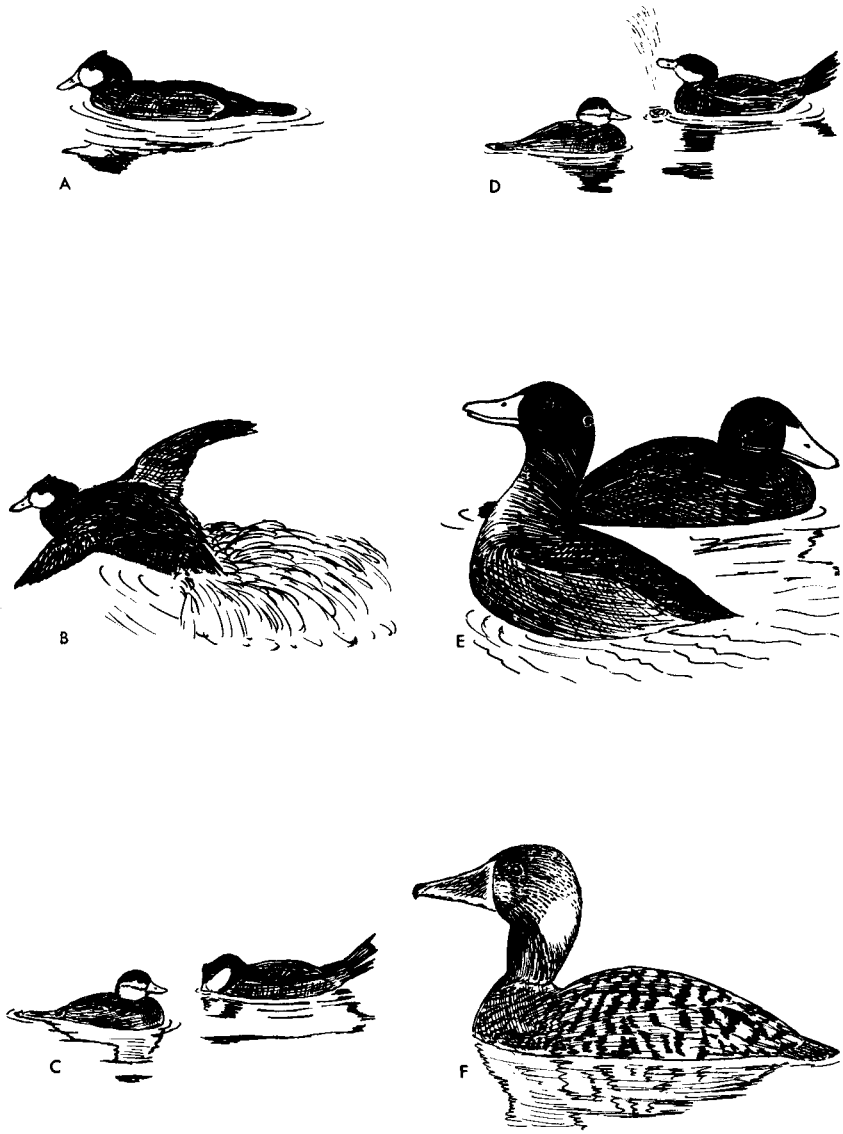


Figure 96. North American Ruddy Duck, Argentine Ruddy Duck, White-backed Duck

A, B. Ringing Rush by male ruddy duck.

C. Precopulatory Bill-dipping, which alternates with *D.*

D. Precopulatory Bill-flicking.

E. Male Argentine ruddy duck performing Head-jerking (*male behind in normal swimming posture*).

F. White-backed duck, swimming posture.

merged. Immediately after treading, the male dismounts rapidly, faces the female, and performs the Bubbling display several times in rapid succession. Both birds then preen and carefully rearrange their plumage.

White-headed Duck (*Oxyura leucocephala*)

It appears probable that the white-headed duck is more closely related to the ruddy duck than to any other species of *Oxyura*. The downy young, juveniles, and females of the two species are very similar. The males differ in that those of the white-headed duck are larger and have a greater amount of white on the head and a markedly higher bill. This higher bill is probably the result of the presumably larger nasal glands associated with the salty or brackish habitat of this species. The body plumage is also less ruddy in color than in the other species of *Oxyura*. There is a definite eclipse plumage in males. The tracheal and esophageal structure is undescribed to my knowledge. No hybrids are known, and there is no sympatry with other stiff-tails.

General behavior. Relatively little is known about the white-headed duck, but except for a tendency to inhabit salt water it appears to be very similar to the ruddy duck. As in that species the nests are large, built over water, and have little down; in addition, the clutch is large and usually consists of six or more eggs.

Agonistic and sexual behavior: female. Females evidently gape aggressively at males, and also occasionally extend their necks (Dementiev, in Delacour, 1959).

Agonistic and sexual behavior: male. Dementiev (in Delacour, 1959) states that males vertically cock as well as spread their tails. They expand their chests and move forward and backward, hitting their chests with their bills in the same manner as North American ruddy ducks. Mountfort (1958) states: "The display consists of the drake swimming in front of its mate while jabbing its short, blue bill rapidly at the water half a dozen times and then jerking its head forward." The behavior described obviously corresponds to the Bubbling display. Dementiev has also described what is clearly the Rush display, saying that males "press the bill against the expanded chest, and press it down into the water; then with a powerful stroke of both feet, they propel their body forward, raising fountains of water."

Copulatory behavior. This is undescribed to my knowledge.

Maccoa Duck (*Oxyura maccoa*)

The African maccoa duck is of uncertain relationships, but possibly it is most closely related to the Argentine ruddy duck. The downy young of the two species are very similar except that the maccoa duck has a striped back and a narrower cheek stripe. Maccoa males are considerably larger than those of the Argentine species, but they have a similar plumage pattern. In both species the bill is relatively narrow and uniform in width. It is uncertain, but doubtful, whether there is an eclipse plumage in males. The tracheal and esophageal anatomy has not been described. The maccoa duck is restricted to Africa and is not sympatric with any other *Oxyura* species.

General behavior. Like the Argentine ruddy duck, this species apparently builds small and frail nests, and lays a small clutch of from three to seven eggs. The male evidently helps care for the young.

Agonistic and sexual behavior: female. Nothing on this has been noted in the literature.

Agonistic and sexual behavior: male. Various authors have described the behavior of this species, the most recent and complete summary being that of Macnae (1959). The male is said to have a relatively loud voice, which is used during various displays. The call has been described as a low, grating *churr, crroooo* . . . , uttered with the head and neck stretched out over the water. It has also been characterized as a loud, snoring *purr, rr-rr,* uttered with the neck arched, the bill pointed toward the water, and the neck swollen. Macnae states that during calling the bill is opened, the head pushed slightly forward and up, the body lifted slightly out of the water, and the tail erected and fanned out. He also mentions the alternate calling position "with head and neck outstretched over the water" as the drake swims forward and backward. No displays corresponding to the Bubble display have been described. A few other male behavior patterns have been described which might also constitute displays. These include "rubbing the bill on its chest" and "rolling its head on the back," which could be either normal or ritualized preening and head-rolling movements respectively. While in front of the female "the drake swam forward with head and neck outstretched, bill pointing downwards, tail stretched back and separated; before doing

this the drake swam with a slight palpitation of the wings. These were not spread but the movement seems to be against the body. The beak is quickly flicked and water splashed up with the tip." This last sentence could refer to precopulatory Bill-flicking. The spreading of the tail feathers mentioned above does not occur in the American ruddy duck, but it has been described for both the white-headed duck and the Argentine ruddy duck.

Copulatory behavior. This has not been described, but Macnae (1959) has described what might be precopulatory behavior occurring between paired birds. He states: "There is some preliminary bill flicking and head rubbing by the drake while the duck preens. The drake swims rapidly up to the duck and stops, almost touching, across her path. Then he lifts and fans his tail, showing the light under tail coverts, pushes his head forward and calls. Then he rapidly back paddles in a small arc to end on the opposite side of his mate. Sometimes he is so close that he forces her around slightly as he revolves."

Argentine Ruddy Duck (*Oxyura vittata*)

The Argentine ruddy duck has at times been considered conspecific with the North American ruddy duck, but this does not appear to be justified. The downy young of this species differ from *jamaicensis* downies in that they have clear white cheeks except for a broad dark stripe. Females have a broad cheek stripe as well, and also have very dark upper-parts. Males have black heads and are otherwise rather uniformly ruddy on the upper parts. The bill increases only slightly in width (about 3 mm. as opposed to 5–7 mm.) beyond the base in the three races of *O. jamaicensis,* and has a relatively straight culmen profile. There appears to be a true eclipse plumage in this species, although such a plumage appears to be lacking in the South American races of *jamaicensis.* The male tracheal structure is simple, with only a weakly developed tracheal air sac, but the esophagus is enlarged and inflatable (Wetmore, 1926). The Argentine ruddy duck is sympatric with the Peruvian ruddy duck in Chile, but no hybrids are definitely known to exist. Hellmayr (1932) mentioned one possible hybrid based on maximum bill width, but the two forms approach each other so closely in this respect (19.4 mm. to 22.2 mm. in 12 male *vittata* vs. 23.0 to 26.1 mm. in 27 male *ferru-*

ginea measured by me) that positive identification of hybrids on this basis is impossible.

General behavior. The Argentine ruddy duck appears to be most readily distinguishable from the Peruvian ruddy duck in that it builds a small, flat, grebelike nest and lays a relatively small clutch of three to five eggs (Goodall *et al.*, 1951). The eggs are also somewhat smaller in size than are those of the Peruvian species.

Agonistic and sexual behavior: female. In limited observations at the Philadelphia Zoo, I noted that the female of this species is much like the North American ruddy duck female in her behavior. Her most common display is a silent gaping, which is performed toward any male that approaches too closely. She also occasionally performs a silent vertical bill-jerking movement similar to the major male display, but done in a much less conspicuous fashion. The only female vocalization I have heard is a high-pitched squeal, very similar to that of the North American ruddy duck female and uttered under similar circumstances.

Agonistic and sexual behavior: male. Little has been published to date regarding male displays in this species; the observations of Kerr (1890) are the only ones known to me. Dr. Martin Moynihan has made extensive observations on the behavior of the Argentine ruddy duck, but these have not yet been published. My own observations are quite limited, but suggest a remarkable difference in male behavior patterns from those of the North American ruddy duck. In fact, in many respects the two species respond in almost opposite ways, which is not surprising considering their sympatric distributions and similar plumages. For example, the Argentine ruddy duck male cocks his tail only rarely, and apparently never during sexual display. He never drums his bill downward on his breast; his commonest display (directed both to females and other males) is instead a very rapid upward jerk of the head with the bill held relatively level (Fig. 96*E*). This display, frequently repeated several times, appears to be silently performed. Although the esophagus is inflatable I did not notice any marked neck enlargement; Kerr (1890), however, did observe this. I once observed a male stretch his head and neck out on the water toward a female, in a posture similar to the Sneak of the pochards, a posture Kerr (1890) also describes. Kerr states that while in this posture the male spreads and cocks his tail, then advances toward the female, but I did not see this.

Other displays or probable displays that I observed include the Hunched Rush, performed in the same manner as by the North American ruddy duck and a silent gaping which also was apparently a threat toward other males. On several occasions I observed a jerking or quivering of the folded wings which strongly reminded me of the black-headed duck's wing movements during display, but which I have never noted in the North American ruddy ducks. Furthermore, the males gave no indication of trying to swim in front of the females in the manner so typical of North American ruddy ducks, in which this tendency forms an important part of the total display activity.

Copulatory behavior. This has not yet been described, and I observed no copulations. I did, however, see one male approach a female and, while facing her, alternately dip his bill and roll his head on the back. This immediately reminded me of the alternate Bill-dipping and lateral Bill-flicking found in North American ruddy ducks as a precopulatory display, and I believe that this was perhaps also a precopulatory display in the Argentine species. The female, however, made no overt response to the male.

Australian Blue-billed Duck (*Oxyura australis*)

The Australian blue-billed duck is of uncertain relationships, but probably belongs near the Argentine ruddy duck and the maccoa duck. Juveniles and females have dusky, unstreaked head patterns unlike those of the other *Oxyura* species. Males have black heads and necks, and otherwise are a uniformly dark ruddy color on the upper parts. A female-like eclipse plumage is evidently present, to judge from personal observations. The bill is relatively narrow throughout, and the culmen profile is concave as in the maccoa duck. A tracheal air sac is lacking, but the esophagus can be inflated. The species is widespread in southern Australia and is not sympatric with any other species of *Oxyura*. No hybrids are known.

General behavior. Descriptions of nests are few, but apparently the nests tend to be larger and more substantial than those of the Argentine or African species. The average clutch apparently consists of five or six eggs. The male evidently never assists the female with rearing the young, but deserts her when incubation begins.

Agonistic and sexual behavior: female. Judging from my observations on this species, females are quite similar to those of other

Oxyura species. Gaping is commonly performed as a hostile display toward males, and is accompanied by a repeated "*tet-tet-tet-tet . . .*" series of notes. In addition, females perform a vertical head-pumping as a dive-intention movement. No Inciting displays have been observed.

Agonistic and sexual behavior: male. Male display patterns in this species have been reported in detail elsewhere (Johnsgard, 1965b), and will only be summarized here. Earlier notes by Brown (1949), Wheeler (1953), and Scott (1958) mention only a few of these displays. Among the most frequent male displays is Dab-preening, a ritualized preening of the breast feathers done in a rapid and repeated fashion, usually while facing the female. Prior to the most elaborate display, the male performs a series of fairly rapid Head-pumping movements that are seemingly identical to the dive-intention movements made by frightened birds. As this Head-pumping progresses, the tail is gradually cocked and the neck expands greatly. Suddenly the bird throws his head forward and downward into the water, and with a series of neck-jerking movements splashes the surface with his bill and throat in a display I have called Sousing. After from five to seven such jerking movements the tail is quickly lowered and simultaneously the head and bill are submerged, so that only the back of the displaying bird is visible. In this posture the male remains motionless or swims backward a varying distance, then retracts his head and completes the display with a series of bill-dipping and head-shaking movements. Like the Bubbling display of the North American ruddy duck, this display produces considerable noise through splashing, but in all probability these two somewhat similar displays were independently evolved. Two displays clearly derived from comfort movements have been frequently observed; these are Head-rolling and Wing-flapping. A sudden Lurching forward in the water often follows Wing-flapping or Head-rolling, producing a conspicuous splashing sound. Similarly a noisy Display Flight is performed in exactly the same manner as the Ringing Rush of the North American ruddy duck, and an aggressive chase, or Hunched Rush, is frequently seen as males threaten one another. In addition, a rapid "surfboarding" type of swimming has been observed, which is similar to that performed by males of the North American species as they return to courted females. In contrast with that species however, this Motor-boating display also occurs in other situations in the blue-

billed duck. Finally, dorsal preening and diving have been observed occasionally during display and may be ritualized.

Copulatory behavior. An adequate description of copulation is still not available. Wheeler (1953) once observed a male chase a female, finally catch her, and copulate with her while she was completely submerged. After copulation there was a lengthy preening which was completely different from the display preening he observed earlier. It seems unlikely that this represents normal copulatory behavior.

Musk Duck (*Biziura lobata*)

The Australian musk duck is certainly a stiff-tail, differing from the other stiff-tails mainly in being larger and in having different body plumage and different feeding habits. The downy young are only slightly patterned, being dark gray above and lighter below. Juveniles and adults of both sexes are essentially alike in plumage, differing only in size and the degree of development of the submandibular lobe, or wattle. Adult males are two to three times as heavy as females, and have an extremely large wattle which is formed by a folding of the integuments. It is not hollow and therefore cannot be inflated, although it can be thickened considerably at the base and made turgid. There is an inflatable subgular pouch immediately behind the lobe, apparently somewhat similar to the throat pouch of the black-headed duck. The trachea is simple and apparently lacks any air sacs, and the syrinx is a simple ossified area at the junction of the bronchi (illustrated in Johnsgard, 1961c). Doubtlessly the syrinx produces the whistling call of the male, but the so-called "plonk call" is mechanically produced by the slapping of the feet on the water. Musk ducks occur over southern Australia and are sympatric with the Australian blue-billed duck. No hybrids are known.

General behavior. Musk ducks build typical stiff-tail nests, and normally lay only two or three large, rough-surfaced eggs. Young birds often ride on the female's back, a behavioral adaptation not known to occur in other stiff-tails. The diet of musk ducks consists of a wide variety of animal material such as amphibians, fish, crustaceans and other invertebrates. Additional notes on the general behavior of this species can be found elsewhere (Johnsgard, 1965a, 1965b).

Agonistic and sexual behavior: female. Females appear to lack any well-defined courtship displays; instead they are simply attracted to displaying males and watch such birds intently, without however actively initiating or regulating display activity. Thus there appear to be no Inciting or other sexual displays present in females, and I heard no calls uttered by them. To my knowledge, the only vocalization recorded for female musk ducks consists of an apparent warning note uttered to ducklings at the approach of possible danger (Johnsgard, 1965a).

Agonistic and sexual behavior: male. Surprisingly little concerning the behavior of this bizarre species has been published. Aside from some short notes, the paper by Serventy (1946) is the only reasonably detailed description of male displays. I have described these in detail elsewhere (Johnsgard, 1965b), so that an abbreviated summary may suffice here. Unlike the sexual displays of nearly all other species of waterfowl, those of male musk ducks do not appear to accomplish the establishment of pair bonds between individuals. Rather, it would seem that males conduct promiscuous relationships with any females that they manage to attract by their conspicuous display activity, and thus their elaborate displays and considerable sexual dimorphism can probably be explained through sexual selection. The female's role is therefore reduced to one of simply observing and presumably visually stimulating the male by her presence alone. The male displays appear to represent a heirarchy of forms, of which three distinct levels can be recognized. These are the Paddling Kick, the Plonk Kick and the Whistle Kick. The Paddling Kick is apparently always used to begin a display sequence. As the bird moves forward through the water he lowers his head and neck toward the surface, holds his body and tail in a straight axis, and with a strong kick sends a sheet of water upward and backward a distance of up to six or eight feet. Often the feet are not kicked in exact synchrony, so that a double or even triple splash may be produced. The only sounds produced are those of splashing water. The tail is often partly cocked between displays, and the submandibular lobe may be somewhat enlarged. The number of Paddling Kicks performed in a sequence and the duration between them is quite variable, but usually less than 20 occur before the male begins to perform Plonk Kicks. The bird remains fairly stationary in the water, tilts the head upward, and sometimes cocks the tail. The lobe is much thickened at the base,

and the cheeks and throat are greatly enlarged through inflation of the subgular pouch. In this posture the bird kicks simultaneously with both feet, sending splashes upward and laterally. Although the amount of water and the distance it is kicked seems less than in the Paddling Kick, the noise produced is greater, for as the feet strike the water they produce a loud, hollow "plonk" or "ker-plonk′," a noise that persons have often concluded to be of vocal origin. These Plonk Kicks are repeated with considerably more regularity than the Paddling Kicks, and are continued for an indefinite period. Often as many as 30 or 40 Plonk Kicks occur in unbroken sequence, spaced with surprising regularity between three and four seconds apart (Johnsgard, 1965b). After an extended series of Plonk Kicks, and especially after one or more females have been attracted to the male, he usually abruptly shifts from Plonk Kicks to Whistle Kicks. Whistle Kicks involve a more extreme extension of the posturing assumed during the Plonk Kick. The tail is spread and usually kept fully cocked and closely pressed against the back. The head is held low in the water with the bill tilted upward, so that the fully turgid lobe is just over the surface. In this posture the bird suddenly flicks his feet simultaneously outward and backward, throwing jets of water out on both sides of the body for a foot or two. Contrary to previous reports, the wings do not produce this splashing, but rather it is caused by the feet alone. With each splash a sharp, clear whistled note is uttered, somewhat similar to the call of the white-backed duck, and at close range a much softer preliminary breathing noise can be heard. In extreme posturing, as when other birds are nearby, the male raises his head and fully cocked tail between splashes, so that the body appears almost U-shaped. This posture is especially frequent when other males approach. Surprisingly, such males will often swim up to within a foot or so of displaying birds, watching them intently. Fights do not usually result until one of these males approaches too closely to one of the females, which are also strongly attracted to displaying males. The timing of the Whistle Kicks is even more regular than that of the Plonk Kicks, and the average time between kicks is again from three to four seconds. It is not uncommon for a series of 50 or 60 Whistle Kicks to occur in unbroken sequence, and such sequences are generally terminated by the females losing interest and swimming away or by the displaying male attacking one of the other males.

Copulatory behavior. I have not observed copulation, but accounts of it made available to me by Angus Robinson and Vic Lowe are fairly similar and the behavior described is probably representative. There is apparently no special precopulatory behavior in musk ducks distinct from the general display activity described above, but instead the male simply displays with particular intensity when a female approaches closely, almost constantly jockeying for position close to her. Finally the male quickly throws a wing over the female, pulls her beneath him, and she is totally submerged during copulation. Both Robinson and Lowe observed an unusual male postcopulatory display, in which the male, with head submerged, rapidly swam away from the female (Lowe's account) or around her (Robinson's account). The female simply surfaced and flapped her wings.

White-backed Duck (*Thalassornis leuconotus*)

Of all the Anatidae, the white-backed duck is one of the most aberrant, and its position in the family is still somewhat tentative. Although it is generally believed to belong to the stiff-tail tribe, there is relatively little evidence to support this view. The tail feathers are very short and only slightly if at all stiffened, there is no inflatable air sac or specialized esophagus in the male, and the feathers lack the grebelike appearance of the typical stiff-tails. The downy young are altogether unique. Juveniles, females, and adult males are essentially identical in plumage, differing only in the brightness and length of the head feathers. The trachea of the male is simple, but the syrinx is an osseous chamber, slightly enlarged and keeled, much like that of female whistling ducks (illustrated in Johnsgard, 1961c). A fact not previously noticed by taxonomists is that the tarsus has a reticulated pattern; the only other ducks which have this feature are whistling ducks and the freckled duck.

General behavior. White-backed ducks dive frequently, but do so in a "leaping" manner much like that of whistling ducks. Their nests are like those of stiff-tails, and are built over water. The eggs, although relatively large, are smooth and glossy, unlike those of the Oxyurini. No down is placed in the nest, suggesting that, as in the whistling ducks, both sexes incubate. It is at least certain that both sexes rear the young; thus pair bonds may be relatively permanent. In two other aspects of its general behavior the white-backed duck is peculiar. First, I have never seen the birds swimming or resting

on the water with the bill tucked in the scapulars in the manner of typical stiff-tails (at least *Oxyura*). Instead the birds go to shore to sleep or rest. Second, the general shake of the white-backed duck is very much like that of a whistling duck in that it is preceded by wing-shaking for several seconds before the bird rises in the water and shakes its head. In addition, white-backed ducks frequently shuffle their wings for extended periods of a minute or more; this is also characteristic of whistling ducks.

Agonistic and sexual behavior. Unlike the typical stiff-tails, white-backed ducks are exceedingly undemonstrative. Both sexes have a clear whistling voice like that of a whistling duck or guinea pig, and when disturbed they utter their plaintive notes with neck outstretched (Fig. 96*F*). So far as I can tell, there is no difference in the voices of the two sexes. The birds do not usually threaten or attack one another, although on a few occasions I saw them rushing over the water like ruddy ducks, as one bird chased another. Although I have watched nine of these birds for extended periods, the only possible instance of display I have observed consisted of one bird (apparently a male, judging from head size and color) swimming toward another while calling repeatedly. The second bird then also began to call, and the two swam along together, calling, for several feet. They then separated and nothing more developed. I have also observed a rapid chin-lifting toward other birds during apparently aggressive calling.

Copulatory behavior. Unfortunately, no information on this is available, and a knowledge of it would no doubt be of assistance in judging the real affinities of the species.

Summary

The major sexual behavior patterns of the species of Anatidae may now be reviewed and summarized, for the purpose of clarifying evolutionary relationships in the family, tracing the evolution of behavior patterns through various taxa, and evaluating the importance of certain behavior patterns as potential isolating mechanisms.

The subfamily Anseranatinae includes the monotypic magpie goose, which exhibits numerous anatomical and behavioral peculiarities. The female, at least in captivity, usually builds several "dummy" nests which are simply heaps of grass or herbs. The male assists in nest-building and incubation, and also defends the nest vigorously. Both parents feed the young, and this represents the only instance of well-developed parental feeding in the Anatidae. Males assist in rearing the young, and family bonds are strong. Threat behavior is not highly ritualized. Wing-shaking appears to be a low-intensity threat, and also seems to function as a rudimentary Triumph Ceremony, occurring after aggressive encounters. Copulation takes place on or near the nest site, and the male evidently does not grasp the female's nape during treading. Preflight signals consist of lateral Head-shaking movements and associated calling.

The subfamily Anserinae (whistling ducks, swans, and true geese) is like the Anseranatinae in that there is little or no sexual dimorphism in plumages, voices, and behavior, and the pair bond is relatively strong and permanent. Although sexual behavior is remarkably uniform throughout the entire subfamily, threat behavior is complex and varies greatly. In both tribes the male assists with

nest building and the rearing of the young, but in only some species do males take part in incubation.

The tribe Dendrocygnini comprises eight species of whistling ducks. Behaviorally, the species differ primarily in their vocalizations and, to a lesser degree, their threat behavior. Aggressive displays are highly developed, and small groups often threaten other birds. There does not, however, appear to be any real Triumph Ceremony present in any species. Mutual preening occurs in most and possibly all species and is not restricted to mated birds. Family bonds appear to be strong, and individual recognition is probably at least in part based on variations in calls. In all the species studied, precopulatory behavior consists of mutual displays that appear to be derived from bathing, bill-dipping, or drinking movements. As a postcopulatory display both birds of a pair call loudly and rise in the water in a Step-dance, side by side, usually raising the wing farthest from the other bird to a position directly vertical but bent at the wrist. Two species lack such an elaborate postcopulatory display, and in these species copulation normally occurs on shore or in shallow water.

The swans and true geese of the tribe Anserini are clearly closely related, and it is concluded that they should be retained in a single tribe. Unlike the whistling ducks they do not become sexually mature before they are two or more years old. All swans and geese except possibly the coscoroba swan have a conspicuous Triumph Ceremony that is performed by members of a pair or family after the extrusion of an "enemy." This ceremony takes different forms in various species. Lower intensities of the Triumph Ceremony are utilized as greeting ceremonies. In swans preflight movements consist of mutual calling with strong upward Neck-stretching movements, or simply of slimming the plumage and holding the neck erect without calling. In the geese, preflight movements are mainly lateral Head-shakes associated with special vocalizations. One type of threat in swans consists of ruffling the neck feathers, whereas in geese it consists of vibrating the neck feathers, and the vertical striations of the neck feathers in most geese appear to function in making this display more conspicuous. Some swans raise their folded wings while threatening; others hold the wings close to the body or spread them wide. In several species of swans the general body shake is used as a threat display, and in a few species wing-flapping serves as a threat display as well. In the true geese the folded wings are often shaken or alter-

nately lifted during threat display, and various neck postures indicate different levels of aggression.

In all the true geese and swans, precopulatory behavior consists of mutual Head-dipping that may be derived from bathing movements. In most geese the tail is strongly tilted upward and thus the undertail coverts are exhibited. Postcopulatory displays vary considerably. The coscoroba swan, which is swanlike in its aggressive behavior, has precopulatory and postcopulatory displays similar to those of some swans and geese, and is possibly a link between the swans and true geese.

The Cape Barren goose is gooselike in its voice and aggressive behavior, possessing a conspicuous Triumph Ceremony and threat displays that include alternate wing-flicking and pumping movements of the neck. Therefore it is included in the Anserini. Copulation in this species occurs on land, and the precopulatory behavior lacks any movements resembling the Head-dipping of true geese. The postcopulatory display is unlike that of the typical sheldgeese, and approaches that of true geese. It is proposed that the freckled duck should also be included in the Anserinae, in a separate monotypic tribe Stictonettini. The behavior of this species, although still inadequately described, supports such a taxonomic placement.

Behaviorally most species of the subfamily Anatinae differ from those of the two preceding subfamilies in that pair bonds are less strong and tend to be renewed every year, often with different mates. The major result of this is that there tend to be two body molts, and thus two plumages, each year. One of these plumages, the nuptial, is associated with pair formation and is generally more elaborate in males than in females. Male courtship patterns tend to be more elaborate and more diversified, since pairs must be formed repeatedly, usually in a matter of a few months each year, throughout an individual's lifetime. Female courtship patterns are more uniform than are those of males, and copulatory behavior patterns tend to be very similar in related species. Unlike the species of preceding tribes, most species of this tribe do not perform Triumph Ceremonies, and pair bonds appear to be developed instead by the combination of female Inciting and the preferred male responding sexually or with appeasement gestures toward the female.

The shelducks and sheldgeese of the tribe Tadornini link, morphologically and behaviorally, the true geese and the true ducks. In

some genera there are no seasonal plumage differences, and there may possibly be only one body molt per year. In the blue-winged goose the voices of the sexes are practically alike, but in all species there are major sexual differences in the tracheal structure. In nearly all genera the female exhibits a distinct Inciting display, and the male usually responds with threats or overt attacks toward the indicated enemy, alternating these with sexual displays toward the female. The sexual displays are often fairly simple, but in the Orinoco goose and some species of *Chloëphaga* the sexual note, a two-syllable call rather than the one-syllable threat note, is accompanied by a Puffing display. A mutual Bowing display also occurs in several species of *Chloëphaga*. Preening-behind-the-wing is encountered in the common shelduck, in which it is used as a precopulatory display as well as a courtship display.

Precopulatory behavior is practically identical in the species of this tribe, and consists of mutual Head-dipping movements. In some sheldgeese, copulation occurs while the birds are standing in shallow water; in the other species it occurs in water of swimming depth. In the genera observed thus far the postcopulatory display consists of the male holding on to the female's nape for several seconds as both call; then the male releases her and assumes a High-and-erect posture, usually lifting the far wing in a manner reminiscent of the postcopulatory display of whistling ducks. The female may lift her wing in the same fashion or may begin to bathe immediately.

Evidence indicates that the steamer ducks differ in numerous behavioral respects from the shelducks and that the two groups should probably be tribally separated. The most elaborate male posture of the three steamer ducks is much like the High-and-erect posture of male shelducks, but it appears that female steamer ducks lack an Inciting display. Precopulatory behavior of the flying steamer duck apparently consists of mutual Head-dipping, and the postcopulatory display involves both birds swimming apart in an alert posture while Grunting and Head-flagging.

Evidence from behavior, tracheal anatomy, and hybridization indicates that the perching ducks of the tribe Cairinini belong between the shelducks and the surface-feeding ducks. The ringed teal (*Callonetta*) is included as a monotypic genus of perching ducks. Behaviorally, the perching ducks resemble shelducks in that the included species are primarily hole-nesters, and some genera require two years

to reach maturity. Pair bonds in the group are temporary, however, and, in some species, practically absent. In the larger forms there is relatively little dimorphism of plumage, and displays tend to be simple, with the same postures used for aggression as for courtship. Hartlaub's duck shows some affinities with these larger forms but differs considerably in downy and adult plumages as well as in behavior; therefore this species is retained in the monotypic genus *Pteronetta*. The rest of the perching ducks are smaller, more specialized forms that mature in their first year and show little dimorphism in size but considerable dimorphism in plumage, with male plumages often being complex in pattern. Pair bonds are stronger in these species, displays and vocalizations more elaborate, and overt aggressive behavior less frequent. Females of these species also possess Inciting displays. Male courtship displays consist of ritualized shaking and drinking movements as well as Preening-behind-the-wing. Turning-the-back-of-the-head occurs in males of some genera, and Chin-lifting is often associated with that display. Among perching ducks the precopulatory displays are unusually variable. In a few genera they are practically absent, while in others Bill-dipping, Head-dipping, or Head-pumping movements are utilized by one or both sexes. Postcopulatory behavior differs in the two sexes, with the female simply bathing immediately and the male usually calling as he swims away from the female or turns and Faces her.

The marked success of the tribe Anatini, in terms of numbers of species and individuals, is probably related to the fact that the included species for the most part have generalized feeding and nesting requirements, that they mature in one year, and that they have a high reproductive potential. The females of all species of *Anas* have marked Inciting displays and distinctive Decrescendo Calls ranging in syllables from one to more than twenty. Males of most and perhaps all species perform a conspicuous Turning-the-back-of-the-head display as well as a courtship call or Burp, and males of most species also perform Preening-behind-the-wing. Preflight movements in all species consist of rapid Neck-jerking and lateral Head-shaking. Precopulatory displays consist of mutual Head-pumping; male postcopulatory displays include calling once, with or without any additional displays. Fairly complex courtship postures are typical of males of most species. The Grunt-whistle, Bridling, the Head-up-tail-up, and

the Down-up are the major *Anas* displays, and are found in most species other than the wigeons, blue-winged ducks, and a few others. It is evident that one or more of these displays has been secondarily lost in various species, and in other species some of these displays are linked in different combinations, which results a display specificity for each species. Courtship displays in the wigeon group consist primarily of ritualized aggressive behavior, and in the blue-winged ducks ritualized feeding and up-ending are the primary courtship postures. The marbled teal deviates from *Anas* in several behavioral and morphological respects, and it is placed in the monotypic genus *Marmaronetta*. The precopulatory displays of the marbled teal, which include Bill-dipping, Drinking, and Preening-dorsally, are unlike those of any species of *Anas* and very much like those of the Aythyini. The postcopulatory displays are likewise almost identical to those of the Aythyini.

The pochard tribe Aythyini consists of a remarkably homogeneous group of species, both behaviorally and anatomically. Besides the two genera included in the group by Delacour and Mayr, the pink-headed duck is included in the tribe on plumage and anatomical grounds. Behaviorally, the pochards differ from the Anatini in that female pochards apparently lack Decrescendo Calls, and the courtship postures of males include the Kinked-neck call, Coughing, Neck-stretching, Sneaking, and the Head-throw. These displays are similar in form in most species, and differ primarily in their associated vocalizations. Females have an Inciting display similar to that of *Anas* females, and males of most and probably all species Turn-the-back-of-the-head to Inciting females. Females of a few species regularly perform the Head-throw and Kinked-neck call displays. Mutual Preening-behind-the-wing also occurs in many species. Precopulatory behavior in most species consists of mutual Bill-dipping and Preening-dorsally, with a rudimentary, *Anas*-like Head-pumping occurring in five species. The male mounts as soon as the female begins to flatten out on the water. The postcopulatory display is the same in all species studied. The male calls once, then swims away from the female in a Bill-down posture. The female may adopt the same posture for a short time, or she may begin to bathe immediately. Preflight signals consist mainly of rapid, repeated Chin-lifting movements and, less commonly, lateral Head-shaking.

The tribe Mergini is here constituted as it was originally by

Delacour and Mayr, and includes the eiders, which were later separated from the other sea ducks by Delacour. The closest relatives of the Mergini are probably the Aythyini, but the two tribes differ in that most species of Mergini are saltwater forms that consume primarily animal material and do not become sexually mature before their second or third year. Behaviorally, females of most and possibly all species have Inciting displays which, although they differ greatly in form, are apparently identical in function and are probably homologous. In several species Inciting is accompanied by marked chin-lifting movements. Male courtship displays vary to an astonishing degree, even among closely related species. The only male displays which occur in more than one genus are the Upward-stretch, Wing-flapping, Head-turning, and Tail-cocking. Copulatory behavior is much more useful in assessing relationships. In all species studied, the female assumes the receptive, or Prone, posture before the male attempts to mount, at which time he performs various precopulatory displays. These usually include movements derived from drinking, shaking, stretching, or preening, which may be different from the corresponding comfort movements or essentially identical with them. In a few species some of the courtship displays are also performed. In some species the male mounts only after performing a complicated, stereotyped sequence of displays. During treading, males of some species loudly Flick-the-wings, and in some the male retains hold of the female's nape for several seconds after treading is completed, so that the two birds Rotate in a circle. Females of all species normally begin to bathe immediately after being released by the male, but male postcopulatory displays are varied. In some genera the male performs a single courtship display immediately after treading, Steams away from the female, or does not display at all. Preflight movements consist only of lateral Head-shaking in all species studied.

The stiff-tailed ducks of the tribe Oxyurini are the most inadequately studied group of the entire family. The black-headed duck appears to be anatomically the least specialized of the group and exhibits some similarities of behavior and structure to the dabbling ducks, which are perhaps the Oxyurini's closest, although distant, relatives. Behaviorally, the Oxyurini is difficult to characterize because so little is known about most species, but it appears that auditory signals may play a more important role in the sexual behavior of the stiff-tails than in the other tribes. Associated with this is the fact

that males of most species have inflatable structures, derived from the trachea, esophagus, or pharynx, which are presumably the sources of most of the male courtship calls. These are lacking in the white-backed duck, and both sexes of this species possess a whistling voice and tracheal anatomy similar to those of the whistling ducks. In at least two species the major courtship display consists of the male repeatedly drumming his bill on an inflated tracheal air sac. In one other species the display appears to consist of the inflation and subsequent deflation of the esophagus by jerky head and neck movements, and also breast preening. Jerky head movements are also a part of the display of male black-headed ducks and may function in a similar way. In all species except the white-backed duck a cocked-tail display occurs, and stretching the neck and head out over the water has been described for several species of *Oxyura,* as well as vertical head-bobbing. Precopulatory and postcopulatory behavior is known for only a few species, and in all cases these displays are distinctly different from copulatory displays in other tribes. In the ruddy duck, precopulatory displays include Bill-dipping followed by lateral Bill-flicking.

Appendix

Synopsis of the Family Anatidae

SUBFAMILY ANSERANATINAE

Tribe Anseranatini

Genus *Anseranas*	
A. semipalmata	Magpie Goose

SUBFAMILY ANSERINAE

Tribe Dendrocygnini

Genus *Dendrocygna*	
D. guttata	Spotted Whistling Duck
D. eytoni	Plumed Whistling Duck
{*D. bicolor**	Fulvous Whistling Duck
{*D. arcuata*	Wandering Whistling Duck
D. a. arcuata	East Indian Wandering Whistling Duck
D. a. australis	Australian Wandering Whistling Duck
D. a. pygmaea	Lesser Wandering Whistling Duck
D. javanica	Lesser Whistling Duck
D. viduata	White-faced Whistling Duck

* Braces indicate superspecies groups.

D. arborea	Cuban Whistling Duck
D. autumnalis	Red-billed Whistling Duck
D. a. autumnalis	Northern Red-billed Whistling Duck
D. a. discolor	Southern Red-billed Whistling Duck

Tribe Anserini

Genus *Cygnus*	
(Subgenus *Cygnus*)	
C. olor	Mute Swan
C. atratus	Black Swan
C. melanocoryphus	Black-necked Swan
(Subgenus *Olor*)	
C. cygnus	
C. c. cygnus	Whooper Swan
C. c. buccinator	Trumpeter Swan
C. columbianus	
C. c. columbianus	Whistling Swan
C. c. bewickii	Bewick's Swan
C. c. jankowskii	Eastern Bewick's Swan
Genus *Coscoroba*	
C. coscoroba	Coscoroba Swan
Genus *Anser*	
A. cygnoides	Swan Goose
A. fabalis	Bean Goose
A. f. fabalis	Western Bean Goose
A. f. johanseni	Johansen's Bean Goose
A. f. middendorfi	Middendorf's Bean Goose
A. f. rossicus	Russian Bean Goose
A. f. serrirostris	Thick-billed Bean Goose
A. f. brachyrhynchus	Pink-footed Goose
A. albifrons	White-fronted Goose
A. a. albifrons	European White-fronted Goose
A. a. frontalis	Pacific White-fronted Goose
A. a. flavirostris	Greenland White-fronted Goose
A. a. gambelli	Tule Goose
A. erythropus	Lesser White-fronted Goose
A. anser	Graylag Goose
A. a. anser	Western Graylag Goose
A. a. rubrirostris	Eastern Graylag Goose
A. indicus	Bar-headed Goose

A. caerulescens	Snow Goose
A. c. caerulescens	Lesser Snow Goose & Blue Goose
A. c. atlanticus	Greater Snow Goose
A. rossi	Ross's Goose
A. canagicus	Emperor Goose
Genus *Branta*	
(Subgenus *Nesochen*)	
B. sandvicensis	Hawaiian Goose
(Subgenus *Branta*)	
B. canadensis	Canada Goose
B. c. canadensis	Atlantic Canada Goose
B. c. interior	Central Canada Goose
B. c. moffitti	Great Basin Canada Goose
B. c. maxima	Giant Canada Goose
B. c. parvipes	Lesser Canada Goose
B. c. taverneri	Taverner's Canada Goose
B. c. occidentalis	Dusky Canada Goose
B. c. fulva	Vancouver Canada Goose
B. c. leucopareia	Aleutian Canada Goose
B. c. hutchinsii	Richardson's Canada Goose
B. c. minima	Cackling Canada Goose
B. c. asiatica	Bering Canada Goose
B. leucopsis	Barnacle Goose
B. bernicla	Brant Goose
B. b. bernicla	Dark-bellied Brant Goose
B. b. hrota	Light-bellied Brant Goose
B. b. nigricans	Lawrence's Brant Goose
B. b. orientalis	Black Brant
B. ruficollis	Red-breasted Goose
Genus *Cereopsis*	
C. novae-hollandiae	Cape Barren Goose

Tribe Stictonettini

Genus *Stictonetta*	
S. naevosa	Freckled Duck

SUBFAMILY ANATINAE

Tribe Tadornini

Genus *Cyanochen*	
C. cyanopterus	Abyssinian Blue-winged Goose

Genus *Chloëphaga*	
C. melanoptera	Andean Goose
C. picta	Magellan Goose
C. p. picta	Lesser Magellan Goose
C. p. leucoptera	Greater Magellan Goose
C. hybrida	Kelp Goose
C. h. hybrida	Patagonian Kelp Goose
C. h. malvinarum	Falkland Kelp Goose
C. poliocephala	Ashy-headed Goose
C. rubidiceps	Ruddy-headed Goose
Genus *Neochen*	
N. jubatus	Orinoco Goose
Genus *Alopochen*	
A. aegyptiacus	Egyptian Goose
Genus *Tadorna*	
(Subgenus *Casarca*)	
T. ferruginea	Ruddy Shelduck
T. cana	Cape Shelduck
T. variegata	Paradise Shelduck
T. tadornoides	Australian Shelduck
T. cristata	Crested Shelduck
(Subgenus *Tadorna*)	
T. tadorna	Common Shelduck
T. radjah	Radjah Shelduck
T. r. radjah	Black-backed Radjah Shelduck
T. r. rufitergum	Red-backed Radjah Shelduck

Tribe Tachyerini

Genus *Tachyeres*	
T. patachonicus	Flying Steamer Duck
T. pteneres	Magellanic Flightless Steamer Duck
T. brachypterus	Falkland Flightless Steamer Duck

Tribe Cairinini

Genus *Plectropterus*	
P. gambensis	Spur-winged Goose
P. g. gambensis	Gambian Spur-winged Goose
P. g. niger	Black Spur-winged Goose
Genus *Cairina*	
C. moschata	Muscovy Duck
C. scutulata	White-winged Wood Duck
Genus *Sarkidiornis*	
S. melanotos	Comb Duck

S. m. melanotos	Old World Comb Duck
S. m. sylvicola	South American Comb Duck
Genus *Pteronetta* ("*Cairina*")*	
P. hartlaubi	Hartlaub's Duck
P. h. hartlaubi	Western Hartlaub's Duck
P. h. albifrons	Eastern Hartlaub's Duck
Genus *Nettapus*	
N. pulchellus	Green Pygmy Goose
N. coromandelianus	Cotton Pygmy Goose
N. c. coromandelianus	Indian Cotton Teal
N. c. albipennis	Australian Pygmy Goose
N. auritus	African Pygmy Goose
Genus *Callonetta* ("*Anas*")	
C. leucophrys	Ringed Teal
Genus *Aix*	
A. sponsa	Wood Duck
A. galericulata	Mandarin Duck
Genus *Chenonetta*	
C. jubata	Australian Wood Duck
Genus *Amazonetta*	
A. brasiliensis	Brazilian Teal
A. b. brasiliensis	Lesser Brazilian Teal
A. b. ipecutiri	Greater Brazilian Teal

Tribe Anatini

Genus *Hymenolaimus*	
H. malacorhynchus	Blue Duck
Genus *Merganetta*	
M. armata	Torrent Duck
M. a. armata	Chilean Torrent Duck
M. a. colombiana	Colombian Torrent Duck
M. a. leucogenis	Peruvian Torrent Duck
M. a. turneri	Turner's Torrent Duck
M. a. garleppi	Bolivian Torrent Duck
M. a. berlepschi	Argentine Torrent Duck
Genus *Anas*	
(Subgenus *Salvadorina*)	
A. waigiuensis	Salvadori's Duck
(Subgenus *Speculanas*)	
A. sparsa	African Black Duck
A. s. sparsa	South African Black Duck

* Where generic allocation differs from that of Delacour (1954–1959), Delacour's genera are indicated in parentheses.

A. s. leucostigma	Abyssinian Black Duck
A. s. maclatchyi	Gabon Black Duck
(Subgenus *Anas*)	
A. penelope	European Wigeon
A. americana	American Wigeon
A. sibilatrix	Chiloé Wigeon
A. falcata	Falcated Duck
A. strepera	Gadwall
A. s. strepera	Common Gadwall
A. s. couesi	Coues' Gadwall
A. formosa	Baikal Teal
A. crecca	Common Teal
A. c. crecca	European Teal
A. c. carolinensis	American Green-winged Teal
A. c. nimia	Aleutian Green-winged Teal
A. flavirostris	South American Teal
A. f. flavirostris	Chilean Teal
A. f. oxyptera	Sharp-winged Teal
A. f. andium	Andean Teal
A. f. altipetens	Merida Teal
A. capensis	Cape Teal
A. gibberifrons	Gray Teal
A. g. gibberifrons	East Indian Gray Teal
A. g. remissa	Rennell Island Gray Teal
A. g. gracilis	Australian Gray Teal
A. g. albogularis	Andaman Teal
A. bernieri	Madagascan Teal
A. castanea	Chestnut Teal
A. aucklandica	Brown Teal
A. a. aucklandica	Auckland Island Flightless Teal
A. a. nesiotis	Campbell Island Flightless Teal
A. a. chlorotis	New Zealand Brown Teal
A. platyrhynchos	Mallard
A. p. platyrhynchos	Common Mallard
A. p. conboschas	Greenland Mallard
A. p. diazi	Mexican Duck
A. p. fulvigula	Florida Duck
A. p. maculosa	Mottled Duck
A. p. wyvilliana	Hawaiian Duck
A. p. laysanensis	Laysan Duck
A. rubripes	American Black Duck
A. melleri	Meller's Duck
A. undulata	Yellow-billed Duck

A. u. undulata	South African Yellow-billed Duck
A. u. ruppelli	Abyssinian Yellow-billed Duck
A. poecilorhyncha	Spot-billed Duck
A. p. poecilorhyncha	Indian Spot-billed Duck
A. p. haringtoni	Burmese Spot-billed Duck
A. p. zonorhyncha	Chinese Spot-billed Duck
A. p. superciliosa	New Zealand Gray Duck
A. p. pelewensis	Pelew Island Gray Duck
A. p. rogersi	Australian Black Duck
A. luzonica	Philippine Duck
A. specularis	Bronze-winged Duck
A. specularioides ("*Lophonetta*")	Crested Duck
A. s. specularioides	Patagonian Crested Duck
A. s. alticola	Andean Crested Duck
A. acuta	Pintail
A. a. acuta	Common Pintail
A. a. eatoni	Kerguelen Pintail
A. a. drygalskii	Crozet Pintail
A. georgica	Yellow-billed Pintail
A. g. georgica	South Georgian Pintail
A. g. spinicauda	Chilean Pintail
A. g. niceforoi	Niceforo's Pintail
A. bahamensis	Bahama Pintail
A. b. bahamensis	Northern Bahama Pintail
A. b. rubrirostris	Southern Bahama Pintail
A. b. galapagensis	Galapagos Pintail
A. erythrorhyncha	Red-billed Pintail
A. versicolor	Silver Teal
A. v. versicolor	Northern Silver Teal
A. v. fretensis	Southern Silver Teal
A. v. puna	Puna Silver Teal
A. punctata	Hottentot Teal
A. querquedula	Garganey
A. discors	Blue-winged Teal
A. cyanoptera	Cinnamon Teal
A. c. cyanoptera	Argentine Cinnamon Teal
A. c. orinomus	Andean Cinnamon Teal
A. c. borreroi	Borrero's Cinnamon Teal
A. c. tropica	Tropical Cinnamon Teal
A. c. septentrionalium	Northern Cinnamon Teal
A. platalea	Red Shoveler
A. smithi	Cape Shoveler

A. rhynchotis	Australasian Shoveler
A. r. rhynchotis	Australian Shoveler
A. r. variegata	New Zealand Shoveler
A. clypeata	Common Shoveler
Genus *Malacorhynchus*	
M. membranaceus	Pink-eared Duck
Genus *Marmaronetta* ("*Anas*")	
M. angustirostris	Marbled Teal

Tribe Aythyini

Genus *Rhodonessa*	
R. caryophyllacea	Pink-headed Duck
Genus *Netta*	
N. rufina	Red-crested Pochard
N. erythropthalma	Southern Pochard
N. e. erythropthalma	South American Pochard
N. e. brunnea	African Pochard
N. peposaca	Rosy-bill
Genus *Aythya*	
A. vallisneria	Canvasback
A. ferina	European Pochard
A. americana	Redhead
A. collaris	Ring-necked Duck
A. australis	Australasian White-eye
A. a. australis	Australian White-eye
A. a. extima	Banks Island White-eye
A. baeri	Baer's Pochard
A. nyroca	Common White-eye
A. innotata	Madagascan White-eye
A. novae-seelandiae	New Zealand Scaup
A. fuligula	Tufted Duck
A. marila	Greater Scaup
A. m. marila	European Greater Scaup
A. m. mariloides	Pacific Greater Scaup
A. affinis	Lesser Scaup

Tribe Mergini

Genus *Somateria*	
S. mollissima	Common Eider
S. m. mollissima	European Eider
S. m. borealis	Northern Eider

S. m. dresseri	American Eider
S. m. faeroeensis	Faeroe Eider
S. m. v-nigra	Pacific Eider
S. spectabilis	King Eider
S. fischeri	Spectacled Eider
Genus *Polysticta*	
P. stelleri	Steller's Eider
Genus *Camptorhynchus*	
C. labradorius	Labrador Duck
Genus *Histrionicus*	
H. histrionicus	Harlequin Duck
Genus *Clangula*	
C. hyemalis	Long-tailed Duck
Genus *Melanitta*	
M. nigra	Black Scoter
M. n. nigra	European Black Scoter
M. n. americana	American Black Scoter
M. perspicillata	Surf Scoter
M. fusca	White-winged Scoter
M. f. fusca	European White-winged Scoter
M. f. stejnegeri	Asiatic White-winged Scoter
M. f. dixoni	Pacific White-winged Scoter
M. f. deglandi	American White-winged Scoter
Genus *Bucephala*	
B. albeola	Bufflehead
B. islandica	Barrow's Goldeneye
B. clangula	Common Goldeneye
B. c. clangula	European Common Goldeneye
B. c. americana	American Common Goldeneye
Genus *Mergus*	
(Subgenus *Lophodytes*)	
M. cucullatus	Hooded Merganser
(Subgenus *Mergellus*)	
M. albellus	Smew
(Subgenus *Mergus*)	
M. octosetaceus	Brazilian Merganser
M. serrator	Red-breasted Merganser
M. s. serrator	Common Red-breasted Merganser
M. s. schioleri	Greenland Red-breasted Merganser
M. squamatus	Chinese Merganser
M. merganser	Goosander

M. m. merganser	European Goosander
M. m. orientalis	Asiatic Goosander
M. m. americanus	American Goosander
M. australis	Auckland Island Merganser

Tribe Oxyurini

Genus *Heteronetta*	
H. atricapilla	Black-headed Duck
Genus *Oxyura*	
(Subgenus *Nomonyx*)	
O. dominica	Masked Duck
(Subgenus *Oxyura*)	
O. jamaicensis	Ruddy Duck
O. j. jamaicensis	North American Ruddy Duck
O. j. andina	Colombian Ruddy Duck
O. j. ferruginea	Peruvian Ruddy Duck
O. leucocephala	White-headed Duck
O. maccoa	Maccoa Duck
O. vittata	Argentine Ruddy Duck
O. australis	Australian Blue-billed Duck
Genus *Biziura*	
B. lobata	Musk Duck
Genus *Thalassornis*	
T. leuconotus	White-backed Duck
T. l. leuconotus	African White-backed Duck
T. l. insularis	Madagascan White-backed Duck

Works Cited

Adams, R. G. (1947). Mating behaviour of wigeon and red-breasted merganser. British Birds, 40:186–187.

Ali, S. (1960). The pink-headed duck *Rhodonessa caryophyllacea* (Latham). Wildfowl Trust 11th Annual Report, pp. 54–58.

Armstrong, E. A. (1947). Bird display and behaviour. Lindsay Drummond, London. 431 pp.

Balham, R. W. (1954). The behavior of the Canada goose (*Branta canadensis*) in Manitoba. Ph.D. Thesis, Univ. of Missouri. 244 pp.

Banko, W. E. (1960). The trumpeter swan. North American Fauna, No. 63. U.S.F.W.S., Washington. 214 pp.

Bennett, K. H. (1891). (Letter to editor on the blue-billed duck.) Ibis, (6)3:143–145.

Blurton Jones, N. G. (1960). Experiments on the causation of the threat postures of Canada geese. Wildfowl Trust 11th Annual Report, pp. 44–52.

Boase, H. (1959). Notes on the display, nesting and moult of the mute swan. British Birds, 52:114–123.

Bretherton, B. J. (1896). Kadiak Island, a contribution to the avifauna of Alaska. Oregon Nat., 3:45–49, 61–64, 77–79, 100–102.

Brown, A. G. (1949). Display of blue-billed ducks. Emu, 48:315.

Cawkell, E. M. and J. E. Hamilton. (1961). The birds of the Falkland Islands. Ibis, 103a:1–27.

Christoleit, E. (1926). Bemerkungen zur Biologie der Schwäne. J. Ornith., 74:464–490.

Collias, N. E., and L. R. Jahn. (1959). Social behavior and breeding success in Canada geese (*Branta canadensis*) confined under semi-natural conditions. Auk, 76:479–509.

Cooch, F. G. (1958). The breeding biology and management of the blue goose, *Chen caerulescens*. Ph.D. Thesis, Cornell Univ. 246 pp.

—— (1961). Ecological aspects of the blue-snow goose complex. Auk, 78:72–89.

Curth, P. (1954). Der Mittelsäger. Die Neue Brehm-Bucherei, Heft 126. 102 pp.

Dane, B., C. Walcott, and W. H. Drury. (1959). The form and duration of the display actions of the goldeneye (*Bucephala clangula*). Behaviour, 14:265–281.

Davies, S. J. J. F. (1962). The nest-building behaviour of the magpie goose. Ibis, 104:147–157.

Delacour, J. (1945). The display of the maned goose. Wilson Bull., 57: 129.

—— (1954, 1956, 1959, 1964). The waterfowl of the world. 4 vol. Country Life, London.

Delacour, J., and E. Mayr. (1945). The family Anatidae. Wilson Bull., 57:3–55.

Dilger, W. C., and P. A. Johnsgard. (1959). Comments on "species recognition" with special reference to the wood duck and mandarin duck. Wilson Bull., 71:46–53.

Drury, W. H., Jr. (1961). Observations on some breeding water birds on Bylot Island. Canad. Field Nat., 75:84–101.

Dzubin, A. (1957). Pairing display and spring and summer flights of the mallard. Blue Jay, 15:10–13.

Finn, F. (1901). Some out of the way ducks. Avic. Mag. (1)7:129–134.

—— (1915). Display of female *Eunetta falcata*. Zoologist, 19:36.

—— (1919). Bird behaviour. London. 363 pp.

Frith, H. J. (1959). The ecology of wild ducks in inland New South Wales. (In four parts.) C.S.I.R.O. Wildlife Research, 4:97–181.

—— (1964). The downy plumage of the freckled duck. Nature, 202: 1352–1353.

Giai, A. G. (1950). Notas de viages. II. Por el norte de Misiones. Hornero, 9:139–164.

Goodall, J. D., *et al.* (1951). Las aves de Chile, su conocimiento y sus costumbres. Vol. 2. Buenos Aires, 445 pp.

Gray, A. P. (1958). Bird hybrids. Commonwealth Agricultural Bureaux of England. 390 pp.

Gunn, D. (1927). The courtship of the common scoter. British Birds, 20:193–197.

Heinroth, O. (1910). Beobachtungen bei einem Einbürgerungsversuch mit der Brautente (*Lampronessa sponsa* (L.)). J. Ornith., 58:101–156.

—— (1911). Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. Proc. V. Inter. Ornith. Congr., Berlin, 1910, pp. 598–702.

Hellmayr, C. E. (1932). The birds of Chile. Field Mus. Nat. Hist. Pub. 380, Zool. Ser., 19:1–472.

Hilprecht, A. (1956). Höcherschwan, Singschwan, Zergschwan. Die Neue Brehm-Bucherei, Heft 177. 151 pp.

Hinde, R. A. (1959). Behaviour and speciation in birds and lower vertebrates. Biol. Rev., 34:85–128.

Hochbaum, H. A. (1944). The canvasback on a prairie marsh. Amer. Wildl. Inst., Washington. 201 pp.

Hollister, N. (1919). The systematic position of the ring-necked duck. Auk, 36:460–463.

Hollom, P. A. D. (1937). Observations on the courtship and mating of the smew. British Birds., 31:106–111.

Hoogerheide, C. (1950). De Eidereenden, *Somateria mollissima* L., op Vlieland. Ardea, 37:139–160.

Humphrey, P. S. (1955). The relationships of the sea ducks (Tribe Mergini). Ph.D. Thesis, Univ. of Michigan. 212 pp.

—— (1957). Remarks on the courtship and voice of the black scoter. Condor, 59:139–140.

—— (1958). Classification and systematic position of the eiders. Condor, 60:129–135.

Humphrey, P. S., and R. S. Butsch. (1958). The anatomy of the Labrador duck, *Camptorhynchus labradorius* (Gmelin). Smithsonian Misc. Coll., 135(7):23 pp.

Humphrey, P. S., and S. D. Ripley. (1962). The affinities of the pink-headed duck. Postilla, 61:21 pp.

Huxley, J. S. (1947). Display of the mute swan. British Birds., 40:130–134.

Johnsgard, P. A. (1955). Courtship activities of the Anatidae in eastern Washington. Condor, 57:19–27.

—— (1959). Evolutionary relationships among the North American mallards. Ph.D. Thesis, Cornell Univ. 153 pp.

—— (1960a). Hybridization in the Anatidae and its taxonomic implications. Condor, 62:25–33.

—— (1960b). Comparative behaviour of the Anatidae and its evolutionary implications. Wildfowl Trust 11th Annual Report, pp. 31–45.

—— (1960c). Pair-formation mechanisms in *Anas* (Anatidae) and related genera. Ibis, 102:616–618.

—— (1960d). A quantitative study of sexual behavior of mallards and black ducks. Wilson Bull., 72:135–155.

—— (1960e). The systematic position of the ringed teal. Bull. Brit. Orn. Club., 80:165–167.

—— (1960f). Classification and evolutionary relationships of the sea ducks. Condor, 62:426–433.

—— (1961a). The taxonomy of the Anatidae—A behavioural analysis. Ibis, 103a:71–85.

—— (1961b). The breeding biology of the magpie goose. Wildfowl Trust 12th Annual Report, pp. 92–103.

—— (1961c). The tracheal anatomy of the Anatidae and its taxonomic significance. Wildfowl Trust 12th Annual Report, pp. 58–69.

—— (1961d). The sexual behavior and systematic position of the hooded merganser. Wilson Bull., 73:226–236.

—— (1961e). The systematic position of the marbled teal. Bull. Brit. Orn. Club., 81:37–43.

—— (1961f). Evolutionary relationships among the North American mallards. Auk, 78:3–43.

—— (1962). Evolutionary trends in the behaviour and morphology of the Anatidae. Wildfowl Trust 13th Annual Report, pp. 130–148.

—— (1964). Comparative behavior and relationships of the eiders. Condor, 66:113–129.

—— (1965a). Observations on some aberrant Australian Anatidae. Wildfowl Trust 16th Annual Report. (In press.)

—— (1965b). Behavior of the Australian musk duck and blue-billed duck. Auk. (In press.)

Johnson, A. W. (1963). Notes on the distribution, reproduction and display of the Andean torrent duck *Merganetta armata*. Ibis, 105: 114–116.

Jones, T. (1948). The Andean crested duck. Avic. Mag., 54:196–199.

—— (1951). Marbled teal. Avic. Mag., 57:183–184.

Kerr, J. G. (1890). (Letter to editor.) Ibis, (6)2:350–365.

Klopman, R. B. (1962). Sexual behavior in the Canada goose. The Living Bird, vol. 1, pp. 123–129.

Koskimies, J., and E. Routamo. (1953). Zur Fortpflanzungsbiologie der Samtente *Melanitta f. fusca* (L). Papers Game Research, Helsingf., 10:1–105.

Kuroda, N. (1942). A bibliography of the duck tribe. Tokyo. 852 pp.

Lebret, T. (1958a). The "jump-flight" of the mallard, *Anas platyrhynchos* L., the teal, *Anas crecca* L., and the shoveler, *Spatula clypeata* L. Ardea 46:68–72.

—— (1958b). Baltsbewegingen van het Nonnetje, *Mergus albellus* L. Ardea 46:68–78.

—— (1961). The pair formation in the annual cycle of the mallard, *Anas platyrhynchos* L. Ardea, 49:7–157.

Lind, H. (1958). Eine Untersuchung über das Balzverhalten der Kolbenente (*Netta rufina* Pallas). Z. Tierpsychol., 15:99–111.

—— (1959). Studies on courtship and copulatory behavior in the goldeneye (*Bucephala clangula* (L.)). Dansk Ornith. Foren Tidssk., 53: 177–219.

—— (1962). Zur Analyse des sexuellen verhaltens der Kolbenente, *Netta rufina* (Pallas). Z. Tierpsychol., 19:607–625.

Lorenz, K. Z. (1941). Vergliechende Bewegungsstudien an Anatinen. J. Ornith., 89 (Suppl.):194–294.

—— (1951–1953). Comparative studies on the behaviour of the Anatinae. Avic. Mag., 57:157–182; 58:8–17, 61–72, 86–94, 172–184; 59:24–34, 80–91.

—— (1958). The evolution of behaviour. Sci. Amer., 199(6):67–78.

Lorenz, K. Z., and W. von de Wall. (1960). Die Ausdrucksbewegungen der Sichelente, *Anas falcata* L. J. Ornith., 101:50–60.

McKinney, D. G. (1953). Studies on the behaviour of the Anatidae. Ph.D. Thesis, Univ. of Bristol, England. 227 pp.

—— (1959). Waterfowl at Cold Bay, Alaska, with notes on the display of the black scoter. Wildfowl Trust 10th Annual Report, pp. 133–140.

—— (1961). An analysis of the displays of the European eider *Somateria mollisima mollissima* (Linnaeus) and the Pacific eider *Somateria mollissima v. nigra* Bonaparte. Behaviour, Suppl. VII. 123 pp.

Macnae, W. (1959). Notes on the biology of the maccoa duck. Bokmakierie, 11:49–52.

Mayr, E. (1931). Zur Anatomie und systematischen Stellung der Salvadori-Ente (*Salvadorina waigiuensis* Rothsch. & Hartert). Orn. Monatsb., 3:69–70.

—— (1942). Systematics and the origin of species. Columbia Univ. Press. 334 pp.

Meanley, B., and A. G. Meanley. (1958). Postcopulatory display in fulvous and black-bellied tree ducks. Auk, 75:96.

Mendall, H. L. (1958). The ring-necked duck in the Northeast. Univ. Maine Bull., 60(16):317.

Mountfort, G. (1958). Portrait of a wilderness. Hutchinsons, London. 240 pp.

Moynihan, M. (1955). Remarks on the original sources of displays. Auk, 72:240–246.

—— (1958). Notes on the behavior of the flying steamer duck. Auk, 75:183–202.

Murphy, R. C. (1936). Oceanic birds of South America. Vol. 1 Amer. Mus. Nat. Hist. 640 pp.

Myres, M. T. (1959a). The behaviour of the sea-ducks and its value in the systematics of the tribes Mergini and Somateriini, of the family Anatidae. Ph.D. Thesis, Univ. British Columbia. 504 pp.

—— (1959b). Display behavior of bufflehead, scoters and goldeneyes at copulation. Wilson Bull., 71:159–168.

Niethammer, G. (1952). Zur Anatomie und systematischen Stellung der Sturzbach-Ente (*Merganetta armata*). J. Ornith., 93:357–360.

Partridge, W. H. (1956). Notes on the Brazilian merganser in Argentina. Auk, 73:473–488.

Phillips, J. C. (1922–1926). The natural history of the ducks. 4 vols. Houghton Mifflin, Boston.

Phillips, S. (1953). An incident concerning the Peruvian torrent duck. Avic. Mag., 59:134.

Poulsen, H. (1949). Bidrag til Svanerne Ethologi. Dansk Ornith. Foren. Tidsskr., 42:172–201.

Prestwich, A. A. (1960). On mandarin duck hybrids. Avic. Mag., 66:5–8.

Ringlegen, H. (1951). Aus dem leben des Mittelsagers (*Mergus serrator* L.). I. Vogelwelt, 72:43–50, 84–87, 119–128.

Ripley, S. D. (1942). A review of the species *Anas castanea*. Auk, 59: 90–99.

—— (1963). Courtship in the ring-necked duck. Wilson Bull., 75:373–375.

Salomonsen, F. (1949). Some notes on the moult of the long-tailed duck. Avic. Mag., 55:59–62.

Savage, C. (1952). The mandarin duck. A. & C. Black, London. 78 pp.

Scott, P. (1954). Behaviour of the Bolivian torrent duck. Wildfowl Trust 6th Annual Report, pp. 69–72.

—— (1958). Notes on Anatidae seen on world tour. Wildfowl Trust 9th Annual Report, pp. 86–112.

Serventy, V. N. (1945). Display in the musk duck. Emu, 45:318–321.

Sibley, C. G. (1957). The evolutionary and taxonomic significance of sexual dimorphism and hybridization in birds. Condor, 59:166–191.

Sibley, C. L. (1938). Hybrids of and with North American Anatidae. Proc. IX Inter. Ornith. Congr., Rouen, 1938, 327–355.

Smith, R. I. (1963). The social aspects of reproductive behavior in the pintail (*Anas acuta acuta* L.). Ph.D. Thesis, Utah State Univ., Logan. 72 pp.

Sowls, L. K. (1955). Prairie ducks. Stackpole Co., Wildl. Mgmt. Inst. 193 pp.

Steinbacher, G. (1953). Zur Ethologie der Türkente. Vogelwelt, 74:7–9.

—— (1960). Zur Balz der Tauschenten. Vogelwelt, 81:1–16.

Stonor, C. R. (1939). Notes on the breeding habits of the common screamer. Ibis, (14)3:45–49.

Stresemann, V. (1948). Eclipse plumage and nuptial plumage in the old squaw, or long-tailed duck. Avic. Mag. 54:188–194.

Timmerman, G. (1963). Fragen der Anatidensystematik in parasitologischer Sicht. Proc. XIII Inter. Ornith. Congr., Ithaca, 1962, pp. 189–197.

Verheyen, R. (1953). Contribution à l'ostéologie et à la systématique des Anseriformes. Gerfaut, 43 (Suppl.):373–497.

Von Boetticher, H. (1942). Gänse und Entenvögel aus aller Welt. Die Neue Brehm-Bucherei, Heft 73. 95 pp.

Von de Wall, W. (1963). Bewegungsstudien an Anatinen. J. Ornith, 104:1–15.

Warham, J. (1958). The nesting of the pink-eared duck. Wildfowl Trust 9th Annual Report, pp. 118–127.

Weidmann, U. (1956). Verhaltensstudien an der Stockente (*Anas platyrhynchos* L.). I. Das Aktionssystem. Z. Tierpsychol., 13:208–271.

Wetmore, A. (1926). Observations on the birds of Argentina, Paraguay, Uruguay and Chile. Bull. U.S. Nat. Mus., Washington. 448 pp.

—— (1951). Observations on the genera of swans. J. Wash. Acad. Sci., 41:338–340.

Wheeler, J. R. (1953). Notes on the blue-billed ducks on Lake Wendouree, Ballarat. Emu, 53:280–282.

Wilson, A. (1829). American ornithology. London and Edinburgh. 3 vol.

Woolfenden, G. E. (1961). Postcranial osteology of the waterfowl. Bull. Florida State Museum; Biological Sciences, 6:1–129.

Wust, A. (1960). Das Problem des Reihen der Enten, besonders von *Anas strepera*. Proc. XII Inter. Ornith. Congr., Helsinki, 1958. pp. 795–800.

Yamashina, Y. (1948). Notes on the Marianas mallards. Pacific Science, 2:121–124.

—— (1952). Classification of the Anatidae based on the cyto-genetics. Papers from the Coordinating Comm. for Research in Genetics, 3:1–34.

Yealland, J. (1951). Hartlaub's duck. Avic. Mag., 57:156.

General Index

The principal page reference for each species or group is indicated by boldface type. Subordinate page references for each species are listed only under the standardized English names used in this book, as shown in the Appendix. Commonly used alternate names, or names referring to certain races or species groups, are included in the index but only principal page references are listed under these names. Page references to illustrations of species or of specific displays are indicated by italics. The Appendix and Summary have not been indexed.

Index of Scientific Names

This index provides a reference only to the page where the principal discussion of each genus or species begins. The general index should be consulted for locations of illustrations and for subordinate references. Several commonly used generic names, here considered synonyms or subgenera, are included for cross reference and are set off by quotation marks.