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Handbook of Waterfowl Behavior: Tribe Anserini (Swans and True Geese)

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

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.

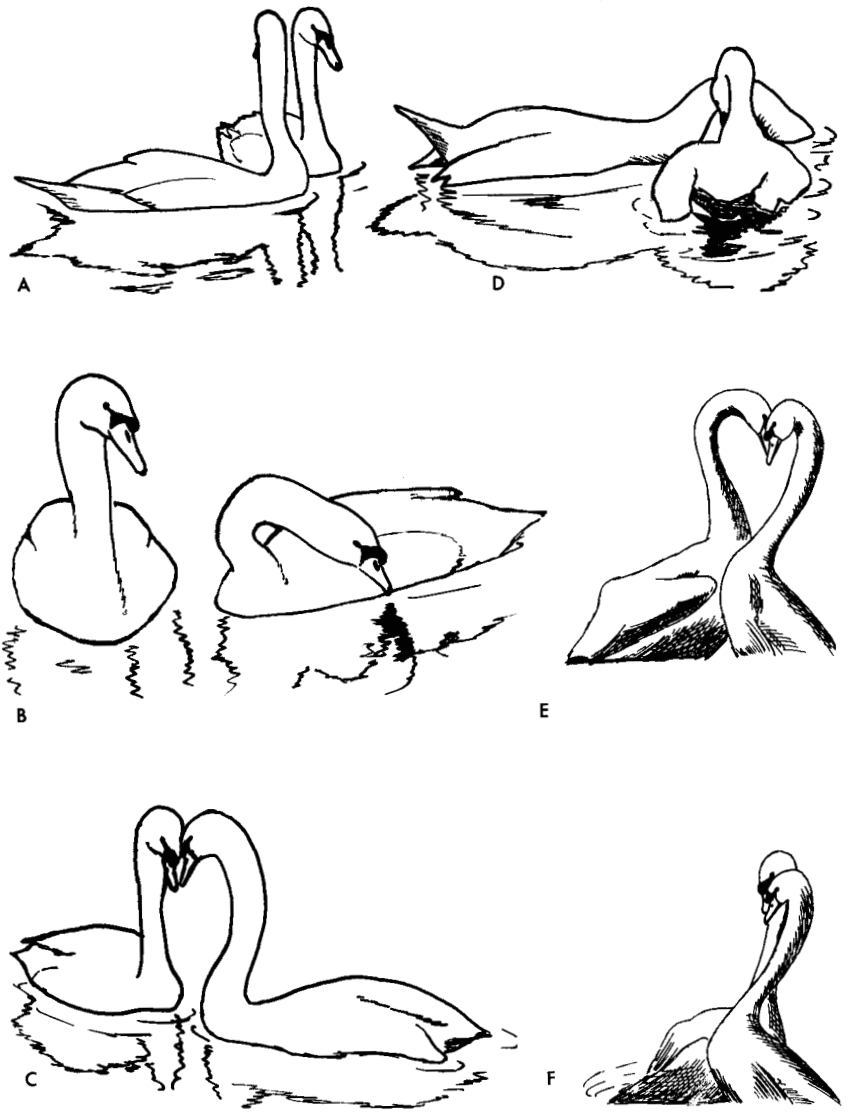


Figure 4. Mute Swan

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

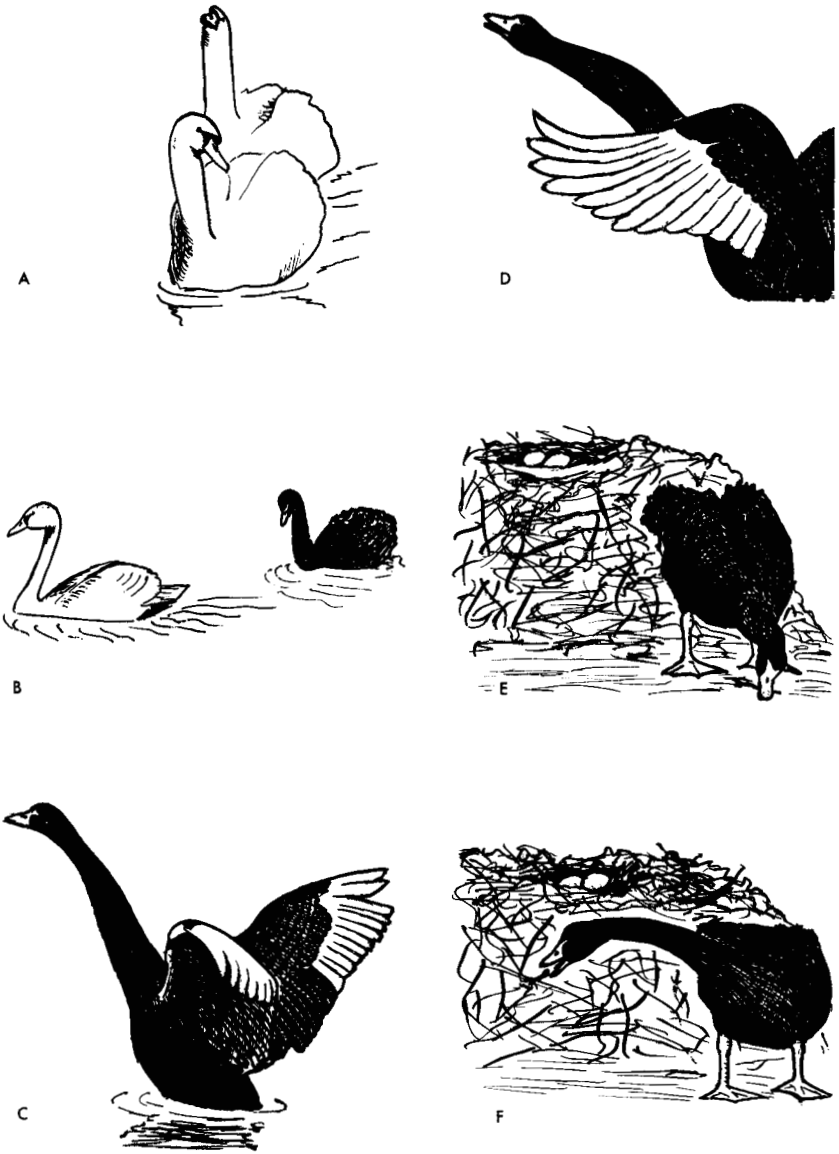


Figure 5. Mute Swan, Black Swan

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.

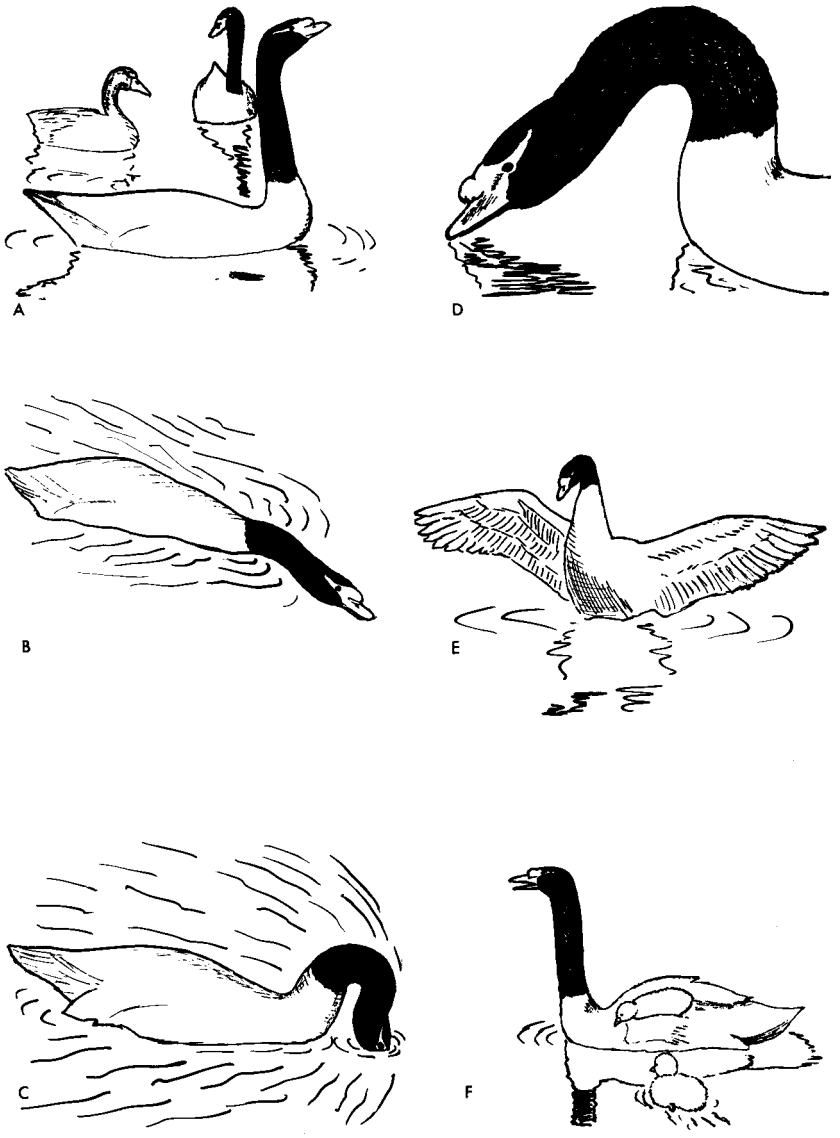


Figure 6. Black-necked Swan

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-

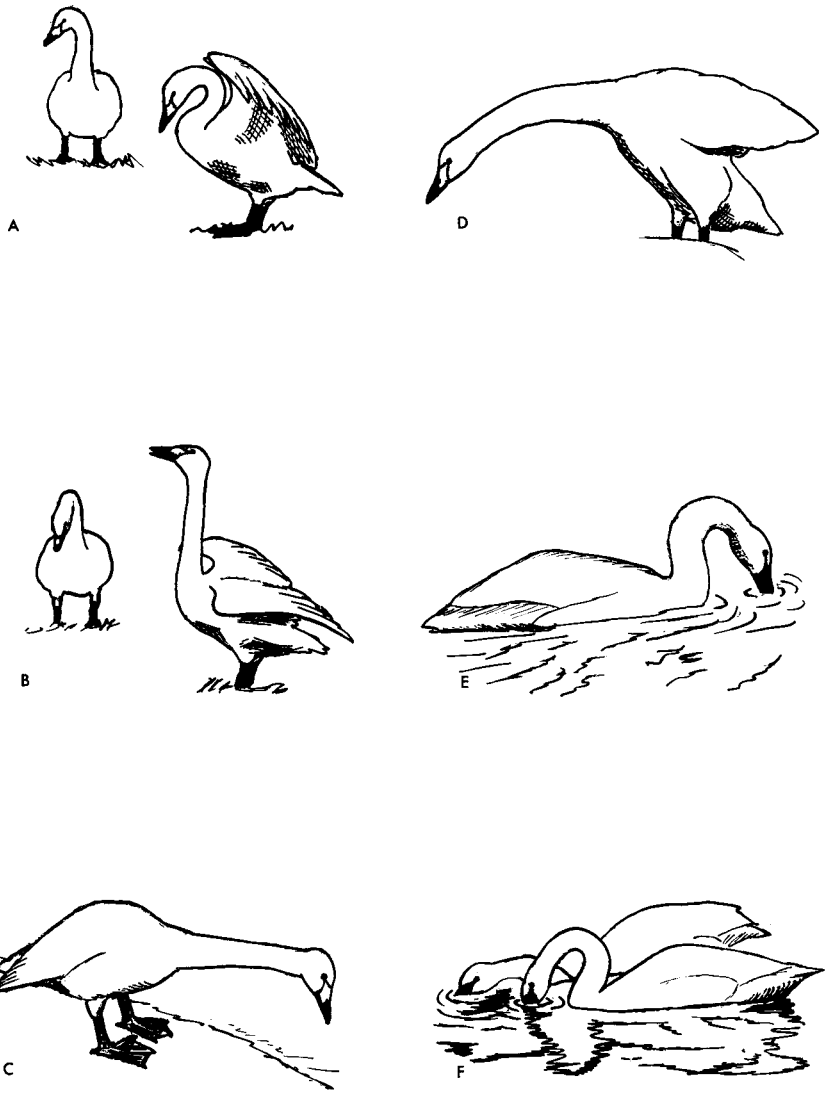


Figure 7. Whooper Swan, Trumpeter Swan

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*).

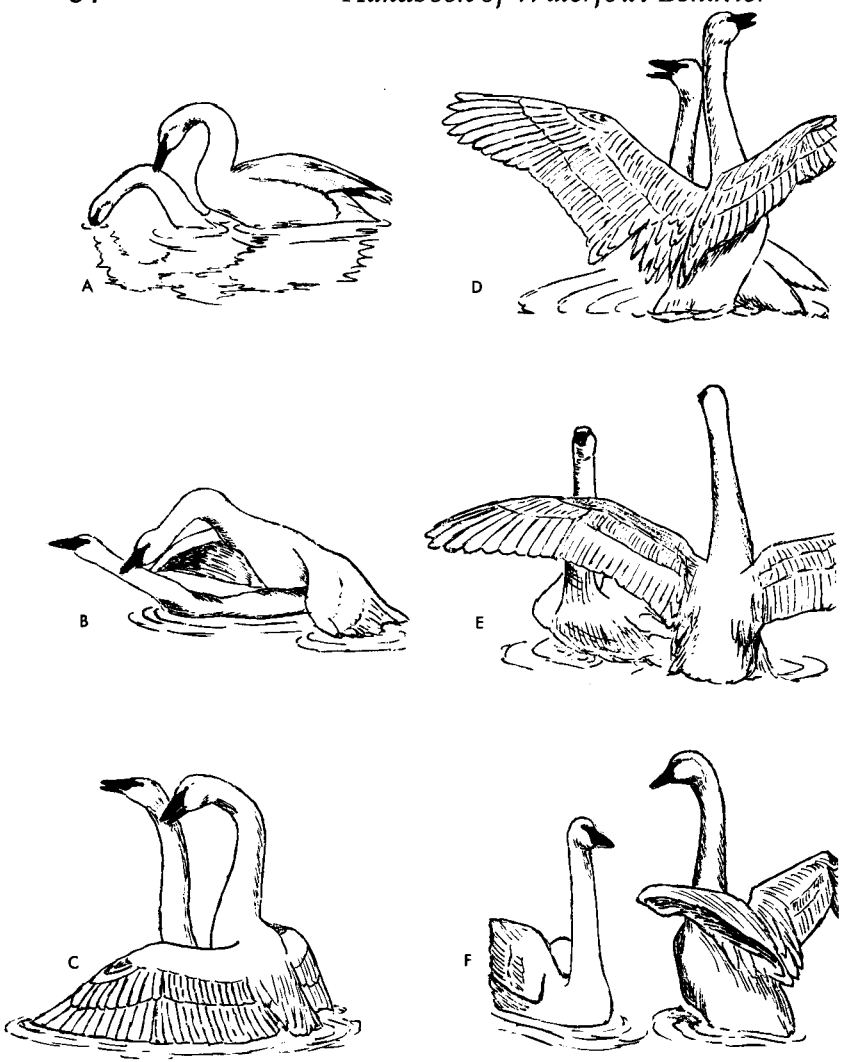


Figure 8. Trumpeter Swan

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

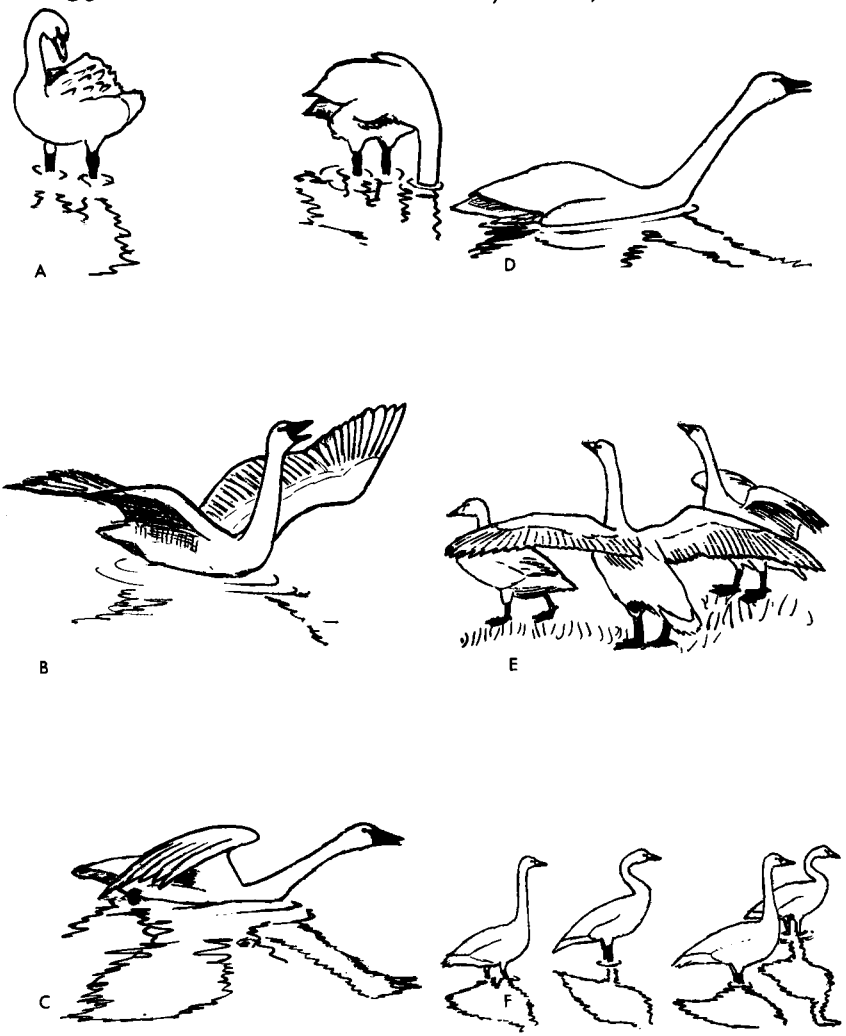


Figure 9. Whistling Swan, Bewick's Swan

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

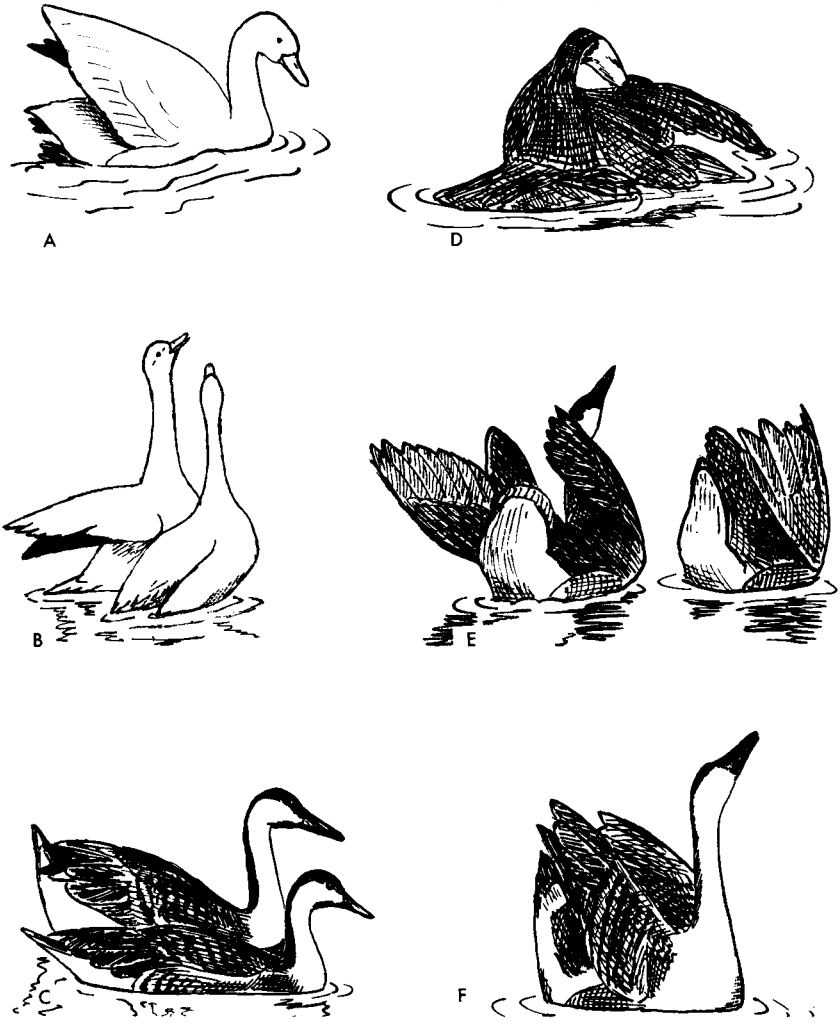


Figure 10. Coscoroba Swan, Swan Goose

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-

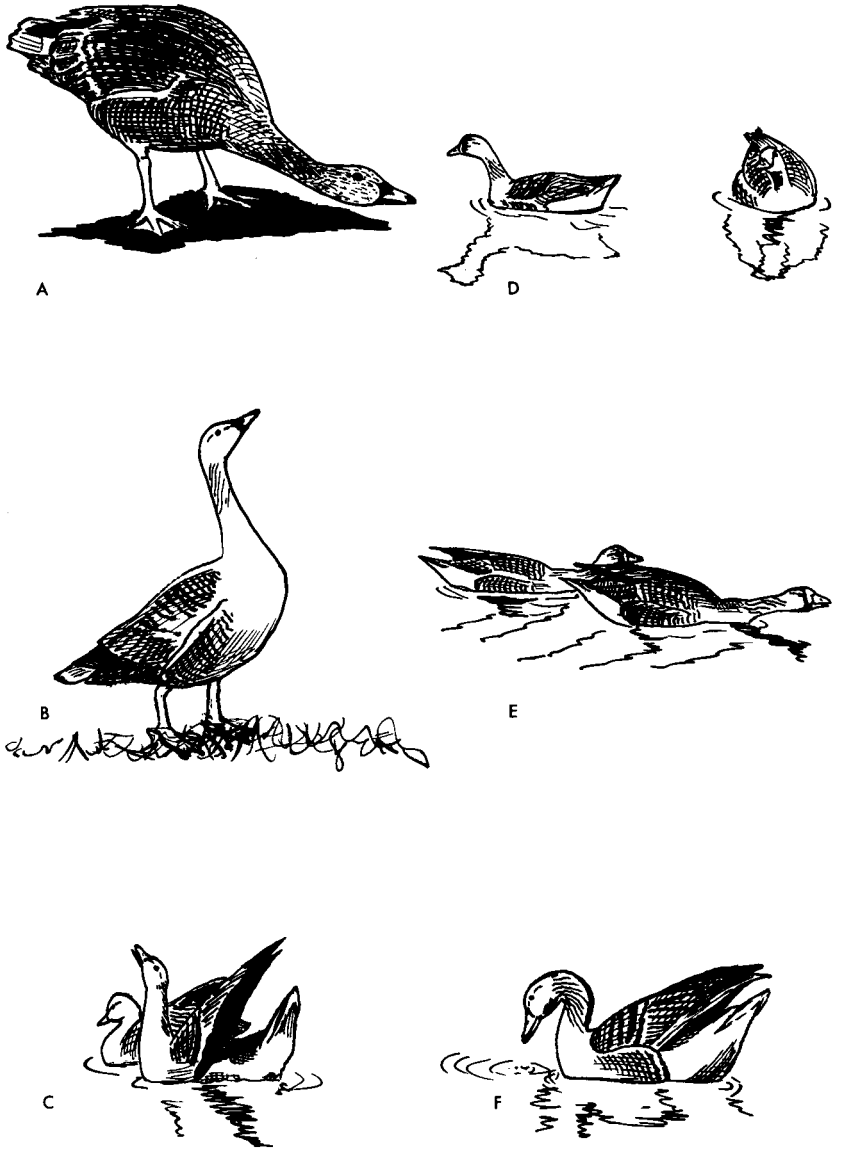


Figure 11. Typical Gray Geese

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

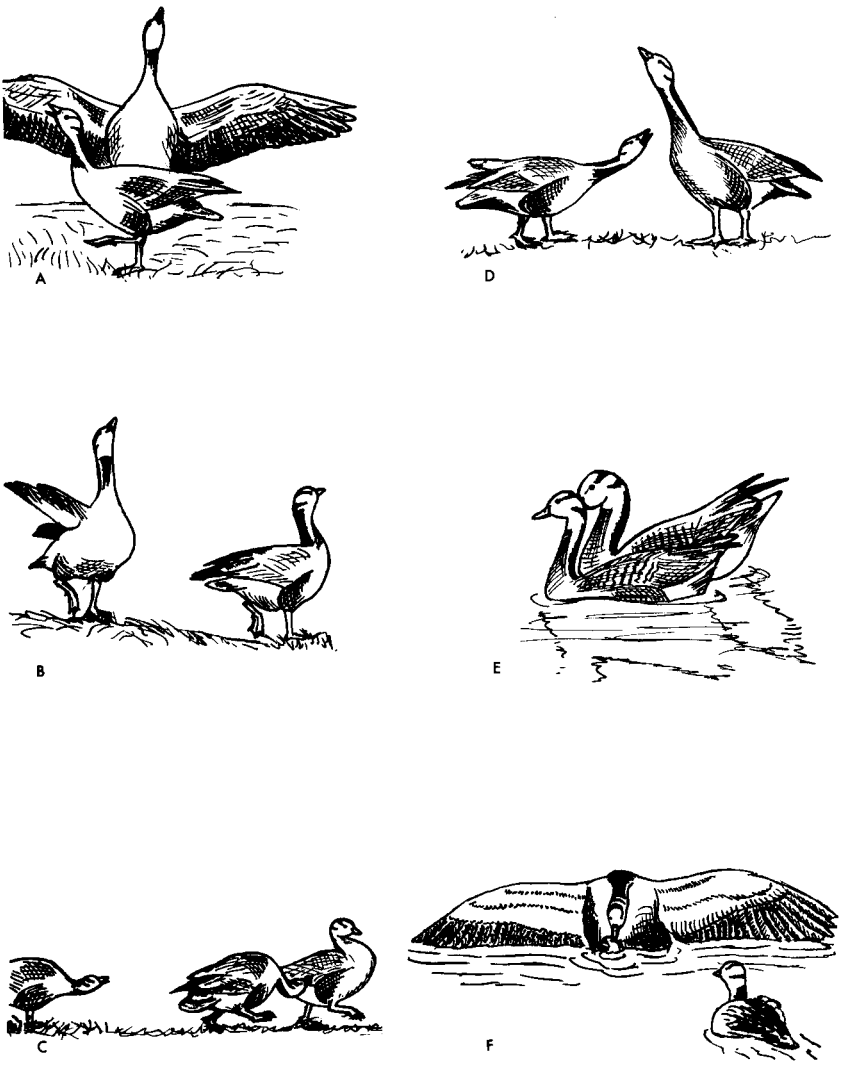


Figure 12. Bar-headed Goose

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.

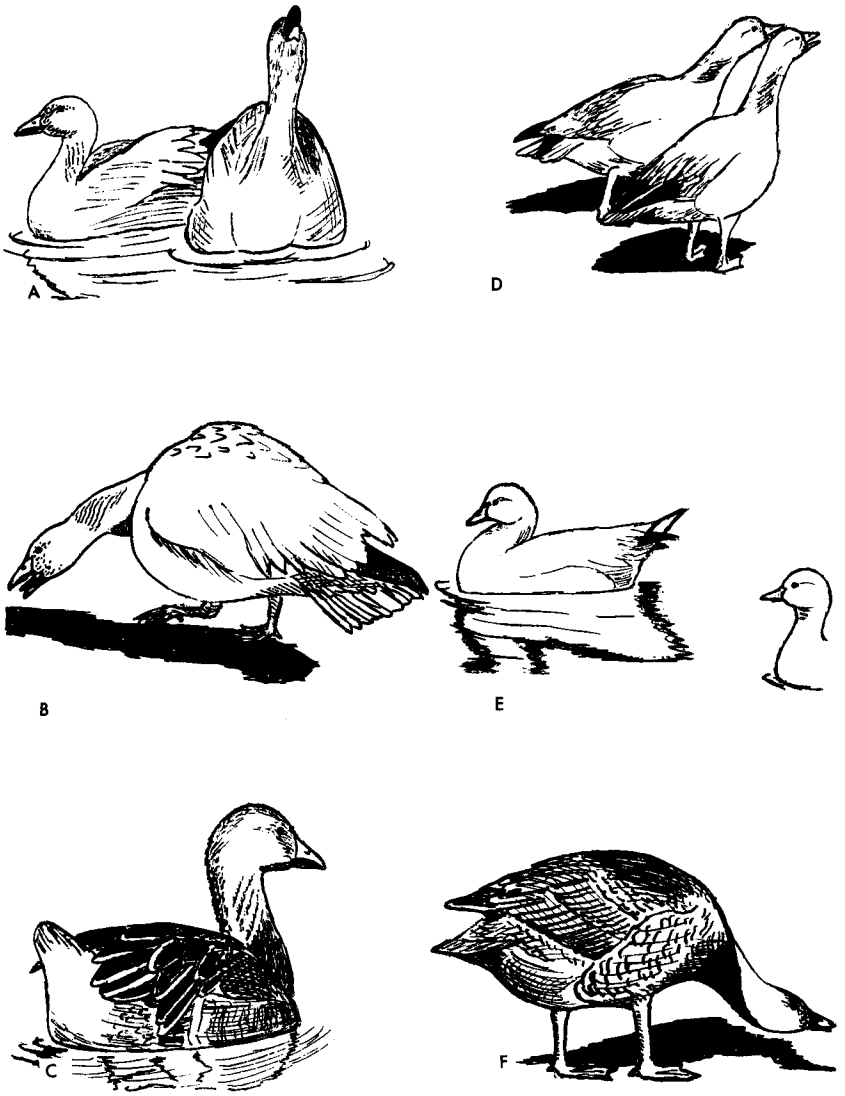


Figure 13. Aberrant Gray Geese

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.

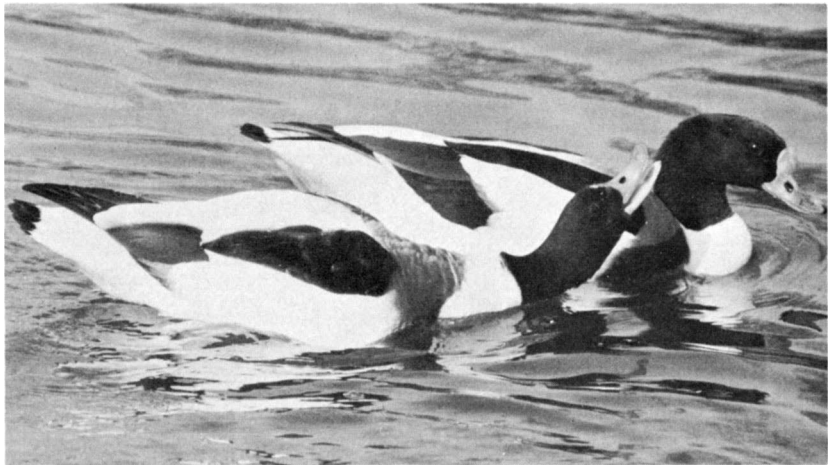
E. Ross's goose male (*left*) courting female. Compare with *C.*

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

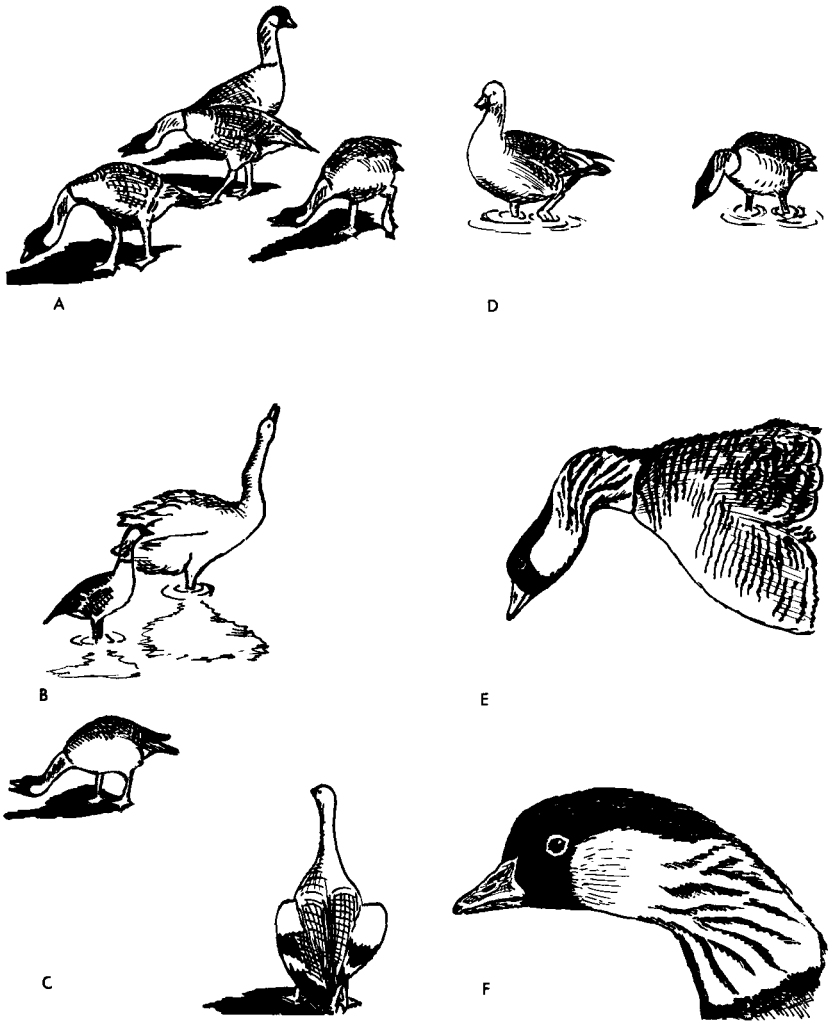


Figure 14. Hawaiian Goose

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.

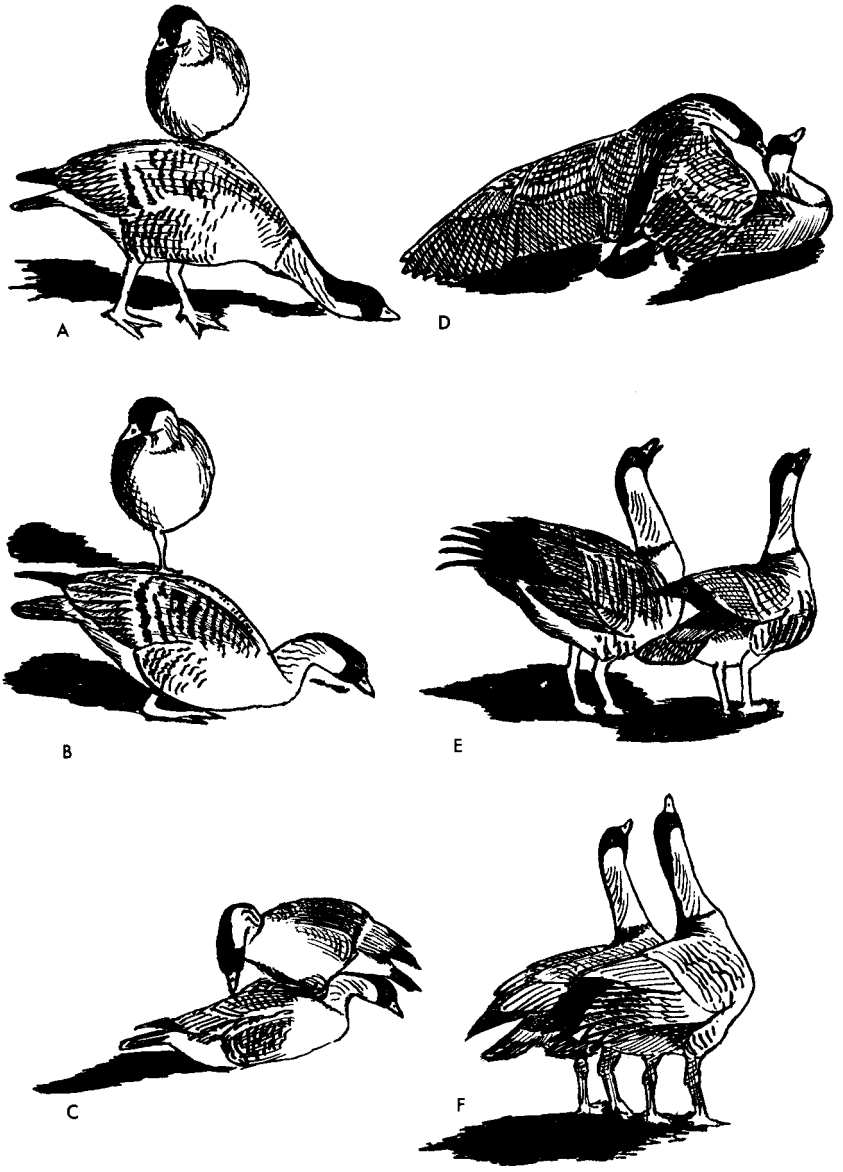


Figure 15. Hawaiian Goose

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

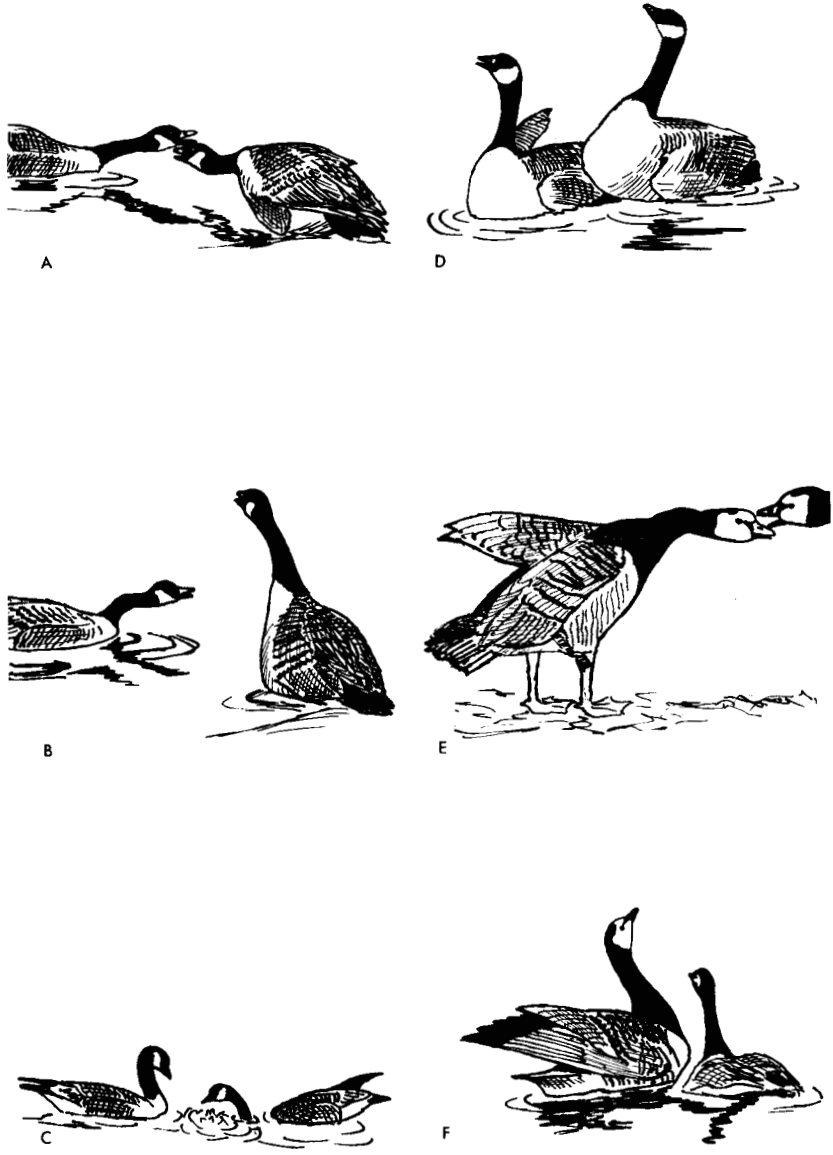


Figure 16. Canada Goose, Barnacle Goose

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-

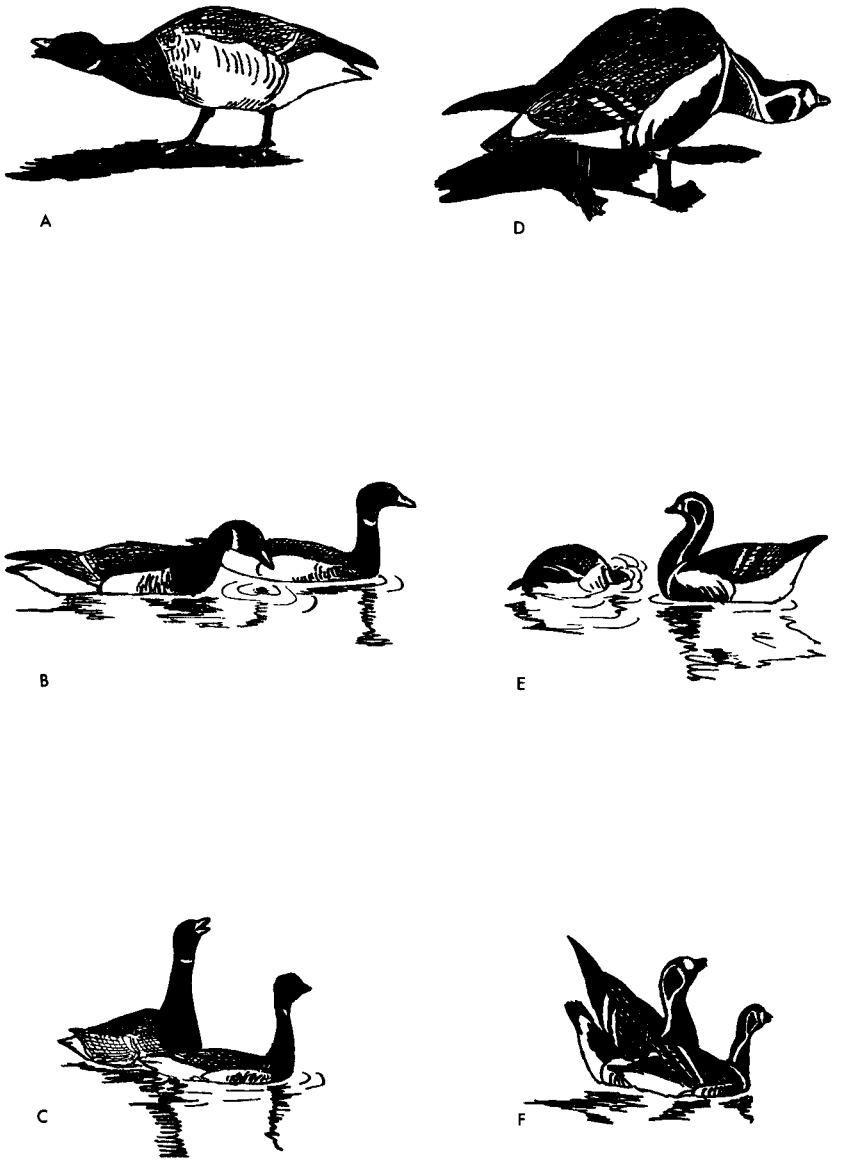


Figure 17. Brant, Red-breasted Goose

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

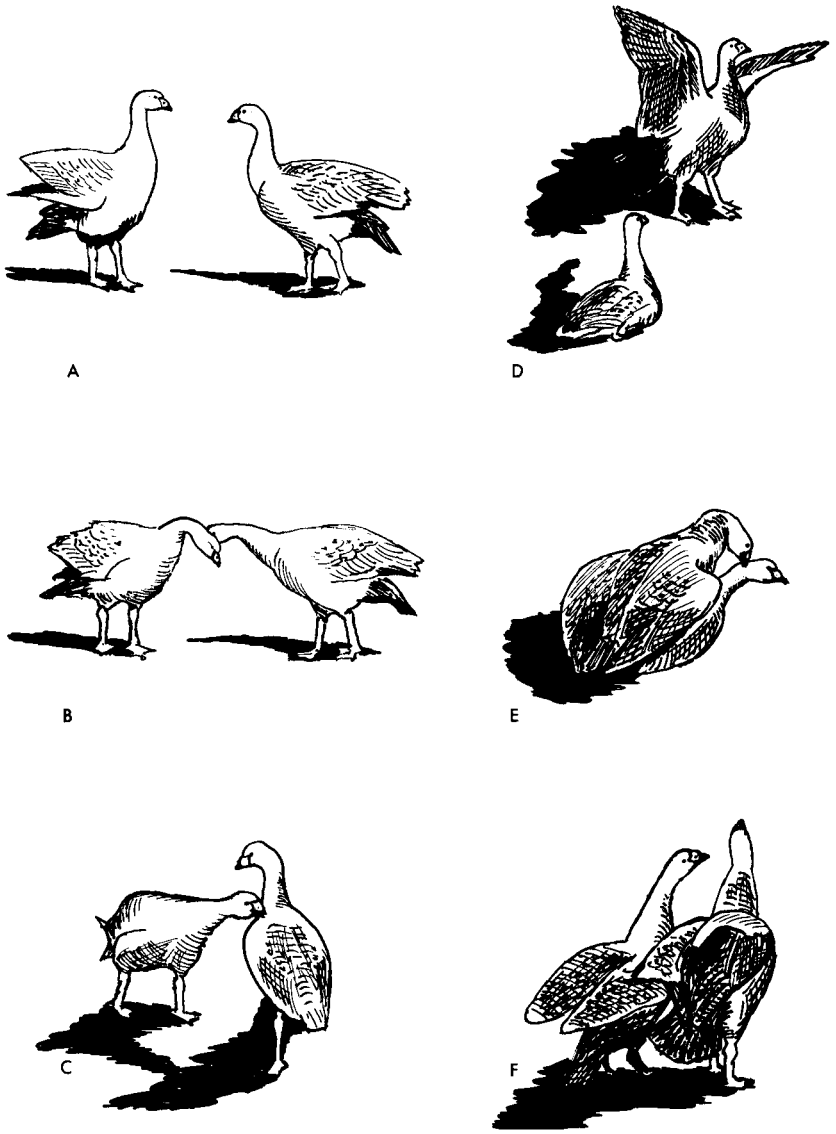


Figure 18. Cape Barren Goose

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*).