

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

---

Waterfowl of North America, Revised Edition  
(2010) by Paul A. Johnsgard

Papers in the Biological Sciences

---

2010

## Waterfowl of North America: The Biology of Waterfowl

Paul A. Johnsgard

University of Nebraska-Lincoln, pajohnsgard@gmail.com

Follow this and additional works at: <https://digitalcommons.unl.edu/biosciwaterfowlna>



Part of the [Ornithology Commons](#)

---

Johnsgard, Paul A., "Waterfowl of North America: The Biology of Waterfowl" (2010). *Waterfowl of North America, Revised Edition (2010)* by Paul A. Johnsgard. 4.  
<https://digitalcommons.unl.edu/biosciwaterfowlna/4>

This Book Chapter is brought to you for free and open access by the Papers in the Biological Sciences at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Waterfowl of North America, Revised Edition (2010) by Paul A. Johnsgard by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

## The Biology of Waterfowl

The term *waterfowl*, at least as it is applied in North America, is generally restricted to the ducks, geese, and swans of the bird family Anatidae. About 140 species of this group of swimming and diving birds have survived throughout the world to the present day, and four more have become extinct during historical times. Many more species have existed in the past; the fossil record of this family extends back roughly fifty million years to very early Cenozoic times, although very little is known of the actual appearance and structure of the earliest form of waterfowl. Presumably these ancestral birds were semiaquatic, perhaps much like the modern-day species of screamers (Anhimidae), which together with the true waterfowl make up the order Anseriformes. These in turn seem to have been derived from land-adapted and fowl-like birds that later diversified into such groups as pheasants, quails, partridges, turkeys, and other “gallinaceous” species.

In part because of their common evolutionary ancestry, waterfowl and the upland, or gallinaceous, birds have certain similarities in their biology that are more fundamental than the obvious differences in their adaptations to aquatic versus terrestrial habitats. One of the most significant of these common attributes is the rather advanced, or precocial, state in which the young are invariably hatched. This implies that they are well covered with down and thus can better maintain a steady body temperature than can birds hatched naked or nearly so. They also are hatched with their eyes open, and they are sufficiently coordinated so that they can begin feeding on their own in a day or less of leaving the egg. They have a variety of calls and can respond quickly and effectively to calls of their parents that may help to keep the family together and safe from danger. They typically remain together as a cohesive “brood” during the period between hatching and initial flight, or fledging, and during this time they undergo the socialization processes that may be impor-

tant later in pair formation at the time of sexual maturity. They also learn the local topography and, especially in the case of females, the landmarks necessary to allow the birds to "home" to their natal area at the time of initial nesting.

Unlike most upland game birds, nearly all North American waterfowl are migratory to some degree, and although the timing and general compass-direction tendencies for movement may be innately transmitted from generation to generation, a considerable part of the specific aspects of migration is dependent on a transmission of migratory "traditions" from the older birds to the younger ones by direct experience. This flexibility in migratory behavior accounts for the surprisingly rapid shifts in migratory pathways and stopover points that waterfowl are able to make when major environmental changes occur, such as the establishment of bird refuges, the filling of impoundments, and the like. On the other hand, this adaptability also may cause an area to be "burned out" of its waterfowl use, when disturbance or excessive mortality disrupts the traditional use of an area. This capability for human manipulation of usage by waterfowl in their migratory or wintering areas poses enormous problems for wildlife biologists, who must choose carefully between the desirability of providing safe and attractive areas for use by large numbers of birds and the potential dangers imposed by such congregations: disease or parasite transmission, crop depredations on nearby private lands, and the encouragement of unrestricted or uncontrolled hunting in areas adjacent to the controlled-usage areas. Interstate and international politics may even become involved, in view of the great economic significance of waterfowl hunting in certain parts of North America.

Usually during their first fall or winter of life, but in the case of swans, geese, and sea ducks in their second winter, the family bonds that promoted the brood's survival and transmission of migratory traditions are broken and are replaced by pair-bonding processes. The strength and duration of pair bonds in waterfowl differ greatly among species and are in general linked to the relative importance of the presence of the male in protecting the female, her eggs, or their offspring during their most vulnerable periods. Swans and geese exhibit a combination of the strongest pair bonds, the smallest clutch sizes, the longest periods of prefledging vulnerability of the young, and the longest deferral of sexual maturity. All of these interrelated characteristics suggest that the gambles associated with reproduction are much greater in these species than in the typical ducks, where conditions variably approach the opposite extreme.

Swans and geese are so large and generally so conspicuous that their nests may be readily apparent to predators, their incubation periods and

fledging periods are so long that renesting attempts in the typically abbreviated nesting seasons of northern latitudes are fruitless, and the requirements for space and food adequate to rear a brood are so great that territorial behavior may limit the density and success of nesting birds in the best habitat. Thus, in keeping with the royalty often ascribed to swans, their social behavior is based on a nonegalitarian doctrine of differential social status and reduced probabilities of successful reproduction in an environment of limited resources and difficult survival.

In contrast, duck species such as mallards and other common "dabbling ducks" represent the ultimate in trends toward a democratic society. Sexual maturity follows hard on the attainment of fledging, and male mallards may begin pair-forming behavior within six months of their hatching. Pair bonds, even after they are formed, are relatively weak, and shifting about of mates may occur even without the needs generated by the death of one member of a pair. The territorial behavior by males of most duck species is weak or may even be lacking, apart from a defense of the female herself, and even this terminates shortly after the female has begun to incubate her clutch of eggs. In most ducks, the males never even see their own offspring, for by the time of hatching they have begun their vulnerable flightless period associated with the postnuptial molt. This molt may be undertaken at a considerable distance from the nesting area, the male undertaking a "molt migration" as soon as he deserts his mate. Should the female in the interim suffer the loss of her clutch or even her brood, she may remate with any available male still in suitable reproductive condition to fertilize her second clutch of eggs, and she may thereby still at least attain her own reproductive success. Parent-offspring bonds in many ducks are rather weak, promoting the development of broods of mixed family origins or even mixed species broods.

Mixing of young of different species is also facilitated by the generally weak territorial defense of male ducks, particularly toward other species. The result is that females of two or more species may nest in close proximity, or one may even inadvertently "drop" one or more of her eggs in another's nest. Nests that are used by two or more females are called "dump nests," and because of frequent fighting over nest possession the eggs are often only ineffectively incubated or not incubated at all. Such dump-nesting is most prevalent in hole-nesting species where suitable nest cavities are limited, and in such species (such as goldeneyes) true territorial behavior involving the defense of the nesting area is well developed, which would help to reduce the occurrence of mixed clutches.

Certain species of duck are much more prone to dropping their eggs in the nest of other females; this is especially true of ruddy ducks and redheads.

Both species are in fact best regarded as incipient nest "parasites," since perhaps as many or more eggs are laid in other nests of their own or other species as are incubated by the females themselves. Studies to date have suggested that the hatching success of parasitically laid eggs is rather low, and virtually none of the adaptations of the highly specialized socially parasitic species of birds are to be found in these ducks. Indeed, only a single species of duck, the South American black-headed duck, is believed to be an obligate nesting parasite, since no nest of this species has yet been found. However, female black-headed ducks have been observed with flightless young, so that some doubt as to this species' dependence on parasitic nesting still remains.

It is characteristic of all species of waterfowl to delay the start of incubation until the last egg has been laid. The length of time needed to complete a clutch varies greatly and depends on the total clutch size and the time interval between successive eggs, which is usually one or two days. During the egg-laying period the female usually spends little time at the nest, leaving it exposed to possible predation or other losses. However, in geese and swans, the male is usually present to guard the nest. As the clutch nears completion the female progressively lines the nest with down and plucked feathers, although the amount used varies considerably in different species. Swans generally use very little down in their nests, geese and ducks tend to use more, and some arctic-nesting ducks use rather large quantities, as in the case of eiders. The tropical-nesting whistling ducks normally have no down in their nests. Usually the nesting down is dark-colored, even if the other underpart feathers are white, although some hole-nesting species do have white down.

In most species of North American waterfowl the actual clutch size is variable, although the "normal" size of initial clutches may be fairly predictable, especially in species having smaller clutches. There is less variation in clutch size among high-latitude nesters than among more tropical ones, and among ground-nesting forms versus hole-nesters. Clutches that are laid late in the breeding season also tend to be smaller than the ones started earlier, and likewise repeat clutches laid by a female who was unsuccessful in her first nesting attempt are appreciably smaller than initial ones. Since the size of the clutch is also a reflection of the female's tolerance for physiological drain, the health and general fat reserves of the particular female also tend to influence the total size of the clutch. In general, clutch size tends to be smallest in swans, slightly larger in geese, larger still in surface-nesting ducks, and largest in hole-nesting ducks. Clutches also tend to average larger in low-latitude species than high-latitude ones, perhaps because of the need for effective covering and warming of the entire clutch under cold conditions, the other demands on energy reserves associated with nesting in arctic environ-

ments, or even the shorter time available for nesting and brood-rearing under these adverse conditions.

In at least some species of whistling duck, one Australian species of swan, and a very few other species of waterfowl, the male actively participates in incubation, often sharing incubation time more or less equally with the female. Among the North American waterfowl, only in the whistling ducks does the male normally participate in this way. Male mute swans, and to some extent the other swans, may regularly tend the eggs in the absence of the female, and in at least the case of the mute swan the male may take over incubation duties should the female die. Active participation by the male in normal incubation duties may also occur among the other swans to a rather greater degree than is currently appreciated, because of the difficulty of distinguishing actual incubation of the eggs from simply guarding them.

Once incubation begins, the female usually becomes very reluctant to leave the nest, and in at least some arctic species of waterfowl she may fast for the entire incubation period. It is common among temperate-zone species of duck that the female takes early-morning and late-afternoon or evening breaks from incubation, so that she may forage for a while. At this time she may be joined by the drake, if he is still in attendance. As hatching approaches, the female sits more continuously, and a certain amount of effective communication between the female and the still unhatched eggs seems to occur. The process of the exit from the egg, called pipping, may require twenty-four hours or more, and although the last-laid egg is often the last to hatch, the entire clutch typically hatches in a remarkably synchronized fashion, often within a total time span of five or six hours. Several additional hours after hatching are required for the down to dry and to fluff properly, so that the brood are likely to remain in the nest for at least the first night of their lives. By the following morning the female generally leads her brood from the nest, sometimes never to return to it. However, a few waterfowl species do use the old nest as a place to brood their young; this is especially typical of swans and of such pochards as canvasbacks and redheads, which usually construct semifloating nests of reeds well away from land. The large, bulky nests of swans also provide a convenient substitute for land-brooding and may be used for a month or more by the family, especially at night.

Although among geese and swans the parental attachment for the young persists through the entire posthatching period and the following migration, the brood bond of female ducks toward their offspring is much weaker and more variable, presumably being dependent on hormonal controls. Generally it persists through most or nearly all of the pre fledging period, which may be as little as about forty days in some surface-feeding ducks and arctic-breeders,

or as much as sixty to seventy days in certain diving ducks. At varying times before the young are ready to fledge, the female typically begins her postnuptial molt, which always includes the flight feathers. Then, like the male, she becomes flightless for a time and thus highly secretive in her behavior, for she is then very vulnerable to predation and, in addition, is usually weak from the stresses associated with molting and reproduction. The length of the flightless period seems to vary considerably among species and even for the same species in different regions, but in general it is probably no less than a month and no more than two months. Thus, females of many species have often just emerged from their flightless period when they are required to begin moving toward their winter quarters. In both sexes molting of the body feathers may thus continue well into the fall migratory period. Whereas among ducks it is typical for the male to begin molting considerably in advance of the female, in geese and swans the molting of the adults is more synchronized, and indeed the female typically molts in advance of the male, often starting shortly after the young are hatched.

The timing of the fall and winter prenuptial molt back into breeding plumage varies even more than that of the postnuptial molt. Geese and swans lack a prenuptial molt altogether, and thus they exhibit virtually no seasonal variation in appearance. Evidently all ducks have a rather extensive prenuptial molt; although it is most conspicuous among males it is also present in females and affects all the feathers except those of the wings and sometimes the tail. In one North American species, the oldsquaw, there is even a third molt and a partially new plumage occurring during the winter, involving some head feathers and the scapulars. For male ducks, the timing of the prenuptial molt and subsequent assumption of the nuptial plumage is closely tied to the timing of pair-forming behavior. Social displays may begin before the males are in "full" plumage, but typically there is a close relationship between the occurrence of courtship activity and the timing of maximum brilliance of feathers and unfeathered areas such as the bill and the legs, as well as iris coloration in some species.

The intensity and complexity of pair-forming or "courtship" displays vary greatly, being under the influence of a multitude of environmental factors. These include the need for stimulating and synchronizing the sexual rhythms of the other sex, the need for sexual and species specificity to avoid homosexual matings or matings between different species, and the ecological counterpressures favoring cryptic or nonconspicuous behavior and appearance in response to varying amounts of predation danger.

With the probable single exception of the muscovy duck, all the species included in this book are ones that form monogamous pair bonds, lasting

either until incubation has begun (in the case of ducks) or indefinitely, and potentially as long as both members of the pair survive (in geese and swans). For such pair-forming species, there is generally a distinction to be made between the pair-forming displays that initially forge the pair bond (which require the sexual and species-specificity previously mentioned) and the pair-maintaining displays that probably serve to synchronize sexual rhythms of the pair. Lastly, displays associated specifically with the facilitation of actual mating, or copulation, are needed in all species. A promiscuous species such as the muscovy duck has no need for the first two categories of display, and thus its social displays are limited to aggressive signals used in male-to-male interactions and heterosexual displays associated directly with mating.

It is interesting to note that although aggressive and threat displays used by males toward other males are obviously functional and serve to facilitate social dominance and achieve preferential opportunities for mating among the fittest males, there is also a surprising component of aggression in the behavior of males toward females and vice versa. The reason for this aggressive component are still speculative but obviously include the fact that the male sex hormone testosterone is closely linked with aggressiveness among vertebrates, and additionally there is a clear relationship between the ability of a male to keep other competing males away from an available female and his subsequent chances of mating with her himself. Likewise, females must be able to repel males effectively if they are to avoid constant harassment and possible rape by the still unmated males, which are usually present in considerable excess over unmated females.

The social behavior of waterfowl, like other birds, is largely dependent on communication by visual, vocal, or tactile methods, with the elements of the communication system being "packaged" in relatively nonmistakable stereotyped behavior patterns, or "displays." The repertoire of displays of any species is usually unique when the displays are considered collectively, even though some components may be identical to those of other species. The recognition of such corresponding, or "homologous," display elements is thus the basis for comparative behavioral analysis, just as the recognition of homologous anatomical elements is the basis for comparative anatomy. Thus displays are usually given descriptive names that, if well chosen, will serve to provide a shorthand means of identification for persons familiar with the corresponding display in other species. Although the same motor pattern associated with a visual display may be nearly identical in two related species, it is apparent that plumage patterns or other morphological differences may confer specificity on the two species. Likewise, differences in the tracheal anatomy of two species, such as length, diameter, and configuration, may



generate acoustical differences in calls made under the same circumstances and motivation. Additionally, tension variations in the sound-producing syringeal apparatus, as well as the volume of air that is passed through it, may produce varying sound frequencies and amplitudes, resulting in characteristic call patterns that are the functional equivalent of human languages.

Following its establishment, a pair bond is maintained and strengthened by various mutual activities by the members of a pair. Among geese and swans the repeated performance of a "triumph ceremony," which is performed after the eviction of a real or symbolic "enemy" from the vicinity of the pair, is the primary behavioral bond that holds the pair together. This is generally marked by excited calling and head-waving movements by the two birds, and often also by wing-shaking or wing-waving movements as well. Among ducks, ritualized drinking and preening movements, which may differ little if at all from those normally performed as functional "comfort activities," provide a corresponding means of providing a simple mate-recognition signal system. In certain species of ducks, and particularly in the pochards and sea ducks, the same or similar signals may serve as early stages of precopulatory behavior by the pair.

Copulation is performed in the water by all the North American species of ducks. Its occurrence may be largely limited to the time immediately preceding and during the egg-laying period (as in geese and swans), or it may be much more prolonged and begin several months before the time when actual fertilization of the female is needed. To what extent such behavior might play an important role in the strengthening or maintenance of pair bonds is uncertain at present. Likewise, the significance of the generally well-developed postcopulatory displays is still rather speculative.

Raping or attempted rapes of females by males is a surprisingly common feature of the social behavior of ducks, but it is either extremely rare or totally absent among geese and swans. It has been argued by some that the raping of females whose eggs have been lost and whose mates have already deserted might provide the functional advantage of assuring the fertility of a second clutch, but this, too, is difficult to state with certainty.

Adaptations associated with foraging and food-getting are another important phase of waterfowl behavior. It is instructive to compare the diversity of bill shape and leg placement that exists among the waterfowl group as compared with, for example, the remarkable similarity of beaks and legs among the upland game birds of North America. There can be little doubt that, by these structural modifications that influence the birds' capabilities for diving, underwater activities, and extracting various kinds of foods, the waterfowl have achieved a maximum degree of habitat exploitation with a minimum

of interspecies competition for the same foods. Thus, with such closely related forms as the blue-winged teal, cinnamon teal, and northern shoveler, there exists a progressive gradient in bill structure involving length, width, and relative development of sieve-like lamellae. These change the bill from a tool adapted basically to probing and picking up materials from below the surface to a surface-straining device of remarkable efficiency. Likewise, the bills of swans are primarily adapted for the tearing and consumption of submerged aquatic plants, whereas those of most geese are much more efficient at clipping or tearing terrestrial herbaceous vegetation close to the ground. Similarly the heavy mollusk-crushing bills of scoters and the larger eiders differ impressively from those of their relatives the harlequin and oldsquaw, which consume large quantities of soft-bodied crustaceans, insects, and much smaller bivalve mollusks.

In parallel with species differences in bill shapes and foraging adaptations, the habitats utilized by various species of North American waterfowl differ remarkably. Freshwater, brackish, and saltwater habitats are all utilized, standing-water and flowing-water communities are likewise used, and water areas of all depths from temporarily flooded meadows to lakes several hundred feet deep are exploited for feeding and resting. Closely related species of birds that have similar bill shapes and foraging methods often differ in the habitats utilized. Thus, brackish to more saline wintering habitats are favored by red-breasted mergansers and Barrow goldeneyes, while freshwater lakes and rivers are the primary wintering areas of their respective close relatives, the common merganser and the common goldeneye. Similarly, the common mallard and black duck are associated, respectively, with open-country marshes and forested swamps for breeding, and the greater and lesser scaups are effectively segregated by habitat preference differences in both breeding and wintering areas. A more comprehensive summary of such breeding habitat differences among species is to be found in the chapter dealing with distribution and migration.

Waterfowl vary appreciably in their capabilities for ready takeoff and prolonged flight; this, too, is understandable in terms of ecological adaptations. The species that are the best divers and underwater swimmers (such as the stiff-tailed ducks and the mergansers) have sacrificed aerial agility and the ease of becoming airborne for anatomical needs associated with foraging requirements. However, in such swimming "generalists" as the surface-feeding ducks that rarely have to dive for their food, the legs are placed fairly far forward and are relatively close together. This improves their walking movements on land and increases the ease of rapid takeoff from either ground or water. On land the birds simply spring into the air, while on water a combined

thrusting movement of the feet and wings downward into the water instantly propels them into the air. By comparison, in order to take flight directly the masked duck must first make a shallow dive and use the associated forward propulsion of the feet and perhaps also the wings to gain the needed momentum to leave the water. Or, as in the ruddy duck, a long pattering run over fairly open water, involving both wings and feet, is required to bring the bird to "flight speed."

Speed of flight, maximum altitudes attained, and maximum duration of flight are all associated with such aerodynamic problems as "wing-loading," the configuration of the wings, and the total weight of the bird. Such heavy-bodied birds as swans are among the most slowly flying waterfowl, averaging about 35 miles per hour on short, local flights and somewhat more on long, migratory trips. On long, migratory flights swans have been found to fly as high as 10,000 feet, presumably to avoid air turbulence associated with lower altitudes. They can cover between 250 and 700 miles in a single "leg," much of which may be done in darkness. Under these conditions a star-filled sky is much more useful than a cloudy one, since overcast conditions obscure the navigational information provided by the constellations. Surprisingly, the moon is evidently of less value than the stars for nocturnal navigation, except possibly as an aid to illuminating surface landmarks.

