

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Papers in Ornithology

Papers in the Biological Sciences

February 1968

The Evolution of Duck Courtship

Paul A. Johnsgard

University of Nebraska-Lincoln, pajohnsgard@gmail.com

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



Part of the [Ornithology Commons](#)

Johnsgard, Paul A., "The Evolution of Duck Courtship" (1968). *Papers in Ornithology*. 31.
<https://digitalcommons.unl.edu/biosciornithology/31>

This Article 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 Papers in Ornithology by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

The Evolution of Duck Courtship*

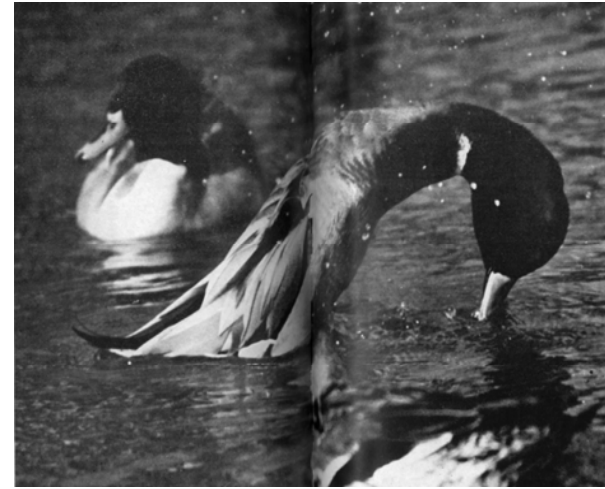
Grunt-whistles, down-ups, shakes, and sneaks are in the bump-and-grind display repertoire by which ducks identify drakes

by Paul A. Johnsgard

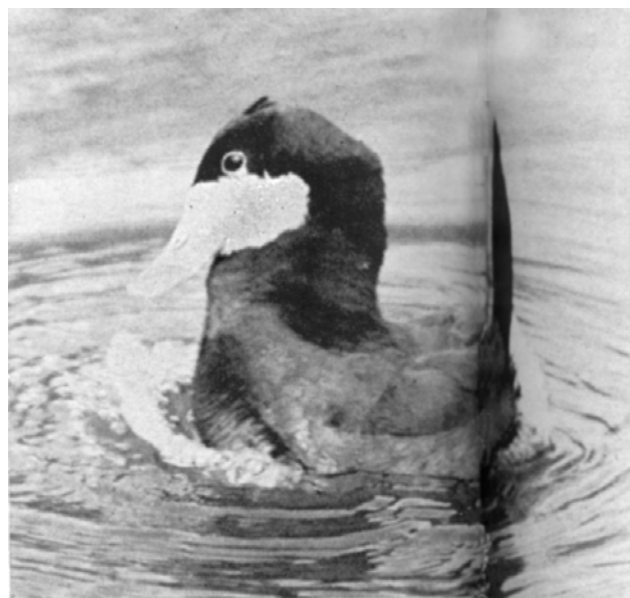
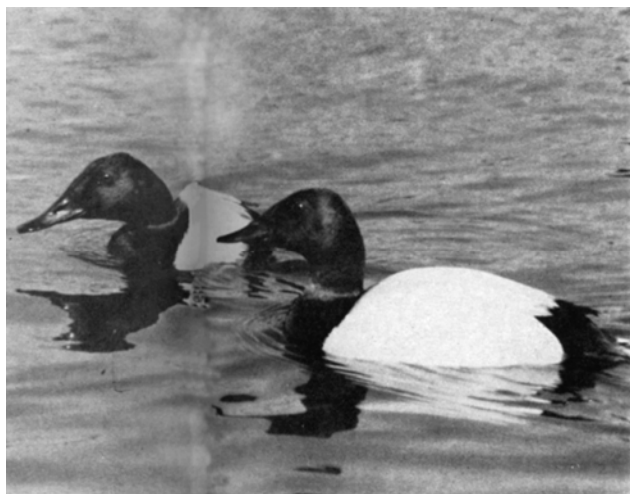
Because the word “courtship” is so imbued with human connotations, it may be debated whether the term should be applied to non-human reproductive behavior patterns. Nonetheless, analogous mating responses can be observed in many vertebrates, and it is instructive to ponder the reasons why such activities often bear a more than passing similarity to human courtship.

The similarities can be partially explained by considering reproductive efficiency. Since terrestrial vertebrates no longer reproduce in a watery medium that would permit simple external fertilization, it is vital that behavioral and structural adaptations be present that will allow for the direct transfer of sperm cells from male to female. Additionally, a prolonged association between reproductively active individuals provides maximum opportunities for synchronizing sexual cycles and preventing mismatings between species. Finally, most of these advanced vertebrates produce relatively few offspring, and it is therefore advantageous if a maximum amount of parental care is available to favor their survival. For such reasons, responses favoring the establishment of individual sexual associations, or “pair bonds,” have evolved in some vertebrate groups.

* Published in *Natural History* 77:2 (February 1968), pp. 58–63. Copyright © 1968 The American Museum of Natural History. Used by permission.



Two of the conspicuous courtship displays mallards perform are the “grunt-whistle,” top, and “head-up-tail-up,” below. Displays such as these usually follow “preliminary shaking,” in which the drake swims high on the water, then thrusts his head up and back, raising his body from the surface. Grunt-whistle derives its name from the sound made during the performance. Head-up-tail-up is self-explanatory.



The canvasback drake with its head lowered, top, performs a display called "sneak," while the ruddy duck, bottom, drums its breast to create a "bubbling" display, which not only attracts females but also wards off male encroachers.

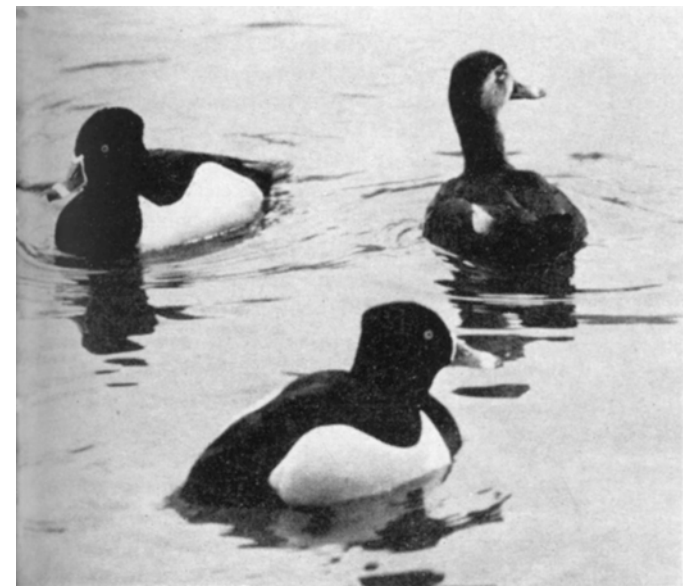
In mammals, monogamous pair bonds are relatively rare and are well developed only among certain groups that give birth to highly dependent, or altricial, offspring. Monogamy among mammals is especially typical of those species, such as various carnivores, in which both the female and young must rely on the male for food gathering. However, the majority of birds produce altricial young and typically form monogamous pairs that normally persist through a single breeding season. Avian polygamy or promiscuity is primarily limited to those species producing precocial young that are easily able to forage for themselves shortly after hatching, to various species that nest near relatively unlimited food supplies so that the female alone can provide for the young, and to socially parasitic species that do not have to rear their own offspring.

It could therefore be expected that ducks, having precocial young, might tend to be polygamous, if not promiscuous. This appears to be the case for only a very few species, such as the Australian musk duck. However, the great majority of ducks annually form relatively clear-cut pair bonds which usually break up when the female begins her incubation. In only a few species does the male remain with the female and help care for the young, and these are mostly tropical species with prolonged or irregular breeding seasons. The biologist is thus inclined to try to account for the possible value of such pre-nesting pair bonds in ducks, and to determine the functions of the elaborate courtship ceremonies performed during the period of pair formation.

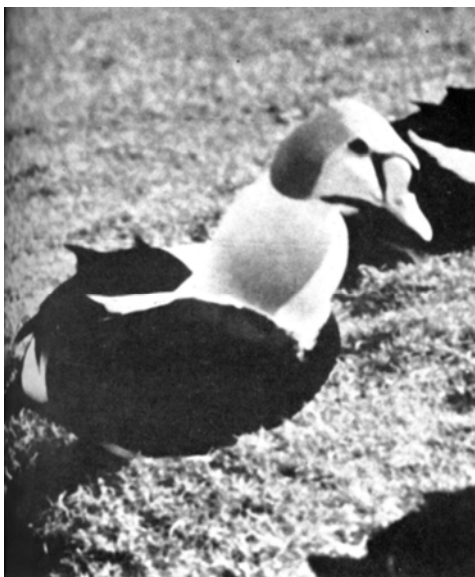
The courtship of ducks is unusual in several aspects. In temperate zones it generally begins very early, usually on the wintering grounds, so courtship is not a manifestation of territorial proclamation and defense as is the case with many songbirds. Nor, because of its early initiation, is courtship closely correlated with gonad growth and fertilization; rather, pair formation is normally completed prior to the period of maximum gonadal activity. Therefore, reproductive behavior in ducks may be conveniently divided into an early phase of conspicuous displays associ-

ated with actual pair formation, followed by the later and less elaborate behavior patterns concerned with pair bond maintenance and fertilization. Two possible advantages of the considerable time lag between pair formation and egg laying are that it decreases the likelihood of uncorrected mismatings between species and, furthermore, provides the female with the protection of a mate to ward off unmated males that might attempt to rape her. An appreciation of the distinctly different functions of early versus later phases of sexual behavior in ducks will help to explain their widely differing behavioral characteristics.

The relatively stereotyped postures and calls, or "displays," associated with pair formation presumably originated as a result of various evolutionary factors. For example, the adult sex ratio of ducks is characterized by an excess of males, probably as a reflection of the greater dangers endured by the females during nesting. As a result, not all males are able to obtain mates, and a spirited competition among them naturally ensues. Therefore, those males having brighter plumages, stronger sexual responses, or increased social dominance will be at an advantage and will tend to be more successful in reproducing. Insofar as these differences have genetic origins a gradual evolution of more elaborate male plumages and displays may be expected. Thus, male ducks have generally more complex displays and brighter plumages than do females, which must remain inconspicuously colored if they are to nest successfully in the presence of predators. If such "sexual selection" were the only factor affecting male plumages and displays, one might well imagine that different species could be very similar in these respects, just as females are relatively similar in their plumages and vocalizations. But this is not the case, and it is a fact that no two species of ducks that are native to the same region have identical plumages or pair-forming displays. Likewise, all North American cricket species living in the same habitats have been found to exhibit diagnostic song repertoires (NATURAL HISTORY, November, 1966).



The "nod-swimming" posture exhibited by the Laysan duck, top, is performed by many mallard-like species and is one of the few courtship displays of females. At bottom, two ringneck males flatten their head feathers to attract a female with a display called "depressed crest."



Even though the neck-stretching display, called "reaching," of the king eider, top, is identical with that of the American eider, bottom, each bird performs it in a specific sequence of displays that identifies the eider as surely as its plumage.

Such diversity would suggest that a major influence in the evolution of male courtship behavior is the need for achieving "species recognition," or a means of ensuring that females will be readily able to recognize and therefore mate only with males of their own species. It is generally true that males of many animal species are much less discriminating in their species-specific attraction to females than are females to males. The maintenance of such species' genetic integrity depends largely upon the females' ability to perceive the "proper" combination of male traits. It is presumably for this reason that such a variety of male plumages and elaborate courtship displays has evolved among birds. On the other hand, displays associated with pair maintenance and fertilization occur only after species recognition has been achieved. Such displays understandably show much less diversity within large groups of waterfowl.

We may therefore predict that distinctive pair-forming displays and male plumages will be present in groups of ducks having a considerable number of closely related species occupying roughly the same geographic area. In North America this criterion is fully met by the typical dabbling ducks (primarily *Anas* spp.). Thus, such abundant and wide-ranging ducks as the mallard, pintail, gadwall, green-winged teal, blue-winged teal, cinnamon teal, American widgeon, and shoveler all have unique display repertoires and brighter male nuptial plumages that readily distinguish the sexes. The remaining dabblers, in which males are inconspicuous and closely resemble females, include the black duck, mottled duck, Florida duck, and Mexican duck. All of these are mallard-like birds, which prior to historical times bred in areas where few, if any, mallards or other dabblers occurred. We might, in fact, regard them as mallards "in disguise," for not only are the males' displays and calls indistinguishable from those of mallards, but also the females' plumages and vocalizations are mallard-like. Indeed, recent changes in the mallard's distribution have resulted in hybridization between mallards and these populations in every region where they have come into contact.



The "bridling" Cape teal, right, throws its head back and its chest up in a variation on the mallard theme. Each mallard-like species has its own diagnostic routine.

The courtship displays typical of mallards may be used as examples of the male pair-forming displays of most dabbling ducks. Not one but several different postures and calls are present, all apparently having evolved from simpler, non-display responses including body-maintenance, or "comfort," activities, such as preening or shaking. Three courtship displays are especially frequent and conspicuous among mallards, and all involve variously stretching the neck and uttering a single or multiple whistle. These displays were first accurately described by the famous German ethologist Konrad Lorenz, who gave them descriptive names that have been translated as "grunt-whistle," "down-up," and "head-up-tail-up." It is fairly clear that the grunt-whistle represents a stereotyped, or "ritualized,"⁵⁵ modification of normal body shaking, and that the down-up is a similarly exaggerated form of drinking; but the head-up-tail-up is of less obvious origin.

This last display is actually only part of a complex sequence of postures, beginning when the male suddenly whistles while stretching his neck vertically, at the same time raising the tail and lifting his folded wings, thus exposing the purple wing-speculum pattern. This head-up-tail-up phase is usually performed at "profile view"⁵⁵ to a specific female, and so provides maximum visual impact. The male then turns his head to point the bill toward the courted bird, and usually holds this rigid posture for a short time as he reorients his entire body toward the female. The male then typically lowers his head almost to the water and swims rapidly past her in a manner called "nod swimming," and finally terminates the sequence by raising his head and simultaneously directing his blackish nape feathers toward the female. Several other postures and calls also occur, but they appear to be of less significance in the mallard's pair-forming activities.

Although the grunt-whistle, down-up, and head-up-tail-up also occur singly or in combination in several of the other North American dabbling ducks, only the mallard-like ducks possess exactly this same repertoire of postures and calls. Thus, the male green-winged teal performs the same three displays much more

rapidly with different relative display frequencies and vocalizations, and additionally has a “bridling” display, which involves drawing the head backward, that is lacking in mallard courtship. The male gadwall lacks both bridling and nod swimming, and, furthermore, its head-up-tail-up display is sequentially “linked” to the immediately ensuing down-up posture. The pintail, however, lacks the down-up display, and in this species there is a significant, although delayed, linkage between the grunt-whistle and the head-up-tail-up, which usually occur about one second apart. The pintail also seemingly lacks a functional nod-swimming display, although it is present in an extremely rudimentary form. The American widgeon, shoveler, cinnamon teal, and blue-winged teal all completely lack these particular displays, and instead have other species-diagnostic responses.

In a similar fashion, such interspecific diversity distinguishing the basic similarities of male plumages and displays can be seen in other North American waterfowl. All of the typical diving ducks (*Aythya* spp.) exhibit certain male displays such as “head-throws,” “sneak” postures, and “kinked-neck” calls, but these displays differ greatly in their visual and acoustical characteristics. Likewise, the three larger species of eiders (*Somateria* spp.) share certain movements and postures associated with cooing sounds, but each species has a diagnostic combination of displays that identifies it as decisively as its male plumage pattern. Several species of ducks having no near relatives in North America also exhibit relatively elaborate male plumages and displays, as does, for example, the ruddy duck. In such species it must be presumed that competition among males for mates has by itself been effective in the evolution and maintenance of these displays. Additionally, the male ruddy duck utilizes its remarkable breast drumming, or “bubbling,” display both as a sexual response toward females and as a territorial advertisement display toward other males.

It has been generally believed that such pair-forming displays are entirely innate, as suggested by their stereotyped performance among all the individual males of a species. Furthermore, hand-

reared male ducks that have never been exposed to experienced males will, when placed in the proper situation, perform their displays without a single mistake from the first time they are attempted. Likewise, downy young ducklings have been stimulated to perform species-typical courtship displays by hormone treatments. Finally, it has been recently reported that when mallards are reared with a foster mother of another species or with foster broodmates of a different species they do not exhibit that species’ displays upon maturing. However, males reared under such conditions will usually become sexually imprinted on their foster species and may later mate with such females in preference to those of their own kind. Similarly reared female mallards, on the other hand, have a strong innate species-recognition mechanism that enables them to mate correctly in a later choice situation.

An additional proof of the hereditary basis for these species-typical displays lies in the intermediate responses performed by hybrid individuals. Hybrid fertility among ducks is unusually great, and it is often possible to hybridize species having widely differing male plumages and displays. For example, mallards and pintails have been repeatedly hybridized in captivity, and a few wild hybrids of this type are shot by hunters almost every year. Their frequency in the wild is small, but their very occurrence poses two important problems: Are they sufficiently fertile and reproductively active enough to compete with the parental types for mates and, if so, what sorts of display repertoires do they possess?

It is well known that first-generation hybrids between mallards and pintails have plumages and bodily proportions almost exactly intermediate between the parental types, as if the parents’ genes were neatly blended in an equal mixture. Of greater interest is that their male display repertoires are also a composite combination of the mallard’s and pintail’s. Thus, such hybrids evidently lack the down-up display altogether, and their nod swimming is performed in a manner that is intermediate between the parental types. The hybrids are fully fertile, but under wild conditions the

males would probably fail to obtain mates because of their intermediate plumages and displays, as well as having apparently reduced competitive responses. In captivity, however, the hybrids may be backcrossed with either parental species or with one another to produce second-generation hybrids. This procedure was first systematically carried out by the great waterfowl authority John C. Phillips, who found that second-generation males exhibit some individual variation indicating genetic segregation of mallard and pintail plumage traits, although less than he observed in crosses that involved only mallard-like species.

We repeated this experiment recently at the Round Lake Waterfowl Station in Minnesota, to obtain more specific information on the degree of plumage segregation in the second generation, and also to determine whether a similar segregation of behavioral traits related to pair formation could be detected. Twenty-three second-generation males were reared, of which about half were selected for behavioral study. These males varied greatly in their nuptial plumages, with some individuals so closely approaching the mallard type that they could scarcely be distinguished from pure mallards, while other males exhibited pintail-like plumages. Of greater interest was my student Roger Sharpe's finding that the mallard-like males performed their displays in a distinctly mallard-like manner. Some of these individuals were the only ones to perform the down-up display, for example. On the other hand, the pintail-like males were also pintail-like in their displays, especially with regard to the details of the head-up-tail-up sequence.

Our results support the view that these male displays are as much a reflection of the species' genetic constitution as are their plumage characteristics, and thus may be used to help characterize or define a species. The degree of individual variation observed in the second-generation males' plumages and displays was surprisingly great, suggesting that perhaps the genetic bases of these traits are relatively simpler than one might have otherwise supposed. Such simplicity of control would help to account for the occasional occurrence of individual mallards and pintails

that perform their courtship displays in an atypical manner. Thus, males of both species have been observed performing bridling as a courtship display, although in these species bridling normally occurs only as a postcopulatory response. Interestingly, this same display anomaly has also been found in some of the hybrid males.

With simple genetic control of male display patterns thus indicated, their resultant susceptibility to changing pressures of natural selection makes the use of male display characteristics less valuable as a criterion of evolutionary relationships than Konrad Lorenz once enthusiastically proposed. However, other behavioral criteria such as female displays and various displays associated with pair maintenance and fertilization are much more uniform among related species and often provide valuable evidence concerning evolutionary relationships. Therefore, the fascination of pair-forming displays in male ducks now lies, not so much in their taxonomic applications, as in understanding their obviously adaptive functions, such as maintaining reproductive isolation between closely related species. Thus, it is a pleasant mental exercise to try to predict what a particular unstudied species' male courtship displays might consist of, based on a prior knowledge of the displays of its nearest relatives, the presence in the same area of related species whose displays are already known, and the clues provided by the male plumage of the species itself, since displays evolve with and frequently expose species-specific plumage features. The usual result of such contemplations, upon learning the facts, is the chagrin of discovering that the results of natural selection often represent a seemingly more imaginative solution to the question than do the musings of flesh-and-blood biologists.