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Handbook of Waterfowl Behavior: Frontmatter and Introduction

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

HANDBOOK *of* WATERFOWL BEHAVIOR

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

Acknowledgments

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

PAUL A. JOHNSGARD

Lincoln, Nebraska
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Introduction

BACKGROUND AND OBJECTIVES OF THIS STUDY

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

Following the remarkably thorough and exceedingly significant behavioral studies of Heinroth (1911), whose observations were strengthened by a firm knowledge of evolutionary principles and a lifetime of intimate study of waterfowl in captivity, many behavioral studies on various species were made. Of these, none are more significant than those of Lorenz (1941; 1951–1953), who intensively studied a number of surface-feeding ducks and by determining and comparing homologous behavior patterns in these species, was able to establish the probable evolutionary relationships existing within the group. More than anything else, Lorenz's fascinating studies stimulated a widespread interest—manifested by the appearance of many recent papers—in waterfowl behavior. Thus McKinney (1953) investigated the family to determine whether comfort movements had the same taxonomic significance as Lorenz found sexual behavior to have. Although he found that they did not have this significance, his descriptions of comfort movements provide a valuable inventory of the behavioral raw materials utilized in the evolution of actual displays. Except for the present work, McKinney's study represents the only attempt to investigate the entire family from a behavioral standpoint, although numerous studies have been done on various smaller groups. Myres (1959a), for example, studied the so-called sea ducks, which Delacour and Mayr (1945) originally placed in a single tribe Mergini, the homogeneity of which had been questioned on anatomical grounds (Humphrey, 1955). Lorenz's student Wolfgang von de Wall (1963) has expanded Lorenz's studies on the surface-feeding ducks, and has attempted to determine the genetic basis for some of the display patterns.

The present study was undertaken to test and evaluate the various taxonomic arrangements of the family, to discover some of the trends of behavioral evolution, and to provide a basis for future workers to use in naming, describing, and evaluating the behavioral patterns observed in waterfowl. Most of the information presented here was obtained during twenty months at the Wildfowl Trust in Gloucestershire, England, under the sponsorship of National Science Foundation and Public Health Service postdoctoral fellowships. Additional observations were obtained during a NSF research grant (GB 1030) while the author was on the staff of the Department of Zoology and Physiology at the University of Nebraska. The Wildfowl Trust comprises—in terms both of species and of individuals—the largest collection of living waterfowl ever brought together at one place in the world. Since 1959 I have been able to study 133 of the 142 extant species of Anatidae, and 40 of the 43 genera accepted by me. For the relatively few species I have been unable to see, I have attempted to extract pertinent information from the literature and from persons who have had firsthand experience with them. For the purpose of description and analysis, 16-mm. motion pictures were made of as many of the behavior patterns as possible, and approximately 7,000 feet of film was utilized in writing the following accounts. All drawings are based on direct photographic enlargements of individual 16-mm. frames or, as in a few cases, 35-mm. photographs.

VALUE AND LIMITATIONS OF BEHAVIOR AS A TAXONOMIC TOOL

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

Of all the activities of any species, none is more significant to that species' survival than successful reproduction. Because of the overriding importance of reproduction, natural selection is particularly strong and effective in maintaining the greatest possible reproductive efficiency. As a result, much of the behavior associated with reproduction is "innate," and any individual whose genetic potentialities deviate from the most effective genotype under the existing conditions is less likely to be effective in producing offspring. Along with this selective pressure toward intraspecific stability and constancy in reproductive behavior, there is another pressure toward species distinctiveness. That is, if a species is to be successful it must not only be able to perpetuate itself but must also avoid disadvantageous hybridization with related species. Of course hybridization is most likely to occur if reproductive behavior (and its genetic basis) is nearly identical in two species, and in such situations those individuals having the greatest genetic capacity for obtaining mates of the same species will be favored by natural selection. As a result, divergences in the sexual behavior of different species are to be expected, especially in behavior related to mate selection. Since all available evidence indicates that with most ducks (some shelducks appear to be exceptions) it is the female which "selects" the mate, it is understandable that male "courtship" patterns are more likely to be affected by this pressure toward divergence. On the other hand, there is normally no strong pressure for the divergence of female behavior patterns; thus these patterns are more constant, or "conservative," and may vary little from one species to another. Likewise, sexual behavior patterns which usually occur after mates have been selected, or which are important in forming and maintaining the pair bond (such as copulatory patterns), tend to be more conservative than pre-pair formation patterns.

We see, therefore, that different aspects of sexual behavior have different degrees of biologic and taxonomic importance, depending on whether they function mainly as species-specific isolating mechanisms (male courtship displays), as pair-maintaining mechanisms (many mutual displays), or are directly related to reproduction per se (behavior associated with copulation). The least conservative patterns, the male courtship displays, are, when proper care and consideration of sympatry are taken into account, useful in determining relationships between very closely related species, but they are practically worthless and may even be misleading at any higher level. Female courtship displays and many mutual displays are generally useful in determining generic relationships within a tribe or subfamily, but are usually of little help in determining affinities within a genus. Copulatory behavior, and especially precopulatory behavior, is in some respects the most conservative of all sexual behavior; hence it is often helpful in assessing tribal relationships. Another very conservative kind of sexual behavior is that related to the actual mechanism of pair formation (as opposed to mate selection). This process is apparently of such fundamental importance that it is relatively immune to selection pressures for divergence; once a potential mate is "chosen," the ensuing patterns which bring about the establishment of a pair bond seem to be relatively uniform throughout the major groups of waterfowl. A few patterns of sexual behavior appear to have little or no taxonomic significance. Among these may be included flights associated with the defense of the female or of territory and those involved with the attempted rape of females. Actual aerial courtship possibly occurs in several species, but this has not been adequately investigated and is so often confused with the other kinds of aerial chase mentioned above that speculation on its evolutionary and taxonomic significance would be totally premature. Recent summaries of studies concerning aerial chases are those of Dzubin (1957), Wüst (1960), and Lebret (1961).

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

BIOLOGICAL CHARACTERISTICS OF THE FAMILY ANATIDAE

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

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

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

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

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

At first glance it would seem a paradox that the family Anatidae, in which some of the most elaborate avian courtship displays are to be found, actually is responsible for the greatest number and variety of interspecific hybrids of any avian family (Gray, 1958). For example, the mallard has been alleged to hybridize with no less than 45 species of anatids, the wood duck with 26 species, and the pintail with 25 species. Among geese, the species most frequently found to have hybridized are the Canada goose and the graylag goose, which are reported to have hybridized with 16 and 17 species respectively. It must be admitted that many of the waterfowl hybrid combinations have been achieved under the artificial conditions of captivity, and are therefore of decreased significance in the consideration of natural isolating mechanisms. They do, however, point out the importance of such mechanisms for the prevention of gene flow between species. Furthermore, many of the hybrid combinations obtained in captivity have also, when geographically possible (i.e., when between sympatric species), occurred under natural conditions. This anomaly then—elaborate sexual display and competition among drakes for mates, combined with a surprisingly high incidence of "incorrect" selection on the part of females—must be examined more closely. Have the elaborate displays and signal characteristics of the males been evolved to prevent interspecific hybridization, or have they been evolved as a result of intraspecific sexual selection? In all probability there is truth in both hypotheses, but the first hypothesis seems the sounder of the two. This topic has been discussed in detail by Sibley (1957), and only the following points need to be made here. In areas where many closely related species of ducks are sympatric on their pairing grounds (generally their wintering areas), they tend to be sexually dimorphic and to engage in rather elaborate courtship displays. And although in closely related species these displays often consist of the same or very similar components of behavior, minor differences of plumage, or of the sequence, form, or frequency of the displays, confer distinctiveness upon them, and probably provide the ducks a basis for species recognition and mate selection. Thus those species which have the widest ranges and the greatest amount of sympatry with other closely related species tend to exhibit elaborate displays and complex male plumage patterns.

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