SEXUAL DIMORPHISM IN THE ANATIDAE

by Tad Lawrence

The fall waterfowl migration has rekindled my interest in the subject of sexual dimorphism in the Anatidae. Specifically, why do the Anserinae (geese and swans) and the Anatinae (ducks), despite the appearance of superficial similarities in ecology, exhibit such divergence in the degree of sexual dimorphism? First, other differences in their breeding systems should be considered. The following life history summaries of several representatives of the Anserinae and the Anatinae are based on material taken primarily from Palmer[1] and Johnsgard.[2]

In general, the Anserinae are large, long-lived, migratory birds that are monogamous and mate for life. Typical of the group are Cygnus buccinator (Trumpeter Swan) and Branta canadensis (Canada Goose). In C. buccinator the average weight of males is about 12,247g., of females, 10,357g. Both sexes have uniform white definitive basic plumage which is molted once per annual cycle. It takes several years to obtain this definitive plumage. Once birds reach the age of 6-10 weeks, life expectancy is 6 years. Pair formation usually takes place during the second winter, and breeding may start the next summer. Eggs are laid and young are reared during the short northern summer before the birds return to their primary wintering grounds in southern Canada.

The situation is very similar in B. canadensis. The average weight of males is 4,300g., and of females, 3,550g. Both sexes share the same mottled gray definitive basic plumage and have black heads and necks with white chin patches. This plumage, molted once annually, is obtained in the Basic II molt. Life expectancy is greatly affected by hunting pressure. Although 60-70% of the yearling birds may be killed by hunters, the possibility of a long life exists, however. Most birds breed in their second winter although many do not. Pair bonds are formed for life. Eggs are laid in the summer, and the young make the long migration to their wintering grounds with their parents.

In general, the Anatinae are medium-sized, often migratory birds that usually show sexual dimorphism, and mate for only one season with the males sometimes helping in the protection of the young but more frequently deserting after mating. Typical of the group are Anas platyrhynchos (Mallard) and Anas acuta (Northern Pintail). In A. platyrhynchos males have an average weight of about 1,240g. and females 1,080g. The plumage of both sexes is very different, with the males having a gray back, chestnut breast, and iridescent greenish head in the definitive alternate plumage, obtained in the second fall. This gaudy breeding plumage is contrasted with the definitive basic plumage or eclipse brownish plumage present for a short time during the summer. Females are a uniform mottled cryptic brown. Both sexes have two molts per annual cycle. Life expectancy is greatly determined by hunting - mortality runs about 50% per year. Pair bonds are usually formed in the late fall and terminate just after incubation is started.

In A. acuta sexual dimorphism is even more pronounced. Males weigh at least 928g., while females weigh approximately 762g. The pattern of plumage cycles resembles that in Mallards for both sexes. However, in the male the definitive alternate plumage is a pearl-gray back, vermiculated sides, white breast and neck, brown head, and a long extension of the central tail feathers - a very elegant bird. The female is much like the female Mallard. It is believed that these birds live for less than three years. Pair termination takes place about a week after incubation starts.

From these life history outlines it can be seen that the Anserinae show little sexual dimorphism. This is accompanied by less promiscuity (pair bonds often being formed for life) and by both parents' contributing to the raising of offspring. The Anatinae exhibit marked sexual dimorphism, greater promiscuity (pair bonds usually terminating just after the start of incubation), and little or no male participation in the rearing of offspring. Clearly on examination, superficial similarities between these two closely related groups of birds break down.

Most authors agree that a review of the Anseriformes phylogeny indicates that the monomorphic condition as well as multi-seasonal pair bonds and male participation in the raising of offspring is the ancestral primitive condition.[3] Hamilton and Barth[4] have compiled a number of possible causes of sexual dimorphism, and several of these are particularly relevant in the evolution of the Anatinae. These theories include the following:

1. Species recognition and hence hybridization minimization[5]
2. Enhanced mate selection[6]
3. Rapid pair formation[7]
4. Rapid sex recognition[8]
5. Predator avoidance[9]
6. Avoidance of competition[10]

Enhanced species recognition and the accompanying lessening of hybridization do not seem to be responsible for the occurrence of sexual dimorphism in the Anatinae. In fact, the evidence indicates that hybridization occurs frequently in this group in association with high fertility.[11] This indicates that not only did sexual dimorphism in this group not evolve due to selection pressures favoring species recognition, but also existing dimorphism serves only a limited recognition function.

The degree to which sexual dimorphism occurs due to selective pressures favoring the female's choice of an optimum mate is extremely difficult to measure. Clearly if secondary sexual characteristics come to reflect accurately the fitness of an individual, then selection can start to take place independently with regard to secondary characteristics. This fact has been substantiated by O'Donald.[12] It follows that in mating systems that involve competitive mate selection the occurrence of sexual dimorphism may be promoted. This must partially account for the lack of dimorphism in the long-pair-bonding Anserinae and the presence of dimorphism in the Anatinae. Reasons for the differences in degree of mate competition will be considered later.

Rapid pair formation seems of little significance in either the Anatinae or the Anserinae as pair formation occurs on the wintering grounds where time pressures are minimal. A similar pressure - rapid mate recognition for pair bond maintenance - has not been satisfactorily considered and may be of some importance in the Anatinae due to the males' rapid mating and nest desertion after arrival on the breeding grounds.

When Hamilton[13] proposed rapid sex recognition as a factor promoting sexual selection, he was considering specifically the Parulidae (wood warblers) and the Icteridae (orioles). In these species dimorphism has evolved from an ancestral state in which both sexes were brightly colored, and hence as territoriality evolved so did more cryptic female plumage, thus minimizing aggressive interaction between the sexes. Exactly the opposite conditions prevail among the Anatidae as the more primitive Anserinae show little sexual dimorphism and much greater territoriality than do the Anatinae. The existence of long pair bonds in the Anserinae and short bonds in the Anatinae suggests that rapid sex recognition is not a primary selective pressure favoring sexual dimorphism in the Anatidae.

Predator avoidance must serve to reinforce the cryptic coloration of Anatinae females but cannot account for its occurrence as more bland plumage seems to be the ancestral norm. However, this conclusion is possibly contradicted by experiments indicating that the male plumage is acquired by both sexes after castration has taken place.[14] Among the Anserinae predation may serve to reinforce ancestral cryptic coloration of both sexes.

Instead of these theories I propose that differences in the degree of sexual dimorphism found in the Anserinae and the Anatinae are primarily the result of the differential effect of high latitude breeding due to differences in biology. Specifically, the Anserinae have maintained the more primitive monomorphic condition due to the requirements of raising their offspring. On the other hand, im the Anatinae a decrease in the investment necessary for the raising of young has caused other selective pressures, namely sexual selection, to favor sexual dimorphism.

In the Anserinae discussed breeding takes place in small northern ponds and tundra puddle-holes during the short northern summer. Trumpeter Swans take 34 days on the average to incubate their eggs, and another 97 days pass before the young are fully fledged and flying! This is a long time in a climate such as Churchill's where only in July and August are the average daily temperature minimums above freezing. Furthermore, before the young migrate, substantial body weight and fat reserves must be built up. This is a substantial job for birds as large as these. In addition, to ensure adequate nest defense and care of the young, the involvement of two parents is required. This may be particularly important with regard to incubation since cold temperatures early in the season could make it unsafe to leave the nest for long periods. Since predation may also be significant, male presence for defense is favored and cryptic coloration reinforced. Thus, environmental factors in conjunction with species biology have favored the maintenance of strong pair bonds and male investment in the care of the young. These factors have served to minimize the selection for sexual dimorphism caused by some of the pressures previously considered, including rapid pair formation and rapid sex recognition. On the other hand, mate selection and predator avoidance exert selection for the maintenance of plain plumage monomorphism due to species biology and breeding requirements.

In the Anatinae, despite similar breeding conditions, time pressures are not so keenly felt. On the average it takes only 27 days for the Anatinae to incubate their eggs and another 55 days until the young are fully fledged and flying. This allows for much greater choice regarding the time of nesting initiation. Furthermore, much less body weight must be put on in these birds than in the larger *Anserinae*. Since males are too small to aid effectively in nest defense, cryptic coloration of the females is maintained by selection and male nest desertion is promoted. Thus, since the male is of little use after the initiation of nesting, the emphasis of selective pressures favors dimorphism. Specifically, bright plumage is selected for to increase the chance of attracting the optimal female, and strong pair bonds are selected against as the presence of a brightly colored male near the nest serves only to attract predators. In short, enhanced mate selection, mate recognition, and predation avoidance exert substantial selective pressures toward dimorphism.

In summary, the differences in the degree of sexual dimorphism found in the *Anatinae* and the *Anserinae* are caused by differences in biology that work through differences in breeding systems induced by environmental conditions. The result is differential sexual selection that favors the development of sexual dimorphism in order to maximize individual fitness in ducks but not in geese.

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