

Sex ratios, sexual selection and sexual dimorphism in waterfowl

“A greater survival of drakes insures natural selection at mating”

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THE MANAGEMENT IMPLICATIONS of disparate sex ratios favoring males in certain waterfowl have long intrigued biologists (Lincoln 1932, Leopold 1933, McIlhenny 1940, Erickson 1943, Petrides 1944, Hochbaum 1944, Beer 1945, Yocum 1949, Johnsgard and Buss 1956, Anderson *et al.* 1969, and Johnson and Sargeant 1977). Hochbaum (1944) and Bellrose *et al.* (1961) convincingly showed that imbalanced sex ratios in most waterfowl species are real, and are the result of greater mortality of females—the sex ratio being essentially 50:50 at hatching. Bellrose (1976) stated that the degree of sex ratio imbalance between species appears related to the length of pair bond, but that the reasons for this relationship are unclear.

Because the preponderance of males increases with time, older-aged populations exhibit a greater disparity than populations having a large percentage of young birds; consequently, imbalanced sex ratios are considered indicative of poor production and an “unhealthy” population. Although it is often difficult to get representative samples owing to differential migration between sexes and age classes (see *e.g.*, Welling and Sladen 1979), most biologists consider accurate sex ratio data of management importance. Some (*e.g.*, Grieb *et al.* 1970) suggested that “excess” drakes could be harvested. A special subcommittee of the Central Flyway Technical Committee was established to determine the function of supernumerary drakes in various populations. Dzubin (1970) in a report to this subcommittee, and later Johnson and Sargeant (1977), raised several questions concerning the origin of disparate ratios and suggested further research into this phenomenon before embarking on special drake-only seasons.

Recently a colleague and I (Brown and Gutiérrez, 1980) showed an appar-

ent relationship between imbalanced sex ratios favoring males and sexual dimorphism in North American quails and hypothesized that male preponderance is a function of sexual selection. We suggested that the need for differential fitness between males in intraspecific competition could explain imbalanced sex ratios favoring males in other *seasonally-monogamous* species, including some waterfowl.

Presentations of waterfowl sex ratios by Bellrose *et al.* (1961), Bellrose (1976), and statistics compiled by the U. S. Fish and Wildlife Service (*e.g.*, Sorenson *et al.*, 1978) are available for most North American waterfowl. Recent findings and investigations on the less dimorphic subspecies of Mottled (Florida) Duck (*Anas fulvigula fulvigula*; Lotter 1968, Stieglitz and Wilson 1968), Mottled Duck (*A. fulvigula maculosa* Stutzenbaker, C. D. *pers. comm.*), and Mexican Duck (*A. platyrhynchos diazi*; Hubbard 1977, Scott and Reynolds 1978) now permit a reasonable discussion of this hypothesis as it pertains to the family Anatidae.

MATING SYSTEMS IN THE ANATIDAE

SEXUAL DIMORPHISM is reduced or absent in members of waterfowl families that maintain lengthy pair bonds—*i.e.*, the subfamily Anserinae (Skutch 1940, Sibley 1957). Studies of Canada Goose (*Branta canadensis*, Imber 1968), Snow Goose (*Anser caerulenscens*, Hanson *et al.* 1972), and Black-bellied Whistling Duck (*Dendrocygna autumnalis*, Bolen 1970) have shown sex ratios slightly weighed in favor of females (Canada Goose), or only slightly in favor of males (Snow Goose, Black-bellied Whistling Duck). Sex ratios in all samples of these species are essentially 50:50.

This is not the case with the Anatinae, a subfamily in which species generally renew mates each year. Bellrose *et al.* (1961) showed that the number of drakes exceeded hens in all species for which data were available. They found that males in most species slightly outnumbered females from shortly after the time of hatching to the first breeding season. After that time drakes greatly exceeded hens, but differential mortality was greater in some species than others (Bellrose 1976). I suspect that differential sex ratios in at least some species are evolutionary strategies insuring intrasexual competition and natural selection. Certainly the conclusion by Bellrose (1976:25) that “the longer a species of duck is without a pair bond, the greater disparity in its sex ratio” supports an evolutionary hypothesis. If sex ratios are indeed a function of sexual selection and intrasexual competition, it would be expected that species possessing the least disparate sex ratios would exhibit the least sexual dimorphism and maintain the longest pair bonds.

Sex ratios and sexual dimorphism in the genus Anas

Although members of the tribe Aythyini (inland divers) have the most exaggerated male to female ratios, they all exhibit pronounced sexual dimorphism, and comparison within this group is difficult. To compare potential relationship between pair bonds, sex ratios and sexual dimorphism, I examined percentages of males in the largest available samples of *Anas* (dabblers)—a genus including species with a wide range of sexual dimorphism and sex ratios (Table 1).

The species are generally arranged by the prominence of drakes in the

Table 1. Percentages of males in shot samples of *Anas* ducks

Species	Shot samples			Shot sample adjusted for differential vulnerability			Breeding season samples
	Adult	Imm.	Total	Adult	Imm.	Total	All
<i>A. acuta</i>	69.3 ^a	53.5 ^a	62.1 ^c				59.4 ^b
	68.6 ^c	53.0 ^c	62.4 ^c				54.3 ^d
<i>A. americana</i>	70.5 ^a	51.8 ^a	—				54.6 ^b
	69.5 ^c	51.9 ^c	60.7 ^c	69.5 ^c	51.9 ^c		56.4 ^d
<i>A. crecca</i>	67.6 ^a	49.8 ^a	55.9 ^c				54.7 ^d
	69.3 ^c	47.4 ^c	56.6 ^c				
<i>A. clypeata</i>	67.8 ^a	42.0 ^a	58.3 ^a				60.1 ^b
	66.2 ^c	52.4 ^c	59.0 ^c				55.1 ^d
<i>A. discors</i>	51.1 ^c	46.3 ^c	—	51.3 ^c	45.0 ^c	—	59.3 ^b
<i>A. cyanoptera</i> and <i>A. discors</i>	56.0 ^c	43.0 ^c	—				57.1 ^d
<i>A. strepera</i>	51.0 ^a	45.8 ^a	47.7 ^a				
	67.6 ^a	50.7 ^a	—				52.8 ^b
	68.8 ^c	52.4 ^c	60.0 ^c				52.8 ^d
<i>A. platyrhynchos</i>	70.1 ^a	57.2 ^a	62.8 ^a	64.2 ^a	51.1 ^a	56.8 ^a	52.6 ^b
	65.2 ^c	50.4 ^c	57.0 ^c	62.3 ^c	50.7 ^c	57.0 ^c	51.2 ^d
<i>A. rubripes</i>	56.9 ^a	—	53.5 ^f	52.3 ^{a,c}	—	55.0 ^c	
	61.3 ^g	48.6 ^g	52.9 ^g			54.8 ^h	
<i>A. fulvigula maculosa</i>			54.6 ⁱ				
<i>A. fulvigula fulvigula</i>			48.2 ^j				
<i>A. platyrhynchos diazi</i>	53.0 ^k		45.7 ^l				51.3 ^m

^aMean weighted total for U.S., 1973-1977 Sorenson *et al.* (1978) ^bBellrose *et al.* (1961:414-415) ^cBellrose (1976) ^dBellrose *et al.* (1961:428) ^eBellrose *et al.* (1961:404) ^fWright (1954:79) ^gBirds in hunter's bags Bellrose *et al.* (1961:405-407) ^hPospahala and Henny (1971) ⁱStutzenbaker, C.D., personal comm. ^jLotter (1968) ^kScott and Reynolds (1978) ^lHubbard (1977) ^mpersonal field notes.

samples and their systematic relationship to each other. The least skewed sex ratios occur in the closely related Blue-winged and Cinnamon teals, the Black Duck, and in non-migratory Mallard-like ducks. These last species appear to have the most balanced sex ratios of any of the species shown and also have the least dimorphic males.

Although the Blue-winged and Cinnamon teals are distinctly dimorphic, Sowls (1955:101) and others observed that Blue-winged Teal drakes were reluctant to abandon their hens until incubation was well advanced, and the Blue-winged Teal is reported as having more intense pair bonds than most other dabblers (Bellrose 1976). Both Blue-winged and Cinnamon teals are early migrants and differential migration to wintering areas out of the United States could also account for less disparity in sex ratios of shot samples of these species (Bellrose 1976:276).

Recent investigations and observations have shown long pair-bond attachments in the resident or nearly resident Mottled (Florida) and Mexican ducks (Engeling 1951, Stieglitz and Wilson 1968, Swarbrick 1975:71, Williams 1975, Scott and Reynolds 1978). Sex ratios of these more monomorphic relatives of the Mallard are as narrow as those in the also rather monomorphic but migratory Black Duck.

The Black Duck is known for early onset of sexual displays, early mate selection and long pair-bonds (Johnsgard 1960, Stotts and Davis 1960).

It therefore appears that disparate sex ratios and sexual dimorphism are related in the genus *Anas* as they are in quail (Brown and Gutierrez 1980). My explanation for this relationship is that differential fitness results in male variation and intra-male competition during female sexual selection. A greater survival of drakes facilitates and insures natural selection at mating. Short mating seasons heighten sexual selection and lead to increased sexual dimorphism. This is not to be interpreted as meaning that females are dying at a greater rate than males as a matter of natural selection—it means that it is important that females have a number of males from which to choose (Fisher 1958). The shorter the period for mate selection, the greater need for more males from which to select. Sexual dimorphism in turn facilitates sexual selection. I suspect these processes were heightened with the post-Pleistocene evolution of species utilizing brief courtship and migration strategies to exploit newly available nesting habitats and the resulting and ongoing competition for these habitats (Sibley 1957). Less migratory and/or longer paired species have longer periods for mate selection; intra-male competition is less

pronounced, sexual dimorphism is reduced, and there is less advantage to differential male survival.

WHAT IS THE biological importance and, therefore, management significance of these relationships? Perhaps the foremost consideration is the recognition that skewed sex ratios, pair-bond duration, and the retention (or assumption) of cryptic coloration are not unrelated phenomena, but functions of natural selection. Drake seasons could conceivably reduce sexual selection and in some species, the increased drake mortality would conflict with evolved mating strategies. On the other hand, an increased hunt mortality of drake Mallards might benefit less dimorphic Mallard-like forms where males of these species are in sexual competition with Mallards (see *e.g.*, Hubbard 1977).

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Male Pintail. Photo/Bob Gress.

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