Differential sex distributions of wintering diving ducks (*Aythyini*) in North America

William C. Alexander

INTRODUCTION

THE ORNITHOLOGICAL LITERATURE is replete with reports of imbalanced sex ratios in natural populations of birds. Although substantial evidence indicates that the sex ratio in young birds is essentially unity (Emlen 1940; Williams 1940; Hochbaum 1944; Selander 1960, 1962, 1965; Darley 1971), adult sex ratios that disproportionately favor males are common (*e.g.*, Mayr 1939, Lack 1954, Bellrose *et al.* 1961, Anderson and Timken 1972, Trauger 1974, Ketterson and Nolan 1976, Welling and Sladen 1979, Brown 1982). No doubt some of the reported distortion in sex ratios can be attributed to inadequate sampling, trapping bias, differential utilization of local habitats, and differential migration by males and females.

For nearly five decades much concern has been expressed about the possible effects of disparate sex ratios on waterfowl population dynamics (*e.g.*, Lincoln 1932, Trauger 1974). Despite the concern over distorted numbers of males and females, little effort has been expended to evaluate waterfowl sex ratios in the field over a broad geographic range. This is somewhat surprising because most waterfowl are flocked during the nonbreeding period and tabulations of males and females can be made easily.

Since 1900 the National Audubon Society has sponsored winter bird censuses on an annual Christmas Bird Count (hereafter, C.B.C.). In recent years scientists have recognized the value of data collected on the C.B.C.s in addressing questions related to specific problems such as population trends (*e g.*, Bock and Lepthien 1972, 1975; Brown 1971, 1973). In 1977 and 1978 I made requests through the National Audubon Society for the tabulation of diving duck (*Aythyini*) sex ratios on the C B.C.s. These data were used to test the hypothesis that male and female Canvasbacks (*Aythya valisineria*), Redheads (*A. americana*), Ring-necked Ducks (*A. collaris*), Greater Scaup (*A. marila*), and Lesser Scaup (*A. affinis*) are distributed independently of latitude in mid-winter. Comments are made relative to the possible evolution of differential male-female distributions in birds.

METHODS

THE REQUESTS FOR sex ratio data on the *Aythyini* were included in the packets of information mailed annually to each count compiler by the National Audubon Society. These requests were for the actual numbers of males and females of each species and the latitude-longitude coordinates of each count area. Where large numbers of birds precluded actual counts, accurate estimates of total numbers and sex ratios were accepted. Estimates of sex ratios accounted for 15% of these data. During 1977 and 1978 most C.B.C.s were conducted between December 16 and January 1.

To evaluate any differences in the distributions of birds by latitude between coastal areas and the mid portions of North America, three regions were designated by longitude: the eastern region included count areas east of 86°W (approximately the location of Chattanooga, Tennessee), the western region included count areas west of 104°W (approximately the location of Denver, Colorado), and the central region included count areas between 86°W and 104°W.

Because these data were collected in two different years, they were evaluated independently to discover annual differences in distribution patterns. Although slight variations in these data existed between years, the trends and subsequent conclusions were the same, therefore, data were combined over the two years.

A simple linear regression analysis was used to analyze the relationship between latitude and sex distribution for each species in each region. This analysis was based upon the proportion of males reported for each individual count within the three respective regions. Arcsine transformations of all proportional data were made prior to statistical analysis (Zar 1974). The regression procedure for each species was weighted by the total number of birds reported for that particular count area, thus placing more emphasis on areas with larger numbers of birds This precludes counts with few birds (*e g*, N = 16, 50% male) from having the same weight in the analysis as counts with large numbers of birds (*e.g.*, N = 10,000, 50% male). Only a few birds were reported above 50°N or below 25°N, and these were deleted from the analysis.

RESULTS

Canvasback.—During the 1977 and 1978 C.B.C.s, 47,761 Canvasbacks were reported from 113 count areas across the United States (Table 1). Major concentrations of Canvasbacks were reported in the east from New York, Ohio, New Jersey, Maryland, Virginia, and Florida. In the west northern California reported good numbers of Canvasbacks. Eighty-seven percent of the Canvasbacks reported across the three regions were located between 35° and 45°N latitude.

The reported sex ratios of Canvasbacks varied among regions with 2.23 1 (males/female) in the east, 1.69:1 in the central, and 1.83:1 in the west. The total Canvasback sex ratio for all three regions was 2.15:1 (68% male).

Results of the linear regression analyses for all three regions indicated that male and female Canvasbacks are partially segregated by latitude during this portion of the nonbreeding season (Table 2). As one progresses from southern to northern latitudes in the United States during this time period,

Table 1. Frequency of count areas and sexes of Aythyini reported on the 1977 and 1978 Christmas Bird Counts across the United States.

Species	Geographic Region			
	Eastern	*Central*	*Western*	*Total*
	52[a]	24	37	113
Canvasback	28,033[b]	1,371	3,216	32,620
	12,570[c]	812	1,759	15,141
	21	12	13	46
Redhead	523	44,465	2,628	47,616
	254	11,185	1,315	12,754
	41	31	35	107
Ring-necked Duck	18,928	4,360	2,402	25,690
	25,761	687	1,522	27,970
	34	2	28	64
Greater Scaup	28,651	571	4,248	33,470
	20,275	740	3,117	24,132
	56	47	44	147
Lesser Scaup	9,003	6,419	6,473	21,895
	4,713	5,191	6,599	16,503

[a]Frequency of reporting areas in each region. [b]Frequency of males reported in each region. [c]Frequency of females reported in each region.

the proportion of male Canvasbacks in wintering populations tends to increase.

Redhead.—On the 1977 and 1978 C B.C.s, 60,370 Redheads were tabulated on 46 counts across the United States and southern Canada (Table 1). The major concentration of Redheads was in the Laguna Madre of Texas (26°N) where 92% of the total birds reported across the United States were tabulated.

Sex ratios of Redheads also varied among regions with 2.06:1 in the east, 3 98:1 in the central, and 2.00:1 in the west. The total Redhead sex ratio over all regions was 3.73:1 (79% male).

Linear regression analyses for the eastern and central regions did not indicate significant relationships between the distributions of the sexes and latitude, but a significant relationship was found in the western region with males being more prevalent in northern areas (Table 2).

Ring-necked Duck.—During the 1977 and 1978 C.B.C.s, 53,660 Ring-neckeds were recorded on 107 counts across the United States (Table 1). Major concentrations of Ring-neckeds were reported in the east from North Carolina, South Carolina, and Florida. In the central region concentrations were reported from Missouri and Arkansas, and in the west from California. Eighty-four percent of the Ring-neckeds reported were located below 35°N latitude.

Ring-necked sex ratios varied among regions with 0.73:1 in the east, 6.35:1 in the central, and 1.58:1 in the west. The sex ratio over the three regions was 0 92:1 (48% male).

Regression analyses for all three regions indicated significant positive relationships between the distributions of the sexes and latitude, with greater proportions of males located in the northerly portions of the winter range (Table 2).

Greater Scaup.—On the 1977 and 1978 C.B.C.s, 57,602 Greater Scaup were tabulated on 64 counts across the United States and southern Canada (Table 1). Concentrations of birds were reported in the east from New York, Massachusetts, Connecticut, and New Jersey. In the west sizable reports came from British Columbia. Ninety-eight percent of the Greater Scaup were reported from areas above 40°N latitude.

Slight variations in sex ratios were reported between the east (1.41:1) and the west (1 36.1), with only a few birds coming from the central region. The total sex ratio was 1.39:1 (58% male)

The regression analysis for the west indicated significant positive relationship between proportions of males and latitude. In contrast the analysis in the east provided a marginally significant negative relationship between proportions of males and latitude. Too few birds and count areas were reported from the central region to make any conclusions about differential sex distributions (Table 2).

Lesser Scaup.—For this species, 38,398 birds were recorded on the two Christmas Bird Counts (Table 1). Concentrations of Lesser Scaup were reported in the east from New Jersey, Maryland, Virginia, and Florida, in the central region concentrations were in Arkansas and Texas, and in the western region from British Columbia, Oregon, and Southern California. Sixty-three percent of the Lesser Scaup reported came from below 35°N latitude.

Sex ratios were variable across regions with 1.91:1 in the east, 1.24:1 in the central, and 1.36:1 in the west. The total sex ratio over all counts was 1.33·1 (57% male).

Regression analyses for the three regions indicated no significant relationships between the proportions of males and latitude (Table 2).

DISCUSSION

THE MID-WINTER DISTRIBUTIONS of the sexes in North American *Aythyini* were examined to test the hy-

Table 2. Relationship between proportions of males and latitude during the 1977 and 1978 Christmas Bird Counts.

Species	Geographic Region		
	Eastern	*Central*	*Western*
Canvasback	Y = −0.66 + 0.04X[a] $r = 0.60$[b] $P < 0.001$[c]	Y = −0.20 + 0.03X $r = 0.61$ $P < 0.01$	Y = 0.12 + 0.02X $r = 0.36$ $P < 0.05$
Redhead	Y = 1.70 − 0.02X $r = 0.38$ $P > 0.05$	Y = 1.71 − 0.02X $r = 0.48$ $P > 0.05$	Y = 0.16 + 0.02X $r = 0.58$ $P < 0.05$
Ring-necked Duck	Y = −0.67 + 0.05X $r = 0.49$ $P < 0.01$	Y = −1.00 + 0.06X $r = 0.66$ $P < 0.001$	Y = 0.51 + 0.01X $r = 0.33$ $P < 0.05$
Greater Scaup	Y = 2.47 − 0.04X $r = 0.33$ $P = 0.05$	——[d] ——[d] ——[d]	Y = 0.40 + 0.01X $r = 0.42$ $P < 0.05$
Lesser Scaup	Y = 0.81 + 0.01X $r = 0.14$ $P > 0.05$	Y = 1.11 − 0.01X $r = 0.11$ $P > 0.05$	Y = 0.68 + 0.01X $r = 0.21$ $P > 0.05$

[a]Regression equation. [b]Product-moment correlation coefficient. [c]Probability values: ≤ 0.05 significant, ≤ 0.01 highly significant. [d]Insignificant number of reporting count areas.

pothesis that males and females in these species occur independently of latitude. This hypothesis was rejected across all three regions of North America for Canvasbacks and Ring-neckeds. In both species significantly greater proportions of males occurred at the more northerly parts of their winter ranges.

In wintering male and female Redheads the respective distribution patterns were more difficult to interpret than those of Canvasbacks and Ring-neckeds. Only a marginally significant relationship was detected in the western region between the proportions of male Redheads and latitude. The low numbers of Redheads tabulated in the eastern region along with the preponderance of birds in the southern portion of the central region probably obscured any detectable patterns of sexual segregation in these areas. Perhaps more systematic and intense sampling of sex ratios over a broader range of latitude in both eastern and central regions would provide added insight into the midwinter distributions of male and female Redheads.

The analyses of sex distributions in Greater and Lesser scaups did not demonstrate any consistent patterns of male-female segregation. The tendency for large numbers of Greater Scaup to occur in the east above 40°N latitude, and for Lesser Scaup to overwinter in the southern United States (Bellrose 1976), results in the concentration of major portions of their wintering populations. Probably these concentrations of birds, as in Redheds, obliterate any potential sexual segregation on a geographic scale. However, this does not preclude the possibility of sexual segregation through differential habitat utilization on a local level in all species (Alexander *in prep.*).

The partial segregation of the sexes documented herein on a geographic scale for nonbreeding Canvasbacks had been suggested earlier (Hochbaum 1944, Palmer 1976), but adequate data were not presented to critically evaluate the problem. Recently in an analysis of banding and recovery data Nichols and Haramis (1980) reported similar trends in Canvasback distribution patterns. In Ring-neckeds, Mendall (1958) alluded to some sexual segregation during migration, but made little reference to post-migratory distributions. Salomonsen (1968) found evidence of latitudinal segregation between the sexes in the Common Pochard *(A. ferina)* and Tufted Duck *(A. fuligula)*, Old World counterparts of Canvasbacks and Ring-neckeds, respectively.

THE LATITUDINAL SEGREGATION of male and female birds during the nonbreeding season has been reported in many species (see review of Gauthreaux 1978). This phenomenon represents an interesting problem from an evolutionary perspective. Why do post-reproductive females in many species undertake the cost of more distant migration to southern latitudes? An argument frequently invoked to explain this separation involves thermoregulatory mechanisms and the "fasting endurance hypothesis" (Calder 1974). Briefly this hypothesis suggests that larger birds can survive during severe cold without feeding for longer periods than can smaller birds. However, Calder (1974) made no reference to sex-related differences in body size and survival, only to differences between species. A number of experimental studies (*e.g.*, Kendeigh 1945, Ivacic and Labisky 1973, Ketterson and King 1977) seem to support the idea that males can survive longer periods of cold without food than females, but under simulated conditions females cannot disperse from approaching cold fronts as they can under natural conditions (*e.g.*, Nilsson 1970, Alford and Bolen 1977, Bennett and Bolen 1978).

A second point relative to fasting endurance is the actual size differential between males and females of a given species. For instance, Nichols and Haramis (1980) suggested that differences in mean weights of 7.8% in January and 10.9% in March (males were larger) between Canvasback sexes could lead to reduced survival by females during cold periods. This appears to be, at best, a highly speculative argument, because good quantitative data exist to indicate that wet-weight in various bird species can vary from 7 to 15% during the diel period (*e.g.*, Owen 1954, Helms and Drury 1960, Helms *et al.* 1967, Helms 1968). Furthermore, Helms *et al.* (1967) reported that in Dark-eyed Juncos *(Junco hyemalis)* males were larger and heavier than females but the sexes did not differ in available body fat, which is the major energy reserve. In a study of wintering Green-winged Teal *(Anas crecca carolinensis)*, Bennett and Bolen (1978) reported no significant sex-related differences in stress as determined by condition index and various blood parameters. In this species males are on the average 8% larger than females (Bellrose 1976). Until sex-specific data are available on various body components (*e.g.*, dry fat-free body weight, total fat, etc.) as well as differences in metabolic rates for individual species, applications of fasting endurance based upon minor variations in total body weight to explain differential distributions in birds are tenuous. As indicated by Helms *et al.* (1967) "water, protein, carbohydrate, minerals, and lipid, as well as their total, vary from species to species, from bird to bird within a species, and from time to time within an individual."

An equally credible hypothesis to explain differences in the distributions of nonbreeding avian sexes that would also include size differences might be behavioral dominance. In most bird species for which data are available, larger males usually dominate smaller females in nonbreeding aggressive encounters (see Gauthreaux 1978), although some exceptions do occur (*e.g.*, Thompson 1960 Samson 1977). In Canvasbacks and Ring-necked Ducks, nonbreeding aggressive interactions are frequent between the sexes and males usually dominate females in competition for food (*e.g.*, Alexander and Hair 1979, Alexander 1980, Alexander *in prep.*). In addition, both species exhibit a partial segregation of the sexes in winter on a latitudinal scale. It is possible that a situation much like that in Common Pochards and Tufted Ducks (Salomonsen 1968) is operating in Canvasbacks and Ring-neckeds. Salomonsen reported that male Common Pochards and Tufted Ducks completed the wing molt before the incubating females, moved south earlier and usurped the available food resources. Therefore, the later-arriving females were forced to migrate farther south. In an earlier paper, Salomonsen (1955) suggested that this type of intraspecific competition would produce an allohiemic distribution in which segments of the same population winter in different areas

A SIMILAR SITUATION prevails in Canvasbacks and Ring-neckeds where large numbers of males also molt before the females (Mendall 1958, Erskine 1972, Bergman 1973), males dominate females in aggressive encounters for food, and a partial geographic segregation of the sexes is evident. I believe that male dominance in intersexual

competition for resources is a likely explanation for the differential sex distribution patterns observed in Canvasbacks and Ring-neckeds, and possibly in many other avian species, particularly those not paired during the nonbreeding season. Increasingly, allohiemic distributions are being recognized as a means of reducing intersexual competition in nonbreeding birds (*e.g.*, Balph and Balph 1976, Ketterson 1979). However, additional information is essential before we can fully document the effects of intersexual dominance on the utilization of winter habitat at both local and geographic levels.

ACKNOWLEDGMENTS

I WOULD LIKE TO THANK S. Gauthreaux, J. Hair, C. Helms, and J. Waide for their confidence and support during my graduate program at Clemson University. My most sincere gratitude is extended to R. Arbib and most especially to the members of the National Audubon Society who tabulated sex ratio data on the 1977 and 1978 Christmas Bird Counts. Their efforts made this research possible. I am also grateful to S. Gauthreaux, R. Taylor, and C. Helms for comments on earlier drafts of this paper. For financial support during this period, I thank the National Wildlife Federation, USFWS (Contract number 14-16-0008-2069), S.C. Wildlife and Marine Resources Commission, and the Clemson University Department of Zoology.

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—*Dept. of Zoology, Clemson University, Clemson, S C 29631,* present address *Department of Biology, Georgia Southern College, Statesboro, Georgia 30460*

Differential sex distributions of wintering. diving ducks (Aythyini) in North America. American Birds 37(1):26-. 29.Â Early pair-formation may be advantageous in wintering dabbling ducks because the resulting higher dominance may give better access to food. Sex ratios differed among the six species. Males predominated in all species; however, species that formed pair bonds early in the winter had less disparate sex ratios than species pairing later. In North America, Rough-legged Hawks breed in tundra or taiga in arctic and subarctic Alaska and Canada and migrate across the boreal forest to winter in open country of southern Canada and the northern United States. A cliff-nesting species, this hawk is likely limited in distribution and numbers in many areas by the availability of suitable nesting sites. Occasionally, pairs exploit areas without cliffs by nesting in trees at the fringe of boreal forest or on human-made structures. In winter, these hawks concentrate in open areas reminiscent of their tundra summer haunts, including pastures,...Â (2000). Differential winter distribution of Rough-legged Hawks by sex in western North America. Journal of Raptor Research 34:157-166. Close. A migratory diving duck of North America. photo: Gerard W. Beyersberger. ÐžÑ‚ÐºÑ€Ñ‹Ñ‚ÑŒ. More information.Â The Australian wood duck, maned duck or maned goose (Chenonetta jubata) is a dabbling duck found throughout much of Australia. It is the only living species in the genus Chenonetta. Traditionally placed in the subfamily Anatinae (dabbling ducks), it might actually belong to the subfamily Tadorninae (shelducks); the ringed teal may be its closest living relative. Tracy Jones. Wild Ducks.