

## SEX-SPECIFIC DIFFERENCES IN WINTER DISTRIBUTION PATTERNS OF CANVASBACKS

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**ABSTRACT.**—Winter band recovery distributions of North American Canvasbacks (*Aythya valisineria*) suggested that males and females exhibit comparable degrees of fidelity to general wintering areas. Of birds banded during the winter, the proportion of males was found to be higher in northern than in southern areas. Winter band recovery distributions of birds banded in particular areas during the summer were found to differ significantly between sexes, with females being recovered farther south. Factors that may have affected the evolution of sex-specific wintering distributions include: (1) possible reproductive benefits derived by males who winter in the north and thus reach northerly breeding areas early; (2) sexual dimorphism in body size, which may render the smaller females especially susceptible to periods of inclement weather and food shortages; and (3) interactions between sexes in which males may control food supply when food is scarce. Two lines of evidence from field data on Canvasbacks in the Chesapeake Bay suggest the existence of competition between males and females. First, Canvasbacks trapped during winter in smaller bodies of water tended to have higher proportions of females and weigh less than birds trapped in large open bodies of water. Second, analysis of aerial photographs of wintering rafts of Canvasbacks showed patterns of intersexual segregation, with females being found more frequently on peripheral areas of rafts.

Lack (1954, 1966) and Fretwell (1972) have suggested that "limitation" of temperate bird populations most likely occurs during the winter or nonbreeding season. It is therefore of interest to examine the distribution and abundance of bird populations during this period of the year. In many species of migratory birds in the Northern Hemisphere, males appear to winter farther north than females (see Nice 1933, Lack 1944, Selander 1966, Ketterson and Nolan 1976 and references therein). It has been suggested, (Witherby et al. 1939:219) that female and young diving ducks in Great Britain generally migrate farther south than adult males. Evidence of such a sexual difference has been provided in North America for Common Mergansers (*Mergus merganser*; Anderson and Timkin 1972) and Buffleheads (*Bucephala albeola*; Erskine 1971), in Europe for Common Pochards (*Aythya ferina*) and Tufted Ducks (*Aythya fuligula*; Salomonsen 1968), Mallards (*Anas platyrhynchos*; Lebreton 1950, Nilsson 1976), European Wigeon (*Anas penelope*), Green-winged Teal (*Anas crecca*), Northern Shovelers (*Anas clypeata*), and Pintails (*Anas acuta*; Lebreton 1950). Bellrose et al. (1961) summarized evidence suggesting that sex

ratios of North American waterfowl vary geographically during the winter. Hochbaum (1944:132) suggested that Canvasbacks (*Aythya valisineria*) may exhibit a differential distribution of sexes on the wintering grounds. Allen (1931:354) and DeGraff et al. (1961:79-80) noted the high proportion of males among Canvasbacks wintering in New York, and suggested that females were more numerous farther south.

The possibility that male and female Canvasbacks winter in different areas is interesting from both biological and management points of view. The continental Canvasback population is thought to exhibit the most disparate sex ratio (65-70% male) of all North American ducks. This ratio (and the low "reproductive potential" which it implies) has been labeled "a fundamental problem in the population dynamics of the Canvasback" (Trauger 1974). Canvasbacks hatch approximately equal numbers of males and females (Hochbaum 1944:51, SOWLS 1955:164); hence, the disparate population sex ratio must be due entirely to differential mortality. Indeed, in an analysis of Canvasback banding and recovery data, we found mortality rates to be significantly greater in females than males in each of the

three populations examined (Nichols and Haramis 1980). The existence of this difference emphasizes the importance of examining any sexual differences that may occur in distribution or general characteristics and habits. If winter mortality is as important to migratory bird populations as has been suggested, then the investigation of possible differences in the winter distribution patterns of the two sexes may help to explain the higher female mortality rates and resultant disparate sex ratios.

Our primary objective was to test the general hypothesis that male Canvasbacks tend to winter farther north than females. If this hypothesis was corroborated, our secondary objective was to explain the phenomenon or at least to obtain information on factors that might have affected its evolution.

## METHODS

Our data were obtained from three sources: the computer retrieval files of the U.S. Fish and Wildlife Service Bird Banding Laboratory (BBL), Laurel, Maryland; aerial photographs of Canvasback rafts in the Chesapeake Bay; and banding and weight records of Canvasbacks trapped in the Chesapeake Bay. The BBL data pertained to the period 1929–77, whereas the other data were collected during the winter of 1977–78. The BBL data used here included 2,663 recoveries and over 55,000 bandings. Only birds categorized as “normal, wild” were used in our analyses. Recovery records were restricted to birds shot or found dead. All birds banded during the winter (January–February) were considered to be adults, whereas summer-banded birds (July–September) were aged as either young (first year) or adult (older than one year).

In two portions of our analysis we tested the null hypothesis that geographic distributions of band recoveries from two samples came from the same population. Each observation (band recovery) is characterized by latitude and longitude of recovery measured to the nearest 10-min coordinate. The statistical problem is thus one of testing whether two-sample distributions belong to the same bivariate population. Kolmogorov-Smirnov test statistics (e.g., Sokal and Rohlf 1969:571–575) were computed to test the null hypothesis that the empirical marginal distributions of latitude and longitude (longitude was transformed via the relationship

$$1^\circ \text{ longitude} = (1^\circ \text{ latitude}) (\cos \lambda),$$

where  $\lambda$  is the latitude; see Raisz 1962:147) were univariate normal. This null hypothesis was rejected ( $P < 0.01$ ) for both latitude and longitude in the first several recovery distributions tested, and we concluded that parametric tests based on the assumption of bivariate normality would be inappropriate for these data.

For testing pairs of empirical distributions of band recoveries we used the nonparametric test suggested by Mardia (1967, 1972:197–201). Briefly, this test first involves computing the centroid or center of gravity of the combined two-sample distribution. Vectors are then considered from this centroid through each sample point (band recovery), and the points are ranked, based on the vector directions. These directions or angular observations are then replaced in the first sample by:

$$\beta_i = 2\pi r_i / (n + m), \quad i = 1, \dots, n,$$

where  $r_i$  is the linear rank of observation  $i$ ,  $n$  is the number of observations in the first sample, and  $m$  denotes the number of observations in the second sample. We then compute the resultant or vector sum of the first sample as:

$$R_1 = \left[ \left( \sum_{i=1}^n \cos \beta_i \right)^2 + \left( \sum_{i=1}^n \sin \beta_i \right)^2 \right]^{1/2}$$

The null hypothesis of no difference between the two bivariate samples is then rejected for large values of  $R_1$ . Mardia (1967) has shown that for  $n + m > 17$ :

$$U = 2R_1^2(m + n - 1)/mn$$

is approximately distributed as chi-square with two degrees of freedom. Under the bivariate normal distribution, the efficiency of Mardia's test relative to Hotelling's  $T^2$  (its parametric competitor) was found to lie between 79% and 93% (Mardia 1968). Our own Monte Carlo simulation work with distributions that more closely resemble band recovery patterns have resulted in approximated powers similar to those obtained using bivariate normal distributions. “Ties” between observations from the two samples occurred in some of our tests with empirical recovery distributions, and we computed approximate chi-square test statistics in the manner suggested by Robson (1968).

Aerial photographs of Canvasback rafts, taken at an altitude of 150 m, were examined under a stereobinocular scope to identify males and females. Negatives were projected with an overhead viewer to map rafts for tests concerning the relative distribution of the sexes.

We investigated the winter weight-loss of Canvasbacks by trapping them in mid-January and again in early March 1978 in upper Chesapeake Bay. Welded-wire diving duck traps baited with corn were used. Trapped birds were held for a minimum of 6 h before weighing to permit the drying of plumage and the passage of much of the ingested bait. This procedure reduced the variance of our data. Before weighing, we inspected the gullet of each bird for corn content; only individuals containing little or no corn were considered in the analysis. Birds were weighed to the nearest 5 g.

## RESULTS AND DISCUSSION

### TEMPORAL VARIATION IN WINTER DISTRIBUTION PATTERN

We wanted to learn whether Canvasbacks return to the same general wintering areas year after year, because we believed that the presence or absence of such a tendency would be important in interpreting any pattern of geographic variation in sex ratio that might exist. We chose to address this question at the population level first by comparing direct (first year after banding) recovery distributions from particular winter banded samples with indirect (second and later years after banding) recovery distributions (similar rationale was employed by Cowardin 1977:6–7). For this analysis we used BBL data from Canvasbacks banded during January and February in particular states during specific years, and recovered during the period from 15 December through 28

TABLE 1. Results of testing the null hypothesis of no difference between direct versus indirect winter recovery distributions of winter-banded Canvasbacks.<sup>a</sup>

State	Year	Total recoveries	Chi-square <sup>b</sup>	df
<i>Males</i>				
Maryland	1956	20	0.24	2
	1957	20	4.48	2
	1964	66	0.07	2
	1965	33	1.57	2
	Total		6.36	8
New York	1955	62	6.01**	2
	1956	81	3.10	2
	1957	198	24.26***	2
	1958	115	11.54***	2
	1965	24	4.76*	2
Total		49.67***	10	
Virginia	1969	24	0.48	2
California	1969	82	3.05	2
<i>Females</i>				
Maryland	1964	21	0.66	2
New York	1957	52	7.20**	2

<sup>a</sup> Includes birds banded during January and February and recovered during the period from 15 December through 28 February.

<sup>b</sup> See Mardia (1967).

\* .05 < P < .10; \*\* .01 < P < .05; \*\*\* P < .01.

February. All such banded cohorts having at least 20 winter recoveries were used. Records were further restricted by excluding all recoveries for which exact (to 10-min block) location data were not available.

A total of 13 banded samples resulting in 778 winter recoveries satisfied our selection criteria. For each of these samples we used Mardia's (1967) test to test the null hypothesis of no difference between the distributions of direct and indirect winter recoveries (Table 1). Maryland and New York contained several years for which selection criteria were met for male Canvasbacks, and summary statistics for these states were thus obtained by summing the chi-square statistics and their associated degrees of freedom. The null hypothesis was rejected for four of the five banded samples of New York males

and for the single banded sample of New York females (Table 1). The summary test statistic for New York males was also significant. We found no difference between direct and indirect recovery distributions for any of the banded samples in other states. Hence, we conclude that birds from these states exhibited the same general wintering distribution patterns year after year. The difference between the direct and indirect recovery distributions of New York birds could be attributable to two factors: 1) Unlike the other tested samples, Canvasbacks banded in New York during the years noted in Table 1 were exposed to large year-to-year fluctuations in winter hunting pressure associated with varying hunting season dates in New York (see Martin and Carney 1977). 2) Some Canvasbacks may tend to winter in New York during some years and in areas farther south during other years, probably depending upon weather conditions. This possibility is consistent with the suggestion of Stewart et al. (1958) and DeGraff et al. (1961) that there is a considerable annual interchange of wintering Canvasbacks between New York and the Chesapeake Bay area.

We also studied annual variation in wintering distribution by examining the proportional distribution of winter recoveries among flyways. In this gross analysis we selected recoveries (15 December through 28 February) of birds banded during January and February, 1929-77, and first grouped them by flyway of banding and sex. The proportional distribution of these recoveries among the four flyways and Canada is presented in Table 2. Birds banded in the Central flyway are omitted from this table because of the small number of recoveries. A high proportion of winter recoveries from both males and females banded during winter in the Atlantic and Pacific flyways occurred in the flyway of banding. Canvasbacks banded in the Mississippi flyway

TABLE 2. Proportional flyway distribution of winter recoveries from winter-banded Canvasbacks (1929-77).<sup>a</sup>

Banding flyway	Sex	Total recoveries	Proportion of total recoveries in recovery flyway				
			Atlantic	Mississippi	Central	Pacific	Canada
Atlantic	Male	1,390	.938	.035	.001	.006	.020
	Female	404	.960	.017	.010	.005	.007
Mississippi	Male	100	.210	.760	.020	.000	.010
	Female	34	.147	.794	.059	.000	.000
Pacific	Male	246	.000	.000	.000	.996	.004
	Female	99	.000	.000	.000	1.000	.000

<sup>a</sup> Includes birds banded during January and February and recovered from 15 December through 28 February.

seem to exhibit less fidelity to wintering areas as indicated by the relatively high proportion (about 0.15 to 0.21) of recoveries occurring in the Atlantic flyway (Table 2). These data are consistent with the conclusion of Stewart et al. (1958) based on winter counts that major shifts of Canvasbacks may take place between the Mississippi Valley and mid-Atlantic regions. Stewart et al. (1958) also noted that numbers of wintering birds may shift between the Detroit River and Lake St. Clair area and the Chesapeake Bay.

Finally, we were interested in whether male and female Canvasbacks seem to exhibit comparable degrees of fidelity to general wintering grounds. Male and female test results presented in Table 1 were similar for both Maryland and New York, suggesting a similar pattern of fidelity in the two sexes. We also addressed this general question using the data of Table 2. We used  $2 \times 2$  contingency tables to test the hypothesis that the proportions of males recovered within and out of the flyway of banding were not different from those of females. The null hypothesis could not be rejected for birds banded in either the Atlantic ( $\chi^2 = 2.89$ , 1 df) or the Mississippi ( $\chi^2 = 0.17$ , 1 df) flyways. Pacific flyway bandings could not be tested in this manner but exhibited virtually identical recovery distributions with all but one recovery occurring in the flyway of banding. Thus we conclude that the general degree of temporal variation in winter distribution patterns was similar for males and females.

#### LATITUDINAL VARIATION IN SEX RATIO OF WINTERING BIRDS

We first approached the question of whether male Canvasbacks tend to winter farther north than females by testing the specific null hypothesis that sex ratios (expressed as proportion male) of banded samples in northern states were higher than those obtained in southern states. Inferences drawn from this test do not require the assumption that male and female Canvasbacks are equally trappable. Petrides (1944) and Bellrose et al. (1961:396-400) showed that in certain ducks (Tribe Anatini) males are more readily trappable than females. However, Bellrose et al. (1961:398) also presented evidence of an instance in which no sex-specific difference in tendency to enter traps existed for Blue-winged Teal (*Anas discors*). In our analysis of latitudinal variation in sex ratio of banded birds, we did not assume that these sex ratios were nec-

TABLE 3. Sex ratios of Canvasbacks banded during January and February (1929-77).

Flyway	State	No. birds banded	Proportion male
Atlantic	New York	15,161	0.78
	New Jersey	1,372	0.71
	Delaware	3,288	0.56
	Maryland	16,788	0.74
	Virginia	3,793	0.68
	North Carolina	729	0.50
	South Carolina	117	0.31
Mississippi	Michigan	1,325	0.79
	Alabama	403	0.40
	Louisiana	1,444	0.67
Central	Texas	118	0.51
Pacific	Oregon	729	0.67
	California	5,239	0.64

essarily equivalent to those of the sampled populations at the time of banding. Instead we simply assumed that any inherent sex-specific difference in trappability would be reflected in all of the samples, and that differences in trap sex ratios between different areas would indicate differences in population sex ratios.

In this analysis we used 50,862 winter banding records from BBL files summarized by state of banding. We selected only birds banded during January and February, and pooled data for all years (1929-77). Banding sex ratios for states in which at least 100 Canvasbacks were banded are presented in Table 3. A number of  $2 \times 2$  contingency tests was conducted to test for differences in banded sex ratios between various pairs of states. In the Pacific flyway, Oregon bandings had only a slightly higher sex ratio ( $\chi^2 = 3.1$ , 1 df,  $P < 0.10$ ) than the California sample. However, the two northernmost states of the other flyways, New York and Michigan, had significantly higher ( $P < 0.001$ ) sex ratios than all other states when tested via a series of individual comparisons. In the Atlantic flyway, where the banded sample was largest, the southernmost state (South Carolina) showed a significantly lower ( $P < 0.001$ ) sex ratio than all other flyway states. In addition, the North Carolina banded sample had a lower sex ratio than all Atlantic flyway states to its north ( $P < 0.001$ ). The latitudinal trend in sex ratio is not consistently shown within the mid-Atlantic states (New Jersey, Delaware, Maryland, Virginia); Delaware exhibited a lower sex ratio than Virginia. We suspect that the differences in sex ratio between areas of similar latitude can be in-

TABLE 4. Results of testing the null hypothesis of no difference between winter recovery distributions of male versus female Canvasbacks banded during the summer.<sup>a</sup>

State or province	Age of birds	Total recoveries	Mean latitude		Chi-square <sup>b</sup>	df	P
			Male	Female			
Alaska	Adult	119	41°	39°	5.73*	2	0.06
Saskatchewan	Young	51	37°	34°	0.82	2	0.66
Manitoba	Young	72	37°	34°	9.88***	2	0.01
Minnesota	Young	56	36°	34°	3.16	2	0.21
Nevada	Young	55	37°	37°	0.01	2	0.99
Total					19.60**	10	0.03

<sup>a</sup> Includes birds banded during the period July through September, 1950-77, and recovered during the period 15 December through 28 February.

<sup>b</sup> See Mardia (1967).

\* .05 < P < .10; \*\* .01 < P < .05; \*\*\* P < .01.

terpreted in terms of factors affecting sex-specificity of local geographic distribution patterns (see later discussion). Most of the birds banded in these mid-Atlantic states come from similar latitudes. Similarly, differences existed among the three Gulf Coast states (Alabama, Louisiana, and Texas), but they all showed lower winter sex ratios than Michigan. Thus, we conclude from the summary of banding data presented in Table 3 and the corresponding chi-square tests that winter-banded samples in southern states generally showed lower sex ratios than those in northern states. On the basis of this sample (most major Canvasback wintering areas are included among the states analyzed; Stewart et al. 1958), we suggest that southern latitudes generally contain proportionately more wintering females than northern latitudes.

Our second approach to the general hypothesis of latitudinal variation in sex ratio was to examine the sex-specific winter band recovery distributions of birds banded during the summer on the breeding grounds. The null hypothesis was that males and females banded in the same general breeding areas showed equivalent winter recovery distribution patterns. The alternative hypothesis was that male and female recovery distributions differed. Specifically, we wondered whether females were recovered farther south than were males from the same breeding area. We used BBL data on birds banded during July, August, and September. Unfortunately, because of the low density and generally poor trappability of Canvasbacks on the breeding grounds, sample sizes of banded birds were quite small. We therefore pooled data for years 1950 through 1977 for these tests, rather than consider groups of birds banded during specific years. We required that the combined male and female sample of winter (15 December through 28 February) recoveries include at

least 20 records within a single age category (either young or adult). All recoveries (both direct and indirect) resulting from summer bandings were considered. Only five states and provinces met the sample size criterion: Alaska, Saskatchewan, Manitoba, Nevada, and Minnesota. Male versus female recovery distributions were compared using Mardia's (1967) test. Results of these tests, as well as mean latitudes of the recovery distributions, are presented in Table 4. Winter recovery distributions of males and females differed significantly for birds banded in Alaska and Manitoba. The summary test statistic computed over all areas also showed a significant difference between male and female recovery distributions. In addition, the mean latitudes of the male recovery distributions (see Table 4) were higher than those of females for all five banding areas (even in Nevada where the rounded means were equal, the mean female latitude of recovery was actually 0.7° less than the mean for males). Thus, we conclude that females from particular breeding areas tend to winter farther south than males from the same areas.

#### FACTORS AFFECTING THE EVOLUTION OF SEX-SPECIFIC WINTER DISTRIBUTION PATTERNS

Our results corroborate the general hypothesis that females tend to winter farther south than males. We assume that this difference in distribution reflects a sex-specific difference in the evolutionary costs and benefits associated with wintering at specific latitudes. We can easily envision benefits that might accrue to birds wintering at southerly latitudes (see later discussion). Thus, there must be some cost associated with such behavior or we would expect natural selection to favor male Canvasbacks wintering as far south as females. The existence of a "cost of migration" is either im-

plicitly or explicitly assumed in most hypotheses dealing with the evolution of bird migration (e.g., see Lack 1944, 1954, Cohen 1967, Cox 1968, von Haartman 1968, Gauthreaux 1978). Although migration certainly costs energy, this cost must reduce either survival or fecundity expectations in order to be of importance in natural selection. Ketterson and Nolan (1976:686–687) discussed several types of mortality risks (increased predation, severe weather, difficulty in finding sufficient food in unfamiliar stop-over locations) that “may be in rough proportion to the time (distance) spent migrating.” We have no reason to suspect that such migratory costs would be any greater (per unit of migration distance) for males than females.

Another potential cost to males wintering in southerly latitudes involves possible disadvantages of arriving on courtship or breeding grounds later than males wintering farther north. Data on temporal changes in Canvasback flock composition in an area of the Chesapeake Bay led Welling and Sladen (1979) to conclude that males left the Bay earlier in spring than did females. Hochbaum (1944:26–27) found that most pair formation and associated courtship activities at Delta Marsh, Manitoba, occurred after the birds’ arrival in April and May. Observations at Lake Christina, a migration concentration area in Minnesota, indicated the occurrence of considerable courtship activity and pair formation in April (Smith 1946). Smith also observed that the very first spring flights into Lake Christina were made up predominantly of males and suggested that males fly northward ahead of females and wait on the breeding grounds for the arrival of potential mates. By wintering in the north, males may attain a competitive advantage in obtaining appropriate breeding territories and mates. However, as noted for Dark-eyed Juncos (*Junco hyemalis*) by Ketterson and Nolan (1976), it would probably be possible for males wintering in the south to start spring migration earlier than northern birds, thereby erasing any potential advantage to northern birds associated with early arrival at the breeding ground.

The principal “benefit” expected to be derived by birds wintering in the south is an increased probability of surviving the winter in a milder climate. Sex-specific differences in winter survival probabilities have been demonstrated and hypothesized in other avian species. In cold-room experiments with White-crowned Sparrows (*Zonotrichia leucophrys*), Ketterson and King

(1977) found that males endured fasting significantly longer than females. Similarly, experiments on the effects of simulated winter storms on Mourning Doves (*Zenaidura macroura*) led Ivacic and Labisky (1973) to suggest that adults (particularly males) possessed a greater potential for surviving winter storms than juveniles (particularly females). Kendeigh (1945) found that female House Sparrows (*Passer domesticus*) died sooner than males when starved at various temperatures. Ketterson and Nolan (1976) suggested that sex-specific differences in fasting endurance may have been important in the evolution of the latitudinal variation in winter sex ratio observed in Dark-eyed Juncos. In a later experiment, they found no sex-specific differences in short-term (overnight) fasting ability in Dark-eyed Juncos, but suggested that differences may exist over longer periods (Ketterson and Nolan 1978). Among field studies, Harrison and Hudson (1964) found that female European Wigeon and Sheld-Duck (*Tadorna tadorna*) died in disproportionate numbers during a period of severe winter weather. In addition, female movement away from areas during periods of harsh winter weather have been noted in Common Goldeneye (*Bucephala clangula*; Nilsson 1970a), Green-winged Teal (Bennett and Bolen 1978), Pintails (Alford and Bolen 1977), and Common Mergansers (Anderson and Timkin 1972), possibly suggesting increased vulnerability of females to such conditions.

We can envision two factors that could render female Canvasbacks less likely to survive winter than males. The first factor involves body size and is a consequence of the “fasting-endurance hypothesis” (Calder 1974:115) which has been proposed as a possible “explanation” for the geographic variation encompassed by Bergmann’s Rule (see Lindsey 1966, Rosenzweig 1968, Boyce 1979). This hypothesis basically asserts that the ability to endure periods of fasting should increase with increasing body size. The energetic arguments and rationale underlying this hypothesis have been discussed by Calder (1974:110–115).

In the Common Goldeneye, Nilsson (1970a) found that females (the smaller sex) foraged and fed especially actively during the coldest periods of the winter. During a period of severe winter weather, Harrison and McLean (1947) found female European Wigeon to be “considerably thinner and more wasted than the drakes.” If the fasting-endurance hypothesis is true for Canvasbacks, then males should be able to endure

periods of fasting better than females because they are larger. We used weights of adult male and female Canvasbacks trapped in Chesapeake Bay during winter 1978 as a measure of the difference in body size. At Bay Ridge, Maryland, 18-21 January, the mean weight for adult male Canvasbacks ( $\bar{x} = 1,326 \text{ g} \pm \text{SE of } 5.44, n = 247$ ) was 96 g (7.8%) greater than that for adult females ( $\bar{x} = 1,230 \pm 5.56 \text{ g}, n = 208$ ). Later in winter at Gibson Island, Maryland, 7-10 March, the mean weight of adult males ( $\bar{x} = 1,224 \pm 3.57 \text{ g}, n = 496$ ) was 120 g (10.9%) more than that for females ( $\bar{x} = 1,103 \pm 6.97 \text{ g}, n = 96$ ). The group of Canvasbacks found at Gibson Island during March (after ice break up) was essentially the same group trapped at Bay Ridge in January. Weights of birds obtained during these two trapping periods can thus be used to estimate average weight loss between mid-winter and early spring. The difference between mean weights for males trapped during the two periods was 102 g representing a 7.7% average decrease in weight between January and March. The difference for females was 127 g, representing a 10.3% average decrease in weight over the two months. The greater proportional decrease in the average weight of females supports the plausibility of the hypothesis that females may not be able to survive harsh winter periods as well as males.

Another factor, intersexual competition, may also contribute to the lower probabilities of overwinter survival in female Canvasbacks. Both Lack (1954, 1966) and Fretwell (1972) suggested that winter shortages of food are "limiting" to temperate bird populations. Lack (1954:245) further suggested that the observed tendency among male partial migrants to remain in the breeding area over winter, results from their ability to compete and survive better than females because of their higher position in the "pecking order." Gauthreaux (1978) has recently suggested that dominant individuals of migratory species generally occupy the nonbreeding habitat that is closest to the breeding grounds and that subordinates must travel farther to nonbreeding areas. The importance of intraspecific interactions and dominance relationships to obtaining resources and surviving during the winter has been demonstrated for some passerines by Fretwell (1968, 1969, 1972). Ketterson (1979) and Ketterson and Nolan (1976, 1979) have discussed the relevance of behavioral dominance to winter sex ratios of Dark-eyed Juncos. Sheld-Duck populations are thought to be limited during the winter by conflicts

in which dominant individuals exclude subordinates from the best feeding areas (Jenkins et al. 1975, Patterson 1977). In a study of diving ducks wintering in South Carolina, Alexander and Hair (1979) found that Canvasbacks established and defended individual foraging sites and that adult males won a large proportion of encounters with females. In addition, the sex ratio in a concentration area of a preferred food source was found to be much higher (74% males) than in other areas (48% males). Alexander and Hair (1979) concluded that male Canvasbacks seemed to be dominant over females during the winter.

If intersexual competition and resultant interactions are important aspects of the wintering ecology of Canvasbacks, then we would predict that some degree of local geographical segregation of the sexes should exist, in addition to the latitudinal segregation noted earlier (see Gauthreaux 1978). If males are dominant over females, for example, we would expect to find intersexual differences in habitat occupation, with males occupying the more attractive habitats. In the Chesapeake Bay area, mid-winter trappings and observations of Canvasbacks indicate that higher proportions of females occur in small flocks frequenting outlying water areas (creeks, ponds, and other small and confined bodies of water) than in main estuaries and tributaries (large, open bodies of water), where large rafts of predominantly males are found (Haramis, pers. observ., Welling and Sladen 1979). Similar differences between the sexes in local habitat occupation have been noted in other diving ducks by Nilsson (1970b). We used trapping data from one area where a few birds occupied a small body of water (Castle Haven trap site, trapped 14-18 February 1978) and another area where many birds occupied a large body of water (Bay Ridge trap site, trapped 18-22 January 1978) to test the hypothesis that a greater proportion of females was trapped in the smaller water area. The chi-square test statistic indicated that a significantly greater proportion of females (38.2% female in the small area,  $n = 76$ , versus 20.6% female in the open area,  $n = 1,085$ ;  $\chi^2 = 11.77, 1 \text{ df}$ , 1-tailed test,  $P < 0.01$ ) was trapped in the smaller body of water. A similar difference between the proportion of female Canvasbacks captured at trap sites for puddle ducks (creeks, ponds and other small water bodies) versus those for diving ducks (main estuaries adjacent to large rafts of birds) was noted during 1978 winter trapping opera-

TABLE 5. Results of tests on the distribution of male and female Canvasbacks within wintering rafts in the Chesapeake Bay area, February 1978.

Raft photo ID number	Total Canvasbacks	Sex ratio (proportion male)	Coefficient of segregation <sup>a</sup>	Nearest neighbor chi-square <sup>b</sup>	Edge chi-square <sup>c</sup>	(O - E) females on edge <sup>d</sup>
19	2,474	0.914	0.05	7.38***	8.27***	5.7
15	701	0.889	0.11	8.48***	2.21*	5.5
1	536	0.920	-0.09	—	4.98**	7.0
3	499	0.864	0.01	0.08	3.04**	6.7
5	494	0.903	-0.04	—	—	—
73	475	0.905	0.17	12.95***	33.08***	16.7
49	249	0.827	-0.06	—	—	—
55	227	0.899	0.17	6.69***	—	—
2	220	0.932	0.01	0.02	—	—
53	140	0.807	0.07	0.68	2.26*	3.4
18	131	0.779	0.16	3.29**	1.55	2.9
39	92	0.913	0.07	0.51	—	—
26	72	0.653	-0.06	—	—	—

<sup>a</sup> Computed as described in Pielou (1961, 1969). Coefficient has a range of [-1, 1].

<sup>b</sup> Computed as suggested by Pielou (1961, 1969). A one-tailed test was used. Test statistics not presented for  $S < 0$ .

<sup>c</sup> Computed as described in text. A one-tailed test was used.

<sup>d</sup> Shows the difference between the observed number of females (O) and the expected number (E) on the edge. Positive values indicate more females on the edge than expected under a null hypothesis of no sex-specific difference in distribution. A negative value indicates fewer females on the edge than expected.

\*  $0.05 < P < 0.10$ ; \*\*  $0.01 < P < 0.05$ ; \*\*\*  $P < 0.01$ .

tions by Maryland Department of Natural Resources (DNR) personnel (V. Stotts, unpubl. data). We compared the sex ratio of Canvasbacks obtained in Maryland DNR puddle duck traps (32.1% female,  $n = 56$ ) with the sex ratio of the Bay Ridge birds and again found significantly more females in the puddle duck traps ( $\chi^2 = 4.21$ , 1 df, 1-tailed test,  $P < 0.05$ ). Thus, we conclude that the distribution patterns of male and female Canvasbacks differ at the local geographic level.

In addition, Canvasbacks captured at small sites generally appeared in worse condition than those trapped in large water areas, so we compared weights of birds from these two types of areas. Adult males and females trapped at Castle Haven, 16–18 February 1978, weighed 234 g and 189 g, respectively, less than birds trapped at Bay Ridge, 18–22 January 1978. However, Canvasbacks trapped before ice in January would be expected to weigh more than birds taken in February regardless of trap location. We therefore compared weights of Canvasbacks from the February Castle Haven sample with those from a large body of water taken after ice (Gibson Island site trapped 7–10 March 1978). The mean weight of Castle Haven adult males ( $\bar{x} = 1,092$  g,  $n = 31$ ) was lower than that of Gibson Island adult males ( $\bar{x} = 1,224$  g,  $n = 496$ ), and the difference was significant ( $t' = 11.3$ ,  $P < 0.001$ , Snedecor and Cochran 1967:114–116). Similarly, the mean weight of Castle Haven adult females ( $\bar{x} = 1,041$  g,  $n = 29$ ) was lower than that for Gibson Island adult females ( $\bar{x} = 1,103$  g,  $n =$

96), and the difference was significant ( $t = 20.8$ , 123 df,  $P < 0.001$ , Snedecor and Cochran 1967:104–106). The small bodies of water containing higher proportions of females therefore also contained birds in poorer physical condition. This finding is consistent with the hypothesis that the presence of females in such areas may have resulted from their subordinate relationship with males.

Finally, if intersexual dominance is important to wintering Canvasbacks, we would expect interactions to be reflected in the sex-specific dispersion patterns within flocks. Field observations suggested that male and female Canvasbacks tended to segregate to varying degrees within wintering flocks or rafts and that females tended to occur more frequently on the periphery of rafts. These observations were formulated as hypotheses and were tested using the aerial photographs of Canvasback rafts taken in the Chesapeake Bay on 9 February 1978. The 13 rafts used in this analysis ranged in size from 72 to 2,474 birds; sex ratio varied from approximately 65% to 93% male (Table 5).

For each raft, we tested the hypothesis that the sexes were spatially segregated by determining nearest neighbor relationships for all birds in the raft, and constructing a  $2 \times 2$  contingency table based on the numbers of intersexual versus intrasexual nearest neighbor relationships as suggested by Pielou (1961, 1969). We also computed Pielou's (1961) coefficient of segregation ( $S$ ) as:  $1 - (\text{observed number of intersexual nearest neighbor relationships}) / (\text{expected number}$



of intersexual nearest neighbor relationships). Values of  $S$  near zero indicate an unsegregated population, whereas positive values indicate segregation of males and females. Negative values indicate a tendency for intersexual aggregation or pairing. Of the 13 rafts, 9 exhibited positive  $S$  values, and the test statistics (presented only for rafts with  $S > 0$ ) suggested a significant degree of segregation in five of these rafts (Table 5). We conclude that the birds in at least some of the rafts tended toward intersexual segregation. This conclusion is consistent with a general hypothesis of behavioral interactions occurring between males and females, although other interpretations are possible.

We tested the hypothesis about the tendency of females to occur on the edges of rafts using an ad hoc procedure. For each raft for which the concept of edge seemed applicable, we drew a band of equal width (two times the approximate average distance between neighboring birds in that raft) around the periphery of the raft. We then totaled the males and females occurring in this band as well as those judged to be stragglers or outliers (birds occurring outside the main raft body). We then compared the proportions of males and females in the edge area with those occurring in the raft interior, using a  $2 \times 2$  contingency test. The concept of edge has little meaning when associated with "linear" rafts or with widely dispersed rafts. We therefore chose seven rafts for the edge versus interior test. The null hypothesis of equal proportions of the two sexes in the edge and interior areas was rejected ( $P < 0.10$ ) for six of the seven tested rafts (Table 5). All seven of the tested rafts contained more females on the edge than expected under the null hypothesis. We thus conclude that females in these winter rafts tended to occur on the edges of the rafts rather than in the interiors.

The observations of Alexander and Hair (1979) together with our test results indicate that behavioral interactions are an important component of competition between the sexes for winter food. We believe that intersexual competition is, at least to some degree, an active and ongoing ecological process. However, current differences in sex ratios found in particular habitats, and even at different latitudes, could also be the result of sex-specific habitat affinities or preferences that have evolved historically in response to intersexual competition for resources (see Selander 1966). For example, segregation of the sexes in Canvasbacks also

occurs during the post-breeding period with males congregating early on large lakes to molt and females remaining with young and later molting individually or in small groups in marshes (see Hochbaum 1944, Oring 1964, Olson 1965, Bergman 1973). Our corroborated hypothesis that females occur in higher proportions in creeks and small outlying water areas than in large water areas during winter is consistent with both the ideas of behavioral dominance relationships and of different habitat preferences. The tendency of females to winter farther south than males may thus result partially from a preference for certain habitats (e.g., creeks and small water areas) that may be more abundant in the south. The observation, however, that Canvasbacks in the small water areas in the Chesapeake Bay tend to be in worse condition than birds trapped in open water areas, and the tests demonstrating sex-specific dispersion patterns within flocks seem to support the notion of ongoing behavioral interactions that can become especially important during periods of winter stress. We conclude that intersexual competition in Canvasbacks probably contributes importantly to the latitudinal differences in wintering areas of the two sexes. Effects of this competition for food may include the historical evolution of some degree of differential habitat preference of the sexes, as well as ongoing behavior that promotes segregation of the sexes.

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**Journal V, 1979-1980.**—The World Pheasant Association. 132 p. Paper. £ 5.50. Source: Secretary, W.P.A., Daws Hall, Lamarsh, Bures, Suffolk, CO8 5EX, England. This volume offers 11 articles about various gallinaceous birds in nature or captivity. The studies of pheasants in the Himalayas and southeast Asia and of megapodes in New Britain yield useful census data and information on habits. The volume includes an annual review of the W.P.A. book reviews, and a list of recent periodical literature. Maps, diagrams, and photographs, many in color.