

FACTORS AFFECTING WINTER DISTRIBUTION AND MIGRATION DISTANCE OF WOOD DUCKS FROM SOUTHERN BREEDING POPULATIONS¹

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Abstract. We used direct band-recovery records of Wood Ducks (*Aix sponsa*) banded 1 April–15 September (1960–1987) in the southern and southeastern reference areas of Bowers and Martin (1975, Fig. 1) to test whether winter distribution and migration distance were age- and sex-specific. Effects of variation in early-autumn temperature and precipitation conditions on winter distribution patterns also were studied. Latitude and longitude of winter band recoveries did not differ by age and sex in the southern reference area; but adult Wood Ducks tended to migrate shorter distances than young. In the southeastern reference area, recovery distributions of males and females also did not differ; but adults were distributed north and east of young birds, and migrated shorter distances.

We predicted that Wood Ducks would move farther south in winter when early-autumn (October–November) temperature and spring–summer (April–September) precipitation were below normal. Adults were recovered farther south when precipitation was below average, but deviations from average temperatures were not associated with winter distribution. Young Wood Ducks occurred farther south when rainfall in spring–summer was less than normal and when average November temperature was colder than normal. We conclude that winter distributions of male and female Wood Ducks did not differ, but that adults migrated shorter distances than young. Variation in winter distribution was associated with early-autumn habitat suitability.

Key words: Migration; winter distribution; age and sex differences; Wood Duck; *Aix sponsa*.

INTRODUCTION

Winter distributions of migratory birds of north temperate regions frequently differ according to age and sex classes (Ketterson and Nolan 1976; Gauthreaux 1978, 1982). In many avian species, males are distributed farther north than females, and adults are found at higher latitudes than young. Several hypotheses have been proposed to explain differential distribution of age and sex classes (Ketterson and Nolan 1983, Gauthreaux 1988), but testing of some of these has been difficult. It is likely that intraspecific variation in winter distribution patterns is not the result of one factor, but of a combination of factors (Nolan and Ketterson 1990).

Some duck species are known to exhibit sex-specific differences in winter distribution patterns; however, relatively little is known about

the extent of age-specific variation (but see Nichols and Hines 1987). Winter band recoveries of male Canvasbacks (*Aythya valisineria*) were distributed farther north than those of females, and it was suggested that intersexual competition contributed to latitudinal segregation (Nichols and Haramis 1980). Alexander (1983), using Christmas Bird Count (CBC) data, reported that more male than female Canvasbacks and Ring-necked Ducks (*A. collaris*) occurred at northern latitudes. The extent of sexual segregation in wintering ducks may be partly related to the time of pair formation; species of dabbling ducks (Tribe Anatini) that form pair bonds in early winter have less disparate sex ratios than species pairing late (Hepp and Hair 1984, Nichols and Hines 1987).

A variety of avian migration systems exists and results in distribution patterns that range from being fixed and predictable to ones that are facultative and flexible. In some migrants, initial movements are endogenous, but are followed by

¹ Received 29 March 1991. Final acceptance 20 May 1991.

a facultative phase in which additional migratory activity depends on prevailing habitat conditions and social status (Terrill and Ohmart 1984, Gwinner et al. 1988). Many species are able to respond to changing environmental conditions and adjust winter distribution patterns. The degree to which individuals alter migratory movements in response to changing habitat conditions may vary according to a number of factors. For example, immature Mallards (*Anas platyrhynchos*) showed greater flexibility in winter distribution than adults (Nichols et al. 1983), and caged subordinate Dark-eyed Juncos (*Junco hyemalis*) had higher levels of migratory restlessness than dominant conspecifics when food was restricted (Terrill 1987).

The Wood Duck (*Aix sponsa*) is distributed primarily east of the Mississippi River drainage system (Bellrose 1980). It is migratory, and populations at northern latitudes move greater distances than southern populations (Nichols and Johnson 1990). Consequently, breeding and wintering ranges overlap substantially (Bellrose 1980).

In some years, Wood Ducks from southern populations may be essentially nonmigratory. There are several potential advantages of being sedentary. First, nest sites may be limiting for cavity-nesting species, such as Wood Ducks (Jones and Leopold 1967, Eadie and Gauthier 1985), and pairs that remain near breeding areas may improve their chances of obtaining a nest site (Lundberg 1979, Fretwell 1980). Second, migration may be costly in terms of fitness. In the European Robin (*Erithacus rubecula*), a partial migrant, resident males had higher survival rates than males that migrated (Adriaensen and Dhondt 1990). Nichols and Johnson (1990) reported lower annual survival rates of Wood Ducks from northern latitudes compared to Wood Ducks from southern latitudes and proposed that differences were related to the greater migration costs of northern populations. Third, because time and energy are not spent migrating, resident females may begin nesting earlier than migrants. Early-nesting females may have greater probabilities of producing second broods (Kennamer and Hepp 1987) or of renesting if the first nest is unsuccessful.

In this study, we examined factors influencing the distribution and migration distance of Wood Ducks from southern breeding populations. Specifically, we tested whether migration distance

and winter distribution were age- and sex-specific. We also considered effects of temperature and precipitation on annual variation in winter distribution.

METHODS

BAND RECOVERIES

We used Wood Ducks that were banded in the southern and southeastern geographic reference areas described by Bowers and Martin (1975) and shown in Figure 1. Band recovery records were obtained from computer files of the U.S. Fish and Wildlife Service, Bird Banding Laboratory (BBL), Laurel, Maryland. We used direct recoveries (occurring the first winter after banding) of normal, wild birds that were banded 1 April–15 September 1960–1987 and shot or found dead in December or January. At the time of banding, birds were sexed and aged as either young (HY) or adult (AHY).

Recovery records specified the latitude and longitude (southeast corner of a 10-min block) of the banding and recovery sites. From these data, we computed the distance (km) between the banding and recovery sites, using methods described by Cowardin (1977).

TEMPERATURE AND PRECIPITATION

Weather data were obtained from NOAA (1960–1987) for 14 stations, six in the southern reference area and eight in the southeastern reference area (Fig. 1). Tests involving the effects of temperature and precipitation on winter distribution of Wood Ducks were based on birds banded at sites $>34^{\circ}\text{N}$ latitude; therefore, reporting stations above 34°N latitude were selected. Tests were limited to birds banded at these higher latitudes, because we thought they would be more likely to respond to annual variation in temperature or precipitation. Winter movements of Wood Ducks at more southern latitudes probably would be more restricted, because they would have less to gain by moving (i.e., environmental conditions would be similar).

For each weather station, we recorded (1) the average monthly temperatures for both October and November, and (2) the cumulative precipitation (mm) during April–September. Cumulative precipitation in April–September should provide a good index to wetland availability and hence habitat suitability during early autumn. We chose to examine effects of environmental

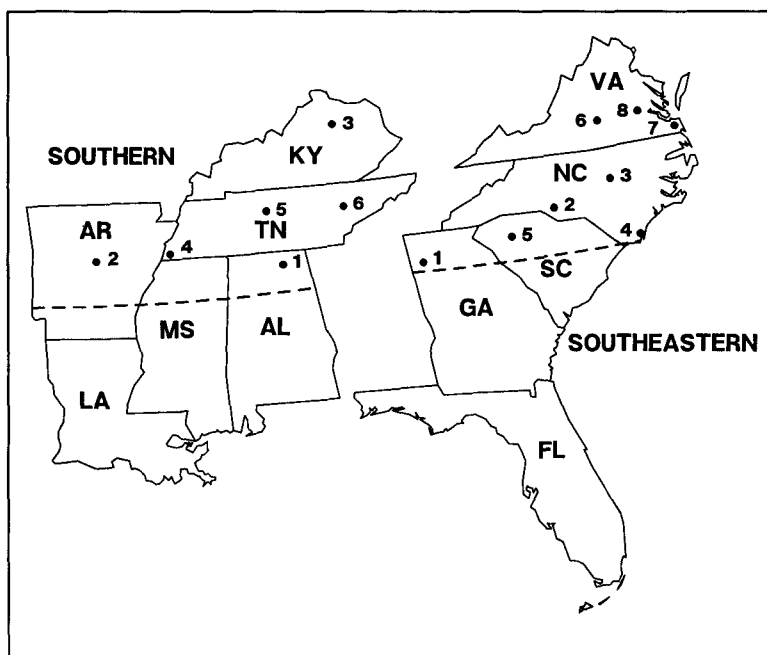


FIGURE 1. Southern and southeastern banding reference areas and locations of the reporting stations that provided temperature and precipitation information (see Appendix A). Dashed line denotes 34°N latitude.

factors in early autumn, because facultative response of some migrant birds to environmental stimuli decreases as the migratory season progresses (Terrill 1987). In essence we predicted that winter distribution of Wood Ducks breeding at southern latitudes would be determined at least partly by suitability of habitats early in the migratory period.

For each temperature and precipitation variable (items 1 and 2), a 28-yr (1960–1987) mean was computed for each of the 14 stations. Annual deviations from these 28-yr averages were calculated for each station, and mean deviations over all stations were computed each year. We used these annual deviation statistics to indicate the relative magnitude by which temperature and precipitation varied.

ANALYSIS

Age- and sex-specific differences in recovery latitude, recovery longitude, and distance between banding and recovery sites were tested with analysis of covariance (ANCOVA). Banding latitude was used as the covariate in analyses testing for differences in recovery latitude and distance of migration. Longitude of banding was the covariate in analysis of variation in recovery longi-

tude. Mean values of the dependent variables and their covariates were computed by age, sex, region, and year. These mean values were used in the ANCOVA. Years with <7 band recoveries were excluded from the analyses, and reference areas were tested separately.

Associations between deviations from average environmental conditions and mean recovery latitudes of adult and young Wood Ducks were tested with partial correlation analyses. Reference areas were combined, and analyses controlled for latitude of banding because of its effect on recovery latitude. We predicted that lower than average temperatures (October–November) and precipitation (April–September) would influence habitat suitability at latitudes >34°N, causing Wood Ducks to move farther south. SAS (SAS Institute 1988) was used for all statistical summaries and analyses.

RESULTS

AGE- AND SEX-SPECIFIC DISTRIBUTIONS

Number of direct band recoveries varied by reference area and by age and sex class (Table 1). More banded Wood Ducks were recovered in

TABLE 1. Frequency of direct band recoveries by age and sex of Wood Ducks banded in the southern and southeastern reference areas and recovered during December–January.

Reference area	Age	Sex	<i>n</i> ^a	Direct recoveries
Southern	Adult	Male	21	265
		Female	16	189
	Young	Male	25	707
		Female	23	500
Southeastern	Adult	Male	12	131
		Female	5	52
	Young	Male	19	317
		Female	9	110

^a Number of years (1960–1987) in which there were ≥ 7 direct band recoveries in December–January.

the southern reference area ($n = 1,661$) than in the southeastern reference area ($n = 610$); and, within reference areas, more young were recovered than adults. Males were recovered in greater numbers than females, within reference area and age class (Table 1). Differences in band recovery numbers were reflected in the number of years that could be used in subsequent analyses (i.e., band recoveries ≥ 7).

TABLE 2. Summary of analyses of covariance that test age- and sex-specific differences in mean band recovery latitude, mean band recovery longitude, and mean migration distance of Wood Ducks from the southern and southeastern reference areas.

Reference area	Dependent variable	Source	<i>F</i>	df	<i>P</i>
Southern	Recovery latitude	Age	0.1	1,80	ns
		Sex	0.0	1,80	ns
		Blat ^a	0.0	1,80	ns
		Age \times Sex	0.4	1,80	ns
	Recovery longitude	Age	1.7	1,80	ns
		Sex	0.4	1,80	ns
		Blong ^b	21.2	1,80	<0.001
		Age \times Sex	0.1	1,80	ns
	Distance ^c	Age	2.7	1,80	0.10
		Sex	0.6	1,80	ns
		Blat	26.7	1,80	<0.001
		Age \times Sex	0.1	1,80	ns
Southeastern	Recovery latitude	Age	3.6	1,40	0.06
		Sex	0.8	1,40	ns
		Blat	17.8	1,40	<0.001
		Age \times Sex	0.0	1,40	ns
	Recovery longitude	Age	9.6	1,40	0.004
		Sex	0.2	1,40	ns
		Blong	26.8	1,40	<0.001
		Age \times Sex	1.2	1,40	ns
	Distance	Age	12.4	1,40	0.001
		Sex	0.1	1,40	ns
		Blat	10.2	1,40	0.003
		Age \times Sex	1.3	1,40	ns

^a Banding latitude is used as the covariate in tests of age- and sex-specific differences in recovery latitude and migration distance.

^b Banding longitude is used as the covariate in tests of age- and sex-specific differences in recovery longitude.

^c Distance (km) between banding site and recovery site.

In the southern reference area, latitude and longitude of winter band recoveries did not differ by age and sex class (Table 2). However, there was a tendency ($P = 0.10$) for adults to migrate shorter distances than young (least squares mean \pm SE: adult = 364.0 ± 14.8 km; young = 396.1 ± 12.9). In the southeastern reference area, there were no sex-specific differences in winter distribution and migration distance, but there were age-specific differences (Table 2). Band recoveries of adults were centered at higher latitudes than young (adult = 33.0 ± 0.2 ; young = 32.5 ± 0.1), and the average longitude of recovery for adults was east of that for young birds (adult = 81.4 ± 0.3 ; young = 82.4 ± 0.2). Adults of the southeastern reference area also migrated shorter distances than young (adult = 202.2 ± 29.8 km; young = 336.8 ± 21.9).

EFFECTS OF PRECIPITATION AND TEMPERATURE

Males and females were combined, because recovery latitude did not differ ($P > 0.10$) by sex. Reference areas also were combined to increase sample size (i.e., years with ≥ 7 band recoveries).

Mean annual deviation statistics of the three environmental variables were computed for each reference area to examine whether environmental conditions varied between areas. We found no overall difference between reference areas (Paired *t*-tests, all tests $P > 0.90$), and mean annual deviation statistics were positively correlated (Spearman's rank correlation; all tests $P < 0.01$) between areas.

Partial correlation analysis that controlled for banding latitude was used to test the association between deviations from "normal" weather conditions and mean band recovery latitudes of adult and young Wood Ducks. Adults were recovered at higher latitudes when the spring–summer precipitation was greater than normal (Spearman's rho: $r_s = 0.38$, $n = 26$, $P = 0.06$), but deviations from average October and November temperatures were not significantly correlated ($P > 0.85$) with mean recovery latitude. Young Wood Ducks also remained farther north in winter when spring–summer precipitation was greater than average ($r_s = 0.38$, $n = 26$, $P = 0.06$). Deviation from the average October temperature was not correlated ($P = 0.28$) with recovery latitude of young ducks; but when November temperatures were warmer than normal, young were recovered farther north ($r_s = 0.33$, $n = 26$, $P = 0.10$). Deviation statistics for spring–summer precipitation and November temperature were independent ($r_s = 0.01$, $n = 26$, $P = 0.96$), indicating that both variables were associated with winter distribution of young Wood Ducks. Relationships between mean recovery latitude in winter and deviations from "normal" temperature and precipitation conditions were not strong, but suggest that Wood Ducks in the northern part of the southern and southeastern reference areas adjusted their winter distributions in response to annual variation in early autumn environmental conditions.

DISCUSSION

AGE- AND SEX-SPECIFIC DISTRIBUTIONS

Many studies have documented sex-specific differences in geographic distribution of birds during the nonbreeding period (review in Gauthreaux 1982). Male and female Wood Ducks, however, did not differ either in winter distribution or migration distance. Mallards and Black Ducks (*Anas rubripes*) also lacked sex-specific

winter distributions (Nichols and Hines 1987, Diefenbach et al. 1988), but male diving ducks (genus *Aythya*) tended to be distributed farther north in winter than females (Nichols and Haramis 1980, Alexander 1983).

Recent studies of ducks suggest an association between the degree of sexual segregation in winter and the timing of pair bond formation. Species in which segregation of the sexes is limited in winter, such as Wood Ducks, are those that form pair bonds early in autumn–winter. Reasons for this association are unclear. Dominance rank of paired female ducks is higher than that of unpaired females (Hepp and Hair 1984), hence, dominance and the protection given paired females by their mates (see Ashcroft 1976) might be partly responsible for this difference.

Winter distribution also differs by age class in some species of birds (Gauthreaux 1988). Young Wood Ducks in the southeastern reference area were distributed south and west of adults, but age-specific differences in winter distribution were equivocal in the southern reference area. Winter distribution differs between age classes of Mallards (Nichols and Hines 1987), but not of Black Ducks (Diefenbach et al. 1988). Gauthreaux (1988) suggested that age-specific differences in foraging efficiency of birds may be responsible for spatial segregation of age classes during winter, but this explanation may be too simplistic.

Young Wood Ducks may experience greater migration costs than adults, because they travel greater distances. High costs of migration are thought to decrease probabilities of survival and reproduction in other avian species (Adriaensen and Dhondt 1990). Yearling Wood Ducks nest later than adults, and age-specific differences in reproduction are more evident at northern breeding sites (Haramis 1990). The additional time and energy that young Wood Ducks spend migrating may help to explain these age-related reproductive characteristics.

PRECIPITATION AND TEMPERATURE

Bottomland hardwoods that are seasonally flooded are selected by Wood Ducks during autumn and winter (Heitmeyer and Fredrickson 1990, Kirby 1990). Availability of forested wetland habitats in winter varies annually and is positively associated with amount of precipitation (Heitmeyer et al. 1989). Winter rains appear to be particularly important, because they recharge forested wetlands that may have dried in

the summer. Forested wetlands in the Mississippi Alluvial Valley (MAV) are important habitats for wintering Mallards and Wood Ducks (Reinecke et al. 1989). Availability of habitats in the MAV may influence winter survival (Reinecke et al. 1987) and future reproduction (Heitmeyer and Fredrickson 1981) of Mallards. Consequently, Mallards show considerable flexibility in winter distribution in response to annual and seasonal variation in habitat availability (Nichols et al. 1983, Reinecke et al. 1987).

Similar studies of Wood Ducks are not available, but Wood Ducks may be even more dependent on forested wetlands in winter than are Mallards. Rice and soybeans, for example, comprised a large percentage of the winter diet of Mallards in the MAV, whereas Wood Ducks relied more on natural foods, primarily acorns (Delnicki and Reinecke 1986). Thompson and Baldassarre (1988) reported that Wood Ducks in northern Alabama exclusively used flooded hardwood habitats in December as these areas became available.

We found that adult and young Wood Ducks were distributed farther south in winter when spring–summer rainfall was below average. Precipitation during this period may affect habitat availability, and hence the probability of migrating in at least two ways. First, a wetter than normal spring–summer season may simply increase the overall availability of forested wetlands and allow Wood Ducks to stay farther north rather than moving south where these wetlands may be more permanent (see Heitmeyer et al. 1989). Second, increased soil moisture in early autumn resulting from wet conditions in April–September may enhance wetland availability in winter by enabling lowland forests to saturate and flood more easily. In the Mingo Swamp of southeastern Missouri, for example, summer flooding in some years had a substantial effect on water levels in autumn (Heitmeyer et al. 1989). Our results support the idea that rainfall during spring–summer affects availability of wetland habitats in autumn, which in turn influences winter distribution of Wood Ducks breeding at southern latitudes.

Warmer than average temperatures in November were associated with more northern winter distributions of young Wood Ducks, but distribution of adult recoveries was not affected by temperature in early autumn. These results are consistent with findings of Jorde et al. (1984),

who reported that subadult Mallards were more likely to winter in Nebraska when temperatures were warm. Nichols et al. (1983) also showed a stronger and more consistent relationship between winter temperature and recovery latitudes of young Mallards compared to adults. Low temperatures affect habitat suitability by increasing individual energy requirements and by reducing food availability, if wetlands freeze. Adult ducks have greater body mass in winter than young (Delnicki and Reinecke 1986, Conroy et al. 1989), which gives adults greater physiological tolerance to low temperatures and may allow them to winter at higher latitudes. Dominance status is another factor that may influence spatial distribution of wintering birds (Gauthreaux 1978). In some species, subordinate individuals exhibit greater migratory restlessness than dominants (Terrill 1987). Because young ducks are subordinate to adults (see Hepp 1989), they may be more likely to move south as habitat suitability decreases and competition intensifies (Jorde et al. 1984).

ACKNOWLEDGMENTS

We thank the many people who banded Wood Ducks over the years. L. Ramage assisted with gathering the weather data. H. Bart, T. Best, C. Guyer, J. Nichols, V. Nolan and an anonymous reviewer provided helpful comments on the manuscript. The senior author was supported in part by the Alabama Agricultural Experiment Station during preparation of the manuscript (AAES Journal No. 15-912961P).

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APPENDIX A. Location of weather reporting stations.

Reference area and state	Reporting station	Latitude, longitude	Map symbol ^a
Southern			
Alabama	Huntsville	34.39N, 86.46W	1
Arkansas	Little Rock	34.44N, 92.14W	2
Kentucky	Lexington	38.20N, 84.36W	3
Tennessee	Memphis	35.03N, 90.00W	4
	Nashville	36.07N, 86.41W	5
	Oak Ridge	36.01N, 84.14W	6
Southeastern			
Georgia	Rome	34.15N, 85.09W	1
North Carolina	Charlotte	35.13N, 80.56W	2
	Raleigh	35.52N, 78.47W	3
	Wilmington	34.16N, 77.54W	4
South Carolina	Greenville-	34.54N, 82.13W	5
	Spartanburg		
Virginia	Lynchburg	37.20N, 79.12W	6
	Norfolk	36.54N, 76.12W	7
	Richmond	37.30N, 77.20W	8

^a See Figure 1.