AMERICAN WOODCOCK WINTER DISTRIBUTION AND FIDELITY TO WINTERING AREAS

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ABSTRACT.—We examined winter distribution and fidelity to wintering areas for the American Woodcock (*Scolopax minor*), which exhibits reversed, sexual size dimorphism. Band-recovery data revealed no difference in winter distributions of different age/sex classes for woodcock from the same breeding ares. Similarly, band recoveries from woodcock banded on wintering grounds revealed no difference in fidelity to wintering sites. Males may winter north of a latitude that is optimal for survival based on physiological considerations, but they gain a reproductive advantage if they are among the first to arrive on the breeding grounds. This may explain our results, which indicate males and females have similar distribution patterns during winter. *Received 5 December 1989, accepted 12 May 1990.*

MANY migratory bird species exhibit sex- and age-specific differences in where they winter (see reviews in Ketterson and Nolan 1976, 1983; Nichols and Haramis 1980; Myers 1981). Three hypotheses have been invoked to explain differences. One concerns physiological differences associated with body size, another considers behavioral dominance of age/sex classes, and a third concerns differences in time of arrival on breeding grounds (see Hypotheses and Predictions). Unfortunately, most previous investigations of differential distribution patterns on the wintering grounds have been conducted on species for which the observed distributional differences are consistent with predictions of two or all three of these hypotheses.

We investigated winter distribution patterns of American Woodcock (*Scolopax minor*). They are an appropriate choice for two reasons. First, the hypothesis of behavioral dominance among age/sex classes can likely be rejected *a priori* for this species, while the two remaining hypotheses yield opposite predictions (see Hypotheses and Predictions). Second, band-recovery data are available. Band-recovery data permit unambiguous inferences about distribution patterns during winter of birds from specific breeding areas (Nichols and Haramis 1980, Nichols et al. 1983, Perdeck and Clason 1983, Nichols and Hines 1987, Diefenbach et al. 1988a, b). Most studies of winter distribution patterns use samples (e.g. museum specimens) of birds obtained at specific wintering locations without prior knowledge of their origin on the breeding grounds. The geographic variation in age or sex ratios of such samples is ambiguous. Previous investigators have inferred that such variation reflected variation in wintering-ground destination among birds from the same breeding areas. An alternative explanation is that geographic variation in age or sex ratios exists on the breeding grounds and that birds from the same breeding areas migrate together to the same wintering areas (see Nichols and Hines 1987: 35). In this instance, age or sex ratios on the wintering grounds simply reflect ratios on breeding grounds, and proposed explanations of different migration patterns may be unnecessary.

In addition to examining winter distribution of the different age/sex classes of American Woodcock, we tested hypotheses about age- and sex-specific variation in fidelity to wintering areas. To date, such questions about fidelity to wintering grounds have been restricted primarily to waterfowl (Nichols et al. 1983, Nichols and Hines 1987, Diefenbach et al. 1988a, b).

Our objectives were to test two null hypotheses. First, male and female woodcock from the

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same breeding areas have the same pattern of distribution in winter. Second, male and female woodcock have similar degrees of fidelity to specific wintering areas. Both of these hypotheses were tested for young, adult, and both age-classes combined.

METHODS

BAND RECOVERIES

Records of band recoveries for woodcock were obtained from the U.S. Fish and Wildlife Service (USFWS) Bird Banding Laboratory in Laurel, Maryland. For the analyses of distribution patterns, we used all recoveries from preseason (10 April to 31 August) 1961–1984 bandings of normal wild birds that were shot or found dead during December and January. Band recoveries were restricted to December and January because autumn migration should be nearly complete and spring migration not yet begun (Pursglove and Doster 1970). Each banded bird was sexed and aged as either young (calendar year of hatching) or adult (older than one year) (Martin 1964).

Band recoveries from normal wild birds banded in Louisiana in December, January, and February, 1939–1960, and shot or found dead in December and January at least one year later, were used to compare the fidelity to wintering areas of male and female woodcock. Banders after 1960 also aged birds, which allowed comparisons between males and females for both young and adults banded during 1962–1977.

STATISTICAL TESTS

Our analysis of distribution patterns of woodcock compared the bivariate distributions (latitude and longitude) of band recoveries from each age/sex class. We used a nonparametric test (Mardia 1967, 1972: 197) to test the null hypothesis that distribution patterns of band recoveries of males and females for both adults and young, and both age-classes combined, were equivalent for birds banded in the same breeding area. Data for comparisons were limited, so we combined recoveries from bandings in all years. When band recoveries from the same 10-min block occurred for both samples (i.e. ties), the test statistic was computed as suggested by Robson (1968).

Our analysis of the fidelity of woodcock to wintering areas compared the location of band recoveries with the location of winter banding. We tested the null hypothesis that males and females exhibited similar tendencies to return to the same wintering area from one year to the next. To test this null hypothesis, we selected degree-blocks of banding and based our tests on all band recoveries of these birds in December and January. A recovery in either the degree-block of banding or one of the eight degree-blocks contiguous to the block of banding was defined as occurring in the vicinity of banding. The proportion of recoveries occurring within the area of banding is an indication of fidelity to a wintering area. We used the *Z*-test for proportions to compare males and females for each class.

HYPOTHESES AND PREDICTIONS

Distribution patterns.—Female woodcock are larger than males. Because larger birds can endure longer periods of fasting (Calder 1974: 110), female woodcock may have the ability to winter in colder environments. Thus, based on physiological considerations alone, we would predict that female woodcock should winter farther north than male woodcock (Ketterson and Nolan 1976).

However, two additional factors may influence age/sex segregration on the wintering grounds (Ketterson and Nolan 1976, 1983) and may work in combination (see Byrkjedal and Langhelle 1986). One potential influence on age/sex segregation on the wintering grounds is behavioral dominance among age/sex classes. We rejected this possibility in woodcock because no evidence of age/sex dominance on the wintering grounds has been reported, and detailed observations of woodcock feeding in groups (Mendall and Aldous 1943) and woodcock maintained in captivity (Stickel et al. 1965, Vander Haegen unpubl. data) have failed to demonstrate social aggression. Another potential influence involves arrival times on breeding grounds. Under this hypothesis, segregation by sex on the wintering grounds occurs because the first individuals of one sex to return to breeding areas gain a reproductive advantage. Members of this sex winter closer to the breeding grounds. Based on the arrival-time hypothesis, we would predict that male woodcock should winter north of females. The physiological and the arrival-time hypotheses applied to woodcock give opposite predictions about sex-specific distribution patterns in winter. Presumably our analyses would permit us to reject one of these alternatives.

Fidelity to wintering areas.—If one age/sex class is more sensitive to environmental changes, then we might expect differences in fidelity to wintering grounds. Female woodcock are larger than males and can endure longer periods of fasting (Calder 1974: 110). Therefore, during periods of harsh weather conditions, we might expect male woodcock to exhibit greater facultative migration than females (Pulliam and Parker 1979, Nichols et al. 1983, Terrill and Ohmart 1984), and less fidelity to wintering areas.

RESULTS

Distribution patterns.—Only 2 of 9 comparisons from the Mardia tests indicated differences in distribution patterns during winter ($P < 0.05$)

TABLE 1. Results of testing the null hypothesis of equivalent winter band-recovery distributions for recoveries of male and female American Woodcock banded during the preseason (10 April to 31 August) in 1961–1984. For each test, df = 2.

Banding location	Age	No. of recov.	Center of recoveries: Males Lat.	Males Long.	Females Lat.	Females Long.	χ^2	P
Maine	Young	39	34.4	82.3	34.0	83.6	2.16	0.34
	Adult	21	32.8	84.6	34.7	79.8	7.22	0.03
	Both[a]	61	34.0	83.1	34.3	82.2	2.63	0.27
New York	Both	18	34.1	83.0	32.5	86.2	0.78	0.67
Michigan	Both	13	33.1	86.3	31.2	91.5	9.16	0.01
Wisconsin	Young	63	31.5	92.1	31.6	91.0	1.13	0.57
	Both	71	31.4	92.0	31.6	91.1	2.40	0.30
Michigan, Wisconsin, Minnesota	Young	73	31.5	91.8	31.6	91.2	0.22	0.90
	Adult	18	31.9	89.5	31.2	91.3	0.19	0.91

[a] Includes one bird of unknown age.

(Table 1). Furthermore, the center of the distribution pattern of females was north of that of males in only 1 of 2 tests with significant results, and 5 of 9 tests overall.

Fidelity to wintering areas.—We found no difference between sexes in fidelity to wintering areas during the period 1939–1960 ($P = 0.13$) (Table 2). Likewise, we found no sex-specific differences during the period 1962–1977 for adults ($P = 0.47$), young ($P = 0.75$), or ages combined ($P = 0.30$).

DISCUSSION

Distribution patterns yielded little evidence for sexual segregation on the wintering grounds. Several studies that examined sex ratios on localized wintering areas found disproportionate numbers of males or females (Stamps and Doerr 1976, Pace and Wood 1979, Stribling and Doerr 1985). However, these results may reflect differences in collecting methods or in habitat use (Stribling and Doerr 1985). Our results indicate that male and female woodcock from the same breeding grounds do not winter in different geographic areas.

The power of our statistical tests to detect differences in distribution patterns may have been reduced by small sample sizes and the relatively small latitudinal wintering range of woodcock (e.g. compared with the Dark-eyed Junco [*Junco hyemalis* Ketterson and Nolan 1976]). The power of Mardia's test is sufficient, even with small sample sizes, to detect differences in distribution patterns likely to be of biological relevance (Diefenbach et al. 1988b). Whereas the latitudinal range of woodcock may be limited, the size dimorphism of woodcock (M:F ratio = 0.81; Owen and Krohn 1973) is greater than for species in which differences in distribution patterns have been detected (e.g. Dark-eyed Juncos, F:M ratio = 0.93; data in Ketterson and Nolan 1976: 689). We also recognize that the northern extent of the winter range probably fluctuates with winter severity (Sheldon 1967, Wood et al. 1985), and combining data over years masked any intra- or inter-year variation in distribution patterns. These factors should not have reduced significantly our ability to test differences in central tendencies of distribution patterns.

Migratory birds would be expected to winter in areas that optimize their overall fitness. We suggest that mechanisms of both the body-size and arrival-time hypotheses may act together

TABLE 2. Test of the null hypothesis that the proportion of December and January recoveries of male vs. female American Woodcock occurring within the area of winter banding in Louisiana are equivalent. Number of recoveries is in parentheses.

Years	Age	Proportion of recoveries in banding area: Males	Females	Z	P
1939–1960	Both	0.75 (20)	0.55 (31)	1.51	0.13
1962–1977	Young	0.64 (33)	0.68 (25)	−0.32	0.75
	Adult	0.44 (18)	0.65 (23)	−0.73	0.47
	Both	0.57 (51)	0.67 (48)	−1.03	0.30

to produce the observed pattern of winter distribution of woodcock. Females probably winter in areas that are a compromise between the energetic cost of migration and food availability. They migrate just far enough to ensure an adequate food supply. Males may winter farther north than is optimal with respect to their energetic requirements and have reduced survival. However, the risk of dying for a male may be offset by greater reproductive success with earlier arrival on the breeding grounds. The effect on winter distribution of woodcock is that both sexes may winter on the same areas to optimize their fitness, but as a result of different influences on their reproductive success.

Along with the advantage of an early arrival on the breeding grounds, male woodcock may gain an additional reproductive benefit by wintering sympatrically with females. Unlike many shorebirds, woodcock do not have disjunct wintering and breeding ranges, and considerable reproduction occurs on wintering areas (Wood et al. 1985). Thus, males that winter with females may have the opportunity to breed before and during the flight north. Nesting has been observed as early as January in North Carolina (Stamps and Doerr 1977) and Alabama (Roboski and Causey 1981), and February in Texas (Whiting and Boggus 1982), although most nesting occurs later. Because males initiate migration sometime in February, receptive females are available for breeding before and during migration. How female woodcock select mates is unknown, as is the likelihood that a male courting on his wintering grounds or migration stopovers could mate with a female. Nevertheless, the opportunity for wintering or migrating males to breed on wintering areas does exist and could influence the winter distribution of males.

The winter banding data indicate no difference between sex and age classes in fidelity to wintering grounds. This was unexpected considering the size difference between sexes, nor does it support our hypothesis that males are wintering north of optimal latitudes. A possible explanation for this discrepancy lies in the origin of the winter banding data. A sufficient number of recoveries was available only for woodcock banded at sites in south-central Louisiana, which is near the southern edge of the winter range for woodcock. Similar analyses for woodcock banded in northern regions of their winter range, where weather conditions are harsher or more variable, might yield different results.

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ERRATUM

In "Renesting by American Woodcocks (*Scolopax minor*) in Maine" by Daniel G. McAuley, Jerry R. Longcore, and Greg F. Sepik (1990, Auk 107: 407–410), the range of distance moved by females that abandoned nests or had nests destroyed by predators (p. 408) should read: "range = **1.0–15.5**" and the values in the "Distance moved (km)" column in Table 2 (p. 409) should read down the column: "**1.01, 11.34, 1.22, 4.17, 15.54, 0.65, 0.36, 1.14, 0.88, 0.24, 0.80, 0.16.**" Corrected values are in boldface type.