

RACIAL AND SEXUAL DIFFERENCES IN MIGRATION
IN *SPHYRAPICUS VARIUS*

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THE subspecies of the Yellow-bellied Sapsucker (*Sphyrapicus varius*) are strongly characterized not only in morphology but in migratory habits as well. General outlines of the breeding ranges and winter ranges of the four subspecies are given in figures 1 and 2. These illustrate the well-known facts that *S. v. varius* is the most highly migratory of North American woodpeckers, *S. v. nuchalis* is moderately migratory, *S. v. daggetti* is still less so, and *S. v. ruber* is almost sedentary. Such racial differences in migration are by no means unique among polytypic species. In the course of investigating the ranges of these forms, however, I was struck by what seemed to be an unusually high proportion of female specimens of *S. v. varius* taken in the peripheral regions of its winter range. To determine if this apparent disproportion were real and if it extended to other races within the species, examination of a large series of specimens from all parts of the winter range of *Sphyrapicus varius* was necessary.

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MATERIALS AND METHODS

Mimeographed forms were sent to the above-listed institutions requesting the sex, date, and locality of wintering specimens of *S. v.*

varius and *S. v. nuchalis*. Data on *S. v. daggetti* and *S. v. ruber* were also requested from the Museum of Vertebrate Zoology, and specimens of all four races were examined in the Dickey Collection, University of California, Los Angeles, and in the Los Angeles County Museum.

It was decided to include as "winter" specimens only those taken from November 1 through March 31, during which time populations would be relatively sedentary. A few birds taken in the early part of November or the latter part of March may have been migrants, but these dates are outside the time of main migratory movements and exclusion of all birds taken in early November or late March would probably eliminate many more winter residents than migrants from the data. All records for which the sex of the specimen or the date of collection was absent or questioned were discarded. Estimates of the significance of the data were determined by the chi-square method, and the customary value for chi-square of 3.841 or more was taken as an indication of significance. Adjusted chi-square values are given for samples of less than 200.

RESULTS

S. v. varius.—The number of winter specimens of each sex from the United States, Mexico, the Central American republics, and the West Indies are given in table 1.

TABLE 1
NUMBERS OF EACH SEX OF WINTER SPECIMENS OF *S. v. varius*. NO WINTER SPECIMENS FROM BRITISH HONDURAS WERE AVAILABLE

<i>Locality</i>	<i>Males</i>	<i>Females</i>
United States	126	100
Mexico	29	96
Guatemala	3	17
Honduras	0	6
Salvador	1	5
Nicaragua	0	1
Costa Rica	3	6
Panama	0	2
West Indies	11	30

The greater number of wintering females of *S. v. varius* from areas south of the United States is at once evident. Of the non-United States specimens, there are 164 females to 47 males, or approximately 77.5 per cent to 22.5 per cent (chi-square = 64.8). On the other hand, among winter specimens from the United States, males are more abundant—about 55.9 per cent to 44.1 per cent (chi-square = 3.0)—but the difference is not statistically significant.

As shown by the range maps, Middle America (including Mexico) and the West Indies form roughly an arc representing the periphery of the winter range of *S. v. varius*. It is arbitrary, of course, to fix a northern boundary for the peripheral part of the winter range at the Mexico-United States border, but the data indicate that this is not as unnatural as it might seem. Of 29 specimens from the eastern Mexico

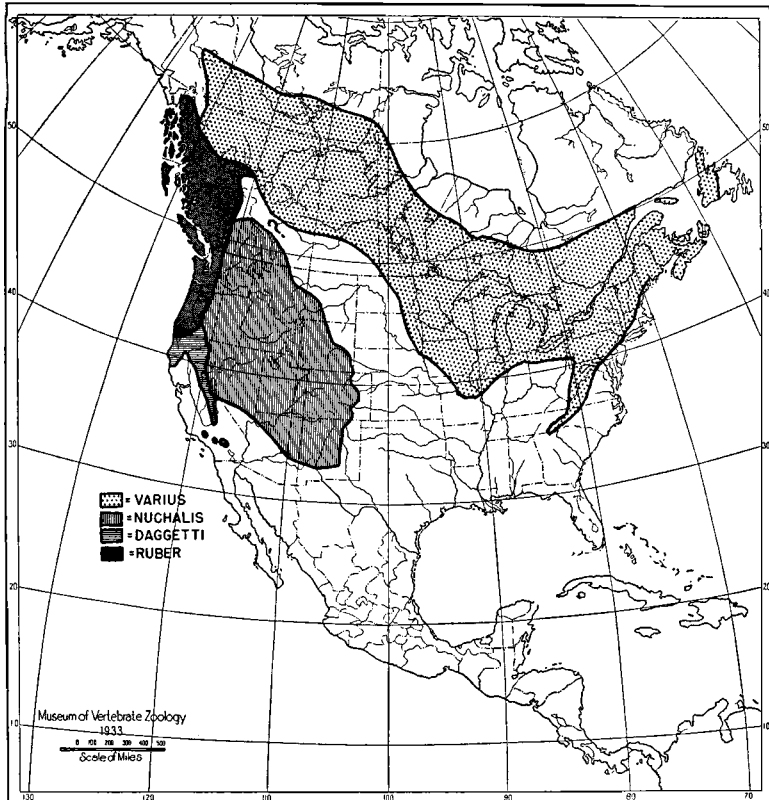


FIGURE 1. Approximate outlines of breeding ranges of the four subspecies of *Sphyrapicus varius*.

border states of Coahuila, Nuevo León, and Tamaulipas, the only border states from which winter specimens of *S. v. varius* are available, 22 are females and 7 are males (chi-square = 6.7). Of 33 winter specimens from Texas, however, the proportion of males to females is almost exactly equal—16 males to 17 females. The Gulf of Mexico appears to form a natural gap between the rest of the United States and the Middle America-West Indies periphery. To check this

supposition, winter specimens from the Gulf Coast states of Texas, Louisiana, Alabama, Mississippi, and Florida were tabulated; the proportion of the sexes was 69 males to 50 females, which contrasts strongly with the much higher proportion of females to males from Middle America and the West Indies.



FIGURE 2. Approximate outlines of winter ranges of the four subspecies of *Sphyrapicus varius*. A few records for *S. v. nuchalis* mentioned in the text are outside the main winter range.

The disproportion of sexes in the peripheral areas of the winter range is significant if one assumes that the specimens represent a random sample of the wintering population over a period of many years. A spread of 92 years, from 1859 to 1951, was covered by the specimens examined. The year most abundantly represented was 1891, in which 23 out of 31 birds were females. The next most abundantly represented year was 1939, in which 14 out of 18 specimens

were females. It is evident, therefore, that the apparent disproportion of sexes among these wintering birds is not an artifact of sampling resulting from heavy collecting during unusual years.

It is also highly probable that the specimens from south of the United States represent a true random sample, for the two sexes of *S. v. varius*, although distinct, are not so strikingly different as to attract the attention of the collector to one or the other. The females are less brightly colored than the males and are, if anything, less conspicuous, and to my knowledge they are no more curious or less wary than the males.

At this point it may be asked why, if the disproportion of sexes is real, the ratio of females to males is not more or less exactly reversed in the northern part of the winter range? Although wintering male *S. v. varius* from the United States do outnumber the females, the difference falls short of statistical significance. One might expect instead that the males would outnumber the females by about $3\frac{1}{2}$ to 1, since that is the ratio of females to males in more southern areas. A possible explanation may appropriately be offered at this point.

Many of the Middle American and West Indian specimens were taken by professional collectors who were paid by the specimen, or by museum parties wishing to get as large a series as possible in a short time; such collecting tends to be random and to produce a random sample if sufficient numbers are taken. On the other hand, collecting of a relatively common species in easily accessible areas in the United States may be more selective. A museum finding itself with 3 or 4 times as many males as females of *S. v. varius* from the United States might then attempt to acquire some more females to even up the representation of the sexes. Such a practice is especially prevalent in private collections, many of which have been incorporated into the collections of large institutions such as those which contributed to this survey.

This hypothesis on the lack of a more pronounced preponderance of wintering males from the United States is by no means definitive; it is merely offered as a plausible suggestion in the absence of conclusive evidence.

An alternative explanation would be that the total number of females in the entire population of the subspecies is consistently much greater than that of the males, at least in winter. There is no evidence, however, of a great surplus of female *S. v. varius* during the breeding season. One would have to propose, then, that more female than male young are produced, that most of these females migrate to the

periphery of the winter range, and that the surplus of females is somehow eliminated before the beginning of the breeding season.

To the present writer the first hypothesis seems much more reasonable than the alternate. It may then be proposed that the data indicate a sexual difference in the migration of this subspecies—that most of the females migrate to the periphery of the winter range whereas most of the males remain in more northern areas.

S. v. nuchalis.—Migration is much less extensive in this subspecies than in *S. v. varius*. *S. v. nuchalis* breeds as far south as southern New Mexico and southern Arizona, and it rarely winters south of central Mexico. Data were gathered on specimens collected in Mexico from November through March, and these showed approximately equal proportions of the sexes—36 males to 32 females. To determine if some peripheral disproportion of sexes might not be present on a minor scale, the specimens were further divided into those from the relatively northern areas of Coahuila, Chihuahua, Sonora, and Baja California north of latitude 30°, and those from the more southern areas of Yucatán, San Luís Potosí, Jalisco, Sinaloa, Durango, and Baja California south of latitude 30°. Of the northern group, the proportion was 30 males to 20 females (chi-square = 1.62), and in the southern group there were only 6 males to 12 females (chi-square = 1.4). Although these differences are not statistically significant, there is at least a suggestion that females are more abundant at the periphery of the winter range and that the proportions are reversed in the northern part, where males are in the majority.

S. v. daggetti.—Migration in this race is relatively slight and no real periphery of its winter range can be defined. However, since the Pacific Coast from the San Francisco Bay area south to northwestern Baja California represents the farthest limit to which any large part of the population moves, data were gathered from California museums on the proportions of the sexes from those areas. Specimens from Los Angeles County were excepted, since this coastal county is only a few miles from isolated breeding populations in the San Bernardino and San Jacinto mountains. Of 40 of these winter specimens of *S. v. daggetti*, 16 are males and 24 are females, and the difference is not statistically significant (chi-square = 1.2), although females are in the majority.

S. v. ruber.—Examples of this race normally do not winter outside some part of the breeding range of the subspecies. Only 10 winter specimens from the coasts of Alaska, British Columbia, Washington, and Oregon were available in three large California museums, and of these specimens 6 are males and 4 are females. Since this subspecies

is virtually non-migratory, no significant disproportion of sexes in wintering birds is to be expected.

DISCUSSION

Although sexual differences in extent of migration may not be confined to *Sphyrapicus varius*, discussion must necessarily be limited to that species. No broad generalizations can be made from the data presented here, but some implications of interest may be mentioned.

Observers have stated that males of *S. v. varius* arrive first on the breeding grounds in the spring (Merriam, 1879; Eaton, 1914). This may be the result not only of earlier migration but also of having generally less distance to cover than most of the females.

It has long been known that in the races of *Sphyrapicus varius* there is a curious inverse correlation between intensity of pigmentation and migratory tendency. *S. v. varius*, the least heavily-pigmented race, is highly migratory, and at the other extreme is *S. v. ruber*, of saturated pigmentation and virtually sedentary habits. The data presented here indicate that this inverse correlation seems to hold not only among the four subspecies but even in the males and females within each race. The female *S. v. varius* is less heavily pigmented than the male, and it appears certain that most females migrate farther than the males. In *S. v. nuchalis* the females are slightly less heavily pigmented than the males, and there is an indication although not a certainty that the former migrate farther. In *S. v. daggetti* there is only a faint indication of less pigmentation in the female, detectable chiefly as occasional white spotting in the outermost rectrices and in more frequent occurrence of a small white postocular spot in that sex, and in this subspecies a sexual difference in migration is completely or almost completely lacking. The pigmentation of the sexes is identical in *S. v. ruber*, and there is no evidence of a migratory difference. It should be recalled at this point that color differences between the sexes and races of *Sphyrapicus varius* are entirely quantitative, for all the variation is produced by greater or lesser deposition of red, yellow, and black pigments, particularly the first and last.

Evidence has been presented in a previous paper (Howell, 1952) that pigmentation in these sapsuckers is under genetic rather than endocrine control, and there can be little doubt that extensive, periodic migration has a genetic basis although the physiological stimulus for it may be an endocrine mechanism. In view of the correlation discussed above, the possibility of a common genetic influence on both pigmentation and migration merits consideration.

One suggestion is that sex-linked multiple factors, acting as modifiers, affect both intensity of pigmentation and extent of migration; in other words, they may act as pleiotropic genes. Possibly a genetically determined physiological process which results in heavier pigmentation may also represent a physiological adjustment which inhibits migration, and vice versa. Recalling that in birds the female is the heterogametic sex, one might suggest that these hypothetical modifiers are located on the X-chromosome, and that their effects are cumulative. Thus, a sufficient number of them on either one or a pair of X-chromosomes would result in maximum pigmentation and minimum migration in both sexes—i. e., *S. v. ruber*. If the number of modifiers were less, pigmentation would decrease and migration would increase. If a very few modifiers were present, the females, with only one X-chromosome, would express the effects more strongly, as in *S. v. varius*.

An alternative but related explanation is that different but closely associated alleles, influencing pigmentation and migration, respectively, compete with each other for a common and limited substrate with which they must interact for expression. Such a concept of gene action has been suggested by Stern (1943, 1949). This hypothesis could explain why intensity of pigmentation and extent of migration in the sapsuckers seem to increase at the expense of one another, and if the alleles were on the X-chromosome the differences between the sexes in these characters would also be explicable.

Previous investigators have pointed out correlations between pigmentation and other characters in birds. Maw (1935) concludes that plumage color and size are sex-linked characters in some domestic fowl, and Lee and Keeler (1951) mention numerous cases among birds in which pigmentation changes are correlated with variation in anatomy, physiology, and behavior. It is hardly necessary to emphasize, however, that the present discussion concerning sapsuckers represents a speculative approach to the data. Correlation does not necessarily mean common or even similar causality, of course, but the possibility that more than coincidence is involved is worthy of consideration until shown otherwise. Perhaps the sexual differences in migration herein described may be paralleled in other picids or other avian groups without regard to pigmentation. Members of the Picidae often show remarkable similarity in habits, and other species in this family may be found to exhibit tendencies like those of the sapsuckers discussed here. It is hoped that this paper may stimulate investigations leading toward more conclusive data on subjects of this nature.

SUMMARY

The four subspecies of *Sphyrapicus varius* differ markedly both in coloration and in migratory habits. *S. v. varius* is highly migratory, *S. v. nuchalis* is less so, *S. v. daggetti* is only slightly migratory, and *S. v. ruber* is practically sedentary. Data on wintering birds indicates that there are also differences in the extent of migration of males and females in *S. v. varius* and possibly in *S. v. nuchalis*. Among specimens from the southern part of the winter range (Mexico, the Central American republics, and the West Indies), females outnumber the males by about $3\frac{1}{2}$ to 1, but in the United States winter specimens of males are in the majority. In *S. v. nuchalis*, wintering females are in the majority in the southern part of the range and males outnumber females in the northern part although the differences fall short of statistical significance. *S. v. daggetti* and *S. v. ruber* do not show comparable phenomena. There is a curious inverse correlation between extent of migration and saturation of pigmentation not only among the races but among the two sexes within the races. Possible genetic linkage of factors affecting pigmentation and migration is discussed.

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